The Afterlife of a Tree

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Second edition, expanded and revised

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The Afterlife
of a Tree

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Contents

A word from the Publisher

In 2004, a book called "The Afterlife of a Tree" was published as part of a project run by WWF Poland in the Białowieża Forest. Its publication stemmed from the need to educate the public about the protection of the remaining natural lowland woods in the Białowieża Forest and their natural processes. In the end, the book became more universal in character, because it addressed the need to conserve biodiversity as a whole. It is estimated that nearly two-thirds of all plant, animal and fungi species occurring in terrestrial ecosystems are associated with forests. As many as 50% of forest species are dependent on dead and dying trees to a greater or lesser degree. Undoubtedly, therefore, "dead wood" is a source of life and one of a forest's most valuable assets, and hence, a prerequisite for the maintenance of many important natural processes taking place in forest ecosystems.

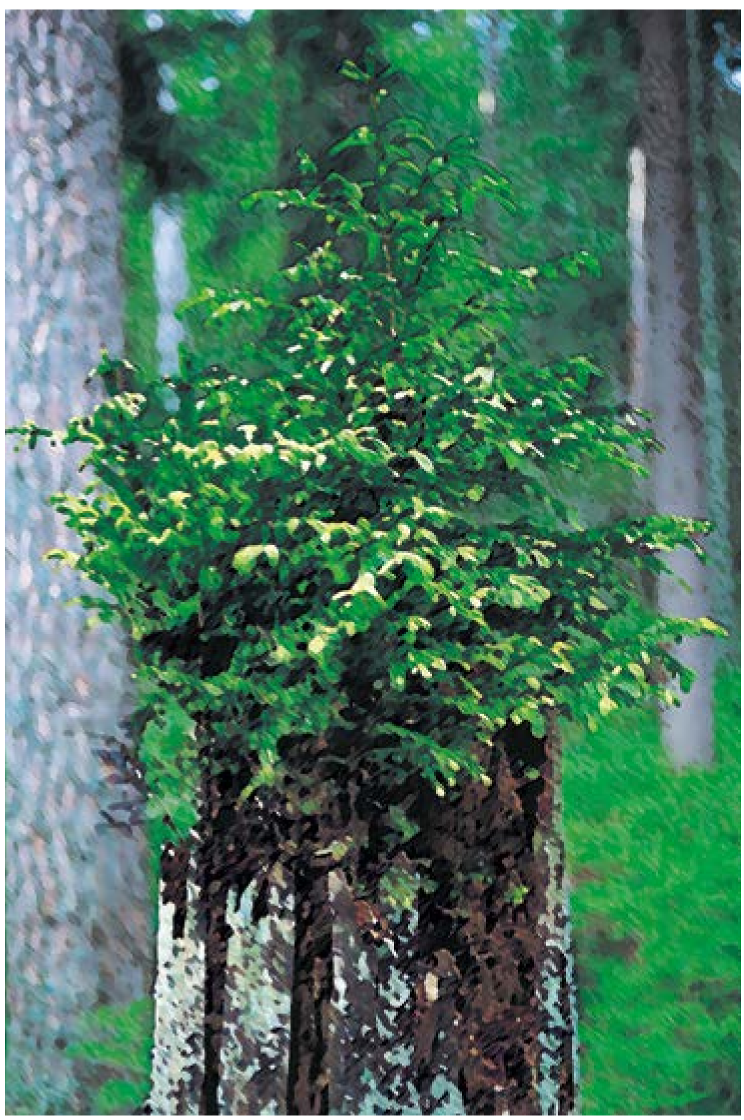
Eighteen years have elapsed since the first edition came out. In the meantime, a new generation of foresters and naturalists have grown up. Today, the significance of dead trees in maintaining conservation values is no longer disputed. What may still be debated, and perhaps even contested, is the question of how much "dead wood" should be left, in what form, and where. Educational programmes and nature trails illustrating these issues are present in nearly every national park, and in many forest districts, therefore in managed forests as well. The topic of "dead wood" is included in out-of-school programmes, high-school curricula (e.g. "Matura" exams) and college courses in the Natural Sciences. This is of utmost importance if we wish to gain greater public acceptance for retaining dead trees in forests. Nevertheless, difficulties still persist as regards presenting large-scale disturbances caused by high winds (gales, hurricanes, tornadoes) as opportunities for the initiation of natural processes that will increase the proportion of dead and dying trees in managed forests. We hope that this problem will meet with greater understanding on the part of decision-makers, who should take steps to exclude human intervention from at least some disaster areas, so that they can be treated as reference sites, where observations of natural regeneration processes in forest ecosystems can take place. This is becoming ever more important in the context of adaptation to climate change.

Over the past 20 years or so, scientific research into many different aspects of the role of "dead wood" in nature has advanced significantly, both in Poland and abroad. For many years now, we have been encouraged to update and reissue this very popular publication. And so the time has come for the second edition of "The Afterlife of a Tree". Its overall concept and layout are based largely on its predecessor. However, compared to the first edition, its scope has been expanded and the contents have been brought up to date. This is due principally to the involvement of new authors, which has allowed for a much broader exploration of matters connected with the parts played by so-called habitat trees and tree-related microhabitats in forests. The chapters discussing fungi, lichens and myxomycetes and their associations with "dead wood" have been completely rewritten, and the other topics covered in the first edition have seen considerable changes, too. Chapter 5: "Dead wood in forest management and nature conservation" has been expanded to include new topics and content. A broader view of the role of dead wood in water bodies has been introduced. Other chapters have been supplemented and updated as well, mainly with new literature. Many new superb photographs have been added.

We are placing in your hands what we hope is a much awaited and important book, which will provide new outlooks on the forest environment and inspire the protection of its most valuable assets.

Stefan Jakimiuk
WWF Poland

Introduction 1



[...] If you were
To enter, deep within you'd find a tangle
Of trunks, logs, roots, amid a swamp — a jungle
Guarded by myriad streams, whose rampant brakes
Hide ants, wasps, hornets, writhing nests of snakes.
[...]
Down below, though, the forest has the look
Of a devastated city: A toppled oak
Leans like a fallen edifice; atumble
Against it, like broken pillars and walls, a jumble
Of earth, boughs, rotten beams [...]

A. Mickiewicz, *Pan Tadeusz or The Last Foray in Lithuania*. Translated by Bill Johnston. Archipelago Books, 2018

A forest ecosystem is not just an assemblage of living trees or "a stand", the most significant part of the forest biomass; it also includes all the other plants and organisms living within this environment. Along with the soil, it is a space in which wooded areas are interspersed with open patches (glades, canopy gaps) populated by heliophilous herbaceous plant species and their associated fauna and funga. From this perspective, a forest is a dynamic system in which the growth, development and death of trees determine the temporal and spatial patterns of a great many simultaneously ongoing processes. This network of interdependent species and species complexes is fundamental to the relative dynamic equilibrium that ensures the forest's permanence. The constant changes in the quantitative relations between the various components of the forest resulting from both natural and human-induced ecological disturbances and interactions between species, intensified by the fact that the ecosystem needs to adapt to climate change, mean that the forest is always evolving.

Forests are the main component of the green infrastructure and as such play a key role in sustaining life on Earth. Therefore, it is in our own best interests to make the most of their biological potential and the ecosystem services they provide while keeping the ecosystem and all of its typical biodiversity in as best a state as possible. Dead wood plays a crucial role in this respect.

Polish forests exhibit a broad spectrum of "naturalness", from monoculture plantations and multi-purpose managed forests retaining many natural traits to forests free from direct human activity. In the latter, dead wood usually plays an especially prominent part. However, a certain amount of decaying wood is necessary in all types of forest ecosystems if they are to function properly and preserve their biodiversity, including many threatened species.

In recent years, much has been said about the significance of dead wood to a variety of forest organisms and its role in the ecosystem. Scientific knowledge on this subject is extensive and growing rapidly. There are already some good reviews, meta-analyses and syntheses available in the international research literature. However, there is still a need for a much more comprehensive work addressing the role and importance of dead wood, targeted at audiences who may not necessarily have a background in the natural sciences.

The first edition of this book, intended for just such a purpose, was published in 2004. At that time, awareness of the importance of dead wood, as well as the idea of leaving it in forests, was just dawning, even among foresters and professional conservationists. The ensuing 18 years have witnessed an exponential growth in knowledge about the significance of wood in ecosystems, in particular forest ecosystems. Issues relating to dead wood, its ecological importance and associated biodiversity have become the topic of hundreds of scientific papers, and their number is increasing by the month. Several publications of fundamental importance have been produced, among them a book entitled *Biodiversity in Dead Wood* (Stokland et al. 2012), which is a compendium of expert knowledge on this topic. Public awareness has shifted significantly as well. Today, many professionals working in forest management and nature conservation are convinced that forest ecosystems need dead wood. Moreover, further questions regarding dead wood are being asked: How much of it "should" there be? How do we balance conservation requirements with utility considerations? How are we to reconcile the need to leave wood in the forest with the economy's demand for wood? How do we sensibly replenish the dead wood stock in those forests which have been depleted of it through improper management? Do dead trees pose a threat to humans? How do we compromise between ecological needs and safety aspects? Will leaving dead and dying trees *in situ* in order to provide habitats for insects and fungi jeopardize the stability of forest stands? What should be done in the case of a natural large-scale disturbance to the stand? Despite the growing recognition of the importance of once-undesirable dead wood, bringing knowledge of its ecology and its importance to the functioning of ecosystems into the public consciousness remains a difficult task. Furthermore, we are only just beginning to comprehend the role of dead trees in non-forest ecosystems like aquatic ecosystems or urban parks.

In light of these circumstances, we have decided that a second, updated edition of the book is necessary. We have tried as far as possible to retain the layout and contents of the first edition. But some parts have had to be thoroughly reworked or even written anew in a few instances. Nevertheless, this book cannot possibly contain the totality of knowledge available today, so we hope those readers who develop a greater interest in the subject will be encouraged to turn to more specialized sources. Some of the most important and especially noteworthy works are highlighted at the end of each chapter, while a more comprehensive list of references is provided at the end of the book.

Dead wood – what exactly is it? Generally speaking, wood is the basic structural material that supports trees and shrubs. It is composed mainly of dead tissue (over 90%), i.e. a tissue in which metabolic processes do not take place, although it does also contain living cells. Besides tissues composed of living cells, organisms with a complex tissue structure also grow tissues where there are few or no living cells. An example of such a tissue in woody plants is wood. Wood is produced by a formative tissue, the cambium, which lies under the bark. Although it plays a key role in the tree's physiological processes, wood is predominantly made up of dead cells. In this context "dead wood" is not a precise term, but we use it here for convenience. Death refers to the whole organism of the tree (much like an animal organism). Likewise, we cannot speak of the "death" of wood when it stops participating, as a conducting tissue, in the tree's life processes. In heartwood species (see Chapter 1.1), the heartwood does not perform conducting functions and can at best be described as a non-living mechanical tissue. Thus, the category of "dead wood" does not follow common logic, according to which the state of being dead is a consequence of ceasing to live; rather, it is a broadly accepted convention, used to distinguish those woody tissues which become decomposed by the living organisms inhabiting it. Paradoxically, the term "dead wood" is used to describe wood which has been "brought back to life" in this manner, whereas wood as such remains a non-living tissue.

Sometimes, we also speak of the "decaying" wood of dead woody plants or of their parts. This is not a precise term either, because wood does not decay on its own: it is a process involving a multitude of different organisms, in particular fungi and invertebrates.

When we talk about wood, we do not mean growing, living trees, but rather dead specimens (standing or fallen trees) or their parts (sections of trunks, boughs, branches, roots, snags, stumps). We rarely mean the wood of a living tree or shrub. It would therefore be sufficient to refer to wood without any additional descriptors; nevertheless, we have decided to use the adjective "dead" to avoid any misunderstanding.

Forests are among the most complex and species-rich land environments on Earth. More than half of all terrestrial organisms are associated with forests. Dead trees and shrubs and

Photo 1 (J. Walencik)
Moribund trees are a valuable component of the forest ecosystem

their parts are integral components of a forest (Photo 1), essential for the proper functioning of its ecosystems and for maintaining its biodiversity [specialized terms are explained in the margins], thereby ensuring its long-term stability.

At our latitudes in the Northern Hemisphere, it takes 10-100 years for wood to fully decompose, depending on the species and size of the tree, its position relative to the ground, the manner of death, the climate and weather conditions, and the microclimate where it is standing/lying. In natural forests, there may locally be more dead wood than the wood of living trees, and over a larger area, the volume of dead wood usually makes up as much as 50% of the entire wood volume of the living stand. If forests lacked such an essential component as dead wood, we would be discussing tree stands rather than functioning ecosystems.

Although here we are discussing the role and importance of dead wood on the basis of our own studies and observations, we have also drawn from the vast amount of information on dead wood available in the international literature.

One of the most prominent examples of forests abounding in dead wood in Poland is the relatively well studied Białowieża Forest, the largest and best-preserved remnant of an unmanaged, semi-natural deciduous and mixed forest on the European Plain. All the authors of this book have had experience of working in this forest, which is why many of the examples are taken from it. Even so, the subject of this book is not the Białowieża Forest; rather, it is

Biological diversity (biodiversity): the variety of life forms in a given area, usually considered at three levels of the ecological hierarchy: genetic diversity (i.e. the variety of genes within given populations), species diversity (i.e. the number of different species in a given area) and ecological diversity (i.e. the variety of ecosystem types, plant communities, habitats and landscapes). In the literature, sometimes used synonymously with "nature".

Stand volume: a term used in forestry to refer to the volume of wood (m^3) in all trees growing in a given stand (then expressed in m^3) or a portion of its area, usually 1 ha (then expressed in m^3/ha).

dead wood, a component that should not be lacking in any forest. Our aim is to show readers how "alive" dead wood can really be. We will explore various aspects of its non-commercial significance and introduce them to the mysterious world of plants, animals and fungi associated with decaying logs, tree throws, trunks, stumps and boughs.

We will generally use the English vernacular names of species, but we will also use Latin scientific names, the latter exclusively for any organism that does not have an English name. To ensure there is no doubt as to which species we are referring to, the index at the end of the book can also serve as an English-Latin and Latin-English glossary of species names. A separate index records the lesser-known terminology used in the book.

At this point, we would like to thank all those who have contributed to this book. Acknowledgements for the first edition go to: Stefan Jakimiuk for his inspiration; Małgorzata Bobiec for drawing most of the illustrations and providing comments on the first draft of the manuscript; Mirosław Waszkiewicz for drawing the illustrations of certain insect species; Piotr Galicki for drawing the illustrations of woodpeckers; Jan Baake, Cezary Bystrowski, Marek Czasnojć, Wojciech Janiszewski and Zbigniew Kołudzki for their photographs; Jan Walencik and the late Janusz Korbel for their photographs and input to the first draft of the manuscript; Roman Królik, Daniel Kubisz, Andrzej Lasoń, Tomasz Majewski, the late Andrzej Melke and Marek Wanat for compiling the list of beetle species associated with spruce trees; Anna Bujakiewicz for allowing us to use information about relict species of fungi; Ireneusz Ruczyński for sharing unpublished data on bats; Dorota Szukalska for sharing unpublished materials about plants; Kazimierz Borowski for his technical assistance with the illustrations; Krzysztof Sućko for his help with the indexes and certain figures, and for sharing a photograph; Lech Buchholz, the late Janusz B. Faliński, Dawid and Kosma Gutowski, Bogdan Jaroszewicz, Wiesław Mułenko, the late Czesław Okołów, Aleksander W. Sokołowski, Alina Stankiewicz, Arkadiusz Szymura and the late Krystyna Wojtkowska for their constructive comments on the manuscript. As their contributions apply in equal measure to the present edition, we extend our gratitude to them once again. Those who are no longer with us will forever be in our memory. Yet again, we were inspired and motivated by Stefan Jakimiuk to produce this second edition. Special thanks also go to Sylwia Kiercul for consultations on lichens; Szymon Konwerski, Roman Królik, Daniel Kubisz, Marek Miłkowski, Tomasz Mokrzycki, Radosław Plewa, Krzysztof Sućko and the late Henryk Szołtys for discussions and consultations on insects; Rafał Ruta for additional information about tree-related microhabitats and their insect inhabitants; Piotr Klub and Łukasz Misiuna for information about areas with valuable relict saproxylic insects; Lech Buchholz and Jerzy Szwagrzyk for their efforts in reading and reviewing the manuscript of the second edition and providing invaluable comments on the text; Hanna Graczyńska for her meticulous technical editing, working on the indexes and proofreading the manuscript; and Andrzej Poskrobko for the typesetting and his patience with the corrections. The authors are solely responsible for any possible shortcomings of this book.

1.1. What is wood?

Vascular plants: a group of plants with fully developed conducting tissues. They do not form a homogeneous taxonomic unit in modern taxonomy, albeit the term is well established in traditional botany. Vascular plants have been traditionally divided into pteridophytes (ferns and allies) and spermatophytes (seed plants). Mosses, liverworts and hornworts are non-vascular plants.

According to the botanical definition, **wood (xylem)** is a complex tissue of vascular plants consisting of vessels and tubes that transport water and minerals, the supporting components (woody fibres, tracheids) and parenchyma. It commonly occurs in the stems and roots of woody plants. The vessel elements in the stems form layers of sapwood, which transports water, and heartwood, which does not transport water and which contains lignified parenchyma cells and vessels clogged with tyloses (Fig. 1).

In some woody species, e.g. birch, aspen, alder, hornbeam, sycamore and maple, all of the wood has a conducting function throughout the lifespan of the tree, provided that it is healthy and not damaged, e.g. by fungi or insects. In most tree species in Poland, such as oak, ash, beech, lime and pine, the inner (older) layers of wood lose this active functionality over time, becoming the heartwood characterized by lignified parenchyma cells and vessels clogged with tyloses. The outer, physiologically active layers of wood in these species are called the sapwood.

From the technical point of view, wood is a raw material derived from harvested trees and processed into different grades. Wood is very resilient even at low densities: its relative resistance matches that of steel, and it also has low thermal and acoustic conductivity. However, from a technological standpoint, wood has disadvantages, such as high hygroscopicity (water absorption potential), swelling, shrinking, cracking and relatively low durability. This is, of course, a generalization, because the properties of wood depend largely on the tree species, growth conditions and the method of season-

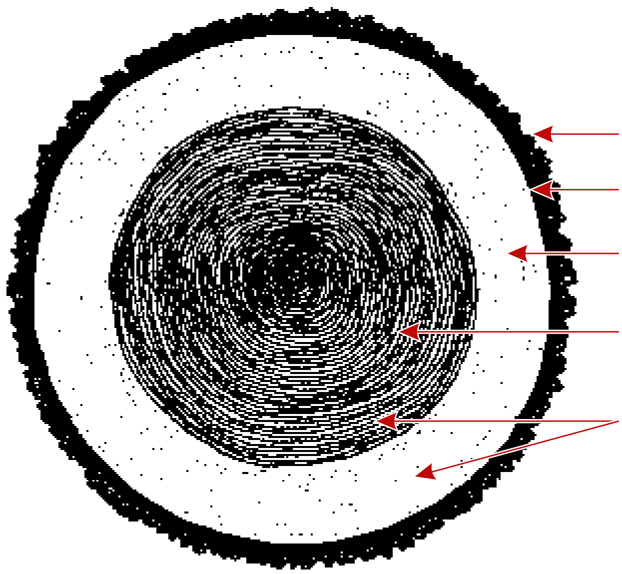


Fig. 1 Cross-section of a tree trunk (M. Bobiec)

ing. The possibility of selecting wood possessing specific properties combined with appropriate processing and application technologies enables a wide range of uses, which means that wood continues to be an almost irreplaceable material in the 21st century.

In temperate climates, trees form concentric annual growth rings visible in the cross-section. The number of rings corresponds to the age of the tree. We can distinguish the rings of early (spring) wood and late (summer) wood. The latter are darker in hue and 1.5 times denser than the early wood. In terms of chemical composition, wood is a mixture of several macromolecular organic compounds: cellulose (40-60%), hemicelluloses (ca 23-35%), lignin (21-30%) and other substances such as resins, waxes, fats, tannins, alkaloids and minerals.

Wood can last for hundreds of years if it is stored under dry conditions, at a constant humidity level or if it is permanently submerged in water. The blackened wood of bog oaks, preserved for hundreds of years under thick layers of peat or silt in anaerobic conditions, is considered a very valuable material for furniture. The durability of wood can be enhanced by sat-

Tyloses: outgrowths of parenchyma cells growing into the cavities of vessels or canals (resin, gum) through pits, thus blocking conduction processes.

Photo 2 (J. Walencik) Cross-section of a snapped, rotting spruce with visible annual growth rings

urating it with anti-decay agents or by processing it into wood-based materials, such as plywood, lignostone (compressed solid wood) and lignofol (laminated compressed wood).

Depending on the species, wood exhibits different physical and chemical properties and durability. For instance, lime wood is very soft, light and easy to process, and is a favourite among sculptors. The wood of balsa trees *Ochroma pyramidale* from Central and South America is also exceptionally light: its density is about 0.1 g/cm^3. Balsa was used as the construction material for Thor Heyerdahl's famous raft, the Kon-Tiki.

Hornbeam and oak wood is relatively hard and heavy. One of the heaviest and most hardwearing is the wood of the lignum vitae tree, which grows in Central America. In fact, it is so heavy (its density is ca 1.1 g/cm^3) that it sinks in water. It is used as a bearing material for ship propellers because of its high resistance to friction and durability at 100% humidity. Equally hard and durable is the wood of the so-called ironwood trees. A few dozen species of ironwood are found mainly in the tropical zone, e.g. *Metrosideros*, *Sideroxylon*, hackberry, casuarina, Persian ironwood, ostrya.

Ebony is a very valuable wood obtained from various tropical species. Its dark brown or black-coloured heartwood is hard, heavy and does not easily splinter. The most precious is the black ebony wood of the genus *Diospyros* (mainly Ceylon ebony *Diospyros ebenum*). It is used to make luxury furniture and musical instruments, among other things. Rosewood obtained from trees of the genus *Dalbergia*, growing in the tropics of America, Asia and Oceania, has similar properties. It is fragrant and has a dark, irregular colouring.

Well-known is the mahogany wood of various tree species growing in both Americas and in Africa, e.g. American mahogany *Swietenia mahogani*. This cinnamon-coloured or red-brown wood is moderately hard and relatively resistant to moisture and cracking. It is used in the production of furniture and veneers. The red-brown, fragrant resinous teak wood of *Tectona grandis* from India, Indochina, Laos, Myanmar (Burma) and Thailand is very durable and very resistant to insects and fungi.

1.2. How big can trees grow and how long do they live?

Sclerenchyma:
a tissue usually made up of dead cells with strongly lignified cell walls; it is composed of fibre cells and sclereids (stone cells).

DBH:
diameter at breast height; the thickness (diameter) of a tree at 1.3 m above ground (at adult breast height); a term used in forestry. If a tree is very thick, then the circumference at 1.3 m is usually measured and recorded instead of the diameter; this is easily calculated using the following formula: circumference = 3.14 × DBH.

Woody plants are a group of vascular plants with perennial lignified stems that includes trees (e.g. pine), shrubs (e.g. common hazel *Corylus avellana*), shrublets (e.g. bilberry *Vaccinium myrtillus*) and lianas, also known as vines (e.g. common ivy *Hedera helix*). They contain considerable amounts of lignified or sclerenchyma tissues, often reach enormous sizes (height, thickness) and can live for thousands of years.

Trees have been on Earth for more than 300 million years. Undecomposed remains of prehistoric woody plants have turned into black and brown coal. In Poland, there are currently more than 70 tree species and about 220 shrub species. These numbers include non-native species that have long been present and are commonly grown, but exclude the whole abundance of recently introduced exotic plant species.

In Poland, pedunculate oaks *Quercus robur*, white poplars *Populus alba* and black poplars *Populus nigra* usually have the largest diameters.

There are a number of individual trees in Poland with a DBH exceeding 3 m, i.e. with a circumference of more than 10 m. The Napoleon Oak in Zabór (Lubuskie Province) and a white poplar in Leszno (Province of Mazovia) were both ca 10.8 m in circumference, but unfortunately, both trees have been lost. In 2020, the famous Chrobry Oak in Piotrowice near Szprotawa (Province of Lower Silesia) died in the aftermath of a fire. Other well-known, imposing Polish trees include the Chrześcijanin Oak in Januszkowice (Province of Podkarpacie), the Bażyński Oak in Kadyny (Province of Warmia-Masuria), the Bartek Oak in Zagnańsk (Świętokrzyskie Province) and the Jan Kazimierz Oak in Warlubie (Province of Pomerania). The multi-trunk small-leaved lime *Tilia cordata* in Cielętniki (Province of Silesia) was a real record-breaker: it boasted a circumference of 10.8 m at its widest point. Sadly, it snapped during high winds in 2017, leaving only the butt portion standing. Two oriental planes *Platanus orientalis* in parks in Chojna (Province of Western Pomerania) and Dobrzyca (Province of Wielkopolska) have reached a circumference of over 10 m. At Komorów near Gubin (Lubuskie Province), there is a European white elm *Ulmus laevis* with a circumference of nearly 10 m. Although it was broken by during a gale in 2020, the remaining part is alive and the dead remains of the stump have been left in place.

The tallest of the native Polish tree species are the silver firs *Abies alba* and Norway spruces *Picea abies* growing in the Beskidy Mountains. It is estimated that one silver fir, called the Thick Fir, on Babia Góra was 60 m tall when alive. Precise measurements of the so-called "Anderson's spruce" in Istebna determined that the tree, which was toppled by the wind in 2006, had been 53 m tall. One spruce and one fir in the Śrubita Nature Reserve in the Beskid Żywiecki Mountains are 51-52 m in height. A 53-m tall silver fir was recently discovered in the Bieszczady National Park. It is matched by the tallest spruces found in the Białowieża Forest: there, the latest survey revealed 5 specimens exceeding 50 m (data correct as of 1 January 2019). All five trees, the tallest of which was 52.2 m high, were growing in the strictly protected part of the Białowieża National Park. However, Douglas firs *Pseudotsuga menziesii*, a North American species introduced by foresters in the past, are the tallest trees in Poland. Until recently, Douglas firs growing near Meszna at the foot of Mt. Klimczok in the Beskid Niski Mountains were thought to be the tallest at up to 57.3 m. One Douglas fir in nearby Szczyrk is almost as tall. In 2020, there were news reports about the discovery of a 58.2 m high Douglas fir near Glinka in the Ujsoły Forest District. In 2021, a 59.4 m high Douglas fir was found in the Bardzkie Mountains in the Sudety Massif. In the arboretum in Karnieszewice near Koszalin (Province of Western Pomerania), trees of this species reach heights of 49.4 m.

Probably the widest tree on Earth is a Montezuma bald cypress *Taxodium mucronatum* in Santa María del Tule in the Mexican state of Oaxaca. Its circumference was measured at about 40 m, although the tree itself is formed of several conjoined trunks. Giant redwoods *Sequoiadendron giganteum* from California are believed to be the thickest single-stem trees. The General Grant Tree in Kings Canyon National Park in California is ca 27 m in circumference and stands about 81 m tall, while the General Sherman Tree in the Sequoia National Park has a circumference of about 26 m and is ca 83 m high. Their volumes are estimated at 1,300 and 1,490 m^3 respectively, which makes them the two largest individual trees on Earth (in comparison, the average stand volume in Polish forests, i.e. the volume of all trees in a given area, is 283 m^3/ha). Sequoias face competition from the baobab *Adansonia digitata*: in 2019, a specimen with a circumference of "ca 28 m" was reportedly found in Gravelotte, South Africa. Many baobabs in Africa may have a circumference exceeding 15 m. The world's record-holders also include an oriental plane in Şıx Dursun in the Nagorno-Karabakh region (ca 27 m in circumference), a camphor tree *Cinnamomum camphora* in Aira, Japan (22.5 m in circumference) and a Sitka spruce *Picea sitchensis* in the state of Washington, USA (20 m in circumference).

At up to 115 m, the world's tallest trees are coastal redwoods *Sequoia sempervirens* growing in the Redwood National and State Parks in California. The tallest Douglas fir in Oregon, USA, stands ca 100 m high; the tallest Australian mountain ashes *Eucalyptus regnans* in Tasmania and Australia can reach similar heights. There is a report, dating back to the 19th century, which mentions a 143 m high mountain ash, but as this tree no longer exists, it is impossible to verify this information. In Europe, there is a 73 m high karri tree *Eucalyptus diversicolor* in the Valle de Canas (Portugal), and there are 67 m tall Douglas firs in Betws-y-Coed, Wales, and near Freiburg in Baden (Germany). The tallest specimens of species native to Europe are found predominantly in mountain areas at sites that are sheltered from the wind and have fertile soils, where the forest has had sufficient time to develop. Other confirmed very tall

Photo 3 (P. Pawlaczyk)
An oak tree in Orisaare, Saaremaa (Estonia), which is still protected even though it stands in the middle of a football pitch

Clone, clonal organism: a cluster of genetically identical but visually distinct or partially distinct plant shoots arising through spontaneous vegetative reproduction. Individual parts of a clonal organism, called ramets, can be functionally joined, e.g. by a shared system of roots, rhizomes or shoots, or they can exist independently.

specimens include, for instance, firs up to 65 m high and spruces up to 64 m high in the Perućica Nature Reserve in the Sutjeska National Park in Bosnia and Herzegovina, European beeches *Fagus sylvatica* up to 49 m tall in the Havešova Nature Reserve in the Poloniny National Park in Slovakia, and European ashes *Fraxinus excelsior* up to 49 m high, sycamores *Acer pseudoplatanus* up to 45 m tall and wych elms *Ulmus glabra* up to 41 m high in the Hrončecký grúň Nature Reserve in the Polana Range in Slovakia.

In this European context, oaks, which are traditionally fabled for their size, pale in comparison with the examples listed above. This is not to say that they do not reach significant ages or dimensions. The thickest of them, with a circumference just shy of 14.8 m, is the famous pedunculate oak named Kvilleken, situated at Rumskulla in south-eastern Sweden. A large-leaved lime *Tilia platyphyllos* in Emsland, Lower Saxony (Germany), is slightly thicker with a 15.3 m circumference.

The competition for the title of the oldest tree in the world, Europe and Poland is likewise fascinating. But while the size of a tree is easily measured, it is possible to determine its age precisely only in rare cases. Although the annual growth rings typical of trees can show the exact number of years, the core portion of an old trunk has usually long since rotten away, which means that the age of the tree can only be estimated by extrapolating from the growth rate. In the case of some trees, their age as stated in publications is purely speculative.

Great Basin bristlecone pines *Pinus longaeva* (formerly identified as bristlecone pines *Pinus aristata*) in Nevada and California, USA, are considered the world's oldest trees. The most ancient representatives of this species have been dated at ca 4,900 years old, which is quite well documented. One dating exercise produced an age of 5,700 years, but this figure has not yet been adequately verified. The age of a Patagonian cypress *Fitzroya cupressoides* in Chile was estimated at about 3,600 years old. The common yew *Taxus baccata* is also a long-lived species. The age of a monumental yew in Gümeli, Turkey, has been estimated at over 4,000 years, and a specimen in Fortingall, Scotland, is thought to be ca 2,500 years old. A few specimens of the giant redwood have been determined to be 2,000-3,000 years old. In Europe, the age of three specimens of the European larch *Larix decidua* in Santa Geltrude in South Tyrol, Italy, was estimated at about 2,300 years. There are three contenders for the title of the oldest pedunculate oak: in Montravail (France), Cartelos (Spain) and Stelmužė (Lithuania). Each of these trees is close to 2,000 years old. The Bosnian pine *Pinus heldreichii* is another of the most ancient tree species in Europe: in Greece, Bulgaria, Montenegro and Italy there are specimens which have been credibly dated to be 1,100-1,300 years old. A Scots pine *Pinus sylvestris* in Finland is believed to be ca 830 years old.

The figures given above refer to the age of particular stems. Some species can regenerate vegetatively by producing sprouts from roots, the root collar, or branches which are in contact with the ground. In such cases, the lifespan of the whole organism may be much longer than that of its individual stems. Attempts are made to determine the age of such clones by performing radiocarbon dating on the oldest remains of the wood or by extrapolating the rate of the tree's outward growth. According to this concept of age, it turns out that the oldest tree organism in the world is a clonal stand of the quaking aspen *Populus tremuloides* in Utah, USA, spread over an area of 43 ha and approximately 80,000 years old. The age of clones of the box huckleberry *Gaylussacia brachycera* in Pennsylvania, USA, has been estimated at 13,000 years old, and the clonal colonies of small creosote bushes *Larrea tridentata* growing in the Mojave Desert at 12,000 years old. A Norway spruce named "Old Tjikko" in the Fulufjället National Park in Sweden, which has been producing new shoots from rooted low-lying branches probably for as long as 9,560 years, would also be considered a world record-holder. A common olive *Olea europaea* in Luras, Sardinia, and a sweet chestnut *Castanea sativa* called "the Hundred-Horse Chestnut" in Sicily are both roughly 4,000 years old.

The oldest trees in Poland are common yews. At around 1,300 years old, the most ancient representative of this species stands in Henryków Lubański (Province of Lower Silesia). The yews in Wilkowice (Province of Silesia) and Bystrzyca near Wleń (Province of Lower Silesia) have an estimated age of ca 800-900 years. An 820-year-old pedunculate oak in the Kołobrzeg Forest (Province of Western Pomerania; Photo 4) was believed to be the oldest one in the country, but it was blown over during a gale in 2016. The next specimen on the list, the earlier-mentioned 780-year-old Chrobry Oak in Piotrowice, ultimately perished in 2020 after having been set on fire in 2014. The estimated age of the Bażyński Oak in Kadyny (Province of Warmia--Masuria) is 720 years. One has to bear in mind, however, that this information on the age of oaks is rather imprecise. At the beginning of the 21st century, a pine tree on Mt. Sokolica in the Pieniny Mountains was estimated to be 550 years old. A silver fir on Mt. Babia Góra also reached the impressive age of 435 years, but this tree does not exist anymore. In the Radęcin Forest (Drawa National Park) there are 470-year-old sessile oaks *Quercus petraea* and 340-year-old beeches.

In the Białowieża Forest, there are a very great many old trees, among them oaks, pines, limes and ashes. Tomasz Niechoda, who has been studying the stands in Białowieża, estimates that there may be ca 3,000 monumental oaks with circumferences of over 400 cm.

Photo 4 (P. Pawlaczyk)
The Bogusław Oak near Ustronie Morskie – a former contender for the title of the oldest oak in Poland; today it is impressive as a giant dead tree left to decompose naturally

Table 1 Minimum circumference requirements for the recognition of trees as natural monuments according to the Regulation of the Minister of Environment of 2017 (Journal of Laws 2017, Pos. 2300). According to the Polish Nature Conservation Act, trees recognized as natural monuments and situated on undeveloped land are protected even after death until their complete spontaneous decomposition, provided that they do not pose a threat to people or property

Tree species/type	Required tree size – minimum circumference at 130 cm above ground level
red elder, common yew, juniper, alder buckthorn, sea buckthorn, common buckthorn, spindle	50 cm
black elder, false cypress, bird cherry, wild cherry, hawthorn, apple, rowan, Swedish whitebeam, common hazel, white cedar	100 cm
pear, field maple, blue magnolia, ginkgo, jack pine, Swiss pine, goat willow, western red cedar	150 cm
silver birch, downy birch, hemlock, European hornbeam, grey alder, walnut, Weymouth pine, aspen, tulip tree, wych elm, field elm, European white elm, bay willow	200 cm
Douglas fir, honey locust, European ash, silver fir, horse chestnut, sycamore, Norway maple, Turkish hazel, larch, black alder, Japanese pagoda tree, black pine, Scots pine, Norway spruce	250 cm
European beech, sessile oak, pedunculate oak, lime, plane, white poplar, white willow, crack willow	300 cm
other *Populus* spp. not mentioned above	350 cm

Moreover, the old oaks in this forest complex are particularly impressive because of their tall, slender and branchless trunks. The broadest Scots pine in the Białowieża Forest has a circumference of ca 390 cm, and the tallest is 44 m high; another of these pines is about 390 years old. Spruces in the Białowieża Forest grow up to 400 cm in circumference, 52 m in height and reach ages of ca 270 years, while oaks can be up to 780 cm in circumference, 44 m in height and 400 years old, and lime trees up to 470 cm in circumference and 38 m in height. Another noteworthy specimen growing in the Białowieża National Park is a splendid European ash

Photo 5 (P. Pawlaczyk)
The "Krocząca Sosna" ("walking pine"), a natural monument at Kuźnica Żelichowska in the Drawa Forest. It died in 2020 and has since dried up

(45 m in height and 500 cm in circumference). A comprehensive study, recently conducted in the Polish part of the Białowieża Forest, showed that there were over 20 million trees there, 273 of which more than 45 m high (as of 2015).

Many imposing trees can also be found in other forests throughout Poland. Those of the Carpathian Mountains abound in beeches and firs. The "Lasumiła" fir, growing in the Baligród Forest District, has been recorded as the widest in Poland with a circumference of 520 cm, and the unofficial record-holder with a circumference of 560 cm stands near the village of Hulskie in the Bieszczady National Park. In addition, there are many large trees growing in the forests of Pomerania.

Some idea of which trees are considered "unusual" in Poland may be gained from the set of dimensions that a tree of a given species is required to have reached in order to be recognized as a natural monument. Of course, circumference is just one of the qualifying parameters, and even some thinner trees may be declared natural monuments if they have other distinguishing features. The current requirements are laid down in the Regulation of the Minister of Environment of 12 December 2017 (Table 1). Similar sets have been drawn up for local needs, e.g. for individual forest complexes.

Photo 6 (P. Pawlaczyk)
One of the older trees in Europe – a Bosnian pine *Pinus heldreichii* in the Pirin Mountains of Bulgaria

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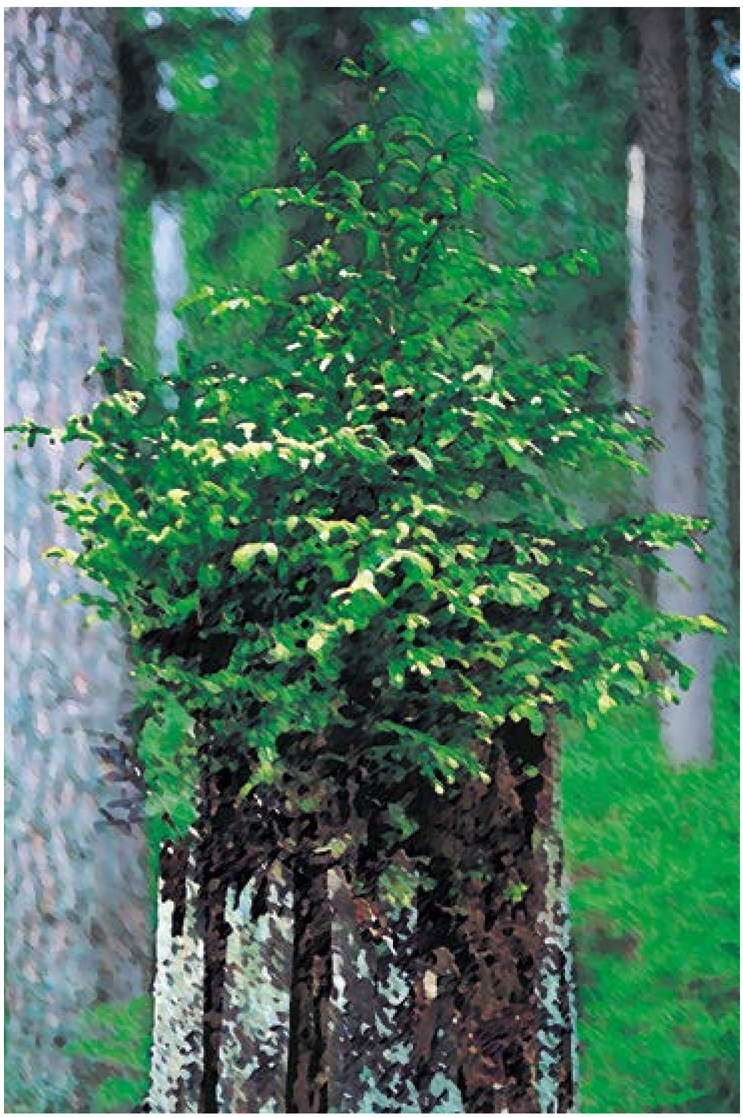
Chapter 1: Summary

Wood is a complex plant tissue consisting of vessels and tubes that transport water and minerals, the supporting components (woody fibres, tracheids) and parenchyma. It is a mixture of cellulose (40-60%), hemicelluloses (ca 23-35%), lignin (21-30%) and other substances. Wood is found in all vascular plants (including herbaceous plants), but it grows and accumulates annually in trees, shrubs, shrublets and lianas. Although wood comprises mainly dead cells, it is widely accepted that the term "dead wood" refers to the wood of dead woody plants or larger-sized dead parts of such plants.

Worldwide, trees can reach enormous sizes (more than 100 m in height, up to ca 40 m in circumference) and ages (up to ca 5,000 years for individual tree parts and up to several thousand years in the case of vegetatively regenerating woody organisms). Trees in Poland, however, are neither as big nor as old, but they are still among the most imposing in Europe. The state of forest preservation in Poland is average compared to the rest of Europe, although some forest complexes such as the Białowieża Forest and some regions of the Carpathians are exceptionally well preserved, which is reflected by the abundance of large and old trees.

2

Sources, dynamics and characteristics of dead wood



2.1. Dead wood in a living tree – tree-related microhabitats

Tree-related microhabitat: a structure forming on a living or dead tree that is or can be a unique habitat for particular species of plants, fungi or animals. In particular, such microhabitats come into being as a result of various kinds of damage sustained by a tree: tree holes, rotting wood, woodpecker feeding signs, rot-holes, cavities between roots, tree throws, holes containing water (phytotelmata), signs of insect feeding, dead boughs, breakages of the trunk or branches, fruiting bodies of tree fungi, masses of slime, sap and resin runs, carpets of epiphytes, witches' brooms, dense clusters of shoots on the bark (water shoots), cankers, bark injuries, tree nests of vertebrates and invertebrates.

The boundary between the life and death of a tree is not easily defined. A tree, considered as an individual organism with a unique genotype, remains alive as long as its assimilation system is still functioning, which means that the overwhelming majority of its tissues may already be dead. It is possible to imagine an imposing tree, which has just a single branch or twig with leaves or needles, as a living organism, despite the fact that most of its parts have already begun to slowly decompose. An excellent illustration of this slow process of dying are monumental oaks in the valleys of large rivers, beeches growing on the former sites of old woodland pastures in mountain areas, or single trees left amid fields, which may only have leaves on one or two boughs, and are often crooked and badly damaged. In such cases, the dead or dying portion of the tree creates excellent conditions for the development of a whole range of different microstructures that can host other, often highly specialized organisms.

These structures, referred to as "tree-related microhabitats", allow for the emergence of plant, fungi or animal species with specific requirements by providing space where they can reproduce, grow, develop, feed, shelter or perform other functions. They are crucial for organisms with narrow ecological requirements, so-called "habitat specialists", which may be inextricably linked to a given microhabitat. Nearly eighty types of tree-related microhabitats have been identified in temperate forests, and their number is constantly growing as a result of new research covering other plant communities and associated tree species being undertaken in different regions around the world.

Among the best-known examples of tree-related microhabitats are hollows. In general, a hollow is any type of opening, cavity, rot-hole, fissure or crack in a tree. Regardless of the type, however, all hollows are important for different organisms. For example, Leisler's bat *Nyctalus leisleri* prefers hollows (and the associated rot-

Photo 7 (P. Pawlaczyk)
Multiple microhabitats (including rotting wood microhabitats) in an old pollarded willow

ting wood) originating from naturally occurring cracks in the trunk or branches, whereas the common noctule bat *Nyctalus noctula* favours holes excavated by woodpeckers. The significance of "hollow trees" should thus not be considered solely in relation to birds, nor should it be limited to just those trees which have hollows suitable for birds.

Rotting wood is a very valuable microhabitat from the point of view of biological diversity. It can develop inside hollows, but also externally (often at the base of the trunk) or internally as heart rot, encompassing the entire core of the trunk and accessible only through a hollow or an opening at the top of the bole. Rotting wood microhabitats are very complex. Depending on the species and size of the tree, the species of wood-decomposing fungi, the location within the trunk, humidity conditions or species of co-occurring animals, they can be used by extremely diverse communities of saproxylic organisms. Within a single rotting wood microhabitat, a number of zones occupied by various species can be identified. For instance, rotting wood microhabitats with nests of the European hornet *Vespa crabro* have their own unique fauna: they are often co-inhabited by the hornet rove beetle *Quedius dilatatus*, which usually occurs together with a number of other valuable beetle species such as *Hesperus rufipennis*, *Quedius brevicornis*, *Quedius invreae*, *Quedius ochripennis* and *Quedius xanthopus.* If a hollow containing a rotting wood microhabitat is inhabited by birds, one can usually expect the co-occurrence of the hide beetle *Trox scaber* (Trogidae) and larder beetle *Dermestes bicolor* (Dermestidae), among others. The fauna of rotting wood microhabitats colonized by ants (Formicidae) is equally rich. Jet-black ants *Lasius fuliginosus* usually live alongside sap beetles *Amphotis marginata* (Nitidulidae). The brown tree ant *Lasius brunneus* co-occurs with species such as the rove beetle *Thoracophorus corticinus*, species of the genera *Scydmaenus* and *Batrisodes*, as well as *Pycnomerus terebrans* (cylindrical bark beetles Zopheridae). Dry, rotted oak wood, sometimes reduced to powder, can be colonized by click beetles, e.g. oak click beetle *Lacon querceus* (Elateridae), darkling beetles, e.g. *Pentaphyllus testaceus* (Tenebrionidae) and hairy fungus beetles, e.g. *Mycetophagus piceus* (Mycetophagidae). The smallest of the Polish stag beetles (Lucanidae) – *Aesalus scarabaeoides* – is also found there. Included on the Polish Red List of Threatened Species and not seen in Poland for a long time, the very rare violet click beetle *Limoniscus violaceus* (Elateridae) requires microhabitats forming at tree bases, where the wood is in a stage of advanced decomposition.

Naturally, the list of tree-related microhabitats is much longer and covers a variety of structures, e.g. old bird or animal nests, especially those belonging to long-lived species with larger body sizes, which remain in use for many breeding seasons, or structures associated with invertebrates, mainly larval tunnels or exit holes of cambio- and xylophagous insects. Some trees feature phytotelmata (photo 8G), i.e. cavities in the trunk, boughs and flutes filled with stagnant water, which can host distinctive invertebrate species, most often gnats and other dipterans, but also e.g. the beetle *Prionocyphon serricornis*. Spots of exposed wood on living trees, such as mechanical injuries, side necroses or even beaver gnaw marks, are used by e.g. powderpost beetles *Lyctus* (Bostrichidae), wood-eating beetles of the genus *Ptilinus* (Ptinidae), and the predatory beetles *Teretrius fabricii* (Histeridae) and *Pelecotoma fennica* (Ripiphoridae), the larvae of which develop inside the larval tunnels of *Ptinidae* beetles. Also, some species of wasps use such places to gather wood fibres to build their nests.

Other microhabitats found on trees include sap runs (Photo 9), cankers or outgrowths, perennial and annual fungal fruiting bodies, cracks, crevices and indentations of the bark, fire scars (resulting from naturally occurring fires), dead boughs, and epiphytes growing on the trunk or branches.

The development of tree-related microhabitats can be influenced on the one hand by a variety of biotic factors, such as the activity of microorganisms, fungi, invertebrates or vertebrates (primarily birds and mammals), and on the other by abiotic factors such as extreme heat or cold, strong winds, snow load, intense sunlight or high humidity, lightning strikes or fires, which over the years can bring about more or less severe mechanical injuries or cause physiological stress in trees. At the same time, the impact of biotic and abiotic factors may unfold over different spatial scales and involve entire stands or be restricted to just a single tree. Some microhabitats, especially large hollows formed through wood decay, can arise from the complex and sometimes prolonged effects of a combination of biotic and abiotic factors. An example of this is when, on one or more occasions, abiotic factors mechanically damage a tree or a part of one, the resulting injuries opening up spaces where biological decay processes generated by prokaryotes, fungi and xylophages can persist for many years.

It usually takes a long, even a very long time for the vast majority of microhabitats to develop on a given tree, regardless of the underlying causes. This is due to the slow growth of trees. Recurring mechanical damage, physiological stress induced by extreme weather conditions or the slow decay of wood can take place over very many years. Destructive events occur even as the tree continues to grow and its damaged tissues heal. These two opposing processes – destruction and growth – mean that

Rotting wood microhabitats:
rotting pieces of wood on standing living trees, e.g. side necroses, cavities left after dead branches have fallen off, rotting cores of old trees, dead and dying woody tissues inside tree cavities.

Side necrosis:
outer layer of wood killed by the local destruction of the cambium as a result of fire, intense insolation, severe frost, and damage caused by animals or machines.

Phytotelmata:
water-filled recesses and holes on trees. They may occur in the crotch of a bifurcated trunk, in cavities, side necroses with an area enclosed by leftover bark where water can accumulate, holes in basal flutes and in calluses developing on stumps still connected to the root system of a living tree.

Photo 8 Examples of tree-related microhabitats: **A** – a natural cavity formed during the protracted process of decomposition (M. Ciach); **B** – a hole excavated by a woodpecker (A. Wajrak); **C** – a spacious cavity in the butt portion of the trunk (M. Ciach); **D** – insect exit holes and larval tunnels (M. Ciach); **E** – perennial fungal fruiting bodies (M. Ciach); **F** – carpet of epiphytes (M. Ciach); **G** – a water-filled hole in a flute (phytotelma) (M. Ciach); **H** – a snapped trunk (P. Pawlaczyk); **I** – canker (P. Pawlaczyk)

the older the tree, the greater the chances that numerous and often unique microhabitats can form. However, some studies have suggested that this relationship is not linear, i.e. that the diversity and number of microhabitats increase rapidly once a tree has reached a really advanced age (150-200 years for most species, but just 100 years in the case of birches, willows, poplars and alders). Other studies have shown a similar correlation between the number of tree-related microhabitats and the thickness of a tree. A consequence of this strong association with trees of large size and old age is that rare types of tree-related microhabitats occur almost exclusively in old forests, which have resisted the effects of human activity for at least decades or even centuries and are not subjected to typical forest management practices.

The deficit of microhabitats often observed in managed forests is caused by the fact that trees in such forests are cut down when they are relatively young and rarely have a chance to grow to the age and size necessary for them to form.

Certain types of microhabitats, such as exposed wood, dead branches or the cover of mosses and lichens on bark, are relatively common. Other types, in contrast, are comparatively rare and thus extremely valuable, for example, fire scars (where pyrophilous organisms are found) caused by lightning strikes and small fires, which under natural conditions only occur sporadically and locally (Photo 10). Another example of a rare microhabitat type are large natural cavities forming in the butt-log near the ground. They provide perfect concealment and hibernacula for mammals. The formation of certain microhabitat types requires a suitably sized and sometimes appropriately structured tree, and this is inevitably linked to its long and natural growth. Some of the microhabitats found on large trees include what are known as chimneys, i.e. deep cavities formed where the top of a tree has been broken off, as well as large nests belonging, for example, to birds of prey of the order *Accipitriformes* or black stork *Ciconia nigra*. Another important type of microhabitat are dead branches and boughs in the crowns of living trees. Dead wood in the crowns of smaller trees is not a significant resource in terms of quantity, but on larger trees an individual dying bough can sometimes be bigger than a whole medium-sized tree.

Numerous studies have shown a strong correlation between the number and diversity of microhabitats, and the size and age of a tree: microhabitats are the most diverse in old trees of significant size, often characterized by a unique trunk (crookedness, multiple stems) or crown structure (horizontal boughs, unbalanced crown).

Photo 9 (J.M. Gutowski)
Sap run on a hornbeam in the Białowieża National Park – a habitat for some species of beetles and dipterans

Tree-related microhabitats act as refuges for biodiversity within a forest complex. The number of organisms and diversity of communities in tree-related microhabitats contribute to the overall level of forest biodiversity.

The role of some microhabitat types, e.g. hollows made by birds, cavities formed during the decomposition of wood, perennial fruiting bodies and cavities with stagnant water, in shaping the biological community of organisms

Photo 10 (J.M. Gutowski)
A Scots pine scarred by ground fires in northern Kazakhstan

Photo 11 (M. Ciach)
Montane deciduous forest featuring many tree-related microhabitats (Magura National Park)

Funga (= mycobiota): all species of fungi occurring in a given area. Past publications also used the term "mycoflora", but this is now regarded as obsolete, because fungi are considered a distinct kingdom in the taxonomy of living organisms, separate from plants.

is quite well documented. Nevertheless, the typical fauna and funga of a vast number of tree-related microhabitats are still poorly researched. There is a lack of specialist knowledge regarding the diversity of organisms colonizing nests of birds and mammals, sap runs and patches of organic matter accumulated on trees. Examples of some of the species associated with these specific microhabitats will be given in the later chapters of this book.

The abundance and diversity of tree-related microhabitats are associated with specific features of a given tree, of which age and size are the most important, as mentioned before. Also, the species of the tree, the structure of its crown and trunk, and its longevity all have a significant influence on the number and diversity of tree-related microhabitats. Usually, deciduous trees foster a greater diversity and abundance of tree-related microhabitats than conifers. In Polish forests, a species particularly likely to host a wealth of microhabitats, especially tree hollows, is European hornbeam *Carpinus betulus*, but there is also no shortage of hollows in birches and alders. Old oaks and very old, sprawling or wind-damaged beeches are hotspots of microhabitat diversity.

Furthermore, standing dead trees host more tree-related microhabitats than living ones. In this context, the life history of an individual tree, including all the environmental factors that have affected it over the years, takes on great importance as well.

Hence, it is crucial to maintain a variety of large trees that could act as sources of microhabitat diversity for the whole forest. Data from natural forests show that large trees are a relatively rare component in the ecosystem. In temperate forests, the number of trees with a diameter over 50 cm is on average less than 100 per hectare, sometimes exceeding 100, and only rarely reaching 200. Studies where only trees with a DBH over 70-90 cm were considered large have shown that their density is not usually more than 20 per hectare. With regard to species diversity, it can be assumed that in some forest types, large trees are represented by single specimens of particular species. The most important consideration when implementing conservation measures for big trees is to retain the existing ones. Long-term planning needs to create opportunities for trees to attain large dimensions. From the ecological point of view, these opportunities should first and foremost be provided for trees with unique characteristics, such as a well-developed multi-branch crown, curved trunk, patches of exposed wood or the presence of natural hollows in the early stages of formation. If suitable trees cannot be found, an appropriate number of any other trees should be given a chance to grow old on the assumption that microhabitats will develop on them as they mature. In the future, these specimens will form the pool of large trees exhibiting unique characteristics and an abundance of microhabitats. In this context, regardless of the harvesting method adopted, the key to the future biodiversity of managed forests is to leave pockets of old growth or individual trees so that they can grow old and become part of the next generation of the stand, develop the broadest possible spectrum of microhabitats, and eventually die and turn into coarse woody debris.

In forests growing on former agricultural land, meadows or pastures, single trees predating the afforestation (usually with a characteristic spreading growth habit, indicating they had been growing in an open space environment) are of crucial importance for the community, precisely because of the richness of microhabitats. In subsequent generations of the stand, this key function is usually performed by trees surviving from the previous generation.

Features of the surrounding forest, including its species composition, structure, spatial diversity, habitat parameters and microclimate, especially light and humidity conditions, may also play an important role in shaping tree-related microhabitats. At the forest level, the natural processes of tree growth and death and, most importantly, the impact of damaging factors, also contribute to the formation of tree-related microhabitats. In order to maintain the richness of microhabitats in the forest, trees that have been damaged in some way need to be retained. After all, it is the damage suffered by a tree, and the structures that develop as a consequence, that give rise to the microhabitats that are integral to forest biodiversity.

Also important for the emergence of tree-related microhabitats is the activity of certain species – ecosystem engineers – which can strongly influence the appearance and functioning of an ecosystem. For instance, the presence and activity of medium-sized and large mammals, such as Eurasian beaver *Castor fiber*, elk *Alces alces* or European bison *Bison bonasus* (Photo 14), often translate into very specific types of damage sustained by trees. Nests built and maintained by birds, breeding cavities excavated by woodpeckers almost every year, and extensive larval tunnels produced by insects such as great capricorn beetle *Cerambyx cerdo*, also create characteristic tree-related microhabitats. Fungi have a special place here: by decomposing wood, they take part in the development of rots and contribute to the formation of snags; some species can kill whole trees or cause branches to die, and the fruiting bodies of tree fungi are themselves important microhabitats.

Indicative of a forest's degree of naturalness and ecological complexity, the number and diversity of tree-related microhabitats are a reliable gauge of the ecosystem's biodiversity. The density of tree-related microhabitats varies significantly between forests and depends on the type of ecosystem, the species, age and size of trees, conservation measures in place, as well as past and current management practices. This density in semi-natural managed forests is ca 100 per hectare, whereas their number may reach 1,000 per hectare in natural forests or in forests enjoying long-term protection. In temperate climate zones, tree-related microhabitats seem to be the most abundant in natural montane beech or beech-fir forests, albeit lowland beech forests are only slightly less plentiful in this respect. Some truly remarkable densities of tree-related microhabitats have been reported from the most natural of forests: for instance, the oak-hornbeam stands in the Białowieża Forest boast more than 1,300 tree-related microhabitats per hectare. Over 800 tree-related microhabitats per hectare have been reported in the oak-hornbeam forests of the Middle Vistula River Valley, and more than 500 per hectare in the projected "Mała Puszcza Kleszczowska k. Krakowa" nature reserve near Kraków. On the other hand, most Polish forests do not usually have more than 100 tree-related microhabitats per hectare, even if they are in protected areas like nature reserves, national parks, landscape parks or Natura 2000 sites, and managed lowland forests have just a few per hectare.

Forests that have not been utilized for a long period of time are particularly important for studying these regularities, as they are likely to have reached their maximum microhabitat potential. Some forests in Poland, although sadly their number is very limited, could serve as reference sites for the majority of temperate forests in Europe. The Białowieża Forest, selected areas of the Carpathians and small patches of forests under long-term protection within nature reserves scattered throughout the country, can be viewed as unique research plots, where the interrelationships between the forest, tree-related microhabitats and their resident organisms can be studied.

Forest management and the biodiversity and abundance of tree-related microhabitats are very closely linked. The aim of forest management is to produce wood of a specific quality, and therefore promotes trees with branch-free boles that are straight, regular and undamaged – the polar opposite of what a habitat tree should look like. Habitat trees are those ecologically valuable specimens which are predominantly damaged or "sick", and are therefore removed during intermediate cutting. In managed forests, trees are harvested once they have reached cutting maturity, which is long before they achieve biological maturity and far earlier than the age at which they would possess the most tree-related microhabitats. Moreover, forest management practices usually focus on species of significant commercial value, thereby restricting the occurrence of species that are economically less valuable but more important for the environment, e.g. European hornbeam or aspen *Populus tremula*. In this way, a substantial proportion of tree-related microhabitats is either removed or simply has no chance to form. As a result, the level of tree-related microhabitat diversity in managed forests is greatly diminished, so the fewer tree-related

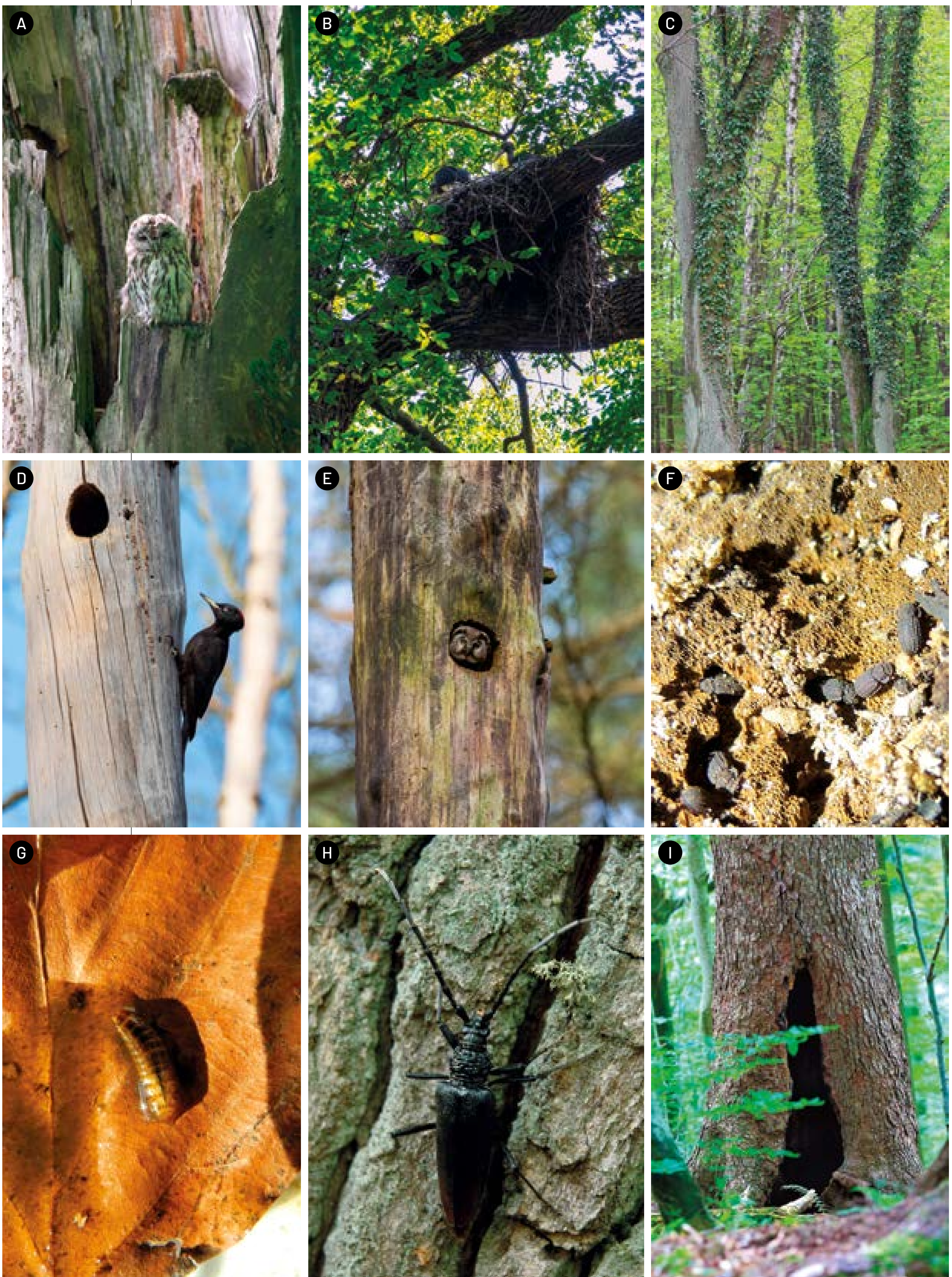


Photo 12 Examples of species associated with specific tree-related microhabitats: **A** – a tawny owl *Strix aluco* nesting in a decayed trunk (M. Ciach); **B** – a nest of the black stork *Ciconia nigra* where numerous saproxylic organisms are found (M. Miłkowski); **C** – common ivy *Hedera helix* growing on tree trunks (M. Ciach); **D** – a black woodpecker *Dryocopus martius* near its nest hole (A. Wajrak); **E** – a black woodpecker's hole taken over by a Tengmalm's owl *Aegolius funereus* (A. Wajrak); **F** – a mycophilous beetle *Eledonoprius armatus* on the fruiting body of a bracket fungus of the genus *Inonotus* (R. Ruta); **G** – a larva of the beetle *Prionocyphon serricornis*, whose life cycle is played out in phytotelmata (water-filled holes in a tree) (R. Ruta); **H** – the great capricorn beetle *Cerambyx cerdo* is an example of a species whose adult forms leave many exit holes in oak trunks (J.M. Gutowski); **I** – a lair of the brown bear *Ursus arctos* in the trunk of a fir (B. Pirga)

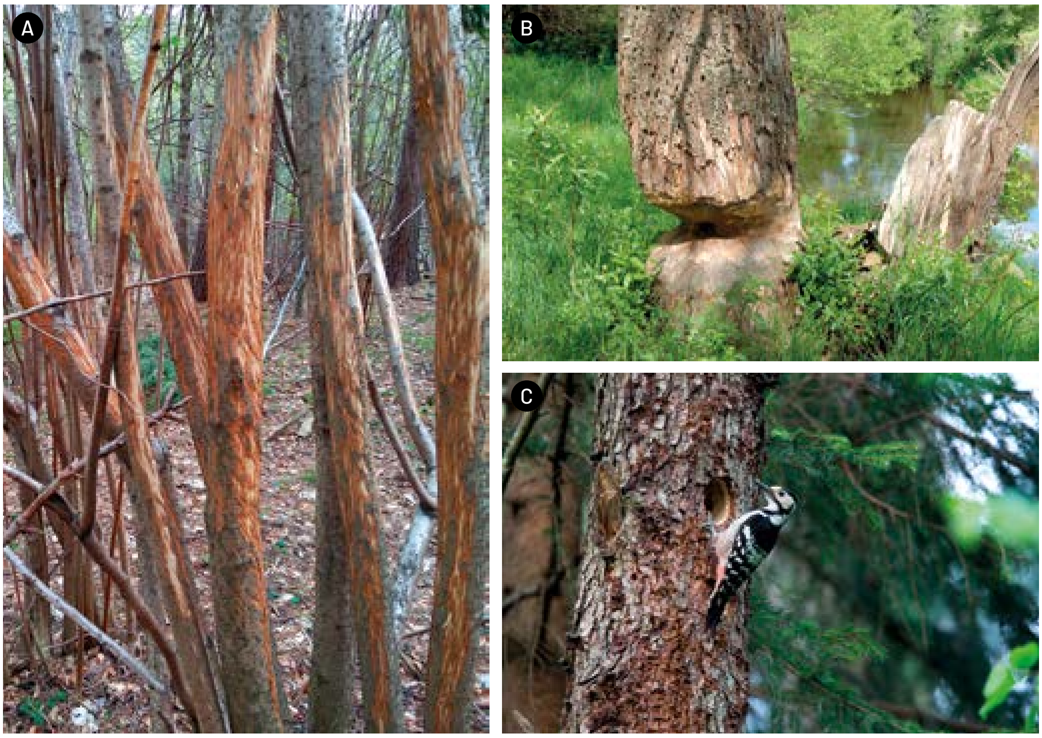


Photo 13 Examples of ecosystem engineers and the effects of their activities: **A** – intensive bark stripping by red deer *Cervus elaphus* has exposed large portions of the phloem on hazel (M. Ciach); **B** – signs of chewing left by Eurasian beavers *Castor fiber* (J.M. Gutowski); **C** – a white-backed woodpecker *Dendrocopos leucotos* excavating a nest hole (A. Wajrak)

microhabitats there are, the less likely that new ones will arise.

Knowledge of the relationships between tree-related microhabitats and the organisms which use them can help us to better protect particular species or groups of organisms in managed forests. At present, the good practice is taking hold of seeking out and retaining habitat trees (see Chapter 5.1), including trees with microhabitats. These are usually large, sometimes partially moribund trees, with a well-developed crown or visible tree-related microhabitats, mainly hollows or perennial fungal fruiting bodies. In some parts of the world, the technique of veteranization, i.e. deliberately damaging trees, is occasionally applied to induce the formation of certain microhabitat types (see Chapter 5.2).

Leaving habitat trees is a commonly declared practice in Polish forests, although care is rarely taken to provide suitable growth conditions for such trees. In practice, therefore, the retention of habitat trees is inconsistent. Sometimes only a few selected trees with the most prominent habitat features are left in place, but it also happens that habitat trees are removed because of purported safety concerns (see Chapter 5.4).

Habitat tree: a tree whose characteristics make it or potentially make it particularly important for biodiversity conservation. This is most often due to the abundance of tree-related microhabitats which have developed on that tree. In Poland, the Instructions for Forest Protection recommend leaving habitat trees until their death and natural decay. Specifically, these can be partially or completely rotten trees, trees with visible fungal fruiting bodies, trees with more than one-third of the crown dead, trees with hollows or dry rot, trees which have lost their crowns as a result of fracture, trees with atypical growth habits or morphologies, and trees of significant age or size (see also Chapter 5.1).

Photo 14 (J.M. Gutowski) European bison *Bison bonasus* and their rubbing site. Animals transform the fallen tree by rubbing their bodies against it

2.2. Dead trees in forests

When wood comes to life

Dead wood occurs as dead pieces of living specimens (e.g. rotten parts of trunks, dead boughs and branches, dead roots, internal rot-holes) or entire standing or fallen trees. Studies from North American forests show that dead wood may cover up to 25% of the forest floor. Decaying wood is a microhabitat that is indispensable to such an ecosystem. While the wood of living trees, the primary construction material of a forest stand, is capable of resisting diseases and infestation by insects, the death of a tree or of its parts opens the door to myriad organisms that are waiting for just such an opportunity. And in a natural forest there are plenty of opportunities.

In natural stands in the Białowieża Forest, the annual average increment of the wood volume of living trees is ca 3.3 m^3/ha. If we assume that these ecosystems are in some kind of dynamic equilibrium, then more or less the same amount of wood dies. 3.3 m^3 is approximately the volume of a 40 m tall spruce tree with a DBH of 45 cm, or a 23 m tall hornbeam with a DBH of 55 cm. These numbers suggest that, on average, 100 such trees are expected to die on every 1 km^2 of forest annually (Photo 15). In actual fact, however, many more trees fall or break: indeed, research shows that it is primarily smaller trees that succumb.

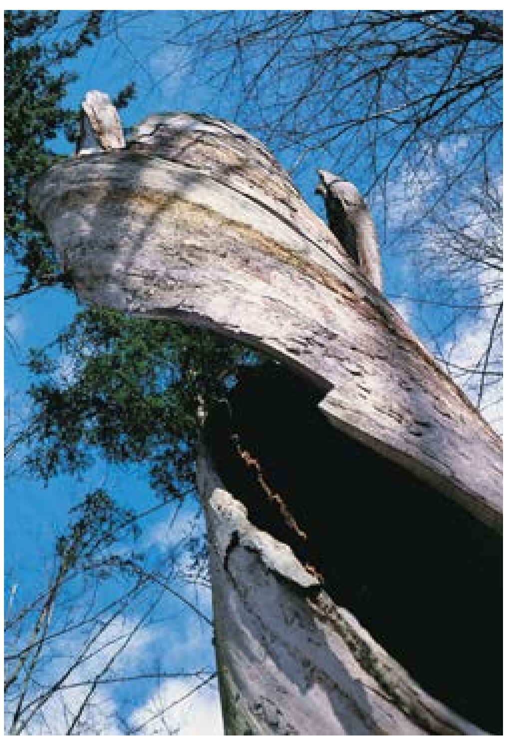


Photo 15 (J. Walencik) A dead pine in the Białowieża Forest. Every year over 100 trees die on 1 km^2 of natural forest

If dead wood did not decay, the ground would eventually become covered by the accumulated woody debris. So, for a forest ecosystem to function properly, a balance has to be maintained between the growth, dying and decomposition of wood. To revisit the example from the Białowieża Forest, what we end up with on the forest floor is 3.3 m^3/ha of fresh, i.e. this year's, material along with ever smaller proportions of the previous years' inputs that have been gradually decaying. As mentioned in the Introduction, the oldest recognizable remnants of wood in the Białowieża Forest may be up to 100 years old. Such a rate of decay results in a relatively constant average of 120 m^3 of dead wood lying on the ground per hectare of forest (Fig. 2).

In our example from the Białowieża Forest, the average volume of wood decomposed by various organisms, along with the standing dead trees and sections of trunks, is 130-140 m^3/ha. This indicates that, in a natural forest, dead wood makes up more than one-fifth of all the terrestrial biomass (locally, even half or more). What part does it play in this ecosystem? It is a treasure trove of ecological niches and microhabitats. Let us imagine how a smooth wooden cylinder placed on the ground might enrich the habitat's microclimate. Where it touches the ground, we have the zone of contact with the soil; the side of the cylinder that is exposed to the sun can be termed the insolation zone, characterized by intensive evaporation and abrupt temperature changes; and the opposite side of the cylinder will be in shade, i.e. the shadow zone, where the humidity and relative thermal stability will both be higher. And that is just a smooth cylinder, a highly simplified model of a real piece of wood lying on the forest floor. A real wood "cylinder" is an intricate microrelief of cracks, furrows, knots, insect-bored galleries and other imperfections. Each of these features introduces its own variability and microclimate. But the surface itself, rich and varied though it is, does not exhaust all the microhabitat resources of dead wood. Its interior is just as interesting and provides a diverse environment and food for a multitude of organisms. Some of them bore tunnels and chambers in hard, fresh wood, whereas others (especially fungi) cause it to decay, the disintegrated wood eventually becoming available to other groups of organisms that require either loose, powdery material or wet, sponge-like rot.

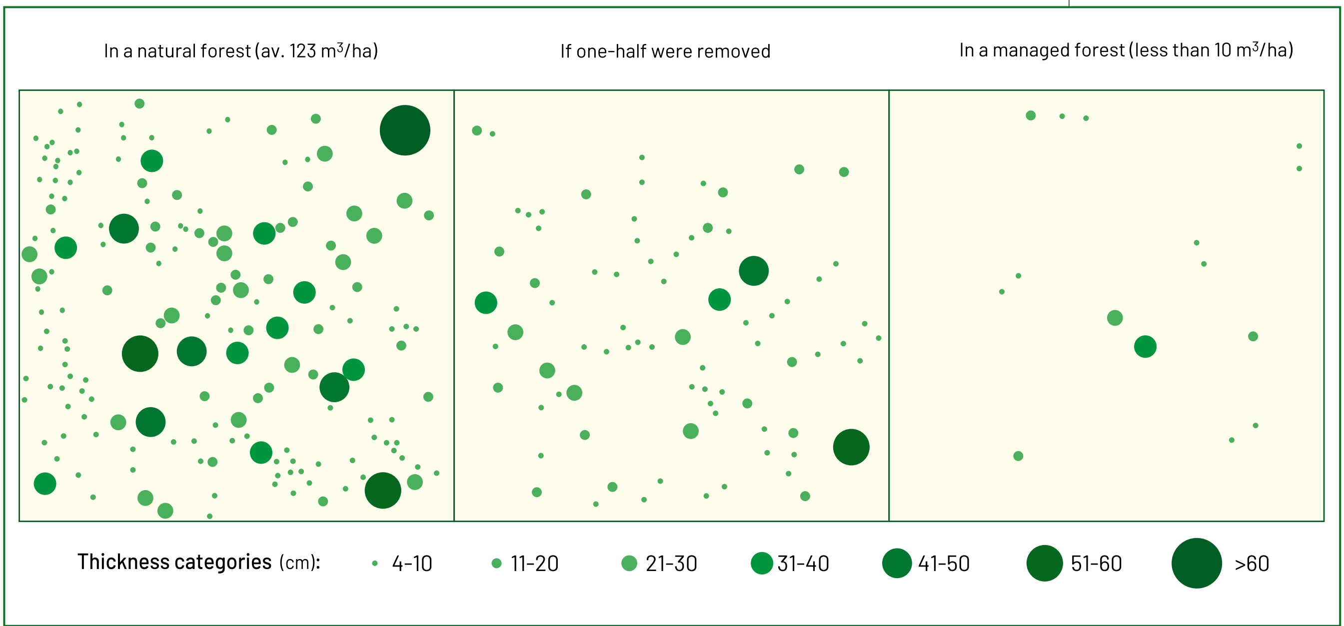


Fig. 2 If fallen dead wood were evenly cut into 1 m sections, this is what an average 100 m^2 of forest would look like (after Bobiec 2002)

If dead wood consisted of absolutely smooth cylinders with different diameters, it would on average provide 65 m^2 of additional surface area for each 100 m^2 of forest floor. However, the additional surface area provided by the complex exterior and porous interior must be very much greater than that. Hence, the magnitude of habitat loss caused by the removal of dead wood from forests is scarcely imaginable.

In other European forests the rate of dead wood build-up varies and ranges from fractions of m^3/ha to a few m^3/ha annually. A rough estimate of ca 1 m^3/ha per year in European old growth forests gives just a glimpse of the actual average intensity of the tree mortality process, which, in reality, is hardly ever linear or steady (see also below). Rather more common are sudden spikes in tree deaths, e.g. as a result of high winds or heavy loads of snow, or longer periods of increased mortality due to outbreaks of insects. The availability of dead wood is a consequence of processes and phenomena occurring

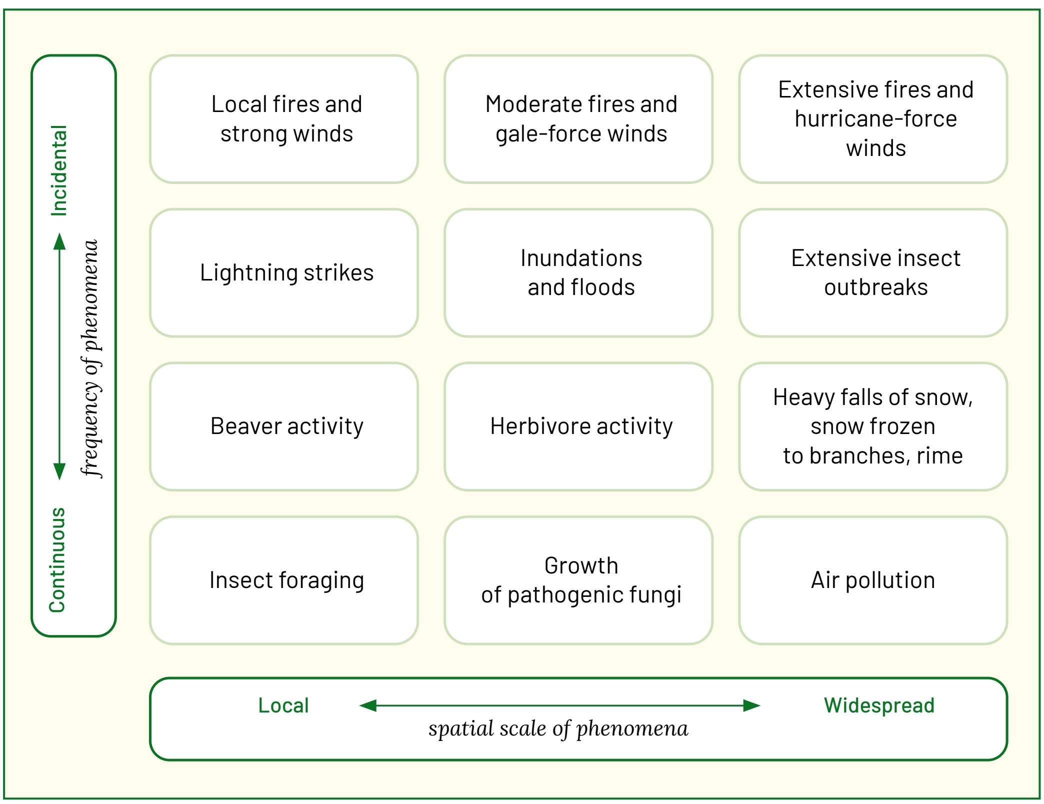


Fig. 3 Temporal and spatial variability of processes and phenomena leading to the supply of dead wood (M. Ciach)

Ecological disturbance: a relatively sudden and transient event, difficult to predict, involving the partial or complete destruction/disturbance of the living plant cover. The disturbances in a certain area follow a certain spatial and dynamic pattern and are characterized by the type of disturbance, its spatial extent and intensity, repetition and frequency. Although disturbances are usually caused directly by an external phenomenon, e.g. wind, fire, flood, avalanche, animals feeding, herbivorous insects, fungal diseases and management practices, the pattern of disturbance is heavily influenced by the characteristics of the community, which determine its susceptibility or resistance to specific types of disturbance. Thus, the continuous growth of vegetation and the development of forests implies changes in disturbance patterns

Stage of stand development: a phase in the life of a stand; in simplified terms these stages include, e.g. a regeneration stage, an optimum stage, a terminal stage (ageing). Natural forests usually feature a mosaic of different stand development stages.

Cleaning: silvicultural practice of removing young trees from plantations and sapling stands in order to adjust the species composition, distribution and regeneration structure, regulate density and improve growth conditions for saplings.

Thinning: silviculture treatment applied in commercial stands after the sapling stage; thinning of the stand; removing trees considered to be defective or hampering the growth of crop trees. To a certain degree, thinning can be used to adjust the species structure of a stand.

in the forest environment at different temporal and spatial scales (Fig. 3). The characteristics of the individual factors contributing to a tree's death are different: they may be almost ever-present or occur intermittently, they may take place at a very local level or influence a very large area. The death of single trees and the local provision of dead wood associated with it is an ongoing process at the stand level.

The activities of insects, fungal pathogens, viruses and single-cell organisms, competition within and between species and local abiotic factors can bring about the death of one tree or a part of it (bough, branch, portion of the trunk) or a small group of trees standing next to each other. Therefore, even though the number of dead trees in large stands may be locally significant, the volume of dead wood per unit of area may be quite small. On the other hand, one of the consequences of periodic events, mainly abiotic ones, may be the simultaneous death of trees over a large area and thus a one-off, very significant increase in the number of dead trees. In this case, the measured ratio of locally accumulated dead wood to the stand area will show that its volume is high, sometimes equal to the volume of the original living stand. Although large-scale disturbances have become increasingly common in recent years, catastrophic events resulting in the death of all trees over a large area are still relatively rare. However, it is worth mentioning that in the age of climate change, phenomena such as extreme drought and hurricane-force winds are becoming more common, and so the simultaneous dying of trees over vast tracts of land and the ensuing ample supply of dead trees may become more frequent.

The temporal and spatial variability of processes and phenomena occurring in forest environments are responsible for the substantially different amounts of dead wood biomass deposited in them. In central European forests that have not been exploited for a long time, the average volume of dead wood ranges from ca 30 to ca 300 m^3/ha and may locally reach 500-700 m^3/ha, usually as a result of major disturbances. Average values recorded, for example, in German beech forest reserves were 94 m^3/ha or one-third of the living stand volume in Serrahn, 193 m^3/ha in the Heilige Halle reserve, and 149 m^3/ha on the island of Vilm. In unexploited forests in the Romanian Carpathians, this figure was around 100 m^3/ha. According to the 2017 survey in the Białowieża Forest, the average volume of dead wood was 157 m^3/ha within the strictly protected zone of the Białowieża National Park, 125 m^3/ha in the nature reserves of the Białowieża Forest and 74 m^3/ha in other complexes. On average, the volume of dead wood in the Polish part of the Białowieża Forest was 94 m^3/ha, almost 12 times more than the national average (8 m^3/ha).

The amount of biomass deposited as dead wood depends on many factors, such as the forest type (deciduous, mixed, coniferous), location (lowlands, mountains), species composition, stage of development (juvenile stand, stand at the breakdown stage) or productivity of a given habitat, including the total volume of living trees achievable within a specific area under existing site conditions. More dead wood is found in forests in cooler climates, where the rate of decomposition is slower. On average, under natural conditions, the volume of dead trees makes up 20-50% of the volume of living trees, although locally this proportion can be higher and sometimes significantly exceeds the total volume of living trees as a result of the accumulation of dead wood.

An important consequence of the temporal and spatial variability characterizing the vast majority of phenomena and processes leading to the emergence or disappearance of dead wood is their randomness. In other words, we cannot predict in natural forests exactly how the quantity, quality and distribution of dead wood is going to change, although we can determine how likely such changes will be. Organisms associated with dead wood are forced to constantly colonize new sites where the increase in the amount of dead wood compensates for the loss of dead wood elsewhere. The population dynamics of saproxylic organisms brings to mind the metapopulation model, a concept well-established in ecology, in which a population is viewed as a group of islands inhabited by subpopulations. In this model, some islands are already colonized, while others represent the potential range; moreover, individual specimens are free to move between inhabited and uninhabited islands. This paradigm of how the populations of species associated with dead wood function comes with two major implications for their conservation. First, it will necessitate securing the future availability of dead wood in places where it is currently lacking; and second, it will require ensuring opportunities for relocation between the current and future (potential) habitats of a given species.

The supply of dead trees

The quality, amount and distribution of dead wood in a forest depends on the rate and mode of its input and output, and that is determined by the stand dynamics, i.e. the phase of stand development and other, often related, factors influencing tree mortality.

Starting with the seedling and sapling stages, young trees in stands compete for nutrients and light. Faster growing trees outcompete less well-adapted ones, which gradually die. This natural self-thinning corresponds to silvicultural thinning as applied in commercial forests. The difference is that in a natural forest, nature alone designates the trees to be eliminated, and, most importantly, ensures that their remains stay in the forest.

The gradual development of the stand during this period is accompanied by a constant and relatively even supply of dead wood to the ecosystem. After the most intensive self-thinning (stem exclusion) stage (at age 20-60 years, depending on the species), the contribution of fallen boughs and branches to the overall dead wood volume increases. With time, individual mature trees die of natural causes and become the source of coarse woody debris (Photos 16 and 17).

In places, this state of relative dynamic equilibrium can last for quite a long time, probably for more than 200 years. In general, it is characterized by a relatively small amount of dead wood (on average 40-80 m^3/ha) and the fact that the species composition of dead wood at any given time reflects the species composition of the stand. Exceptions to this pattern are the "reorganizing" pioneer stands, i.e. the spontaneous succession of shade-intolerant and fast-growing species (mainly birches, aspens and goat willows *Salix caprea*) on abandoned fields, clearcuts and areas affected by catastrophic events such as fires or hurricanes. In the transitional stage, having reached the age of 80 years, these pioneer stands enter a period of accelerated mortality and are replaced by shade-tolerant, climax species: in the Białowieża Forest, these are usually hornbeams and limes in the oak-hornbeam complexes. In such a case, therefore, at a certain stage of stand development, the type of dead wood does not reflect the current species composition of the living stand (Photo 18).

An integral aspect of forest dynamics are various types of disturbance during which the existing flora (mainly trees) is locally destroyed by some biotic or abiotic factor. In the context of forest ecosystem dynamics, these phenomena should not be underestimated. Not only do they rejuvenate the forest, they also introduce spatial variability to its various communities. The process of tree mortality or loss followed by tree regeneration in the new gaps creates a mosaic of patches which are crucial for the stability of the forest as a whole. Paradoxically, the forest lives on because of the death of its constituent trees. Disturbances can be natural (e.g. high winds, insect outbreaks) or anthropogenic (e.g. a clearcut or arson). Natural disturbances are irregular and unpredictable, both spatially

Oak-hornbeam forest: Humid deciduous or mixed forest with dominant hornbeam, oak or lime, and a rich ground layer, growing on fertile soils.

Abiotic factors: factors not associated with the activity of living organisms, mainly precipitation, wind or frost.

Biotic factors: the impact of living organisms: insects, fungi, bacteria, etc.

Photo 16 (K. Zub). Dead pines in the Białowieża Forest

Photo 17 (A. Bobiec)
The Białowieża Forest. A patch of oak-hornbeam forest in a state of relative equilibrium – relatively small amounts of dead wood come from the gradual shedding of branches and death of individual trees

Photo 18 (A. Bobiec)
The natural transformation of a beech-aspen stand into a hornbeam-lime stand results in an abundant supply of dead wood to the ecosystem

Photo 19 (K. Zub)
The Białowieża Forest: natural disturbances are responsible for local accumulations of large amounts of dead wood

and temporally. When a disturbance affects a stand, gaps are created and an immense local stock of dead wood may be produced (Photo 19). The pattern of currently observed disturbances often has its origins in the ecosystem's history. For instance, the disintegration of a large-scale spruce stand in the Beskidy Mountains would not have occurred, had its typical lower montane beech-fir forests not been cut down and replaced with spruce. Similarly, the death of spruce stands attacked by the European spruce bark beetle *Ips typographus* in the Białowieża Forest is due, among other things, to a ban on burning the forest floor imposed by the tsarist administration in the first half of the 19^{th} century. Once the many-hundred-year-long practice of burning had ceased, fire-resistant pines, which had benefitted from it, were gradually supplanted by spruces, which became the dominant species within a few decades.

Disturbances in natural forests may occur at very different spatial scales: the effects of very strong winds can range from a single uprooted tree to perhaps hundreds of hectares of windblown trees. Some such large-scale events, such as the blowdowns in Masuria in 2002 or in Pomerania and the Kujawy region in 2017, or certain spruce bark beetle outbreaks, are viewed as natural disasters. Indeed, the forest is no longer the same as it was prior to such an event; the ecosystem has been severely disturbed and many of its functions have been reduced, at least temporarily. The destruction of a stand by fire (Photo 21) or wind (Photo 22) means the destruction of the basic structural element of natural habitats of flora, funga and fauna; this may also spell death to valuable trees, including monumental and habitat trees, although the devastation is rarely ever total. Some trees do survive, even if severely damaged. If the damage has been inflicted by outbreaks of insects or fungal disease, the surviving trees may acquire immunity, so their survival is important for this immunity to continue. This is the case with, for example, the large-scale ash dieback that is happening in Europe at present. Studies conducted in North America have shown that those specimens of lodgepole pine *Pinus contorta* which survive an outbreak of the mountain pine beetle *Dendroctonus ponderosae* have more robust resin canals. The remains of living and dead trees contribute to a high diversity of microhabitats in the disturbed area. In ecology, all such remains are known as the "disturbance legacy". This has been identi-

Photo 20 (P. Pawlaczyk)
Changes in water levels can cause massive tree mortality in marshland habitats

Photo 21 (J.M. Gutowski)
After a massive fire in the Augustów Forest (Płaska Forest District, 2019), a few clumps of burned trees were left in order to protect its biodiversity

fied in many studies as a very important element, mediating the subsequent regeneration of the ecosystem.

According to modern research, large-scale disturbances are not aberrations, but rather normal ecological occurrences driving the development of the forest. Individual types of forest ecosystems may differ in terms of the frequency, characteristics and extent of the disturbances they are exposed to. Disturbance regimes may influence the functioning of ecosystems. Some forest types, e.g. mountain spruce forests, are directly dependent on them, in other words, periodic disturbances are part and parcel of their natural dynamics. Disturbances over large areas occur in forests worldwide; indeed, they appear to be increasing in frequency as a consequence of climate change. There is no means of effectively preventing them.

Once there has been widespread destruction of trees in a forest, the natural and understandable human response to such an environmental disaster is usually to "clean up" the mess and to restore the "destroyed ecosystem". In forest areas, this often means cutting down and re-

Photo 22 (P. Pawlaczyk)
Landscape after the catastrophic storm in the Tuchola Forest (near Rytel). Although the remains of broken trees were cleared away and a new generation of trees was planted, a group of snapped pines was left in place

moving the remains of dead trees and planting new ones in the cleared space, which is justifiable from the point of view of the fastest possible restoration of the productive and economic functions of the ecosystem. However, the impact of large-scale disturbances on the biodiversity and functioning of the forest ecosystem at broader spatial and temporal scales is far from obvious. Many studies have suggested that although disturbances do have some, usually temporary, negative effects on an ecosystem, they are also beneficial to biodiversity, even though many components of the biodiversity of the disturbed area are damaged. In some cases, forests disturbed and "destroyed" by blowdowns or insect outbreaks become havens for species which are endangered elsewhere. This happens, for example, because a significant stock of dead trees is created in the process. Most importantly though, removal of the disturbance legacy often harms the ecosystem more than the disturbance itself, hampering and slowing down the regeneration processes. Relevant examples are examined in greater detail in Chapter 5.1.

The quality of dead wood – variability under natural conditions

Of key importance to forest ecology and the occurrence of species associated with dead trees is not so much the total amount of wood deposited in a specific area, as its quality, and especially its form, degree of decay, the sizes of individual pieces of woody debris and their spatial distribution.

The microclimatic conditions to which woody debris is exposed are an important aspect influencing dead wood quality. On the one hand, a high degree of shade and/or humidity, and on the other, strong insolation and/or desiccation, mean that dead trees and their associated debris may acquire vastly different characteristics over time, which in turn determines their suitability for various groups of saproxylic organisms. When discussing environmental factors, we must first and foremost consider the trophic conditions, i.e. the presence of chemical elements and compounds necessary for the growth of saproxylic organisms. Also important are the microclimatic conditions, i.e. the thermal and moisture characteristics of the substrate and their variations. As a consequence, the quality of dead wood in a natural forest is highly variable, and it is this that creates the diversity of conditions under which the organisms using this substrate can live and evolve.

The gradual decomposition of wood gives rise to a long-term succession of specific microhabitat conditions: from hard wood, especially on standing trees, to dry rot transitioning into the topsoil in the final stages of decay (see also Chapter 3). The rate of dead wood decomposition depends on a number of factors, such as moisture content/insolation, the tree species from which the dead tissue comes, or the size of a single piece of wood and its associated community of organisms degrading it.

Because larger pieces of dead wood have a higher surface area to volume ratio, they usually decompose more slowly than smaller ones. The protracted process of decomposition enables organisms inhabiting a given piece of wood to use it for a longer period of time, which could be especially important for insect species with a long life cycle or for low-mobility species. In case of the latter, the slow decay of a piece of dead wood creates an opportunity for the long-term generational succession of organisms at a particular site. The period during which dead trees remain standing usually extends from a few years to a few decades, and in extreme instances, to more than 100 years, as in the case of Norway spruces in boreal forests. Fallen logs may take even longer to decompose, usually a few decades, but the period between the fall and complete decomposition can be as long as 200 years. Beech wood decomposes fairly quickly: in central Germany an average beech log loses 50% of its volume after around 50 years and breaks down completely after ca 85 years. In Swiss forests, beech logs degrade faster, within 27 to 54 years. Oak logs usually need twice as long to decompose. The decomposition of coniferous logs, e.g. of pine or spruce, is also a prolonged process.

Since fungi are the most effective decomposers of wood in temperate climates, climatic conditions unpropitious to the development of saproxylic mycobiota – low winter temperatures and a dry growing season – are the principal factors prolonging the decomposition of dead wood. Such conditions favour the progressive accumulation of poorly decomposed dead wood; in many such ecosystems, fires are a natural factor contributing to its reduction.

As a result of the long-drawn out process of decomposition, dead or dying trees or pieces of them offer the organisms inhabiting them a great diversity of forms and qualities of woody necromass. In consequence, a number of saproxylic species have become highly specialized, i.e. they have very demanding requirements regarding the amount and form of dead wood, the degree of decomposition or the size of the various pieces of woody debris.

Cambiophagous species: a species feeding on phloem and cambium, living in or under the bark of trees or shrubs.

Saproxylic species: a species living in dead wood.

Species of dying trees – sources of dead wood

A dying tree is a source of dead wood having the characteristics typical of a given species. The physical properties of the wood, especially its density and hardness, its chemical composition, including the levels of individual elements, and the distinctive anatomy of the tree all contribute to the considerable variability of the dead wood stock. As a result, the species of the dying tree plays an important role in determining which particular saproxylic organisms will be able to colonize it. The differences between the dead wood of deciduous and coniferous trees alone illustrate the great variability in the communities capable of populating a given substrate. The dead wood of a particular species can be colonized by a cohort of species consisting of both polyphages (organisms with a broad spectrum of requirements, able to inhabit a range of tree species) and monophages (specialized species whose development cycle requires the dead tissues of one particular tree species).

Analyses of the use of dead wood by saproxylic organisms reveal significant differences among various tree species. Many studies emphasize the pivotal role of dead oaks, which harbour a particularly valuable assemblage of invertebrate species. The dead wood of hornbeams is also exceptionally important to the species richness of the organisms that inhabit it. Thus, the dead wood of some tree species can fulfil the habitat demands of a substantial number of saproxylic organisms. However, the significance of a tree species as a source of dead wood may vary somewhat in different habitat or even geographic settings. Scandinavian and Polish studies indicate that a greater diversity of organisms inhabits the wood of deciduous species than that of coniferous species. Nonetheless, admixtures of dead conifer wood in deciduous forests will encourage the occurrence of additional species. It is therefore essential to have forest habitats with a wide range of tree species providing dead wood biomass. In this context, pioneer species are of importance, although in the absence of disturbances there are very few of them in mature forests, especially of oak-hornbeam or beech. Sources of distinctive dead wood types are willows and poplars, as well as wild cherry, rowan, pear and apple trees, all of which are rarely found in forests today and are more common in semi-natural landscapes and ecotones.

At the same time, it is important to bear in mind that the role of dead trees should not be assessed solely on the basis of the number of species inhabiting them. It can happen that the dead wood of some woody species is suitable for only a small number of species, but which are unique, i.e. not found in/on the dead wood of other trees. In this case, what matters is the specific trophic relationship between a given tree species and the organisms using it. This can be exemplified by the link between *Pseudogaurotina excellens*, an endemic species of beetle found only in a few ranges of the western Carpathian Mountains, and the wood of the only shrub species on which its larvae feed, the black-berried honeysuckle *Lonicera nigra*. In the case of fungi, studies have shown that even though some are capable of colonizing the wood of different tree species, they only develop fruiting bodies on one particular species of host plant. The specificity of a number of trophic associations requires further research, and it may well turn out that dead wood derived from shrubs or even climbers, such as elders, dogwoods, currants, cotoneasters, yew or common ivy, is important for the occurrence of certain species.

Forms of dead wood

Dead wood in the forest environment comes in a variety of forms, which are the result of a long-term process triggered by the weakening and the subsequent death of a tree and culminating in the complete breakdown of the woody biomass. As a result, dead wood is present in the forest ecosystem in the form of whole, standing, desiccated dead trees; snags, i.e. parts of standing trees, usually trunks from which branches and boughs have snapped off; stumps, i.e. shorter, lower sections of trunks of felled or broken trees; dead trees lying on the ground whole or often in the form of smaller parts fragmented in consequence of a fall (downed woody material). Dead wood also occurs in the form of branches and boughs, either still attached to living trees or broken off and lying on the ground.

Disturbances, especially high winds, can cause trees to be uprooted. The resulting windthrows (tree throws) are a particular form of dead wood, as there may sometimes be significant amounts of mineral soil among the tangle of roots above ground level. This mixture of decaying roots coated in clay, sand or pieces of rock, often exposed to direct sunlight, is a unique microhabitat. In living trees, parts of the root system are continually dying off in a process that is a source of dead organic matter in the soil. When an entire tree dies, a significant amount of biomass appears in the soil at one time, also in the form of thick roots, which decompose in much the same way as dead wood lying on the ground, providing a habitat for distinctive saproxylic organisms.

Degrees of dead wood decomposition

The degree of decay of the substrate is one of the qualitative characteristics determining the occurrence of saproxylic organisms on dead wood. The processes of wood decomposition along with their modifying factors are described in greater detail in Chapter 3. The interplay between the properties of wood, the environmental conditions to which woody debris is exposed and the degree of wood decay, i.e. the changes in the physical and chemical properties of wood, gives rise to shifts in the species composition and the abundance of organisms successively colonizing individual pieces of dead wood. As the decomposition of dead wood progresses, new organisms or their groups start moving in, depending on the degree of decomposition and the occurrence of other organisms. For example, the occurrence of saproxylic insects depends on the presence of specific fungi, the nutrient-rich hyphae of which constitute a source of food for their larvae.

By influencing growth conditions for saproxylic invertebrates, the degree of decomposition of the wood can indirectly affect the organisms feeding on these invertebrates, especially birds and mammals. It has been shown that the choice of feeding site is governed by the diet specific to a given species. For some species, trees that are weakened and have recently begun to die are of crucial importance, as they host numerous and dynamic populations of cambium-eating insects, usually bark beetles. This is the case with the three-toed woodpecker *Picoides tridactylus*, which prefers weakened and moribund spruces. Other predators (higher-order consumers) will depend on the occurrence of the larvae of xylophagous insects inhabiting wood at various stages of decomposition, from hard wood to dry rot. Yet other organisms may rely on the presence of saproxylic species inhabiting only heavily degraded wood.

Birds excavating holes in which to lay their eggs and rear their young have strong and varied preferences regarding the degree of wood decay. In the case of woodpeckers, the preferred degree of decomposition depends on the species and its ability to excavate cavities in hard wood, as well as on the species of the tree. In softwood species, such as willows and poplars, hollows are readily excavated even in undecomposed wood, but where hardwood trees such as beeches and oaks are concerned, birds prefer specimens that have been at least partially decomposed by fungi.

Photo 23 (K. Zub)
Thick standing dead pines are a rare form of dead wood, but they are important for biodiversity

The sizes of individual pieces of woody debris

Many studies have found that dead trees of a large size are essential for forest biodiversity. Coarse woody debris mediates the occurrence of certain species of fungi, mosses or saproxylic insects, which do not inhabit pieces of wood that are too small. This could be due to the conditions within differently sized pieces of wood, e.g. their microclimate or moisture content. Also, a dead trunk, log or bough can provide sheltered, secluded internal cavities, which simply cannot form in smaller pieces of dead wood. For saproxylic species requiring these types of environments to complete their life cycle, and especially those with long development times, coarse woody debris is an invaluable resource. Studies of fungi show that even though some of them can colonize woody debris of various sizes, they only develop fruiting bodies on large pieces. What is more, certain species of wood-decomposing fungi colonize trees that are still alive, and their life cycle requires trees which are at least 60 years old. Large dead trees are also crucial for birds known as primary hole-nesters, which more frequently choose trees with a large DBH in which to excavate their hollows. Bats, too, prefer cavities in larger trees for roosting or repro-

Photo 24 (J.M. Gutowski)
The Białowieża Forest: a cavity inside a decayed oak log

duction. Hole-nesting animals are more likely to choose large, standing, dying or dead trees, because hollows in larger-diameter trunks offer a better microclimate (Photo 24). The greater thickness of the walls of a such a tree hollow insulate it from the external environment, which is important in the breeding season, but also in winter, when tree hollows may serve as hibernacula. Organisms inhabiting cavities in large trees are less sensitive to daily and yearly amplitudes in temperature and humidity.

Birds feeding on trees tend to prefer standing dead trees of significant size, as they are a richer source of food (larvae of xylo- and cambiophages) concentrated in one place. The opportunity to exploit spatially concentrated food resources means that a smaller home range may be sufficient for survival, and that less time and energy need to be expended on feeding and maintaining the territory. In these circumstances, it is preferable to have fewer large trees growing in a smaller area than many smaller trees scattered over an extensive area. The presence of large trees cuts down the time spent on finding food and optimizes the overall energy balance, which may increase the survivability rate and the reproductive success of a given species. The results of many studies provide evidence that a smaller amount of coarse woody debris cannot be replaced with a large amount of fine woody debris, because there are many species that cannot occur on woody debris, the size of which is below a certain threshold necessary for colonization.

Under certain conditions, however, a significant portion of the dead wood stock will consist of fine woody debris. Scandinavian studies indicate that nearly half the biomass of a fallen dead tree may consist of a great many small pieces. Given that eurytopic saproxylic species usually develop in fine woody debris, a significant proportion of small fragments in the stock of dead wood may be critical for the prevalence and overall abundance of such organisms. If there is a profusion of fine woody debris, some of the less demanding saproxylic species may be widespread and numerous, which is important for the organisms feeding on them.

Microclimatic conditions

The colonization of woody debris depends very closely on where it is lying. Microclimatic factors are of prime importance here. High humidity and temperatures facilitate decomposition, so places with high levels of precipitation, near surface waters and strongly shaded, are where the moisture content of wood can increase, thus accelerating its breakdown. On the other hand, the stronger influx of light resulting from direct insolation enhances the thermal conditions in the substrate. This promotes microbiological activity, which in turn can improve growth conditions for some invertebrates. On the other hand, too much exposure to sunlight may tend to dry the material out, which may slow down the rate of decomposition. The diversity of climatic conditions is the cause of further variance in the properties of individual dead wood pieces, which, combined with the tree species and the form of dead wood, may lead to considerable qualitative differentiation among dead wood stocks.

A large group of rare and endangered beetle species prefer dead wood situated in at least partially insolated sites, i.e. they exhibit some degree of thermophily. These are mostly species which used to be associated with periodically pastured, open forests and woodland ecotones. It is thought that strongly insolated forests used to be products of local disturbances and the activities of large herbivores, such as the aurochs *Bos primigenius*, European bison and cervids. Historically, these factors were replaced by the widespread silvopasturing of livestock, mainly cattle. Nowadays, sparsely wooded and therefore strongly insolated forests are disappearing, and pastured forests are relict features in the landscape (see also Chapter 2.3). The distinctive microhabitat of coarse woody debris exposed to the sun is crucial for the conservation of this group of beetles, although guaranteeing their occurrence may require active conservation measures (see also Chapter 5.2).

The insolation requirements of species associated with dead wood vary widely. Some clearly prefer sites with copious amounts of sunshine, others choose spots with moderate exposure to the sun, and yet others avoid direct sunlight altogether, finding the best living conditions in strongly shaded places. Moreover, preferences regarding the degree of insolation of dead wood may vary between taxa, and the key requirements of one group, e.g. insects, may not be consistent with those of another group, e.g. fungi. Some species thought to be thermophilic are in fact not that at all: until recently, it was believed that the hermit beetle *Osmoderma barnabita* prefers rotting wood in trees growing in open terrain, but it turns out that it flourishes just as well in dense forests, just so long as there are enough suitable rotting trees in it.

The quantity and quality of dead wood in a managed forest

An obvious consequence of forest management is the felling of trees, especially those that have reached a significant size. As a result, large, dead trees are virtually non-existent in a traditionally managed forest. In order to enable trees to reach harvesting maturity, traditional forestry tends to cultivate younger stands and removes trees perceived as blocking the development of large specimens – the desired end product of such forest management. Trees that would have died naturally of various causes, thereby increasing the dead wood stock, are often removed in the process. Although forest management guidelines allow for the retention of so-called sterile standing dead trees, active snags are cleared indiscriminately. Simply put: long-dead trees are allowed to remain, but weakened and recently dead trees are not, which ultimately hinders the continuous renewal of the dead wood stock.

Consequently, traditional forest management poses the greatest risk for species closely associated with dying, dead and decaying trees, and especially those which require trees with specific characteristics, like large trees.

The average volume of dead wood in managed forests in Poland is just a few cubic metres per hectare. Moreover, the bulk of this woody debris is fine, such as treetops and branches left after felling, and so is of no real significance for the conservation of saproxylic species, particularly those with highly specific requirements regarding the quality and availability of dead wood.

However, in some managed forests, especially in the mountains, amounts of dead wood can be significant. Around 47 m^3/ha were recorded in managed forests in the Romanian Carpathians. In Poland, the average stock of dead wood in managed forests supervised by the Regional State Forest Directorate in Krosno is more than 24 m^3/ha. These examples show that it is possible to reconcile forest management with maintaining a considerable stock of dead wood. Often, within forests that are generally lacking in dead wood, there are some places particularly rich in this resource, e.g. less accessible sites on steep slopes, in ravines and gorges, or marshy stands such as alder carrs or beaver ponds. Substantial amounts of dead wood can also occur in managed forests as a result of disturbances like blowdowns or insect outbreaks.

Snag (standing dead tree): in forestry, snags are trees that are either dead or dying as a consequence of diseases (including invasions of "pests", i.e. certain species of insects or pathogenic fungi), competition between individual specimens and changes in the environment. Fallen logs are usually referred to as coarse woody debris, although in practice the differentiation between snags and woody debris is not always consistent.

Active dead wood: standing dead or dying trees colonized by "pests", which can reproduce and may infect other trees, killing them.

Sterile dead wood: standing dead trees on which "pests" are no longer present; colonized by other organisms; not considered a risk to neighbouring trees.

Stenotopic species: a species with highly specific requirements, which can live only in strictly defined environmental conditions; very demanding in terms of humidity or other abiotic and biotic environmental features, exhibiting a narrow range of tolerance to environmental factors.

The opposite of a stenotopic species is a **eurytopic species**, i.e. cosmopolitan, with a broad spectrum of tolerance.

Around the world, modern forestry targets the regeneration and maintenance of an abundant inventory of dead wood in managed forests; this is discussed in greater detail in Chapter 5. Enrichment strategies for managed forests which aim at increasing the volume of dead wood and bringing it closer to natural levels are possible, although they usually require commercial operations to be scaled down.

A frequently asked question is how much dead wood actually needs to be provided in a managed forest in order to conserve most of its natural wealth or regenerate its diversity, impoverished by earlier management practices. There have been some attempts at determining these threshold levels by analysing correlations between the biological diversity of individual groups of forest organisms and available amounts of dead wood. Depending on the forest type (coniferous, mixed, deciduous, montane, lowland) and the species group in question, these levels for European forests have been identified to be from 10 to 150 m^3/ha, most frequently 20-50 m^3/ha.

As mentioned previously, the actual amount is not sufficient on its own. The relationship between the ecological richness of a forest and the stock of decaying wood, though significant, is far more complex. The diversity of forms, size, species, location and degree of decomposition of dead wood is more important than its quantity. Its distribution across the forest landscape is no less important. The few dozen cubic metres of dead wood required by one species does not have to be the same few dozen cubic metres of wood needed by another. The difference lies in the quality of the substrate. Many researchers have gone so far as to state, not without reason, that the amount is of secondary importance and that it is the actual presence of dead wood of appropriate quality that really matters. Standing trees, both whole and in sections, large dead trees in insolated locations and fallen logs in humid microclimatic conditions all play a meaningful role.

Nevertheless, the amount in m^3/ha, which is easier to measure, does in fact count, because there is usually a strong, positive correlation between the total volume of dead wood and its diversity. Any accumulation of large volumes of dead wood can be assumed to be qualitatively very diverse, which means that it will support a broad range of saproxylic species.

The key issue here is to conserve stenotopic species in managed forests, i.e. species with very specific requirements regarding the amount and quality of dead wood. Therefore, the next step in planning for the volume and quality of dead wood resources should take into account knowledge about the habitat requirements of particular rare and endangered species. The presence of these taxa in the ecosystem does not always indicate that the management strategy and the state of dead wood stock are right: sometimes it is merely an echo of how the forest performed in the past.

The spatial distribution of the dead wood stock is also important, as one has to take account of the mobility of individual saproxylic organisms. The distance between suitable habitats must be conducive to dynamic colonization, i.e. it must be smaller than the distance a given species is able to travel effectively. The space over which new habitats can be colonized determines the required density of areas with higher amounts of dead wood and the location of corridors for possible migrations. It is worth noting that a very local, and thus usually isolated accumulation of dead wood may not yield expected results. Some studies indicate that only a substantial supply of dead wood over a large area can have a positive impact on the diversity of saproxylic organisms. This correlation is stronger for rare species, which tend to have specific habitat requirements. Local accumulations of dead wood resources positively affect species that are relatively more common, whereas rare taxa require a rich dead wood stock accumulated both locally and at a larger spatial scale. In practice, enabling the occurrence of an entire cohort of saproxylic species would mean that the largest possible network of protected areas along with the corridors to connect them would have to be planned and interspersed throughout managed forests.

2.3. Dead trees beyond forests: parks, groves and other environments

The disappearance of forest ecotones and pasture forests

Any forest that we visit today, whether it is part of a natural park or a nature reserve, or simply an "ordinary managed forest", is not the same kind of forest our ancestors experienced. Changes wrought by the development of modern forestry and the "strict" separation of forests from agricultural land have resulted in the almost total disappearance of broad ecotone zones, where the adjoining environments of forests, meadows and pastures used to blend into each other. For hundreds of years, people used these zones as pastures, but also for many other purposes associated with traditional farming systems. They were the source of brushwood (young trees, shoots, boughs), leaved branches and shrubs used for fodder, and leaf litter (used as an insulating material in houses and cattle sheds). That is also where single large trees would be felled. Owing to this diverse use, the level of tree cover, i.e. the degree to which a stand utilizes the production potential of a given habitat, in forest ecosystems used to be relatively low, which meant that they had a very favourable photoclimate. With the competition from neighbouring specimens being much lower and access to sunlight almost unrestricted, the growth habits of trees developing in these circumstances were a far cry from the modern "ideal" forest tree, which should be as straight as possible, have the greatest possible marketable height and as few branches as possible. Unlike the majority of trees in today's forests, the trees of past ecotonal "groves" were bulky, relatively short and had broad, low-set crowns. Many of those trees were continually being subjected to pollarding, brashing and irregular pruning, or exposed to bark stripping by animals or localized charring, thus acquiring the traits of "veteran" trees, which are immensely rich in such tree-related microhabitats as scars, hollows and semi-hollows, cracks, necrotic tissues and dry rot. It may seem counterintuitive, but with full access to sunlight even injured trees did not become weak, because they were able to regenerate and scar over the damaged tissues more quickly. What is more, the lower height, especially of pollarded and regularly pruned trees, greatly increases their longevity compared to trees of the same species growing in dense forests. For instance, while the oldest oaks in the Białowieża Forest are an estimated 400 years old, hundreds of the most ancient oaks in Europe are remnants of old groves, pastures or parks, similar to the ones described above.

Photo 25 (M. Ciach)
Pastoral beeches in the Beskid Niski Mountains, a remnant of past silvopasture, which left behind uniquely shaped, very old trees with an immense wealth of tree-related microhabitats

Photo 26 (A. Bobiec)
Rotting wood beyond the forest: a "veteran" elm in Sweden

"Veteran" trees are the most resilient living "manufacturers" and hosts of dead wood of shapes and forms hardly ever found in modern forests. This is because a significant proportion of trunks and boughs are directly exposed to the warming and lighting effects of solar radiation. Often, these "veteran" trees, despite their advanced age, are extremely vigorous, which means that the tree holes and other saproxylic microhabitats they contain persist for much longer than their counterparts on rapidly dying or dead forest trees.

There are many studies confirming the crucial and indispensable role that habitat "veterans" play for a multitude of saproxylic insects, especially thermophilic species. At the Eurasian level, the oak pasture forests of the Taşeli plateau in the Taurus Mountains (southern Turkey) are a true haven for these species. The misshapen trees, which for hundreds of years have been regularly pruned and brashed by shepherds living on the plateau, are home to numerous species of saproxylic species, including many listed in the Turkish and peri-Mediterranean Red Lists of Endangered Species. Species, which in Europe are already considered critically endangered, are still represented there in large numbers. Unfortunately, "degraded" by humans and their goats, this landscape of wounded and technically useless trees is threatened by a "redevelopment" plan to convert it into productive pine stands.

Indeed, in the whole of western Europe and the Mediterranean region, traditional wooded pastures are among the most valuable habitats for organisms associated with dead wood, as the trees growing there reach very old ages and host a wealth of microhabitats. Such areas are a unique element in the traditional landscape of England or southern Sweden (Photo 26). The rotting wood of these grassland "veterans" hides the most precious biological legacy of past forests. In Italy, among the very important habitats are the "orchards" of the sweet chestnut *Castanea sativa*, full of old trees with many microhabitats. Regardless of the location, however, ecosystems like these are vanishing, because the traditional management systems that formed them are becoming obsolete. This is true also for Poland, particularly in the Carpathians, where patches of old pasture forests still remain, albeit most of them are currently under forestry management, which results in groups of habitat trees being cleared and gradually replaced with sapling stands.

Is this era in the long history of "veteran trees", standing among fields and inviting livestock to find shelter under their canopies, definitely over? Will these landscapes disappear once and for all? The growing interest in the history of cultural landscapes in Europe, and especially the enormous success of such initiatives as the Ancient Tree Forum (ATF), offer grounds for some optimism. More and more is being written and said about the positive role that agroforestry can play in moderate climates, and silvopasture is its most ancient version. The ecological and aesthetic void left after the elimination of old "veterans" should be filled, little by little, with a new generation, which should slowly be readied to take over the duties of their predecessors. It would be worthwhile for authorities and associations involved in environ-

Photo 27 (J.M. Gutowski)
A dead oak in Rogalin

mental conservation to make use of the extensive expert literature and guidelines on the protection of old "veterans" and the "veteranization" of younger trees.

Parks

In traditionally maintained urban and rural parks, there is almost no dead wood. Every dying tree or shrub is removed, as are dying boughs or branches lying on the ground, because they are thought to be an eyesore and a safety hazard. Of course, the park services cannot always keep up with clearing it all away, so in practice dead or dying trees and dead boughs can be encountered even in these environments. Many species with short life cycles have a chance to colonize such places and successfully produce a new generation. Hence, our parks are not completely devoid of fauna associated with wood, and various species of insects or other invertebrates can be found there. The situation is rather better as regards retaining the underground portions of dead woody plants. After a tree has been felled, the stump is generally left in place, providing a valuable living environment and food resource for all sorts of saproxylic organisms.

From the late 20th century onwards, there was a rapid expansion of the "naturalist" movement in landscaping, whose objective was the broader integration of natural processes into planned green spaces. An example of this is the growing acceptance of dead trees in some parks, where "wild" zones are being set up. In such zones, dead and dying trees are retained or even highlighted (Photo 28), so long as they do not pose a risk to the safety of visitors. This approach is becoming more and more common. Environmental psychology suggests that relative wildness in recreational areas is important

Photo 28 (P. Pawlaczyk)
A dead oak "exhibit" in the Wisława Szymborska Park of Love (Park Miłości im. Wisławy Szymborskiej) in Lubniewice

to the people using them, even if it is a somewhat subconscious process, and having at least single dead trees in the landscape is what makes this wildness perceptible. In the USA, it has been recommended for several decades to leave standing or lying dead trees even on golf courses in order to ensure a living environment for saproxylic organisms and to increase awareness of these issues among players and spectators. In parks all over Europe, and Poland is no

Photo 29 (M. Miłkowski)
A dead Norway maple in the Tadeusz Kościuszko Park in Radom serves both people and various invertebrates and fungi

Photo 30 (S. Jakimiuk)
In the parks and city squares of Białystok, it has been decided to leave sections of selected trees blown down and broken by storms, allowing them to decompose naturally. This offers an opportunity to educate the public about the importance of dead wood

exception here, retaining selected dead monumental trees is slowly becoming the norm. One such positive example comes from Radom. When two monumental Norway maples *Acer platanoides* died in the city's Tadeusz Kościuszko Park in 2014, the Naturalist Club of the Radom region put forward a proposition to keep them in place. Once felled (the safety of passers-by had been at risk), both trees were included in research on invertebrate succession (Photo 29). This way of thinking is increasingly being adopted by other cities, too. In Białystok, some trees downed or broken by storms are left in parks (Photo 30). A lot of dead trunks were also kept in Poznań's Citadel Park. In Grabów nad Prosną, a wind-thrown monumental oak tree was turned into a sculpture – a monument to the history of this town.

Photo 31 (J.M. Gutowski)
An old hollow willow is not a blot on a park's reputation; rather, it provides a habitat for the lichens on the bark and invertebrates in the rotten wood

Parks and groves provide habitats which are sometimes absent in managed forests – old trees with hollows (Photo 31 and 32); such trees, if alive, are still found there fairly frequently. They contain hollows with rotting wood, which are a unique habitat for stenotopic invertebrate species. Sometimes, as part of maintenance measures, a monumental tree is "treated" in that all of the substrate accumulated in its hollows is removed and its tissues impregnated with chemicals. Sadly, such "treatment" kills all the organisms living in tree holes and side necroses. These are often species which are critically endangered within their ranges. The consequent loss to nature is irrecoverable, especially that this "treatment" is rarely effective and does not really prolong the life of the tree. Thankfully, modern arboriculture is moving away from such practices, recognizing tree-related microhabitats, including rotting wood, as valuable assets, which are not only worth keeping, but whose emergence should be initiated and facilitated (see also Chapter 5.2).

Although interventions motivated by safety concerns, such as removing trees with nests of European hornet *Vespa crabro*, are sometimes necessary, they are undertaken far too frequently and may thus do a lot of damage to park ecosystems. The complexities of balancing the risks to people with the value of habitat trees and tree-related microhabitats are discussed in detail in Chapter 5.4.

Former parks, now overgrown and wild, are particularly valuable. The Bielany Forest (Las Bielański), a designated nature reserve in the Warsaw metropolitan area, is an example of a park where old hollow trees exist and are retained, harbouring interesting, rare and even endangered species of invertebrates, e.g. great capricorn beetle *Cerambyx cerdo*, hermit beetle *Osmoderma barnabita*, *Rhamnusium bicolor*, variable chafer *Gnorimus variabilis*, *Protaetia speciosissima* (=*aeruginosa*) and rusty click beetle *Elater ferrugineus*. Such species are more numerous there in a relatively small area than in most homogeneous and impoverished commercial forests. Similarly, many rare species of birds find favourable nesting and breeding habitats in the Bielany Forest, e.g. black woodpecker *Dryocopus martius*, white-backed woodpecker *Dendrocopos leucotos* and stock dove *Columba oenas*.

Unless there is a safety issue, it is worth considering whether the practice of leaving dead trees, shrubs and their parts in parks and groves until their complete decomposition should not be more widespread. This also applies to dead parts of living trees (tree-related microhabitats, see also Chapter 2.1). In particular, trees with cavities or hollows should be cared for, and under no circumstances should their rotting wood microhabitats be disturbed. The same attention should be paid to trees in wooded pasture landscapes, small patches of which are still found within or near cities.

Photo 32 (A. Bobiec)
Old and dying oaks are unique habitats for many saproxylic organisms; southern Sweden

Groves

Groves sometimes prove to be important sources of dead trees and associated microhabitats. Although groves are not subject to forest management, the law stipulates an administrative procedure and that a permit be obtained from local authorities before a larger tree – even a dead one – may be cut down in such a habitat. Therefore, many groves, though not all, are left undisturbed. The wooded shores of lakes and watercourses, steep slopes or patches of trees

Groves: single trees and shrubs or their groups beyond forests and urban areas, fulfilling ecological, aesthetic and (to a decreasing degree) productive functions through the supply of wood, fruit, etc; groves can exist in isolation, in rows, groups, belts or patches, and can occur on roadsides, in fields, meadows, pastures, near bodies of water, etc.

Photo 33 (P. Pawlaczyk)
Cycles of the germination, growth and death of trees are typical for some peatlands, reflecting the variable nature of peatland hydrology, which leads to the periodic appearance of larger stocks of dead wood

in fields may turn out to be places with more dead wood than in forests – over 100 m^3/ha at times. Quite large amounts of dead wood can be found in marshy groves where the water level has risen, e.g. as a result of the activity of beavers *Castor fiber* or following a particularly wet year, causing trees to die.

Paradoxically, many species associated with tree-related microhabitats such as tree hollows and rotten wood, especially invertebrates and lichens, find refuge in man-made habitats – rows of old trees along roads – which are an important feature of modern landscapes. Habitat trees, which are nowhere to be found in modern managed forests, are still present there.

In urban landscapes, dead trees are usually removed from heavily frequented avenues and groves for safety reasons alone, but even there, individual dead trees are sometimes kept, especially dried-out oaks, which can remain standing for many years without posing any risk.

However, many of the groves less visited by people are places with potentially high concentrations of dead wood. This is often the case with some of the more inaccessible groves in the middle of fields and meadows, on steep slopes, in wooded swamps, etc. For saproxylic species, such places can sometimes be more valuable than present day forests.

Waters and their surroundings

It may not be immediately obvious that bodies of water, and especially watercourses and lake shores, are places where dead trees and their debris tend to accumulate. Formally, they are owned by a water management entity, which is not interested in managing and harvesting wood. Hence, the natural processes of tree growth and death are not disturbed, and larger amounts of woody debris can gradually accumulate. Processes occurring at the boundary between water and land, such as periodic but persistent inundations, erosion of soil around roots and the felling of trees by beavers, often lead to tree mortality, and in an aquatic environment the decomposition of wood may be slowed down. Dead trees and their parts can be transported down watercourses, especially when water levels are high, forming piles and jams. Dead wood in European and American forests is crucial for the ecology of natural water ecosystems, a topic that we shall explore in greater detail in Chapter 4.3.

Under natural conditions, the amounts of coarse woody debris in aquatic ecosystems vary greatly. The quantitative and qualitative characterization of woody debris in watercourses is much more challenging than in forests. Different indicators are used, e.g. volume of dead wood per unit of watercourse surface area (m^3/

Photo 34 (P. Pawlaczyk)
Dead trees are an essential component of forest watercourses

ha), mass per unit of watercourse surface area (t/ha), volume of dead wood per unit of water volume (m^3/m^3), volume of dead wood per unit of watercourse length (m^3/km), or number of logs above a certain size per unit of watercourse surface area or length (pcs./ha, pcs./km), which makes it difficult to directly compare data taken from various studies. Regardless of the measurement methods and their limitations, however, the aquatic habitat itself can be highly variable. The variety of indicators for different rivers is enormous and depends on many factors: the characteristics of the river; the shape of the riverbed; the proportion between the width of the riverbed and the length of logs (which determines the mobility of woody debris); the type of forest environment surrounding the riverbed (including the species structure, age and health of tree stands on the banks); the supply of dead wood to the riverbed (continuous processes of tree mortality vs. catastrophic processes); the hydrological regime, which influences the transfer of materials; places where driftwood can potentially accumulate; the rate of wood decomposition (depending e.g. on the tree species, but also on the parameters of the water flowing over it); and the history of anthropogenic transformations of the watercourse. The amounts of woody debris will be vastly different in a narrow stream, a larger river with a rapid current and a gravel substrate, a medium-sized river with a sandy substrate, and a large lowland river. In various natural watercourses around the world, from 10 to 4,000 m^3 of dead wood per ha of watercourse surface area and 20-600 logs/km of watercourse have usually been reported. Sometimes these values are much higher. The large amounts of dead wood, typically found in the streams of Pacific North America, for instance, can be partly explained by the dominance of coniferous species, the wood of which decomposes more slowly in water. The natural amounts of wood in watercourses flowing through European deciduous forests may be somewhat smaller, if only because the wood of deciduous trees decomposes faster.

Forms of coarse woody debris in rivers include whole trees with roots, long and thick logs, sections of broken branches, smaller and shorter trunk pieces, and broken smaller twigs and branches. Different watercourses may feature different structures of woody debris. This depends on the size and species of trees growing next to the watercourse (individual trees differ in their susceptibility to fracture, breakage or overturning and uprooting), the habitats surrounding the watercourse (the vulnerability of trees to various destructive factors also depends on habitat characteristics, including the parameters of the soil in which they are rooted, landslide processes, etc.), the supply of dead trees to the river (mortality of individual trees vs. large-scale mortality, insect outbreaks, blowdowns, landslides) or the mobility of individual pieces of dead wood, either remaining *in situ* or transported by the river and deposited elsewhere. In this context, important features

Photo 35 (P. Pawlaczyk)
Dead trees on the shores of Lake Żabiak in the Wielkopolska National Park

include log size, possible branching and tree species. An important feature of coarse woody debris in streams is its location relative to the channel. Some logs are suspended above the watercourse, resting on both banks, while others are lodged in the bank on one side with the other end submerged in the water. Some logs lie crosswise or diagonally in the current, entirely submerged in water or completely or partially buried in the alluvium. Logs carried by the river can form jams, pieces of wood can be deposited in mid-channel and on point bars. What is important is the angle at which they are situated relative to the current. Some logs may not be submerged all the time: if deposited on an alluvial plain they are out of range of average water levels, but when flow rates and water levels are both high, they will be within reach. The primary or secondary location of woody debris is also of significance.

Dead wood resources comprise logs that are still at the fall site, but they also include pieces transported by the river and re-deposited in new, sometimes remote, locations. Each river has a unique structure of dead tree resources.

The ecological importance of dead wood in watercourses is discussed in more detail in Chapter 4.3.

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Chapter 2: Summary

Unlike phloem or cambium, wood is a non-living tissue. Biologically speaking, it usually remains barren as long as the tree can defend itself against foreign organisms. Paradoxically, wood "comes to life" just as soon as external pathogenic agents overcome the tree's defence mechanisms. The moment when previously lifeless wood is "brought to life" marks the "birth" of dead wood. The organisms inhabiting it gradually change its characteristics by means of mechanical breakdown and chemical transformations associated with physiological processes. The suitability of wood as a microhabitat increases as dying proceeds. The weakening and recession of natural defence mechanisms, preventing various organisms from penetrating the tree's tissues, enables wood to be colonized by numerous species of forest flora, fauna and funga, the life cycles of which are associated with dead wood.

Living trees can carry dead wood, e.g. portions of the trunk colonized and decomposed by fungi, dry rot, dead boughs, tree hollows, rot-holes, breakages and cankers, which form the majority of tree-related microhabitats. Occurring on trees both within and beyond forests, they are the richest and most abundant in natural forests. Traditional forest management usually restricts their number, however. The presence, diversity and density of tree-related microhabitats are key to the development and conservation of biodiversity in forest ecosystems. Generally speaking, the more microhabitats, the greater the natural value of the tree. Their number and diversity depend on many aspects, but usually rise abruptly when the tree reaches maturity. In many forest tree species, this happens at the age of >150 years and on achieving a significant size – around >60-90 cm in diameter, depending on the species. Trees that are particularly rich in such microhabitats are sometimes called "habitat trees" in forestry and "veterans" in dendrology.

Entire dead trees, or "autonomous" dead wood, not associated with living trees, e.g. whole standing dead trees, fallen logs and branches, are important components of ecosystems. Dead trees and shrubs, standing portions of trunks, fallen logs and branches vastly increase the surface area of the forest habitat. Given the multitude of shapes, species of wood and degrees of decomposition, this is a highly diverse habitat, which enables many species with differing requirements and life cycles to occur together within a relatively small area. Dead wood is a very dynamic habitat with constantly changing characteristics, which is the result of changes in its position (e.g. when a tree falls) and the ongoing degradation of dead tissues.

A necessary prerequisite for maintaining forest biodiversity is a constant supply of fresh wood to counterbalance decomposition. This means that on forest floors in moderate climates, such as in the Białowieża Forest, there should be on average at least 120 m^3/ha of dead wood, in other words, one-fifth of the above-ground tree biomass. If these amounts are smaller, then there is a risk of many species associated with dead wood being lost. The supply of dead wood in a forest is governed by two basic processes: competition between trees or their branches, and disturbances, i.e. relatively violent, non-continuous phenomena caused by biotic factors like outbreaks of European spruce bark beetles and abiotic ones such as strong winds. Careful study of dead wood in forests in terms of species, volumes, degree of decomposition or spatial distribution, also in relation to living stands, can provide very valuable insights into past and current forest development trends. In a typical growth cycle of a natural stand, the dynamics of dead wood mirror the volume of the stand: the initial stages of stand development are usually accompanied by large amounts of dead wood left over from the previous stand. As decomposition advances, these resources diminish, falling to a minimum at the time when the newly developing stand reaches its optimal phase and peak volume. Along with ageing processes in the terminal phase, a living stand decreases in volume in favour of the renewing dead wood resources, which achieve their maximum volume when decomposition is at its most intense and another cycle of forest development is being initiated. In reality, dead wood dynamics are usually influenced to a much higher degree by the effects of unpredictable disturbances due to both abiotic and biotic factors, such as blowdowns, tree diseases or insect foraging. Sometimes these disturbances affect much bigger areas, but even then, removing all the remains of damaged trees is ecologically not an optimal solution, even in managed forests.

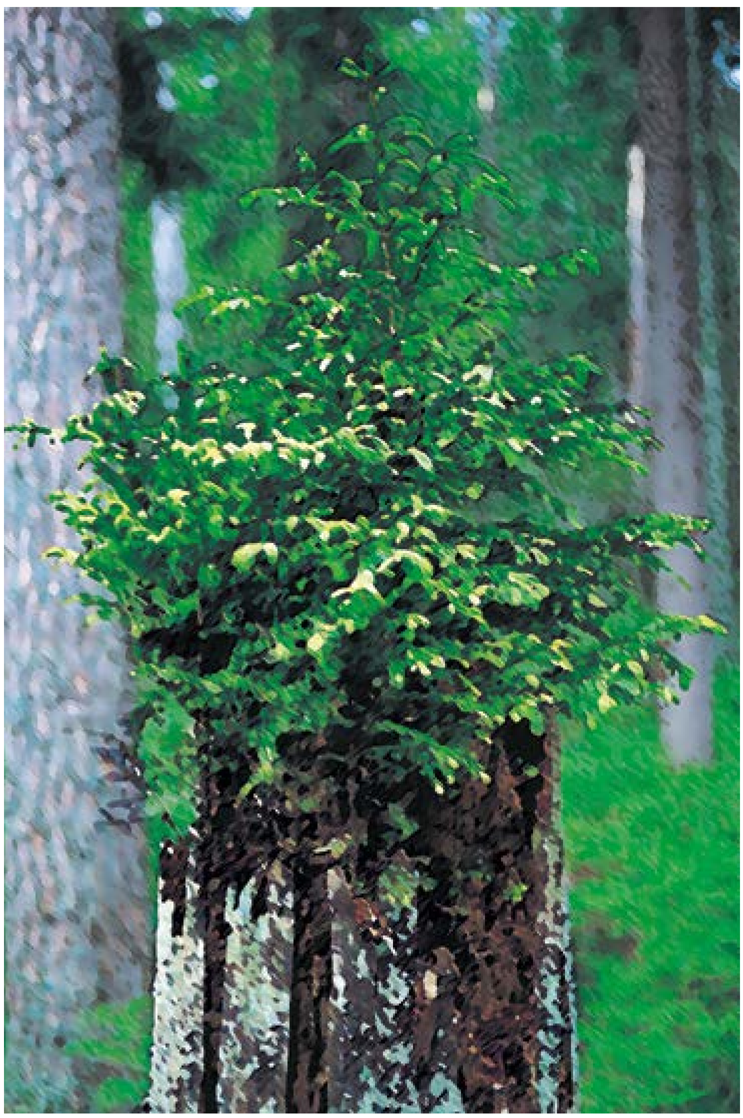
A considerable amount of dead wood is a basic indicator of a forest's natural character. The volume of dead wood in a natural forest can be as much as 50% of the volume of living trees. Forests distorted by management are usually much poorer in dead wood, although significant amounts of it can appear following various kinds of disturbances. Similarly, the number and diversity of tree-related microhabitats in natural forests is usually one or two orders of magnitude higher than in traditionally managed forests. Nowadays, modern forestry around the world is aiming to restore and maintain a significant stock of dead wood and tree-related microhabitats, also in managed forests.

Today, paradoxically, conditions are often more favourable to the longevity of trees outside forests, in groves, avenues and pastures, where they are not under pressure from competitors and, above all, from forest management. Although they are shorter, thicker and have broad crowns, these trees are more likely to reach a very old age and become "veterans" than their forest counterparts, and they may often host more microhabitats than trees in managed forests. Dead sections of trunks and boughs exposed to direct sunlight provide a system of exceptionally valuable microhabitats for many thermophilic species.

Historically, the majority of such trees used to be associated with open and semi-open silvopasture environments shaped by traditional forms of land use, mainly by agroforestry management practices. Abandoning the old ways of using the environment around those trees triggered succession processes that rapidly reduced their longevity and increased their mortality, at the same time impoverishing their unique biodiversity. Parks and groves are present-day remnants of those past environments, often providing rich habitats for species associated with dead parts of old living trees. This is especially true for groves on the shores of water bodies or in all but inaccessible sites, such as clumps of trees growing in the middle of fields or meadows, on small patches of dry land in marshes, or on steep slopes. The importance of dead trees is also increasingly being recognized in landscaping: it is becoming standard practice to leave dead trees in city parks and to protect monumental trees even after their death. The "surgical" procedures, once commonly performed on old hollow trees in order to clean, impregnate and seal off the rotten wood, do not significantly extend the life of such trees; rather, they bring about irreparable losses among rare species of insects and other organisms dependent on these environments. Modern arboriculture is moving away from such procedures.

Life after death

3



3.1. Stages and consequences of tree death

A great many different factors can cause the death of a tree. They include strong winds overturning whole trunks with its roots (windthrows – Photos 36, 37) or trees snapping at various heights (windsnap); a heavy snow load breaking boughs, branches or even whole trunks (snowbreak); long-lasting drought lowering the water table; a general shortage of soil moisture; competition for light in dense, compact stands; old age; fire; floods; periodic inundations; lightning strikes (Photo 38); insects, fungi and mammals, e.g. beavers (Photo 39) and wild boar (Photo 40).

Photo 36 (J.M. Gutowski)
Windthrows

Photo 37 (J.M. Gutowski)
Windthrow; tree throw

Every weak, moribund and dead tree (in various stages of decay) provides a habitat (a place used as a home, shelter, hunting ground, etc.) for many species, especially invertebrates.

The death of a tree gives rise to substantial environmental changes in its neighbourhood. More water and light reach the forest floor. The habitat conditions change for soil bacteria, fungi and animals, i.e. organisms that decompose dead organic matter into simple mineral compounds. The cessation of mineral uptake by roots and the gradual decomposition of wood contribute to a better supply of nutrients, which, coupled with additional light, stimulate the growth of plants. Those seedling and sapling trees, whose growth was limited by the dense canopy, now have a chance to rise into the canopy.

Let us take a closer look at a tree uprooted by the wind (Photo 41). The activity of fungi – the pioneers of wood decomposition – becomes evident already in the first months, when sporocarps start appearing, drawing out the nutrients stored directly in the phloem beneath the bark. The outermost layers of the wood gradually break down. The thinnest twigs break off first, followed by the thicker branches and, ultimately, the largest boughs. At this point, the tree, which up to that moment was supported by these boughs like stilts and was not in contact with the soil, sinks lower and lower until it finally rests on the ground. Decomposition accelerates as a result of the additional moisture absorbed by the woody tissues and the deeper penetration by soil organisms, which can now move unimpeded under the bark or into the increasingly soft wood. In addition, the wood is mechanically broken down by insects, making it easier for bacteria and fungi to reach the core

Photo 38 (J.M. Gutowski)
Sometimes the death of a tree is caused by a lightning strike

of the trunk. Wood decomposes at different rates. The fastest decaying tissues in many trees are those lying immediately under the bark (phloem), followed by the sapwood. The hard wood of the trunk's interior (heartwood) and the bark, which contain the toxic alkaloids and tannins that protected the tree throughout

Photo 39 (J.M. Gutowski)
In riparian environments, dead wood is supplied by beavers *Castor fiber*

its life, generally decompose more slowly. This process is particularly well illustrated by pine trees.

In our temperate latitudes, frost plays an important role in the decay process, especially in its more advanced stages, when logs contain more moisture. The ice forming in the intercellular space tears the woody tissue apart, softens it and alters its structure. Sharp temperature fluctuations and severe frosts allow the wood to be more easily penetrated by animals, fungi and plants.

With time, the initially relatively smooth surface of a log becomes a patchwork of softer and harder wood. The emerging cracks and hollows capture the spores of liverworts, mosses, ferns and the seeds of herbaceous plants. But initially, only certain species attached to the log surface can cope with such difficult living conditions.

As the soft rotting layer expands, the log is colonized by various species of mosses and

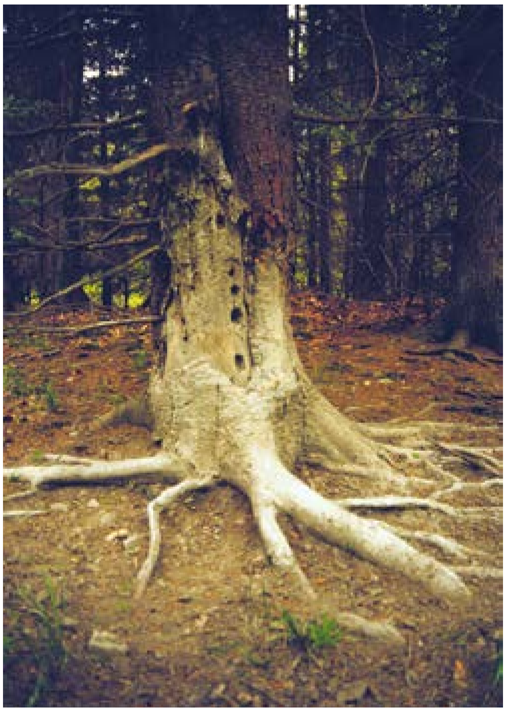


Photo 40 (J. Korbel)
A spruce next to a wallow used by wild boars *Sus scrofa*; visible signs of activity by woodpeckers looking for carpenter ants in the trunk

Liverworts (Marchantiophyta): a division of plants within the bryophyte group; found predominantly in damp habitats.

Photo 41 (J.M. Gutowski)
Windblown spruces are the start of the succession of many organisms developing on and under the bark and in the wood

Photo 42 (A. Bobiec)
The Białowieża Forest: this dead oak is home to about 1,000 different species

liverworts, which require more moisture than is available on its surface. They partially displace the previously established species, but after some time are themselves gradually replaced by ferns, herbaceous plants and tree seedlings (Photo 42). The dense carpets of bryophytes covering some logs maintain a high level of humidity inside them, which increases the rate of wood decay by fungi and modifies the local microclimate. The greater the degree of decay, the more suitable the woody substrate becomes for invading plants. Herbaceous plants usually cannot colonize, persist and grow until the rotting layer is several centimetres deep.

Each year the decaying log sinks deeper and deeper into the ground, its shape and consistency changing from hard wood to a crumbling, wet rotten mass (Photos 43, 44). In time, the disintegrated log becomes just an elongated hillock overgrown by vegetation only slightly different from that in the surrounding area (Fig. 4).

The decay of standing dead trees is different and takes place much more slowly, but there is no universal pattern or model for this process. As in the case of woody debris, the decay of a snag depends on the species, DBH, site, slope (exposure, aspect and steepness), insolation, etc. (Fig. 5).

As mentioned earlier, the complete decomposition of wood in lowland central Europe usually takes from one to several decades. But in other climates, this process can take place more slowly. In more arid conditions or at high altitudes in mountainous regions, for example, it can take hundreds of years. Douglas fir logs in North America can persist for up to 250 years. Wood submerged in water, an environment poor in oxygen and hostile to fungi and wood-boring invertebrates, decays extremely slowly. In 1985, an interesting experiment was started in Oregon, USA, the objective of which was to carry out an in-depth study of rates of wood decomposition and all aspects associated with this process, including the significance of the tree species and the part played by insects. The experiment is to be continued for 200 years!

Photo 43 (J. Walencik)
A dead spruce, damaged by wild boars *Sus scrofa* looking for insect larvae, is sinking into the ground

Exposure: the compass direction which a slope faces.

Photo 44 (J.M. Gutowski)
The final stage of decomposition of a fallen spruce log

Decomposition of a log

FEATURES OF A LOG	class 1.	class 2.	class 3.	class 4.	class 5.
Bark	Intact	Intact	Fragments	None	None
Branches < 3 cm	Present	None	None	None	None
Texture	Intact	Intact to partially soft	Larger harder pieces	Small, fine fragments	Soft and powdery
Shape	Round	Round	Round	Oval to round	Oval
Colour of the wood	Original colour (natural)	Original colour	Original colour to faded	Pale brown, faded or yellowish	Faded to pale yellow or grey
Section on the ground	Log supported by branches	Still supported but sagging	Almost all of the log is lying on the ground	The whole log on the ground	The whole log on the ground

Fig. 4 Decomposition classes, illustrating the gradual decay of a standing spruce and a fallen log (M. Bobiec after Maser et al. 1979)

3.2. How dead trees "come to life": the colonization of dead trees and dead wood

The decomposition of wood is principally the effect of the activities of various organisms, especially bacteria, fungi and invertebrates, which penetrate into dead wood or colonize its surface, feeding on its biomass. As a result, the chemical elements contained within the wood are slowly released and temporarily deposited in the topsoil, from which they are taken up by other plants. The rate of wood decomposition depends on a number of factors, but above all on the characteristics of the individual tree species. The chemical makeup of woody tissues, including the content of nutrients, resins, gums, tannins, terpenes and their derivatives, as well as the characteristics of the lignin, cellulose and hemicelluloses building the cells and tissues of trees, all have an impact on how quickly wood-decomposing fungi can develop and how active they are. In general, the wood of coniferous species degrades more slowly than that of deciduous trees. The average rate of decomposition of the latter varies significantly. Research has shown that during the initial phase of decomposition, spanning the first few years after the death of the tree, oak and ash wood decomposes the slowest, whereas beech and hornbeam wood breaks down the fastest. The rates of decomposition of lime, maple, poplar, birch and wild cherry wood are intermediate. The decomposition rate also depends on the presence of heartwood and the thickness of the bark covering the wood. As mentioned previously, because external factors, mainly the local climate, play an important role in the dynamics of dead wood, wood of the same species may become degraded at very different time scales, depending on the environmental conditions.

As a tree decomposes, its mechanical resistance changes. Consequently, in the late stages of degradation, dead wood is present mostly in the form of lying trees. Nonetheless, under favourable conditions, some trees can remain standing for a long time, despite their high degree of degradation. As the decomposition of wood in the trunk progresses, the proportion of standing trees falls sharply, leaving just a few specimens, which become very valuable components of the ecosystem. The rate of wood decomposition is by no means constant. For instance, more of the dead wood mass is usually lost in the early stages of degradation than later on. Wood in the initial stages of decomposition is available only for the first few years after the tree's death, slightly more decomposed wood is available for a few dozen years, while the highly degraded wood can persist for several decades.

Besides the properties of the wood, the rate of decomposition also depends strongly on external factors, mainly the climate and microclimate. High levels of humidity and temperatures facilitate decomposition. Wood on sites with high levels of precipitation, near surface water bodies, or strongly shaded, contains higher levels of moisture, which will accelerate its breakdown. On the other hand, better access to light as a result of direct insolation raises the temperature of the woody substrate, thus intensifying microbiological activity and possibly enhancing the living conditions of some invertebrates. But if exposure to sunlight is excessive, the wood may become too dry, so that the rate of decomposition will slow down. Changeable climatic conditions, in turn, further differentiate the properties of individual pieces of woody debris. In combination with the tree species and the form of dead wood, this can lead to considerable differences in the quality of dead wood stocks. In the context of climatic factors and the increasingly recognized role of insolation in the development of saproxylic organisms, species associated with dead wood exhibit a wide spectrum of insolation requirements. Some species evidently prefer sites with copious amounts of sunshine, others choose spots with moderate exposure to the sun, and yet others avoid direct sunlight altogether, finding the best living conditions in strongly shaded places. In addition, preferences regarding the degree of exposure of dead wood to sunlight may vary between taxa, so that the key requirements of one group, e.g. insects, may stand in contrast with those of another group, e.g. fungi.

Another factor governing the rate of wood decomposition is the species structure of the communities inhabiting its various parts. The characteristics of the wood itself and the external factors that influence them, especially climatic factors, make for a high degree of variability in its parameters, creating specific microhabitat conditions suitable for various living organisms, e.g. microorganisms, macrofungi and invertebrates, both on the surface and inside dying trees, whether blown down by the wind or recently cut down (Photo 45). This colonization is often facilitated by insects, such as European spruce bark beetle *Ips typographus*, which transmits to spruces the spores of *Ceratocystis polonica*, a fungus staining the wood blue. Enzymes, secreted by the fungi and present in the alimentary canals of the larvae of numerous insect species foraging in dead and dying trees, decompose cellulose completely and hemicelluloses partially in reactions that produce monosaccharides on which the larvae feed. In the wood of pine snags and stumps, the quantities of these sugars increase, reaching

Photo 45 (J.M. Gutowski)
Perennial sporocarps of bracket fungi ("conks") provide a habitat for many insect species

Blue staining of wood: a change in the wood's colouration caused by fungi, manifested by irregular bluish to almost black streaks or spots of various size in the sapwood.

Ambrosia beetles: not all insects that bore into and live in wood also consume it. Several species feed on fungi, which they spread and "cultivate" on the walls of their galleries. Such a strategy is used by the striped ambrosia beetle, a common species in Polish forests, which feeds on hyphae. Other species of the genus *Trypodendron*, as well as *Xyleborus* species, ambrosia weevils and the large timberworm beetle feed in a similar way.

a peak about five years after the tree's death, after which time they begin to decrease. Apart from this, the humidity and temperature of the wood change significantly, which is critical for the organisms invading it. The changing food resources and microclimatic conditions of a given dead tree or its parts thus offer a broad spectrum of niches to countless arthropods, fungi (including lichens), slime moulds and other organisms.

With such a diversity of ecological demands exhibited by organisms associated with wood, every stage of decay attracts its own distinct assemblage of species, each gradually replacing its predecessor as one stage merges almost imperceptibly into the next. On pine stumps, for example, five distinct successional stages can occur during the decay process, each represented by a slightly different insect community.

During stage I, lasting less than one year, insects feed in and under the bark. These may include timberman beetle *Acanthocinus aedilis* of the longhorn beetle family (Cerambycidae) and common pine shoot beetle *Tomicus piniperda*, one of the scolytid bark beetles. Only a few bore deeper into the wood, like large timberworm beetle *Elateroides dermestoides* (Lymexylidae) and striped ambrosia beetle *Trypodendron lineatum* (Scolytinae). At this stage, the bark adheres closely to the wood, which is still hard and not yet exhibiting any obvious signs of decay. Ambrosia beetles, which feed on fungi rather than on wood, are often among the wood-boring insects.

In stage II (from the second half of the first year to the fourth year), the bark starts to peel and the cambium gradually dies. There is a steady increase in the number of insect species capable of digesting wood with the aid of their own enzymes or symbiotic microorganisms living in their digestive canals. These include longhorn beetles, like rust pine borer *Arhopalus rusticus*, and jewel beetles (Buprestidae), such as flatheaded pine borer *Chalcophora mariana* and *Buprestis rustica* (Photo 46). Also, more and more insect species are accompanying the xylophages (wood eaters), along with their predators and parasitoids.

Stage III (5-6 years after the tree's death) involves insects requiring or preferring partially decayed wood, such as red longhorn beetle *Stictoleptura rubra*. Under the remnants of bark, ants (Formicidae) can be observed, principally common black ant *Lasius niger*. Fairly soft wood becomes an ideal hibernation site for ground beetles.

In stage IV (7-9 years), wood decay proceeds apace. The sapwood is now already very rotten, but the stump still retains its shape. The moisture content of the wood is higher. Ants, click beetles (Elateridae) and darkling beetles (Tenebrionidae), as well as the larvae of robber flies (Asilidae) and crane flies (Tipulidae), are typical of this stage. Predatory insects are common.

In stage V, only the heartwood of pine stumps remains. It is extremely moist, and the dead wood fauna is dominated by earthworms (Lumbricidae), myriapods (Myriapoda) and springtails (Collembola). Insects are represented, for example, by earwigs (Dermaptera), ground beetles (Carabidae), rove beetles (Staphylinidae).

Large decaying oak trees and logs can be inhabited sequentially by invertebrates belonging to four successional stages: I – longhorn beetles (Cerambycidae), e.g. *Plagionotus detritus*, and jewel beetles (Buprestidae), e.g. oak jewel beetle *Agrilus biguttatus*; II – stag beetles (Lucanidae), such as *Aesalus scarabaeoides* and rhinoceros

Photo 46 (J.M. Gutowski)
Buprestis rustica
is associated with
the wood of conifers

stag beetle *Sinodendron cylindricum*, dipterans of the family Sciaridae, click beetles (Elateridae), e.g. the genus *Ampedus*, etc.; III – mainly ants; IV – wood decay and humification now proceed mainly with the participation of earthworms and myriapods.

In general, we can distinguish three distinct phases in the decay of wood:

- colonization (invasion and colonization by specialized organisms of hard wood with closely adhering bark and live phloem and cambium),
- decomposition (decay; the crumbling and decomposition of the wood tissue caused by various organisms associated with dead wood),
- humification (further decay and mineralization of wood as a result of the increase in soil organisms, such as springtails, myriapods, earthworms, enchytraeids, mites, bacteria and fungi).

In a natural forest, one can observe many significantly different sequences of succession on dead wood (Fig. 5, 6). The colonization of snags differs from that on fallen or lying logs, and which again differs from the processes occurring in stumps or woody debris. Another different and highly specific succession occurs in the rot powder inside the cavities of living trees (Fig. 8). This differentiation is associated with the size of the tree, even within a single tree species. The sequence and rate of colonization vary between insolated and shaded sites. Interestingly, wood decomposition in arid, insolated locations is slower than in places with no direct sunlight. The wood of some species decomposes quickly (e.g. lime, hornbeam), whereas other woods decompose more slowly (e.g. oak, pine with a high proportion of heartwood). Although there is immense variability in the patterns of succession, there are certain similarities and functional regularities charac-

Cambium:
the layer of living cells between the bark and the wood, which grows and increases the thickness of the plant; it produces wood inwards and phloem outwards.

Xylophages:
this and other related terms are explained in Chapter 4.1.2, which deals with invertebrates.

Parasitoid:
a parasite that always causes the death of its host; parasitoids are particularly numerous in the insect world, e.g. hymenopterans representing the families of ichneumons (Ichneumonidae), braconids (Braconidae) and chalcids (Chalcididae). They usually parasitize other invertebrates.

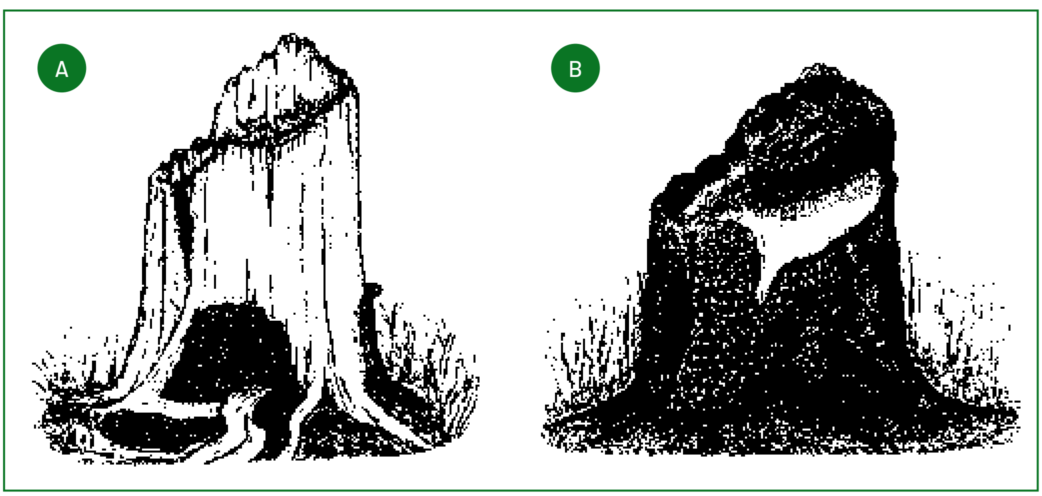


Fig. 5 Decaying stumps:
A – in a sunny spot,
B – in the shade
(M. Bobiec)

Fig. 6 Dead fallen wood – an environment full of life; the gradual decay of wood and the succession of organisms colonizing it (M. Bobiec based on *A richer forest*, modified)

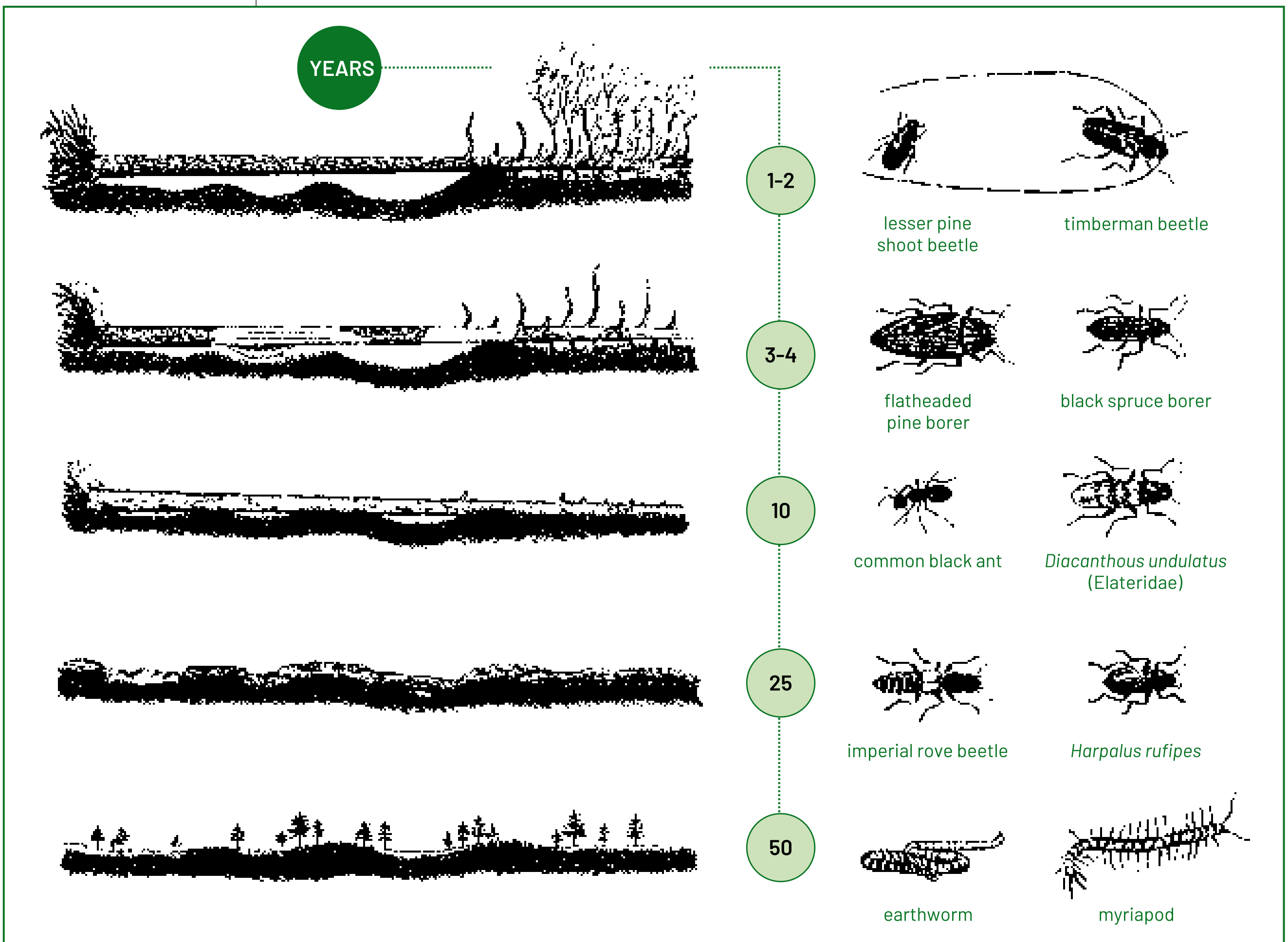
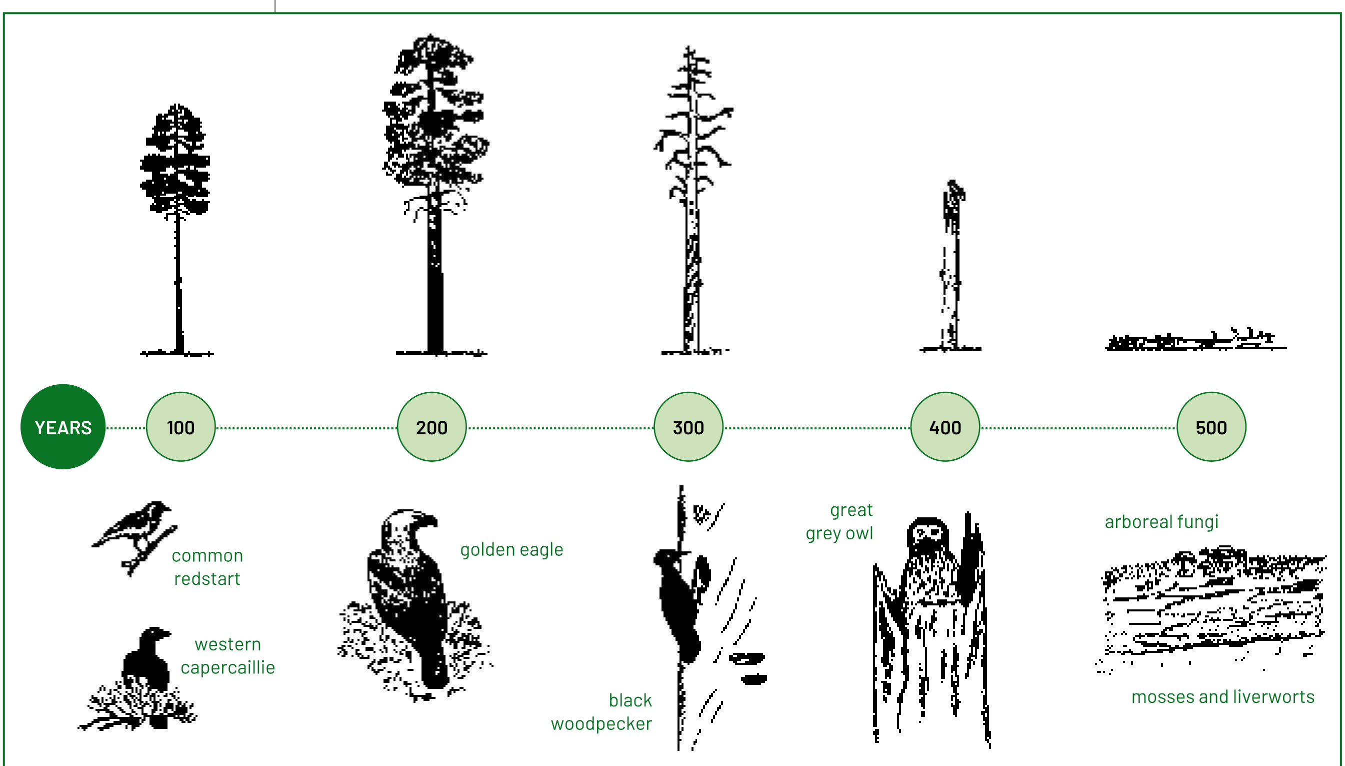


Fig. 7 A living and a dead tree – an environment full of life
(M. Bobiec based on *A richer forest*, modified)



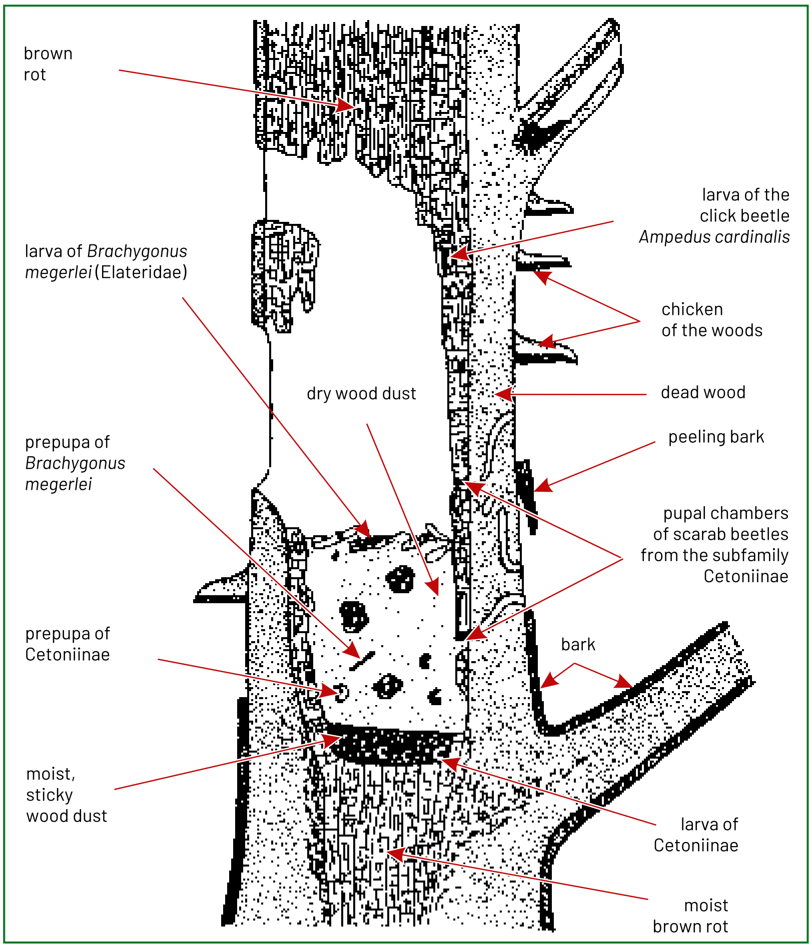


Fig. 8 Longitudinal section through a nest hole (M. Bobiec, based on Iablokoff, 1943, as modified by Speight, 1989)

terizing the successive groups of organisms. Also, the more advanced the stage of wood decay, the more the associations of organisms colonizing dead wood regardless of tree species resemble one another.

Finally, it is important to stress that thick trunks and logs provide more stable microclimatic conditions and are therefore preferred by many organisms. Moreover, most of the endangered invertebrate species are associated with coarse woody debris.

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Chapter 3: Summary

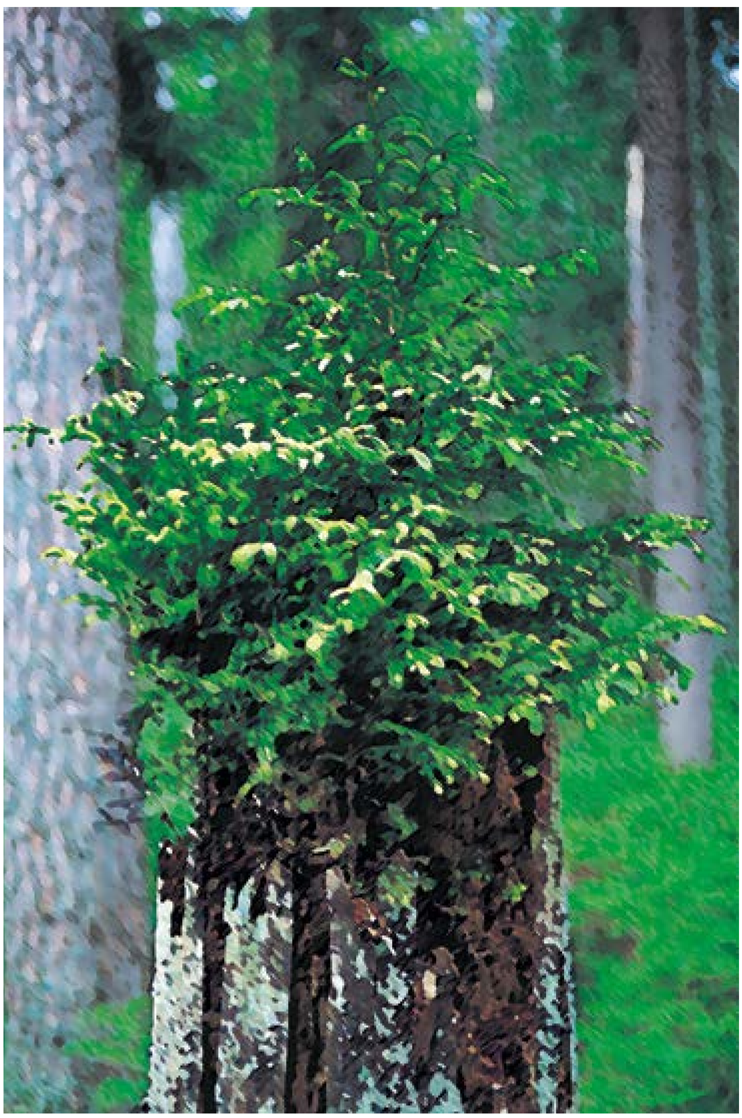
The death of trees is one of the natural processes occurring in forests. Not only does it ensure the supply of dead wood, but it also modifies the tree's immediate neighbourhood, among other things, the amount of light, humidity and availability of nutrients. The gradual breakdown of the dead tree's woody tissues takes place in parallel with the release of chemical elements into the soil.

Once a tree is dead, it is starts to be colonized by various groups of organisms. This succession is characterized by gradual changes in the type and number of species and the quality of habitat (in terms of feeding, reproduction, development and shelter sites). The process is initiated by insect species living under strongly adhering bark and boring galleries in hard wood. They are followed by organisms preferring ever more decayed and softer wood, and finally by those that live in the dry rot. The speed of succession varies and depends on the species, the size of the tree, and the environmental conditions in which the tree finds itself, e.g. humidity, temperature, geochemical conditions, the types and activity of micro- and macroorganism communities taking part in the decomposition.

Although they have certain features in common, patterns of succession can vary substantially, depending on the tree species, size, light regime, humidity and position (standing dead trees vs. fallen logs). During the period from a tree's death to its complete decay, usually many decades, a single tree is colonized by dozens to hundreds of species of fungi, plants and animals.

4

Dead and dying wood in a living forest



4.1. Dead and dying wood as a living environment

Besides the most obvious, though still poorly understood, role of dead wood as a microhabitat for a myriad of species, from mammals and birds to invertebrates, fungi, plants, protozoans and bacteria, dead wood performs a number of other very important functions. Several of them, such as carbon sequestration and the storage of minerals that are slowly but steadily released into the soil, are inseparable from the decay and mineralization processes that occur in every forest ecosystem. There are also functions connected with specific types of environments, where processes associated with dead wood influence the structural and dynamic character of the ecosystem.

4.1.1. Vertebrates

In the same way as there are a variety of factors involved in tree death and a multitude of forms of dead wood in forests, there are also many ways in which woody debris is utilized by animals. The more diverse and numerous a vertebrate group is in a given region, the greater the number of ways its members can make use of dead wood. Dead wood can also influence organisms that are not directly related to the forest ecosystem, e.g. fish. Dead trees in watercourses can provide refuges and breeding space for some fish species, and the decaying wood fertilizes the waters and changes their chemistry. For terrestrial organisms, however, the role of dead wood is far more immediate. In the Blue Mountains (USA), for instance, 179 vertebrate species were found to be dependent on dead tree trunks and logs. The importance of woody debris to mammals, birds, reptiles and amphibians will be discussed and illustrated with observations and studies carried out in the Białowieża Forest, as well as in boreal and temperate forests in Europe and North America.

A humid cave or a sunny beach – amphibians and reptiles

Highly decayed wood provides amphibians with shelter and food. It is where toads (Photo 48) find abundant invertebrates to feed on. Other species, such as moor frog *Rana arvalis* and all the Polish species of newt (smooth newt *Lissotriton vulgaris*, crested newt *Triturus cristatus*, Alpine newt *Mesotriton alpestris*, Montandon's newt *Lissotriton montandoni*) use rotting trunks and stumps as hibernacula. What is also important is that wood lying on the ground holds substantial amounts of moisture and strongly impacts the microclimate in its immediate vicinity. Such conditions are attractive to amphibians, which are particularly sensitive to changes in humidity. Experimental research carried out in Maine, USA, has shown that the presence of dead wood creates favourable living conditions for adult amphibians, but it also facilitates the dispersal of juveniles, especially when an area is abruptly stripped of

Photo 47 (K. Kujawa) Fire salamander *Salamandra salamandra*. This montane amphibian often seeks shelter under fallen logs, protruding pieces of moist bark or strongly decomposed, damp wood

tree cover as a result of the old stand being cleared.

In montane and submontane areas, the humid environment of decaying wood is preferred by fire salamanders *Salamandra salamandra* (Photo 47). Coarse woody debris is thought to be an obligatory element of the habitat for all salamander species. Fallen trees are used by some predatory Oregon salamanders, e.g. Oregon slender salamander *Batrachoseps wrighti*, ensatina *Ensatina eschscholtzii* and clouded salamander *Aneides ferreus*, as feeding areas, but also as egg-laying sites and places where their larvae can grow.

Reptiles are not numerous in temperate forest ecosystems in terms of either species diversity or population densities. These thermophilic animals prefer open, well-insolated habitats. Nonetheless, in broad-leaved forests with abundant herbaceous vegetation, logs provide favourable conditions for reptiles to thermoregulate. Lizards are frequently seen basking in the sun on barkless logs. Gaps created by dying trees are preferred by other species, such as slow worm *Anguis fragilis*, grass snake *Natrix natrix* and adder *Vipera berus*. Besides basking sites, logs, snags and stumps offer a multitude of refuges or hideouts, enabling animals to escape from predators. Old decomposing logs can also be used as a habitat for hibernation. The Aesculapian snake *Zamenis longissimus*, found in south-eastern Poland, lays its eggs in piles of decaying wood and uses single broken trees and fallen logs for shelter. European pond terrapins *Emys orbicularis* often soak up the sun on logs lying in water.

Birds' homes

Birds are the best represented group of vertebrates in forest ecosystems. The Białowieża Forest, for instance, can boast as many as 251 bird species, 177 of which are breeders, but no more than 80 species of amphibians, reptiles and mammals combined. In the Polish part of the Białowieża Forest, 111 breeding bird species are closely associated with the forest ecosystem.

At the level of entire bird assemblages, it has been demonstrated that the species diversity and abundance of birds are closely correlated with the presence of dead wood and old trees. This is especially true for insectivorous birds and hole-nesters, which are far more numerous in natural stands in the Białowieża Forest than in comparable habitats in managed forests. Similarly, in mixed forests in western Hungary, one of the two most important factors (the other was the role of old trees) determining the abundance and species diversity of birds was the volume of dead wood. In fact, it had the greatest impact on the species diversity and abundance of hole-nesters. On the west coast of Canada, too, the number of hole-nesters rose along with the increasing density of standing dead trees. Removing dead trees, especially standing ones, significantly lowers the density of bird species populations, but affects hole-nesters the most. This has been demonstrated both in experimental research in North America and in comparative research in the Białowieża Forest. Studies carried out in Carpathian forests indicate that the presence of even a single dead tree can have a positive impact on species diversity and the abundance of birds.

Photo 48 (K. Kujawa)
A hideout of common toad *Bufo bufo* in dead wood

Photo 49 (J. Korbel)
Hollows excavated by black woodpecker *Dryocopus martius*, a connoisseur of carpenter ants, which often build their nests inside old, rotted spruces

Many bird species nest in cavities in dead trees. In general, hole-nesting birds can be classified as primary hole-nesters, i.e. those that excavate holes themselves – primarily woodpeckers (Photo 49), and secondary hole--nesters, i.e. those that use cavities formed in the process of wood decay or excavated by woodpeckers.

Woodpeckers are the group of birds that are the most closely associated with trees and dead wood. They exhibit numerous adaptations facilitating their arboreal way of life. The orientation of their toes, two pointing forwards and two backwards (in the case of three-toed woodpecker *Picoides tridactylus* only one points backwards), allows them to climb tree trunks with ease. Short, stiff tail feathers provide excellent support while the bird is moving and foraging. The anatomy of the beak, skull and tongue are the most remarkable of the woodpecker's adaptations. The beak is so strong that it is capable of excavating holes in oak wood. The shock of impact is effectively absorbed by a special buffering tissue, which prevents its transmission to the skull and brain. The tongue is fixed to the prolonged hyoid bones, which are anchored at the very back of the skull, permitting the tongue to be extended deep into galleries beneath the bark and into the underlying wood to extract insects. The tip of the tongue is barbed and operates much like a harpoon, easily piercing and securing the soft bodies of insect larvae.

There are nine breeding species of woodpeckers in the Białowieża Forest, most of them being typical primary hole-nesters. They are: Eurasian green woodpecker *Picus viridis*, grey-headed woodpecker *Picus canus* (Photo 50), black woodpecker *Dryocopus martius* (Photo 12), great spotted woodpecker *Dendrocopos major* (Photo 51), middle spotted woodpecker *Dendrocoptes medius* (Photo 52), white-backed woodpecker *Dendrocopos leucotos* (Photo 53), three-toed woodpecker (Photos 54, 58) and lesser spotted woodpecker *Dryobates minor* (Photo 55). Only one species – Eurasian wryneck *Jynx torquilla* – does not excavate nest holes. It nests in existing cavities and hollows, but feeds primarily on ant pupae, which it

Photo 50 (K. Zub) (left)
Grey-headed woodpecker *Picus canus*, female

Photo 51 (K. Zub) (right)
Great spotted woodpecker *Dendrocopos major*

Photo 52 (K. Zub) (left)
Middle spotted woodpecker *Dendrocoptes medius*

Photo 53 (K. Zub) (right)
White-backed woodpecker *Dendrocopos leucotos*

extracts from anthills. A tenth species, Syrian woodpecker *Dendrocopos syriacus*, is not as closely associated with forests as the other woodpeckers and is mainly found in groves, parks and old orchards.

Cavities in dead trees probably provide a better microclimate than natural hollows in living trees; even species capable of excavating the hard wood of living trees often choose dead trees when they are available.

Such cavities in dead trees or dead parts of living trees, used for nesting or roosting, are usually less accessible to predators. Rotten trunks may not bear the predator's weight, and the bare wood provides little texture on which paws or claws can get a grip. Great spotted woodpecker, the most common woodpecker species in the Białowieża Forest, excavates around 35% of its nest holes in dead trees. More than 70% of the nest holes of middle spotted woodpecker are situated in dead trunks or boughs. Lesser spotted and three-toed woodpeckers excavate their holes almost exclusively in dead trees. The latter nests mostly in dead or

Photo 54 (A. Wajrak) (left)
Three-toed woodpecker *Picoides tridactylus*

Photo 55 (K. Zub) (right)
Lesser spotted woodpecker *Dryobates minor*, female

dying spruces. Another species closely associated with dead trees, albeit almost exclusively broad-leaved, is white-backed woodpecker. Nearly half of its cavities are found in dead trunks, most of the remainder being in dead boughs of living trees. The distribution of this species in the Białowieża Forest has been found to be significantly correlated with the volume of dead wood in stands.

Black and grey-headed woodpeckers also excavate their nest holes in dead trees. Considering that almost all woodpecker nest holes are freshly excavated each year, the demand for dead trees by these birds is large, so a shortage of dead trees may seriously reduce the potential number of woodpeckers nesting in a given area. Not surprisingly, in managed forests, where dead wood has been largely or entirely removed, the density of those woodpeckers that are associated with dead wood is on average half as great as in the protected natural stands of the Białowieża Forest (Fig. 9). Similar relationships have been observed in western Europe and North America. In Oregon, forested areas, where logs cover more than 10% of the ground surface, are clearly favoured by woodpeckers.

Data from central Sweden indicate that the trees most preferred by woodpeckers for excavating holes are aspens, goat willows and pedunculate oaks.

Most woodpecker species are capable of excavating holes in relatively hard wood (such as the middle spotted woodpecker in oaks), although some of them, e.g. the North American Lewis's woodpecker *Melanerpes lewis*, excavate them in heavily degraded wood.

Dead trees not only provide woodpeckers with breeding habitats, they are also an important food supply. The only exceptions in this re-

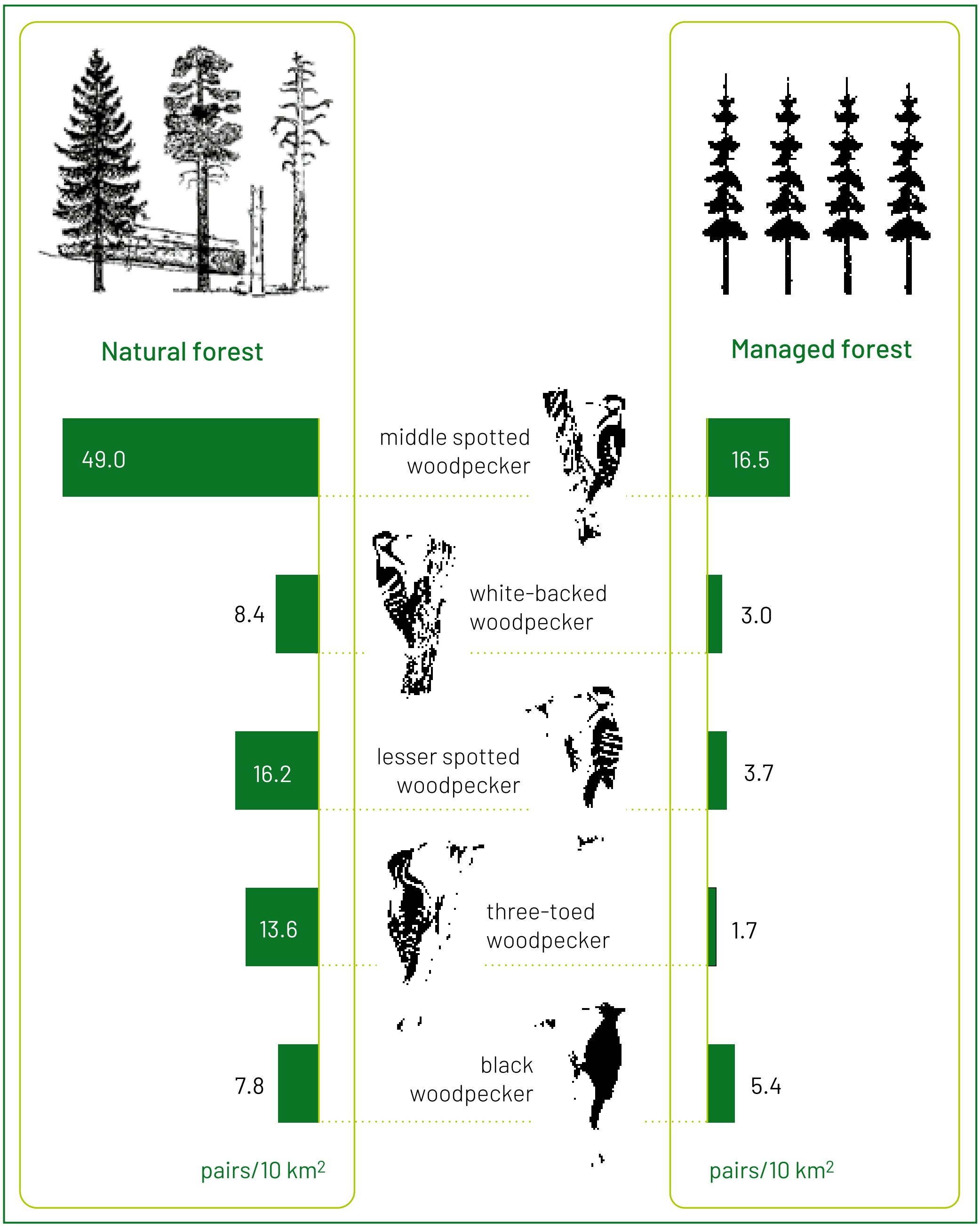


Fig. 9 The density of woodpeckers utilizing dead and dying trees; a comparison between natural and managed stands in the Białowieża Forest (after Pugacewicz 1997; modified)

Table 2 Locations of white-backed woodpecker *Dendrocopos leucotos* nest holes in the Białowieża Forest [%] (according to Wesołowski 1995, modified)

Tree status	Alder	Hornbeam	Oak	Other	Total
living	28	64	70	69	52
dead	44	21	10	15	27
dead trunk	28	14	20	15	21

spect are Eurasian wryneck and Eurasian green woodpecker, which feed primarily on ants. The remaining woodpecker species feed on other insects and their larvae extracted from under bark. Studies from Germany have shown that most woodpeckers forage more than 70% of the time on dead trees or the dead parts of living trees. Dead trees or their dead parts are particularly important for three-toed woodpeckers, which spend more than 80% of the time foraging on dead trees (Fig. 10). In the Białowieża Forest, three-toed, black, and white-backed woodpeckers search for food on dead wood more often (60% of instances) than on living trees, while the other species (great spotted, middle spotted and lesser spotted woodpeckers) forage on dead wood 20% of the time. The size of dead trees is also important as regards the woodpeckers' preferred diet: the larger trees are far more attractive foraging sites than smaller, young trees (Fig. 11). In the Białowieża Forest, woodpeckers clearly prefer trees with a DBH >20 cm. Thus, it comes as no surprise that the density of the woodpecker population is correlated with the amount of dead wood (Fig. 12). However, smaller woody debris is equally important for some species, e.g. lesser spotted woodpeckers or female three-toed woodpeckers, which commonly forage on the dying boughs of old spruces.

Even though in the summer, middle spotted woodpecker most often consumes insects picked out from cracks in the bark of both dead and living oaks, it prefers dead trees to feed on in the winter; indeed, without them it could not survive.

It turns out that besides using dead wood for foraging, woodpeckers also have a direct influence on its supply in the forest. Studies conducted in Oregon show that there are far more hyphae and spores of fungi (including yeasts) in the beaks of woodpeckers than in the beaks of other bird species which do not excavate cavities, and the damage woodpeckers cause to trunks facilitates the wood's decomposition. Not only do woodpeckers mechanically weaken the structure of wood, making it more susceptible to fungal infections, they also transmit

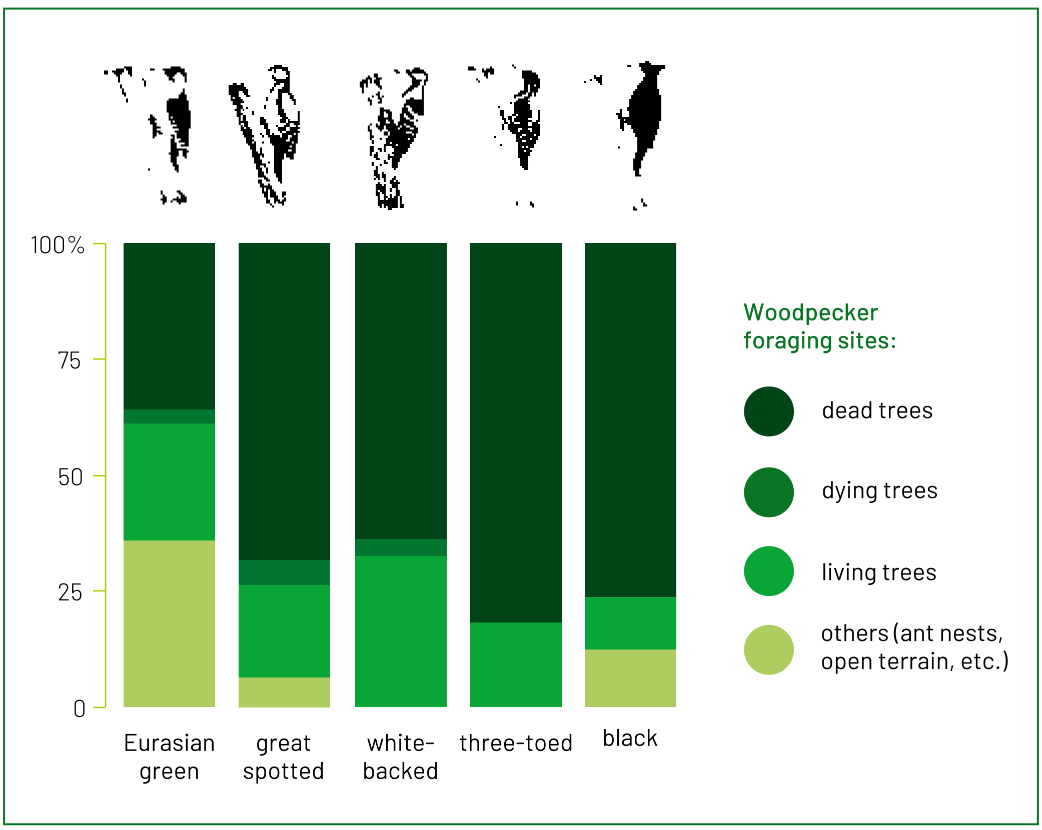
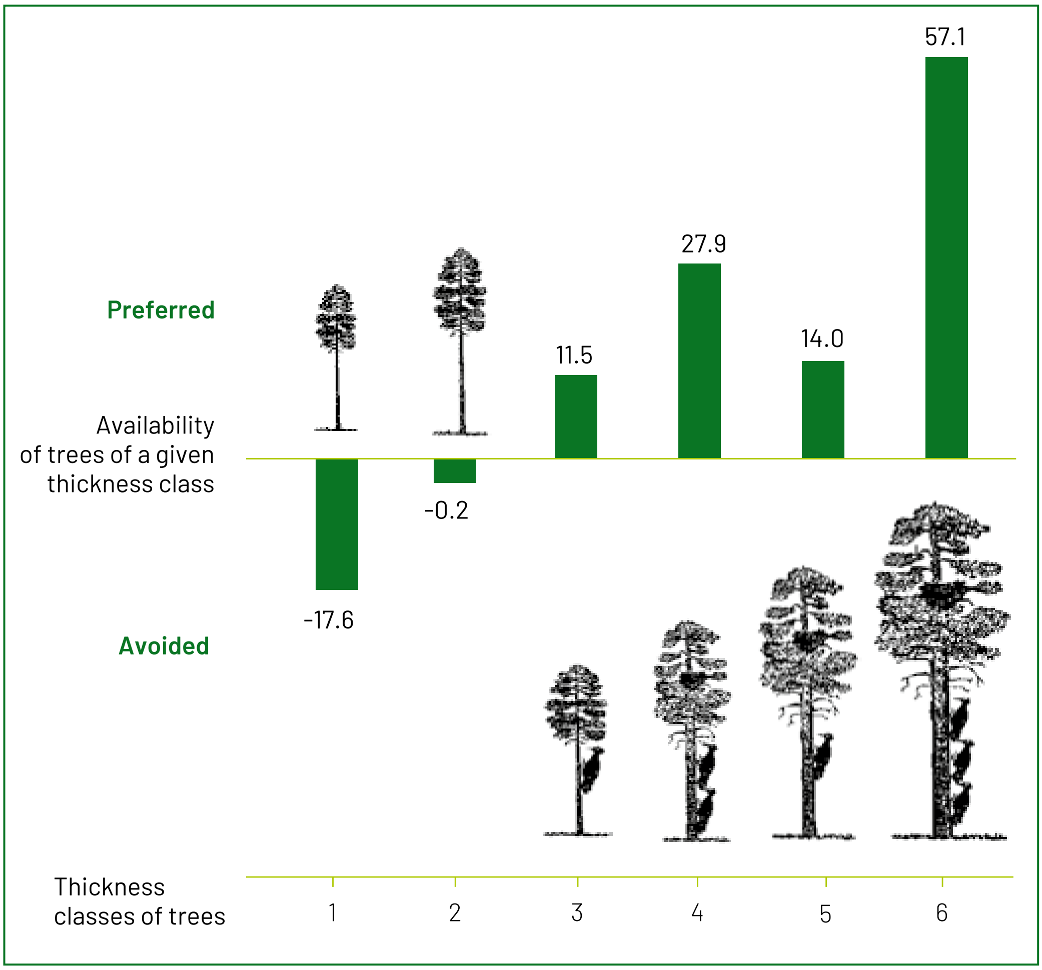


Fig. 10 Preferences of woodpeckers for different types of feeding substrates in the Berchtesgaden National Park, Germany (after Pechacek 1995 and Scherzinger 1996; modified)

Fig. 11 Preferences of foraging woodpeckers for trees of different diameters; the bars denote the selection or avoidance of a given DBH class relative to its proportion in the stand (according to Swallow et al. 1988, after Scherzinger 1996; modified)



spores and fragments of mycelia of species that colonize wood.

Dead trees and dry boughs also play another role in the life of a woodpecker: they provide ideal drumming sites. Drumming is caused by quick rhythmical hits of the beak on resonating, dry but hard parts of trees, as well as other resonating structures. A very important mating behaviour, it serves as a way for pairs to communicate and is used to mark their territories.

Secondary hole-nesters mostly make use of existing cavities, either natural ones or previously excavated by a primary hole-nester. Only the willow tit *Poecile montanus* and the Eur-

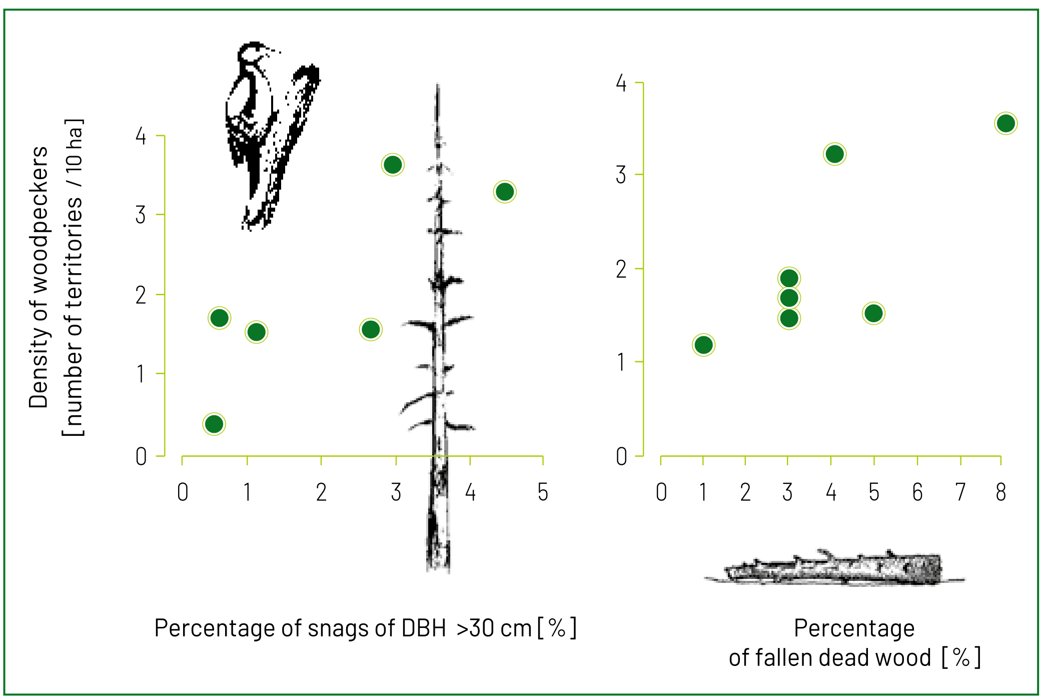


Fig. 12 Relationship between woodpecker density and the proportion of dead trees in a forest (according to Komdeur and Vestjens 1983, after Scherzinger 1996; modified)

asian nuthatch *Sitta europaea* are capable of excavating new cavities in soft wood or improving existing ones. The availability of tree hollows and cavities in the unmanaged and more natural patches of the Białowieża Forest is many orders of magnitude greater than in intensively managed, commercial forests.

Besides nuthatches, flycatchers, tits and starlings also commonly occupy nest holes. Almost half of European pied flycatcher *Ficedula hypoleuca* and collared flycatcher *Ficedula albicollis* nesting sites are situated in dead trees. Similarly, the nest holes of about 25% of common starling *Sturnus vulgaris* and 10% of European blue tit *Cyanistes caeruleus* and marsh tit *Poecile palustris* are found in dead wood. Other species utilizing cavities are spotted flycatcher *Muscicapa striata* and red-breasted flycatcher *Ficedula parva*, and also stock dove *Columba oenas*. An interesting peculiarity of the Białowieża Forest is that cavities are often used by species which normally build open nests, i.e. Eurasian blackbird *Turdus merula*, European robin *Erithacus rubecula* and dunnock *Prunella modularis*. If possible, these birds will prefer natural cavities formed through the decomposition of wood over holes excavated by woodpeckers, which may steal and eat eggs or nestlings of other species: great spotted woodpecker does so in Europe (it is also capable of breaking into nesting boxes and natural cavities), red-bellied woodpecker *Melanerpes carolinus* in North America.

Large woodpecker species, like black woodpecker and its North American relation pileated woodpecker *Dryocopus pileatus*, often excavate holes in rotted trees, making vast spaces available inside the trunk. Woodpeckers themselves utilize such cavities as roosts, but are far less likely to raise their brood there. But other animals, like northern flying squirrel *Glaucomys sabrinus* and American red squirrel *Tamiasciurus hudsonicus* in North America, regularly make use of them. In the Białowieża Forest, such holes are used by tawny owl *Strix aluco* (see below), and in North America by Vaux's swift *Chaetura vauxi*, a close relative of our common swift *Apus apus*. Also, American northern flickers *Colaptes auratus* use these spacious cavities for roosting.

Owls are another group of birds closely associated with hollows and cavities. Three species found in the Białowieża Forest typically inhabit tree holes and cavities: tawny owl, European pygmy owl *Glaucidium passerinum* (Photo 56) and Tengmalm's owl *Aegolius funereus*. In natural forests of the Carpathians, Ural owl *Strix uralensis* is a cavity-dwelling species. Tawny owls are fairly large birds that most often nest in large naturally-formed hollows, whereas Eurasian pygmy owls and Tengmalm's owls do so in cavities excavated by woodpeckers. Tengmalm's owls breed less frequently in dead trees,

Photo 56 (J. Walencik)
A hollow in an old, dead pine occupied by a Eurasian pygmy owl *Glaucidium passerinum*

because they prefer hollows made by black woodpeckers in living pines, whereas Eurasian pygmy owls favour cavities excavated by three-toed and great spotted woodpeckers, many of which are located in dead wood. In North America, a species breeding in abandoned woodpecker holes is the northern saw-whet owl *Aegolius acadicus*.

Other owls, such as great grey owl *Strix nebulosa*, breed almost exclusively in open nests placed on the top of broken dead trees (snags). Ural owls and northern hawk owls *Surnia ulula* use similar sites in Scandinavia.

Both woodpeckers and secondary hole-nesters prefer to nest in cavities in trees of a relatively large diameter. For instance, the average DBHs (in cm) recorded for such trees in the Białowieża Forest are: white-backed woodpecker – 59, middle spotted woodpecker – 91, three-toed woodpecker – 39, great tit *Parus major* – 54 and European pied flycatcher – 48. In North America, pileated woodpecker forages most often on dead Douglas firs *Pseudotsuga menziesii* and western larches *Larix occidentalis* with a DBH > 38 cm.

In view of the shortages of dead wood in managed forests in many parts of the world, its quantities are artificially increased by girdling, removing the crown or applying chemicals in order to induce the tree's death (veteranization) (see also Chapter 5.2). In most cases, areas with artificially increased numbers of standing dead trees featured both a greater abundance of birds and a higher bird species diversity. Comparative research carried out in Texas, USA, showed that this was particularly important in the case of

Table 3 Polish birds that nest in hollows, root plates and snags

BIRD SPECIES	Excavation of hollows	Nesting in hollows	Nesting on uprooted trees and windsnaps
common goldeneye *Bucephala clangula*		+	
goosander *Mergus merganser*		+	
stock dove *Columba oenas*		+	
Eurasian pygmy owl *Glaucidium passerinum*		+	
Eurasian scops owl *Otus scops*		+	
little owl *Athene noctua*		+	
Tengmalm's owl *Aegolius funereus*		+	
tawny owl *Strix aluco*		+	
Ural owl *Strix uralensis*		+	
great grey owl *Strix nebulosa*			+
common swift *Apus apus*		+	
European roller *Coracias garrulus*		+	
common hoopoe *Upupa epops*		+	
Eurasian wryneck *Jynx torquilla*		+	
grey-headed woodpecker *Picus canus*	+	+	
Eurasian green woodpecker *Picus viridis*	+	+	
black woodpecker *Dryocopus martius*	+	+	
great spotted woodpecker *Dendrocpos major*	+	+	
middle spotted woodpecker *Dendrocoptes medius*	+	+	
white-backed woodpecker *Dendrocopos leucotos*	+	+	
Syrian woodpecker *Dendrocopos syriacus*	+	+	
lesser spotted woodpecker *Dryobates minor*	+	+	
three-toed woodpecker *Picoides tridactylus*	+	+	
northern wren *Troglodytes troglodytes*			+
dunnock *Prunella modularis*		+	+
European robin *Erithacus rubecula*		+	+
common redstart *Phoenicurus phoenicurus*		+	
Eurasian blackbird *Turdus merula*		+	+
song thrush *Turdus philomelos*			+
redwing *Turdus iliacus*			+
spotted flycatcher *Muscicapa striata*		+	+
red-breasted flycatcher *Ficedula parva*		+	+
European pied flycatcher *Ficedula hypoleuca*		+	
collared flycatcher *Ficedula albicollis*		+	
marsh tit *Poecile palustris*		+	
willow tit *Poecile montanus*	+	+	
crested tit *Lophophanes cristatus*		+	
Eurasian blue tit *Cyanistes caeruleus*		+	
great tit *Parus major*		+	
coal tit *Periparus ater*		+	
Eurasian nuthatch *Sitta europaea*	+	+	
common treecreeper *Certhia familiaris*		+	
short-toed treecreeper *Certhia brachydactyla*		+	
Eurasian jackdaw *Corvus monedula*		+	
common starling *Sturnus vulgaris*		+	
Eurasian tree sparrow *Passer montanus*		+	

hole-nesters living exclusively in these areas. In Douglas fir forests in Oregon, where the quantity of dead trees was increased artificially, 20% of snags were used as nesting sites, and cavities were present in as many as 80% of them. Such trees played a greater role in managed forests where clear-cutting rather than selective cutting was employed.

Not all such artificial replenishments of dead trees deliver the desired results. A study in Scotland involved the cutting of pine trunks at a height of ca 1.0–1.2 m above the ground. Five years on, none of the cut trunks had been colonized by crested tit *Lophophanes cristatus*, which was expected to have benefitted from this treatment. The probable reasons behind this outcome were the insufficient degree of wood decomposition and the inappropriate height of the trunks: nest holes of this species are typically found at an average height of over 7 m. Similar observations were made during a 25-year-long study regarding the level of occupancy of Douglas fir snags: only 11% of them were used by four out of twelve bird species recorded on the study site (more than 90% of which were chestnut-backed chickadees *Poecile rufescens*). These examples serve to illustrate that our ability to imitate natural processes occurring in forest ecosystems remains extremely limited.

As is the case in forests, dead and hollow trees play a very important role in groves. Single dying trees are used by certain species of woodpeckers, e.g. green and black woodpeckers, in which they excavate holes. In subsequent seasons, abandoned woodpecker nest holes are taken over by European rollers *Coracias garrulus*, a rare and endangered species in Poland, and other birds like little owl *Athene noctua* (Photo 59) and common hoopoe *Upupa epops*. Little owls and hoopoes also frequently inhabit old, hollow roadside willows, which are becoming ever rarer in the Polish landscape. Syrian woodpeckers use dying trees in parks and orchards for nesting. Certain species of secondary hole-nesters, including relatively rare ones like Eurasian wryneck and common redstart *Phoenicurus phoenicurus*, choose the same kind of habitat. The populations of many of these birds are in decline, the prime cause being the loss of their favoured suitable breeding sites in old and dying trees.

Birds associated with old, dead and dying trees constitute a significant part of forest fauna, not only in Poland. In the boreal zone of Fennoscandia, for instance, 45 species build their nests in or on such trees, while in central and southern Sweden, 15 species inhabit cavities and hollows, and in North America as many as 86 species use such sites for nesting.

Another important form of dead wood are the root plates of uprooted trees. They are important breeding sites for numerous species of birds, e.g. thrushes, European robin, dunnock, spotted and red-breasted flycatcher and northern wren *Troglodytes troglodytes* (Photo 57), the last-named building ca 80% of its nests in the root plates of fallen trees in the swamp stands of the Białowieża Forest. Eurasian eagle-owls *Bubo bubo* often perch on top of large root plates (Photo 60), and common kingfishers *Alcedo atthis* sometimes excavate their nesting burrows in tree throws, even if these are situated some distance away from water. Tree throws closer to water are regularly used as nesting sites by goosander *Mergus merganser*.

Photo 57 (K. Zub)
Northern wren
Troglodytes troglodytes

Photo 58 (K. Zub)
Three-toed woodpecker *Picoides tridactylus* foraging on a dead spruce

For some birds, dead trees are an important element of their biotope, even if they do not use them for nesting. Although white-tailed sea-eagle *Haliaeetus albicilla* nests on living trees (predominantly old, over 120-year-old pines with umbrella crowns), it requires standing dead trees as observation points. Common kingfisher, which nests in holes in the soil, makes use of coarse woody debris in the river as a vantage point when hunting.

Large-scale tree mortality, e.g. due to high winds or insect outbreaks, leads to significant amounts of dead wood being produced in a relatively short time. As a result of the European spruce bark beetle *Ips typographus* outbreak in the Białowieża Forest, which has been ongoing since 2012, the number of three-toed woodpeckers (Photo 58) in this area has more than doubled. This species, which had previously nested mainly in protected areas, where it was able to find a sufficient quantity of old and dying trees, has begun to migrate to dying stands in managed forests. At the same time, however, the death of nearly all the trees over a large area dramatically depletes the woodpeckers' food resources. After only a few years, three-toed

Photo 59 (J. Baake)
Little owl *Athene noctua* in a hollow on a fruit tree

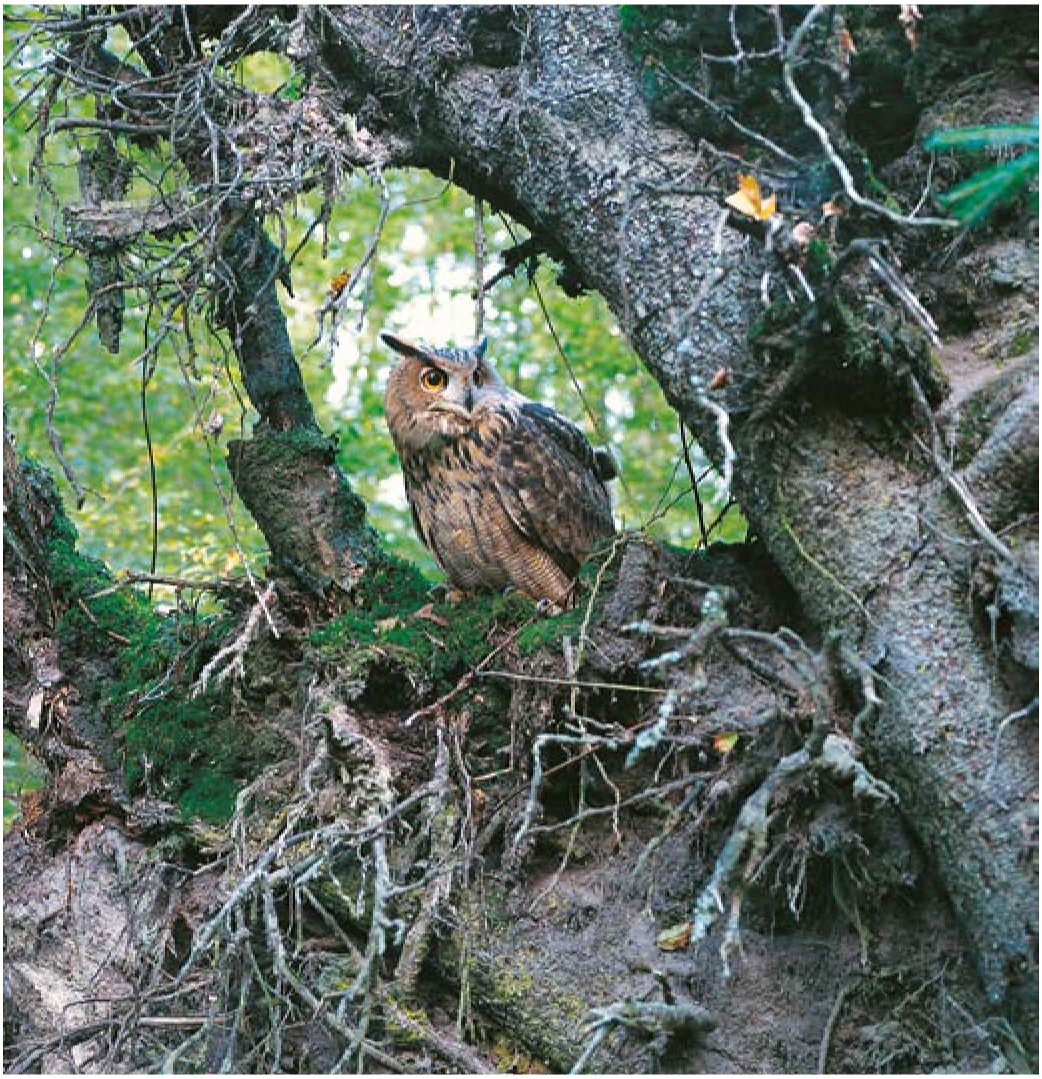


Photo 60 (J. Walencik)
Eurasian eagle-owl *Bubo bubo* on the roots of a downed spruce

woodpeckers start avoiding sites with large amounts of dead wood. Likewise, white-backed woodpeckers in the Białowieża Forest are more likely to forage and nest in woodland with a higher proportion of dead deciduous trees, shunning areas where large amounts of dead spruce wood have accumulated. Nevertheless, despite being associated mostly with broad-leaved trees, this species does occasionally feed on spruces attacked by bark beetles. An analogous situation occurred in the Bavarian Forest: at first the number of woodpeckers in spruce forests invaded by the European spruce bark beetle increased, but then decreased, as the outbreak died down.

Be that as it may, one has to bear in mind that the long-term effects of disturbances in forests could have an additional positive impact on the populations of many animal species in that they modify the landscape and create new ecological niches. Large accumulations of dead wood could improve nesting conditions for hazel grouse *Tetrastes bonasia* and other ground-nesting birds. Such spaces also attract species favouring more open stands, like common redstart and tree pipit *Anthus trivialis*.

Hideouts and hunting grounds – mammals

Among the mammals inhabiting the Białowieża Forest, insectivores, bats, rodents and certain carnivores have a particularly strong relationship with dead wood.

Coarse woody debris does not have the same significance for ungulates, but it can effectively prevent them from accessing seedlings and advanced regeneration. It is also an important element of the so-called landscape of fear, which influences how animals behave, minimizing their negative impact (in the case of abundant populations) on forest regeneration. Fallen logs are perceived by red deer *Cervus elaphus* and other ungulates both as a place where predators can lie in wait and as an obstacle, hindering effective escape. Thus, in the face of a heightened threat from predators, they become more vigilant and avoid foraging near logs (Photo 61). Studies carried out in the Białowieża Forest have shown that in areas where the risk of predation is low, e.g. near human settlements, the radius of this effect is 4 – 6 m around the logs, keeping the browsing of young trees to under 20%. In places frequented by wolves *Canis*

Advanced regeneration: a young generation of trees exceeding 50 cm in height, developing under the canopy of the established stand; given its condition and species composition, it is likely to form the future canopy.

Photo 61 (J.M. Gutowski)
Fallen tree trunks restrict access to ungulate mammals, allowing a new generation of trees to grow (here: Scots pines, pedunculate oaks and Norway spruces in the Białowieża Forest)

Landscape of fear: a space where animal behaviour is determined by the threat of predation. Animals may, for example, avoid certain places or increase their vigilance in places where they are more likely to be attacked by predators.

lupus, browsing is reduced by more than 35%, and the impact radius extends to 16 m. Interestingly, similar research conducted in Pomerania indicated that the presence of wolves in an area increased the level of alertness of foraging deer, but did not limit the damage sustained by seedlings in tree plantations. It may well be that the absence of dead wood in these areas meant that the landscape of fear was incomplete, so that its influence on ungulates was much weaker than anticipated.

Dead wood plays an entirely different role during the sprouting season of seeds, as it provides protection to rodents, which are their main consumers. An experiment carried out in the Białowieża Forest has demonstrated that when dead wood is present, all acorns are taken by rodents and wild boars *Sus scrofa*, whereas in areas devoid of dead wood less than half are removed. This goes to show that the regeneration of many tree species in forest ecosystems is a complex process and that dead wood may impact it in many different ways, depending on the phase.

Larger ungulates sometimes use dead wood as a food resource. European bison *Bison bonasus*, for example, sometimes eat sporocarps of honey fungi and other fungi growing on fallen logs, and wild boars search for insects and rodents under decaying wood.

Rotten logs, especially in the later stages of decomposition, offer an excellent habitat for three species of shrews *Sorex* in the Białowieża Forest: pygmy shrew *Sorex minutus*, common shrew *Sorex araneus* and masked shrew *Sorex caecutiens*. Logs not only provide them with refuges or hideouts, but are also sources of food in that they may harbour small invertebrates. In North America, the populations of many shrew species (e.g. southern short-tailed shrew *Blarina carolinensis*, south-eastern shrew *Sorex longirostris* and Trowbridge's shrew *Sorex trowbridgii*) are larger in areas with a higher proportion of fallen dead trees.

Fallen logs play an equally important role in the life of rodents. Bank voles *Clethrionomys glareolus* and common pine voles *Microtus subterraneus* construct their burrows underneath logs, and if the wood is well rotted, rodent burrows may extend into the tree trunks. In Oregon, USA, the radiotelemetry tracking of California red-backed mice *Clethrionomys californicus* revealed that they spent 98% of their time under or near fallen dead trees, even though these occupied only 7% of the study area. Moreover, these rodents were more likely to inhabit significantly decayed wood rather than only slightly decomposed logs. Dead and decaying logs are often used to store food, including tree and shrub seeds, but this is not their only function: they are also sources of food. Sporocarps of fungi growing on dead wood are a significant dietary component of California red-backed mice and southern red-backed voles *Clethrionomys gapperi*. Poland's native bank voles also regularly feed on sporocarps, which they find both on the surface of dead wood and under the ground.

Red squirrels *Sciurus vulgaris* make similar use of dead trunks and stumps. However, besides using them as food stores, they utilize cavities, both excavated by woodpeckers and natural ones, for concealment and breeding. Dormice, i.e. fat dormouse *Glis glis*, forest dormouse *Dryomys nitedula* and common dormouse *Muscardinus avellarius*, as well as north-

Photo 62 (J. Walencik)
Northern birch mouse
Sicista betulina

ern birch mouse *Sicista betulina* (Photo 62), hibernate in rotten hollow trunks.

While voles and shrews choose habitats that are predominantly under or inside fallen dead trunks, yellow-necked mice in Europe and deermice in North America prefer to stay on the surface or in the vicinity of dead wood. That is why in South Carolina, the population density of cotton mice *Peromyscus gossypinus* was found to be almost twice as high in tornado-stricken areas from which dead wood had not been removed. In burnt areas in the Myszyniec Forest District (Poland), both yellow-necked mouse *Apodemus flavicollis* (Photo 63) and bank vole (Photo 64) were the most abundant where dead wood had been left in place. In the Białowieża Forest, too, there were twice as many yellow-necked mice in areas with large stocks of dead pine wood, although no such correlation was found for bank voles.

Bats are often closely associated with dead trees. At least 11 of the 17 bat species occurring in the Białowieża Forest use cavities and hollows for summer roosts or concealment, and two of them sporadically hibernate in trees.

Sometimes, even closely-related species exhibit distinctly different preferences for cavities and hollows. Common noctules *Nyctalus noctula* almost exclusively use holes excavated by woodpeckers, while Leisler's bats *Nyctalus leisleri* generally use natural ones. Most of the cavities used by the common noctule bat are located in dying trees. The characteristics of the habitat adjacent to suitable cavities or hollows are often important. Bats often select tall trees either at the edge of an opening in the forest or extending well above the average canopy height. Such locations permit easy entrance and exit from cavities and hollows; presumably the microclimate of these also varies in suitability. Conditions are often ideal in old and dying trees. In the Białowieża Forest, 40% of breeding colonies of five bat species (barbastelle bat *Barbastella barbastellus*, Leisler's bat, soprano pipistrelle *Pipistrellus pygmaeus*, Nathusius' pipistrelle *Pipistrellus nathusii* and brown long-eared bat *Plecotus auritus*) were found in dead trees, while there were breeding colonies of a sixth species – Natterer's bat *Myotis nattereri* – in cavities or holes that formed as a result of

Photo 63 (K. Zub)
Yellow-necked mouse
Apodemus flavicollis
on the stump of a dead spruce

Photo 64 (K. Zub)
Bank vole
Clethrionomys glareolus

branches breaking off. Curiously, most barbastelle bat colonies and nearly half of the brown long-eared bat colonies were located under the loose bark of dead trees, mainly spruces. Soprano pipistrelles and Nathusius' pipistrelles preferred to establish their colonies either under peeling bark or in crevices in the trunks of dead trees.

Similar observations concerning the selection of roost sites by bats have been made in North America, where these mammals choose taller, better insolated trees, standing farther away from others. In Canada, individual silver-haired bats *Lasionycteris noctivagans* prefer to roost in tight crevices in trunks or under the bark, although the breeding colonies of this species are typically situated in cavities. In the warmer Californian climate, where insolation is not the most important factor as regards the choice of roost, bat breeding colonies are often found in spacious cavities at the bases of coastal redwoods *Sequoia sempervirens*.

Carnivores, especially pine martens *Martes martes*, often use tree cavities and hollows for roosting and breeding. In North America, 22% of hideouts and 73% of breeding sites of American marten *Martes americana* were found to be located in hollows, but during the breeding season this species would also often use rotten logs lying on the ground. Likewise, raccoon dogs *Nyctereutes procyonoides* often rest and breed in fallen rotten logs. In fact, in natural forests they use such sites more readily than burrows dug in the ground, even for hibernation. Pine martens, however, often leave their tree cavities and hollows and take refuge in logs when temperatures drop below -20°C. In particular, they prefer logs covered with a thick covering of snow, which insulate them from the cold better than cavities and hollows in standing trees.

For pine martens and weasels *Mustela nivalis* (Photo 66), logs are also an ideal hunting environment. These animals clearly favour such locations when searching for food (Fig. 13).

Lynxes *Lynx lynx* often use logs as "stepping stones" when moving across the forest floor (Photo 65). Mammals also use wood for other purposes. To cross forest streams, small mammals run along logs bridging them, wild boars make their lairs from thin branches (Photo 68), while beavers *Castor fiber* build their dams with logs, boughs and branches (Photo 69). For many predator species, areas with an abundance of dead wood provide important breeding sites.

In North America, fallen logs are often used by cougars *Puma concolor*, wolverines *Gulo gulo*, and especially by lynxes, as they provide excellent protection for their cubs. Black bears *Ursus americanus*, too, regularly make use of large hollows at the bases of standing trees or fallen logs to breed in. Such cavities are most often found in grand firs *Abies grandis* and are associated with the Indian paint fungus *Echinodontium tinctorium.*

European brown bears *Ursus arctos* hibernate in hollows at the bases of trees. In the Bieszczady Mountains, they do so in cavities in old firs (Photo 67) or under fallen fir trees.

As in the case of birds, a deficiency of old hollow trees can reduce the numbers of certain mammal species. Bats, dormice and small carnivores, such as pine martens, are particularly sensitive in this regard. These animals will also readily use artificial nest boxes, but such "hollows" do not provide such suitable nesting con-

Table 4 The use of hideouts by bats in the Białowieża Forest (according to I. Ruczyński, unpublished data)

Species	Summer hideouts	Winter hideouts (hibernacula)
Myotis alcathoe	unknown	
Natterer's bat *Myotis nattereri*	cavities	cellars
Brandt's bat *Myotis brandtii*	cavities	
pond bat *Myotis dasycneme*	unknown	
Daubenton's bat *Myotis daubentonii*	cavities	cellars
parti-coloured bat *Vespertilio murinus*	cavities/buildings	
northern bat *Eptesicus nilssonii*	cavities/buildings	
serotine bat *Eptesicus serotinus*	buildings	cellars
common pipistrelle *Pipistrellus pipistrellus*	buildings	
soprano pipistrelle *Pipistrellus pygmaeus*	cavities/buildings	
Nathusius' pipistrelle *Pipistrellus nathusii*	cavities/buildings	
greater noctule bat *Nyctalus lasiopterus*	unknown	
noctule bat *Nyctalus noctula*	cavities	
Leisler's bat *Nyctalus leisleri*	cavities	
brown long-eared bat *Plecotus auritus*	cavities/buildings	cavities/cellars
grey long-eared bat *Plecotus austriacus*	unknown	
barbastelle bat *Barbastella barbastellus*	cavities/buildings	cavities/cellars

Photo 65 (J. Walencik)
This young lynx on a spruce log gets a better view than on vegetation-covered ground

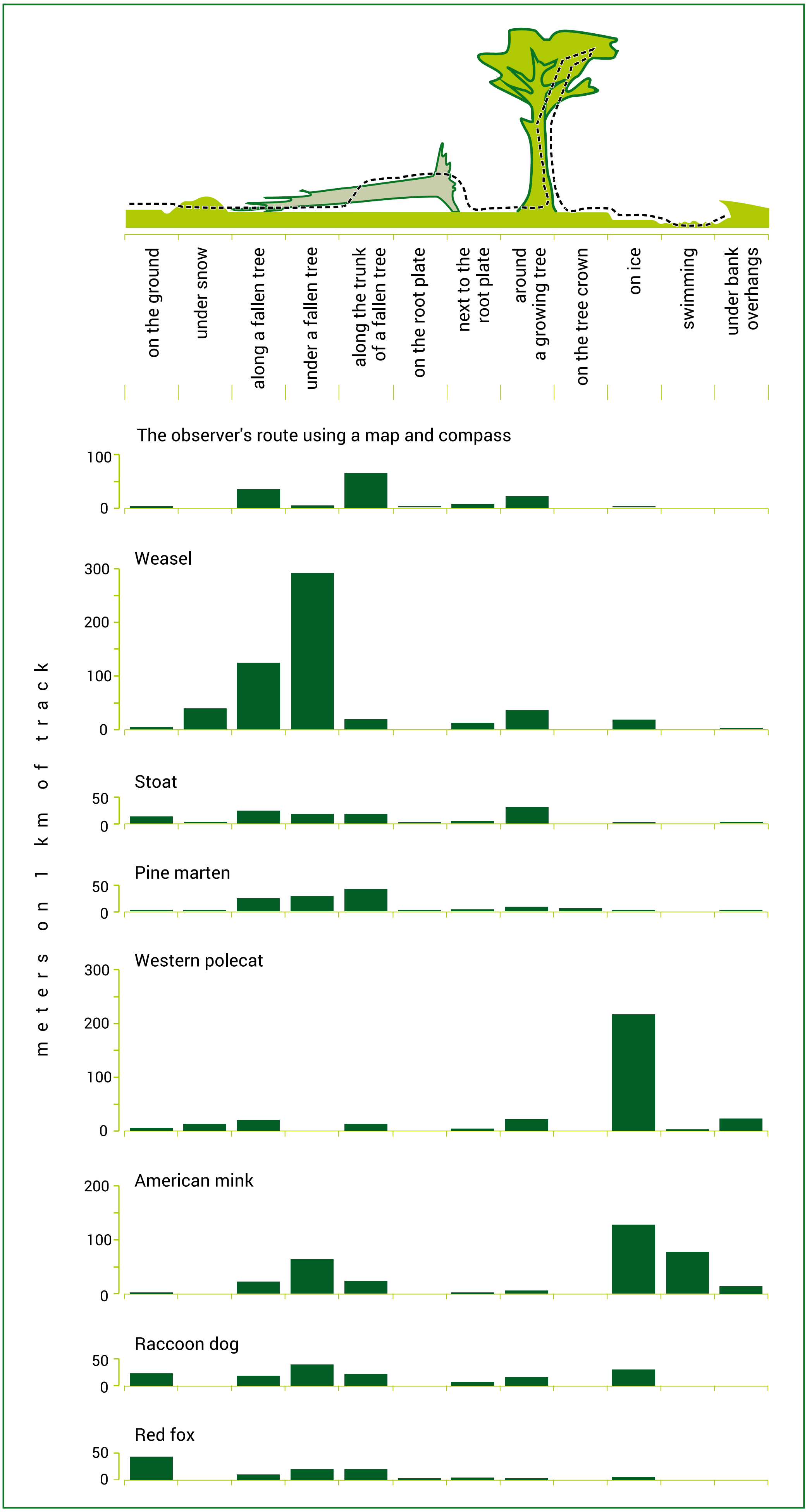


Fig. 13 Paths of communication and terrain penetration by selected predatory mammals in the Białowieża National Park. Data collected by an observer on foot using a map and compass show the relative availability of various components of the forest (after Jędrzejewska and Jędrzejewski 2001, modified)

Photo 66 (K. Zub)
Weasel *Mustela nivalis*

ditions as natural cavities do. Besides, the need to constantly change hiding places (in order to avoid parasites and predators) means that there are too few artificial refuges to provide optimal conditions for all species.

Research in the USA has shown that, in order to ensure appropriate living conditions for American martens, at least 18 m^3/ha of dead wood should be left in managed forests, with the trunks, stumps and fallen logs for preference being at least 80 cm in diameter and 10 m in length.

Photo 67 (B. Pirga)
Lair of brown bear *Ursus arctos* in a hollow at the base of a thick fir (over 5 m in circumference)

Photo 68 (J.M. Gutowski)
Lair of wild boar *Sus scrofa* bedded with dry branches

Photo 69 (J.M. Gutowski)
Beaver dams are made mainly from dead wood

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Chapter 4.1.1: Summary

Dead trees and their parts are used as hiding places by members of all vertebrate classes, although they are most important for birds, which utilize them for breeding, roosting and feeding. The species most closely associated with dead and hollow trees are woodpeckers, tits, flycatchers and owls. Two woodpecker species – white-backed and three-toed – excavate cavities and forage almost exclusively on dead and dying trees. The presence of dead trees is vitally important for the survival of many rare and protected bird species, like the aforementioned two woodpecker species, collared and red-breasted flycatchers, Eurasian pygmy owls, Tengmalm's owls, European rollers and stock doves. Tree throws are also important breeding sites for many birds.

Mammals use dead trees for shelter and food. Dead and hollow trees are crucial for bats, insectivores, rodents and small predators. By providing rodents with sites where they can conceal themselves, fallen tree trunks allow them to eat more tree seeds, but being an important element of the "landscape of fear", they also facilitate forest regeneration by protecting seedlings and advanced regeneration from ungulates.

4.1.2. Invertebrates

Invertebrates (Invertebrata) are an artificial taxonomic unit, distinguished for practical reasons, which includes multicellular animals that lack bone tissue or an internal (axial) skeleton consisting of a spine and a skull. Invertebrates exhibit a wide variety of shapes and forms, characteristic of individual systematic groups. There are more than a million known species of invertebrates worldwide, making up around 97-99% of modern animal species; their percentage in the total biomass is similar.

Around 60% of invertebrates in Poland live in forests. How many of them are saproxylic? It is hard to say. It is estimated that up to 50% of plant, fungi and animal species in forests may be directly or indirectly dependent on dead wood. In the UK, for example, there are approximately 1,800 saproxylic invertebrate species.

In Poland, there are more than 35,000 species of animals, most of which are invertebrates, including more than 28,000 insects. Invertebrates are an extraordinarily diverse group of organisms, comprising numerous phyla with varying degrees of association with dead and dying trees. They include nematodes, many of which are linked to either dead wood or other organisms inhabiting dead wood; annelids: for example, some earthworm species live under the bark or in the wood of highly decomposed tree stumps, broken trunks (Photo 70) and fallen logs; arthropods, including crustaceans, arachnids, myriapods and especially insects; and molluscs (snails). Mites (Acarina), which belong to the arachnids (Arachnidae), are a diverse group. Many are associated with coarse woody debris, in particular with cavities, hollows and the spaces just beneath the bark. Mites include wood-eating species such as *Rhysotritia duplicata* and *Steganacarus carinatus*, pseudoscorpions (Pseudoscorpionida) resembling miniature scorpions, and spiders, e.g. predatory species living under the bark, including the walnut orb-weaver spider *Araneus umbraticus* and tube web spider *Segestria florentina*. Among the myriapods inhabiting dead wood, including the interstices beneath the bark and abandoned larval tunnels, are many centipedes and millipedes.

Also worth mentioning are springtails (Collembola), formerly classified as insects, a rich and diverse group of small forest-dwelling organisms, some of which are associated with dead wood, wood and tree fungi, and tree hollows. These types of environments are also used by members of the related orders Protura and Diplura, which are less common in Poland.

Certain species of velvet worms (Onychophora), a relict type of terrestrial invertebrate not found in Poland, prefer wood with a high moisture content. They have 5 – 15 cm long worm-like bodies, one pair of antennae and numerous legs armed with claws. Onychophorans possess characteristics of both annelids and arthropods. Around 200 species have been described to date, most of which are found in the tropical zones of the southern hemisphere, and some in temperate areas of Australia and New Zealand.

Without any doubt, the most diverse group of species associated with dead wood habitats are insects. Insects are *the* group of organisms exhibiting the greatest species richness in the world. It is estimated that they comprise about 50% of all living species on Earth. Insects include certain groups that, despite their relatively small size, are crucial for the functioning of ecosystems owing to their sheer numbers, and thus exert an enormous influence on the human economy.

Saproxylic insects are the most typical of the forest, which, though rich in species, are the most endangered group. These are insects that at some point in their life cycle depend on dying trees and dead wood at various stages of decay, or on fungi or other insects inhabiting such substrates. One of the orders best represented by saproxylic species are beetles – in central Europe there are about 1,500 species of saproxylic beetles. Gutowski (2006) provides a summary of the current state of knowledge regarding these beetles.

There are more than 70 families of saproxylic beetles in Poland. Most of them belong to the families Cerambycidae (longhorn beetles) (Photos 71-73, Figs. 14-20), Curculionidae (snout beetles, weevils) (particularly the subfamily

Photo 70 (A. Bobiec)
This decayed spruce snag is a valuable habitat for numerous fungi and invertebrates

Photo 71 (J.M. Gutowski)
Pine sawyer beetle *Monochamus galloprovincialis* – a longhorn beetle whose larvae live under the bark and in the wood of pines

Photo 72 (W. Janiszewski)
Akimerus schaefferi – a very rare beetle, whose larvae live inside the dead roots of large, ancient oaks

Scolytinae – bark beetles), Buprestidae (jewel beetles) (Photo 46, Fig. 21), Oedemeridae (false blister beetles), Ptinidae (deathwatch and spider beetles) (Photo 75), Elateridae (click beetles), Scarabaeidae (scarab beetles) (Photo 74), Lucanidae (stag beetles), Staphylinidae (rove beetles), Carabidae (ground beetles) (Photo 76), Anthribidae (fungus weevils), Cucujidae (flat bark beetles), Lymexylidae (timberworm beetles), Nitidulidae (sap beetles), Alleculinae (comb-clawed beetles), Eucnemidae (false click beetles) (Fig. 22) and Tenebrionidae (darkling beetles).

But many saproxylic insects belong to other taxonomic groups. They include heteropterans, e.g. the family Aradidae – flat bugs; hymenopterans, e.g. Siricidae – horntails, certain ant species (Photo 77); lepidopterans, e.g. Cossidae – carpenter moths (Photo 78), Sesiidae – clear-winged moths; mayflies; stoneflies; caddisflies; snakeflies; net-winged insects; psocids; thrips;

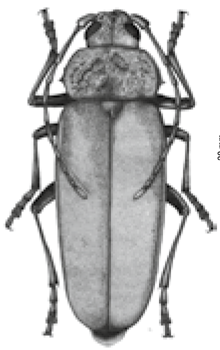

Fig. 14 *Ergates faber* occupies insolated stumps, snags and the lower portions of thick dead pines (M. Waszkiewicz)

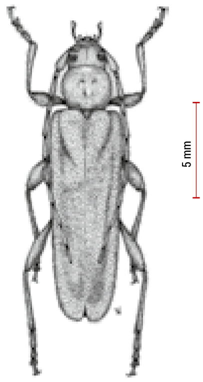

Fig. 15 *Leioderes kollari* – a very rare species associated with old maples (wg Gutowskiego 1988)

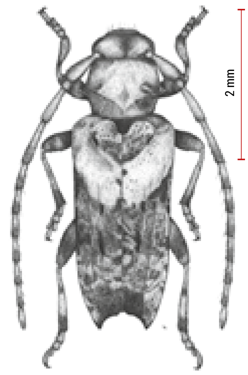

Fig. 16 *Pogonocherus hispidus* – this beetle is associated with the thin branches of many deciduous trees and shrubs (M. Waszkiewicz)

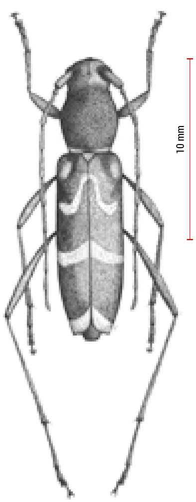

Fig. 17 *Rhaphuma gracilipes*, a very rare beetle, which develops in the branches and boughs of deciduous trees and shrubs (after Gutowski 1992)

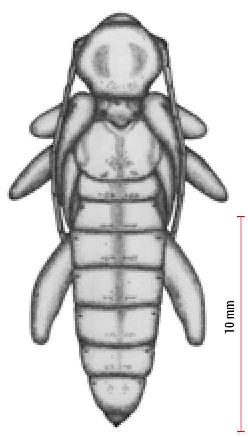

Fig. 18 The pupa of *Callidium coriaceum* – dorsal side; this species is associated with coniferous trees, in particular spruce (after Gutowski 1983)

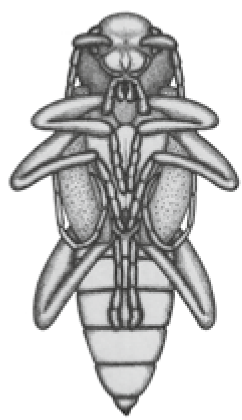

Fig. 19 The pupa of *Callidium coriaceum* – ventral side (after Gutowski 1983)

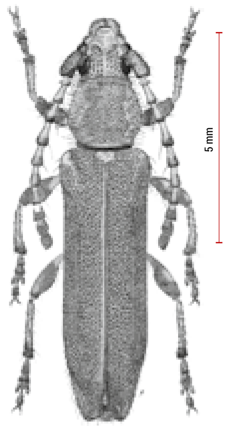

Fig. 20 *Deilus fugax* – a longhorn beetle associated with a distinctive breeding substrate – the dying branches of brooms, small shrubs from the family Fabaceae (after Gutowski et al. 1994)

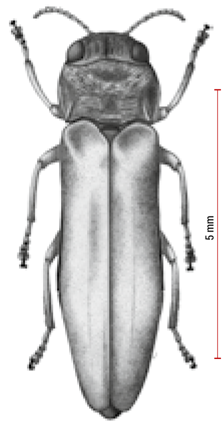

Fig. 21 Jewel beetle *Agrilus pseudocyaneus* – a vanishing species ecologically associated with aspens (after Gutowski 1993)

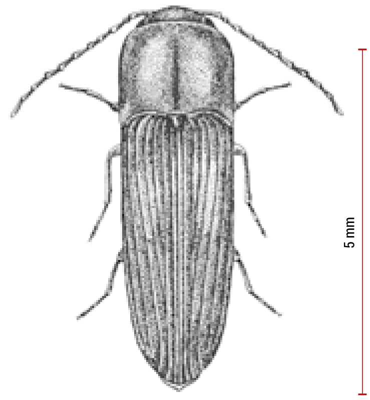

Fig. 22 *Dirrhagofarsus attenuatus* – a very rare, relict species of false click beetle (Eucnemidae) associated with fungi-infested dead wood mainly of alders and aspens growing in damp, often marshy habitats (after Burakowski 1989)

Photo 73 (J.M. Gutowski) Two-banded longhorn beetle *Rhagium bifasciatum* – a species widespread in the mountains and foothills, whose larvae live in snags or stumps left after snapped or felled trees

Photo 74 (J. Walencik) A typically C-shaped larva of the scarab family (Scarabaeidae) in a pupal chamber lying in a rotting wood microhabitat

Photo 75 (J. Walencik) Feeding signs of spider beetles (Ptinidae) on a hornbeam

Photo 76 (J. Walencik)
Blue ground beetle *Carabus intricatus* – a representative of the family Carabidae that commonly hibernates in the decaying wood of stumps, snags, fallen logs or under loose bark

Photo 77 (J. Walencik)
Carpenter ant *Camponotus* sp. on the trunk of a spruce perforated by its feeding tunnels

earwigs; true flies, e.g. the families Asilidae – robber flies (Fig. 23), Syrphidae – hover flies (Photo 79, Fig. 24), Tipulidae – crane flies, Cecidomyiidae – gall midges, Stratiomyidae – soldier flies (Photo 80). For example, there are 72 saproxylic hover fly species in Poland. Several of these, such as buff-tailed bear-hoverfly *Criorhina floccosa*, *Caliprobola speciosa*, *Chalcosyrphus eunotus*, *Criorhina pachymera*, *Mallota cimbiciformis*, *Pocota personata* and *Sphecomyia vittata* are endangered (most of the listed taxa do not have English vernacular names).

Though not found in Poland, termites (Isoptera), a very important group of insects associated with wood, are an insect order comprising some 2,000 species. Termites live mainly in tropical and subtropical regions, but a few species have been found in southern Europe, e.g. yellownecked dry-wood termite *Kalotermes flavicollis* and *Termes lucifugus*. They feed mostly on plant tissues containing large amounts of fibre such as wood, but they also eat other organic substances. Some species excavate their nests (termitaria) in wood. Termites are often treated as "pests", because their activity cause tree mortality and structural damage in buildings.

The greatest richness of saproxylic species is found in natural, unmanaged forest ecosystems, e.g. in the Białowieża Forest or in certain areas of the Carpathians, usually protected as national parks.

Saproxylic invertebrates, i.e. organisms that depend unconditionally on dead wood for their

Photo 78 (J.M. Gutowski)
The characteristically coloured larva of goat moth *Cossus cossus*, which lives in the wood and under the bark of various deciduous tree species

Photo 79 (Z. Kołudzki)
A beautiful specimen of the hover fly *Temnostoma vespiforme* (Syrphidae). Its larvae live in the moist, decaying wood of birches and alders

Photo 80 (J.M. Gutowski)
Larva of a predatory dipteran of the genus *Xylophagus*, which lives under the bark of dead trees

habitat or foraging substrate, or simply prefer dead wood, can be further classified as:

1. **Cambiophages** – organisms that feed on the phloem and live under or in the bark of trees and shrubs (Photo 81, Fig. 25). For these animals, the presence of weakened trees, recently dead trees or trees in the early stages of decay in the ecosystem is crucial. The relationship between cambiophages and recently dead trees arises from the fact that there is scarcely any bark left on trees in more advanced stages of decomposition and that the phloem, which lies directly beneath the bark, is one of the tissues that fungi break down the fastest, making it a short-lived resource.
2. **Saprophages** – organisms that feed on wood, including wood eaters (xylophages – Photo 82) and cariophages (Photo 83). However, it is worth noting that the wood consumed by these insects is often overgrown with mycelia or colonized by bacteria, protozoans and other microscopic invertebrates taking part in the decomposition of the woody tissues. As a result, the presence of particular saprophagous species is increasingly ascribed to the presence of particular species of fungi and bacteria that break down cellulose and, by incorporating nutrients into their bodies, become a kind of concentrated source of food.
3. **Mycophages** – species that consume mainly the mycelia and sporocarps of fungi growing on dead and dying trees. The most notable examples are insects inhabiting the perennial sporocarps known as brackets (conks), which develop on dead or dying trees.

Fig. 23 Robber fly *Laphria ephippium* (Asilidae) – the larvae of this species live as predators in dry standing dead beeches (after Speight 1989)

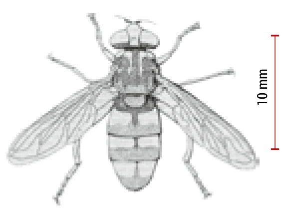

Fig. 24 Hover fly *Milesia crabroniformis* (Syrphidae); its larvae live in the moist, decaying wood at the base of deciduous tree trunks (after Speight 1989)

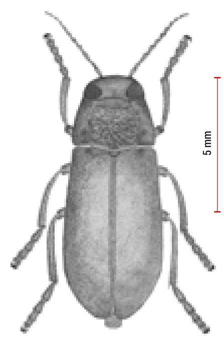

Fig. 25 *Phaenops knoteki*, known in Poland from only a few localities in the south-eastern part of the country, in the Świętokrzyskie Mountains and the Kozienice Forest (after Gutowski and Królik 1996)

Photo 81 (J.M. Gutowski)
Feeding signs of jewel beetle larvae under pine bark

4. **Predators** – organisms indirectly associated with dead wood, and directly linked to organisms inhabiting this substrate. Their larvae and often also adult forms (imagines) feed on other invertebrates, including insects inhabiting coarse woody debris (Photo 84, Fig. 23).
5. **Parasitoids** – organisms whose larvae parasitize saproxylic insects (Photo 85).
6. **Coprophages** – organisms that feed on the excrement of other organisms inhabiting dead wood.
7. **Necrophages** – organisms that feed on dead animals or parts of their bodies in dead wood or in tree cavities and hollows.

Photo 82 (J.M. Gutowski)
The impressive southern European beetle *Morimus asper* funereus is dependent on coarse woody debris from deciduous trees

8. Organisms that live in the sap leaking out on to the bark.
9. Organisms that use wood as a construction material for nest building, e.g. wasps.
10. Organisms that use dead trees or coarse woody debris as nesting sites, e.g. termites, some ants, and wood-boring bees of the genus *Anthophora*.
11. Organisms that use dead wood as a refuge from predators and extreme weather conditions.
12. Organisms that use dead wood as hibernacula.

The most information has been acquired about cambio- and saprophages, as well as those organisms associated with wood and tree fungi, although this knowledge is essentially restricted to insects. Much less is known about other organisms inhabiting these substrates and their interactions. Our knowledge is rather limited as regards, for example, the various organisms that hibernate in strongly decomposed dead wood and under the bark of dead trees.

Saproxylic invertebrates inhabit various dead wood microenvironments, such as dead standing trees, broken trunks, stumps, roots, broken-off boughs and branches lying on the ground, dead boughs in the crowns of trees, trunks of trees leaning against other trees, necroses on living trees, leaking sap, cavities and hollows, soil adhering to the exposed roots of uprooted trees (this is a crucial microhabitat for the development of chestnut click beetle *Anostirus castaneus*), fungi growing inside dead wood, as well as the perennial and annual sporocarps of fungi developing on the surface of wood.

Photo 83 (J. Walencik)
Well-rotted wood provides a habitat for European rhinoceros beetle *Oryctes nasicornis*

Photo 84 (J.M. Gutowski)
A predatory larva (wire worm) of *Melanotus villosus* (Elateridae), a click beetle that lives under bark

Photo 85 (C. Bystrowski)
The parasitoid *Xorides alpestris* (Ichneumonidae), which attacks longhorn beetle larvae living in the wood of deciduous trees and shrubs

The relationships between saproxylic beetles and mites are interesting – from the incidental penetration of feeding sites to an interdependence based on trophic specialization and phoresy. Many mite species feed on wood-decomposing fungi and move from one dead or dying tree to another by attaching themselves to saproxylic beetles. An extreme example of a relationship involving phoretic mites, the species of fungi they feed on and their carriers is hyperphoresy: fungal spores are transferred by mites which themselves are transported phoretically by the beetles. Some mites have specialized organs in which to store the spores (sporothecae), while other species lacking this type of organ carry the spores on their bodies. The European spruce bark beetle *Ips typographus*, common in European forests, is associated with numerous mite species, such as *Urobovella ipidis* and *Dendrolaelaps quadrisetus*, which transfer different species of fungi as the beetle colonizes new trees. Another form of interaction between these organisms is the predation of mites on the eggs of saproxylic beetles.

Saproxylic beetles include a group of species which are more or less dependent on forest fires (pyrophilous species). They exhibit a preference for charred materials. Some species actively move in the direction of burning trees. The pyrophilous beetles of this family include the black fire beetle *Melanophila acuminata*, steelblue jewel beetle *Phaenops cyanea* and *Phaenops formaneki*; the longhorn beetles are represented by *Euracmaeops marginatus* and the genus *Asemum*. Among the species more or less associated with naturally occurring fires in northern Europe are, besides the ones already mentioned, *Agonum bogemanni*, *Agonum quadripunctatum*, *Pterostichus quadrifoveolatus* (ground beetles); *Paranopleta inhabilis* (rove beetle); *Denticollis borealis* (click beetle); *Stephanopachys linearis*, *Stephanopachys substriatus* (false powderpost beetle); *Laemophloeus muticus* (lined flat bark beetle); *Corticaria planula* (mould beetle); *Sphaeriestes stockmanni* (narrow-waisted bark beetle); and *Platyrhinus resinosus* (cramp-ball fungus weevil). A recent study carried out in a burnt area in the Białowieża Forest confirmed the presence of as many as 61 pyrophilous species, including *Stephanopachys linearis* (Photo 86) and *Asemum tenuicorne*, both species new to Poland.

Invertebrates can be found in wood at various stages of decay: hard wood with the bark still present, wood at different stages of decomposition, and very soft rot.

Saproxylic invertebrates are one of the groups of organisms determining the overall level of biodiversity of a forest ecosystem. Being an indispensable and irreplaceable component of its dynamic equilibrium, they participate in many processes taking place within it.

Among other things, invertebrates are involved in:

- the decomposition and mineralization of organic matter (with the aid of macro- and microfungi, bacteria, protozoans),
- limiting the numbers of phytophages, mainly through predation and parasitism,
- preparing nesting and roosting sites suitable for numerous species of birds, mammals and a great variety of invertebrates, e.g. by killing off weakened trees, after which primary hole-nesters, mainly woodpeckers, can excavate cavities in them.

Saproxylic insects, one of the most numerous groups of invertebrates, are themselves important food for woodpeckers and other birds, as well as other animals. At the same time, these insects can become microhabitats for many microscopic organisms, predominantly bacteria, protozoans, and parasitic and symbiotic nematodes, and they can also become carriers of fungal spores. The excrement of insects is consumed by coprophagous species, and their dead bodies become food for necrophagous species. The nutrients contained in the dead tissues are thus restored to the biogeochemical cycle.

Phytophages: herbivorous animals adapted to consuming and assimilating living parts of plants, e.g. leaves, seeds, fruits, the wood of living trees, etc.

Photo 86 (M. Sławski) *Stephanopachys linearis* – an obligate pyrophilous beetle inhabiting the outer bark of pines scorched by fire (after Borowski et al. 2018)

How strongly individual insect species are associated with dead wood resources may depend on one or more stages of their life cycles. The adult forms (imagines) of some species, whose larvae prefer or are dependent upon dead wood, feed on the pollen and/or nectar of flowers, thus contributing to their pollination. That is why members of Cerambycidae, Buprestidae, Scarabaeidae, Cleridae, Mordellidae and Syrphidae are considered to be pollinators, an ecologically important group of organisms. Some saproxylic species cease feeding altogether on metamorphosing into the imagine, so all the resources an individual managed to accumulate during the larval stage spent in dead wood habitats will have a bearing on the remainder of its life.

Saproxylic insects play a particularly important role in the comminution of wood. Larval feeding leads to changes in the structure of wood tissues, and the resulting larval corridors provide a microhabitat for other organisms, which can then find their way into dead trunks and branches. Simultaneously, the spores and hyphae of saprotrophic fungi transferred by insects initiate or accelerate the decomposition of wood. Dying trees and their parts are decomposing continuously because of the activity of saproxylic insects, among other things, as a result of which they do not accumulate in large amounts in the forest. Under the temperate climate conditions of Europe, longhorn beetles are the leaders when it comes to breaking down

Photo 87 (J.M. Gutowski)
The longhorn beetle *Strangalia attenuata*; its larvae live in decaying wood but the imagines pollinate flowers

Photo 88 (J.M. Gutowski)
The longhorn beetle *Alosterna ingrica*, which in Poland is currently found only in the Białowieża Forest

Photo 89 (J. Walencik) *Evodinellus borealis* – its larvae live in the moist wood of spruce, but its imagines feed on pollen and pollinate anemones

and decomposing wood (Photos 90-92, Figs. 27, 28, 32), although jewel beetles (Photo 46, Figs. 21, 25), timberworm beetles, stag beetles, spider and deathwatch beetles (Photo 75), bark beetles, hymenopterans of the family Siricidae and dipterans of the family Tipulidae also play significant parts in this process. In tropical and subtropical regions, the decomposition of wood is influenced mostly by termites, a key group of organisms in intertropical ecosystems.

Worth mentioning are certain saproxylic species inhabiting sap runs on living trees, a highly specific habitat, as they are often rare or endangered. Long-lasting, copious sap exudations from damaged tree tissues are uncommon and occur only locally. This microhabitat usually comes into being on single, fairly isolated, old trees of certain species, mainly elms, oaks, hornbeams and birches (Photo 9). In groves and parks, sap runs sometimes occur on chestnuts. This ephemeral (short-lived) environment is used by certain species of dipterans (hover flies, biting midges) and beetles for their development. The latter group includes the only Polish member of the family Nosodendridae – *Nosodendron fasciculare*. It is a rather small (4-4.5 mm), oval, black beetle with characteristic tufts of red-brownish hairs on the elytra. Rare species of hover flies living in sap run habitats include *Brachyopa dorsata*, *Brachyopa panzeri*,

Photo 90 (J.M. Gutowski) *Leiopus punctulatus* – a very rare longhorn beetle associated with aspens

Photo 91 (J. Walencik)
The larvae of *Prionus coriarius* forage on the underground parts of dead trees, which underscores the importance of roots and tree-throws as microhabitats

Photo 92 (J. Walencik)
This subspecies of the black fir sawyer beetle *Monochamus sartor urussovii* inhabits the taiga, but also occurs on spruces in the Białowieża Forest, at its south-westernmost range boundary

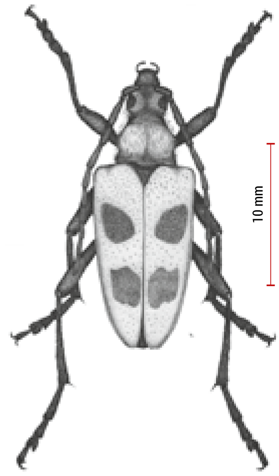

Fig. 26 *Pachyta quadrimaculata*, a beetle belonging to the family Cerambycidae; its larvae develop in the dying roots of pines, but the imagines feed on the pollen of flowering plants (M. Waszkiewicz)

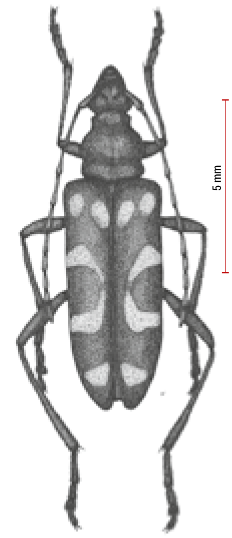

Fig. 27 *Evodinellus borealis* – the only known localities of this boreal longhorn beetle in Poland are in the Białowieża, Borki and Augustów Forests (after Gutowski and Karaś 1991)

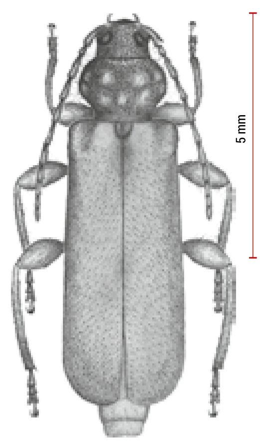

Fig. 28 *Phymatodes pusillus* – a rare longhorn beetle associated with oaks (after Gutowski and Hilszczański 1997)

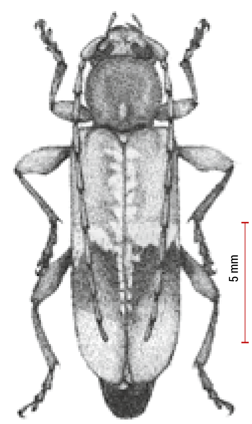

Fig. 29 The longhorn beetle *Trichoferus pallidus* lives in dying oak boughs (after Gutowski 1986)

Brachyopa scutellaris, *Ferdinandea nigrifrons* and *Ferdinandea ruficornis*. The main threat to these insects is that there are fewer and fewer diseased trees exuding sap, mainly because of the removal of such weak trees to meet forest management objectives and the tendency to have a narrow range of species in artificial regenerations. In the case of elms, this is also connected with Dutch elm disease, caused by two species of fungi from the genus *Ophiostoma*, which is causing these trees to die off in European forests.

Dead wood submerged in water is a wholly separate living environment for saproxylic invertebrates (Photo 97). Not much is yet known about this group, but a number of publications from around the world (including Poland) are already available, providing insight into these aquatic species and their interactions with dead wood. Although the species diversity in this environment is far lower than that on land, it is highly specific. Submerged wood hosts, among others, beetles of the family Elmidae (riffle beetles), certain species of dipterans of the families Chironomidae (non-biting midges) and Tipulidae (crane flies), mayflies (Ephemeroptera), caddisflies (Trichoptera) and stoneflies (Plecoptera). The larvae of the wharf borer *Nacerdes melanura* (Oedemeridae) live in wet wood periodically submerged in sea water. Research has shown that 15 obligate and 22 facultative xylophagous species can be found in central European streams. The former group includes the caddisfly *Lype phaeopa*, the beetle *Potamophilus acuminatus* (Elmidae) and the dipteran *Brillia modesta* (Chironomidae).

The species richness of saproxylic insects is positively correlated with the quantity and quality of woody debris in the ecosystem, as well as with the diversity of natural fluctuations in the successional stages of forest development.

The number of saproxylic insect species associated with individual tree species/types varies greatly (data for Germany): oak – 900, birch – 700, European ash – 700, European beech – 600, willow – 600, alder – 500, Norway spruce – 300, lime – 300. With regard to the species inhabiting it, dead wood is indeed often "more alive" than living trees. According to Swedish estimates, for example, there are nearly twice as many insect species inhabiting a dead oak than a living one. The diversity of organisms occupying dead wood has been evidenced by an experiment conducted in Germany, during which 1.7 m^3 of oak and birch wood was kept in a forest for one year under various insolation conditions. 36,000 insect specimens were captured from this wood, including 10,000 coleopterans (beetles) (122 species), 7,500 dipterans and 2,500 hymenopterans.

The immense species diversity of insects developing on tree fungi is excellently exemplified by data collected in the Białowieża Forest, where 4,184 were reared from one sporocarp of the hoof fungus *Fomes fomentarius*; they belonged to 9 families with 11 species from the orders Coleoptera, Lepidoptera, Diptera and Hymenoptera. A handful of rotten wood may contain up to 7,000 microscopic arthropods (mites, springtails), and a 10 m long pine log can host as many as 400 million specimens. Mycetophilous beetles associated with tree fungi are a species-rich group among the saproxylic beetles. In Poland, there are around 500 such species. They are to be found in the following families, *inter alia* Anthribidae, Bostrichidae, Ciidae, Cryptophagidae, Curculionidae (Scolytinae), Endomychidae, Erotylidae, Latridiidae, Leiodidae, Lymexylidae, Melandryidae, Mycetophagidae, Nitidulidae, Peltidae, Ptiliidae, Ptinidae, Scraptiidae, Silvanidae, Sphindidae, Staphylinidae, Tenebrionidae, Tetratomidae, Trogossitidae and Zopheridae.

The Białowieża Forest can boast a greater abundance of unique saproxylic insect species than any other forest in Poland, and probably any other temperate forest in Europe as well. Although not as rich in saproxylic insects as the Białowieża Forest, a few other areas in Poland still harbour rare and endangered species. Certain parts of the Carpathian Forest, especially in the Bieszczady Mountains, the Beskid Niski Mountains, the Sanok-Turka Mountains and the Przemyśl Foothills, as well as larger forest complexes in the Świętokrzyskie Mountains and the Suchedniów Plateau, are important for the conservation of saproxylic organisms at the European level. Research carried out in commercial and protected forests has indicated that the longer a forest remains devoid of dead wood, the more its biodiversity is impoverished. The long history of maintaining a "high standard of hygiene" in European forests by consistently removing diseased and dying trees and dead wood has led to considerable "sterilization" of the ecosystem, reflected by the disappearance of species closely associated with dead wood. It is estimated that over 160 species of saproxylic beetles in Europe, indicators of the state of natural forests, are now rare and disappearing.

Old living trees with dying boughs and branches, hollows and side necroses provide exceptionally rich living environments for many saproxylic insect species. Many of these occur only on the very old trees that incorporate numerous distinctive microhabitats. Among such stenotopic species (having a narrow range of habitat requirements) are *Eurythyrea quercus* (Buprestidae), *Tragosoma depsarium*, great capricorn beetle *Cerambyx cerdo* (Photos 93, 94), *Nothorhina muricata*, *Trichoferus pallidus* (Fig. 29) and *Stictoleptura variicornis* (longhorn beetles).

Some species of insects find suitable conditions for development on ancient trees, which are sometimes 200 or even more years old. They include *Boros schneideri* (Boridae), which lives in dead trees, mainly pines; *Protaetia speciosissima*, inhabiting spacious tree hollows; hermit beetle *Osmoderma barnabita* (Scarabaeidae); and oak click beetle *Lacon querceus* (Elateridae) associated with old oaks. Cavities and hollows of old trees are often occupied by woodland bees and other hymenopterans. Humans have long exploited the tendency of bees to inhabit natural hollows in forests, and semi-wild colonies of these insects in old and often giant oaks and pines were cultivated in the Białowieża Forest until the end of the 19th century. Traditionally, the tops of selected pines in the Dainava Forest (Lithuania) were deliberately damaged in order to induce lateral rather than vertical growth. After about 100 years, such a tree was ready to be utilized as a bee nest. Dead pines also turned out to be highly suitable for this purpose. Today, dead pines with wild bee nests are one of the local attractions of the Dzūkija National Park. Attempts are being made to reintroduce bee colonies to forests in different parts of Poland, albeit at a very small scale (Photo 95). It must be noted, however, that the presence of large honey bee colonies can have a negative impact on the diversity and abundance of other pollinators, as competition for food may reduce populations of wild hymenopterans.

The trophic relationships of saproxylic invertebrates, though still incompletely understood, suggest that most species depend on deciduous trees, especially oaks, but also hornbeams and limes. Moreover, conifers like pines

Photo 93 (J.M. Gutowski)
Visible feeding signs of the great capricorn beetle *Cerambyx cerdo* on an oak

Photo 94 (J.M. Gutowski)
Great capricorn beetle *Cerambyx cerdo*

and spruces are home to a great many species, too. Relatively few saproxylic invertebrate species are found in ash trees. Many saproxylic species are polyphagous and colonize the wood and rot of various tree species. However, there are also many monophages that depend on a single species or genus of tree or shrub. A smaller number of species feeding on a given plant does not necessarily mean that it is less useful for biodiversity conservation, because it may be crucial to a unique species. A good example here is black-berried honeysuckle *Lonicera nigra*, a small bush growing in upper montane spruce forests, whose branches are used by the larvae of the very rare beetle species *Pseudogaurotina excellens*, which is endemic to the western Carpathians. Therefore, it is of the utmost importance that forests contain the wood of all tree and bush species occurring naturally in a given region or ecosystem.

The colonization of dead wood by insects depends on the species of the tree or shrub, its thickness (size), insolation and humidity conditions, but very often also on the type of decomposition that is taking place on a particular part of the tree (trunk, bough, stump). A lot of species have a very narrow range of requirements regarding substrate quality and exhibit an exclusive preference towards wood degraded by either brown, white or soft rot fungi (more detailed data on the types of dead wood rot are given in Chapter 4.1.4). There is also a large group of species with no specific substrate quality requirements that can develop in wood in various states of decay (wet rot, for example).

Dead wood in forest ecosystems or groves situated in agricultural or urban areas provides hibernacula for many invertebrates, not only forest species, but also those living in adjoining meadows, steppes and crop fields. Myriapods, hemipterans, hymenopterans, dipterans and beetles find refuge from severe winter weather under the bark and in the humid wood of fallen logs, stumps, or the low parts of trunks. Dead wood is especially important for predatory ground beetles (*Carabidae*).

Evidence shows that dead wood on the forest floor has a positive effect on the diversity of non-saproxylic insects, e.g. epigeal beetles, but this effect is strongly influenced by the canopy density.

It is worth discussing not only the relationships existing among the groups of organisms inhabiting dead wood, but also those between them and species using other habitats. Saproxylic insects serve as food for numerous species of amphibians, reptiles, birds and mammals, mediating the numbers, and in some cases the distribution, of animals from the higher levels of the trophic pyramid. The overall relationship is simple: the more dead wood in forests, the more saproxylic invertebrates there are, and hence the more numerous and diverse the fauna feeding on the invertebrates. The ultimate beneficiaries of the growing volume of dead wood are also humans: the opportunity to observe rich and diverse groupings of organisms as a form of recreation improves people's mental and physical health and is a source of income from wildlife tourism. More and more

Photo 95 (J.M. Gutowski)
A log hive on an oak in the Białowieża Forest (Browsk Forest District, 2016)

Photo 96 (P. Pawlaczyk)
A dead pine with former (below) and extant (above) wild bee nests in the Dzūkija National Park, Lithuania

studies have demonstrated that contact with nature relatively unchanged by human activities provides the emotional and spiritual input necessary for the proper functioning of our own organisms. The opportunity to admire the natural beauty of the forest landscape, recognized and appreciated by a growing number of walkers and nature lovers, is key to maintaining human health. Moreover, humans as a species depend on the quality of their living environment and the ecosystem services provided by it. The number and quality of the services provided by natural ecosystems are greater than those of other ecosystems that have been altered, disturbed and simplified.

Threats to invertebrates associated with dead wood

With respect to their rarity and distinctiveness, the habitats of saproxylic invertebrates in temperate forests are amongst the most highly endangered in Europe. The habitats of insects foraging on living plants, e.g. leaves, can be re-created within one to several years or decades at most, but the habitats of certain stenotopic saproxylic species may take centuries to regenerate. In Europe, about 40% of saproxylic species are threatened with extinction, and the populations of most of the remaining species appear to be declining.

Although various forms of nature conservation have been implemented in Poland for many years, these organisms still face significant threats. This is especially true for stenotopic species with a narrow ecological tolerance, i.e. species dependent on specific environments like coarse woody debris, which is still lacking in many forests in Europe. But even if we replenish the dead wood stock, a hiatus in the continuous presence of dead wood may still fail to enable the return of certain distinctive species that once became extinct because of the absence of such wood.

Suitable conditions for the emergence and persistence of old and dying trees (shrubs) are currently possible almost exclusively in forests subject to long-term passive conservation, usually designated as strictly protected reserves or strict protection zones within national parks. However, their total area in Poland is very small and far from sufficient to ensure adequate living conditions for saproxylic insects. Moreover, not all habitat types are suitably represented in such areas. The history of the protected area is also important. Reserves established on the remnants of primeval forests will have a different value for the conservation of saproxylic invertebrates from those established in secondary or degraded forests, restored following previous damage or transformation. Until recently, dead wood also used to be removed from nature reserves. Saproxylic insects classified as primeval forest relicts are good indicators of the continuity of natural processes. The lack of these species is a reliable sign that the forest was significantly or completely degraded in the past, either by intensive management practices, which would have temporarily eliminated the habitats of wood-feeding organisms, or by conversion into arable land, and later restored.

The most comprehensive list of European primeval forest relict insect species was compiled by A. Eckelt et al. (2017). It was divided into relicts *sensu stricto* (found only in old-growth forests) and *sensu lato* (found in other types of forests, albeit rarely). Most of the species listed are also present in the Polish fauna. The European Red List of threatened saproxylic beetles (edited by A. Nieto and K.N.A Alexander) was

Polyphages: omnivorous organisms with a broad diet feeding on many different species of fungi, plants and animals.

Monophages: organisms feeding on just one single species or genus of fungus, plant or animal.

published in 2010; it was later revised by Cálix et al. (2018). Species on the European lists are usually rare in Poland as well, although some of them are somewhat more common there. And they may not always be true forest relicts – some species are more frequent in other environments, where old trees are also present, e.g. avenues or parks. The classification of some Polish species as relicts *sensu stricto* can sometimes prove problematic.

The basic condition for the existence of endangered saproxylic species is to preserve the temporal and spatial continuity of their food resources. Because many invertebrate species have very limited migratory capabilities, even a brief interruption in the availability of a substrate suitable for colonization in a given patch of habitat can result in the extinction of a local subpopulation, which is unable to move to more suitable neighbouring habitats. Saproxylic insects do not normally undergo traditional migrations, i.e. periodic long-distance movements, and a population may change its range/distribution over many years almost exclusively through local movements of individuals searching for breeding material during a given breeding season. Monophagous insects are a good illustration of this process: if, on emergence, an adult cannot find a suitable tree or shrub (meeting specific criteria, i.e. an acceptable species, favourable insolation, suitable size, appropriate degree of decomposition of wood and/or cambium) within a few hundred metres, its subpopulation will be at risk of extinction. The darkling beetle *Bolitophagus reticulatus*, inhabiting perennial sporocarps of the hoof fungus and willow bracket *Phellinus igniarius*, does not migrate farther than 30 m from the site where it metamorphosed. The hermit beetle (Scarabaeidae) migrates, on average, up to several hundred metres and is therefore vulnerable to local extinction when suitable trees are distributed too sparsely across the landscape. A large flightless longhorn beetle found in southern Europe and the Balkans – *Morimus asper funereus* (Photo 82) – also exhibits very limited mobility: research carried out in Italian forests has demonstrated that it does not usually travel beyond a few dozen metres (although migrations of almost 500 m have occasionally been recorded as well). The consequence of this reduced mobility is population fragmentation (also evident even when a forest with suitable trees itself becomes slightly fragmented), which is one of the main problems associated with the conservation of this species.

Obligate saproxylic species:
organisms that develop solely in wood.

Facultative (occasional) saproxylic species:
these can develop in a different environment, such as soil, if wood is not available.

Photo 97 (J. Walencik)
Dead wood in a flooded carr in winter

Red List: the accepted name for a list of species threatened with extinction. Modern Red Lists are compiled on scales from local to global, usually under the auspices of the International Union for Conservation of Nature (IUCN), according to standardized criteria.

At present, the following threat categories are used: EX – extinct; EW – extinct in the wild; RE – regionally extinct; CR – critically endangered; EN – endangered; VU – vulnerable; NT – near threatened. Additionally, species whose threat status cannot be assessed for lack of data are classified as DD (data deficient), and those not endangered as LC (least concern).

A "Red Book" is a publication in which an assessment of threat categories is accompanied by broader species descriptions. Red Lists and Red Books do in fact usually have red covers.

Table 5 Primeval forest relicts (Eckelt et al. 2017) and species included in the European Red List of Saproxylic Beetles (Cálix et al. 2018; only categories CR, EN, VU) found in the Polish fauna

Scientific name	Common name (if any)	Relict category according to Eckelt et al. (2017)	IUCN Red List threat category (Cálix et al. 2018)
Rhysodidae			
Rhysodes sulcatus		s. stricto	EN
Histeridae			
Abraeus parvulus		s. lato	
Platylomalus complanatus		s. lato	
Platysoma deplanatum		s. stricto	
Leiodidae			
Dreposcia umbrina		s. stricto	
Staphylinidae			
Abemus chloropterus		s. lato	
Batrisodes hubenthali		s. lato	
Bolitochara lucida		s. lato	
Gyrophaena nitidula		s. lato	
Hesperus rufipennis		s. lato	
Lordithon pulchellus		s. lato	
Lordithon speciosus		s. lato	
Olisthaerus substriatus		s. lato	
Phymatura brevicollis		s. lato	
Quedius infuscatus		s. lato	
Quedius truncicola		s. lato	
Sepedophilus binotatus		s. lato	
Tachyusida gracilis		s. stricto	
Thoracophorus corticinus		s. lato	
Lycidae			
Lopheros lineatus		s. lato	
Cleridae			
Dermestoides sanguinicollis		s. lato	
Derodontidae			
Derodontus macularis		s. lato	
Trogossitidae			
Calitys scabra		s. stricto	
Grynocharis oblonga		s. lato	
Peltis grossa		s. stricto	
Elateridae			
Ampedus cardinalis	cardinal click beetle	s. stricto	
Ampedus elegantulus		s. lato	
Ampedus melanurus		s. lato	
Ampedus suecicus		s. stricto	
Ampedus tristis		s. lato	
Cardiophorus gramineus		s. lato	
Crepidophorus mutilatus		s. lato	
Denticollis borealis		s. stricto	
Elater ferrugineus	rusty click beetle	s. lato	
Ischnodes sanguinicollis		s. lato	VU
Lacon lepidopterus		s. stricto	EN
Lacon querceus	oak click beetle	s. stricto	VU
Limoniscus violaceus	violet click beetle	s. stricto	EN
Podeonius acuticornis		s. stricto	EN

Scientific name	Common name (if any)	Relict category according to Eckelt et al. (2017)	IUCN Red List threat category (Cálix et al. 2018)
Brachygonus dubius		s. stricto	
Cerophytidae			
Cerophytum elateroides		s. lato	VU
Eucnemidae			
Dirrhagofarsus attenuatus		s. stricto	EN
Nematodes filum		s. lato	
Otho sphondyloides		s. stricto	
Xylophilus testaceus		s. lato	
Buprestidae			
Acmaeodera degener		s. stricto	
Buprestis splendens	goldstreifiger	s. stricto	EN
Dicerca aenea		s. lato	
Dicerca alni		s. lato	
Dicerca berolinensis		s. lato	
Dicerca furcata		s. stricto	
Dicerca moesta		s. lato	
Eurythyrea austriaca		s. stricto	
Eurythyrea quercus		s. stricto	
Bothrideridae			
Oxylaemus variolosus		s. lato	
Teredus cylindricus		s. lato	
Teredus opacus		s. stricto	
Cerylonidae			
Philothermus evanescens		s. lato	
Monotomidae			
Rhizophagus brancsiki		s. lato	
Cucujidae			
Cucujus haematodes		s. stricto	CR
Erotylidae			
Dacne notata		s. stricto	
Triplax collaris		s. lato	
Triplax elongata		s. stricto	
Tritoma subbasalis		s. lato	
Cryptophagidae			
Cryptophagus confusus		s. lato	
Cryptophagus quercinus		s. lato	
Laemophloeidae			
Laemophloeus muticus		s. stricto	
Latridiidae			
Corticaria interstitialis		s. lato	
Corticaria lapponica		s. lato	
Corticaria lateritia		s. lato	
Corticaria orbicollis		s. lato	
Latridius brevicollis		s. lato	
Mycetophagidae			
Mycetophagus ater		s. lato	
Mycetophagus decempunctatus		s. lato	
Zopheridae			

Scientific name	Common name (if any)	Relict category according to Eckelt et al. (2017)	IUCN Red List threat category (Cálix et al. 2018)
Colydium filiforme		s. lato	
Lasconotus jelskii		s. stricto	
Pycnomerus terebrans		s. lato	
Rhopalocerus rondanii		s. lato	
Synchita separanda		s. lato	
Endomychidae			
Leiestes seminiger		s. lato	
Ciidae			
Dolichocis laricinus		s. stricto	
Ennearthron palmi		s. lato	
Endecatomidae			
Endecatomus reticulatus		s. stricto	
Bostrichidae			
Lichenophanes varius		s. lato	
Stephanopachys linearis		s. lato	
Stephanopachys substriatus		s. lato	
Ptinidae			
Anitys rubens		s. lato	
Dorcatoma ambjoerni		s. stricto	
Ernobius explanatus		s. lato	
Ernobius kiesenwetteri		s. lato	
Xestobium austriacum		s. lato	
Oedemeridae			
Ditylus laevis		s. stricto	EN
Pythidae			
Pytho abieticola		s. stricto	
Pytho kolwensis		s. stricto	EN
Prostomidae			
Prostomis mandibularis		s. lato	
Melandryidae			
Dircaea australis		s. lato	
Dircaea quadriguttata		s. stricto	
Phryganophilus auritus		s. stricto	
Phryganophilus ruficollis		s. stricto	
Tetratomidae			
Mycetoma suturale		s. lato	
Tenebrionidae			
Allecula rhenana		s. lato	
Bius thoracicus		s. stricto	
Bolitophagus interruptus		s. stricto	
Corticeus bicoloroides		s. lato	EN
Corticeus fasciatus		s. lato	
Corticeus suturalis		s. stricto	
Corticeus versipellis		s. stricto	EN
Eledonoprius armatus		s. stricto	
Hymenophorus doublieri		s. stricto	VU
Mycetochara obscura		s. lato	
Neatus picipes		s. lato	
Platydema dejeanii		s. lato	VU

Scientific name	Common name (if any)	Relict category according to Eckelt et al. (2017)	IUCN Red List threat category (Cálix et al. 2018)
Prionychus melanarius		s. lato	
Tenebrio opacus		s. stricto	
Boridae			
Boros schneideri		s. stricto	
Scarabaeidae			
Gnorimus variabilis	variable chafer	s. lato	
Osmoderma barnabita	hermit beetle	s. lato	
Lucanidae			
Aesalus scarabaeoides		s. lato	
Ceruchus chrysomelinus		s. lato	
Cerambycidae			
Akimerus schaefferi		s. lato	
Alosterna ingrica		s. lato	VU
Cerambyx cerdo	great capricorn beetle	s. lato	
Cornumutila lineata		s. lato	
Evodinellus borealis		s. stricto	
Leptura thoracica		s. stricto	
Necydalis ulmi		s. lato	
Nivellia sanguinosa		s. lato	
Nothorhina muricata		s. lato	
Rosalia alpina	rosalia longicorn	s. lato	
Saperda punctata		s. lato	
Stictoleptura variicornis		s. lato	
Tragosoma depsarium		s. lato	
Curculionidae			
Euryommatus mariae		s. lato	
Gasterocercus depressirostris		s. lato	
Rhyncolus reflexus		s. lato	
Additional species from the European Red List of Saproxylic Beetles (Cálix et al. 2018) not considered as relicts by Eckelt et al. (2017); all species listed below are classified as CR, EN or VU			
Elateridae			
Ampedus hjorti			VU
Eucnemidae			
Hylochares cruentatus			EN
Tenebrionidae			
Corticeus fraxini			VU
Corticeus suberis			EN
Mycetochara roubali			VU
Cerambycidae			
Rhamnusium bicolor			VU
Pachyta lamed			EN
Pseudogaurotina excellens			EN
Euracmaeops angusticollis			CR
Euracmaeops marginatus			EN
Pedostrangalia revestita			VU
Lepturalia nigripes			EN
Anisarthron barbipes			VU
Ropalopus ungaricus			EN
Xylotrechus ibex			VU

Population: a group of organisms of the same species living in a specific area at a particular time;

subpopulation – part of a population in a specific area or environment;

metapopulation – a system in which the population of a species functions as dispersed subpopulations which ensure, to varying degrees, that individuals can move between patches of suitable habitat.

Taking into account the fact that many species occupy only a handful of localities in Poland, and some are known from just a single refuge (some of these species are unique and not found elsewhere in Europe or the world), their loss would be irretrievable. According to estimates, a strictly protected forest reserve with an area exceeding ca 50 ha is able, in theory, to ensure the continuing existence of all stand development stages. This implies that only within such a minimum area is there a high probability of the permanent presence of all wood decomposition phases and DBH classes of dead trees – suitable sites for the development of individual species with diverse environmental requirements – and only when the forest dynamics are "small-scale", dependent on local, rather than widespread, disturbances. In practice, this usually requires several hundred hectares of forest shaped by natural processes.

Even the presence of the best quality forest habitats, but which are otherwise small, sparse and scattered, may not be enough to prevent the extinction of a local population in the long term. For this reason, in order to protect invertebrates associated with dead wood, it is crucial to provide them with a whole network of areas abundant in suitable microhabitats (which most often means passive conservation in national parks, reserves, long-term reference sites, refuges for saproxylic organisms, streamside zones) that would enable individual species to live and migrate across the landscape on a large scale.

In forest areas where species associated with the primary forest once died out, the repopulation of such an area, even though desired habitat features have been restored, may prove impossible owing to the limited mobility of individual species. In this case, the widest possible availability of ecological corridors featuring rich and diverse dead wood resources is a basic condition for the conservation of saproxylic invertebrates.

Many species of invertebrates live in hollows, or more specifically in the rotting wood within them. In terms of biomass, mites are the most abundant, followed by springtails, beetles and dipterans. Many of the members of this ecological group, i.e. insects and other invertebrates like mites, pseudoscorpions and beetles associated with tree cavities and hollows in old oaks, limes, beeches and other veteran trees, are among the least mobile. The small number and wide spread of old trees with hollows in managed forests means that many of these species are becoming extremely rare and in danger of extinction. In Poland, about 100 species of beetles alone live in cavities and hollows; most are considered endangered.

In these environments numerous generations of invertebrates have lived continuously under relatively unchanged conditions for as long as 100 years. Therefore, the most endangered saproxylic species are those unable to disperse beyond short distances, requiring old, but still living, well-insolated trees with hollows, situated either at the forest edge or in open stands. The presence of these rare invertebrate species suggests that these microhabitats have persisted since prehistoric times (both in natural forests periodically affected by disturbances and within "veteran trees" standing in open forests).

A major threat to saproxylic organisms in Poland, as well as in most European countries, are traditional forest management practices. The basic canon of modern forestry is the cultivation of trees, but it also continues to profess the deep-rooted conviction that the forest needs to be sanitized. The concept of "forest sanitary status" is related to the health of the trees that make up a stand and supply a valuable raw material. Silvicultural practices promote the selection of trees with desired technical and commercial features. As a result, the cultivation of trees and the maintenance of an acceptable sanitary status requires the removal of all dead

Beetles (Coleoptera) living in rotting wood microhabitats inside the cavities and hollows of living trees in central Europe

Histeridae – hister beetles (clown beetles)
Abraeus granulum
Abraeus perpusillus
Dendrophilus punctatus
Dendrophilus pygmaeus
Myrmetes paykulli
Onthophilus punctatus
Plegaderus caesus
Plegaderus dissectus
Ptiliidae – feather-winged beetles
Ptenidium gressneri
Ptenidium turgidum
Leiodidae – fungus beetles
Anemadus strigosus
Catops morio
Catops picipes
Dreposcia umbrina
Leptinus testaceus
Nemadus colonoides
Staphylinidae – rove beetles
Batrisodes adnexus
Batrisodes delaporti
Euplectus bescidicus
Euplectus brunneus
Euthiconus conicicollis
Hapalaraea pygmaea
Microscydmus nanus

Quedius dilatatus **– hornet rove beetle**
Quedius infuscatus
Quedius microps
Quedius truncicola
Saulcyella schmidtii
Scydmaenus hellwigii
Scydmaenus perrisi
Thoracophorus corticinus
Trogidae – hide beetles
Trox scaber
Lucanidae – stag beetles
Dorcus parallelipipedus – lesser stag beetle
Scarabaeidae – scarabs
Cetonia aurata – rose chafer
Gnorimus nobilis – noble chafer
Gnorimus variabilis – variable chafer
Osmoderma barnabita – hermit beetle
Protaetia speciosissima
Protaetia marmorata
Protaetia metallica
Valgus hemipterus
Scirtidae – marsh beetles
Prionocyphon serricornis
Eucnemidae – false click beetles
Eucnemis capucinus
Elateridae – click beetles
Ampedus cardinalis – cardinal click beetle
Ampedus elegantulus
Ampedus hjorti
Ampedus nigroflavus
Ampedus rufipennis – red-horned cardinal click beetle
Brachygonus dubius
Brachygonus megerlei
Cardiophorus gramineus
Crepidophorus mutilatus
Elater ferrugineus – rusty click beetle
Ischnodes sanguinicollis
Lacon lepidopterus
Lacon querceus – oak click beetle
Podeonius acuticornis
Procraerus tibialis
Lycidae – net-winged beetles
Platycis minutus
Cantharidae – soldier beetles
Malthinus frontalis
Malthodes pumilus
Dermestidae – larder beetles
Attagenus punctatus
Ctesias serra – cobweb beetle
Dermestes bicolor
Globicornis corticalis
Trinodes hirtus
Ptinidae – spider beetles
Dorcatoma dresdensis
Dorcatoma flavicornis
Oligomerus ptilinoides
Xestobium rufovillosum – deathwatch beetle
Trogossitidae – bark-gnawing beetles
Tenebroides mauritanicus – cadelle
Lophocateridae
Grynocharis oblonga
Peltidae
Peltis ferruginea
Dasytidae – soft-winged flower beetles
Charopus flavipes
Monotomidae – root-eating beetles
Rhizophagus cribratus
Cerylonidae – minute bark beetles
Cerylon fagi
Cerylon histeroides
Cryptophagidae – silken fungus beetles
Cryptophagus confusus
Cryptophagus fuscicornis
Cryptophagus labilis
Cryptophagus micaceus
Cryptophagus pallidus
Cryptophagus quercinus
Mycetophagidae – hairy fungus beetles
Mycetophagus populi
Melandryidae – false darkling beetles
Conopalpus testaceus
Hypulus bifasciatus
Hypulus quercinus
Zopheridae – cylindrical bark beetles
Pycnomerus terebrans
Rhopalocerus rondanii
Synchita variegata
Tenebrionidae – darkling beetles
Allecula morio
Allecula rhenana
Hymenophorus doublieri
Mycetochara axillaris
Mycetochara flavipes
Neatus picipes
Pentaphyllus testaceus
Prionychus ater
Pseudocistela ceramboides
Tenebrio opacus
Uloma culinaris
Oedemeridae – false blister beetles
Calopus serraticornis
Ischnomera caerulea
Ischnomera sanguinicollis
Nacerdes melanura – wharf borer
Aderidae – antlike leaf beetles
Aderus populneus
Euglenes oculatus
Euglenes pygmaeus
Scraptiidae – false flower beetles
Scraptia fuscula
Cerambycidae – longhorn beetles
Alosterna tabacicolor
Anisarthron barbipes
Rhamnusium bicolor
Dryophthoridae – grain weevils
Dryophthorus corticalis
Curculionidae – weevils (including bark beetles)
Cossonus linearis
Phloeophagus lignarius
Phloeophagus thomsoni
Phloeophagus turbatus
Stereocorynes truncorum

and dying trees with irregular growth habits, hosting all kinds of microhabitats inhabited by saproxylic insects and other organisms. Another premise of silviculture is that trees should be cut down and the forest regenerated long before the trees have reached old age. Given this management paradigm, trees are never allowed to grow old enough to start developing a range of tree-related microhabitats and become old, large dead wood of various forms. Constant interventions and removals of trees of low material value, combined with limited opportunities for trees to reach an old age, inevitably impoverish the ecosystem's biodiversity.

There are no "pests" in a natural forest

No discussion of the role of dead wood in the forest ecosystem should overlook the European spruce bark beetle *Ips typographus*. This species contributes to the periodic supply of dead wood in forests, so it is an important component in the dynamics of forest stands with spruce trees. Studies from forests in Bavaria show that there are 173 species of beetles and 181 dipterans associated with spruce wood. In this context, this beetle can be viewed as a keystone species, determining how the whole ecosystem functions.

Sanitary state of a forest: a term used in forestry to describe the degree to which a forest has been cleared of potential food resources for insects and saproxylic fungi – dead and dying trees, windthrows, windsnaps, portions of branches; the sanitary state of a forest is determined by the percentage of dead trees in the total stock of trees. It used to be believed that the better the sanitary state (a small proportion of dead and dying trees), the healthier the forest and the less likely that forest diseases would lead to tree mortality, e.g. large-scale outbreaks of so-called pests – organisms whose ecological role is associated with economic losses. This view is not supported by modern ecological knowledge: rather, research results indicate that a forest with as much biodiversity as possible, similar to a natural forest in this respect, is the most resistant to disturbances.

The european spruce bark beetle populations tend to have cyclical outbreaks that can result in great economic loss wherever its host plant the Norway spruce grows (in Poland these trees grow mainly in the south and north-east of the country). During outbreaks, this species may kill weakened trees, e.g. weakened by fire, windstorms, fungal infection by honey fungus or annosum root rot *Heterobasidion annosum*, and infestation by so-called "primary pests", but also apparently healthy spruces that have experienced prolonged periods of drought, or very old specimens. Together with other associated species, European spruce bark beetles can cause significant spruce mortality.

The hasty removal of trees attacked by bark beetles (with visible symptoms of tunnel boring in the form of boring dust) in the middle of the growing season can cause significant losses in other components of the forest ecosystem. On the other hand, the leaving of such trees in passively protected areas, e.g. national parks or reserves, is contested by foresters managing adjoining forests, who attempt to impose on the managers of protected areas what they believe are necessary measures to combat bark beetle outbreaks. The received wisdom is that the presence of dead trees in nature reserves and national parks has a negative impact on the health of surrounding managed forests. Protected areas are often perceived as "pest hatcheries", but in many cases this could not be farther from the truth: protected areas are a source of natural enemies of the beetles – parasitoids, predators and competitors – which keep their populations at a relatively low level or reduce their numbers during outbreaks.

While bark beetle outbreaks do elicit undeniable negative economic effects (inferior quality timber) in commercial forests, there is a growing awareness of the positive ecological role of this group of insects and its importance to other elements of the forest environment. We are beginning to understand the role that this and similar species play in properly functioning ecosystems in protected areas. However, in Poland, as in most of Europe, this point of view remains controversial, although attitudes towards bark beetles and their importance in shaping natural forests are starting to shift.

Recent findings by forest ecologists and some entomologists show that natural disturbances, including outbreaks of spruce bark beetles and other cambiophages, are not necessarily disastrous for ecosystems, but merely recurring episodes in the natural forest's life cycle (see Chapters 2.2 and 5.3). Periodic massive mortality of conifers happens even in the most primeval parts of the Siberian or Canadian taiga. At most, these events cause damage to a certain number of trees of a certain age and species (usually abundant and common), simultaneously enriching an entire community of other organisms in the forest by changing the structural and species diversity of habitats. Thus, we need to acknowledge the fact that insect outbreaks are inevitable in protected areas. Their intensity and range are positively correlated with the extent to which a given stand (not the whole forest!) deviates from the natural model.

Current theories in forest ecology suggest that outbreaks of European spruce bark beetles and other species are an intrinsic part of the natural processes occurring in dynamic forest ecosystems in which spruce is a prominent component. Hence, one has to accept that outbreaks cannot be eliminated. On the other hand, the changes in ecosystems caused by human activities, and sometimes even attempts to stop outbreaks by cutting down the affected trees, may increase their intensity, frequency and duration.

Photo 98 (J. Gutowski)
This "jewel of the insect world" – the musk beetle *Aromia moschata* – used to be described in old handbooks as a "pest of willows

The European spruce bark beetle in the Białowieża Forest

The European spruce bark beetle is one of the most important cambiophages of Norway spruces in the Białowieża Forest (Photo 99).

Palynological analyses (palynology attempts to describe past vegetation compositions based on the analysis of fossilized pollen preserved in old layers of peat; palynological research is usually carried out in raised bogs) show that spruces have been continuously present in the Białowieża Forest for at least 8,000 years. At the same time, there is absolutely no reason to conclude that cyclical outbreaks of European spruce bark beetles, at times on an enormous scale, have not been an ever-present feature of the ecosystem since spruces first appeared in this forest, and certainly since it became one of the main stand-forming species (around 1,500 years ago). Bark beetle outbreaks may have been more intensive following various natural disturbances (fire, high winds, drought), but would inevitably have declined after a few years.

The history of fires in the Białowieża Forest is crucial for understanding the contemporary population dynamics of the European spruce bark beetle. Fires were quite common between the 1650s and 1850s, especially in coniferous habitats, and were caused almost exclusively by humans, just as they are nowadays. The frequent fires in coniferous habitats meant that spruces were found almost only in fertile oak-hornbeam forests, riparian stands and alder carrs. Hence, spruces were probably absent from mixed and coniferous forests for some 300 years. Unlike pines, spruces are more vulnerable to ground fires, which at the time made it impossible for them to persist in nutrient-deficient habitats. In the first half of the 19th century, Brincken (1826) noted that in the monotonous "sea of pines", which then covered ca 70% of the Białowieża Forest area, there were only a few "green islands" of oak-hornbeam forests, where spruces were also present. He expressed surprise that there were no outbreaks of the European spruce bark beetle. It is safe to assume, then, that before the 19th century the dynamics of the bark beetle populations differed from that of the present day. Later on, as this species became more prominent, its numbers were reported to rise significantly at certain times. The available data indicate there have been at least eight European spruce bark beetle outbreaks in the Białowieża Forest since the late 1800s: 1882-1883, 1919-1922, 1951-1955, 1963-1966, 1983-1988, 1994-1997, 2001-2003, 2012-2019. Most of these events happened in periods when the thermal and hydrological conditions were unfavourable to spruces (growing seasons with low precipitation and high temperatures). The latest outbreak coincided with weather conditions (recurring extreme drought over a number of years) particularly disadvantageous for spruces, which are sensitive to low soil moisture levels, and this is why it lasted as long as it did.

At the turn of the 19th and 20th centuries, the number and extent of fires in the Białowieża Forest decreased, wild ungulates became overpopulated and the mass grazing of cattle began. The resulting gradual shift to pure spruce forests and spruce-dominant stands increased the probability of more frequent and severe spruce bark beetle outbreaks. This was an obviously

Photo 99 (K. Sućko)
The European spruce bark beetle *Ips typographus* – the larval tunnels of this species are habitats for many rare saproxylic insects

anthropogenic effect; because there was a high proportion of fertile habitats, broad-leaved and mixed woodlands ought to have been dominant.

Research on the European spruce bark beetle and its role in the forest ecosystem, carried out in the Białowieża Forest, has yielded interesting and useful information. For instance, the natural drivers of ecosystem resistance, e.g. diverse and numerous populations of predators, parasitoids and fungi, reduced the European spruce bark beetle population by 95.7% in the Białowieża National Park (BNP) but by only 82.5% in Polish managed forests. More recent studies have shown that very high mortality rates of European spruce bark beetles in the strictly protected zones of the BNP result in about half as many adults emerging per unit of spruce bark surface compared to the managed part of the Białowieża Forest.

Large-scale outbreaks of the European spruce bark beetle are triggered by a number of factors causing the increased abundance of weakened spruce trees of a certain age – the usual food resource for this species. The predisposal of spruces to bark beetle attack can be aggravated by long periods of drought (because they have a very shallow root system, spruces are highly susceptible to deficits of soil water), when even a single season (no matter whether this is winter or the growing season) during which trees have to endure water scarcity may cause physiological stress and consequently facilitate fungal infections. Also significant are random events, such as the sudden accumulation of large numbers of windsnaps or clearcutting, which induces severe physiological stress in trees abruptly exposed to direct sunlight and increased evaporation from the soil. Paradoxically, actively combatting a bark beetle outbreak by removing infested trees actually makes it worse. Studies in strictly protected areas indicate that outbreaks tend to stabilize and subside faster in spruce stands attacked by bark beetles where no interventions have taken place.

The basic factors that limit the European spruce bark beetle population in the Białowieża Forest are parasitic hymenopterans, predatory insects, woodpeckers, parasitic fungi and weather conditions. The dispersal and age diversity of spruce trees is an important aspect of the bark beetle's food resources, which limits the growth of its population at least during some stages of an outbreak.

Generally speaking, after 2-3 years, an outbreak is followed by such a high accumulation of antagonistic species (parasites, parasitoids, predators) that the number of beetles drops very sharply, even to below the foraging requirements of the parasitoids and parasites, especially the highly specialized ones. The decrease in the bark beetle population is followed by a decline in the numbers of its natural enemies. Then, for several years after the end of the outbreak, the population of bark beetles gradually increases, and the natural cycle of the dynamics of a forest with large numbers of spruce trees is repeated. Wet, rainy years may delay the timing of the next outbreak, but all the other circumstances that may weaken the trees (mentioned above) may accelerate the outbreak. It is clear, however, that endogenous (internal) factors of the European spruce bark beetle population are not in themselves sufficient to bring about an outbreak. For this, large numbers of stressed trees vulnerable to attack are necessary, but the outbreak usually dies out as a result of biotic factors (parasitoids, predators, fungal pathogens).

Observations of natural mixed forests in temperate climates (including the Białowieża Forest) show that pest control measures do not have much influence on the duration of outbreaks. After three to four years, the outbreak usually breaks down of its own accord, both in strictly protected reserves and also in managed forests, where every effort is made to control the outbreak. The results may be different in artificial spruce monocultures with a unified age profile. Adjacent patches of old, usually passively protected stands abundant in dead trees may play an important role here as refuges of insect populations antagonistic to bark beetles. However, a discussion of the underlying causes and how to minimize the effects of insect outbreaks in commercial forests is beyond the scope of this book, even though it is a major issue from the point of view of rational, science-based forest management. It is worth noting that in recent years ever larger numbers of the sharp-dentated bark beetle *Ips acuminatus* are being recorded in pine stands. Because Scots pine is a dominant species in central European forests, this increased activity of cambiophagous insects has serious economic and environmental implications. In this context, knowledge of the relations between the European spruce bark beetle and Norway spruce could be very helpful in understanding the future dynamics of pine forests.

From a scientific standpoint, European spruce bark beetle outbreaks in the Białowieża Forest, as well as in other near-natural lowland and montane forests, are a normal and necessary component of the functioning of forest ecosystems in which spruce is predominant, but their frequency may increase as the climate changes. Heightened spruce mortality, induced in part by the European spruce bark beetle, is also an environmental response to past anthropogenic disturbances, aiming to restore a state of relative equilibrium. Much like the previous outbreaks, the latest one served to eliminate the unnatural imbalance resulting from direct and indirect human intervention. Despite claims from some quarters, the Białowieża Forest is not dying because of the bark beetles. Neither the spruce as a species nor the Białowieża Forest as a whole are at all threatened by the European spruce bark beetle. An excellent illustration of this assertion is the Bavarian Forest, where stands decimated by a bark beetle outbreak managed to self-regenerate without human intervention. Spruces, which are one of the more than ten main tree species in this complex, can readily renew their stands in suitable habitats. The retreat of this boreal species from some forest environments, also observed elsewhere in central Europe, has more general underlying causes, one of which is climate change.

A bark beetle outbreak is an excellent, selective ecological mechanism, which restores and maintains the natural mosaic structure (both spatially and temporally), as well as the species composition and dynamics of the woodland ecosystems within the Białowieża Forest. Outbreaks are also essential providers of food resources for saproxylic organisms, which are among the most valuable components contributing to its functioning. In Poland, many unique and endangered species associated with spruces, e.g. *Lasconotus jelskii*, *Pytho kolwensis* (Fig. 30), *Bius thoracicus*, *Pityogenes saalasi* and *Orthotomicus starki*, are only found in the Białowieża Forest, or if still found elsewhere, only in a few, widely scattered localities. Outbreaks also supply more food for animals whose diets rely largely on the European spruce bark beetle, e.g. birds (mainly woodpeckers), predatory insects and arachnids, or those which use this species as a living environment (protozoans, nematodes, mites, insects).

Pest control in the Białowieża Forest, carried out according to forest protection guidelines, substantially alters the natural mechanisms of ecosystem dynamics and can impoverish its unique biodiversity. These ecosystems are deprived of the dead spruce wood "due" to them, and even if the average level of dead wood resources in the Białowieża Forest remains high, we lose the opportunity to study the natural processes by which the post-outbreak dead wood resources are integrated into the ecosystem. Moreover, measures aimed at combatting the European spruce bark beetle directly destroy the eggs, larvae and pupae of many other insect species that start to colonize dead spruce trees as soon as the outbreak begins. Peeling, burning or burying the spruce bark containing the eggs, larvae and pupae of these insects, as well as removing them with timber from the forest, can deprive this of specimens of many valuable species (Photos 100-103). Over 100 species of rare beetles alone, not to mention a similar number of endangered fungi species, could be killed during such procedures. It is worth bearing in mind that 50 endangered species of fungi have been confirmed in just one compartment of the Białowieża Forest (see the CRYPTO research programme). No less significant is the inevitable devastation caused by timber harvesting, which has an impact on many other species.

Pathogen:
a biotic disease vector; an organism that causes disease in its host.

Rhysodidae – wrinkled bark beetles
Rhysodes sulcatus (Fig. 31)
Histeridae – hister beetles (clown beetles)
Platysoma deplanatum
Platysoma elongatum
Platysoma angustatum
Plegaderus saucius
Leiodidae – fungus beetles
Agathidium plagiatum
Staphylinidae – rove beetles
Atheta boletophila
Atheta liturata
Atheta pilicornis
Atheta taxiceroides
Atrecus longiceps
Atrecus pilicornis
Bolitochara pulchra
Cyphea curtula
Dadobia immersa
Euryusa castanoptera
Euryusa sinuata
Gyrophaena minima
Gyrophaena nitidula
Gyrophaena pulchella
Gyrophaena strictula
Dropephylla linearis
Ischnoglossa prolixa
Leptusa fumida
Leptusa ruficollis
Olisthaerus substriatus
Phloeopora angustiformi
Phloeopora nitidiventris
Phloeostiba lapponica
Phymatura brevicollis
Placusa atrata
Placusa depressa
Placusa incompleta
Lucanidae – stag beetles
Ceruchus chrysomelinus
Buprestidae – jewel beetles
Buprestis haemorrhoidalis
Buprestis splendens – goldstreifiger
Chrysobothris chrysostigma
Chrysobothris igniventris
Eucnemidae – false click beetles
Hylis procerulus
Elateridae – click beetles
Ampedus elegantulus
Ampedus melanurus
Ampedus praeustus
Ampedus suecicus
Ampedus tristis
Diacanthous undulatus
Lacon lepidopterus
Lycidae – net-winged beetles
Platycis minutus
Lymexylidae – timberworm beetles
Elateroides flabellicornis
Peltidae
Peltis grossa
Nitidulidae – sap beetles
Epuraea angustula
Epuraea fussi
Epuraea muehli
Monotomidae – root-eating beetles
Rhizophagus grandis
Cucujidae – flat bark beetles
Cucujus cinnaberinus
Cucujus haematodes
Cryptophagidae – silken fungus beetles
Micrambe longitarsis
Pteryngium crenatum
Bothrideridae – dry bark beetles
Bothrideres bipunctatus
Endomychidae – handsome fungus beetles
Symbiotes latus
Latridiidae – mould beetles
Corticaria interstitialis
Corticaria longicornis
Stephostethus alternans
Stephostethus pandellei
Ciidae – tree fungus beetles
Cis dentatus
Cis quadridens
Dolichocis laricinus
Melandryidae – false darkling beetles
Abdera triguttata
Phryganophilus ruficollis
Tetratomidae – polypore fungus beetles
Mycetoma suturale
Mordellidae – tumbling flower beetles
Curtimorda maculosa
Zopheridae – cylindrical bark beetles
Lasconotus jelskii
Tenebrionidae – darkling beetles
Bius thoracicus
Corticeus longulus
Corticeus suturalis
Hymenophorus doublieri
Mycetochara obscura
Prostomidae – jugular-horned beetles
Prostomis mandibularis
Boridae – conifer bark beetles
Boros schneideri
Pythidae – log bark beetles
Pytho abieticola
Pytho kolwensis (Fig. 30)
Cerambycidae – longhorn beetles
Callidium coriaceum (Figs. 18, 19)
Etorofus pubescens
Euracmaeops angusticollis
Euracmaeops septentrionis
Evodinellus borealis (Photo 89, Fig. 27)
Lepturobosca virens
Monochamus saltuarius – Sakhalin pine sawyer beetle
Semanotus undatus
Stictoleptura variicornis
Tragosoma depsarium
Curculionidae – weevils (including bark beetles)
Cryphalus saltuarius
Orthotomicus starki
Pityogenes saalasi
Pityophthorus morosovi
Polygraphus punctifrons
Rhyncolus sculpturatus
Xylechinus pilosus

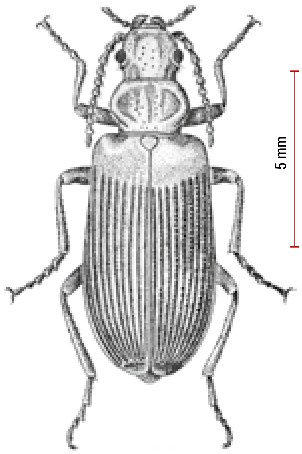

Fig. 30 *Pytho kolwensis* – an extremely rare, boreal species of beetle that lives under the bark of thick, dead spruces (after Burakowski 1962)

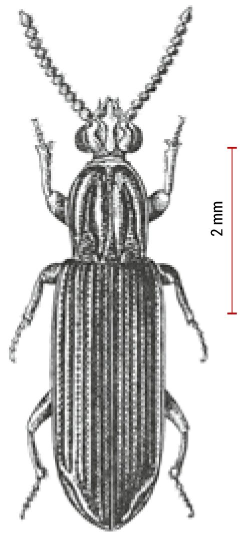

Fig. 31 *Rhysodes sulcatus* – a relict of primeval forests; it lives under the bark and in the rotting wood of thick trees (after Burakowski 1975)

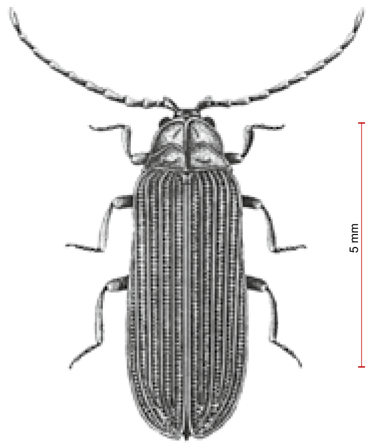

Fig. 32 *Lopheros lineatus* (Lycidae) is known only from Japan, the Far East, central Russia and the Białowieża Forest; it develops in thick, moist, fallen trunks of ash trees (after Burakowski 1990)

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Photo 100 (J.M. Gutowski) Felling and barking this enormous spruce in the Białowieża Forest has annihilated the habitat of many rare species of invertebrates living under the bark and in the wood

Photo 101 (J. Korbel)
Felling, barking and burning the bark of spruce is a common method of combatting the European spruce bark beetle *Ips typographus* in Polish forests

Photo 102 (J.M. Gutowski)
This natural forest is now just a distant memory

Photo 103 (J. Korbel)
Stacks of marketable timber – the effect of the battle against the European spruce bark beetle *Ips typographus* in the Białowieża Forest at the turn of the 20th and 21st centuries

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Chapter 4.1.2: Summary

Thousands of invertebrate species, i.e. nematodes, annelids, arachnids, myriapods, insects, molluscs and others, depend on the presence of dead wood in the forest (saproxylic species). These include the species that live in and under the bark, in the wood, as well as in the rotting tissues of woody plants; species that feed on the hyphae and sporocarps of wood-decomposing fungi growing on dead and dying trees; predatory and parasitic invertebrates feeding on insects and other organisms inhabiting this environment; species that feed on the excrement of other saproxylic animals; scavenging invertebrates that feed on animal remains they find in dead wood or in cavities in old trees; species that live in the sap exuded by trees; species that use wood as a construction material to build their nests; invertebrates that use wood to conceal themselves from predators, to shelter from extreme weather conditions and as hibernacula.

The large majority of saproxylic invertebrates are very rare and endangered. To prevent their extinction, it is necessary to preserve in the forest sufficient numbers of standing dead trunks, fallen logs, standing living hollow trees, tree throws, dead boughs, branches, windsnaps and other diverse forms of dead wood. It is also of the utmost importance to preserve the temporal and spatial continuity of dead wood in all its variety, because saproxylic species often have highly specific and diverse requirements, yet have only a very limited ability to move about the environment.

Invertebrates inhabiting rotten wood in old hollow trees and thick standing or downed trunks of dead trees are among the most seriously threatened with extinction.

Only the passive conservation of large forested reserves (at least a few hundred hectares in size), from which no living, weakened or dead trees are removed, can ensure viable conditions for saproxylic invertebrates and a continuous supply of dead wood.

The Białowieża Forest is Europe's most unique forest and its richest reservoir of saproxylic invertebrates. Certain areas of the Carpathian Forest and some small patches of forest in the Polish lowlands, e.g. in the Augustów, Borki, Bukowa, Knyszyn, Romincka and Świętokrzyska Forests, can also be regarded as natural, crucial to the preservation of biodiversity at the national and central European level.

The cyclical outbreaks of the European spruce bark beetle are an indispensable element of the functioning of natural forests containing substantial proportions of spruce in their stands. By killing weakened trees, spruce bark beetles are nature's perfect selective tool for restoring and maintaining the forest's functional, mosaic structure. The gaps in the canopy thereby produced increase the amount of open space, which provides a variety of warm and insolated habitats required by heliophilous species, and the accumulated dead wood becomes a food resource for other vulnerable saproxylic species that are dependent on spruce.

4.1.3. Algae, liverworts, mosses and vascular plants

Epiphytes: autotrophic plants (but also lichens) that grow on other plants, mainly the trunks and branches of trees, thus gaining better access to light; epiphytes are typical of forest communities, especially wet tropical forests. In the flora of temperate regions, the most common epiphytes are algae, lichens and mosses.

A dead tree provides a distinctive and dynamic habitat for innumerable organisms, including plants. However, its properties change dramatically during the decay process.

When a tree or parts of it fall, they are usually covered completely or partially by bark. The bark is virtually impenetrable to the roots of vascular plants. When their host tree dies as result of falling or snapping, for example, the epiphytes, i.e. the plants (mainly mosses and lichens) that were growing on the trunk and branches of the still living tree, suddenly find themselves in a different environment with radically altered light and humidity conditions. The change in the trunk's position, from the vertical to the horizontal, is in itself enough to trigger the emergence of a mosaic of microhabitats offering a diversity of living conditions for plants colonizing the bark, replacing the more or less homogeneous environment of the upright bole's bark. Among the most distinctive habitats is the nearly horizontal, upper surface of the trunk, sometimes trampled by small animals, which use it as a communication route. The lower surface of the fallen trunk, being close to the ground, offers more shade and usually a higher moisture level. The trunk's original, fairly homogeneous assemblage of epiphytic bryophytes thus has to gradually transform itself into a mosaic of different floral assemblages occupying the newly established niches.

The initiation of the wood decay process, described in more detail in Chapters 3.1 and 4.1.4, forces further environmental changes on the plants inhabiting the dead tree. The bark begins to peel and are some of it usually falls off. The now exposed sapwood surface, initially hard and smooth, gradually becomes a loosely compacted material. Mosses adapted to life on bark now start to be replaced by other species, and the ongoing fungal decomposition of the wood enables the roots of vascular plants to penetrate it.

For plants, however, even very rotten wood is a habitat very different from soil. As described by Mirosława Hackiewicz-Dubowska, an ecologist who studied the flora of decaying wood in the Białowieża Forest in the first half of the 20th century, rotting wood is "a highly humidified substrate, with very loosely bound particles" that cannot offer firm support to rooting plants. Hence, it can be colonized only by certain species with characteristics such as shade tolerance and stem and root morphologies that allow growth and development on and in rotting wood. Touch-me-not balsam *Impatiens noli-tangere*, for example, grows additional adventitious roots, which penetrate the unstable substrate and support it. Other plants, such as herb Robert *Geranium robertianum* and wood stichwort *Stellaria nemorum*, also "prop themselves up" using their lowest leaves.

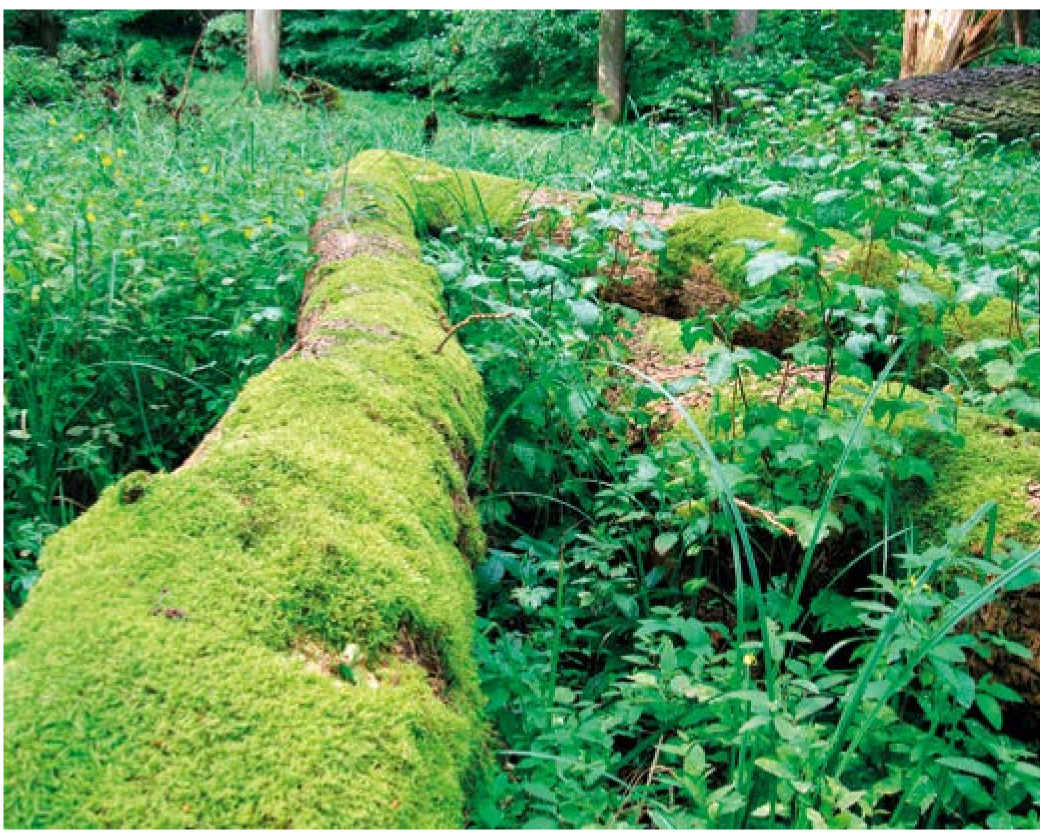

Photo 104 (P. Pawlaczyk) A fallen tree trunk introduces a completely new substrate and a new microhabitat to a marsh in a beech forest (the Bukowa Forest near Szczecin)

Notwithstanding the difficult living conditions, rotting wood is an attractive habitat for vascular plants. Being an empty niche, it is ripe for colonization, and moreover, is a site that usually lies above the surrounding forest floor. Thus, there is no competition from the dense ground cover at such spots, which in addition are less exposed to ground frost, and to inundation in moist and boggy woodlands. In certain types of forests like alder carrs, only the bases of standing and fallen tree trunks provide a suitable habitat for non-hygrophilous plants.

The fall and gradual decomposition of a tree trunk on the forest floor is merely one consequence of a tree's death. The collapse of a tree usually produces a gap in the canopy that instantly changes the light and thermal regimes; it also eliminates local inter-root competition. At the same time as the wood continues to decay, such a canopy gap soon begins to close as a result of the growth of young trees or the expansion of the tree crowns around the edges of the gap. Plants living on a decaying trunk are affected by these processes as well. Unfortunately, however, a detailed discussion on how the ground cover reacts to these phenomena lies beyond the scope of this book.

If the tree died because it snapped, the resulting debris would consist of the fallen part of the trunk and the part of it that remained standing, i.e. the snag, or, if less than ca 1 m high, the stump, both of which are also subject to gradual decay. The soil surrounding the root collar of a decaying snag is locally enriched by the falling particles of bark and wood. Enriched by decaying woody material, this soil may support a luxuriant growth of nitrophilous plants. A characteristic feature of snags in ancient beech forests in Pomerania (north-western Poland) are the wreaths of stinging nettles that surround them.

The site where the crown falls also becomes a very distinctive habitat. Small branches and twigs usually decompose quickly, releasing substances that enrich the substrate. If the forest floor is then exposed to large amounts of sunlight entering through the gap in the canopy, patches of heliophilous vegetation may develop locally.

An even more profound diversification of ecological niches occurs when a tree is uprooted (Photo 105). Such a tree creates a characteristic microtopography of the forest floor consisting of a mound formed from the soil gradually falling from the uplifted root plate, a patch of ground cover that has been shifted to a new position, the fallen trunk and the crown. All of these habitats can be colonized by plants (Fig. 33). Windthrow pits are often moist and may fill up with water; in many types of forest they are the only refuges of hygrophilous and small aquatic plants. Vertical clumps of soil within the displaced root plates or root balls provide microhabitats for specialized mosses and liverworts. These sites, too, gradually change as the material (both the mineral and humus layers) adhering to the root plates is slowly washed away, forming a characteristic windthrow

Hygrophilous species: moisture-loving species; species of moist and wet habitats.

Photo 105 (J.M. Gutowski)
An uprooted spruce in the Białowieża Forest

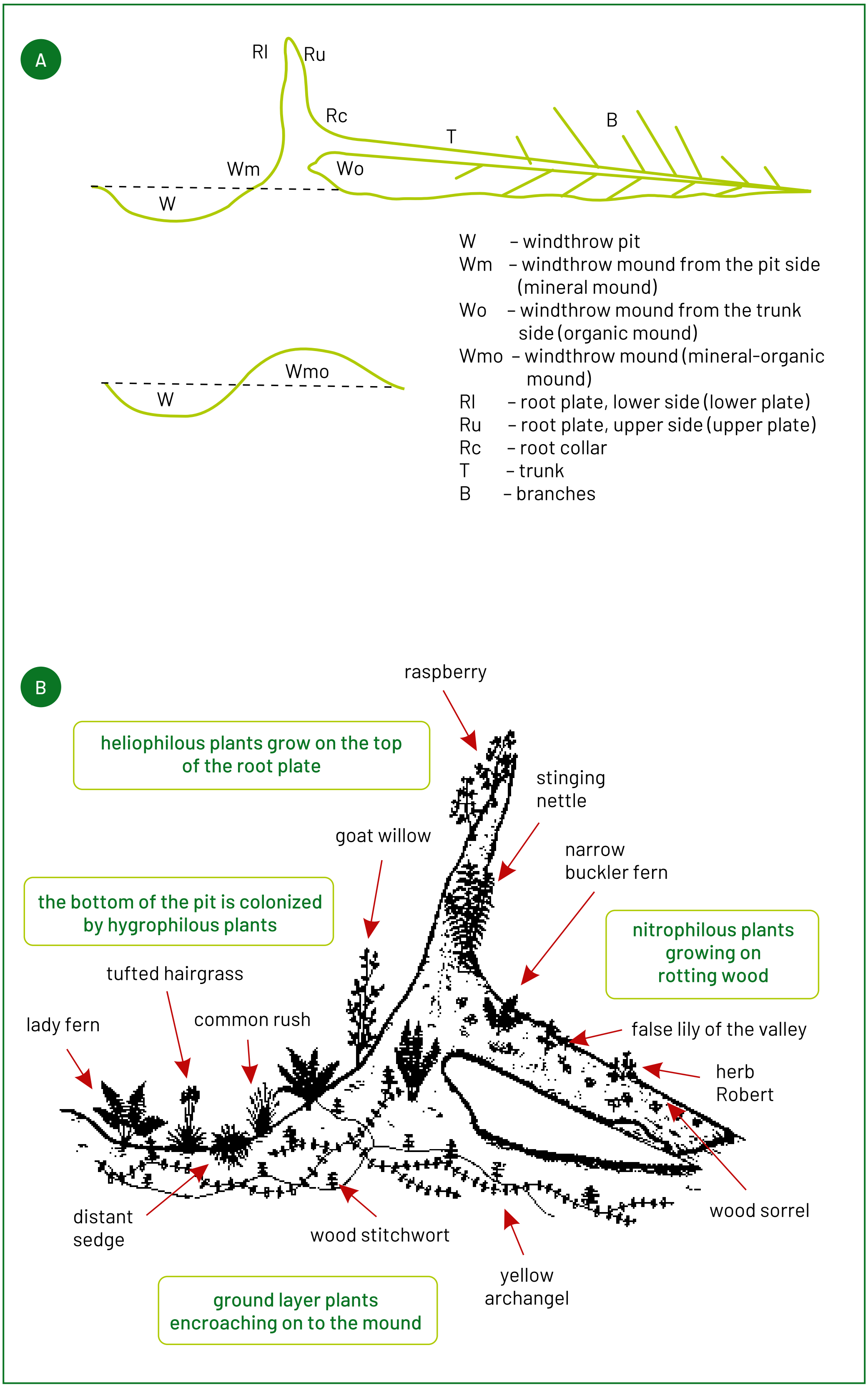

Fig. 33 The division of an uprooted spruce into its constituent parts (A); vegetation on the uprooted system on the floor of a mesic oak-hornbeam forest (B) (M. Bobiec, after Masalska 1997, slightly modified)

mound, while the bottom of the pit fills up with sediment from its edges and locally produced organic matter. Concurrently, the conditions in the whole area below the canopy gap are changing, too, as it imperceptibly closes as a result of the growth of the new generation of trees and shrubs.

Algae – aquatic ecosystems and beyond

Algae are a traditional group of simple, mainly autotrophic (able to synthesize organic compounds from inorganic compounds using solar energy), unicellular, or thalloid (having no distinct organs) organisms, which are currently classified into different kingdoms (bacteria – cyanobacteria, chromists, plants, fungi, protists). A significant proportion of organisms traditionally referred to as algae occupy aquatic habitats, especially standing waters, e.g. ponds, clay pits and lakes. Their distribution in the environment is, however, much wider. Some species, e.g. certain chrysophytes, live in humid spots in forests, like tree hollows and tree bark, and also on the bark of dead trees. Even though their diversity and role in the ecosystem is still poorly understood, assemblages of many very interesting species can be found, particularly in water-filled tree cavities (phytotelmata). For example, one such phytotelma inside an old willow in the Gorce Mountains (southern Poland) was found to host seven species of xanthophytes, among which *Botrydiopsis arhiza* and *Heterotrix bristoliana* were the most abundant, along with protozoans (flagellates) and invertebrates (rotifers and nematodes).

Algae include the green algae (Chlorophyta) commonly found on tree trunks, usually on the northern side. Species belonging to the genus *Trentepohlia* produce spectacular orange or rust-coloured patches on the bark of trees growing on the edges of forests or in groves (Photo 106). They usually colonize living trees, although they can be seen on the trunks of dead ones as well. Many *Trentepohlia* species live in symbiotic relationships with fungi as lichens.

Photo 106 (J.M. Gutowski) Rust-coloured algae of the genus *Trentepohlia* (Chlorophyta) often grow on the bark of the lower parts of trees, both dead and living

Photo 107 (A. Sulej) Pendulous wing-moss *Antitrichia curtipendula*, a rare and protected epiphytic moss often inhabiting the trunks of over 150-year-old, partially moribund hornbeams in the Borki Forest

Liverworts and mosses – dead trees mediate the occurrence of specialized species

The microhabitats that emerge following the death of a tree are of particular importance to the richness of the bryophyte flora (Photos 108-110, Fig. 34). A few dozen moss species can usually be found growing on decaying logs. 75 species of mosses and 24 species of liverworts were found in such habitats in a single compartment of the Białowieża Forest. The species composition of mosses and liverworts (bryoflora) on dead wood obviously depends on the species of the downed tree (ash, spruce and oak logs usually host the greatest abundance, while beech and pine logs are relatively poorer in this regard), but it is first and foremost influenced by the log's stage of decay, humidity, light regime, and the characteristics of the surrounding environment.

The bryoflora of a rotting trunk includes epiphytic species, which had previously been growing on the living tree and now have to live under altered ecological conditions after its death. Understandably and as expected, the viability of these species gradually decreases as decomposition progresses. In the final stages of decay, woody debris is almost completely dominated by ground bryophyte species, most often recruited from the immediate vicinity of the log.

Besides the two ecological groups of epiphytic and ground mosses and liverworts making up the bryophyte community at the initial and final stages of wood decay, there are other, more specialized species for which a rotting trunk is an optimal habitat. Consequently, there are distinctive species compositions of these plants typical of rotting trunks. Even though botanists describe them as separate plant communities, they are nonetheless wholly integrated with the rest of the forest ecosystem. As the wood decays, it is sequentially colonized by leafy creeping liverworts, e.g. flapworts *Jungermannia* and crestwort *Lophocolea*, followed by the loose leafy mats and upright stalks of notchworts *Lophozia*, fingerworts *Lepidozia*, pincerworts *Cephalozia* and earworts *Scapania*, and later by thallose liverworts, e.g. germanderworts *Riccardia*. In the further stages of succession, various species of mosses begin to dominate.

The typical mosses of rotting wood include smooth-stalk feather-moss *Brachythecium salebrosum*, Silesian feather-moss *Herzogiella seligeri*, pellucid four-tooth moss *Tetraphis pellucida*, beautiful branch moss *Callicladium haldanianum*, beaked bow-moss *Dicranodontium denudatum* and shaded wood-moss *Hylocomiastrum umbratum*. Having a very wide ecological spectrum, Cypress-leaved plait-moss *Hypnum*

Photo 108 (J. Walencik)
Moss on the surface of a dead tree (cypress-leaved plait-moss *Hypnum cupressiforme* in the form typifying the phase of expansion into a new habitat)

cupressiforme is usually the most common one, being able to grow on the ground, on stumps, and often also on decaying logs (Photo 108).

Rotting logs are also the preferred habitat of the rare green shield-moss *Buxbaumia viridis*, protected under the EU Habitats Directive and the Natura 2000 network (Photo 111). In the forests around the Turnica Hill in the Przemyśl Foothills, it is found predominantly on decomposing logs in stream valleys, where no tree harvesting normally takes place. This species exhibits similar preferences elsewhere in the Carpathians and in other mountain ranges in Europe. However, in the Bieszczady Mountains, for example, it does not shun forest subcompartments where trees have recently been harvested, as long as there are still spots with a stable, humid microclimate and plenty of dead wood. It has been estimated that the amount of dead wood is the most important environmental variable governing the distribution of green

Photo 109 (J. Walencik) Ample moisture in the lower portion of a standing dead trunk encourages the growth of mosses and fungi (red-belted bracket *Fomitopsis pinicola*)

Photo 110 (K. Zub) Interrupted clubmoss *Lycopodium annotinum*; mosses and lichens on a dead spruce stump

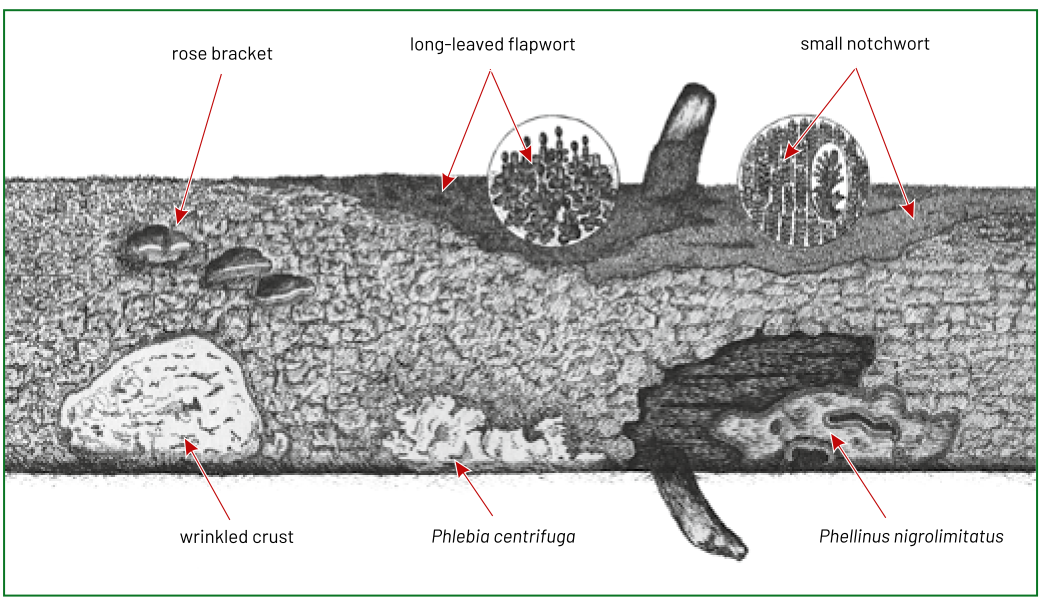

Fig. 34 A log covered in liverworts, mosses and fungi (M. Bobiec)

Photo 111 (M. Książek)
Green shield-moss
Buxbaumia viridis

shield-moss in the Alps, where it is most likely to inhabit forests with 48-61 m^3/ha of dead wood. Even so, in the "Tricity" Landscape Park in Pomerania (near Gdańsk, Sopot and Gdynia, northern Poland), where suitable logs are in short supply, green shield-moss can develop on stumps left after felled beeches or even directly on very humic soil.

Nevertheless, there are not many moss species exhibiting a clear preference for dead wood. The moss species considered to be "natural forest indicators" are usually epiphytes growing on tree trunks. They include *Anacamptodon splachnoides*, slender tail-moss *Anomodon attenuatus*, long-leaved tail-moss *Anomodon longifolius*, *Anomodon rugelii*, rambling tail-moss *Anomodon viticulosus*, pendulous wing-moss *Antitrichia curtipendula*, blunt feather-moss *Homalia trichomanoides*, *Neckera besseri*, flat neckera *Neckera complanata*, crisped neckera *Neckera crispa*, feathery neckera *Neckera pennata*, dwarf neckera *Neckera pumila* and Lyell's bristle-moss *Orthotrichum lyellii*. Shining hookeria *Hookeria lucens*, typically found in old forests, can colonize logs, although it usually prefers shady, humid spots on rocks or on the ground.

Rather more typically epixylic species can be found among the liverworts. One of the most common on dead wood is variable-leaved crestwort *Lophocolea heterophylla*, but dead wood habitats are also preferred by palmate germanderwort *Riccardia palmata*, bog germanderwort *Riccardia latifrons*, greater featherwort *Plagiochila asplenioides* and hairy threadwort *Blepharostoma trichophyllum*, along with certain protected species, e.g. rustwort *Nowellia curvifolia*, chain pincerwort *Cephalozia catenulata*, stipular flapwort *Harpanthus scutatus* and pointed earwort *Scapania apiculate*. The Polish Red List of Threatened Species includes 12 species of xylobiontic liverworts, the rarest of which – Michaux's anastrophyllum *Anastrophyllum michauxii*, Swedish pouchwort *Calypogeia suecica*, horned notchwort *Lophozia longidens*, Heller's notchwort *Crossocalyx hellerianus* – are concentrated in old forests in north-eastern Poland, mainly the Białowieża Forest.

In the oak-hornbeam forests of the Wielkopolski National Park, slightly decomposed, barkless logs of pines, and less frequently oaks, are usually occupied by variable-leaved crestwort, accompanied by cypress-leaved plait-moss and several other species that take root in cracks in the wood. Silesian feather-moss finds an optimal habitat on rotting oak bark and well-decayed pine wood. Bud-headed groove moss *Aulacomnium androgynum* and pellucid four-tooth moss form a typically epixylic association characteristic of well-rotted and cracked wood on the sides of logs. The tops of logs are occupied by bryophyte associations of cypress-leaved plait-moss and mountain fork-moss *Dicranum montanum*, whereas the sides and lower surfaces of logs are overgrown by mosses dominated by curved silk-moss *Plagiothecium curvifolium* or bright silk-moss *Plagiothecium laetum*.

As in the Wielkopolski National Park, decaying wood in the forests of the Roztocze region (south-eastern Poland) is dominated by associations of pellucid four-tooth moss, variable-leaved crestwort and Silesian feather-moss. Decaying silver fir and spruce trunks in this hilly landscape are occasionally occupied by germanderworts (*Riccardia* spp.) and rustwort. In shady ravines, alder carrs and riparian forests, fallen spruce trunks are overgrown by hygrophilous liverworts dominated by Nees' pouchwort *Calypogeia neesiana*. Six other moss communities occur on living trees in these forests.

Epixylism:
Epixylics are organisms (the term is usually applied to plants) that live on the surface of wood. In practice, epixylics are considered to be all plants (tracheophytes and cryptogams) and lichens growing on dead trees at various stages of decay, regardless of whether they occur on wood, bark or humus. As certain species (some mosses) are obligatorily associated with dead wood and do not occur elsewhere, they are referred to as obligate epixylics. Other species can make use of several optional substrates, including wood when it is available. These are facultative epixylics, and all vascular plants occurring on dead wood belong to this group. In general, obligate epixylics are rare and stenotopic, i.e. they can tolerate only a very narrow range of variability in their immediate environment. It is not surprising then that their occurrence is often limited to minimally transformed, near-natural areas.

Epixylic associations of variable-leaved crestwort with pellucid four-tooth moss and Silesian feather-moss are also among the most frequent in the Carpathian Forest in the Babia Góra massif (southern Poland). Clusters of beaked bow-moss and waved silk-moss *Buckiella undulata* are commonly found on decaying logs in this area. In upper montane spruce stands, clumps of Nees' pouchwort and compact cushions of the liverwort Taylor's flapwort *Mylia taylori* grow on logs. A detailed study in the Babia Góra National Park revealed more than 40 different bryophyte communities associated with decaying logs!

A very diverse flora of tree mosses and liverworts with many protected species and "natural forest relicts" has been found in the Bieszczady Mountains and the forest around the Turnica Hill in the Przemyśl Foothills.

In the spruce forests of the Karkonosze Mountains, variable-leaved crestworts grow on every other log. However, beech logs have proved to be much poorer in liverworts than spruce logs.

Moss communities on decaying logs are equally diverse in other natural sites, such as the Białowieża Forest, the beech forests in Pomerania, the forests of the Sudety Mountains (south-western Poland) and the Beskid Sądecki Mountains (southern Poland), not to mention many other forests that have yet to be comprehensively studied.

As mentioned earlier, the decaying wood and bark of dead trees are not the only microhabitats that develop after a tree dies. Although a comprehensive review of the variety of microhabitats would far exceed the scope of this book, the significance that soil disturbed by a wind-thrown tree and upended root plates or root balls have for bryophytes deserves some attention. This kind of microhabitat is often colonized by pioneer bryophyte species, e.g. the mosses juniper haircap *Polytrichum juniperinum* and nodding thread-moss *Pohlia nutans*, or species of the genera *Calypogeia* and *Cephalozia*, before vascular plants become established and come to dominate these sites.

Geobotanical studies conducted in various types of forests have demonstrated that microhabitats related to dead and decaying trees and their immediate neighbourhood make a considerable contribution to the diversity of mosses in the forest ecosystem, because they are biotopes for specialist species and moss communities. In numerous national parks and nature reserves, it is on decaying wood that the most interesting bryophyte assemblages are found.

Epixylic moss communities are integral components of forest ecosystems. Although different types of bryophyte associations growing on dead wood occur in various types of forest and stand developmental phases, woody debris habitats are always among the more important for mosses and liverworts in forests.

The importance of dead wood as a habitat for rare bryophyte species is not restricted to forests with intact natural components and processes. Older pine plantations growing on former deciduous forest habitats sometimes yield sufficient amounts of dead wood to support some of the valuable bryophytes associated with this habitat.

An outstanding example of this relationship was found in a strictly protected area within the Wielkopolski National Park, encompassing a number of artificial pine stands growing in an oak-hornbeam forest habitat. A considerable number of standing dead trees emerged following the 1975-1982 outbreak of the black arches moth *Lymantria monacha*. After 15 years, the decaying logs had developed into a habitat for nine bryophyte associations consisting of a few dozen species. These associations included a rare liverwort – rustwort – not previously known from the Wielkopolska region, and fragile fork-moss *Dicranum tauricum*, for which this was only the eighth locality in Poland. Similarly, even in young and modified mixed forests in Silesia, a random selection of 32 dead logs featured 39 bryophyte species.

However, it is not always the case that an increase in dead wood abundance translates into a more diverse bryoflora. In the Bukowa Forest near Szczecin, the bryoflora of decaying logs was found to be quite poor, even in nature reserves, where there are larger quantities of dead wood. Especially noticeable was the paucity of liverwort species in this area. Similar observations were made in Silesian forests. This is most likely due to the historical lack of continuity in the dead wood supply, caused by former forest management practices, which led to local extinctions of the more specialized species.

The true species richness of bryophytes on dead wood manifests itself in forests of a more natural character, particularly in places with a slightly more humid microclimate and especially on conifer logs.

The abundance of epixylic bryoflora and the diversity of their associations coupled with the occurrence of rare species are recognized indicators of the condition of natural forest ecosystems.

Vascular plants – dead trees form a mosaic of habitats

Unlike the bryophytes, there are no vascular plants that are strictly associated with or exhibit a strong preference for dead wood. That being said, however, the death of trees and the deposition and decay of wood have a profound influence on these plants.

Bryoflora:
the flora of bryophytes; these are mosses (Bryophyta) and liverworts (Marchantiophyta).

Photo 112 (P. Pawlaczyk)
Wood sorrel *Oxalis acetosella* and herb Robert *Geranium robertianum* on the rotting wood of an old hornbeam

Partially or thoroughly rotted wood, though difficult to colonize, is gradually occupied by vascular plants regardless of location. The most distinctive sites inhabited by such plants include rotten wood microhabitats situated high on the trunks of old, but still living trees, even outside of forests. The trunks of old willows, maples, limes and other tree species provide sites where other plants, like raspberries, greater celandines *Chelidonium majus*, common polypodies *Polypodium vulgare*, or even woody plants such as spruces, rowans or birches can germinate and grow. Birches growing out of willows or pear trees rooted in old willow trunks have often been reported. Incidentally, this latter observation may have given rise to the Polish saying "promising pears on a willow" (obiecać gruszki na wierzbie), i.e. to make empty promises.

Photo 113 (J. Walencik)
Plants growing in the hollow of a downed tree: wood sorrel *Oxalis acetosella*, early dog violets *Viola reichenbachiana* and mosses

Photo 114 (J. Walencik)
Plant succession on an uprooted spruce

Much more common and ecologically significant is the colonization of rotting logs by vascular plants, although only a relatively small number of species are involved. In Sweden, for instance, 40 species of vascular plants were recorded on decaying logs, and 47 in the Białowieża Forest (including 8 tree species). The most common plant species growing on decomposed logs in the oak-hornbeam stands in the Białowieża Forest are wood sorrel *Oxalis acetosella* (Photo 113), ground ivy *Glechoma hederacea*, touch-me-not balsam, oak fern *Gymnocarpium dryopteris*, herb Robert, wood meadow grass *Poa nemoralis* and stinging nettle *Urtica dioica* (Photo 114). Two species that are rather rare in the Białowieża Forest – common polypody *Polypodium vulgare* and ivy *Hedera helix* – are found more often on decaying logs than on the ground. Alpine enchanter's nightshade *Circaea alpina* also occurs on this type of substrate in many other forests.

Photo 115 (J. Walencik)
Vascular plants benefit from the moist environment of dead wood

Myrmecochory: dispersal of seeds by ants.

The above species are also components of the usual ground layer vegetation growing on mineral soils in places devoid of dead trees. The colonization of decomposing trunks affects the spatial patterns of their populations, however. In many forests, there are belts of wood sorrel indicating the position of completely decomposed logs or glittering clusters of alpine enchanter's nightshade on rotting wood.

Dead wood habitats are particularly important in marshy and wet forests such as alder carrs. In these environments, fallen logs are one of the very few habitats elevated above the surface of water, which can remain stagnant for many months (Photo 115).

Logs are also colonized by woody vascular plants. Spruce seedlings in particular prefer decaying wood in various types of forests. Therefore, the presence of decomposing wood in ecosystems plays an important role in the regeneration of this species; this will be discussed in Chapter 4.2.5.

Although the elimination of dead wood does not automatically lead to the loss of any vascular plant species, its removal does give rise to a different species composition and spatial structure of the ground layer, and by influencing population processes, indirectly affects the plants involved. A spectacular example can be seen in the beech forests of the Drawa National Park. In the Radęcin sector, where fallen trees are left in place, each canopy gap resulting from the death of an old beech enables the development of a mosaic of ground vegetation dominated by stinging nettles, clumps of oak fern and other components. Its structure is certainly influenced by the presence of beech logs and branches, although other factors, such as the greater amount of light reaching the forest floor, also play an important role. In these openings a variety of herbaceous species can flourish, e.g. wood melick *Melica uniflora*, coral root bittercress *Dentaria bulbifera* and narrow-leaved bittercress *Cardamine impatiens*, typical of Pomeranian beech forests (northern and north-western Poland). In neighbouring forests, from which fallen trees are immediately removed, the vegetation under the canopy gaps is much less diverse and dominated by wood small-reed *Calamagrostis epigejos*, with little regeneration of beech. Similarly, though under the very different ecological conditions of subalpine spruce forests degraded by air pollution, the retention of dead tree trunks leads to the development of a more diverse plant mosaic, in which growing conditions are propitious for spruce and rowan seedlings and saplings. In contrast, where such dead wood is removed from these high-altitude forests, the resulting community inhabiting the gap is completely dominated by hairy reed grass *Calamagrostis villosa*.

The associations between vascular plants and dead wood may also be indirect. The colonization of second-growth forests by typical forest species is dependent on the presence of at least single stumps and dead trunks, because the species covering the forest floor often rely on myrmecochory, and at least some of the species of ants dispersing the seeds build their colonies in dead wood.

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Chapter 4.1.3: Summary

Numerous bryophytes live exclusively in or on dead wood. In most forests, dead wood is a key habitat as regards perpetuating the diversity of this group of plants.

Increasing the amounts of woody debris in both natural and degraded forests usually enhances the species composition of mosses and liverworts, which often includes very rare and interesting species.

Although there are no vascular plant species whose development is strictly related to dead wood, several species readily colonize fallen logs, especially in the later stages of decomposition.

Despite having no direct influence on the presence or absence of vascular plants, dead wood substantially modifies the population structure of these species and affects their regeneration. The lack of dead wood may hamper these processes and make it difficult for many plants, including trees, to regenerate.

4.1.4. Fungi

Phyla of fungi: according to Spatafora et al. (2017) fungi are divided into the following phyla: Basidiomycota, Ascomycota, Mucoromycota, Zoopagomycota, Chytridiomycota, Blastocladiomycota, Cryptomycota, Microsporidia.

Fungi are among the most important, yet underestimated components of forest ecosystems, in which they play important roles. First of all, they form symbiotic relationships with living plants (including trees and shrubs), the most common of which is known as a mycorrhiza (an association between the mycelium and the roots). Secondly, saprotrophic fungi decompose dead organic matter, e.g. dying woody material, and thirdly, parasitic fungi growing in living trees contribute to the formation of various microhabitats used by numerous organisms, including many invertebrates and birds. In addition, fungi perform many other functions, such as increasing the absorption area of roots, thereby enhancing water and nutrient uptake, accumulating nitrogen-based substances, or regulating plant and animal populations. They also participate in soil formation processes, the cycling of chemical elements and the flow of energy through ecosystems. The paramount role of fungi in the environment derives primarily from their widespread occurrence, diversity of associations with other species, great species richness and variety of life forms.

It has been estimated that there are more than 10,000 species of fungi in Poland. The macrofungi (fungi that produce sporocarps or stromata, which can be seen with the naked eye) alone comprise some 5,000 species. Even so, we are far from fully understanding the diversity of this group of organisms and there are quite a few "mycological blank spots" on the map of Poland. Even the fungi of national parks is poorly researched. Between 1,250 and 1,400 macrofungi species on average have been recorded in larger, relatively well-studied forested areas like the Kampinos National Park, the Bieszczady Mountains and the Knyszyn Forest. The diversity of fungi in the Białowieża Forest is particularly noteworthy in this context. During the CRYPTO research programme, 1,380 species of micro- and macrofungi were identified in a 1.5 km^2 area of the Białowieża National Park. At the same time, the number of macrofungi species known to occur in the Białowieża Forest is already in excess of 2,000. Many among them are related to dead trees and shrubs, both standing and fallen, as well as to the woody debris in the form of fallen boughs and branches. We can obtain a fairly good idea of this if we consider that 454 (40%) of the 1,144 species of fungi collected for 25 exhibitions organized so far in the Białowieża Forest (many of which were shown to the wider public) grow on dead wood.

CRYPTO research programme: some of the data presented in this chapter are derived from the CRYPTO research programme carried out from 1987 to 1996 by a team of experts, one of whose aims was to analyse the relationships between the occurrence of non-flowering plants and fungi, and the diversity of forest environments. The research took place in a 144 ha study area in the Białowieża National Park.

Neither a plant nor an animal – why are fungi a separate group of living organisms?

For centuries, fungi were classified as plants. It was not until the 1950s that advances in science enabled researchers to demonstrate considerable differences between fungi and other organisms, and to group them under a separate taxonomic unit equivalent to plants and animals; indeed, it is the latter that fungi are more closely related to. The singularity of fungi is manifested in a wide range of characteristics unique only to them. First of all, no fungus contains chlorophyll and is incapable of synthesizing its own food. Instead, it has to absorb nutrients from the environment. Without exception, therefore, all fungi are heterotrophic organisms. Furthermore, the walls of fungal cells are made from chitin, the substance from which the exoskeletons of insects are also built. As in animals, fungi store energy in the form of glycogen. There are also many anatomical features and means of reproduction that are exclusive to fungi. No wonder, then, that fungi were eventually elevated to a separate kingdom on a par with plants and animals, and that the terms flora and fauna were complemented with "funga".

Mycorrhizae – essential associations supporting the growth and development of trees

In any discussion of fungi growing, for example, on roadsides, in parks, groves and other green spaces, though primarily in forests, brief mention should be made of mycorrhizae. Although such fungi are associated solely with living trees (and other plants), they play a very important role in ecosystems. There are many forms of mycorrhizae, but the one most often come across is the ectomycorrhiza (Photo 116), where the hyphae wrap themselves tightly around the fine roots of trees and penetrate them. This very close association facilitates nutrient exchange. For example, fungi help to transport water containing mineral salts from the soil to the plants and in return use organic compounds produced by their partner tree. Mycorrhizae enable trees to make use of substances present in the soil that are not available to them directly. This is possible because of the enzymes secreted by the hyphae. The protective function of mycorrhizae is equally important. Because hyphae form a dense layer around the tree's roots, many pathogens are denied access to them. Almost every species of tree and shrub enters into a symbiotic relationship with fungi, usually right after sprouting. These are often species-specific relationships, where a given species of fungus coexists with just one particular tree species, e.g. larch boletes *Suillus grevillei* form mycorrhizae exclusively with

Photo 116 (R. Wilgan)
Mycorrhiza formed by *Tomentella bryophila* (Photo 142) – a fungus which develops sporocarps on rotten wood

larches. So it is no coincidence that, in order to find *Leccinum* boletes, we visit aspen and birch stands, whereas we look for saffron milkcaps *Lactarius deliciosus* under pines, false saffron milkcaps *Lactarius deterrimus* under spruces, and scarletina boletes *Boletus erythropus* under beeches and spruces. However, many species of fungi are capable of forming symbiotic relationships with more than one tree species. Moreover, the composition of the mycorrhizal fungi in the roots changes along with the growth of the tree. Mycorrhizae are especially important for seedlings and saplings. That is why it is often difficult to afforest non-wooded land, where the soil is virtually devoid of fungi capable of coexisting with trees. Rodents, for example, play an important part in transferring the spores of mycorrhizal fungi. This applies both to fungi that develop sporocarps on the ground, such as boletes or amanitas, and to mycorrhizal fungi that produce subterranean sporocarps, such as truffles, false truffles or species of the genus *Choiromyces*.

Dangerous, though equally essential associations – fungi causing trees to die and supporting the cycling of nutrients in ecosystems

Apart from the saprotrophic (developing on dead organic matter) and symbiotic fungi, there is a large group of parasitic fungi capable of colonizing living organisms. They develop in the seeds, seedlings, leaves and needles, and also in the trunks and branches of living trees and shrubs. Fungi have plenty of opportunities to colonize a living tree during its lifetime. Any kind of injury to branches or the trunk of a tree (fractures, cuts, scars), or its weakening as a result of drought or unsuitable habitat conditions, for example, clear the way for fungi to develop. Stress factors weaken the resistance of trees, enabling parasites to bypass their defences. The older the tree, the more parasitic fungi can develop on it. The growth of a mycelium inside the tree produces a great number of diverse microhabitats for many organisms. How quickly an infected tree dies depends on a number of factors, e.g. its ability to defend itself and the conditions allowing the parasite to develop, but parasitic fungi grow slowly and can live inside the host's tissues for decades. These species include members of the genus *Phellinus* (bracket fungi), e.g. pine bracket *Phellinus pini*, which most often colonizes 60-80-year-old pines, willow bracket *Phellinus igniarius*, which grows on willows, and robust bracket *Phellinus robustus* (Photo 117), developing on oaks.

Photo 117 (K. Kujawa)
The development of robust bracket *Phellinus robustus* facilitates the decomposition of wood, and thus the excavation of cavities

Photo 118 (K. Zub)
Chicken of the woods *Laetiporus sulphureus* breaks down the tissues of a dead tree

Another common species found on healthy trees is chicken of the woods *Laetiporus sulphureus* (Photo 118) with its impressive yellow sporocarps. This species develops mainly on deciduous trees (willows, ashes, oaks, false acacias, wild cherry and cherry plum) in varying states of health. Sometimes it kills the tree quite quickly, but on the other hand it can live within it for decades. It worth noting that it can take many years from the time a parasitic fungus colonizes a tree until the sporocarps appear, during which time the mycelium grows inside the trunk or bough. In many cases, parasitic fungi continue to decompose wood after the death of the host. Simply put, a tree fungus is considered to inhabit the host tree until its complete decomposition, because, even when no new sporocarps are visible, the living mycelium may still be present in the wood.

Many species of fungi colonize weakened trees, accelerating their death. They include hoof fungus *Fomes fomentarius* (Photo 125), oyster mushroom *Pleurotus ostreatus* (Photo 119), red-belted bracket *Fomitopsis pinicola* (Photo 120) and birch polypore *Piptoporus betulinus*.

Apart from common species, there are also rare and protected species among the parasitic fungi, e.g. short-stemmed cauliflower fungus *Sparassis laminosa*, developing on the roots of oaks, and hen of the woods *Grifola frondosa* (Photo 121). Another important protected species is beefsteak fungus *Fistulina hepatica* (Photo 122), which grows most often on the lower portion of oak trunks. And the trunks of maples, beeches and other broad-leaved trees are where the rare northern tooth fungus *Climacodon septentrionalis* can be found.

Photo 119 (K. Kujawa)
Sporocarps of oyster mushroom *Pleurotus ostreatus* on standing dead ash trees

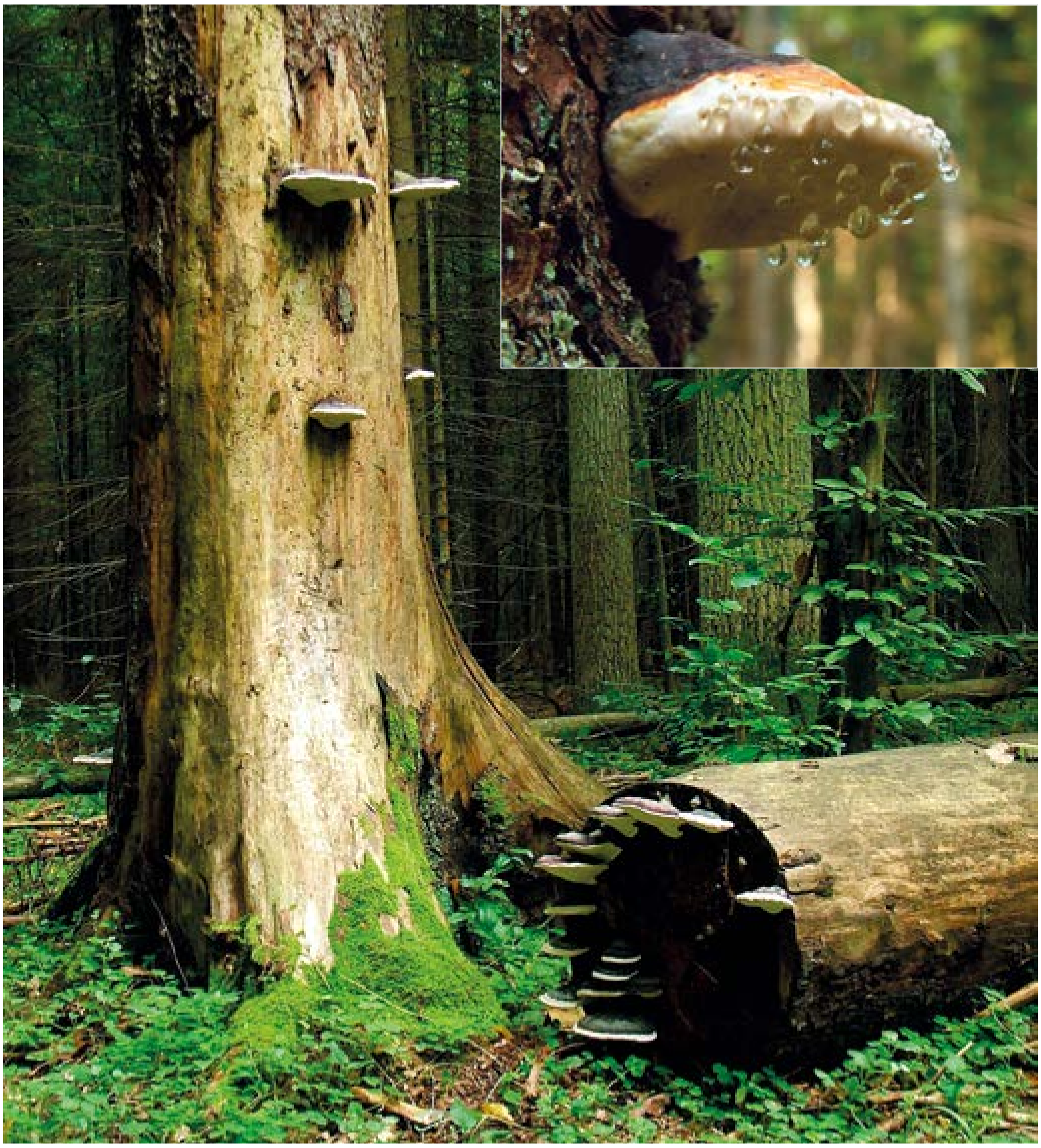

Photo 120 (K. Kujawa)
Red-belted bracket *Fomitopsis pinicola* on a dead spruce – a perennial sporocarp with visible droplets (guttation)

Photo 121 (K. Zub)
Hen of the woods *Grifola frondosa* – a sporocarp growing at the base of a living oak

Photo 122 (J. Walencik)
Ephemeral sporocarps of beefsteak fungus *Fistulina hepatica* at the base of an oak trunk

Types of wood rot: according to Ważny (1968), after Mańka (1981):

- **brown rot** (often called red rot) makes the wood appear darker than the original colour; it is mainly cellulose that is broken down, while the intact lignin is the cause of the red hue (Photo 123); the lack of cellulose causes cell disintegration and the breakdown of the wood into prismatic blocks; the brown or red rot is caused by chickens of the woods (Photo 118), birch brackets and beefsteak fungi (Photo 122), among others);
- **white rot** brings about a paler hue compared to the original colour of the wood; all the wood's components decompose uniformly, but because of the greater amount of cellulose in the wood, it turns the wood pale; white rotted wood crumbles and falls apart into fibrous fragments; the white rot is caused by members of the genus *Phellinus* on broad-leaved trees, hoof fungus (Photos 125, 153) and oyster mushroom (Photo 119), among others;
- **white pocket rot** can be distinguished by the regularly distributed white pockets of cellulose on a dark background; it is caused by pine bracket *Phellinus pini* and annosum root rot *Heterobasidion annosum* s.l., among others.

The breakdown and redistribution of nutrients by saprotrophic fungi

As stated in the Introduction, wood consists largely of cellulose, hemicelluloses and lignin (ca 96-97% of its dry mass), along with waxes, fats, tannins etc., which make up the remaining 3-4% of the dry wood mass. The wood of both coniferous and broad-leaved species contains similar amounts of cellulose but differs in the ratio of hemicellulose to lignin. In general, the former have fewer hemicelluloses and more lignin than the latter. These differences affect the rate at which wood is colonized by various organisms and the characteristics of decomposition specific to particular tree and shrub species. The presence of substances like flavonoids and terpenoids may also inhibit the growth and development of living organisms. Wood-building compounds cannot be directly utilized, and only a few organisms have the ability to decompose them. Carbon bound up in the form of cellulose, hemicellulose and lignin is only available to organisms producing enzymes (ligninases and cellulases) that decompose these compounds. Compared to the green parts of plants, wood contains only a small amount of nitrogen. Only basidiomycetes can cope with this problem. The enzymes produced by the hyphae of these fungi act as catalysts initiating the decomposition of wood cell walls, and the shortage of nitrogen is partially compensated for by the fixing of free nitrogen from the air or partnering with microorganisms.

The visible effect of the activity of both parasitic and saprotrophic fungi is wood decay, which in forest phytopathology is known as rot, i.e. "the chemical breakdown and subsequent decomposition of the woody substance" (according to Mańka 1981). There are many classifications of rot, but one of the simpler ones is that based on decay symptoms: it distinguishes brown rot, white rot and white pocket rot.

Fungal enzymes change not only the structure of wood (Photo 124) but also its chemical composition. As decomposition progresses, the nitrogen content of wood increases and its pH decreases. Fungi also secrete various sugars, acids and proteins that can be utilized by other organisms. Thus, the decomposition of wood primarily involves the activation of nutrient reserves stored by trees and shrubs, which is handled by a veritable army of species specialized to varying degrees. We usually only know about a few of them. The most visible sign that wood has been colonized by macrofungi is the appearance of their sporocarps. However, the crucial part of fungal development takes place out of sight inside the wood tissue. Some species may not produce sporocarps even once during their lifetime on a given log. Many form sporocarps sporadically, perhaps once every few months or years, and may often be very inconspicuous, like those of many ascomycetes (Fig. 127), or short-lived. In some cases, the mycelium may not have the right conditions for producing sporocarps if, for example, it is confined to a small space inside the log. Perennial sporocarps are comparatively easy to spot.

Photo 123 (J. Walencik)
Brown rot of spruce wood

Studies using mycelial isolation and identification or modern molecular methods give a much more complete and up-to-date picture of the composition of the fungal community. This is well illustrated by the results of a study carried out in Sweden, where an old spruce log that had lain on the ground for seven years was found to have been colonized by 15 species of fungi, only three of which actually produced visible sporocarps.

The aforementioned parasitic species have the ability to decompose dead wood saprotrophically. After a tree dies and topples over, these fungi continue to grow and feed by digesting its dead tissues. Here, we can observe an interesting phenomenon, known as geotropism, where the hymenophore of the sporocarps is facing downwards. This can be clearly seen on old sporocarps (conks), which grow at right angles to the trunk. On the standing tree, they were parallel to the ground, but after its fall, new, smaller conks start growing on their undersides, again parallel to the ground, in accordance with the new growing conditions (Fig. 35, Photo 125).

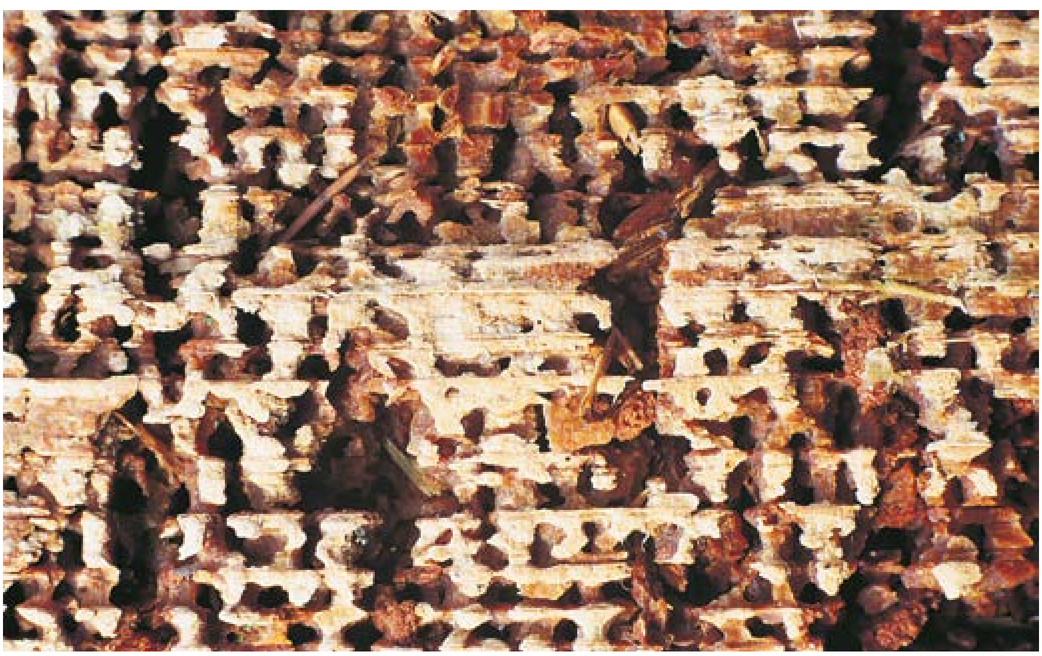

Photo 124 (J. Walencik)
The distinctive structure of spruce wood decayed by fungi

Photo 125 (K. Kujawa)
A perennial sporocarp of a hoof fungus *Fomes fomentarius* that initially developed on a living beech and then continued to grow for many years on the dead, fallen trunk

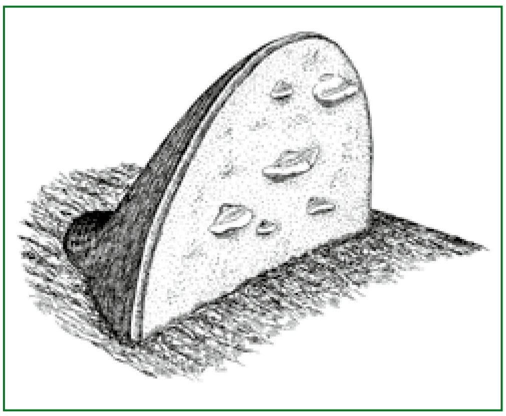

Fig. 35 The sporocarp of red-belted bracket *Fomitopsis pinicola* that originally developed on a standing tree and then adapted to life on a fallen log after the tree fell; new structures grow at right angles to the existing ones, whereas the hymenophore is still oriented horizontally (M. Bobiec)

Dead wood in forests (but also in groves, parks, on roadsides, in old gardens, green spaces, cemeteries, etc.) can exist in a variety of sizes and forms, from fine debris that is easily moved around (twigs, parts of boughs and logs), to coarse debris, i.e. fallen logs and standing trunks, snags and stumps, the remnants of felled and snapped trees and shrubs. Each of these forms offers fungi different conditions of humidity, insolation or durability. Therefore, even a single log can have a mosaic of micro-habitats with quite different microclimates. The diversity of woody material translates into the

Photo 126 (K. Zub)
A perennial sporocarp of artist's bracket *Ganoderma applanatum*

Photo 127 (K. Kujawa)
Green elfcup *Chlorociboria aeruginascens* decomposes the wood of deciduous trees; its mycelium gives the wood a distinctive bluish-green colour; its sporocarps appear for a short time, are very small – a few millimetres in size – and are often hidden in crevices in the wood

species diversity of tree fungi. Twigs, pieces of bark, chips and small pieces of wood derived from thicker branches offer little food for fungi and are usually decomposed by species with small sporocarps, many of which belong to the genera *Marasmius* (parachute) (Photo 128), *Mycena* (bonnet) (Photo 129) or *Tubaria* (twiglet). Scarlet elfcup *Sarcoscypha austriaca*, one of the earliest fruiting fungi (it can be found during mild winters and in spring) and the most common elfcup in Poland, also develops on small pieces of wood (Photo 130).

The assemblage of fungi inhabiting dead wood is significantly influenced by a tree's life history, e.g. the species composition of fungi will be different on a tree suddenly blown over by the wind from that on a standing, slowly dying tree. The phloem and sapwood of recently broken branches and snapped trunks offer more nutrients than just cellulose and lignin. This, therefore, is where we find pioneer decomposers, i.e. organisms that are unable to decompose cellulose and lignin, but can take up the simple sugars, starch and proteins contained in the wood of recently dead trees. These

Photo 128 (K. Kujawa)
Collared parachute *Marasmius rotula* decomposes the wood of small branches

Photo 129 (K. Kujawa)
Clustered pine bonnet *Mycena stipata* (its sporocarps smell of chlorine) decomposes both the coarse and the fine woody debris of coniferous trees

include two species of ascomycetes – common tarcrust *Diatrype stigma* and birch blackhead *Diatrypella favacea* – and two woodwart species – beech woodwart *Hypoxylon fragiforme* (Photo 131) and *Hypoxylon howeanum*. Occasional parasites, such as coral spot *Nectria cinnabarina*, also use this type of substrate. The easily absorbed nutrients are quickly consumed, and the wood is subsequently colonized by other species able to decompose more complex compounds. In the Białowieża Forest, 142 species, including 83 ascomycetes and 59 basidiomycetes, were recorded on the bark of fallen dead trees and branches during CRYPTO. Among the ascomycetes exhibiting a strong relationship with this type of substrate are black bulgar *Bulgaria inquinans* (Photo 132) and the protected *Holwaya mucida* (Photo 150). 10 species of

Photo 130 (K. Zub)
Scarlet elfcup *Sarcoscypha austriaca* – a beautiful fungus whose sporocarps can be encountered in early spring; its mycelium decomposes fine woody debris that is usually buried in the substrate

Photo 131 (K. Kujawa)
Beech woodwart *Hypoxylon fragiforme* develops on beeches – like other woodwarts, it is a pioneer decomposer

Basidiomycota were found exclusively on this substrate. In a study of 30 wind-broken trees (birches, oaks and pines) in the Kampinos National Park, conducted one year after the blowdown, 62 species of macrofungi were found, including numerous species classified as pioneers of wood decay.

Fallen logs are a typical habitat for fungi associated with dead wood. The CRYPTO survey in the Białowieża Forest yielded 282 species of fungi, 109 of which were obligatorily dependent on fallen logs. Owing to the different water content in logs lying directly on the ground, significantly more fungi were associated with them than with logs leaning on stumps or root plates, for example.

Among the 90 species of ascomycetes found during CRYPTO on fallen logs, 38 occurred exclusively on this substrate. Woodwarts were the most common: birch woodwart *Hypoxylon multiforme*, rusty woodwart *Hypoxylon rubiginosum*, *Hypoxylon serpens*, dead moll's fingers *Xylaria longipes*, common eyelash *Scutellinia scutellata* (Photo 136), pedicel cup *Peziza micro-*

Photo 132 (J. Walencik)
Black bulgar *Bulgaria inquinans* on the trunk of a fallen hornbeam

Photo 133 (J.M. Gutowski)
Hericium flagellum – a protected species – on a fallen fir log

Photo 134 (J. Korbel)
The spectacular sporocarps of fungi growing on fallen beech trunks sometimes grow to enormous sizes

Photo 135 (J. Walencik)
Sporocarps sometimes occur en masse on fallen trees – an inkcap *Coprinus* sp. on a downed spruce

Photo 136 (K. Kujawa)
Common eyelash *Scutellinia scutellata* usually develops on moist pieces of wood

pus and brittle cinder *Kretzschmaria deusta*, often growing in company with mosses on the large trunks of broad-leaved trees. As many as 192 species of basidiomycetes were found on fallen logs, 67 of them being restricted to this type of substrate. These logs also hosted four species belonging to other systematic groups. It is primarily the ability of this group of fungi to break down cellulose and lignin that gives them a competitive advantage over other organisms inhabiting dead wood, hence the great diversity of species recorded here. Fungal species developing annual sporocarps, which may be visible for many weeks or months, were quite abundant on the trunks of dead trees. These included brownflesh bracket *Coriolopsis gallica*, blushing bracket *Daedaleopsis confragosa*, *Dentipellis fragilis* and fragrant bracket *Trametes suaveolens*, as well as silverleaf fungus *Chondrostereum purpureum*, other species of the genus *Trametes* (Photo 138) and a great many *Stereum* species. Spectacular fruiting bodies that persist for many weeks are produced by the protected coral tooth fungus *Hericium coralloides*. Also abundant on this type of substrate were the genera *Pluteus* (shield) – 11 species, *Pholiota* (scalycap) – 5 species (Photo 137), *Lentinellus* (cockleshell) and *Crepidotus* (oysterling) – 3 species each. Species with perennial sporocarps were the most abundant. They belonged to many genera, notably *Ganoderma* (bracket) (Photos 126, 160), *Hymenochaete* (crust, curtain

Photo 137 (K. Kujawa)
Shaggy scalycap *Pholiota squarrosa* – its sporocarps often appear on weakened trees and continue to grow after their death

Photo 138 (K. Kujawa) Turkeytail *Trametes versicolor* – one of the fungi with medicinal properties that is being increasingly cultivated

crust), *Fomitopsis* (Photo 144), *Gloeophyllum* (Photo 145) and *Daedalea*.

During a more recent field survey carried out in the Białowieża National Park involving 32 oak logs at different stages of decomposition, sporocarps of 187 fungi species were found, including protected (*Hapalopilus croceus* and beefsteak fungus – Photo 122) and threatened ones, such as ceramic fungus *Xylobolus frustulatus* (Photo 158) and *Antrodia gossypium*.

Stumps of felled trees and snags with broken tops offer far less favourable conditions to fungi than fallen logs, because of the low levels of humidity, particularly in the upper parts, and the intensive insolation. The fungi found on this substrate during CRYPTO included 10 species of sac fungi, e.g. brittle cinder, and representatives of the genus *Xylaria*, i.e. dead man's fingers *Xylaria polymorpha*, dead moll's fingers (Photo 139) and candlesnuff fungus *Xylaria hypoxylon* (Photo 140). Only 6 out of the 58 basidiomycetes found on this substrate occurred exclusively on this form of dead wood.

Equally difficult conditions for fungal development occur on the trunks of standing dead trees or snags. During CRYPTO it was found that the trunks of spruces were the most frequently colonized, followed by alders and

Photo 139 (K. Kujawa) Black stromata of dead moll's fingers *Xylaria longipes* on a moss-covered log

Photo 140 (K. Kujawa)
Candlesnuff fungus *Xylaria hypoxylon* is often found on the stumps of deciduous trees

birches. Apart from a few Acsomycota, only 18 species of Basidiomycota were recorded on standing dead trees, although most of them were also common on other substrates, for example, hoof fungus (Photos 125, 153), red-belted bracket (Photo 120) and dryad's saddle *Polyporus squamosus*.

The relationships of fungi with dead wood range from strong to weak. As discussed earlier, certain parasitic species may function as saprophytes after the death of the tree. Similarly, many species growing on strongly decomposed wood can also grow on the leaf litter, e.g. fluted bird's nest *Cyathus striatus* (Photo 141) and numerous species of *Mycena*. Conversely, some of the fungi most often recorded growing on leaf litter can also grow on strongly decomposed wood. Moreover, certain mycorrhizal fungi normally found growing on the soil, can do so on rotten wood or still quite intact pieces of wood. Among them, we find common earthball *Scleroderma citrinum*, curry milkcap *Lactarius camphoratus* and the very common bay bolete *Xerocomus badius*. What is more, there are species of mycorrhizal fungi, e.g. of the genus *Tomentella* (Photos 116, 142), which are incapable of producing sporocarps in the absence of wood.

Photo 141 (J. Walencik)
Cup-shaped sporocarps of fluted bird's nest *Cyathus striatus* sometimes develop on bits of wood lying on the ground

Associations between fungi and different tree species

Fungi tend to prefer particular tree species. Of the 11 tree species analysed in this context during CRYPTO, birches hosted the largest number of fungi (68 species) and rowans the fewest (only 5) (see Table 6).

A study carried out in the Kashubian Landscape Park, focusing exclusively on aphyllophorioid fungi, showed that out of 31 species of trees and shrubs, this group of fungi was the most abundant on beeches (149 species), then on spruces (125 species) and pines (100 species). The lowest numbers – 1 species each – were recorded on apple, bird cherry, cherry plum, black elder and elm trees.

In light of this, it ought to be possible to draw up measures to support the populations of particular fungi species by planting appropriate trees. This applies in particular to trees outside of forests – on roadsides, in groves, parks, green spaces, cemeteries, etc. A study carried out in the Wielkopolska region regarding substitute habitats for the protected hen of the woods, which occurs naturally in oak-hornbeam and oak forests, found that this species emerges spontaneously on very old oaks growing in village parks, groves and roadside avenues. This was also the case for another protected species – beefsteak fungus (Photo 122) – which was found in groves and village parks, but it has been recorded in urban green spaces as well. Knowledge of the fungi that inhabit particular tree species can help maintain populations of rare species as well as the species diversity in managed forests and wherever the deficit of dead wood is a significant yet neglected problem, e.g. in cities and in rural landscapes beyond forested areas. The results of a study carried out in a park on the outskirts of the city of Poznań, where 333 species of fungi were found (on various substrates), 19% of which were rare species, highlight the importance of parks in preserving biodiversity in urban environments

Table 6 The number of epixylic fungi species occurring on particular tree species in the Białowieża Forest (according to Chlebicki et al. 1996; modified)

Tree species	Total number of epixylic fungi species	Species occurring exclusively on a given tree species	Number of rare species of fungi
black alder *Alnus glutinosa*	59	7 (+4 species showing a strong preference)	53
birches *Betula pendula* + *Betula pubescens*	68	9	59
European hornbeam *Carpinus betulus*	54	5	45
Norway spruce *Picea abies*	54	18	50
Pedunculate oak *Quercus robur*	61	7	55

Photo 142 (T. Leski) A flat, spread-out sporocarp of *Tomentella bryophila*. In order to form sporocarps, this mycorrhizal fungus requires both a symbiotic relationship with tree roots and the presence of dead wood

Photo 143 (A. Szczepkowski)
Bondarzew's polypore *Bondarzewia mesenterica*, a species closely associated with firs

and the need to move away from traditionally accepted methods of caring for green spaces, which include the removal of dead wood. The maintenance of avenues likewise requires a change in attitude towards dead wood. Whenever the felling of dying trees is deemed necessary for reasons of safety, a tall stump (1.1-1.3 m) should be left to decompose naturally.

There are many examples of specific tree-fungi associations, one of the best known being the exclusive occurrence of birch polypore on birches. Oaks, in turn, are preferred by the aforementioned protected beefsteak fungus, but also by oak polypore *Buglossoporus quercinus*, as well as by species such as robust bracket (Photo 117) and oak mazegill *Daedalea quercina* (both unprotected). *Holwaya mucida* (protected) can be found on limes (Photo 150), the wood of pines is decomposed by pine brackets, while larches are associated with the extremely rare and protected agarikon *Fomitopsis officinalis* (Photo 201) and firs with the protected *Hericium flagellum* (Photo 133) and Bondarzew's polypore *Bondarzewia mesenterica* (Photo 143). Many species are exclusive to pine wood, e.g. the protected rose bracket *Fomitopsis rosea* (Photo 144), common species such as anise mazegill *Gloeophyllum odoratum* (Photo 145), jelly tooth *Pseudohydnum gelatinosum* and pinewood gingertail *Xeromphalina campanella*, and the rare benzoin bracket *Ischnoderma benzoinum*. Spruce trees are also where extremely

Photo 144 (K. Zub)
The protected rose bracket *Fomitopsis rosea* on a spruce log

Photo 145 (J.M. Gutowski)
Anise mazegill
Gloeophyllum odoratum
grows only on spruces

rare species, known from single localities, are found. These species are associated with natural forests and, in order to thrive, require conditions resembling those of primeval forests. Such fungal rarities associated with spruce include protected species – *Amylocystis lapponica* (Photo 206) and orange sponge polypore *Pycnoporellus alboluteus* (Photo 156) – as well as others that are not protected, like *Sarcoporia polyspora*, *Phellinus ferrugineofuscus*, *Postia minusculoides* and *Asterodon ferruginosus*.

However, a lot of species of fungi can flourish on trees of different species, e.g. the protected coral tooth fungus and bearded tooth *Hericium erinaceus* can be found on beeches, oaks, maples, elms and birches. Examples of more common fungi capable of inhabiting a wide range of substrates include widespread species with conspicuous sporocarps, such as dryad's saddle, hoof fungus (Photo 125), stump puffball *Lycoperdon pyriforme* (Photo 151), sheathed woodtuft *Kuehneromyces mutabilis* (Photo 154), and the less conspicuous witches' butter *Exidia glandulosa* (Photo 146) and silky rosegill *Volvariella bombycina* (Photo 149), which grow on the wood of deciduous trees. Among the fungi commonly found on both broad-leaved and coniferous trees are honey fungi *Armillaria*, especially dark honey fungus *Armillaria ostoyae* (Photo 148) and sulphur tuft *Hypholoma fasciculare*. Also worth mentioning are fungi that appear to develop on wood but in fact parasitize the mycelia of saprotrophic wood fungi, for instance, species of the genus

Photo 146 (K. Kujawa)
The forms of sporocarps are sometimes intriguing – witches' butter *Exidia glandulosa*

Photo 147 (J. Walencik)
Honey fungi *Armillaria* and hoof fungi *Fomes fomentarius* on a birch tree

Tremella (brain) – leafy brain *Tremella foliacea* (Photo 152) and orange brain *Tremella aurantia* – which are parasites of *Stereum* species inhabiting deciduous trees, as well as conifer brain *Tremella encephala*, which grows on bleeding conifer crust *Stereum sanguinolentum* found on the wood of coniferous trees.

A characteristic shared by all the tree species is the very high proportion (up to 80-90%) of rare fungi species associated with them that occur in Poland at just a few, sometimes single localities. This is mainly because this group of fungi has been poorly researched: since the 19th century only a few mycologists in Poland have studied fungi growing on trees and wood, and their associated fungi have largely been neglected. This state of affairs is exemplified by research from Wielkopolska, a region fairly well studied in comparison with other areas of Poland, where some otherwise common species have been recorded only at single localities. Nowadays, when surveying the fungal diversity of a particular area, mycologists specializing in wood fungi frequently identify species new to the mycobiota of Poland, e.g. in the Kashubian Landscape Park, the Białowieża Forest and the Kampinos National Park.

Photo 148 (K. Zub)
Dark honey fungi *Armillaria ostoyae* – one of the most common *Armillaria* species

Because fungi prefer particular tree species and substrate types, their abundance across forest types varies. Depending on the forest environment, the richness of tree and shrub species, the amount of dead wood, and the moisture and light conditions are different. Unsurprisingly, therefore, the more fertile habitats can boast a greater diversity of epixylic fungi. Thus, we find the most species in oak-hornbeam forests but the fewest in dry coniferous forests, more in near-natural forests but fewer in even-aged and single-species managed forests (Photo 159). Local accumulations of large amounts of dead wood in various stages of decay can significantly increase the species richness of fungi, even in poorer environments.

Photo 149 (K. Kujawa)
The sporocarps of silky rosegill *Volvariella bombycina* often grow in wounds, cavities and crevices of trees

Colonization of dead wood by fungi

Pinpointing the moment a fungal succession on wood begins is difficult and depends on many factors, though mainly the species of the tree and its life history. Colonization will take place differently when a tree dies suddenly, such as when it is blown over or damaged by fire, differently when it dies as a consequence of insect activity, and differently again when it reaches a very old age and becomes a "veteran tree". In mature trees, some fungal species may remain in a latent form in the sapwood and not appear until the prevailing conditions become more favourable, i.e. when the moisture content decreases and the gas regime changes. Other fungi colonize different parts of a living tree one after the other as a result of a branch being broken off, damage to the bark or insect activity. We should bear in mind that the colonization of a tree by fungi does not conform to a single pattern: the fungal communities inhabiting a particular tree come into being in accordance with its distinctive individual characteristics. Colonization depends intimately on the tree's condition, the number and variety of defects it has, the physical conditions and microclimate of its environment, as well as the

Photo 150 (K. Zub)
Holwaya mucida – a protected species – decomposes the wood of lime trees

Photo 151 (J. Walencik)
Stump puffball *Lycoperdon pyriforme* – one of the very few species of puffballs growing on trees

Photo 152 (K. Kujawa)
The sporocarps of leafy brain *Tremella foliacea* appear to be growing on the wood, but its mycelium actually parasitizes the mycelium of saprotrophic fungi of the genus *Stereum*

succession of other epixylic species, be they fungi, lichens, mosses, liverworts or vascular plants. The colonization of a dead tree by fungi often begins many years before it actually falls; some trees can remain standing for at least 50 years after they die. Research conducted in the Białowieża Forest has shown that ca 45% of trees are already dead when they collapse. Hence, we can distinguish two phases of colonization: 1) parasitic, beginning when the tree is still alive, during which facultative saprophytes and facultative parasites take pride of place, and 2) saprotrophic, beginning after the tree or shrub has died, during which typical saprotrophs play the leading part. In the initial stages of succession, fungi colonizing mainly the branches and trunks still covered with bark are of major significance. These are primary (early) saprotrophs, consuming the simple sugars, starches and proteins contained in the fresh wood. Importantly, these fungi deactivate phenolic compounds that retard the growth of basidiomycetes. Through their activity, the early saprotrophs decompose the outer layers of the tree, thereby exposing its deeper tissues. By colonizing thin branches and bark crevices, these fungi can successfully compete with other species, causing substantial desiccation of the wood. Fungi associated with the advanced stage of decomposition play a crucial

Photo 153 (K. Kujawa)
The composition of fungi on dead wood depends on many factors – the sporocarps of hoof fungus *Fomes fomentarius* visible on this beech trunk weakened the tree, finally causing it to break; also visible are the sporocarps of common splitgill *Schizophyllum commune* – a fungus which occurs at early stages of decomposition

Photo 154 (K. Kujawa)
Sheathed woodtuft *Kuehneromyces mutabilis* decomposes the wood of deciduous trees – it is cultivated and used commercially in many countries

role in the decay of the woody substance. Their succession is facilitated by the prior activity of other groups of fungi and epixylic plants. The facilitating function of mosses and liverworts is key to the establishment of these fungi, as they retain substantial amounts of water, modify the microclimate, filter solar radiation, regulate the exchange of gases between wood and atmosphere, and moderate temperature amplitudes in the neighbourhood of fallen logs. The very last stage of wood decay permits colonization by fungi that grow on the leaf litter or the ground (including the typically mycorrhizal species), e.g. bitter bolete *Tylopilus felleus*. Some fungi are associated only with a particular stage of wood decay and, as conditions change, they are replaced as a result of competition from fungi better adapted to the later stages of decomposition. Nevertheless, some species can be observed for many years, from the moment a tree becomes weakened almost through to its complete breakdown. For instance, bleeding broadleaf crust *Stereum rugosum* and common mazegill *Datronia mollis* are capable of colonizing beeches and produce sporocarps from the earliest stages of decomposition almost until the very end of this process.

In general, the diversity of wood fungi is governed by a whole range of factors that includes the species and age of the tree, its life history, manner of death (slow dying or sudden fall, e.g. caused by the wind), how a given section of the forest has been managed, the degree of naturalness of the forest and the size of the forest complex, the generational continuity of trees of a given species, and the local richness of arboreal and wood fungi associated with the continuity of dead wood resources in different stages of decomposition.

Risks of biodiversity loss among wood fungi

As mentioned earlier, among the fungi associated with dead wood there are many species with single populations restricted to a certain area in Poland. The Polish Red List of macrofungi features several hundred protected and endangered species. These data do not reflect the actual threat many of these species are facing: firstly, because knowledge of wood fungi is far from complete, and secondly, because the Red List of fungi requires updating, which will most likely result in many other wood fungi being added to the highest risk categories. We can therefore say that although the circumstances surrounding this group of fungi in forests has been improving very gradually for several years (recall that the majority of rare species require coarse woody debris that has been present in natural forests for decades), outside of forests, i.e. in 70% of the area of Poland, wood fungi have very limited opportunities for development. Their situation can be improved by the careful management of all green spaces beyond forests and by recognizing dead wood as a biologically valuable material that should be preserved in various forms wherever possible, especially in urban green spaces, on roadsides, in groves and along watercourses.

More than 40% of the fungi on the Polish Red List are species associated with wood, some of which are thought to be extinct in Poland. Very rare species growing on dead wood at just a handful of localities include *Trametes pubescens* (Photo 157) and *Pycnoporellus fulgens* (Photo 155). Certain species are found only in the Białowieża Forest or are quite abundant only there. They include *Antrodiella foliaceodentata*,

Photo 155 (K. Zub)
Pycnoporellus fulgens – a very rare species in Poland

Boreostereum radiatum, ceramic fungus (Photo 158) and a few protected species (see Chapter 5.2) like orange sponge polypore (Photo 156). Localities particularly rich in wood fungi should be treated as hotspots of their diversity. One exceptionally valuable refuge of wood fungi is the Białowieża Forest, where studies of polyporoid fungi (including brackets and other wood fungi with a typically spongy hymenophore) have yielded 210 such species (over 50% of all such species known in Europe and nearly 90% of those known in Poland).

It is worth reiterating the positive value of coarse woody debris for preserving the species diversity of arboreal and wood fungi. Research carried out in the Kashubian Landscape Park involved a detailed analysis of the occurrence of fungi in the individual size classes of dead wood (Table 7), from twigs (less than 1 cm in diameter) to thick logs. Most species produced sporocarps on coarse woody debris, although the results of studies performed in other countries highlight the fact that smaller woody debris can actually host a relatively richer mycobiota.

Photo 156 (A. Szczepkowski)
Orange sponge polypore *Pycnoporellus alboluteus* – a protected fungus which in Poland occurs only in the Białowieża Forest

Recent studies in the Białowieża Forest have confirmed that in order to conserve the biodiversity of wood fungi, dead wood must be lying on the soil surface; dead wood lying beneath the surface, e.g. dead roots, is not as important a habitat for fungi. The amount of dead wood and the species of the tree is also important, but the type of forest community is of little consequence to the diversity of fungi growing on wood.

Photo 157 (K. Kujawa)
Trametes pubescens – very rare in Poland

Table 7 Number of species of fungi in/on individual size classes of dead wood (Karasiński 2016)

Class of dead wood	Number of specimens collected	Number of species	Number of species exclusive to a given class
Fine woody debris	119	59	19
Medium-sized woody debris	1051	189	46
Coarse woody debris	1567	259	122
Logs and their parts	934	217	99
Stumps (mainly of felled trees, rarely of natural origin)	480	104	10

Non-obvious associations – fungi and animals

When discussing arboreal fungi, it is important to point out some relationships that are often overlooked. As mentioned earlier, colonization of a living tree by wood-associated fungi begins just as soon as the spores of parasitic fungi enter through wounds on the tree and mycelia start to grow inside the trunk. Naturally, this results in the decomposition of wood, which locally becomes very soft. It is in these spots on living or dead trees that birds excavate their hollows (sporocarps of e.g. robust brackets on oaks can often be seen growing near them; Photo 117), which are later used by other animals, such as bats, squirrels, hornets, ants and spiders. The rot inside the tree trunks, formed by the enzymatic activity of fungal hyphae, is a separate world with a multitude of microhabitats populated by specialized inverte-

Photo 158 (K. Zub)
Ceramic fungus *Xylobolus frustulatus* is an endangered species found at numerous localities in the Białowieża Forest

Photo 159 (K. Kujawa)
An example of a forest where arboreal and wood fungi have limited opportunities to develop and survive

brates, many of which are nowadays found less and less frequently. The sporocarps of fungi are also breeding sites for many invertebrates, some of which are closely dependent on a particular species of fungus; for example, artist's bracket *Ganoderma applanatum* (Photos 126, 160) is linked to the dipteran *Aganthomyia wankowiczi*, while resinous polypore *Ischnoderma resinosum* and benzoin bracket are associated with the beetle *Mycetoma suturale* (Photo 161), which very often co-occurs in sporocarps with another rare species – *Derodontus macularis*. Hundreds of mite species and dozens of springtail species develop in the sporocarps of wood fungi, and the compositions of their assemblages change as the sporocarp develops and then decays. There are more such associations and many of them have yet to be discovered.

Photo 160 (K. Kujawa)
The dipteran *Aganthomyia wankowiczi* develops in the sporocarps of artist's bracket *Ganoderma applanatum*

Photo 161 (M. Miłkowski)
The beetle *Mycetoma suturale* on a sporocarp of benzoin bracket *Ischnoderma benzoinum*

4.1.5. Lichens

Lichens (lichenized fungi) are pioneer organisms that colonize very poor environments, e.g. wood with a considerable degree of desiccation and a highly variable water content. The acids secreted by lichens can, on the one hand, effectively inhibit the development of fungi, but on the other hand accelerate wood decay. Lichens can successfully compete with other epixylic organisms in strongly insolated sites. Best predisposed to these warm, sunny sites are foliose lichens, such as monk's hood lichen *Hypogymnia physodes*, hammered shield lichen *Parmelia sulcata*, varied rag lichen *Platismatia glauca* and tree moss *Pseudevernia furfuracea*.

Because they are sensitive to sulphur and nitrogen compounds, lichens are considered indicator organisms (bioindicators) of air quality in a given environment. Less well known is the fact that they have been successfully used as bioindicators to evaluate the naturalness of forests where the continuity of natural processes characteristic of forest ecosystems has remained intact. In Great Britain and Sweden, for instance, such recognized indicator species of naturalness are tree lungwort *Lobaria pulmonaria* and elm gyalecta *Gyalecta ulmi*. Most of these indicator species grow on either dead wood or old trees. Be that as it may, strongly insolated and desiccated wood provide the best conditions for epixylic lichens: a higher moisture content would increase the pressure from bryophytes and vascular plants, which are better suited to growth in moist environments.

Research has highlighted the significance of the Białowieża Forest as a refuge for lichens in north-eastern Poland. To date, 400 species have been confirmed there, 121 of which are epixylic. However, only a dozen or so of them are closely associated with dead and decaying wood. They include an interesting montane species – spray paint lichen *Icmadophila ericetorum* – and the rare textured lungwort *Lobaria scrobiculata*.

During CRYPTO, 86 species of epixylic lichens were found in the 144 ha study area within the Białowieża National Park. 15 of them were obligate epixylics, i.e. occurring exclusively on dead wood. The following species display a strong preference for such a substrate: *Micarea elachista*, mottled-disc lichen *Trapeliopsis granulosa*, board lichen *Trapeliopsis flexuosa* and white-collar stubble lichen *Calicium glaucellum*. Some other interesting species occurring on dead wood include Laurer's thelocarpon lichen *Trapeliopsis laureri*, *Strangospora moriformis* and Notaris' soot lichen *Cyphelium notarisii*.

Most lichens associated with dead wood inhabit the trunks of both standing and lying dead trees.

Photo 162 (K. Kujawa)
Oak moss *Evernia prunastri* is a common lichen inhabiting both living and dead wood

During CRYPTO, 72 lichen species were found on fallen logs in the Białowieża Forest, 13 of which were growing only on this substrate. Fast-growing foliose and fruticose lichens were dominant (44 species), e.g. species of the genus *Cladonia* (Photo 164), monk's hood lichen, hammered shield lichen, varied rag lichen, tree moss, green starburst lichen *Parmeliopsis ambigua* and salted starburst lichen *Imshaugia aleurites*. Crustose lichens, e.g. *Lecidea granulosa*, were less common (28 species).

Some lichen species usually grow on the ground, although they can often be found on the trunks of dead trees as well. They include shrubby cup lichen *Cladonia arbuscula*, reindeer cup lichen *Cladonia rangiferina* and lipstick cup lichen *Cladonia macilenta*. Dead wood is also the habitat of dog lichen *Peltigera canina*, a rare species in danger of extinction.

The trunks of standing trees were found to host 55 lichen species. In contrast to the previous substrate, crustose lichens were the most abundant, whereas the proportion of *Cladonia* species was negligible. Most of the lichens grew on the lower parts of the trees, where humidity levels were more favourable. Most of the common species included white-collar stubble lichen, mottled-disc lichen, *Micarea melaena* and brown-head stubble lichen *Chaenotheca brunneola*. These show a clear preference for this type of substrate. Species such as snag whiskers *Chaenotheca xyloxena*, Schaerer's disc lichen *Buellia schaereri*, *Lecanora saligna* and *Lecidella elaeochroma* occurred exclusively on the trunks of standing dead trees. This substrate was also particularly suitable for epiphytic species that develop on living trees. These species also inhabited the bark-covered trunks of fallen trees.

An interesting study of the colonization and succession of lichens on pine stumps in a dry forest habitat was conducted in the Tuchola Forest. Four stages of colonization were identified: 1. initiation – up to 4-5 years after felling; 2.

intensive colonization – 4(5)-10(11) years after felling; 3. optimum – 10(11)-15(16) years after felling; 4. regression – more than 15(16) years after felling. Once the fresh stumps have been colonized by the primary colonizers (stage 1), the intensive growth of mainly crustose species such as *Trapeliopsis glaucolepidea* or *Lecidea granulosa* follows (stage 2). The third stage, dominated by crustose species and cup lichens (*Cladonia*), is characterized by the highest species diversity: 39 lichen species were found occupying pine stumps in the research area, with wooden soldiers cup lichen *Cladonia botrytes* occurring exclusively on this substrate. The wood of rotting stumps is clearly preferred by the following species: *Trapeliopsis glaucolepidea*, powdered cup lichen *Cladonia cenotea*, Floerke's cup lichen *Cladonia floerkeana*, fingered cup lichen *Cladonia digitata* and lipstick cup lichen. In stage 4, the lichens gradually recede.

Structural timber is an important substrate for lichens. A wooden barn in Wawrzonowo in the commune of Brusy (northern Poland) (Photo 165) was officially designated a natural monument because of the rare beard lichens *Usnea* spp. growing on it.

Photo 163 (K. Kujawa)
Pale-footed horsehair lichen *Bryoria fuscescens* – a protected species – develops on living trees (predominantly larches) and dead wood

Photo 164 (K. Kujawa)
Common powderhorn *Cladonia coniocraea* grows on rotting, dry wood

Photo 165 (K. Kujawa)
A wooden barn covered in rare lichen species – a natural monument

4.1.6. Slime moulds

Slime moulds (myxomycetes) are a group of organisms currently classified as protozoans but which used to be included in the fungi kingdom (which themselves were once classified as plants). Their life cycle is rather peculiar: depending on the prevailing conditions, the spores germinate into either myxamoebae or flagellated swarm cells, which assimilate to form a plasmodium. Therefore, they can move, first as myxamoebae and swarm cells, and later as plasmodia. Plasmodia are clusters of multinucleate cytoplasm, which are capable of amoeboid movements. In this form, slime moulds can absorb and digest bacteria, fungal spores, fragments of mycelia and even small sporocarps. A mature plasmodium can form distinctively shaped sporangia, peculiar to each species (Photos 166–169), from which, following division of the nuclei in the multinucleate cytoplasm, the spores arise, mature and are relased. Their preferred substrate is highly decayed wood – in fact, the survival of many species depends on it.

Photo 166 (K. Kujawa)
Coral slime *Ceratiomyxa fruticulosa* in poroid form; different stages of plasmodium formation are visible

Photo 167 (K. Kujawa)
The plasmodium of *Hemitrichia* forms an intricate pattern

Photo 168 (K. Kujawa)
Tapioca slime mould *Brefeldia maxima* can cover a significant area of wood (seen here on a maple stump)

Photo 169 (K. Kujawa)
Some slime moulds which have already developed sporangia are very inconspicuous and hard to spot

The sporocarps of slime moulds usually emerge on wood previously occupied by fungi. During unfavourable periods, like drought or winter, slime moulds can survive in a latent state as spores or endospores, i.e. microcysts and sclerotia. Thus, certain species change into their "active" form only once every few years. 103 slime mould species have been recorded in the Białowieża Forest (there are ca 250 in Poland), and 124 in the nearby Wigry National Park. During CRYPTO, 44 species of slime moulds were found in the study area, the majority of which (38) are associated with dead wood. Among the slime mould species commonly occurring in the Białowieża Forest are the pinkish-red wolf's milk *Lycogala epidendrum* (turning brown with time, with pale beige spores), the lemon-yellow flowers of tan *Fuligo septica* and the white coral slime *Ceratiomyxa fruticulosa* (Photo 166). In addition, very rare species on the Polish Red List can be encountered here, e.g. *Badhamia lilacina*, *Hemitrichia abietina*, *Perichaena chrysosperma*, *Perichaena vermicularis*, *Physarum sulphureum*, *Stemonaria irregularis* and *Stemonaria longa*.

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Chapters 4.1.4-4.1.6: Summary

Although most fungi occur in forest environments, they also perform crucial functions in open-terrain ecosystems. They improve growing conditions for trees by forming symbiotic relationships with them (mycorrhizae); saprophytic species decompose dead organic matter, taking part in soil-forming processes and providing plants with essential nutrients; parasitic species regulate plant and animal populations; and all fungi participate in the cycle of chemical elements and the flow of energy through ecosystems. The functional diversity and species richness of fungi make them important components of ecosystems, associated with other components through a network of complex relationships.

Fungi are among the few organisms capable of breaking down the cellulose and lignin of which wood is composed; *Basidiomycota* do so with particular ease. Fungi colonize both fine woody debris as well as the trunks of standing and fallen trees, and also shrubs. Their activity breaks down long-chain organic compounds, unavailable to other organisms, into simpler, easily assimilable ones.

Most species of wood fungi occur on fallen logs. Fungi colonize wood in a definite sequence. The process may be initiated by parasitic fungi, colonizing weakened trees, or by endophytic fungi, inhabiting living, healthy trees. These fungi become saprotrophic after the tree dies. They are followed by species utilizing relatively simple organic compounds contained in fresh wood tissues (especially the phloem), and later by those that break down more complex compounds (cellulose and lignin). The final stage of decay sees the emergence of fungi able to live on the soil.

Dead wood provides a substrate on which grow many rare, often protected, fungi. They include coral tooth fungus *Hericium clathroides, Hericium flagellum*, bearded tooth *Hericium erinaceum*, orange sponge polypore *Pycnoporellus alboluteus*, rose bracket *Fomitopsis rosea*, beefsteak fungus *Fistulina hepatica* and ceramic fungus *Xylobolus frustulatus*.

The majority of lichens are epiphytic organisms, but many of them also occur on dead wood. Most species of lichens growing on coarse woody debris colonize the trunks of fallen trees. This substrate hosts mainly foliose and fruticose forms. Stumps and strongly decayed logs are generally colonized by terrestrial (epigeal) lichens, mainly cup lichens and species with crustose thalli. Epiphytic lichens form an ecologically important group. Although more often found on living trees, they are sometimes encountered on the trunks and branches of dead trees, and can become abundant on dying parts of trees. However, some lichen species prefer dead wood, such as spray paint lichen *Icmadophila ericetorum*, an interesting montane species, or the rare textured lungwort *Lobaria scrobiculata*. Some lichens associated with dead wood serve as indicators of forest naturalness and the continuity of its natural processes.

Dead wood, usually colonized by fungi, is the most important substrate for slime moulds, a distinctive group of organisms formerly thought to have been related to fungi and currently classified as protists. Their plasmodia – often spectacular and colourful – are capable of amoeboid movements.

4.2. From forest "fuel" to water retention in forests

4.2.1. Forest "fuel"

Forest fires caused by lightning strikes are among the chief factors underlying the dynamics of boreal forests in Siberia and Scandinavia, and coniferous forests in North America. Under natural conditions, the frequency and intensity of fires depends on the amount of accumulated fuel, including dead wood. However, forest fires are mainly fuelled by small plant remains, like needles, twigs, litter and dry vegetation. Thick trees can be killed by fire but are rarely burned down: in most cases, their trunks are merely scorched. The same applies to the large trunks of dead trees. On the one hand, the frequency and intensity of fires is mediated by the volume of available dead wood (usually fine woody debris), but on the other, fires are one of the factors determining the amount of coarse woody debris.

The many effective techniques developed in the 20th century for rapidly detecting and extinguishing small to medium-intensity fires are favourable to the deposition of large amounts of organic matter which, if it should become accidentally ignited, can lead to intense and catastrophic and uncontrollable events. Such experiences have forced managers of fire-prone forests to periodically light controlled fires, thereby reducing the amount of "fuel" in them in an attempt to simulate their natural dynamics. Controlled fires are standard practice in American pine forests; they are also one of the nature conservation measures employed in pine forests in Finland and Sweden. The fact that fires break out locally in boreal forests is a prerequisite for the occurrence of certain specialized animal species (mainly insects) (Photo 170) and the regeneration of some plants (e.g. jack pine *Pinus banksiana* in North America).

Numerous plants, fungi, and animals depend on forest fires, and also on the presence of dead trees killed by fire or microhabitats that develop on scorched tree trunks. Sometimes this dependence is very close – obligate pyrophiles do not occur in forests where fires do not break out. On the other hand, species for which the occurrence of fires provides suitable habitat or substrate, but which can also exist in substitute habitats, are called facultative pyrophiles. Forest litter fires stimulate richer species compositions, so they can be employed as a biodiversity conservation measure. Pyrophilous organisms include many very rare species that have been declining in abundance in recent decades. Even species that used to be relatively common and locally abundant have now become rare, as forest fires are quickly detected and effectively nipped in the bud.

Pyrophiles, pyrophilous species:
species that prefer habitats formed as a result of fire, e.g. beetles with a preference for scorched wood, plants preferring burn sites, or whose development is mediated by fire, e.g. some species of American pines, most of whose cones open only after a fire has heated them.

Photo 170 (J.M. Gutowski)
Upis ceramboides – an obligate pyrophilous beetle that inhabits northern regions of the Holarctic

Boreal forests: forests growing in the far north; mainly coniferous with admixtures of birches and willows.

Weight of wood: one cubic metre (m^3) of air-dry wood weighs around 0.5 tons, although this value can vary widely depending on the tree species and the conditions in the local microenvironment.

In Sweden, forests where natural fires occur were found to be preferred by species from as many as 50 beetle families, i.e. about half of the families found in the region. A spectacular example of a beetle responding to smoke and fire from a great distance (even more than 20 km), and migrating in the direction of the fire, is the black fire beetle *Melanophila acuminata*, also present in Poland.

Until not so long ago, it was believed that in central Europe, including Poland, natural forest fires only occurred sporadically because the moisture conditions and the great abundance of wood-decomposing organisms prevented larger amounts of combustible material from accumulating in forests. The flagship pyrophilous beetle, the black fire beetle, was not recorded during recent surveys at burn sites in the Białowieża and Augustów Forests. However, a recent study by Ewa Zin (2016) in the Białowieża Forest, based on the analysis of fire scars in cross-sections of pine trunks, suggests that fires (in large part probably related to human activity) were until about 100-150 years ago a regular, major factor in the dynamics of tree populations in the boreal parts of the Białowieża Forest, to a large extent governing the species composition of forests (favouring pines and partly oaks, but limiting the development of spruce). Similar conclusions were drawn by Kujawa-Pawlaczyk following analyses of peat profiles. Without doubt, fires play an important role in the preservation of semi-natural heathlands, e.g. in military training areas, and prescribed burning would probably be justified to some extent also in Poland. The first successful experimental attempts to use prescribed burning on heathland in this country were made in the Przemków Landscape Park in western Poland. But in spite of this, controlled burning is still prohibited in Poland; in fact, virtually any type of burning is banned.

4.2.2. Storage of organic matter

In natural forests, dead wood sequesters huge reserves of organic matter (Photos 171, 172). Depending on the geographic location, the type of forest site and the phase of stand development, the average volume of coarse woody debris may range from 100 to 200 m^3/ha, possibly more. A mere 20 m^3/ha is accumulated in the natural boreal forests of northern Europe, but dead wood deposition in the mixed beech-fir-spruce forests of east-central Europe may amount to 500-1,000 m^3/ha. Certain forests in North America (California, Oregon), where Douglas firs *Pseudotsuga menziesii*, eastern hemlocks *Tsuga canadensis* and giant redwoods *Sequoiadendron giganteum* grow, may stock as much as 1,100-1,400 m^3 of dead wood per hectare. The input rate of coarse woody debris varies from 0.5 to 2.5 (7.0 in rare instances) tons per hectare per year and is lower in broad-leaved than in coniferous stands. The amount of dead wood is directly proportional to the volume of tree biomass. In North America, the mass of coarse woody debris (diameter > 10 cm, length > 1 m) is 30-40 tons/ha in pine forests, 20-25 tons/ha in warm broad-leaved oak-maple for-

Photo 171 (J.M. Gutowski) Huge oak trunks such as these can only be seen in only a few places in Europe: the Białowieża Forest

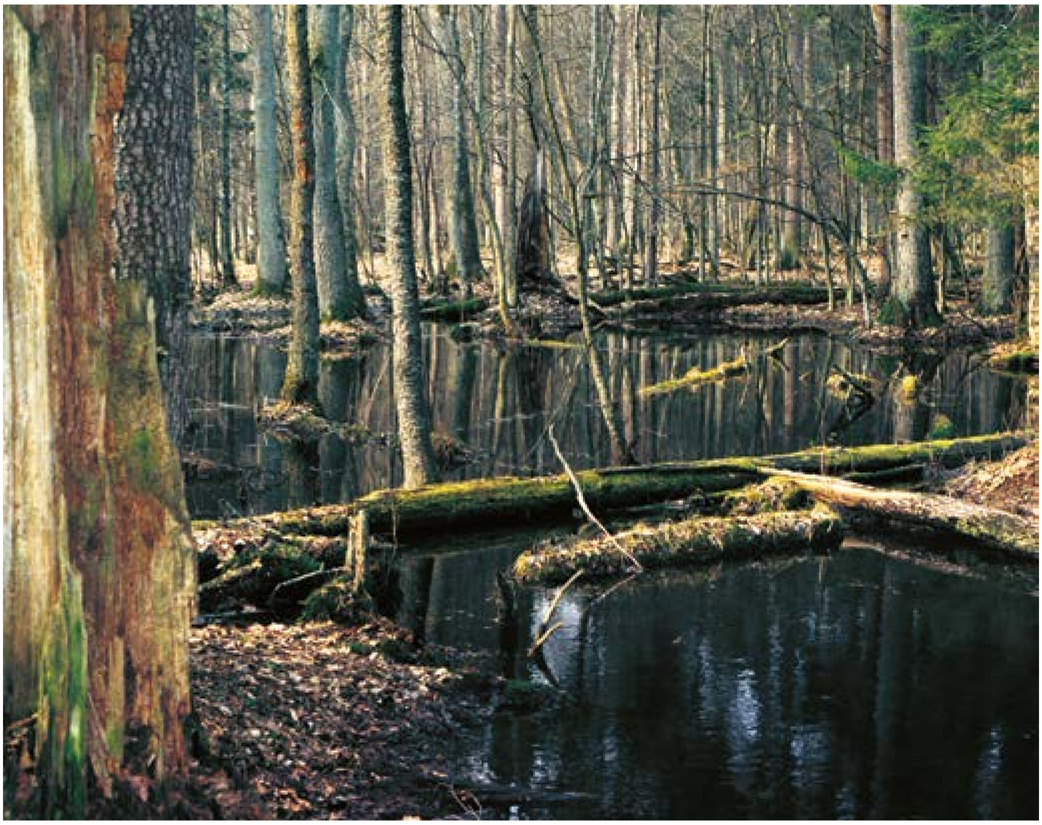

Photo 172 (J.M. Gutowski)
Dead wood in an alder carr

ests, and as much as 580 tons/ha in natural Douglas fir forests (these figures refer to the weight of wood under normal conditions, not to the dry mass). In Europe, the amounts of dead wood in deciduous and coniferous forests differ from those in North America, which means that in Europe, natural broad-leaved forests contain more dead wood.

Quite the reverse situation prevails in managed forests, however. In pine stands, which have usually replaced natural forest communities in Poland and central Europe, the volume of dead wood does not usually exceed 3 m^3/ha, and very often is less than 1 m^3/ha. Such a negligible amount of dead wood obviously cannot provide sufficient food resources and growth conditions for many saproxylic species, and the biodiversity of these forests is therefore very poor. Intensive, plantation-based forest management over large parts of Europe has driven many species of saproxylic invertebrates to extinction. This is exemplified by the dramatic reduction in the number of saproxylic beetle species in some countries of western Europe (see Chapter 4.1.2).

Once a tree (or shrub) dies, the macro- and micronutrients accumulated in its tissues slowly return to the soil. The activity of saproxylic organisms breaks down organic matter, releasing elements that plants can take up. It is important to bear in mind that this is a very long-drawn out process, guaranteeing a steady, slow and gradual supply of the nutrients required by living plants. On the other hand, there is no risk that the excess of mineral compounds (as is often the case with artificial fertilization) will be flushed out by heavy rains into the deeper layers of the soil or will run off into rivers and be irretrievably lost. This is particularly significant as regards the stabilization of natural processes, especially after natural disturbances like gale-force winds or fires, which give rise to large amounts of dead wood in the forest.

A study in North America found that 215 tons of coarse woody debris accumulated on one hectare of forest contained about 330 kg of calcium, 46 kg of potassium, 14 kg of phosphorus and 7 kg of sodium.

Therefore, when wood is taken out of the forest, as is the case with managed forests, each harvesting cycle and each clearing or thinning removes all the accumulated elements from the environment.

The amounts of these essential nutrients in wood are relatively small compared to their pool in the soil, which nowadays is also increased by eutrophication as a result of wet and dry precipitation. Removing nutrients with harvested timber does not seriously impoverish habitats, at least on a perceptible time scale. However, depletions of some microelements are potentially more important, although this is an issue that has not yet been thoroughly researched.

Content of elements in 1 m^3 of wood:
(after Prosiński 1969)

Pine:
0.1743 kg of potassium (K)
0.0371 kg of sodium (Na)
0.0965 kg of magnesium (Mg)
0.5218 kg of calcium (Ca)
0.0437 kg of phosphorus (P)

Oak:
0.3155 kg of potassium (K)
0.1113 kg of sodium (Na)
0.0904 kg of magnesium (Mg)
2.0086 kg of calcium (Ca)
0.1004 kg of phosphorus (P)

4.2.3. Carbon and nitrogen accumulation

The insufficient amount of nitrogen and, more commonly, its limited availability in many types of forest is an important factor restricting plant growth. Dead wood has a relatively low nitrogen content. This element may be incorporated into wood in two ways. Firstly, the hyphae of mycorrhizal fungi develop a close association with tree roots, facilitating nitrogen uptake from the soil. Besides fungi, some species of trees form symbiotic relationships with Actinobacteria, which have the ability to fix atmospheric nitrogen. Secondly, nitrogen in wood comes from the decomposition of microorganisms, dead hyphae, dead invertebrates and the excreta of invertebrates and other animals.

A North American study found that 215 tons of coarse woody debris accumulated on one hectare of forest contained almost 300 kg of nitrogen.

Carbon is accumulated by a woody plant only when it is alive. The average annual rate of carbon accumulation in central European forests is about 1.4 tons per hectare. The overall amount of carbon sequestered in one hectare of forest varies significantly, but the average is about 150-250 tons in temperate forests (with two-thirds stored in the soil) and 200-280 tons in tropical forests. As decay progresses after the death of a tree or shrub, carbon is slowly released back into the soil. However, it is bound up in dead wood for many years, which is of great consequence for the global carbon balance in the atmosphere. This, in turn, has a major influence on the greenhouse effect. In 2021, an international team of researchers, headed by Sebastian Seibold, estimated the amount of carbon accumulated in dead wood in forests around the world at 67-79 × 10^{12} kg, which is around 8% of all the carbon in forests and around 8.5% of all the carbon present in the atmosphere.

The carbon balance of natural forests is currently the subject of intense scientific debate. It used to be assumed *a priori* that levels of accumulated carbon in living trees and dead wood were constant: because the stand volume in a natural forest is in dynamic equilibrium, roughly the same amounts of dead wood are being produced and decomposed at the same time. We now know that this is far too idealistic and simplistic an assumption. Critically, moreover, the cycle is not closed: some of the carbon from rotting wood becomes permanently bound up in the organic matter of the soil. Field studies (just a few as yet) show that more organic matter is accumulated than released. While the magnitude of this difference is still a matter of debate, it is safe to say that its existence is not, although the mechanisms and underlying causes remain unclear. It is, however, (especially now, in 2021) one of the most keenly discussed issues in forest ecology, particularly as it is of crucial importance to understanding the role of forests in the balance of greenhouse gases.

On a global scale, harvesting trees in managed forests increases overall carbon emissions to the atmosphere by 20-25%, assuming that the carbon contained in harvested trees is immediately oxidized and released as CO_2. This assumption is true if the wood is burned. But whenever wood is processed into wood products, the emission of CO_2 is slowed down. This has given rise to opinions that carbon accumulation in wood can be optimized by intensively exploiting forests and storing the carbon in products made from the harvested wood. But this argument is fallacious, as the lifespans of most wood products are much shorter than the time it takes for dead wood to decompose naturally in the forest.

Slash burning

Until recently, all branches and other types of post-harvest residue (slash) in managed forests in Poland were gathered, piled up and burned. This was supposed to prevent the spread of those insects which forestry regards as "pests of trees". Here, we must highlight the fundamental difference between natural fires and the intentional burning of slash. In a natural fire, it is usually only a small proportion of wood that gets burned; there still are standing dead trees left, and neither thicker logs nor stumps are incinerated. In pine forests, for example, naturally occurring fires facilitate the regeneration of pines and enable the emergence of distinctive organisms, e.g. pyrophilous insects and fungi, intimately associated with burn sites.

Whereas the burning of slash might be justifiable in coniferous forests, which under natural conditions can sometimes be ignited by a lightning strike (though very rarely in Poland), this should not take place in deciduous and mixed forests. Even in coniferous forests, the clearing up and burning of post-harvesting remnants should not include the whole material, otherwise where would the food resources come from to enable saproxylic organisms to flourish in this environment?

Polish State Forests have already abandoned the practice of slash burning, and even a formal ban has been in effect since 2004. But in exceptional circumstances, such as insect outbreaks, the Forest Protection Instructions make provision for the burning of bark and branches.

In some forestry districts, the slash is not burnt but comminuted into chips which are then scattered over the cleared area. Although this technique eliminates certain disadvantages of burning, it is still inconsistent with natural processes, as it removes the structure of dead wood, which is key to the establishment and development of many dead-wood-related organisms. There are only a handful of forest districts where slash is left unprocessed or, at the very most, piled or stacked up. Foresters' observations suggest that this, the most environmentally friendly way of managing slash, is not only good for saproxylic organisms, but can also help protect regenerating stands from browsing by deer.

4.2.4. Dead wood as a water reservoir

The water-holding capacity of a fallen log generally increases with time. There are two sources of water in dead wood: precipitation, and the release of water as a result of the chemical decomposition of woody tissues by bacteria and fungi. Within a few years to a decade after the fall of a tree, the water content in a log lying on the forest floor can be so high that it can be squeezed out like from a sponge. Therefore, fallen trunks should be considered an important water storage reservoir in the forest and a factor moderating the microclimate under the tree canopy. Such logs, especially the larger ones, provide enough moisture for tree seedlings to take root. This is particularly important in rocky areas or arid regions. The water storage capacity of logs is substantially improved if they have a covering of mosses, lichens, liverworts, ferns and flowering plants.

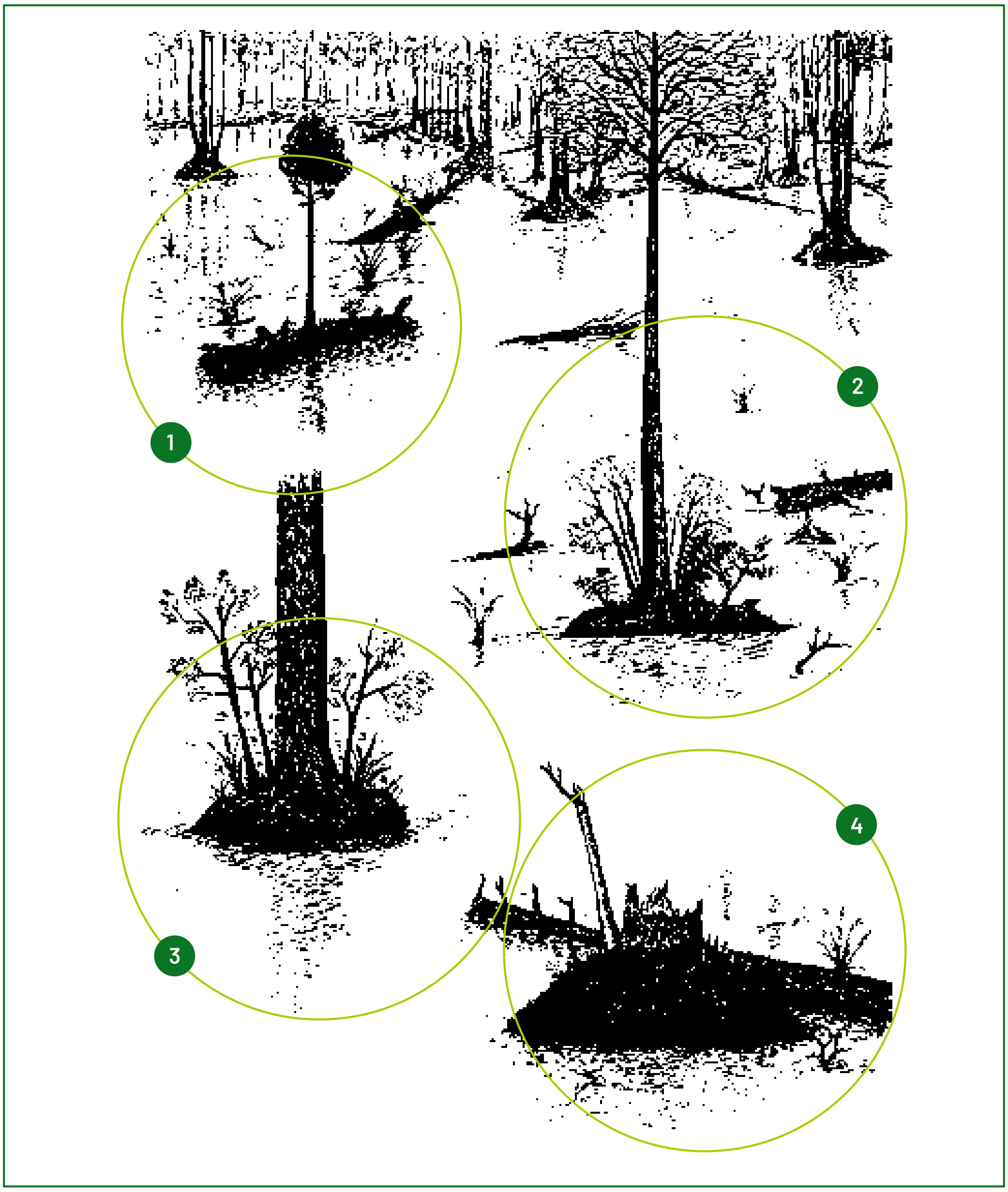

Fig. 36 The development of a tree on a "nurse log" (formation of a hummock in a carr): 1 – the emergence of seedlings and young trees on the log; 2 – the formation of a new hummock: the gradual disintegration of the "nurse log" and the accumulation of organic matter around the roots of the young trees; 3 – a mature alder on a well-developed hummock; 4 – a vacant hummock, ready to be taken over by a new tree (M. Bobiec)

Photo 173 (A. Bobiec)
An alder carr in the Białowieża Forest: “nurse” logs and their “charges”

Retention: the temporary accumulation of rainwater within a catchment area; usually beneficial, it reduces the likelihood of very high or low water levels downstream.

Dead wood contributes to the retention of water from rain and snow melt in the forest. Dead wood on the ground accumulates water from the spring thaw, delaying its runoff and so reducing the danger of flooding. This happens, firstly, because decomposed logs become saturated with water, and secondly, the fallen logs dam the surface water runoff. The immediate “retention capacity” of rotting wood, i.e. its ability to absorb and hold water, is about 0.1-0.85 m^3 of water/m^3 of dead wood. These values depend on the degree of decomposition and the species, e.g. fir wood has the highest capacity to absorb and store water: a single log can retain several hundred litres of water. Wood in the most advanced stages of decay absorbs water particularly well, so dead wood on the forest floor contributes significantly to preventing the soil from drying out, which is very important during dry spells.

The second mechanism, i.e. the blocking of runoff by logs lying on the forest floor, is much more influential. In riparian forests or wet oak-hornbeam forests, one can see how a large fallen tree blocks the path of periodic water runoff: this first forms a pool, then dams up, and finally has to flow around the log. This may cause the channel to widen or a “relief channel” to form around the obstacle. Frequent changes of the runoff course as more trees fall down prevent the development of permanent rills along which the water would run off faster. The overflowing water seeps into the soil, moistening it. A similar mechanism operates on slopes and the smallest streams in the mountains (Photo 183).

In 2019, the Gdańsk Forest District developed a plan for water retention in the forested parts of the catchment areas of the Oliwski Potok and Potok Strzyża streams, which involved the collection and redistribution of coarse woody debris. These measures are aimed at mitigating the effects of periodic heavy rainfall and protecting Gdańsk from local flooding. They would increase the amount of dead wood in the areas covered by the plan by 9-24 m^3/ha (from the current average of 11.4 m^3/ha). The logs, placed across the runoff paths, are intended to act as small dams retaining surface runoff in the catchment. By increasing the amount of dead wood, a volume of water will be retained that is estimated to be equivalent to ca 9.3% of the total retention capacity of the forests growing in the catchments of these two streams.

4.2.5. Importance of dead wood in forest regeneration

Forest “nurses”

How do trees regenerate in swampy forests, where surface water becomes stagnant for several months each year (as in alder carrs) or in forests regularly flooded by brooks in the spring (as in riparian communities)? Tree seedlings germinating in places that are later flooded will ultimately be drowned or destroyed by ice. Under such conditions, all sites above the water level are important for tree regeneration. Hummocks typically remain above the water level in alder carrs. They form around the trunks of old

Photo 174 (J. Walencik)
A fallen log offers spruce seedlings ample moisture and nutrients

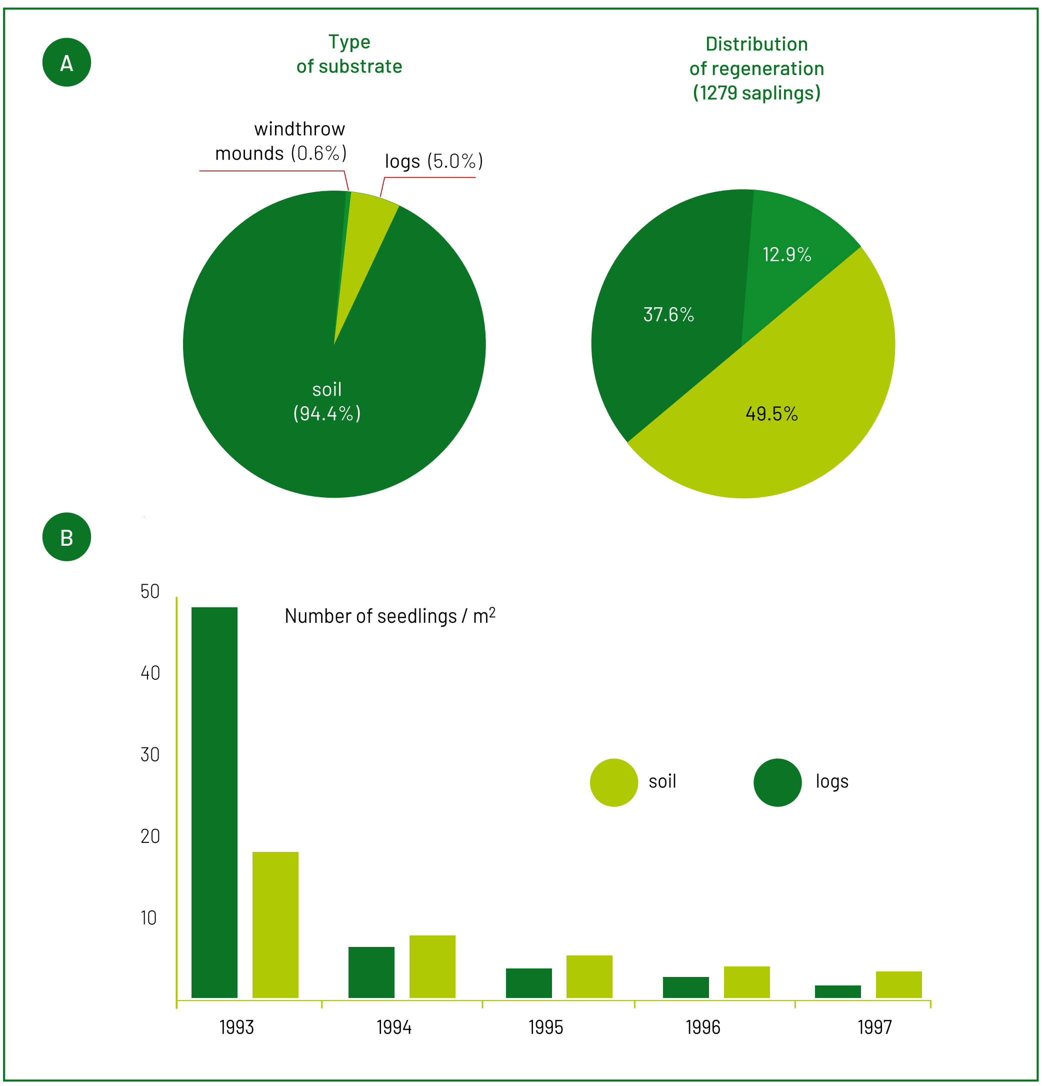

Fig. 37 The importance of decaying log microhabitats for spruce regeneration in the upper montane forests of the Babia Góra mountain (southern Poland);
A – the distribution of advanced spruce regeneration on various types of sites, depending on their relative richness,
B – changes in seedling numbers of a cohort established in 1993, depending on site type (according to J. Holeksa, after Danielewicz and Pawlaczyk 1998; modified)

Photo 175 (J. Walencik)
A new generation of trees growing on an old snag

trees, which once germinated on rotting "nurse logs", providing the dry substrate that young trees need. Straight rows of young trees, usually "the charges" of the same "nurse", are commonly seen in natural alder carrs and riparian communities. To gain access to the soil, the saplings' roots wrap around and gradually overgrow the decaying log. In this way, each "nurse" "teaches" the young generation of trees "the appropriate posture" that they should adopt in order to survive high water levels. As the young trees gradually develop their root system, this provides the necessary access to air and forms the skeleton for a new alder hummock (Fig. 36). Although single (sometimes more numerous) examples of "nurse logs" can be seen in other types of forests, those found in wet, boggy environments are crucial to the dynamics of the whole community.

Processes analogous to those occurring in alder carrs and riparian forests also occur in various types of natural spruce stands. The relationship between spruce regeneration and decaying wood is actually quite spectacular. Dense aggregations of spruce saplings and seedlings entirely covering decaying logs are very characteristic of high-altitude coniferous forests in the Alps and Carpathians, and also at lower elevations in the Scandinavian taiga and the Białowieża Forest (Photos 174-176). Detailed studies have highlighted the great importance of this phenomenon (Fig. 37). For instance, in a

Photo 176 (J. Korbel)
Young spruces growing on a decaying log

nature reserve in Lapland, 40% of advanced spruce regeneration occurs on decaying logs that cover a mere 6% of the forest floor. And in the forests of the Babia Góra mountain in southern Poland, almost 50% of advanced spruce regeneration takes place on logs covering just 5% of the ground surface.

Research carried out in the Polish mountains has confirmed that the diameter of lying logs is an important factor in their role as regeneration beds for young spruce trees. It turns out that seedlings very rarely take root on logs less than 20 cm in diameter, and those with diameters exceeding 40 cm are the most suitable. Natural spruce regeneration is severely limited in the absence of coarse woody debris on the ground.

In oak-hornbeam and coniferous stands in the Białowieża Forest, young spruces can often be seen growing on the tops of their predecessors' stumps. By utilizing stumps as microhabitats, young spruces are freed from competition with herbs and shrublets, obtain an abundant supply of water and can become closely associated with mycorrhizal fungi. Trees growing in such locations develop and retain a distinctive stilt-like form (Photo 177).

Photo 177 (J. Walencik)
This stilted spruce grew up on a thick log, now completely decomposed

Animals play a crucial role in depositing seeds in decaying wood: it is not just a matter of seeds passively falling from trees or being carried by the wind. Certain birds, such as Eurasian nuthatch *Sitta europaea*, actively transport tree seeds to fallen logs (as a food supply that they sometimes forget about), where they are covered and hidden. This makes it harder for other potential consumers to locate the seeds and ensures more favourable conditions for their germination compared to seeds that have randomly fallen onto the dead wood without the birds' participation.

The regeneration of trees on logs is known from many forests around the world. It occurs e.g. in eastern hemlocks in North American forests, Engelmann spruces *Picea engelmannii* and subalpine firs *Abies lasiocarpa* in the montane forests of British Columbia, Japanese clethras *Clethra barbinervis* in the montane forests of Japan, trees in the coastal Pacific forests of North America, and certain species of trees in tropical forests. A number of different explanations have been put forward as to why this happens, e.g. better and more stable moisture conditions, seeds are prevented from being covered by a thick layer of fallen leaves, avoidance of dense litter or dense moss cover, guaranteed warmer microhabitats, seeking beneficial mycobiota and escaping common soil pathogenic fungi. In the Patagonian Andes, a petrified forest dating back 300 million years has been discovered in which trees regenerated in precisely this way.

Forest "pens"

The expression "damage caused by game" is well known to foresters. It basically implies damage to and loss of seedlings and young trees in forest plantations and sapling stands as a result of large forest herbivorous mammals (red deer, elk, roe deer *Capreolus capreolus* and European bison *Bison bonasus*) browsing shoots and buds, stripping fresh bark and phloem with their incisor teeth, and rubbing their maturing antlers against trees. Such damage entails financial losses in managed forests because the effort required to plant and take care of the trees has been wasted and the wood has become unsaleable. Measures suggested or employed in order to prevent or limit such damage include the culling of ungulates, the erection of fences around plantations or the individual protection of each planted tree.

In natural forests, where herbivores behave in the same way as in managed forests and cause the same kinds of injuries to trees, this concept of damage does not apply. These same species of trees and animals have coexisted for aeons, yet the forest remains intact. In such a forest, the fate of the vast majority of young trees (starting from seeds and seedlings) is to be consumed by herbivores: birds will eat the seeds, caterpillars will eat the leaves and red deer will strip the bark. Only a tiny proportion of young trees (regeneration) will survive to maturity and grow to an immense size. How is that possible, given the much greater pressure exerted by ungulates per unit of area (for instance, in the strictly protected zone of the Białowieża

Photo 178 (A. Bobiec)
Fallen spruces offer a new generation of trees effective protection from deer browsing

Photo 179 (A. Bobiec)
The Białowieża Forest: remnants of the spruce "fortifications" that protected young trees from browsing animals, facilitating the regeneration of broad-leaved trees

National Park, the density of the red deer population is 2-3 times higher than in the commercially utilized areas of the Białowieża Forest) and the absence of artificial protection against "damage"? Quite simply, the forest has its own natural defences. These are predominantly windthrows or sections of trees lying on the ground, which set up a barrier or "pen", making it more difficult for herbivores to gain access to sites where trees can safely regenerate (Photos 61, 178, 179). Furthermore, herbivorous animals avoid these sites for fear of being attacked by predators. This is an effect of the landscape of fear, described in more detail in Chapter 4.1.1.

Particularly effective protection is provided by fallen spruces, whose trunks are spiked with hard, sharp and very durable branches. Dense regeneration belts of broad-leaved trees that have found "asylum" along spruce logs in natural forest communities are common; even more so are entire complexes with perhaps 15 to 50 fallen trees, enabling the simultaneous development of a new generation of trees over areas from 500 to 1,500 m^2 on average.

The mortality of whole groups of trees, initially brought about mainly by fungal infections and finally by insects, as well as strong pressure from herbivores precluding continuous, even regeneration, are among the principal factors responsible for the exceptionally rich spatial diversity of the natural oak-hornbeam woodlands within the Białowieża Forest.

4.2.6. Dead trees stabilize steep slopes

Human activities are increasingly being blamed for catastrophic avalanches and landslides. Analyses of these events often point the finger at the deforestation of mountain areas. In mountainous terrain, dead trees are as important as living ones. Their roots hold thin, fragile layers of soil as well as fragments of rock in place on slopes, while fallen trees or their parts, lying across slopes or anchored to living or dead trees or to rocks, are exceptionally effective as anti-avalanche "retaining walls" (Photo 180).

Photo 180 (J. Korbel)
Fallen logs on mountain slopes prevent soil erosion

Removing dead trees and other coarse woody debris from steep slopes or montane forests (particularly near the tree line) as well as harvesting living trees increases the risk of landslides and leads to the erosion of the soil by wind and water and the muddying of streams.

One more aspect of the importance of dead wood in mountainous regions is worth noting. Studies from the Gorce Mountains (southern Poland) have shown that upper montane coniferous stands, declining as a result of air pollution, high winds, insect outbreaks or fungal infections, are quickly replaced by rowan thickets, which effectively limit soil erosion and allow the forest to regenerate rapidly. Rowan seeds are dispersed mainly by birds that perch on dead trees – the removal of spruce snags would make their dispersal far more difficult.

4.2.7. Significance of tree throws and dead wood for soil processes

Tree throws – forest "orogeny"

Root systems torn out of the soil along with a windthrown tree play a very important role in forest ecosystems (Photos 36, 37, 41, 105, 181). Spruces are the most frequently uprooted trees, as they have very shallow root systems and are therefore especially vulnerable to strong winds.

The root plate of a freshly windthrown tree still has large clumps of soil and rocks sticking to it. Thus is created a unique microrelief, typical of natural forests, consisting of pits, and also mounds accumulating from the material falling off the root plates (Fig. 33). Because the topmost layers of soil have a significantly different composition and grain size (they consist mainly of sand and particulate matter) from the deeper layers (which are heavier, less permeable and clayey), the structures formed when a tree is uprooted offer the organisms colonizing them a great variety of substrates. While the mounds of sand and much organic matter accumulated on the root plate (e.g. mor humus and a thick layer of spruce needles) are less moist and more acidic than intact soil, the clayey floor of the

Photo 181 (J. Walencik) We intuitively associate primeval forests with large trees lying on the ground

pits holds water for a long time. Uprooting, an event inseparably connected with the death of trees and the production of dead wood, is thus a process which diversifies and rejuvenates forest sites. Falling trees cause temporary (given the lifetime of a natural forest) disturbances that permit species with a variety of ecological demands to coexist in a very small area (Fig. 34).

By minimizing the "risk" of trees uprooting, forest management practices impoverish and homogenize habitats. When windblows do occur, they are treated as catastrophic events, and their effects, as in the case of other disastrous occurrences, are quickly removed. This is done by cutting the fallen trees from their root plates and removing the logs from the forest. The now unbalanced root plates often fall back into the hollow created by the uprooting, wiping out the newly created microhabitats. Moreover, the common practice of manually or mechanically "preparing" the soil in managed forests does not remotely resemble the dynamics and soil structures exposed by the uprooting of trees.

When a tree "returns to dust"...

...and, buried under a layer of leaf litter and ground cover, blends into the forest floor, it does not automatically mean that the dead wood ceases to exist. Though not easily recognizable, the most persistent elements of wood will remain a distinguishable (because of the deep red hue) component of exogenous humus (ectohumus). Thus, the content and thickness of the uppermost soil layers in a naturally functioning forest are highly variable, both horizontally and vertically. Acidic coniferous sites are generally characterized by a thick ectohumus layer, the depth of which ranges from 0 cm, where uprooting was recent, to a few dozen cm, where a decaying trunk is rotting into the forest floor. In an oak-hornbeam forest, where ectohumus is reported to be generally lacking, its layers (often quite thick) are locally present under natural conditions as the remnants of decomposed logs. The conditions present in the ectohumus microhabitat are quite different from those of the surrounding mineral soil. The retention of large amounts of moisture in ectohumus consisting of rotten wood provides an ideal environment for pteridophytes, i.e. ferns, clubmosses and horsetails. On the other hand, wild garlic *Allium ursinum*, a species that in springtime forms dense carpets in oak-hornbeam stands in the Białowieża Forest, avoids ectohumus, leaving uncolonized patches that recall the outlines of decomposed logs. However, the almost totally decayed wood is inhabited and penetrated by many representatives of the soil fauna, including mites, springtails, myriapods, earthworms and other species; these are discussed at length in Chapter 4.1.2.

Recent studies have shown that a few decades after the removal of wood from coniferous forests has ceased, deposits of coarse woody debris have greatly enriched the site. This has led to changes in the ground vegetation, and species typically found in richer sites, such as broad-leaved trees characteristic of mesic deciduous communities, e.g. hornbeam, are now more common. Besides enrichment, the decomposition of dead wood improves the topsoil structure. Lignin, a major component of wood, provides many of the basic components of humus, and this, in turn, enhances the air-water ratio, absorption capabilities and thermal conditions of the soil.

Humus: Organic remains, mainly of plants, accumulated in soils (in the forest also on the soil surface as overburden humus) and in various stages of decay (humification, mineralization); woodland humus can be divided into the following types: mor, moder and mull, in which the intensity of organic matter decomposition is low, medium and high, respectively.

Fragmentation horizon: overburden humus, the layer of undecomposed or partially decomposed plant remains on the forest floor forming the organic horizon of the soil, overlying the humus horizon.

Absorption capacity of soil: the ability of solid soil particles to retain ions, mainly cations or chemical molecules dissolved in the soil air or in the soil solution; a high absorption capacity hinders the flushing of mineral nutrients from a soil.

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Chapter 4.2: Summary

An important part of the forest, dead wood is an exceptionally rich store of energy and chemical substances, which are indispensable for the proper functioning of forest ecosystems. Solar energy, captured and fixed by leaves during photosynthesis, is accumulated in the organic compounds making up the woody tissues. These substances contain great amounts of carbon derived from carbon dioxide absorbed from the atmosphere. The gradual metabolic oxidation of these compounds provides the energy supporting the life processes of organisms. Natural forest fires, e.g. caused by lightning, are also a way in which certain types of forests use the energy and nutrient residues stored in dead wood to initiate tree regeneration.

Although the relative contents of nitrogen and other minerals are not as high as in leaves, their total amounts in dead wood are enormous because of its much larger total volume. The slow rate of decay of dead wood stabilizes the trophic conditions in the ecosystem.

With its porous, sponge-like structure, dead wood in many forests is a vast reservoir of water supplied by both precipitation and that produced within the wood itself as a result of the metabolic processes of bacteria and fungi. This function is particularly important during periods of drought.

In swampy forests, like alder carrs, and riparian communities that are regularly flooded, young trees can grow only in microhabitats lying above the water level. Such sites are usually formed by decaying "nurse logs". The young trees develop root systems that wrap around and overgrow these logs, so that they can then function independently. A similar phenomenon occurs on a larger scale in montane and taiga spruce forests: there, decaying logs or stumps give a young tree a head start over other herbaceous plants or shrublets, with which it would normally have to compete for space, food and light.

Fallen trees protect developing seedlings and advanced regenerations from herbivorous mammals like red deer. In this way, they act as natural "pens", within the shelter of which young trees can quickly reach a safe height.

Dead wood exerts a critical influence on the quality of forest habitats. In mountainous regions, it counteracts the formation of avalanches and soil erosion, and facilitates tree regeneration after blowdowns. In wet and riparian communities, fallen trees can alter local water flow patterns. Uprooted trees are crucial to habitat formation in that they create a system of windthrow mounds and pits – new mini-landforms with radically different environmental conditions. Forest management practices, however, are intended to eliminate these forms, thereby homogenizing the surrounding environment. Decayed logs, wholly blended into the soil, form belts of thick layers of ectohumus – a distinctive habitat sought by some organisms but avoided by others.

4.3. Dead wood in watercourses

In forested landscapes of the temperate zone, trees usually also grow on the banks of rivers, so it is perfectly possible that dead trees or their remains will find their way into watercourses as a result of natural processes. Such coarse woody debris is a key component of both forest and aquatic ecosystems.

While modern foresters generally understand the necessity for dead wood in forests, its significance for aquatic environments, including rivers, is still not fully recognized by water managers. Moreover, fallen trees in watercourses are widely viewed by the public as rubbish that clutters them up and which should be removed as a matter of course: a river bed strewn with dead wood is perceived as being ill-maintained. Even if water managers ultimately do realize the ecological importance of coarse woody debris, they remain under public pressure to remove it.

Meanwhile, no aquatic ecosystem, at least in central Europe, can be healthy without a certain amount of coarse woody debris. In the European lowlands, wood is often the only hard substrate present in the rivers of sandy or clayey landscapes, providing a habitat that fundamentally enhances growth opportunities for aquatic flora, funga and fauna.

The stability of woody debris in a watercourse varies, owing not only to the characteristics of the wood itself, but also to the nature of the watercourse and its valley. A windthrown trunk with its root system still attached often remains where it has fallen, as does a log with its ends resting on opposite banks. Smaller pieces are more likely to be taken up and carried off by the water. On a river which is narrower than the height of the trees growing on its banks, finer woody debris and sediments start to accumulate when trees collapse into or

Photo 182 (P. Pawlaczyk)
A typical lowland riverbed in a forested landscape is always rich in fallen dead trees lying in the water

across it and remain *in situ* (Photo 182). On wider rivers, wood floats downstream and comes to rest on gravel deposits, where the river is wider and flows more slowly. The stability of these pieces of wood can, of course, be relative, as high waters can shift pieces that have remained stationary for quite a long time.

By generally reducing the energy of flowing water and slowing down the passage of flood waves, dead trees in watercourses boost the accretion of sediment and organic matter. Logs blocking small streams can cause the localized build-up of water and the formation of small cascades (Photo 183).

Coarse woody debris in a river with a gravel bottom prevents it from cutting too deeply into the substrate, limits excessive bank erosion and can even help to restore the bottom sediment structure. Increasing the roughness of river beds significantly reduces the magnitude of flood waves downstream. To give an example: along some rivers in the UK, it was estimated that wood accounted for about 75-98% of flow resistance, and that an adequate supply of dead wood in upstream sections of the catchment could reduce downstream flood surges by 5-10%. At the same time, coarse woody debris in a high-energy watercourse remains under its overwhelming influence and is often shifted, transported and re-deposited on embankments, stabilizing gravel banks in the process. In general, the presence of such debris assists the formation of braided channels and supports the development of banks and islands. However, the exact nature of these processes may depend on the particular river in question. In gravel bed rivers in North America, islands form around large dead trees in the current as a result of gravel deposition behind them. But in gravel bed mountain rivers in Europe, where there are no such trees because of the more radical transformation of the riparian landscape and the large-scale removal of dead wood, finer woody debris accumulates on gravel bars, stabilizing them and stimulating the growth of eyots upstream, where willow and poplar stems can take root and sprout. When water levels are high, coarse woody debris deposited on the alluvium contributes significantly to overbank sedimentation and thus to the development of floodplains. In lower energy rivers, including lowland gravel bed and sand bed rivers, the hydromorphological role of coarse woody debris is no less significant. Here, individual sections of trees and log jams also set up resistance to the flow. Water-borne sediment is deposited in the hydrological shadows of tree trunks and branches, leading to the development of bars. Deeps are scoured out under and behind the logs. Plunge pools, backwater pools, sand shadows (channel bars) and other formations are created (Fig. 38). The frequency and strength of high-water flows, as well as bank erosion govern the supply of logs to the channel; the logs, in turn, alter the pattern of channel formations and shape its course, also by stimulating lateral erosion.

Photo 183 (J. Korbel)
Dead trees slow the flow in mountain streams

In sand bed and sand-gravel bed lowland rivers, woody debris is the most common obstacle forcing the vertical movement of water, thereby regulating channel depths and inducing river water to migrate into the bottom sediments. The presence of woody debris is thus of key significance for the functioning of the hyporheic zone, i.e. the zone of contact between groundwater and river water in the river sediments, which is very important for certain types of river ecosystems (including the so-called *Ranunculus* rivers – a natural habitat protected in the Natura 2000 network).

Dead trees in a river are an important part of the processes underlying the functional links between the river and riparian habitats, including riparian forests. By modifying the shape of braided channels, erosion and accumulation, overbank flow through riparian zones or enabling wood to become embedded in alluvial deposits, coarse woody debris influences not only the river itself but also its floodplain. In doing so, processes triggered by the presence of logs in the stream overlap those associated with the occurrence of living trees on the banks and floodplains. The deposited debris enables trees to colonize the alluvium and facilitates the development of riparian forests, which in their turn become a source of coarse woody debris, further stimulating this process. These natural processes, once far more common, are now –

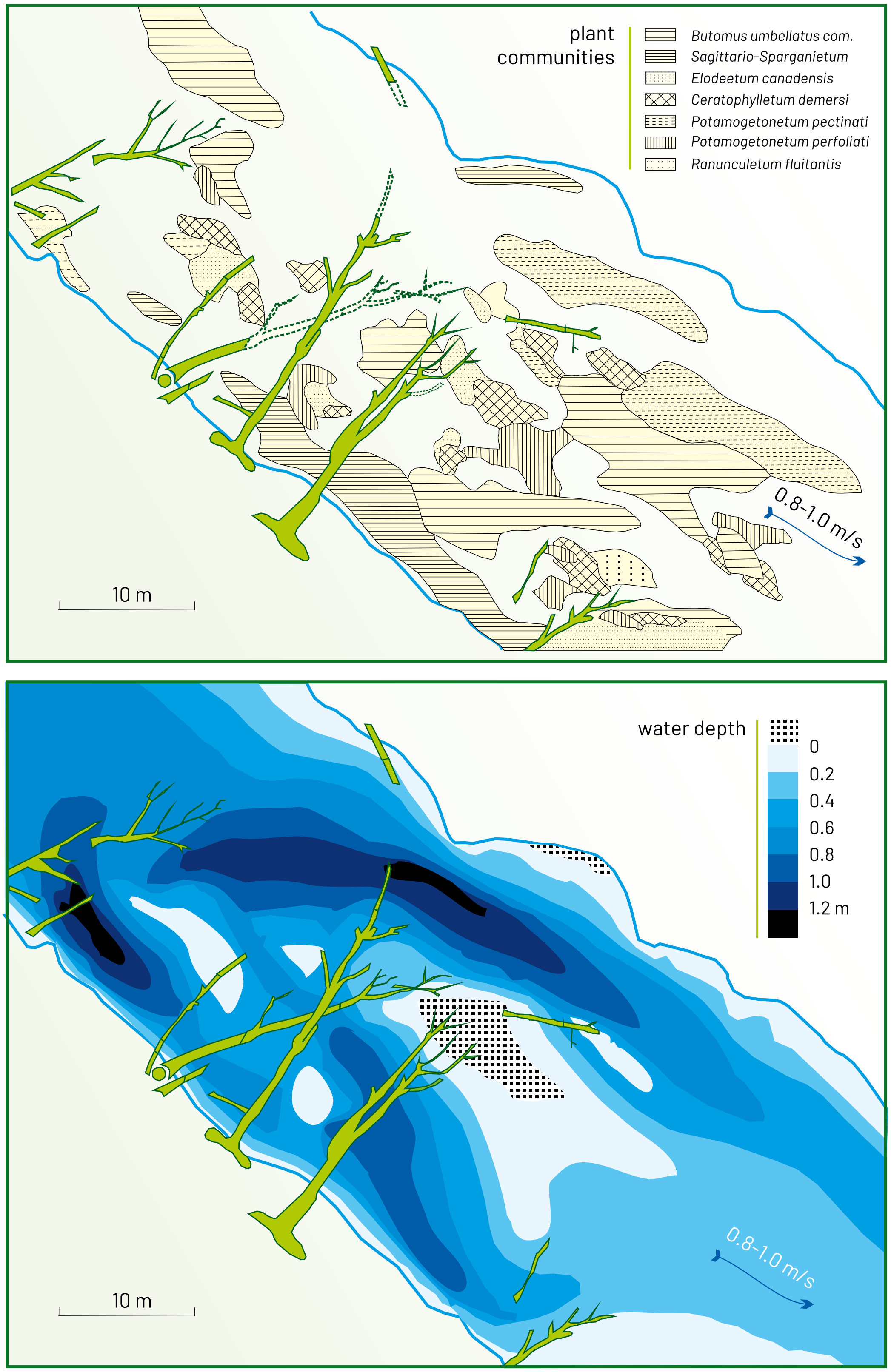

Fig. 38 Changes in river bed relief brought about by dead trees falling into the stream. The River Drawa in the Drawa National Park (after Pawlaczyk 1995)

especially in Europe – much diminished as a result of the significant and widespread anthropogenic reduction of the amount of dead wood in rivers.

These processes have the potential to affect entire landscapes. Researchers speculate that throughout the forested zones of North America, and probably other continents (including Europe), the large-scale removal of woody debris from rivers has dramatically altered entire river landscapes, transforming wide, braided channels retaining their connectivity with the floodplain into single-thread streams. At the landscape scale, coarse woody debris initiates and modifies the meandering of rivers and may locally contribute to bank erosion and the development of meanders, especially when logs divert the current towards the concave bank.

However, it can also stabilize banks undercut by erosion and reduce lateral river migration when logs are concentrated just below the eroded concave bank, deflecting the current away from it.

Both the coarse woody debris itself and the microhabitats it creates are key aspects of watercourse biodiversity. Many river ecologists have become convinced that, at least in the forest climate zone, a river devoid of dead trees will always be ecologically impoverished.

Trees present in a river provide a habitat for unique (not found elsewhere) species of aquatic invertebrates, especially certain species of molluscs, mayflies, caddisflies and water beetles, as well as hygrophilous fungi. Fine woody debris and leaves fallen from the trees are the main source of organic matter, particularly in the middle and upper reaches of rivers. Parts of trunks protruding above the water form habitats for invertebrates which later collapse into the water and become food for fish. Invertebrates on large woody debris can be extremely abundant at times – as many as 10,000 individuals/m^2. Invertebrates colonize the wood, lay their eggs, pupate and feed on the bacterial biofilm coating the surface of the wood. Coarse woody debris is crucial for maintaining biodiversity in rivers lacking hard substrates, e.g. lowland sand bed rivers.

Microhabitats associated with coarse woody debris are of key importance for numerous fish species. Fish congregate near trees, hiding in their hydrological shadow, which helps them avoid the strong currents when the water is high; they also use the pools and bars forming near coarse woody debris as hiding places when flows are low. By modifying the channel morphology and altering the flow of water, coarse woody debris makes rivers and their fish communities more resilient to hydrological extremes (both very low and very high water flows). Insectivores sometimes feed on invertebrates associated with coarse woody debris. Numerous studies have demonstrated the positive influence of coarse woody debris on fish reproduction and the growth of fry, especially in salmonids. Anglers have long known that many species of fish can be found near fallen trees, under which brown trout *Salmo trutta* morpha *fario*, for example, like to hide.

Fallen trees in the river bed are an important component of the foraging habitat of common kingfisher *Alcedo atthis*, and other birds use them for resting. Pools building up behind logs in mountain streams may play a crucial role in the life cycles of amphibians: there, the water flows more slowly, and the channel is deeper and wider.

Certain species of fungi thrive on riverine woody debris; for example, the sporocarps of tiger sawgill *Lentinus tigrinus* are common on logs submerged in rivers.

The dams built across watercourses by Eurasian beavers *Castor fiber* also consist of wood (Photo 69). These beaver ponds effectively retain water and are important biotopes for other valuable taxa, e.g. amphibians, European pond terrapin *Emys orbicularis*, Eurasian otter *Lutra lutra* and the yellow-spotted whiteface dragonfly *Leucorrhinia pectoralis*. Although beaver dams and ponds may locally obstruct fish mi-

Overbank flow:
a flow exceeding the bankfull stage when water flows out of the channel and into the valley. The periodic occurrence of such flows is a normal, natural feature of all rivers and streams which have not been completely regulated. The probability of overbank flows during the year depends on the type of watercourse and its valley, but the average for natural watercourses under the climatic and hydrological conditions prevalent in Poland is about 66%.

Photo 184 (P. Pawlaczyk)
Trees in the River Brda

Deflector: a component altering the direction of the flow, thus changing its course.

grations, they improve the hydrological regime, as well as the quality of water and food resources within the catchment area, and generally have an overall positive impact on river and riparian ecosystems along with their fish communities, including salmonids. At the catchment area level, these benefits usually outweigh the losses caused by beavers flooding grasslands and forests.

Interestingly, logs buried in river sediments preserve important paleogeographic information, making it possible to create a timeline of past geomorphological processes. What is known as bog oak is actually blackened oak wood which has spent a very long time in the alluvium and at one point must have been deposited in the river as coarse woody debris.

Coarse woody debris is without doubt an important and integral element of river ecosystems. Nevertheless, the presence of dead trees in a river often raises questions about safety. In most cases, however, the actual extent of the problem is exaggerated and is often fairly easily dealt with (see Chapter 5).

As our understanding deepens of the ecological significance of dead wood in rivers, the idea that coarse woody debris should be left in rivers or even restored has become an unquestioned aspect of river conservation strategies. The significance of dead trees for fish in trout rivers cannot be underestimated: this has long been recognized by anglers and ichthyologists. It was these groups that first postulated the retention or reintroduction of coarse woody debris to river environments. In North America, such notions began appearing as long ago as the 19^{th} century (an article addressing the need to leave dead trees in rivers as a means to protect trout was published in 1885), but it was not until the 1980s that they gained universal acceptance. American researchers summarized them as follows, "*As a result of the geomorphological and ecological importance of CWD in river channels in forested catchments, such debris requires careful management. In particular, indiscriminate removal of CWD should be avoided.*" Since then, our awareness of the importance of dead trees in rivers, for both the living components of river ecosystems and the hydromorphology and hydrology of entire river systems, has increased markedly. Present-day efforts to restore rivers or optimize fish habitats are very often founded on the premise that rivers are enriched by placing dead trees in their channels. Unlike boulders, for instance, wood is a natural element of almost every aquatic ecosystem in temperate forests, which is why it is very widely used to initiate channel restoration processes. Dozens of river restoration projects involving dead trees have been carried out in Germany, for example.

In the 1990s, on the previously regulated River Wda and its tributary the Trzebiocha in Pomerania (northern Poland), tree trunks together with their branches were purposely felled into the water at an angle of 45° to the river bed in order to improve the spawning conditions of the unique form of lake trout *Salmo trutta* morpha *lacustris* that inhabits Lake Wdzydze (the Wda flows through the lake). The intention being to restore the hydromorphological features of these watercourses, it was

Photo 185 (P. Pawlaczyk) Trees in the River Radunia

assumed that the trees would act as deflectors, initiating erosion of the opposite bank, which would give rise to shallows in their hydrological shadows suitable for trout fry and juveniles. This was one of the first examples of dead trees being intentionally used to improve habitat conditions in a European river. It was successful: these sections of the rivers today betray virtually no signs of their one-time deformations as a result *inter alia* of the processes initiated by dead trees.

The foremost, fundamental and obvious premise for using coarse woody debris to modify rivers is to leave as many fallen trees in the river as possible, that is, to cease their wholly unjustified yet often routine removal. This has already become an obvious basis for river conservation. More comprehensive approaches involve the active regeneration of wood resources in rivers. Coarse woody debris can be used in water maintenance measures, in particular the upkeep and protection of the channel's banks in such a way as to preserve its microhabitat diversity. Dead trees or their parts can become structural elements strengthening the banks of a watercourse and regulating the water flow as root wad revetments: trunks of dead trees built into the concave, eroded bank of a watercourse with the root wads exposed to the current, thus protect the bank from further erosion. Other techniques employed in river restoration projects include installing deflector logs; repairing banks using entire felled trees, tree logs and finer woody debris; anchoring logs in the current to enrich habitats; or felling trees crown-first into the current. Another approach involves building structures mimicking beaver dams out of wooden posts and branches.

The most advanced concepts of river restoration assume the comprehensive regeneration of the natural dynamics of coarse woody debris, including the processes relating to its supply, transportation and deposition. This means shaping the forests along streams in such a way that ensures the most effective continuous supply of dead wood to the watercourse. In most cases, this involves leaving entire patches of riparian forest undisturbed so that the trees in them can grow to larger sizes, die and ultimately fall into the water.

The idea of rebuilding the dead wood stock in watercourses, principally by not removing logs and coarse woody debris, has become recommended good practice in water management and surface water rewilding in Poland as well.

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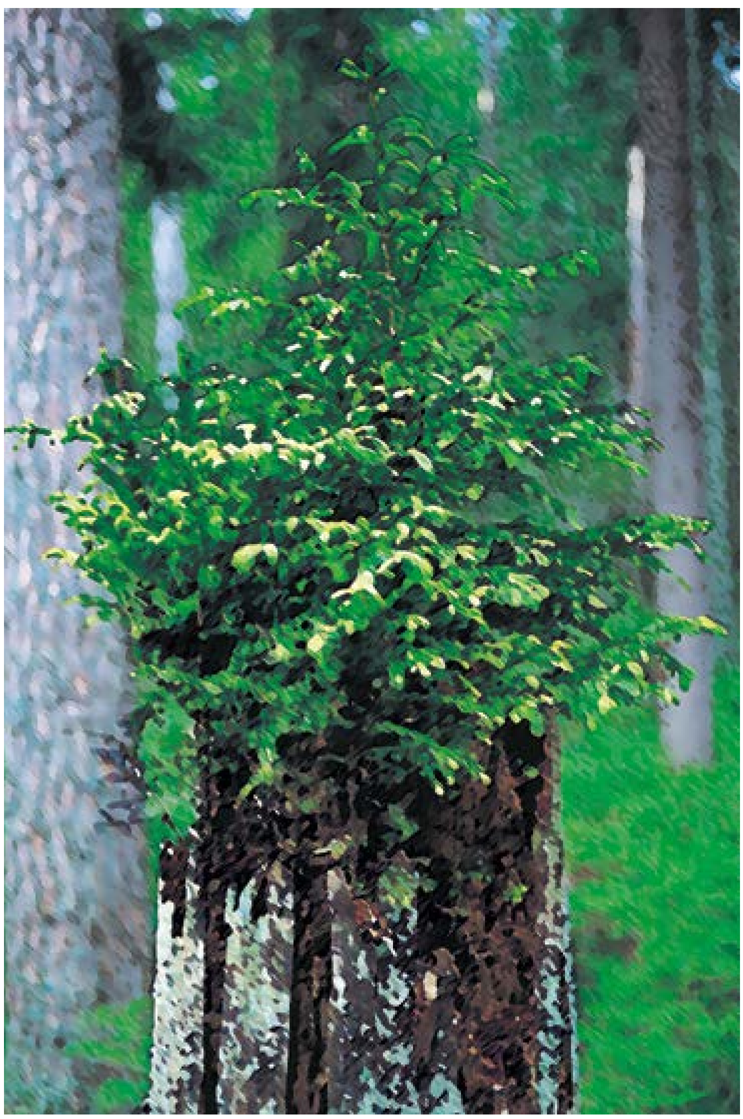
Chapter 4.3: Summary

Dead wood in streams and rivers benefits both abiotic and biotic aquatic environments. Among other things, it helps to dissipate the energy of floodwaters, increases the ability of watercourses to accumulate bottom sediments and rebalance the intensity of its transport, enhances the stability of gravel bars and variability in flow velocity and depth. The wood of fallen trees shapes the ecosystems of rivers and streams by providing habitats and enriching their physical diversity. It also serves as food for many aquatic organisms. Coarse woody debris is an integral component of aquatic ecosystems, without which they would not be able to function properly. Good maintenance practice for watercourses must involve leaving as many dead trees in the channel as possible. Stream rewilding often involves the restoration of submerged wood resources. Proper management of the watercourse and its catchment should also include maintaining the ability of riparian forests to continuously supply dead wood to the watercourse.

5

Dead wood in forest management and nature conservation



5.1. Dead wood in the forest – a growing understanding

Good taste and bad habits

Dead wood, in particular dead and fallen trees, has fascinated people for a long time, prompting them to reflect on the power of nature and the inevitability of death and decay – phenomena that eventually affect every living thing. These notions echo in romantic depictions of primeval forests, where dead trees play a prominent role. We find them in the beautiful verses of *Pan Tadeusz* by Adam Mickiewicz (see the Introduction), in the drawings of M. E. Andriolli and even in the tunes of Edvard Grieg's *Peer Gynt* suite. Dead wood symbolizes the untamed and mysterious ancient forest. Our sense of aesthetics favours a natural, wild, "chaotic" landscape over the orderliness of a "well-managed forest." When presented with a choice of decorations, such as photo calendars featuring images of wild and unmanaged forest full of dead wood and fallen trees or a properly tended and managed forest, we usually ask for the former.

Our intuitive, innate idea of the untamed primeval forest has been displaced by a landscape of managed forests modelled on intensively managed agricultural fields. Since wood has become a valuable commodity, forestry has been dominated by the determination to eliminate anything that would reduce the commercial value of timber. The old concept of forest protection, understood as the protection of habitats for game animals, has been replaced by forest protection equated with the fight against tree pathogens and "pests." The profitability of forest products depends upon a reliable supply of raw materials of the requisite quality, so, in order to meet this objective, foresters have modified species compositions and limited the maximum ages of harvested trees to reduce the risk of waste. Natural tree mortality due to old age, fungal infection or insect infestation is highly undesirable and perceived as a waste of the commodity. The swift removal of trees inhabited by "pests" is supposed to reduce the loss of marketable timber and prevent the further dispersal of unwanted species. Such a forest no longer embraces the complete life cycle of trees from seedling to death and the natural decomposition of the woody tissue. Slash burning is common practice in many European forests as a preventive measure against "pest" infestation. Unfortunately, these techniques have also been applied extensively in natural forest complexes, such as the Białowieża Forest (Photo 101). The stereotypical reasoning that "dead wood = pest hatchery" has long been dominant in European forest management and has resulted in a regime of forest hygiene that removes every last piece of dead wood, whether it is used by cambiophages or not. The belief that the presence of dead and dying trees is a sign of

Fig. 39 An illustration to "Pan Tadeusz", 1881 (M.E. Andriolli)

bad management still persists, also in the public perception of forested areas. To this day, forest managers and users are weighed down by the idea of protecting forests by pre-emptively removing dead and dying trees, regardless of whether it is actually relevant to breaking the chain of events referred to as "forest disease." There is still a deeply rooted conviction that a forest with lots of dead trees is a "source of disease", spreading "pests" and pathogens to neighbouring stands, even though this is usually untrue. Those foresters who allow dead trees to accumulate in the forest risk being rebuked for failing to apply the "appropriate hygiene standards." Furthermore, the view of dead wood as a waste of a resource that "could be used" plays a large part in shaping public perceptions.

However, even in the times when the vast majority of foresters thought of decaying wood as a threat to forests, some did recognize the ecological significance of coarse woody debris. In 1885, forestry superintendent Tschepske, managing the Pieńsk Forest District in Lower Silesia, wrote about the necessity of retaining ancient, decaying oaks (200-300 years old) in some parts of the forest so that "insectivorous birds had places to nest." In the early 20th century, Wilhelm Rüdiger, a passionate ornithologist and a forester from Żeleźnica on the River Drawa, appealed to his colleagues to leave old, hollow trees, especially oaks and beeches, so they could become nesting sites for common goldeneyes. He would also use pieces of rotted-out beech trunks to make artificial hollows for flycatchers and place them throughout his forest.

A gradual paradigm shift

Naturalists have long been interested in dying and decaying wood as a habitat for a wide variety of interconnected fungi, slime moulds, arthropods and other organisms, many of them very rare. However, it was not until the agreements to protect biodiversity had been made by states attending the Rio de Janeiro Earth Summit in 1992 that decision-makers began to take notice of the biological resources associated with dead wood. As a result, widespread educational campaigns were undertaken already in the 1990s to promote the incredible diversity of the dead wood "microcosm." The aim was to raise awareness of the value of "messy" forests, where the variety of "useful" saproxylic species enriches the ecosystem and makes it healthier. A good example of such a campaign was "A *richer forest*", a project carried out since the early 1990s in Scandinavia, where, among other things, it gradually brought universal recognition of the presence of dead wood as one of the main criteria for assessing the naturalness of an ecosystem. Similar trends started appearing in other countries, becoming especially popular at the start of the 21st century. Another example is the evolution of the UK Forestry Commission's guidance, which in 2002 issued a recommendation with the following long-term target for the management of native British forests: "40-100 *m^3 ha^{-1} of deadwood ≥20 cm diameter*", supplemented by specific short-term goals, "*Maintain at least 20-40 m^3 ha^{-1} of deadwood ≥20 cm diameter. Retain, open up and pollard any existing veteran trees* [the current Polish Instruction for Forest Protection uses an equivalent term – "habitat trees"]. *Identify and retain potential veteran trees or trees with decaying wood (20% of trees in stand). Retain 20-40% of all cut wood on site; leave all fallen deadwood if possible.*" German and French forestry policies suggested maintaining the stock of dead wood at the level of at least 10-15 m^3 per hectare. Forest certification schemes began to include requirements to set aside areas of sufficient size where no tree would be harvested and no dead wood removed. Little by little, the concern to preserve and restore at least some dead wood in forests has become the norm in European forestry. Nearly all modern publications about the opportunities to integrate biodiversity protection into forest management put a strong emphasis on this aspect. The presence of dead wood (along with minimum required quantities in certain instances) has become one of the more important indicators of sustainable forest management within the FSC forest certification scheme.

In the USA, it has been recommended for several decades to leave standing or lying dead trees even on golf courses in order to ensure a living environment for saproxylic organisms and increase awareness of these issues among players and spectators.

In 2003, during the Ministerial Conference on the Protection of Forests in Europe (MCPFE), which is an ongoing process aimed at protecting and preserving the European forest heritage, a set of pan-European Indicators for Sustainable Forest Management were adopted. One of these indicators concerns the amount of decaying wood per hectare of forest. It emphasizes that "*deadwood is a habitat for a wide array of organisms, and after humification it constitutes an important component of forest soil. Many species are dependent, during some part of their life cycle, upon moribund or dead standing and fallen trees or upon wood-inhabiting fungi or other species. Because of the lack of deadwood, many of the dependent species are endangered.*" The design of this indicator takes into account the need to ensure the diversity of dead wood by registering the volume of fallen logs and standing dead trees separately. It was decided that it should cover portions of above-stump woody biomass (excluding stumps and roots, but this does not negate their ecological impor-

FSC, Forest Stewardship Council:
an international organization awarding interested forest managers with certificates confirming "environmentally appropriate, socially beneficial, and economically viable management of the world's forests."

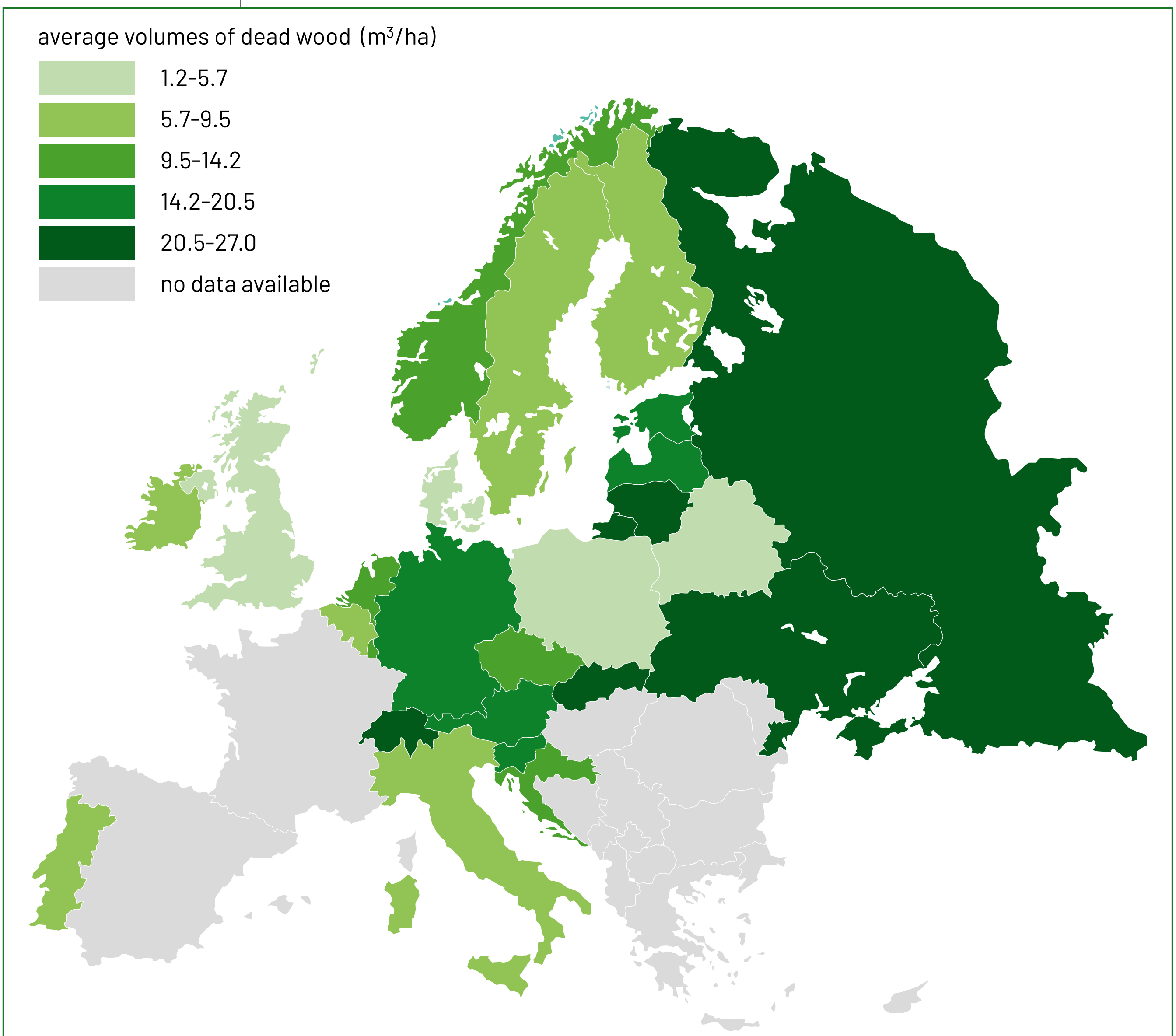
FSC forest management certification confirms that the forest is being managed in accordance with the worldwide FSC standard. Specific indicators included in National Standards are developed for each country based on International Generic Indicators. One of these International Generic Indicators states that "sufficient amounts of dead and decaying biomass are retained in order to conserve environmental values", while the instruction for defining standards in Poland recommends that they should include "thresholds and guidelines for the retention and recruitment of woody debris." The FSC standard also requires the designation of so-called reference ecosystems within forests and leaving them without intervention.

tance) longer than 2 m and wider than 7-10 cm. Since the year 2000, the European Environmental Agency (EEA) in Copenhagen has been collecting statistical data on dead wood based on a similar interpretation as one of the key indicators of sustainable development. Although not all countries have submitted appropriate data, some regularities can already be seen at the European scale (Fig. 40). Between 2000 and 2010, the average reported volume increased from ca 8 to ca 10 m³/ha, while national averages reported by the EEA as of 2010 ranged from 3.9 m³/ha in Great Britain and 5.6 m³/ha in Poland to 26.2 m³/ha in Slovakia, 23 m³/ha in Lithuania, 21.3 m³/ha in Switzerland, 20.3 m³/ha in Austria, 19 m³/ha in Slovenia, 17.7 m³/ha in Latvia and 15 m³/ha in Germany.

Also, within the framework of monitoring the conservation status of natural habitats (in connection with the implementation of the EU Habitats Directive) and developing guidelines and examples of good practice in forest conservation within the Natura 2000 network coordinated by the Directorate General for Environment of the European Commission, it was pointed out that the amount of dead wood, as well as some of its quality characteristics, can be good indicators of the conservation status of biodiversity and natural habitats, including the status of habitats of some species. Species associated with dead wood, such as woodpeckers, have increasingly come to be recognized as key species and indicators of forest health.

In Poland, the volume of fallen and standing dead trees has been monitored since the end of the 20th century under the Large-Scale Forest Inventory (involving the evaluation of forest characteristics on evenly distributed sample plots, which provides meaningful data with average values for larger geographic regions or for large groups of forests). The 2012 version of the Instruction for Forest Management introduced the possibility of assessing the volume of dead wood at the level of individual forest districts during timber cruising.

Fig. 40 Average quantities of dead wood in European forests according to the European Environmental Agency (data correct as of 2020)



The notion that a certain amount of dead wood must be left in the forest began to gain traction in Polish forestry at the end of the 20th century. In the northern and western parts of the country, more than a dozen forest districts have pledged to establish "refuges for saproxylic organisms" in cooperation with the Naturalists' Club (Klub Przyrodników), a non-governmental conservation organization. In 2003, the setting up of such refuges, where dead wood would be permitted to accumulate, was declared mandatory in all forest districts supervised by the Regional Directorate of the State Forests in Piła, and a few other regional directorates followed suit. In this context, the first edition of this book, published in 2004, was one of the more significant Polish publications on the role of dead wood in forests.

Gradually, more and more foresters have become aware of the positive role of dead wood in forest ecosystems. Provisions reflecting the importance of dead wood in forests have also made their way into documents regulating forest management in Poland (Principles of Silviculture, Instruction for Forest Protection), such as the rule stipulating the retention of so-called "sterile" woody debris (dead wood that is not and will not be used by "pests"). According to the current Instruction for Forest Protection from 2012, one of the fundamental principles of forest protection is to enable a specified volume of dead trees and their sections in managed forests to decompose naturally.

At the end of the 20th century, a principle was introduced to retain some trees during final cutting, allowing them to reach maturity and natural death. This would usually be up to 5% of the stand volume, although in the most ecologically valuable forests this proportion could be raised to 7-10%. Such groups of trees would provide a source of coarse woody debris for the next generation of the stand and could increase the chance for the stock of habitat trees to regenerate (very old and large trees host incomparably more tree-related microhabitats). Unfortunately, the new version of the Principles of Silviculture issued in 2012 restricts this practice to clearcutting only, permitting no more than 5% of the stand to be retained. Nevertheless, the criteria of the FSC Certification Scheme require small patches of stands to be left in place, and most of the Regional Directorates of the State Forests continue to boast about having received an FSC certificate.

In accordance with the long-standing principles of forest protection and silviculture adopted in Poland, trees with hollows are also protected. Currently, this type of protection ("leaving in the forest until biological death and natural decomposition") extends to the entire category of "habitat trees", which include in particular trees with *rotted-out cores*, *trunk wounds*, *damage caused by lightning strikes*, *hollows or rot (also formed in wounds left after dead branches have fallen off)*; *trees inhabited by bracket fungi*; *broken trees*; *trees with partially dead crowns (more than one-third)*; i.e. trees with tree-related microhabitats.

The practice of linking spruce regeneration with the presence of decaying wood has even been tried out in high altitude stands. It has been repeatedly demonstrated that the removal of dead trees disrupts regeneration processes in upper montane spruce forests. A common practice, especially in alpine zones, is to leave dead spruce trees to decompose naturally, or even to designate entire patches of upper montane spruce forests as reference stands, which are to be left unmanaged. In rare instances of the artificial regeneration of upper montane forests, spruce seedlings are planted next to the retained logs and stumps.

The idea of retaining so-called "sterile" dead wood was accepted by foresters with almost no resistance. At the same time, however, it was strongly recommended to remove all "active" dead wood, i.e. coarse woody debris colonized by "harmful species". Maintaining "an appropriate state of forest hygiene," based on the application of suitable "pest control" measures, like burning spruce and pine branches or debarking stumps, was still one of the priorities of forest managers (Photos 100, 101, 103), while "sterile" dead wood was often removed and sold as fuelwood. The Instruction for Forest Protection used in 2011-2014 recommended leaving "a certain amount" of wood to decompose naturally, but suggested that this should not exceed 0.5 m^3/ha in coniferous stands and 2 m^3/ha in broad-leaved stands. But any dead wood classified as "sterile" must earlier have been "active". Any suitable piece of "healthy" wood, standing or fallen, is sooner or later colonized by organisms that will gradually break it down. Species that ultimately kill trees are needed to ensure the continuity of microhabitats, which in turn are necessary for the development of thousands of other species associated with the successive stages of wood decay. Therefore, forest ecosystems simply cannot function naturally if dead wood is removed or substantially reduced! What was not completely understood was that merely leaving slash or wood chips in the forest would not be sufficient to conserve the biodiversity of dead-wood related organisms, because many of them require the presence of large logs. Until 2011, there were no effective mechanisms allowing for the comprehensive monitoring of the quantity and quality of dead wood in forests, e.g. controlling this parameter as part of forest management planning activities. Only random studies were available, indicating that the resources of dead wood in Polish forests were several times lower than the minimum required to ensure the survival of the organisms associated with it.

Forest management planning:
an aspect of practical forestry concerned with drawing up detailed 10-year plans for forest district operations.

Instruction for Forest Protection Volume I

Annex to the Ordinance No. 57 of the General Director of the State Forests, Warsaw 2012

Dead wood and habitat trees in the Instruction for Forest Protection: "One of the tasks of modern multi-purpose forestry is to manage dead organic matter in the forest. The wood of dead trees is an important component of the ecosystem with a positive impact on the physical, chemical and biological properties of the soil, ensuring good growing conditions for many organisms. Most endangered and declining species in the forest fauna are at least partially associated at some point during their life cycles with old trees in various physiological conditions (from healthy trees to dead and dying specimens), trees with hollows and stumps. Trees and decaying wood provide habitats and refuges for thousands of forest organisms (bacteria, fungi, algae, lichens, vascular plants, molluscs, insects, amphibians, reptiles, birds and small mammals). These organisms become threatened when, for example, snags, broken trees and windthrows are removed indiscriminately, and slash or branches are burnt.

In order to ensure the stability of forest ecosystems and the continuity of their functions, biodiversity shall be protected by: (...) retaining habitat trees in the forests until their biological death and natural decomposition. Habitat trees are, for instance:

a) living and dead trees with localized rot (decay) and trees hosting the fruiting bodies of bracket fungi (conks):
   - with clearly visible trunk decay, e.g. trees with easily distinguishable open wounds on the trunk, hollows filled with rotted wood, damage caused by a lightning strike, broken trees,
   - with fruiting bodies of fungi (conks),
   - with a partially (over one-third) dead crown (dead boughs and branches in the crown);
b) trees with hollows:
   - inhabited by birds or other animals,
   - containing rot formed in the wounds after a dead branch has broken off,
   - filled with rotted woody material;
c) trees with atypical growth habits:
   - so-called unusual forms,
   - trees without a crown as a result of its having broken off;
d) trees exhibiting unusual morphological forms of cones, bark, branches, etc.;
e) trees of native habitat species, occurring naturally or introduced, enhancing foraging resources for the fauna, and nectariferous trees, improving landscape diversity, such as apple, pear, wild cherry, cherry plum and other trees;
f) trees with birds' nests > 25 cm in diameter;
g) residual trees: trees and groups of trees left to be removed during the next cutting cycle or to die and decompose naturally;
h) trees hosting protected species of fungi, plants and animals;
i) trees clearly differentiated by age or size from other trees in the area;
j) trees representing the heritage of silviculture, e.g. specimens of exotic species (of extraordinary age or size), all experimental plantations established before 1945 (regardless of species);
k) trees that are part of spatial layouts, e.g. avenues, rows of trees.

The following principles shall be applied in the protection of ecosystems: (...) leaving a certain volume of dead trees and their debris in managed forests to decompose naturally.

The aim of protective measures against pests and pathogens is to reduce the occurrence of these organisms to a level that does not cause economically significant damage. Protective measures should be applied only in the case of threats causing significant damage to the forest and disrupting its various functions, and when timber production is at risk.

Preventive measures include: (...) influencing the cycle of matter and energy in forest ecosystems, by e.g.:

- the controlled use of phytophagous insect outbreaks;
- (...) leaving a certain volume of dead trees and their debris in managed forests to decompose naturally;
- abandoning the practice of burning slash, including small branches and needles, during the post-harvesting clear-up, with the exception of endangered areas.

From the point of view of protecting forests and improving their resilience, silvicultural activities should specifically target: (...) the continuity of all phases of tree and stand development and the decomposition of dead trees.

(...) Standing and fallen dead trees, slash and treetops abandoned by species feeding under the bark and colonized by cambiophagous insects should be left in the forest until their biological decomposition."

Most foresters have gradually become aware of the importance of dead wood in the ecosystem and the need to protect its resources. Poland's accession to the European Union and the implementation of the Natura 2000 network in 2004 proved pivotal in this process. Within a few years, almost 40% of Polish forests were included in the Natura 2000 network. Not only was an adequate supply of dead wood required by many species protected within the network (e.g. saproxylic insects, some species of forest birds – see Chapter 5.3), but it was also a factor determining the favourable state of natural habitats. Confronted with contemporary ecological knowledge, both foresters and other naturalists realized that the quantities in question would have to be several times greater than previously imagined.

The new set of principles and instructions for forest management implemented in 2011 brought with it new, binding guidelines for foresters. The new Instruction for Forest Management made it possible to assess the average quantity of dead wood by taking measurements on circular sample plots as part of forest management activities carried out in forest districts. The new Instruction moved away from indicating maximum amounts of dead wood that can remain in the forest, instead emphasizing the need to leave dead trees to decompose naturally. It also clearly specified the need to protect and retain habitat trees, including dead trees, uprooted trees, trees with portions of dead woody tissue and tree-related microhabitats (including trees with hollows, rot etc.).

The question now being discussed in Poland is no longer whether dead wood is needed in the forest, but how much of it is needed, what are the best ways of bringing its amounts up to target levels, how it will impact the economics of forest management, what cost will be acceptable, and also how to address concerns that dead trees could facilitate the dispersal of organisms endangering trees which, though still alive, have been weakened by climate change.

Many foresters are still of the opinion that dead wood can be left in place, but only as individual trees, whereas groups of dead trees should be removed. However, the reality is that tree mortality processes are not normally linear, and trees often die or are broken en masse. These are precisely the kinds of events that should be used as opportunities for regenerating dead wood resources.

Even so, these general principles of dead wood conservation are usually suspended whenever an "extraordinary event" occurs, such as a blowdown affecting a very large area or an insect outbreak. The consequences of climate change are also of great concern to foresters. Natural disasters are becoming more and more common, e.g. large-scale damage caused by very high winds or insect outbreaks on a vast scale induced by the weakening of trees as a result of prolonged dry periods, the unprecedented mass mortality of certain tree species (usually caused by a complex set of factors) and the fact that new species are being designated as harmful organisms, e.g. European mistletoe *Viscum album* and sharp-dentated bark beetle *Ips acuminatus*. The usual response, especially in the face of incomplete knowledge and lack of experience, is to remove all dead and dying trees on the assumption that this will effectively prevent further mortality or with the intention of clearing the area and preparing it for the next generation of trees. From an ecological standpoint, such measures are often misguided (see below) and compromise the opportunity to use the event as a means to increase the supply of dead wood.

In consequence, volumes of dead wood in Polish forests are increasing, albeit rather slowly, and remain very low in some parts of the country. Data collected during the 2020 Large-Scale Forest Inventory indicate that the volume of dead wood in Polish forests increased from 5.8 m^3/ha in 2010 to 8.4 m^3/ha in 2019 (and from 5.2 m^3/ha to 8.0 m^3/ha in forests managed by the State Forests). It was also found that dead wood resources were geographically highly diversified. For example, the volume of dead wood did not exceed 5 m^3/ha in forests supervised by the Regional State Forest Directorates in Toruń, Piła, Zielona Góra and Szczecin, but ranged from 5 to 6 m^3/ha in forests run by the Regional State Forest Directorates in Szczecinek and Warsaw, and exceeded 24 m^3/ha in the forests of the Regional State Forest Directorate in Krosno.

Moreover, implementation of the principle of retaining habitat trees, despite what foresters frequently declare, is very uneven in practice. There have been attempts to whittle down the definition of "habitat trees" to just "trees with hollows", and then only those with hollows suitable for birds. Meanwhile, every cavity inside a tree is a microhabitat important for some organisms and should be treated as one of the features central to a habitat tree. It is often believed that habitat trees, including dead ones, can be protected, but only to the extent that they do not interfere with harvesting and silvicultural operations; in actual fact, however, they should be protected so that they can become part of the future generation of the stand. Under the pretext of "ensuring the safety of people in the forest" (see Chapter 5.4), habitat trees are sometimes removed from places where people seldom go. Because each habitat tree is "damaged" to some extent, it can easily be deemed "unsafe", and this can lead to the wholesale elimination of such trees from forests.

In spite of all this, it seems that we are on the verge of an inevitable paradigm shift as regards

Harvesting methods: A set of principles and activities aimed at creating the most favourable conditions for the regeneration of appropriate species of trees and obtaining the desired structure of the stand; harvesting methods include clearcutting, shelterwood cutting, a mixed system with gap cutting (first stage) and shelterwood cutting or clearcutting (second stage), irregular shelterwood cutting and single-tree selection cutting.

Clearcutting (type I): a type of harvesting method in which all the trees are removed at the same time from a significant area (up to 4-6 ha in size) and usually replaced with young trees (artificial regeneration).

Polycyclic harvest systems: types of harvesting methods in which trees are removed gradually by thinning the stand over the course of several cutting stages (shelterwood cutting, type II), removing trees from smaller areas within a stand several years before removing the rest of the stand (mixed system with gap cutting [first stage] and shelterwood cutting or clearcutting [second stage], type III), a complex sequence of thinning and cutting suited to the biology of particular tree species (irregular shelterwood cutting, type IV), or the continuous removal of individual trees (single-tree selection cutting, type V).

Photo 186 (P. Pawlaczyk)
Examples of habitat trees

how forestry deals with dead trees and tree-related microhabitats. Forestry has moved on, though not without much hesitation, from eliminating dead wood to retaining at least some of it. In contrast, the forestry of the future will strive to shape and maintain forests rich in dead trees and microhabitats, which means actively managing their resources, for example, by earmarking certain trees for this purpose, allowing them to mature, develop their full habitat potential and eventually become dead wood. Around the world and in Europe, there are already examples of forests consciously managed in such a way as to preserve some of their economic value at the same time as restoring, adjusting and maintaining the tree-related microhabitats and large volumes of dead wood needed to optimize the natural and social functions of the forest.

5.2. Dead wood and nature conservation

Dead wood as a component of protected ecosystems and an indicator of their status

As mentioned above, the presence of plants, fungi and animals associated with dead trees, particularly obligate saproxylic organisms, is a reliable indicator of the naturalness of forest ecosystems. Many of these species are rare and endangered, so their conservation is of paramount importance for the maintenance of forest biodiversity. Therefore, from the viewpoint of maintaining all species in forests, the more decaying wood in the forest, the better. Usually, the species richness of a forest is positively correlated with the number of dead trees. Areas with greater amounts of dead wood support more species listed in the Red Book and Red Lists of endangered species than areas where dead trees are not as abundant. Large volumes and a broad diversity of dead wood and tree-related microhabitats are typical of old growth forests, which are increasingly being seen as absolutely crucial. These are also the characteristics that can be deliberately shaped, for example, by restoring old growth features in forests impoverished by former management practices.

Modern conservation plans for the environmentally most valuable areas take this problem into account. Ensuring and restoring an adequate supply of dead wood is usually one of the main conservation objectives.

But in the past, this was not obvious, even as recently as 20 years ago. The approach to nature conservation in Polish national parks and nature reserves was based on the premise that dead wood posed a threat to the forest ecosystem. According to the internal regulations of the national parks, the forests situated within them were to be managed using the standard procedures specified in the Instruction for Forest Protection in force at the time. Exceptions could only be made for parts of a forest subject to strict formal protection, i.e. free in perpetuity from any interference in natural processes. "Moderate control of tree pest infestation" was accepted as the norm in the management of national parks. Passive conservation applied only to small areas of national parks: this ruled out any type of intervention, including the removal of wood from the ecosystem, and was perceived as some kind of extravagance and a risky scientific experiment. It could also be temporarily suspended in some cases. Similarly, the removal of broken trees, windthrows and snags from many nature reserves was sometimes treated as a standard protective measure.

Today, that situation has changed. An important recommendation was made in 2007 by the National Nature Conservation Council: "*Processes of tree mortality caused by various factors are a natural part of the functioning of the forest ecosystem (...). In light of the provisions of the Act on forests, the concept of "harmful organisms" must always be interpreted in the context of the function performed by a given forest. A "harmful organism" can only be understood as one that effectively prevents the forest from fulfilling its function, i.e. the function it was intended for. This means that in forests located within nature reserves, "harmful organisms" are only those that prevent the implementation of nature conservation, the preservation of protected forest ecosystems and their processes, as well as the preservation of biodiversity. Thus, the concept of a "harmful organism" in a nature reserve or national park takes on a completely different meaning than in a multi-purpose forest. In protected forests, organisms whose negative impact is limited to economic losses but does not affect long-term conservation goals, cannot be considered "harmful" (...). It should be the norm to leave all dead and dying trees in the forest eco-*

systems of nature reserves and national parks, and not to focus on eradicating "harmful organisms (...)". Nowadays, most conservation action plans in national parks take into account the risk of "*impoverishment of forest communities, especially with respect to the species richness of fungi and invertebrates, resulting from a smaller proportion of old trees in the stands*" (this notion can be formulated in various ways; the phrasing quoted above, which seems to be one of the most apt, is taken from the Ordinance of the Minister of Environment on the protective measures to be applied in the Świętokrzyski National Park). Similar changes have occurred in relation to the protection of nature reserves. Conservation plans currently being drawn up more and more often include provisions stipulating that all or much of the dead wood should be left in place. Even when active forest protection measures are planned and carried out, i.e. cutting down some trees in order to achieve the natural regeneration of the stand or to create conditions for the growth of young trees, it is sometimes (why only sometimes?) envisaged to leave the felled trees in the ecosystem to decompose naturally.

However, it still happens, though less and less often, that the managers of some national parks and reserves are stuck in the old ways and painstakingly remove dead and dying trees from protected forests, thereby destroying a component of the ecosystem they ought to be protecting. This is especially the case when large-scale tree mortality events occur, e.g. when a forest stand in a protected ecosystem is destroyed by wind or fire (see Chapter 5.3). The removal of dead trees may be sometimes justified by safety concerns (see Chapter 5.4).

The objective of Natura 2000 sites is "the favourable conservation status of natural habitats", which should be considered in the context of Article 2(1) of the Habitats Directive: "*The aim of this Directive shall be to contribute towards ensuring bio-diversity through the conservation of natural habitats (...)*." In view of the links between biodiversity and dead wood resources highlighted in the previous chapters, the search for criteria of that favourable conservation status of forest habitats in all EU countries takes into account, among other things, different forms of dead wood and other microhabitats associated with trees, which are crucial for biodiversity. In virtually all EU countries, the proportion of dead and old trees or trees with specific tree-related microhabitats is factored in when the status of forest habitats is assessed, although the technical details and threshold values may vary. On the other hand, conservation planning in Natura 2000 sites often aims to improve the quantity, quality and diversity of such structural elements.

Photo 187 (P. Pawlaczyk)
The Buczyna Nature Reserve near Długa Goślina in Wielkopolska Province. The naturalness and favourable conservation status of the beech forest ecosystem has been restored as a result of a group of beeches having been snapped by the wind

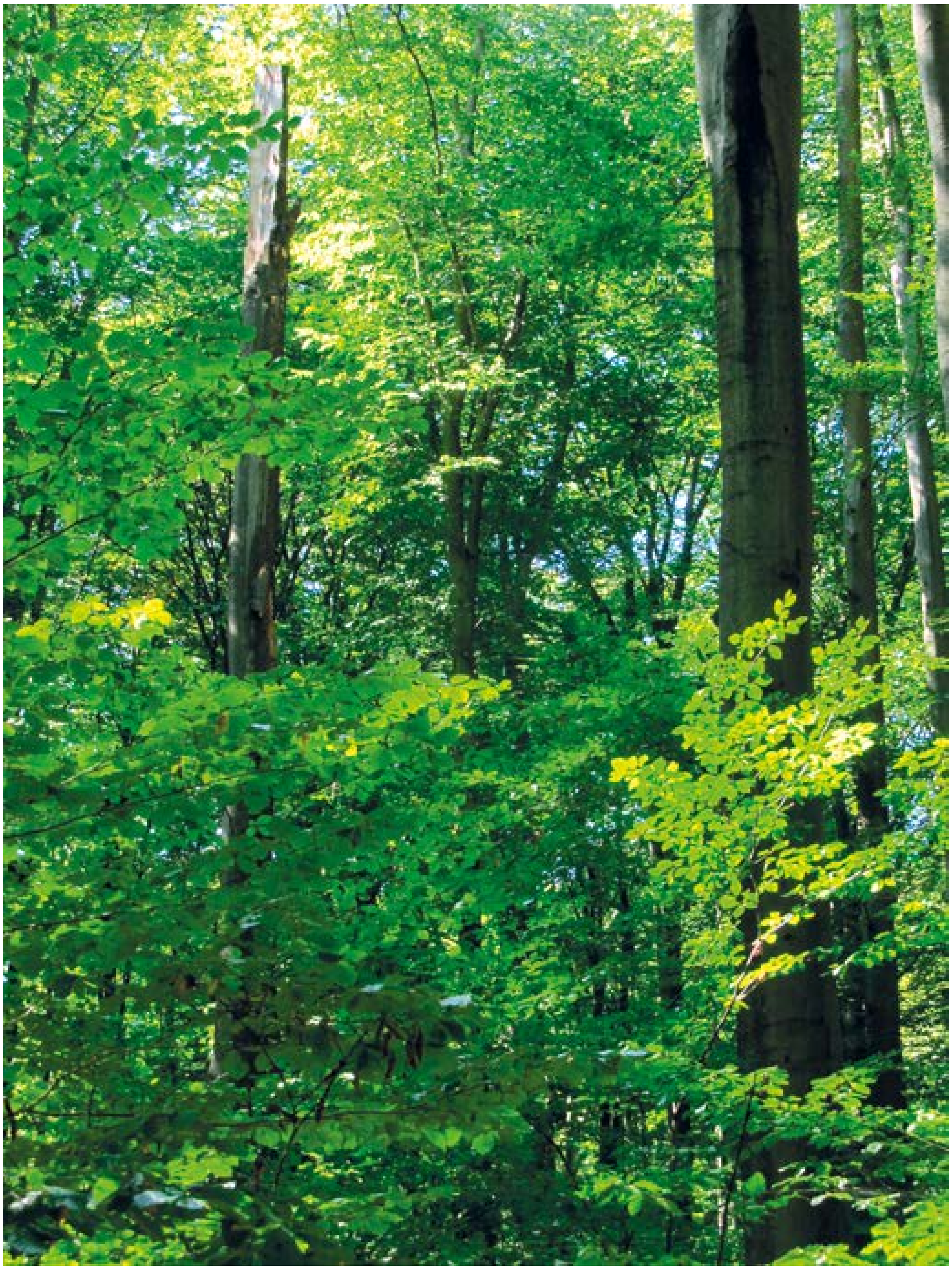


Photo 188 (P. Pawlaczyk)
Before the Drawa National Park was established in 1990, the beech forests in the park were typical managed forests. After 30 years of passive protection, they have returned to their proper conservation status and the natural diversity of their inhabitant organisms is gradually being restored. Tree mortality processes have contributed significantly to this outcome

In connection with the implementation of the Habitats Directive and standardized reporting across the European Union, all EU countries have developed national methodologies for assessing the status of natural habitats, based on a universal set of parameters: the area of the habitat, its structure, functions and conservation prospects. However, criteria vary from country to country in terms of specific indicators for assessing ecosystem structure. The general understanding of the natural significance of dead trees and habitat trees means that there is currently no country that does not use indicators relating to the presence and quantity of such elements to assess forest habitats. But while the idea itself is shared, the ways in which it is put into practice vary significantly. For example, in Brandenburg (Germany), a 40 m^3/ha volume of dead wood was adopted as the threshold for the favourable conservation status of Natura 2000 habitats. In Bulgaria, the team of H. Zingstra, tasked with developing a system to assess the conservation status of natural habitats, assumed that "for a forest habitat to achieve favourable conservation status, dead wood should constitute more than 8% of the stand volume and at the same time there should be at least 10 standing dead trees per hectare." In the Baltic states, it was recommended to keep the volume of dead trees above 50 m^3/ha in natural boreal forests and alder carrs, and at least 20-30 m^3/ha in restored managed forests, while maintaining the full spectrum of decomposition stages. Many other countries adopted criteria that are much less ambitious and sometimes even lacking any ambition whatsoever – a few m³/ha or 1-3 larger-sized dead trees per hectare.

In Poland, dead wood resources are also included in the monitoring and assessment of the status of natural forest habitats. In most instances, the criteria for the assessment of forest habitats assume the favourable conservation status threshold of 20 m³ of dead wood per hectare with more than 5 pieces of coarse woody debris (more than 3 m in length and in principle more than 50 cm in diameter; in forests, where trees do not achieve such dimensions, pieces exceeding 30 cm in diameter are considered). The values of 10 m³/ha and 3 pieces/ha set the borderline between inadequate and bad status. The conservation status of a habitat within a larger area may be considered favourable when at least 25% of the habitat area meets the above criterion for favourable status. Detailed information about the evaluation methodology can be found in the Habitat Monitoring Handbooks published by the Chief Inspectorate for Environmental Protection.

Compared to other European countries, these thresholds are quite ambitious, though still well below those recommended in Brandenburg. In light of knowledge of the ecological requirements of species associated with dead wood and the condition of Polish forests, the criteria adopted in Poland seem to be quite apposite. For example, in the case of *Asperulo-Fagetum* beech forests surveyed in 2015-2018, the overall dead wood volume was rated as favourable at 36% of sites, as inadequate at 26% and as bad at 38%, which seems to reflect quite accurately the condition of forests at these survey points in Natura 2000 sites. The result relating to coarse woody debris was slightly worse: the conservation status was favourable at 32% of sites, but inadequate at 16% and bad at 52%. According to analyses published in 2020, based on data from the Large-Scale Forest Inventory, the average volume of dead wood in forest habitats in Natura 2000 sites in Poland is 12.7 m³/ha, whereas, for example, it is 55.4 m³/ha in upper montane coniferous forests, 28.7 m³/ha in *Asperulo-Fagetum* beech forests, 25.1 m³/ha in alder-ash alluvial forests, 21.5 m³/ha in sub-Atlantic oak-hornbeam forests, and 9.3 m³/ha in central European oak-hornbeam forests. On the other hand, average amounts of coarse woody debris range from zero in Euro-Siberian steppe woods with *Quercus* spp. and central European lichen Scots pine forests to 2.7 pieces/ha in old acidophilous oak woods, 16.3 pieces/ha in *Asperulo-Fagetum* beech forests and 31.1 pieces/ha in upper montane coniferous forests.

Another criterion used to assess the conservation status of forest habitats in most EU countries is the density of habitat trees, i.e. trees with microhabitats, usually representing dead parts of living trees. In Poland, quantitative evaluation of tree-related microhabitats and their host trees was introduced in 2015 as part of the monitoring of several habitat types. Trees were to be counted on a 200×20 m transect, with the recorded specimens including trees with conks, trees with partially broken crowns, trees with dead main branches in the crown, broken trees with splintered trunks, trees with lightning scars, trees with cracked

Photo 189 (K. Zub)
Red-breasted flycatcher *Ficedula parva*, a species protected in some Natura 2000 sites. A suitable habitat for this species is a patch of dense deciduous forest at least 40 ha in area situated within an extensive forest complex, where the average age of stands exceeds 100 years and there are at least 20 damaged, dying or dead trees with a DBH > 25 cm present per hectare

stems, trees with hollows, trees with decaying wood, and uprooted trees. Trees likely to be older than 150 years were to be counted separately, although this would reflect the potential for the emergence of tree-related microhabitats rather than their actual presence. The evaluation was initially calibrated to the threshold value for favourable status set at 20 or more trees with microhabitats per hectare of forest and 10 trees/ha as the threshold for inadequate status, with the caveat that this indicator needed further calibration as the available data were very sparse. As it turned out, however, these assumptions were quite accurate. For the *Asperulo-Fagetum* beech forests surveyed in 2015-2018, the number of trees with microhabitats was evaluated as favourable at 36% of sites, inadequate at 33% and bad at 31%, which seems to correspond well to the current ecological status of these forests.

Sets of indicators to monitor the quality of habitats have also been developed for areas intended for species protection. The quantity and quality of dead wood is included as an important parameter for many species. For example, one of the indicators of favourable conservation status for the habitat of barbastelle bat *Barbastella barbastellus* is the presence of more than 12.5 dead or dying trees of diameter > 25 cm per hectare. In the case of *Carabus variolosus* habitats, achieving favourable conservation status requires, e.g. the presence of 5 or more trunks with a diameter of at least 20 cm or uprooted trees in a 1,000 m^2 sample area. The habitats of *Rhysodes sulcatus* can be considered as having favourable conservation status only when there are 5 or more trunks with a diameter of more than 40 cm, representing all stages of wood decomposition, along a 100 m transect surrounded by forest with a significant proportion of trees over 150 years old. A favourable habitat for white-backed woodpecker *Dendrocopos leucotos* is a patch of at least 100 ha of natural deciduous forest (beech, sycamore, alluvial, alder, oak-hornbeam) with a significant proportion (> 75%) of trees older than 80 years and at least 50 m^3/ha of dead wood or no management activities (including harvesting of dead wood) in the last 20 years. Indicators proposed for other species can be found in the Habitat Monitoring Handbooks published by the Chief Inspectorate for Environmental Protection and the General Directorate for Environmental Protection.

The amount and structure of dead wood (species, diameter, degree of decay), as well as the continuity of its supply have thus become important criteria for assessing the effectiveness of forest conservation. Existing methods of estimating the amount of dead wood can and should be used widely in the daily practice of the nature conservation services (see Appendix I). Monitoring dead wood dynamics in relation to stand dynamics can provide fundamental information on the processes, trends and extent of natural succession.

The principal method of dead wood resource management is to retain trees that are already dead, but also those which have the potential to become coarse woody debris of sufficient quality. Today, it is not so much the removal of individual dead trees that is responsible for the persistent deficit of dead wood in forests, as the removal of dying trees, the removal of "rubble" after local disturbances, such as blowdowns, and, above all, management practices that lead to trees being cut down before reaching biological old age. Hence, passive protection is simply the best solution. It has already proven very helpful in rebuilding the resources of dead wood in Polish national parks. According to data collected during the Large-Scale Forest Inventory in 2020, the current average is about 42.2 m^3/ha, which is quite a good result. That is almost 10 m^3/ha more than in 2010.

Where a compromise between conservation and the commercial use of a forest is necessary, i.e. in multi-purpose forests, the key to improving the situation can be found in solutions that give at least some trees a chance to reach an advanced age (in forestry, typical felling ages for particular tree species are designed to optimize long-term yield per unit area, but they are from ca one-third to one-half of the average age trees of a given species can reach and in no way constitute the threshold of physiological old age for trees). Effective approaches include:

- establishing a network of forest areas intended strictly for nature conservation purposes, no smaller than several dozen hectares (this role should be fulfilled by nature reserves and reference ecosystems);
- leaving unused forest patches a few hectares in area, including areas affected by very high winds or mass tree mortality; ceasing operations in parts of the forest where valuable saproxylic species have been identified;
- consistently retaining "biogroups" of trees from the existing stand during final cutting (also in polycyclic harvest systems in the case of broad-leaved forests); each such biogroup should be several hundred m^2 in area. The retained trees should ideally become part of the new stand, reach a physiological old age, create microhabitats and eventually become coarse woody debris;
- very consistently retaining habitat trees, including groups of trees damaged by wind and other factors, as well as windthrows, windsnaps and other dead trees.

These solutions cannot be viewed as alternatives and should be understood as complementary measures in the conservation of forest biodiversity associated with dead wood and tree-related microhabitats. They are intended to be implemented at different spatial scales.

Protection of animal, plant and fungi species

The list of protected animal species in Poland is based on the Regulation of the Minister of the Environment of 16 December 2016 on the protection of species. Many of the protected species are directly dependent on dead wood and the Regulation states explicitly that the protection measures should include the conservation and regeneration of dead wood stock and trees with hollows in forests and groves. This could provide a legal basis for the protection of dead wood in forests, which is the living environment for these species.

For instance, many beautiful beetles, which are endangered and protected, develop in decaying wood, e.g. *Rhysodes sulcatus* (Fig. 31), hermit beetle *Osmoderma barnabita* (Photo 190), *Protaetia speciosissima* (Photo 191), European stag beetle *Lucanus cervus*, *Ceruchus chrysomelinus*, goldstreifiger *Buprestis splendens* (Photo 192), *Dicerca moesta*, *Eurythyrea austriaca* and *Eurythyrea quercus*, rusty click beetle *Elater ferrugineus* (Photo 193), *Phryganophilus ruficollis* (Photo 194), *Tragosoma depsarium*, *Akimerus schaefferi* (Photo 72), *Pseudogaurotina excellens*, *Stictoleptura variicornis* (Photo 195), *Leptura thoracica*, rosalia longicorn *Rosalia alpina*, great capricorn beetle *Cerambyx cerdo* (Photos 93, 94, 196), and lesser capricorn beetle *Cerambyx scopolii* and *Mesosa myops*. Beetles of the genus *Cucujus* – *Cucujus cinnaberinus* (Photo 197) and *Cucujus haematodes* (Photo 198) – live under the bark of dead trees and large fallen logs. Similarly, under the bark of large fallen spruce trunks is where *Pytho kolwensis* (Fig. 30, Photo 199) can be found, while standing pines, firs, oaks and a few other tree species are inhabited by *Boros schneideri* (Photo 200). Ground beetles of the genus *Carabus* (23 species, Photo 76) and caterpillar hunters (4 species) hibernate in partly decayed wood of stumps and logs. In 2014, *Ergates faber* (Fig. 14) and lesser stag beetle *Dorcus parallelipipedus*, among other species, were deleted from the list of protected species.

Dead trees (or wooden structures) provide a habitat for *Xylocopa valga*, a species of black-violet carpenter bee. Until recently, it was considered extinct in Poland, but new sightings have been reported since the beginning of the 21st century.

Loose bark and rotting wood become hibernacula and occasional hiding places for certain amphibians (fire salamander *Salamandra salamandra* (Photo 47), smooth newt *Lissotriton vulgaris*, crested newt *Triturus cristatus*, Alpine newt *Mesotriton alpestris*, Montandon's newt *Lissotriton montandoni*) and reptiles (lizards, snakes).

Finally, standing and fallen dead trees and shrubs are foraging areas, hideouts, nesting and breeding sites for numerous species of protected birds and mammals, e.g. all species of woodpeckers, owls, shrews, bats, squirrels and dormice.

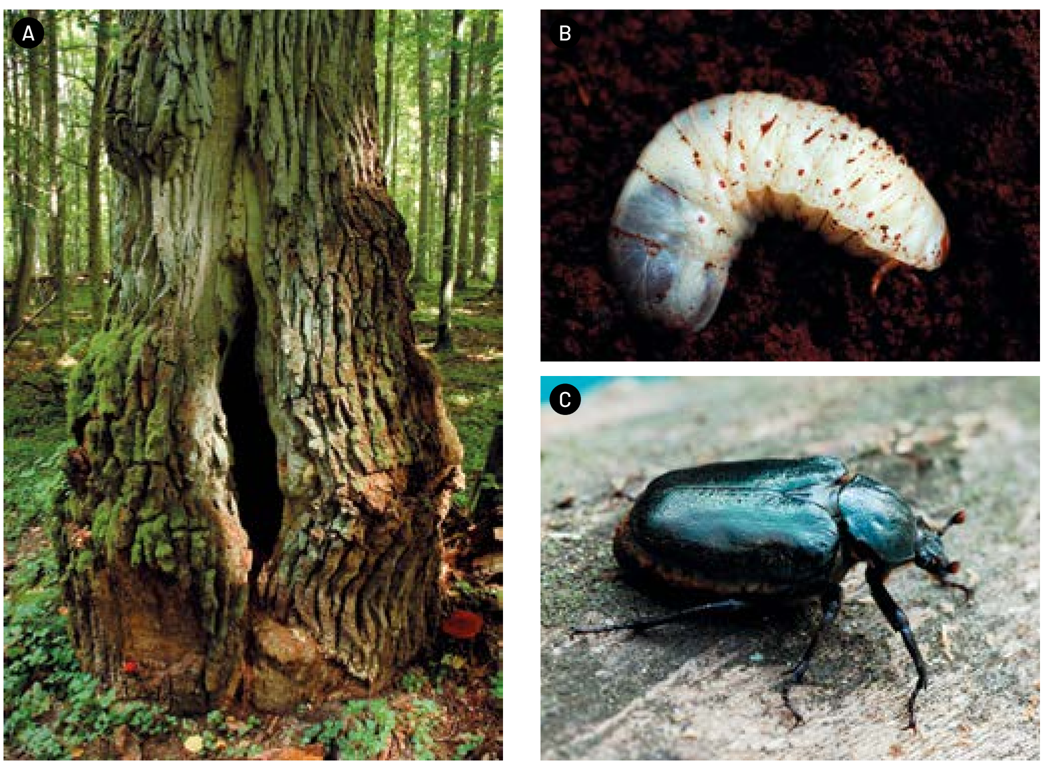


Photo 190 (J.M. Gutowski) Hermit beetle *Osmoderma barnabita* is an impressive beetle inhabiting tree hollows with copious amounts of rotting woody material: **A** – a cavity in an oak, **B** – larva, **C** – imago (female)

Photo 191 (J.M. Gutowski)
Protaetia speciosissima – one of the most beautiful Polish beetles – lives in hollows high up in the crowns of broad-leaved trees

Photo 192 (J.M. Gutowski)
Goldstreifiger *Buprestis splendens* – one of the rarest jewel beetles; a relict of primeval forests

Photo 193 (J.M. Gutowski)
The predatory rusty click beetle *Elater ferrugineus*. Its larvae forage in tree hollows, preying, for example, on the larvae of hermit beetle and other scarab beetles

Photo 194 In Poland, *Phryganophilus ruficollis* is only found in the Białowieża Forest:
A – larva (K. Sućko),
B – imago (J.M. Gutowski)

Photo 195 (K. Sućko)
Stictoleptura variicornis – a very rare species of long-horned beetle; its larvae develop in the wood of coniferous trees

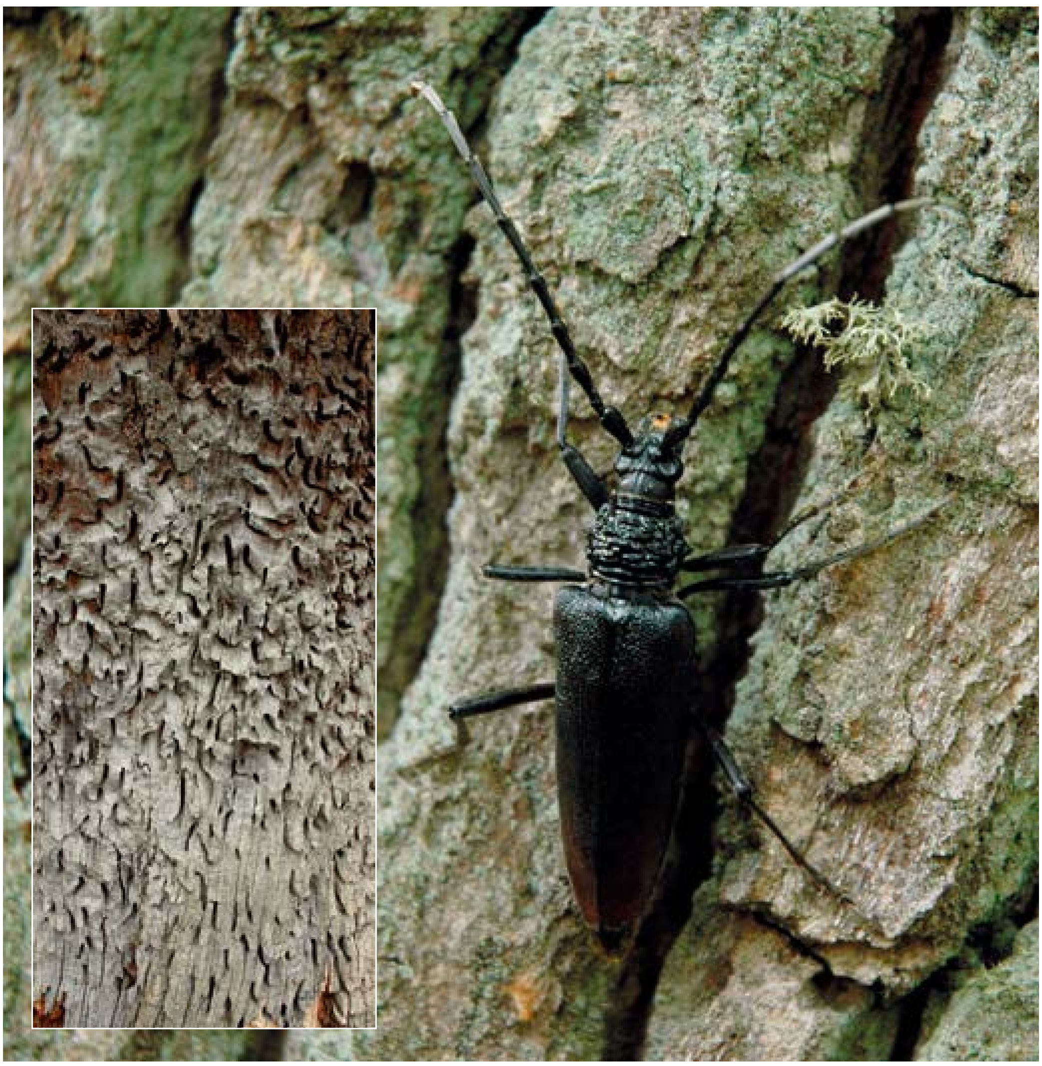


Photo 196 (J.M. Gutowski)
Great capricorn beetle *Cerambyx cerdo* – one of the largest beetles in Poland – leads a nocturnal life. Imago and feeding sites

It is noteworthy that hermit beetle, rosalia longicorn, *Pseudogaurotina excellens*, great capricorn beetle, goldstreifiger, *Cucujus cinnaberinus*, *Phryganophilus ruficollis* and *Pytho kolwensis* are listed in Appendix IV of the EU Habitats Directive, which means that all EU Member States are obliged to protect them (as well as prevent their breeding sites from being inadvertently damaged). Besides these species, Appendix II also includes *Boros schneideri*, violet click beetle *Limoniscus violaceus*, *Mesosa myops* and *Rhysodes sulcatus*, imposing the obligation to protect them by establishing Natura 2000 areas and implementing appropriate protection measures, which correspond to the ecological requirements of the species. Conservation efforts can be financed from European Union funds; protecting the habitats of these species takes priority over all other activities carried out in Natura 2000 sites, with only a few exceptions allowed for overriding reasons of public interest in the absence of alternative solutions. Additionally, hermit beetle, rosalia longicorn and *Pseudogaurotina excellens* are priority species with stricter conservation requirements, which opens up more possibilities to finance projects for their protection, e.g. under the EU's LIFE programme (funding instrument for the environment and climate action).

Photo 197 (J.M. Gutowski)
Cucujus cinnaberinus is a polyphage inhabiting various species of broad-leaved and coniferous trees

Photo 198 (J.M. Gutowski)
Cucujus haematodes – unlike *Cucujus cinnaberinus*, it is not covered by EU regulations; it is less common and more closely associated with natural forests

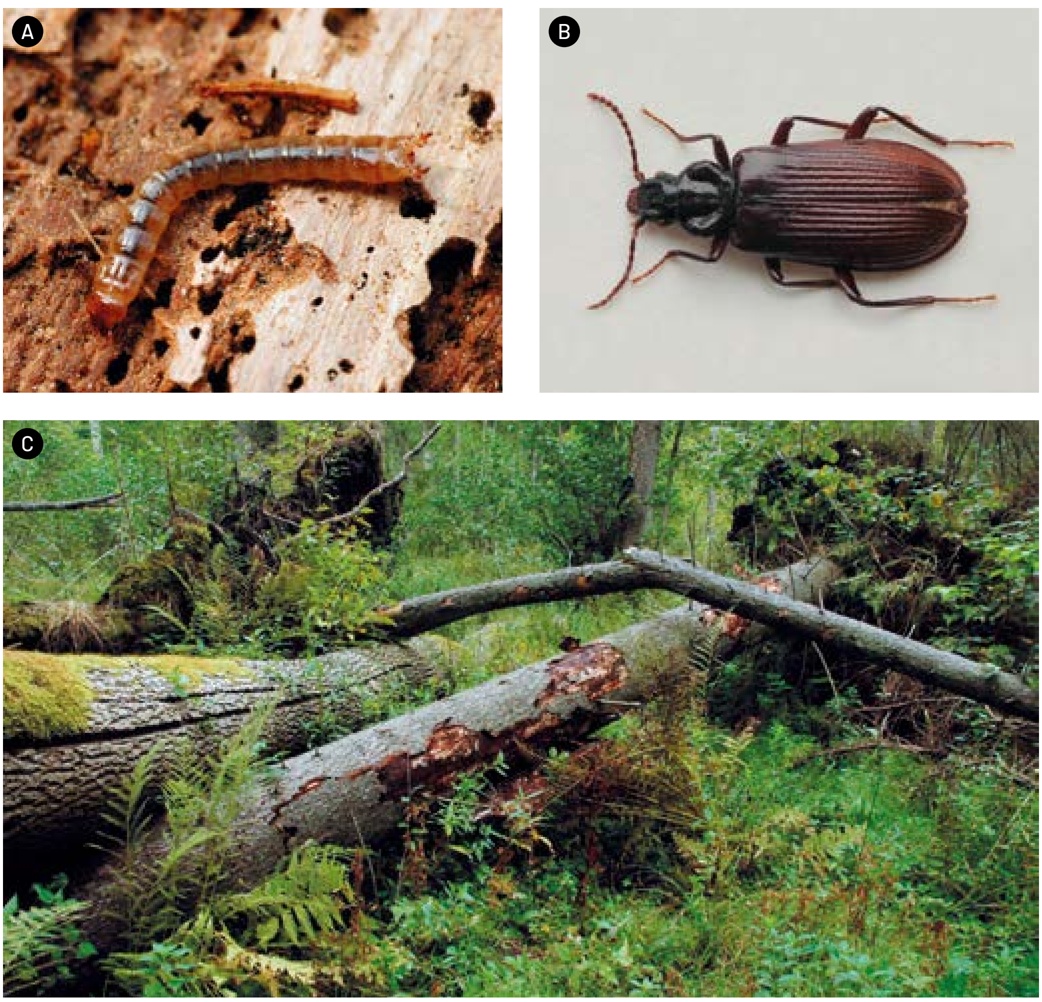


Photo 199 (J.M. Gutowski)
The Białowieża National Park is the only locality in Poland where one can encounter *Pytho kolwensis*: **A** – larva, **B** – imago, **C** – habitat

Habitats Directive:
Council Directive 92/43/EEC of 21 May 1992 on the conservation of natural habitats and of wild fauna and flora; a legal instrument of the European Union which is binding on Member States. The aim of the Habitats Directive is to contribute towards ensuring biodiversity through the conservation of natural habitats and of wild fauna and flora in the European territory of the Member States.

Obligations resulting from the Directive include:
- designating and protecting Natura 2000 sites for habitat types specified in Annex I and species listed in Annex II of the Directive;
- ensuring strict protection of species listed in Annex IV within the whole territory of Member States;
- ensuring that the capturing or killing of species listed in Annex V is sustainable within the whole territory of Member States;
- overseeing national resources of habitats and species from all annexes;
- protecting and shaping landscape features with importance for wildlife within the whole territory of Member States.

Not far from the Polish borders, in Ukraine, the Balkans, Romania and the Mediterranean region, is where one more saproxylic beetle species protected under the EU Habitats Directive is found, namely, the longhorn beetle *Morimus asper funereus* (Photo 82).

The list of protected animals in Poland is relatively short and does not include many endangered and declining species of invertebrates: these, however, are included in Red Lists and Red Books of endangered species. In many groups of invertebrates, 30-40% of the species are sufficiently endangered or declining to appear on Red Lists and should be protected. The percentage of endangered animals is even higher among the taxonomic groups containing saproxylic species, so the protection of dead wood should take the highest priority in forest biodiversity conservation.

The list of protected plant species in Poland is currently defined by the Regulation of the Minister of the Environment of 9 October 2014 on the protection of plant species. As regards the biodiversity of organisms inhabiting dead wood, the moss and liverwort species included in the Regulation are particularly important (see Chapter 4.1.3). Decaying logs are the preferred habitat of green shield-moss *Buxbaumia viridis*. A similar species from the same genus – brown shield-moss *Buxbaumia aphylla* – is also protected. Decaying spruce wood provides optimal conditions for the protected fertile plait-moss *Hypnum fertile*. A few other protected moss species are epiphytes, i.e. species preferring microhabitats situated on the bark of standing trees (usually living), which at the same time are considered to be indicators of natural forests, e.g. *Anacamptodon splachnoides*, slender tail-moss *Anomodon attenuatus*, long-leaved tail-moss *Anomodon longifolius*, *Anomodon rugelii*, rambling tail-moss *Anomodon viticulosus*, pendulous wing-moss *Antitrichia curtipendula*, blunt feather-moss *Homalia trichomanoides*, *Neckera besseri*, flat neckera *Neckera complanata*, crisped neckera *Neckera crispa*, feathery neckera *Neckera pennata*, dwarf neckera *Neckera pumila* and Lyell's bristle-moss *Orthotrichum lyellii*.

Protected species of saproxylic liverworts include chain pincerwort *Cephalozia catenulata*, rustwort *Nowellia curvifolia*, matchstick flapwort *Odontoschisma denudatum*, stipular flapwort *Harpanthus scutatus*, Heller's notchwort *Crossocalyx hellerianus*, horned notchwort *Lophozia longidens* and pointed earwort *Scapania apiculata*.

Another important aspect of the conservation of organisms associated with dead wood is the protection of fungi, which is based on the Regulation of the Minister of the Environment of 9 October 2014 on the protection of fungi species. This Regulation is discussed in great detail in a brochure published by the Polish Mycological Society (Domian et al. 2015).

Nearly 30% of the fungi currently protected are associated with wood. Some of them have only small populations that have survived in the Białowieża Forest (predominantly in the Białowieża National Park); they include *Antrodia albobrunnea*, orange sponge polypore *Pycnoporellus alboluteus* (Photo 156) and *Amylocystis lapponica* (Photo 206). Other protected species, though also found in other parts of Poland, are the most abundant in the Białowieża Forest, e.g.

Photo 200 (J.M. Gutowski)
Boros schneideri:
A – larva, **B** – imago,
C – feeding site (an old, standing dead pine)

Photo 201
(A. Szczepkowski)
In Poland, the protected and critically endangered agarikon *Fomitopsis officinalis* grows exclusively on very old larches

Photo 202 (A. Kujawa)
The protected oak polypore *Buglossoporus quercinus*, known in Poland from three sites outside of the Białowieża Forest

Photo 203 (G. Domian)
The protected bearded tooth fungus *Hericium erinaceus* is an excellent indicator species of the natural value of European beech forests

oak polypore *Buglossoporus quercinus* (Photo 202) and wrinkled peach *Rhodotus palmatus* (Photo 205). Arboreal fungi include a few species that have been protected since 1983, such as hen of the woods *Grifola frondosa* (Photo 121), coral tooth fungus *Hericium coralloides* (Photo 204), *Hericium flagellum* (Photo 133) and agarikon *Fomitopsis officinalis* (Photo 201). Further species were placed under protection in accordance with the Regulations adopted in 1995, 2001, 2004 and 2014, e.g. bearded tooth *Hericium erinaceus* (Photo 203), *Holwaya mucida*, *Pholiota heteroclite* and wrinkled peach. The Regulation of 2014 lifted protection from 22 species, including wood cauliflower *Sparassis crispa*, giant polypore *Meripilus giganteus*, scarlet elfcup *Sarcoscypha austriaca* (Photo 130) and ruby elfcup *Sarcoscypha coccinea*. The same Regulation retained a provision introduced with the 2004 Regulation, which states that *fungi conservation shall consist in ensuring the presence and protection of various types of substrate on which protected fungi species develop, in particular, trees of an appropriate age and species, and decaying wood.*

Photo 204 (K. Zub)
The protected coral tooth fungus *Hericium coralloides* is slightly more common than bearded tooth fungus (Photo 203), but it, too, is an indicator of the natural value of European beech forests

Photo 205 (G. Domian)
The protected wrinkled peach *Rhodotus palmatus* is currently known to grow in just two localities in Poland – the Białowieża Forest and the Carpathians

Witnesses of the past – refugia of relict species

Unique saproxylic species are often indicators of sites (particularly forest complexes) especially worthy of protection. This applies mainly to species-abundant forests that are considered to be relicts of primeval forests, which, because of their ecology, are associated with natural forests. The occurrence of this group of species is a sign that the characteristics of naturalness, the most fundamental of which is the presence of dead wood, especially coarse woody debris and tree-related microhabitats, have persisted continuously in a given area for a long time, which merits calling it an old growth forest.

The Białowieża Forest deserves special attention. Saproxylic organisms are one of the most valuable elements of its fauna, flora and funga and testifies to its naturalness, which makes it a unique place on the European Plain. Saproxylic insects make up the largest proportion of this assemblage.

Because of the good state of these woodlands, their relatively large area and the fact that the processes typical for natural forests have persisted there uninterruptedly for several thousand years, the Białowieża Forest (regarded as the best-preserved mixed lowland forest in Europe) is home to many species which have long been extinct in other parts of the continent as a consequence of more intensive forest management.

Despite its relatively small area (the Polish and Belarusian parts of the Białowieża Forest together cover an area of ca 1,500 km^2), there is a surprising proliferation of animal species compared to most zoogeographic regions in Poland. Many of them are saproxylic species recognized as relicts of primeval forests. Most such relict species are expected in the assemblage of animals intimately associated with dead wood rather than among those inhabiting living trees or herbaceous vegetation, for example. A detailed checklist of such species for the Białowieża Forest has not yet been compiled. However, it is safe to say that among the 124 longhorn beetle species found in the Białowieża Forest, 46 are relicts of primeval forests, e.g. *Tragosoma depsarium*, *Evodinellus borealis* (Photo 89, Fig. 27), *Euracmaeops angusticollis*, *Alosterna ingrica* (Photo 88), *Etorofus pubescens*, *Stictoleptura variicornis* (Photo 195), *Leptura thoracica* and *Lepturalia nigripes*. Similarly, 13 of the 55 species of jewel beetles living in the Białowieża Forest are regarded as relicts, e.g. *Dicerca berolinensis*, *Dicerca moesta*, *Eurythyrea quercus*, goldstreifiger *Buprestis splendens* (Photo 192), *Chrysobothris chrysostigma* and *Agrilus pseudocyaneus* (Fig. 21).

In addition, the Białowieża Forest hosts a large population of hermit beetle *Osmoderma barnabita* (Photo 190), which inhabits trees with hollows in dense woodlands. This species is better known from roadside trees and other insolated wooded areas, which is why these types of habitats are considered optimal for it. It seems, however, that it originally inhabited hollows in ancient trees situated high above the ground, often in the crowns, as is still the case in the Białowieża Forest. Beyond the strictly protected areas, there are very few stands in Polish forests which are sufficiently abundant in old hollow trees able to offer it appropriate living conditions. The felling age of trees in managed forests precludes them from developing cavities with sufficient volumes of rotting woody material (more than 5 litres). However, such old, hollow trees grow in urban and rural parks, in cemeteries and on roadsides, etc. For lack of suitable sites in managed forests, hermit beetle colonizes these secondary habitats in many regions of Europe, which gave rise to the belief that this is its primary and most appropriate environment. Hardly any studies have examined this process in natural forests, although recent research in the Białowieża Forest and in the forests along the River Oder has finally led to a comprehensive assessment of this phenomenon.

Because nearly all vertebrate animals can adapt to some extent to human-modified environments, it is difficult to distinguish the true relicts of the primeval forest from the other species living there. However, the behaviour of a number of animals indicates that they are well adapted to the natural forest environment. Examples include some of the birds nesting in the Białowieża Forest. Many species that are commonly found in open environments, such as Eurasian buzzard *Buteo buteo* and common woodpigeon *Columba palumbus*, feed almost exclusively under the forest canopy in the Białowieża Forest. Common swifts *Apus apus*, familiar in Europe as urban dwellers, nest in the cavities of tall trees in the Białowieża Forest. In the natural forest setting, many species that usually occupy open nests can also utilize tree cavities. These birds include Eurasian blackbird *Turdus merula*, European robin *Erithacus rubecula* and dunnock *Prunella modularis*. Another behaviour common in natural forests is the use of uprooted trees and snags as breeding sites. A typical species that nests on the tops of broken trees is great grey owl *Strix nebulosa*, which generally occurs in northern Europe, but is regularly observed in the Belarusian part of the Białowieża Forest.

Some mammals also exhibit characteristics that could be considered relict-like. Raccoon dogs *Nyctereutes procyonoides*, which usually hibernate in burrows dug in the soil, do so in large, well-rotted fallen logs in the Białowieża National Park. Certain mustelids, such as pine marten *Martes martes*, western polecat *Mustela putorius* or weasel *Mustela nivalis*, also use the trunks of standing and fallen trees as places of concealment. Finally, one bat species, Brandt's bat *Myotis brandtii*, generally thought to exclusively inhabit buildings, has been seen using tree hollows in the Białowieża Forest.

Other apparent relicts of primeval forests among vertebrates include white-backed woodpecker *Dendrocopos leucotos*, three-toed woodpecker *Picoides tridactylus* and Eurasian pygmy-owl *Glaucidium passerinum*.

Table 8 Bioecological groups of primeval forest relicts in a single division (144 ha) of the Białowieża Forest (after Cieśliński et al. 1996; modified)

Taxonomic group	Total number of species	Primeval forest relicts		Epixylites	
		Number of species	Percentage of species	Total	Exclusively on dead wood
Liverworts	41	7	17	6	2
Mosses	104	13	12	7	-
Lichens	164	43	26	15	6
Total	**309**	**63**	**18**	**28**	**8**

Photo 206 (A. Szczepkowski)
Amylocystis lapponica, a protected species which in Poland is found only in the Białowieża Forest

The same applies to fungi and plants, as evidenced, for example, by the results of a detailed inventory of fungi and non-flowering plants carried out during the CRYPTO research programme in just one forest division. Depending on how well they were researched, the inventoried relict species were classified as definite relicts of primeval forests (mosses, liverworts and lichens) and probable relicts of primeval forests (fungi). The former group contains 63 species, many closely associated with dead wood. In the Białowieża Forest, liverworts have a particularly strong relationship with dead wood. One species – Michaux's anastrophyllum *Anastrophyllum michauxii* – is not found anywhere in the Polish lowlands except in the Białowieża National Park.

Based on the results of CRYPTO and other studies of the Białowieża Forest's macrofungi, one can distinguish within the mycobiota of this

Photo 207 (K. Zub)
Fenugreek stalkball *Phleogena faginea*, a threatened fungus species (category E on the Polish Red List of plants and fungi)

entire forest complex a group of species dependent on primeval forest features, indicative of old growth forests. One example is the protected wrinkled peach *Rhodotus palmatus*, which grows on elms in alluvial forests: one hundred years ago it was recorded near Elbląg, but now it is found only in the Białowieża Forest and the Carpathians (and possibly near the town of Piła in north-western Poland). Old-growth indicators also include other protected species, such as *Antrodia albobrunnea*, orange sponge polypore *Pycnoporellus alboluteus* (Photo 156) and *Amylocystis lapponica* (Photo 206), known only from the Białowieża National Park. That said, there must surely be a larger number of relict fungi species inhabiting the Białowieża Forest, a possibility that needs to be thoroughly investigated.

Similar conclusions can be drawn in relation to lichens: the Białowieża Forest hosts a unique assembly of lichens that are considered to be relicts of natural forests. For reasons not fully understood, here too, the lichen flora is currently becoming impoverished, although the strictly protected zones of the Białowieża National Park are unique in Europe where lichen species richness is concerned.

At the European level, the Białowieża Forest is a forest complex without equal, not only because of the great variety of life forms, especially fungi and animals, but also because of the natural (near-primeval) character of the plant communities and animal assemblages inhabiting it. It is a place where one can still study the functioning of ecosystems and the population structures of various species – residents of ancient primeval forests that used to cover much of lowland Europe. The Białowieża Forest should therefore be considered a benchmark. It must be stressed, however, that were it not for the uninterrupted presence of dead wood since prehistoric times, it could not be regarded as a reference point for other lowland forests across Europe.

The Białowieża National Park encompasses the most ecologically valuable and the best-preserved part of the Białowieża Forest (Photo 208), although it lacks certain habitats that are found elsewhere in the forest and are refuges of saproxylic organisms. This is one of the arguments in favour of granting the whole Białowieża Forest national park status, thereby ensuring that it enjoys the highest level of protection possible in Poland.

Photo 208 (J. Walencik)
Dead wood covered in mosses in an oak-hornbeam stand in the Białowieża Forest

Photo 209 (J.M. Gutowski)
Dead wood during the winter

The Białowieża Forest is a prime example of naturally-occurring ecological and biological processes in the evolution and development of forest ecosystems, as well as a refuge for numerous endangered species of outstanding universal value for science or nature conservation. Accordingly, UNESCO has designated it as a World Heritage Site. The species living in the Białowieża Forest and the processes related to dead wood that take place in it have contributed greatly to this distinction.

It is worth noting, however, that historical sources – publications or specimens preserved in museum collections – provide evidence that many species now regarded as relicts of primeval forests used to be much more widespread in the forests of the European lowlands.

Besides the Białowieża Forest, there is one more UNESCO Natural World Heritage site in Poland, the "Ancient and Primeval Beech Forests of the Carpathians and Other Regions of Europe". This is a multinational site, comprising nearly 100 natural beech forests in 18 countries (Albania, Austria, Belgium, Bosnia and Herzegovina, Bulgaria, Croatia, the Czech Republic, France, Germany, Italy, North Macedonia, Poland, Romania, Slovakia, Slovenia, Spain, Switzerland, Ukraine), such as the Stužica beech forest in the Slovakian and Ukrainian parts of the Bieszczady Mountains, the beech forests in the Czech Izera Mountains, and the Grumsin, Hainich, Jasmund, Kellerwald and Serrahn beech forests in Germany. The occurrence of relict saproxylic species is indicative of the region's outstanding natural value, and justifies its placement on the World Heritage List. In 2021, after much effort, the most ancient fragments of beech forests in Bieszczady National Park were added to this list.

Attributes of naturalness and communities of "primeval forest relicts" are also found in other forest complexes in Poland. They include the Augustów Forest, the Knyszyn Forest, the highly fragmented biome of the Świętokrzyska Forest (along with the Świętokrzyski National Park), the Strzelce Forests near Hrubieszów, the former Zwierzyniec Forests in the Roztocze region (now part of the Roztocze National Park, especially its strictly protected zones), certain parts of the highly fragmented Sandomierz Forest, as well as the Carpathian Forest, which comprises the forests of the eastern part of the Polish Carpathians and their foothills (the Beskid Niski Mountains, the Bieszczady Mountains, the Sanok-Turka Mountains and the Przemyśl Foothills). Saproxylic organisms are one of the most valuable components of the fauna, flora and mycobiota in all of these forests. They are exemplified by some beetle species considered to be relicts of primeval forests:

- in the Carpathian Forest: *Rhysodes sulcatus*, *Ceruchus chrysomelinus*, *Eurythyrea austriaca*, *Ampedus melanurus*, *Lacon lepidopterus*, *Boros schneideri*, *Cucujus haematodes*, *Peltis grossa*;
- in the Augustów Forest: *Boros schneideri*, *Ceruchus chrysomelinus*;
- in the Knyszyn Forest: *Rhysodes sulcatus*, *Boros schneideri*, *Cucujus haematodes*, *Peltis grossa*;
- in the Świętokrzyska Forest (in the Świętokrzyski National Park, the Suchedniów Forests, the Cisów-Orłowiny Forests, among other areas): *Rhysodes sulcatus*, *Ceruchus chrysomelinus*, *Ampedus melanurus*, *Boros schneideri*, *Cucujus haematodes*, *Peltis grossa*;
- in the Strzelce Forests near Hrubieszów: *Rhysodes sulcatus*, *Boros schneideri*;
- in the former Zwierzyniec Forests (now part of the Roztocze National Park): *Rhysodes sulcatus*, *Ceruchus chrysomelinus*, *Eurythyrea austriaca*, *Ampedus melanurus*, *Lacon lepidopterus*, *Cucujus haematodes*, *Peltis grossa*;
- in the Sandomierz Forest: *Cucujus haematodes*.

Attention has long been drawn to the presence of relict invertebrates in the Turnica Forests (part of the Carpathian Forest), for more than 100 years, in fact. This forest complex has been proposed as a national park since the 1980s and rightly so. Studies of the area's mycobiota have revealed 26 species new to Poland (so far not found anywhere else in the country) and 31 declining species of fungi, many associated with dead wood. The diversity of lichens is equally impressive. Among the 244 species of lichens recorded to date within the area of the projected park, 18 are indicators of primeval forests, and four of these (tree lungwort *Lobaria*

Photo 210 (P. Pawlaczyk)
A beech log in Serrahn (part of the Müritz National Park in Mecklenburg, Germany) – this forest complex was placed on the UNESCO World Heritage List because of the presence of relict saproxylic organisms

pulmonaria, perforated lichen *Menegazzia terebrata*, powdered ruffle lichen *Parmotrema arnoldii* and barnacle lichen *Thelotrema lepadinum*) are considered to be indicators of the forest's ecological continuity. The projected Turnica National Park will feature at least 23 species of protected bryophytes, e.g. broken fork-moss *Dicranum viride*, shining hookeria *Hookeria lucens* and wall scalewort *Porella platyphylla*, as well as green shield-moss *Buxbaumia viridis*, which grows here almost exclusively on the trunks of dead trees. The protected rustwort *Nowellia curvifolia* is numerous on barkless dead trunks. Of all the mosses and liverworts occurring in the area, eight are recognized as indicators of natural forests. Insects, particularly beetles, are the assemblage of organisms with the highest indicator value and the strongest association with dead wood. Research and inventory work has confirmed the presence of 658 species, most of which are saproxylic, i.e. closely associated with dead wood. Many of them are protected within the Natura 2000 network, are listed in the Polish Red Data Book of Animals or are included in national, European and global Red Lists. Nearly 70 species are indicators of old growth forests, 14 of which are regarded as relicts of primeval forests. Besides the species mentioned above – *Ceruchus chrysomelinus*, *Lacon lepidopterus* and *Peltis grossa* – other species found in the area include *Tachyusida gracilis*, *Ampedus melanurus*, *Ampedus tristis*, *Diacanthous undulatus*, *Dendrophagus crenatus*, *Thymalus limbatus*, *Sternodea baudii* and *Euplectus frivaldszkyi*. Two of these beetle species do not occur anywhere else in Poland, and a number of other species are known from just one or two other localities in the country. This area is the second-most important refuge of relict beetles after the Białowieża Forest, which without doubt is due in no small part to the amount and quality of dead wood occurring here. The area is also important for birds. All the Polish species of woodpeckers can be found here, an aspect in which the planned Turnica National Park resembles the Białowieża Forest. Especially worthy of mention are two woodpecker species associated with dead and dying trees, i.e. white-backed woodpecker and three-toed woodpecker.

Relict species have contrived to survive in some of the above-mentioned forests in spite of contemporary forestry management practices. Therefore, it is sometimes incorrectly claimed that the existence of these species can be reconciled with continuous timber harvesting as part of a sustainable but multifunctional management. Even though these modern management methods should take into account the need for nature conservation, they have by no means improved the situation of relict species. There is no support for the claim that the presence of forest relicts in managed forest conditions is permanent: those species that were rare, still are, and their populations are not recovering. That relict species can still be found in these forests merely reflects the fact that they are indeed relicts of a former, natural forest. The impoverished biodiversity of most other Polish forests (where old-growth forest species are not present) makes a strong case against such claims.

Taking this into account, it would be necessary to start protecting these forests within the shortest possible time by freeing the development of their ecosystems and ecological processes from any human interference whatsoever. Otherwise, with the ongoing disappearance of more and more patches of forests with natural dynamics and a natural ecological structure, we will forfeit the opportunity to preserve and perhaps also restore natural forest biodiversity. The reason for this is the rapid technicization of forest management in often previously inaccessible areas, which until recently had maintained their natural character. In this context, the creation of the long-proposed Turnica National Park, but also the expansion of the Białowieża and Bieszczady National Parks, and the passive conservation of parts of other forest complexes as nature reserves, are crucial for the continued existence of saproxylic flora, funga and fauna. The quality of conservation in some national parks also needs to be improved, e.g. by significantly increasing the area of strict (passive) protection in those parks where primeval forest relict species still survive in some places, e.g. the Roztocze National Park and the Magura National Park.

“Management for decadence”

“Management for decadence” (also known as “morticulture”) is an approach intended to increase the variety and quantity of dead wood in forest ecosystems. Ecological studies, in particular those that have examined the population dynamics of rare invertebrates, often show that even the immediate cessation of dead wood removal from a forest is insufficient to maintain its natural biological diversity. The smaller the volume of dead wood (in cubic metres), the greater the distance between particular pieces of woody debris. A single piece of dead wood inhabited by insects and other organisms cannot provide a permanent home. Rather, it provides a temporary foraging resource, which is gradually consumed, in the process losing the very characteristics that made it suitable for its inhabitants. As a result, new occupants requiring “older” dead wood move in and the former ones leave to look for a fresher substrate.

What would be the fate of an amphibian population inhabiting a drying out pond if there were no other water body within a distance that a sufficient number of individuals could cover? Would a koala kept outside of Australia, having eaten the eucalyptus leaves provided by its caretakers, be able to reach the nearest eucalyptus tree? The occupants of dead wood face the same challenge. Many of them, especially the highly specialized ones, heavily dependent on certain kinds of decaying wood, are also characterized by very limited mobility, like flightless insects, arachnids, nematodes and molluscs. Extending the distance an organism has to traverse beyond its capabilities will have fatal consequences. Meanwhile, the natural forests of the Białowieża National Park can offer any species requiring large decaying logs with diameters exceeding 40 cm a suitable habitat, as there is an average of 7 linear metres of such substrate within a 5.6 m radius (Fig. 2). Conversely, in a typical managed forest in Poland a suitable log may be several kilometres away. Would a small, slow dead-wood dweller be able to find its way to a new suitable microhabitat under such circumstances, or would it find it as difficult as a koala trying to make a journey from Europe to Australia in search of eucalyptus trees?

In such instances, intervention may be necessary to help dead-wood dependent species, especially those that are endangered, to colonize new substrates. This usually involves providing a more reliable supply of dead wood.

At the sight of a decaying hornbeam log covered with numerous fungal fruiting bodies lying in the Białowieża National Park, Ted Green, a prominent advocate of veteran trees in the UK, said, "we could not afford such waste." When asked what he meant by that statement (did he, perhaps, regret the "wasted" timber?), he explained that in the UK this would mean a loss of rare wood decaying fungi. In English forests, such a decaying log could be used to kick-start the regeneration of forest ecosystems elsewhere, so it would function very much like yeast in bread making.

Similar measures are becoming increasingly common and include felling trees and leaving them in the forest (increasing the amount of dead wood), girdling trees (enriching the ecosystem with snags), shooting off parts of trees, inoculating artificially scarred healthy trees with infected wood, damaging trees to initiate the development of tree-related microhabitats, cutting out cavities in trees, etc. There is now an entirely new approach, known as eco-arboriculture, which focuses specifically on enhancing the biodiversity value of single trees. In some cases, eco-arborists may initiate and facilitate the development of rot in trees. The practice of veteranization, i.e. intentionally damaging younger trees (growing in parks, groves and forests) so that they acquire the characteristics of old trees and develop dead fragments, has become one of the tools of nature conservation.

In the Abernethy nature reserve in northern Scotland, the tops of selected old pines are shot off to produce a suitable number of snags in order to improve the breeding habitat of crested tit *Lophophanes cristatus*. In nature reserves in Great Britain and the Netherlands, girdling and felling living trees and leaving the logs in place have become common techniques to make good the deficit of dead wood. There is also an increasing awareness that the quality of decaying dead wood may be even more important than its quantity, and that successful biodiversity conservation requires planning and management for the diversity of forms, sizes and degrees of decomposition of wood, including large logs and standing dead trees.

In the boreal forests of Sweden and Finland, for instance, one such biodiversity protection measure involves the controlled burning of the forest and retaining the killed trees as key habitats for declining species associated with dead wood in warm, well-illuminated places.

In the beech forests of southern Sweden, the ecological value of some commercial forests is improved, for example, by veteranizing beech trees. This is done by cutting cavities in their trunks, partially damaging or completely destroying and stripping the bark, or partially burning the butt.

Between 2010 and 2012, a study was carried out on several plots in Sweden and Norway to determine patterns of colonization in artificially created microhabitats. The microhabitats intended for insects and fungi were made in approximately 120-year-old oaks by cutting holes resembling natural hollows and cavities, damaging the bark on the root collar and breaking or girdling boughs.

In the Bosco della Fontana reserve near Mantua, Italy, tree trunks were intentionally damaged using explosives, and trees were uprooted with the help of a tractor in order to facilitate the quick regeneration of dead wood resources and improve habitat conditions for saproxylic organisms.

Initiating wood rot by slitting trees is sometimes used in the conservation of hermit beetle (Photo 190), especially when habitat continuity and the functioning of ecological corridors needs to be quickly restored. Such measures are included, for instance, in the conservation plans for this species in Lithuania and Latvia.

Another experimental approach in nature conservation is to infect living trees with the mycelia of wood-decaying fungi in order to accelerate the development of certain types of microhabitats, such as rot-outs and hollows. In Poland, similar experiments have been conducted at the Department of Forest Protection at the Warsaw University of Life Sciences (SGGW).

Enriching the forest with dead trees through active conservation usually has positive results, at least in terms of insect and fungal species diversity. The positive effects on other groups of organisms are more equivocal, however. The results depend on many factors, including the current state of biodiversity (the presence of at least residual populations of saproxylic organisms that would be able to colonize the substrate supplied) and the tree species (several studies have shown hornbeam to be particularly valuable in this respect).

The deliberate inoculation (infection) of trees with the mycelia of selected species of rare and protected tree fungi has thus far been tested in Poland on an experimental scale in order to enhance the active protection of, for example, Bondarzew's polypore *Bondarzewia mesenterica* (Photo 143), associated with very old firs; hen of the woods (Photo 121), inhabiting oaks, beeches and hornbeams; and two *Hericium* species – coral tooth fungus *Hericium coralloides* (Photo 204) and *Hericium flagellum* (Photo 133). A few live larches in central Poland were infected with fragments of agarikon mycelia (Photo 201), whose life cycle is associated with old and thick, but weakened and dying larch trees.

5.3. Large-scale disturbances – nature's unwanted gift?

Leaving single dead trees in the forest no longer stirs up controversy. However, the situation is different when significant numbers of trees die over a large area in a short time, which could be the effect (see Chapter 2.2) of such events as hurricane-force winds, fires, tree disease epidemics and outbreaks of certain insect species, which can sometimes reach natural disaster proportions. Often, the intuitive response is to try and "mend the damaged forest": cut down and remove all the damaged trees and plant new ones as soon as possible. Many foresters believe that in the event of such an environmental disaster, all considerations regarding the positive role of dead trees should be set aside. But is this the right approach?

Under natural conditions and without human intervention, a large-scale disturbance is almost always followed by spontaneous regeneration, which in many cases is quite rapid. A forest's regenerative capabilities are often underestimated and reports of total destruction are more the result of shock at the sight of a forest affected by fire, very high winds or flood. Moreover, although a disaster-stricken forest appears to present a scene of utter devastation, some trees usually survive, despite being more or less damaged. Besides live trees, a disturbance may also leave in its wake a number of windsnaps, windthrows, charred trunks or pieces of trees, although what actually happens depends on the type of disturbance, e.g. fire, blowdown. These are crucial components in the structure of a recovering ecosystem and may be important for its future functioning and biodiversity. They are known in ecology as the disturbance legacy, and their influence on subsequent regeneration has received much attention in recent years.

More often than not, clearing up entails removing such components, which turns out to be yet another major ecosystem disturbance, the effects of which actually aggravate the original damage. A lot of the research in this field, including much of the literature cited below, comes from North America, where there is a very long history of studying the ecological effects of large-scale disturbances on forest ecosystems and examples of such disturbances are more numerous. Despite the distinctiveness of North American conditions, the ecological mechanisms appear to be more universal. Though fewer in number, there are also examples from Europe.

One of the best-known examples of a large-scale disturbance is the blowdown and subsequent outbreak of European spruce bark beetle *Ips typographus* that occurred in the 1980s and 1990s in the Bavarian Forest in Germany and the adjacent Bohemian Forest in the Czech Republic. A strategy of passive protection of forest ecosystems, including abandoning bark beetle control measures, has consistently been applied in the Bavarian Forest National Park for more than 40 years. In the midst of the intensifying spruce bark beetle outbreak in the Bavarian Forest National Park (BFNP, ca 25,000 hectares), the authorities responsible for nature conservation in Bavaria decided not to attempt to control the outbreak by employing sanitary cutting, a decision that was heavily criticized by foresters and local communities. "Why waste so many trees?", they asked. The outbreak resulted in massive stand mortality and the accumulation of dead wood at an average level of ca 100 m^3/ha; nevertheless, the affected spruce forests began to regenerate themselves on their own. In the Bohemian Forest, the bark beetle control strategies were spatially and temporally differentiated. Attempts were made to contain the outbreak by removing infested trees and dead stands from large areas, and then to force spruce regeneration, but some sections of the forest were left to recover naturally. This provided a number of opportunities for multi-faceted studies comparing the ecological effects of both approaches.

Some 15 years later, wherever no interventions had been undertaken, young spruce stands had regrown to a density sufficient to restore the forest's basic ecological functions. Interestingly, most regeneration occurred around old dead trees, thus reproducing the spatial structure of the original stand. In the Bavarian Forest, the natural successional stages that developed after the outbreak, representing a mosaic of open and denser patches with large amounts of dead wood, proved to be among the most species-rich mountain forests in central Europe with a very high conservation value. The effects of the bark beetle outbreak, i.e. irregular openings in the forest canopy and large volumes of decaying wood, had a positive impact on the saproxylic beetle community, particularly on the occurrence of species considered highly endangered and declining elsewhere. Because of this, the European spruce bark beetle has even been defined as a keystone species for maintaining biodiversity in forested landscapes in mountain regions.

As a consequence of the large-scale tree mortality, increased rates of nitrogen leaching and higher nitrate concentrations in streams flowing out of the forests were recorded for a few years after the outbreak, but this turned out to be a relatively short-lived effect and was compensated for by a more prolific growth of herbaceous plants. At the same time, after the destruction of the stand in the aftermath of the outbreak, species diversity increased across nearly all systematic groups, and the number of valuable Red List species rose even higher.

How tourists visiting the Bavarian Forest perceived the bark beetle outbreak and its effects, including large-scale tree mortality, was also investigated. Attitudes towards the actual outbreak were neutral, but a small majority of respondents pronounced a negative judgement on possible measures aimed at controlling the insect by removing dying trees and artificial reforestation. The sight of dead trees was perceived more positively by respondents who were more aware of the existence of the BFNP and for whom this was the main purpose of their visit. Within the local community, however, the landscape changes associated with the outbreak became a source of polarization and a point of contention in local politics. For some inhabitants of the Bavarian Forest, the "green spruce forests" were part of their identity, so the bark beetle was seen as a force destroying their homeland – with the tacit approval of the park's administration. Others viewed the processes occurring as a result of the bark beetle outbreak positively as the "return of truly wild nature." Unlike the tourists, the tourist industry was much more critical of the impact of the outbreak on tourism growth: most businesses were of the opinion that the park authorities ought to maintain "healthy, green forests". Curiously, the farther away a given business was from the parts of the park affected by bark beetles, the more negative the attitude of its owners. But what public opinion ignored was the fact that maintaining "green forests" was simply not possible, even across the border in the Czech Republic, where attempts to combat the outbreak had been made.

When in the 1970s the park was designated to be the first national park in Bavaria, its forests resembled those of other well-managed mountain forests, i.e. well-maintained artificial

Photo 211 (P. Pawlaczyk)
Dead spruce trees after an outbreak of European spruce bark beetle *Ips typographus* in the Harz National Park, Germany; the forest was left to regenerate itself naturally

Reference ecosystems: ecosystems designated by forest managers to be left unmanaged (in theory, indefinitely) to serve as benchmarks for stands modified by forest management practices, enabling comparison of processes, structural features and biodiversity levels. In addition, they are usually biodiversity hotspots, providing a living environment for species associated with microhabitats which are typical of natural forests but rare in managed forests. In Poland, they may also be referred to as "representative ecosystems", "areas excluded from management", "biodiversity refuges" or "refuges of saproxylic organisms".

spruce monocultures. Now, fifty years later, because the bark beetle outbreak was allowed to run its course without intervention, the BFNP ecosystem is much more "natural." Nature reorganized what used to be managed and intensively exploited for hundreds of years. After the outbreak, the BFNP became the most popular natural destination in Germany with 2 million visitors each year. Calculations from 1995 showed that the profit gained by tourism in that area was four times greater than the cost of halting timber harvesting and administering the park.

The studies carried out in the Bohemian Forest showed that if a forest was left to itself after a bark beetle outbreak, regeneration would take place rapidly, and the new generation of trees would be more diverse than the original cohort. The sequence of outbreak and spontaneous regeneration has even been considered as a method of restoring the natural characteristics of mountain forests deformed by previous management. Conversely, the measures aimed at reducing the spread of the insect greatly exacerbated the distortion of the ecosystem and hindered forest regeneration. The regeneration of the ground cover was also faster and easier in the areas from which dead trees had not been removed, while the outbreak itself had a much smaller negative impact on the ground cover than the measures taken to combat it. The presence of dead logs with bark was crucial for the natural regeneration of spruce in areas affected by bark beetles. On the whole, the non-interference strategy is thought to be better suited to the requirements for protecting Natura 2000 sites and national parks in both Germany and the Czech Republic.

The experience with passive protection in the Bavarian Forest, also when large-scale bark beetle outbreaks occurred in spruce forests, was evaluated positively in the nature conservation context. This approach was subsequently extended to other protected areas; the same solutions have been applied to most spruce forests in the Harz National Park in Germany (Photo 211). This is in line with the overall objective of protecting natural processes on at least 2% of German territory and at least 75% of the area of each national park, which is set to be achieved within twenty years. Passive protection measures are used quite consistently in German national parks: only the tops of trees growing close to public roads are cut off even if there are safety issues, but dead trees near trails and footpaths are often not felled, let alone removed. The only exceptions are the buffer zones around the parks, where active dead wood is usually removed so as to alleviate the concerns of the owners of adjacent forests.

In Austria, passive conservation strategies, including refraining from interventions during bark beetle outbreaks, have been successfully implemented in the Kalkalpen National Park and the Dürrenstein protected area. It is on this basis that the Austrian National Park Service has developed its approach to bark beetle outbreaks in mountain spruce forests in national parks. It is recommended that the inner parts of the parks should be left free from interference, but that interventions may be undertaken in the several hundred metres wide buffer zone along the borders of the protected area to forestall possible negative impacts on neighbouring areas.

In the Vitosha Nature Park, near Sofia, Bulgaria, it was decided not to interfere in the core sections, but to actively protect the areas around the perimeter. The dynamics of spruce stands in the Vitosha Massif have always depended largely on bark beetle outbreaks, which emphasizes the importance of leaving such areas to regenerate naturally.

In Poland, after much discussion and some not always successful attempts at active conservation, a significant area of a spruce forest with spruce trees damaged by blowdowns and outbreaks of *Cephalcia falleni* and spruce bark beetle has been excluded from active intervention in the Gorce National Park. This approach turned out to be the right one: rowan and spruce soon began to regenerate themselves (also on decaying logs), and areas passively protected have become a significant habitat for three-toed woodpecker *Picoides tridactylus*, boreal owl *Aegolius funereus* and western capercaillie *Tetrao urogallus*. Large areas of spruce forests affected by bark beetle outbreaks (including those previously damaged by blowdowns) have also been left unmanaged within strictly protected zones in the Tatra National Parks in both Poland and Slovakia. Despite the large-scale spruce mortality events still taking place from time to time, no negative consequences for biodiversity have yet been identified.

It seems, therefore, that the experience with passive protection in the context of bark beetle outbreaks in European spruce forests within areas dedicated primarily to nature conservation is generally positive. Even large-scale spruce mortality events have not had catastrophic long-term consequences for biodiversity, so long as the dead trees are left in place.

In Poland, a well-known site where spontaneous forest regeneration processes after a large-scale disturbance (a blowdown in this case) are studied is the "Szast" Protected Forest in the Pisz Forest District (Photo 212). In 2002, extremely strong winds destroyed 17,000 hectares of forest in north-eastern Poland. At that time, it was proposed to leave about 3,000 hectares of the affected area, including fallen trees, to regenerate spontaneously as a reference forest, which would allow researchers to track and study the ecosystem's response to the disturbance. Ultimately, 475 ha were set aside and declared "protected forests of high scientific and ecological value", a unique, ground-breaking approach. This provided the opportunity to study the natural regeneration of an ecosystem after a large-scale disturbance and to compare its effects with the results of the traditional approach applied in neighbouring forests, where damaged and destroyed trees are removed and the stand regenerated artificially. Different aspects of biological diversity and forest condition were examined. The forest regenerating spontaneously after the blowdown and an artificially regenerated stand in the Pisz Forest have been compared in many publications. Despite the impression of a "completely devastated forest", more than 50% of the trees actually survived the high winds. Where wind-snapped trees were left in place and the ecosystem was allowed to regenerate naturally, the restored forest was smaller in area and had fewer trees, but it was much healthier, with a considerably better developed mycorrhizal network, a more diverse age structure and spatial distribution, and a richer species composition. It can be assumed that within a few decades, a new stand of trees from natural regeneration will spontaneously emerge and mature, and that such a forest will be naturally and structurally richer and more resistant to disturbances. On the whole, the environment was more resilient to synanthropic and pathogenic species, including annosum root rot *Heterobasidion annosum*, which causes annosum root disease. Plots with dead trees were also found to be valuable, having a greater diversity of beetle, fungi and lichen species. The strategy of not intervening in natural processes after a large-scale disturbance has proved to be a good way of restoring the ecosystem of the "Szast" Protected Forest, and retaining the wind-broken trees has had a positive impact on the site's natural value.

The Białowieża Forest has faced a similar dilemma several times as a result of recurring bark beetle outbreaks. Until the beginning of the 21st century, any increase in outbreak intensity resulted in an automatic increase in sanitation cutting (at least in the part managed by the State Forests outside the national park), which jeopardized regeneration processes. Yet the bark beetle outbreaks presented an opportunity to quickly restore the natural character of the ecosystems, in terms of both their function (improved balance of dead wood, natural succession of species) and tourism potential. In the early 2010s, it seemed that management of the Białowieża Forest had begun to lean towards a more consistent conservation approach. Forest management plans, conservation action plans for the Natura 2000 site and the principles of operation of the UNESCO World Heritage Site all clearly stated that forests with trees over 100

Photo 212 (P. Pawlaczyk)
The "Szast" forest was left to regenerate naturally following destruction by hurricane-force winds in 2002. The photograph was taken in 2014

years old ought to be left free from interference. However, when a massive bark beetle outbreak occurred after 2012, these arrangements were questioned by foresters and the state authorities. There were attempts to cut down dead spruce trees, but they were thwarted after protests by environmental activists, objections from UNESCO and a judgment of the Court of Justice of the EU of 17 April 2018 (stating that the decisions to fell trees were made in violation of the EU law). As elsewhere, here it is better to allow natural processes run their course in spruce stands with dead spruce trees, especially because the specific ecological value of this forest complex has a great deal to do with its considerable natural character.

5.4. Dead wood and safety concerns

Retaining dead trees often raises questions about people's safety. Nowadays, concerns that such trees can easily break or fall are the main basis for their removal.

Of course, as is the case with living trees, such a risk cannot be ruled out, but misguided safety concerns can easily lead to the elimination of ecologically important components of the ecosystem.

The risk posed by standing dead trees varies and depends closely on the species of the tree, the cause of its death, its root system, the soil conditions and many other factors. Dead oaks or pines can usually remain standing for several decades, but dead beech, ash or spruce trees are typically somewhat more fragile.

The problem of ensuring public safety when retaining dead trees is common worldwide. Usually, the go-to solution is not to remove "potentially hazardous" trees, but to make trade-offs between safety and preserving the ecological, aesthetic and cultural role of dead trees. Solutions are sought to provide an acceptable level of safety while maximizing the retention of dead trees as elements important to biodiversity. Often some risk is accepted and the main focus is on warning people about it. Usually, forests accessible to the public are divided into "more natural" zones, where a higher level of risk is accepted, large numbers of dead trees are left, and safety measures are limited to warning messages, and zones along public roads and trails, where the acceptable level of risk is lower. When establishing the zones and access rules, consideration should be given not only to the risk posed to people by trees, but also to the risk that people pose to trees, e.g. the trampling of soil within the root range of veteran trees. Of course, in protected areas, where people go intentionally and have a good awareness of where they are, e.g. national parks and nature reserves, the acceptable level of risk should be much higher than in places that are frequented by people for other reasons not related to the forest, like public roads. The level of acceptable risk for a forestry worker will be much higher than for the "average passer-by." The acceptable level of risk associated with exercising due diligence by the trees' owner varies from country to country and depends greatly on cultural considerations, including social appreciation of the value of trees. For example, the management guide to veteran trees, edited by David Lonsdale and published by the Tree Council, suggests that in public spaces in the U.K. 1 accident per 10,000 people per year is an acceptable level of risk; in Poland, such a risk would be perceived as very high.

Periodic safety reviews of highly frequented areas are necessary to assess risks. The lower the level of acceptable risk in a given place, the more frequent and comprehensive the reviews need to be. Examples of methodological protocols for such reviews can be found in the literature. The most important thing, however, is to treat review results solely as a basis for weighing a specific risk against other reasons, e.g. ecological, aesthetic and educational, in favour of retaining the tree, rather than interpreting them as an automatic rationale for removing every "hazardous" tree.

Technical methods are sometimes used to reduce risk and preserve at least part of a dead tree, such as shooting, breaking or possibly cutting off the branches. In such cases, the dead trunk can be left standing, as it is usually more stable than the whole tree and can still provide habitat for fungi, insects and other organisms or become hollow. While these approaches are much more expensive and more troublesome than straightforward felling, they do make it possible to preserve much of the tree's ecological value and to raise environmental awareness. In a national park or nature reserve, the stumps of felled trees – even when their felling was justified and necessary – are visual elements carrying an anti-conservation message, which is inevitably at odds with efforts to educate visitors about respecting and protecting nature.

The decision to cut down a dead tree is usually preceded by a risk assessment, which is then compared with an appraisal of its conser-

Photo 213 (P. Pawlaczyk)
A broken tree like this one obviously does not pose any threat – even in a public space. Harz National Park, Germany

vation value. When felling a tree is unavoidable, it should be left on the ground, because in this form it is no longer a danger. Instead of leaving a smooth cut surface, a variety of eco-arboricultural techniques can be applied to shape truncated stems or stubs of severed branches so as to mimic natural fractures, the aim being to initiate the development of appropriate microhabitats, while avoiding negative messaging. Similarly, when part of a fallen log has to be removed, such as when it is obstructing a road or path, the cut surfaces can be treated in the same fashion (Photo 225).

Conservation plans in the majority of Polish national parks emphasize public safety, which is viewed as a rationale for the removal of "hazardous trees" along public roads, hiking trails and other publicly accessible areas, and sometimes even along forest roads. Similar measures are planned even in strictly protected zones, although in most cases, the wood is left on the ground. Safety has been the focus since 2012, when, by order of the Ministry of the Environment, all Polish national parks were required to implement action plans after a tragic accident in the Ojców National Park. Paradoxically, the accident itself had nothing to do with dead trees.

Concern for the well-being of hikers is important, but the safety argument is sometimes abused in national parks and all trees with any kind of damage (and thus all habitat trees), not to mention snags, are removed from a wide zone along the trails. This has a devastating effect on the image of a national park or nature reserve as a wilderness refuge and undoes the message about respecting nature addressed to visitors (see Chapter 6).

An example of how the argument of public safety can be abused were the actions of the State Forests in the Białowieża Forest in 2015 and 2016, where under the pretext of "safety concerns", spruces killed by bark beetles were also removed from places situated far away from frequented roads and trails, without assessing the impact this could have on values central to the recognition of the Białowieża Forest as a Natura 2000 site and a UNESCO World Heritage Site. It was not until a ruling by the EU Court of Justice and an intervention by UNESCO that this practice was stopped.

Some animals inhabiting tree-related microhabitats, such as hornets *Vespa crabro* nesting in tree hollows, can also make people anxious. Destroying the nests, however, means not only destroying the hornets, but also a potential biotope for many valuable invertebrate species (see Chapter 2.1).

It is also argued that the accumulation of dead wood poses a significant fire hazard, but wood, especially at the later stages of decomposition, is not usually readily combustible, because it is relatively moist owing to its considerable hygroscopicity. The risk of fire comes from small branches and desiccated remains of ground cover vegetation rather than from coarse woody debris.

The accident in the Ojców National Park (2012)
In May 2012, a tragic accident occurred: two trees – a ca 40-year-old beech and a ca 20-year-old ash – unexpectedly fell on to children on a school trip. A 13-year-old girl was killed and another child was injured. However, the trees were alive and displayed no visible external damage or signs of dying that could have been observed prior to the accident.

Photo 214 (P. Pawlaczyk)
A small “debris catcher” protects a culvert under a road. With this in place, woody debris can be left in the channel upstream without the risk of the culvert getting blocked. The Bregenz Forest, Austria

Leaving dead wood in watercourses often raises concerns about heightened flood risks. Single, stable logs, e.g. anchored to at least one bank, are unlikely to cause flooding. On rivers where such coarse woody debris is left, such as the Drawa in the Drawa National Park, flooding of riparian areas resulting from this practice is rare. Even when a log does partially block the current, the water level in front of it does not usually rise by more than 5-15 cm. If present in non-urbanized areas, increased channel roughness, reduced flow velocity and slightly elevated water levels, including the occurrence of overbank flows, should be treated as positive phenomena, because they improve water retention, thereby reducing the risk of flooding of urban areas farther downstream.

A significant risk may result from the mobility of coarse woody debris transported by the river, its accumulation in critical locations and subsequent logjams, which may put more pressure on watercourses and greatly increase the likelihood of flooding. Natural narrows and bends are prone to blockages, but not as much as hydraulic structures like bridges with narrow spans, weirs and culverts. However, there is a whole arsenal of technical means for solving such problems. Bridges and culverts have to be designed to minimize the risk of jams. Debris screens can also be used: these can be struc-

Photo 215 (P. Pawlaczyk)
Such a tree lying across the kayak trail is a thrill, not a threat! The River Drawa in the Drawa National Park

Photo 216 (P. Pawlaczyk)
Only small pieces of dead trees that have fallen across popular kayak trails are removed – a compromise between nature conservation and the convenience of kayakers. The River Brda

tures made from steel ropes, posts driven into the bottom, and bars, for example, which prevent woody debris from entering sensitive hydraulic structures (Photo 214). The natural morphological features of the riverbed can also act as “debris traps”. In North America, it has been shown that removing logjams in an effort to make the watercourses available for fish can sometimes paradoxically result in a loss of channel stability and the mobilization of previously stable pieces of wood during the next high-water event. Another solution, which represents a compromise between preserving or replenishing dead wood resources in the river for ecological reasons and reducing the associated flood risk, is to artificially stabilize coarse woody debris, e.g. by anchoring it to the river bed. However, before turning to technical solutions, it is worth considering whether the possible flood risk associated with logjams is at all relevant or potentially acceptable in the context of an entire river or one of its reaches. This applies, for example, to forested sections of watercourses or sections running exclusively through extensively managed land.

Some risk and inconvenience arising from the presence of trees in the channel is associated with rivers used extensively for recreation. Logs in the current can pose a danger to kayakers. On the other hand, the presence of such obstacles determines the attractiveness of a kayak trail, at least for some groups of paddling enthusiasts (see Chapter 6). On popular routes, where there are more inexperienced kayakers, a compromise is sometimes made by cutting through the obstructing trunks to allow passage (Photo 216). “Logjam kayaking” enthusiasts regard such conveniences as undignified, however.

Since 1990, the kayak trail on the Drawa in the Drawa National Park is consistently kept in a wild, unmanaged state, i.e. dead trees lying across the river should not be removed and narrow passages are only cut through them in response to public pressure.

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Chapter 5: Summary

Dead wood is inseparably associated with a primeval, mysterious forest. However, the basic tenet of forest management remains the protection of trees against harmful biotic and abiotic factors. The retention of dead wood and dying trees is still considered a risk to the health of living trees, reducing their commercial value.

Despite the increasing interest in dead wood and its crucial importance to ecological processes and organisms, both the Polish forestry administration and some Polish national parks perceive dead wood as a threat to the health of forests. This non-understanding of the real part that dead wood plays in the forest ecosystem renders "concessions to biodiversity" symbolic and incapable of halting the degradation of forests and their key components.

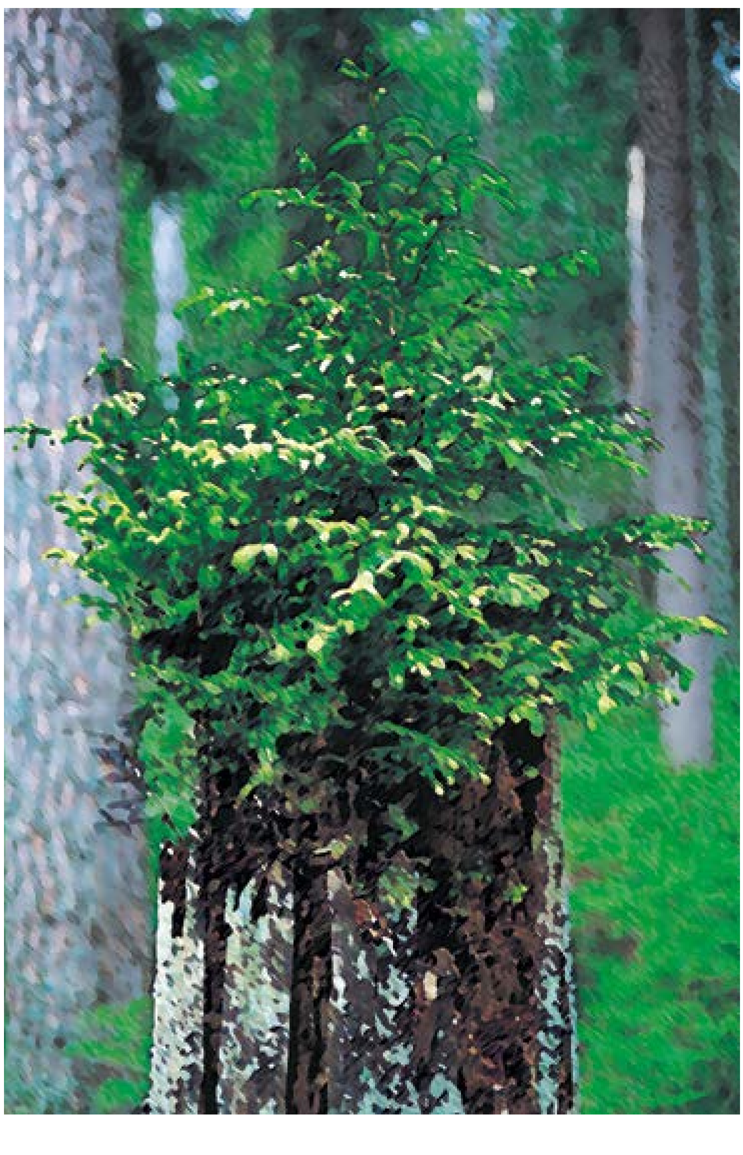
In many countries, special measures are being adopted to increase the amount of dead wood in forests. They are intended to perpetuate the presence of dead wood in the ecosystem, which is in turn necessary to ensure the continuity of the processes inherent to dead wood and the many species that are dependent on it. The restoration of the biological richness of natural forests will not be possible unless effective protection is extended to all remnants of natural forests.

Because of the crucial role of dead wood as a basic and irreplaceable component of forest biodiversity, nature conservation efforts must include measures for conserving dead wood and increasing its volume in forest ecosystems.

The volume and quality of dead wood (species, diameter, degree of decomposition) and perpetuation of its supply is an important criterion when assessing the efficacy of nature conservation in forests.

6

Dead wood in science and the economy



Dead wood as a research subject

Even a few decades ago, few people cared about dead wood, let alone its role in the ecosystem. Scientists, however, had long been interested in dead wood. Numerous studies were carried out to develop the most suitable procedures for assessing quantities and the various forms of coarse woody debris, detecting its spatial patterns at local and larger geographic scales, understanding its association with forest type and stand development phase, etc. In addition, research began to examine the significance of decaying wood, especially for various living organisms. The fundamental monograph on the subject was published by American researchers (Harmon et al. 1986) and much of its content remains valid to this day.

In the first edition of "The Afterlife of a Tree", published in 2004, we stated that hundreds of new publications were appearing annually in both scientific and popular journals. We wrote about the many researchers devoting all of their time to getting dead wood to divulge its secrets, and mentioned the many MSc theses and PhD dissertations addressing the subject of dead wood. One could say that after a very long period during which dead wood had been underestimated if not downright ignored, we were entering a new era when studies of dead wood were now à la mode. There were strong reasons to expect that research on saproxylic fauna could provide crucial information that would help improve our understanding of the processes underlying the evolution of these animals. It was well known that the most primitive groups within numerous taxa (tribes, families, orders) were saproxylic. We knew that if we wanted to track the course of development of primitive characteristics within particular evolutionary lines, we would have to focus our attention on the animals living in dead wood. We also mentioned that the pharmacological exploration of dead wood and the organisms associated with it might result in the development of useful medicines. Some very promising information had been published on the possibilities of exploiting the exceptional properties of the bark of certain tree species or fungi living on dead wood.

Since then, the amount of research on dead wood and its role in the ecology and function of both forest and aquatic ecosystems has grown exponentially. In 2021, academic search engines retrieved around 40,000 publications on the subject, nearly half of them published in the last ten years. Important meta-analyses have also been carried out, covering, among other things, the importance of dead wood for biodiversity in different taxonomic groups, threshold volumes of dead wood in relation to the requirements of different groups of colonizing organisms, and the effectiveness of various methods for artificially increasing the amount of dead wood in the forest. They have provided definitive confirmation of the key role played by dead wood in forest biodiversity (including its association with the amount of dead wood; threshold values usually at the level of several tens of m^3/ha), but they have also revealed the complexity of these issues, e.g. the importance of the "qualitative" and not only "quantitative" aspects of dead wood resources, or the importance of the distribution of dead wood resources at the landscape scale.

Meta-analyses: "studies of studies"; methodical, quantitative syntheses of the outcomes of many different studies. Drawing general conclusions about a specific topic is usually only possible by means of meta-analyses.

Dead wood as a "commodity"

A survey, carried out in 1999 in the Białowieża Forest by TOPB (the Association for the Protection of the Białowieża Forest), showed that among seven possible purposes of tourist visits – social, recreational, seeing the natural forest, encountering bison, learning about forestry, scientific, other – "seeing the natural forest" was the primary objective for the overwhelming majority of respondents. Visitors are keen to experience the most valuable attraction that the Białowieża Forest has to offer, namely, the natural forest. This means that there is no need to generate additional interest (this is the task of the more recently founded, less well-known national parks), because most tourists expect to see the forest and its constituent parts. Thus, the major objective of educational activities in the Białowieża Forest is to give it adequate exposure and to "sell" its natural and primeval character, which is the primary reason for visits to the area. Uprooted trees creating impenetrable thickets or huge half-dead trunks concealing the mysteries of the primeval forest in their hollows are intuitively recognized as attributes of the forest's naturalness.

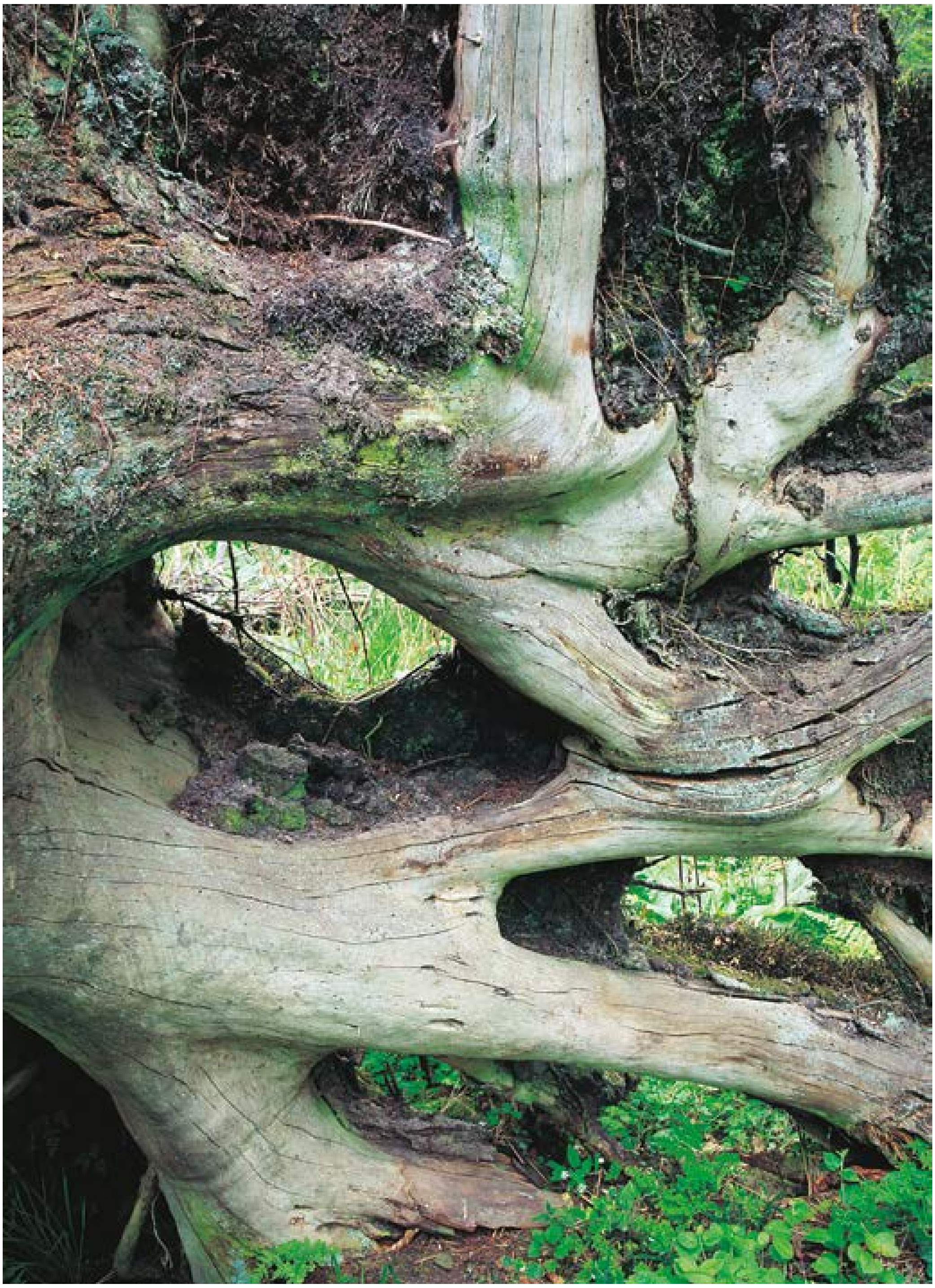
Apart from the European bison, the symbol of the Białowieża Forest and the Białowieża National Park, a major must-see attraction is the Jagiełło Oak, a powerful symbol of Poland's history and culture situated in the strictly protected zone. It comes as a surprise to many visitors that the famous tree is actually a large, half-decayed fallen log, but they nonetheless appreciate the embellished stories told by local guides about the brave king (Władysław Jagiełło) who rested in the shade of the tree in 1409 when hunting, prior to the Battle of Grunwald that took place in 1410. Had the oak been growing beyond the confines of the national park, it would no doubt have shared the fate of so many other old oaks and would have been cut down and the timber sold for a good price. But would that have been a better "deal" than retaining the "famous rotten tree", which continues to make money decades after its death? How many

Fig. 41. A one-off gain or long-term benefits? (M. Bobiec)

groups of sightseers and individual tourists have beheld the "Jagiełło", which has been lying on the ground since 1974? What contribution has it made to the incomes of travel agencies and guides? How many pictures of the oak have been published in books and brochures? And yet this is but a single log (and not even the largest one), with, as it happens, an accompanying legend. How many other stories just as fascinating could make trips to the Białowieża Forest more exciting for people with little interest in the natural world! Since the times of Władysław Jagiełło, almost every Polish monarch hunted in the Białowieża Forest. In the 19th century, the insurgents in the November (1831) and January (1863) Uprisings fought and found refuge in Białowieża's impenetrable forests. Could the atmosphere of those days be conveyed without a large amount of dead and decaying wood with all the emotions and imagery associated with it? And yet, it is not only about "decoration." In fact, we are only "buying" the external "packaging" of dead wood, painted with our own sense of aesthetics and imagination. What is the actual content underneath the wrapping? What is the real "product"?

As is the case with other non-essential, luxury goods, dead wood requires a suitable form of presentation, professional sales people and a discerning customer. Successfully "selling" dead

Photo 217 (J. Walencik)
Dead wood enhances the aesthetic value of the forest



wood (Fig. 41) means fully displaying the richness of its microhabitats and highlighting its function in the ecosystem.

Has anyone ever thought of creating a dead wood trail or a living "museum" of dead wood? Would that be a contradiction in terms? Not at all, because dead wood is not truly dead (and neither is the Dead Sea for that matter). It is actually more alive and dynamic than the healthy wood of living trees! Such a "museum" might include a special trail showing examples of various stages of decay and the different ecological roles of coarse woody debris. Information boards accompanying the "showpieces" along the trail would give an idea of what they looked like when the "museum" was opened and how decomposition progresses. In terms of maintenance costs, this would be the cheapest "museum", where the collection enriches itself and the exhibits do not have to be preserved! Imagine the profit margin from ticket sales!

As in the Białowieża Forest, in many other forests in the world the occurrence of dead wood and habitat trees (including those with various types of damage, hollows, rotting wood or perennial fungal fruiting bodies, i.e. conks) is an important component of the alluring image of "naturalness", which has the power to attract people looking to re-connect with nature or spend time outdoors (Photo 223). And even

Photo 218 (J. Walencik)
Only a forest abundant in dead wood can give the impression of a wilderness

though they may not realize it, they may respond, when asked directly, that dead trees are "bad and ugly," yet still prefer the image of a forest with dead trees to the image of a forest without them. Subconsciously, they seek contact with truly wild nature and that includes forests abundant in dead trees.

Several studies carried out in different locations around the world have shown that the way people perceive dead trees can be easily shaped through education. Providing even simple information about their natural significance can greatly improve their image. Explaining the difference between managed and natural forests, demystifying natural processes and showing how nature deals with natural disturbances significantly increases the subjectively perceived attractiveness of passively protected sites, which are usually rich in dead trees. This is a job for nature educators, but provoking such changes in the public awareness is also one of this book's aspirations.

Photo 219 (J. Walencik)
Amazing forms of fungi are often found on dead wood: orange sponge polypore *Pycnoporellus alboluteus*

Photo 220 (A. Bobiec)
A museum of dead wood is the cheapest one

The presence of dead wood and the variety of tree-related microhabitats in the forest also indirectly affects how a forest is perceived. After all, the soundscape of a spring forest depends on a diversity of bird species, especially woodpeckers – and their occurrence is in turn dependent on the presence of dead trees (see Chapter 4.1.1). Colourful fungal fruiting bodies or imagines of insects (adult forms) are attractive even to the average tourist, even if he/she might not be able to name the species in question, but the occurrence of many of them depends on the existence of suitable forest microhabitats.

Without adequate quantities and diversities of dead wood, no forest can be "sold" as natural and wild. This fact should be of great consequence to the management of protected natural areas like national parks and nature reserves. By demonstrating their respect for dead trees (see

Photo 221 (M. Czasnojć)
One of the last places in Poland where one can still observe the processes involved in the death and decay of old trees in beech forests. The Radęcin Reserve in the Drawa National Park

Photo 224), land managers can show the visitors that they care about nature and its naturalness. Tourists who are determined to experience wildlife in the flesh, as it were, will take a certain level of inconvenience in their stride.

The overzealous removal of dead trees or merely felling them in the vicinity of hiking trails, even if motivated by concern for the safety of hikers (see Chapter 5.4), must inevitably generate the opposite impression. Visitors to some of Poland's national parks are shocked by the frequent sight of felled trees along the trails. If felling/pruning/cutting really is necessary, this negative impression can be minimized by so treating the cut surfaces that they mimic a natural fracture to some extent, blend into the landscape more easily and provide a better habitat for saproxylic organisms (Photo 225).

At Łysy Młyn near Poznań, the Łopuchówko Forest District has opened an educational facil-

Photo 222 (M. Czasnojć)
Trees that have fallen into forest streams enhance the diversity of aquatic environments. The River Płociczna in the Drawa National Park

Photo 223 (K. Zub)
A forest rich in thick, dead trees and a variety of tree-related microhabitats is seen as natural; more and more people today are seeking to connect with such environments

Photo 224 (P. Pawlaczyk)
Such a tree on a hiking trail is not a safety hazard. Leaving it in place is a sign of respect for the ecosystem and a valuable learning opportunity

ity called "The Hermit Beetle Conservation Centre" ("Centrum Ochrony Pachnicy Dębowej"). It features a permanent exhibition devoted to the biodiversity of dead wood, consisting of backlit photos of various organisms inhabiting dead trees, a diorama showing fruiting bodies and animals living on fallen logs, a touch screen providing detailed information, and a mock-up of a fallen oak trunk. In State-managed Forests and national parks, numerous boards describing the importance of dead wood in the forest have been erected in many places along nature trails. At least one such board has probably been put up in just about every single forest district in Poland. Moreover, the national school curriculum addresses themes related to life in dead wood and its importance to the ecosystem.

Some saproxylic species can become "ambassadors of dead wood". They are or can be easily noticed and admired by the average tourist, and their positive image can be further enhanced using standard social techniques. The opportunity to encounter such species can then become part of the tourist product and a tool for promoting the region. Protecting these "flagship" species will be a matter not only of nature conservation, but also of local development; at the same time this will imply protecting dead wood together with all its associated biodiversity aspects, including the less spectacular or better concealed ones. Such species include the aforementioned hermit beetle and the rosalia longicorn *Rosalia alpina*, "the blue gem of old beech forests". Moreover, the common kingfisher *Alcedo atthis* could be the "ambassador of dead wood in rivers", because large woody debris in the current is a crucial part of its habitat.

The general public often finds it difficult to come to terms with large-scale tree mortality events, resulting, say, from bark beetle outbreaks. Whether in the Bavarian Forest, the Black Forest or the Białowieża Forest, there are voices in local communities, saying, "we want a living, green forest, not vast areas of dead spruce trees." But in fact, the choice is stark: between dead spruce trees and the empty space left after they have been cut down. What seems to be a "dead forest" is actually teeming with life in its every nook and cranny, an impressive demonstration of the power of natural regeneration. Indeed, by no means does the image of dead trees and rotting wood detract from the tourist appeal of the area. In the Bavarian Forest National Park in Germany, where a strategy of non-interference during bark beetle outbreaks was adopted some 40 years ago, it was found that the attitudes of tourists were neutral towards dead and dying trees, yet highly critical as regards combatting the insects by removing dying trees and artificially regenerating the forest (see Chapter 5.3). The sight of a "dead forest" was perceived more positively by respondents who had a deeper awareness of the park's existence and for whom the park was the main purpose of their visit. Today, all German national parks are striving to have their forests rich in

Photo 225 (L. Buchholz)
If a fallen log has to be cut through because, for example, it is obstructing an important road or path, it is possible and worthwhile to shape the cut surface so that it at least partially resembles a natural fracture. This is important for the log's decomposition and its colonization by saproxylic organisms, not to mention the image of the forest and its perception by tourists. Świętokrzyski National Park

Photo 226 (P. Pawlaczyk)
In almost every Polish forest district there is now at least one such board providing information about the importance of dead wood

Photo 227 (M. Kulesza)
Overcoming fallen trees in the river is a source of great satisfaction for some kayakers

dead wood and shaped by natural processes, in accordance with the fundamental belief that this is beneficial, among other things, for the attractiveness of the parks and for income from tourism.

Also, the presence of dead trees in watercourses will be appreciated by anglers, because they know how important this aspect of the ecosystem is for fish. And kayakers, too, are inclined to view a river with dead trees as more interesting and natural. They do not expect all such trees to be removed from rivers and streams, but they do like to have narrow passages cut through some of the trees that would otherwise completely block the trail.

Finally, there are those kayakers whose ambition is to overcome all such obstacles, ideally without leaving the kayak: from their point of view, the more fallen trees in a river, the more satisfying it is to navigate. A river with abundant dead trees can therefore be a tourist product addressed to just such a group.

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Müller J., Bütler R. (2010) 'A review of habitat thresholds for dead wood: a baseline for management recommendations in European forests', *European Journal of Forest Research*, 129(6), pp. 981-992.

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Piętka J. (2001) 'Właściwości lecznicze czarnej huby brzozowej', *Las Polski*, 3, pp. 14-15.

Rathmann J., Sacher P., Volkmann N., Mayer M. (2020) 'Using the visitor-employed photography method to analyse deadwood perceptions of forest visitors: a case study from Bavarian Forest National Park, Germany', *European Journal of Forest Research*, 139(3), pp. 431-442.

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Stokland J.N., Siitonen J., Jonsson B.G. (2012) *Biodiversity in Dead Wood*. Cambridge University Press, 509 pp.

Wierzbicka A., Prange M. (2014) 'Martwe drewno – trudny temat. Jak uczyć o roli martwego drewna w lesie', *Studia i Materiały Centrum Edukacji Przyrodniczo-Leśnej w Rogowie*, 16(4), pp. 380-386.

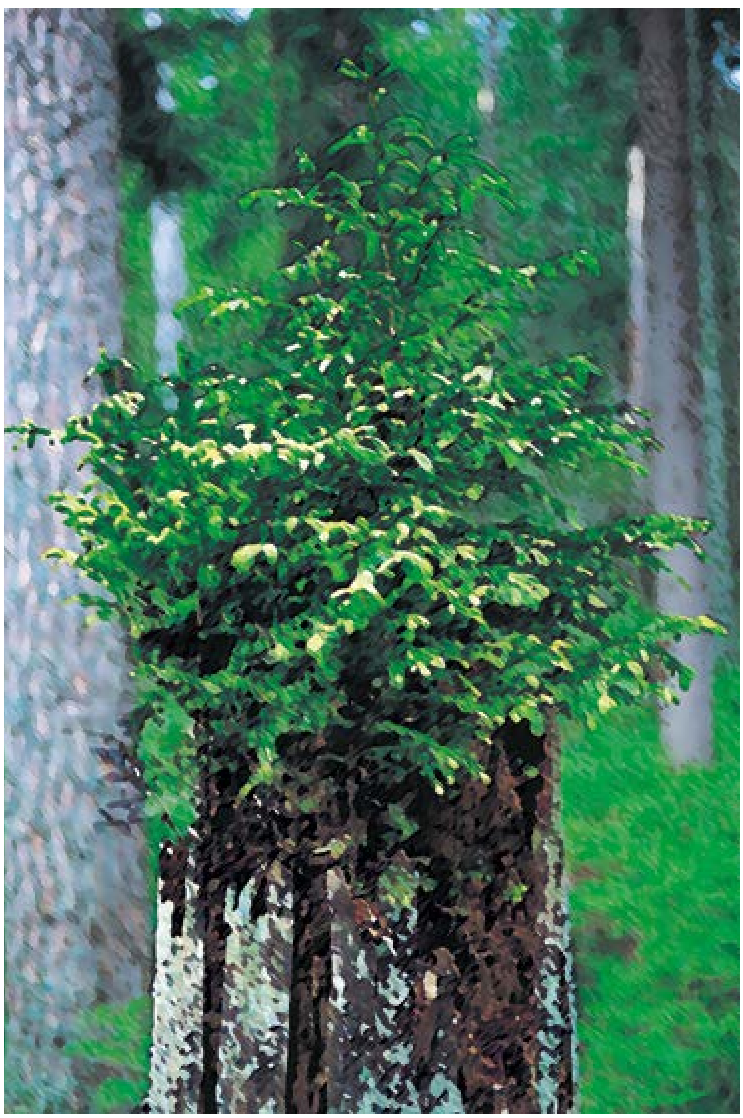
Chapter 6: Summary

Increasing interest in dead wood has given rise to a plethora of studies examining, inter alia, the ecological, biological, biochemical and pharmacological aspects of dead wood. The very extensive subject literature illustrates not only the depth and breadth, but also the popularity of such studies. Some of these may result in discoveries that will cast new light on our understanding of the forest ecosystem or even on the evolution of species. The pharmacological research may perhaps contribute to the development of new medicines.

The unique aesthetic values of dead wood, associated with our atavistic, intuitive perception of ancient woodland, are a major and necessary attribute of any publicly accessible forest that is presented as a "natural" one. Large amounts of dead wood reinforce such a forest's appeal to an increasing number of people keen to experience traces of untamed nature in an urbanized world. Be that as it may, however, dead wood remains underexposed and underutilized as a valuable "commodity" by tour operators and nature educators.

7

Wood as a raw material



Despite the value of dead wood to a functioning forest, it is important to bear in mind that wood is an important renewable commercial commodity, irreplaceable in the construction, mining, rail transport, telecommunications, furniture and chemical industries. In the last-mentioned, it is used for producing cellulose, which in turn is necessary in paper manufacturing. Wood is also a valuable and renewable fuel. The purpose of this book is not to call a halt to the harvesting of timber or its use. We merely wish to point out other valuable aspects of wood that are frequently underestimated or ignored. We want to show that the value of wood as a commodity is often of secondary importance (Photos 103, 228-230), In any case, the place of wood in the construction, paper or furniture industries is self-evident. But we should not overlook the importance of wood in art, including traditional wood crafting, sculpting, and souvenir-making (Photos 231, 232), and also in medicine (Photo 234).

The demand for wood as a raw material or fuel can partly be met by plantations of fast-growing trees or shrubs like willows and poplars. However, the harvesting of wood in forests should also take into account their other functions.

Photo 228 (J.M. Gutowski)
Stacks of harvested alders in the Białowieża Forest (ca 2000)

Photo 229 (K. Zub)
Felled old oaks in the Białowieża Forest (ca 2000)

Photo 230 (J.M. Gutowski)
A charcoal pile. Though picturesque, charcoal production in the Bieszczady Mountains (in the 1970s) destroys the habitats, eggs and larvae of the rare longhorn beetle - rosalia longicorn *Rosalia alpina*, which is protected in Poland

Photo 231 (A. Bobiec)
Dead wood makes for a pensive mood and concentrates the mind. A confessional cut out of a hollow lime trunk in the church of St. Teresa of the Child Jesus in Białowieża (historical photograph)

Photo 232 (J.M. Gutowski)
A wooden wayside shrine on an old dead pine in the Biebrza National Park

Obviously, wood should not be harvested in those forests which still retain much of their natural character; they are far too valuable as wildlife refugia to be exploited commercially. Biodiversity protection is the only function that such ecosystems should fulfil. It is critical to preserve these forests as models, where natural processes can operate, be observed and studied, and as places where we can learn from nature and try to apply natural solutions in managed forests. Apart from scientific research, these forests could be used for education and low-impact tourism.

Photo 233 (P. Pawlaczyk) A bees' nest in a dead log – the bees benefitted from the mosaic of marshy coniferous forests and the *Vaccinio vitis-idaeae-Pinetum* association on sand dunes. Dzūkija National Park, Lithuania

For the same reasons, the removal of wood in national parks and nature reserves should cease. Even if the elimination of certain trees as part of active conservation is unavoidable, their wood should, in principle, be retained in the ecosystem.

A plan to leave at least some dead wood in managed forests can be easily drawn up and quickly implemented as it generates no additional costs. In the case of deciduous trees, there should not be any objections even from traditionally-minded foresters, who usually dread the proliferation of "pests", which they associate with leaving dead coniferous wood in the forest. It is also worth putting even greater emphasis than hitherto on educating the public and raising awareness of the significance of dead wood in the forest ecosystem.

Currently, in both Poland and many other countries, the ecological functions of dead wood are being given much more consideration than 20 years ago. Nonetheless, the inclusion of these issues into conservation and forestry practice is still far from complete.

Photo 234 (J.M. Gutowski) The timber-built graduation tower in Ciechocinek

"When one walks through the rather dull and tidy woodlands – say in the managed portions of the New Forest in Hampshire [England] – that result from modern forestry practices, it is difficult to believe that dying and dead wood provides one of the two or three greatest resources for animal species in a natural forest, and that if fallen timber and slightly decayed trees are removed the whole system is gravely impoverished of perhaps more than a fifth of its fauna.

[…] Logs are considered to be more important as wildlife habitat than are other forms of woody debris since they are stable and persist longer in the environment […].

The size of the material is important for many species […]. In general, the larger the diameter and the greater the length of a log the more useful it is".

Selected tips developed by the USDA Forest Service for managers in the Pacific Northwest:

"At least five uncharred class 1 or class 2 logs per hectare (two/acre) should be retained as wildlife habitat. Furthermore, all class 3, 4, and 5 logs, which have little or no commercial value but are acceptable as fuel loading, should be retained. […] the logs should be at least 30 to 43 centimeters (12 to 17 in) in diameter at the large end and 6 meters (20 ft) or more in length.

The removal of natural, stable woody material, especially logs, may seriously damage the stream channel and the streamside riparian habitat. Such woody material provides excellent habitat for aquatic and amphibious wildlife and for many small terrestrial animals; it should be left in place when possible".

Excerpts from the US Forest Service Handbook

Maser C., Anderson R.G., Cromack K. jr., Williams J.T., Martin R.E. (1979) 'Dead and Down Woody Material', pp. 78-95. in: Thomas J.W. (ed.) Wildlife habitats in managed forests. The Blue Mountains of Oregon and Washington, USDA Forest Service, Agriculture Handbook No. 553.

A call to foresters

In managed forests, the harvesting of wood should be based on a compromise between the demand for wood products and the requirements of resource and species conservation. Depending on the geographic location, habitat type, species structure, stand composition and other factors, this compromise should be sought at different levels. It is important in managed forests to let selected trees grow old and die naturally and to allow dead standing and fallen trees (including coarse woody debris) to decompose fully. What is more, when we decide to harvest timber in a given place, we should not take it in the form of dead wood – **it is just so full of life**.

In forest management, it is important to identify and secure sites with protected species and to consider which particular tools and harvesting methods should be used, including the timing of their application. This should help reduce the negative side effects of removing trees to a minimum. The success depends in large part on the professionalism and goodwill of forest managers.

It is vital to keep in mind that seemingly unimportant details may snowball into a serious, though unintended, risk to certain insects. Sites used for logging operations may become traps for endangered species. For instance, saproxylic insects tend to aggregate in unnaturally large numbers at forest landings, attracted by the stacked logs. There they mate and lay eggs in sites potentially suited to their larval development. Eventually, the wood will be hauled away and both eggs and larvae will be destroyed. Thus, the ecosystem is drained of a large portion of the reproductive output of its distinctive insect life, which often includes critically endangered species; the threat itself is most often the effect of such processes. This mechanism is one of the ever-present threats in the conservation of rosalia longicorn *Rosalia alpina*. All of this could be avoided if the harvesting and stacking of felled trees in the forest took place at a time when valuable insect species did not lay their eggs, i.e. outside of their mating season.

The multi-purpose character of the forest requires that nature is given some space exclusively to itself, where it can remain undisturbed. Meanwhile, the most common practice is to continuously use the entire area of the forest for planting, growing and felling trees. A certain proportion of old growth forests should be excluded from management. Where forestry operations are still ongoing, it is worth retaining 5-10% of the original cohort for the future generation of the stand.

Recommended reading for Chapter 7:

Bobiec A., Buchholz L., Churski M., Chylarecki P., Fałtynowicz W., Gutowski J.M., Jaroszewicz B., Kuijper D.P.J., Kujawa A., Mikusek R., Mysłajek R.W., Nowak S., Pawlaczyk P., Podgórski T., Walankiewicz W., Wesołowski T., Zub K. (2016) 'Dlaczego martwe świerki są potrzebne w Puszczy Białowieskiej?', *Las Polski*, 7, pp. 14-16.

Borowski J., Wójcik R. (1996) 'Stare drzewa – ważny element ekosystemu leśnego', *Las Polski*, 17, pp. 13-14.

Bütler R., Schlaepfer R. (2001) 'Three-toed Woodpeckers as an alternative to bark beetle control by traps', in: Pechacek P., d'Oleire-Oltmanns W. (ed.) *International Woodpecker Symposium. Nationalpark Berchtesgaden. Forschungsbericht*, 48, pp. 13-26.

Gilg O. (2005) *Old-Growth Forests: Characteristics, Conservation and Monitoring*. Habitat and Species Management, Technical Report, 74 bis, 96 pp.

Gutowski J.M., Buchholz L. (2000) 'Owady leśne – zagrożenia i propozycje ochrony', *Wiadomości Entomologiczne*, 18 (supplement 2, pp. 43-72.

Kujawa A., Orczewska A., Falkowski M., Blicharska M., Bohdan A., Buchholz L., Chylarecki P., Gutowski J.M., Latałowa M., Mysłajek R.W., Nowak S., Walankiewicz W., Zalewska A. (2016) 'Puszcza Białowieska – obiekt światowego dziedzictwa UNESCO – priorytety ochronne', *Leśne Prace Badawcze*, 77(4), pp. 302-323.

Schiegg K. (1998) 'Totholz bringt Leben in den Wirtschaftswald', *Schweizerische Zeitschrift für Forstwesen*, 149(10), pp. 784-794.

Vallauri D., André J., Blondel J. (2002) *Le bois mort, un attribut vital de la biodiversité de la forêt naturelle, une lacune des forêts gérées. Rapport scientifique*. WWF France, 34 pp.

Wesołowski T., Gutowski J.M., Jaroszewicz B., Kowalczyk R., Niedziałkowski K., Rok J., Wójcik J. M. (2018) *Park Narodowy Puszczy Białowieskiej – ochrona przyrody i rozwój lokalnych społeczności*. [http://www.forestbiology.org, Article 2: pp. 1-28].

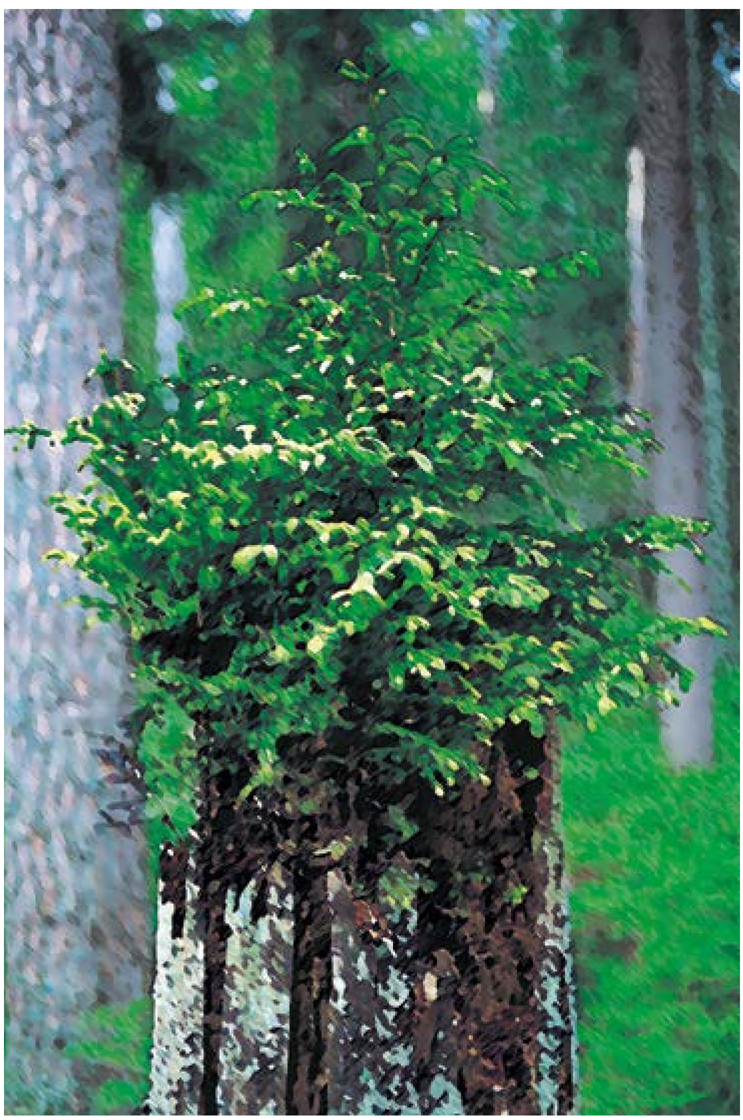
Wolski J. (2003) 'Martwe drewno w lesie: ocena zapasu i propozycje postępowania', *Prace Instytutu Badawczego Leśnictwa*, 2(953), pp. 23-45.

Chapter 7: Summary

For many industries and crafts, wood is a valuable and irreplaceable raw material. However, the significance of dead wood in the functioning of forests and the maintenance of biodiversity continues to be underestimated.

In managed forests, the harvesting of wood should be based on a compromise between satisfying the demand for necessary raw materials and meeting conservation requirements. To some extent, the demand for wood as a raw material or fuel can be met by plantations of fast-growing trees or shrubs. But the extraction of timber from the very few, extant remnants of the natural European forests will lead to the irreversible loss of their biodiversity heritage, which will impoverish the quality of life of future generations.

Summary 8



Dead wood in forests, i.e. standing dead trees and shrubs, snags, stumps, old trees with dying boughs and cavities, fallen logs and branches, etc. provides a great many "services". For example, it:

- greatly enriches the species diversity of fungi, plants and animals,
- makes for a more attractive landscape with greater tourism potential,
- has a positive influence on habitats (soil, leaf litter),
- improves water retention in the forest,
- prevents erosion,
- stores organic matter,
- is a source of elements (carbon, phosphorus, potassium, calcium, etc.) and energy indispensable in the forest ecosystem,
- facilitates, and is sometimes an absolute precondition for, stand regeneration,
- broadens the range of ecosystem services provided by forests,
- increases the resilience of forests to disturbances,
- enhances the quality of the country's green infrastructure.

In light of these points and contrary to popular opinion, dead wood in the forest is neither an "incubator" for harmful insects and fungi nor a "threat to forest continuity", but an important component of the ecosystem, increasing its natural biological resilience and ensuring that the balance of nature is maintained (Fig. 42). As a rule, wood should not be extracted from forests with natural and semi-natural characteristics, e.g. having large, old trees or copious amounts of dead wood. Such forests are irreplaceable sources of biological diversity and models where natural processes can be observed and investigated, and possibly imitated in managed forests. The practice of clearing dead wood out of protected areas like national parks and nature reserves should be abandoned. In multi-purpose forests, a certain acreage of stands should be left untouched and some dead wood, at least, should be retained to ensure habitat continuity for saproxylic organisms. The more important the ecological and landscape functions of the forest, the more dead wood that needs to be retained. These postulates are set out in the conclusions below

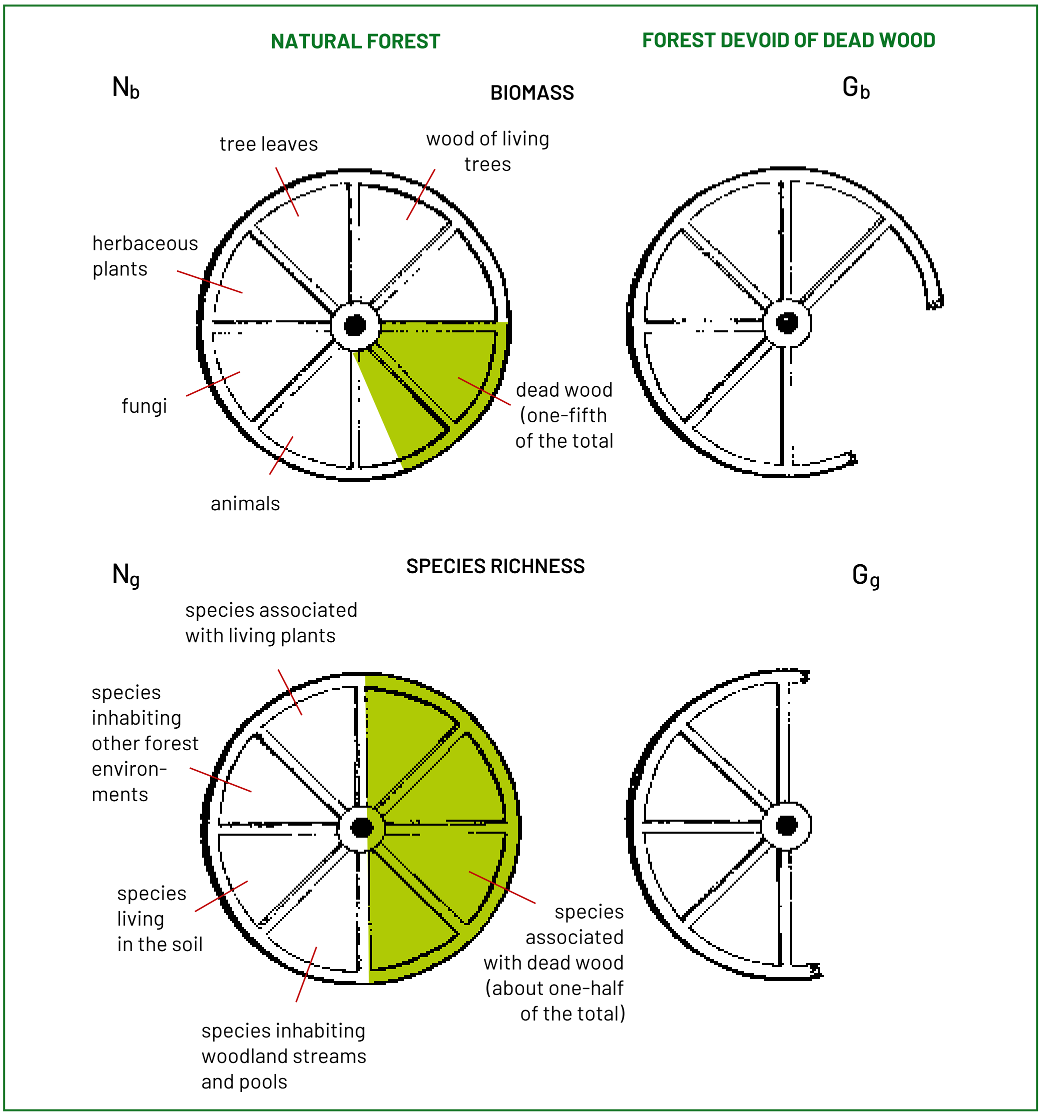


Fig. 42 Let us imagine the ecosystem of a natural forest in the form of a wheel. The biomass of dead wood will then make up about one-fifth of its area (Nb), and the species associated with it will cover almost one-half of it (Ng); but if we remove dead wood from a forest, the ecosystem can no longer function efficiently (Gb, Gg) – in other words, the wheel can no longer serve its purpose (M. Bobiec)

and summarized in a table along with recommended quantitative and qualitative threshold values for dead wood in different forest types.

Conclusions:

1. As much dead wood as possible should be retained in forests. A key component of the forest, dead wood is as important as living trees or shrubs, if not more so. Removing and utilizing dead wood, e.g. as fuel, can cause greater damage to the forest ecosystem than felling a living tree.
2. Dead wood resources should reflect the same diversity of species composition and size structure as the living stand. It is vital to facilitate a continuous "supply" of dead wood, especially of coarse woody debris. Ensuring the presence of dead trees with a DBH > 40 cm is particularly important, as they are crucial to many endangered organisms.
3. The mere non-removal of dead trees will not suffice to achieve this, however. At least some trees in the forest must be allowed to reach an appropriate size, grow old and die of natural causes.
4. In near-natural forests, especially in national parks and nature reserves, dead and dying trees (shrubs) should be left *in situ*, and no living trees should be felled or removed. The quantity and structure of dead wood should be solely the result of natural processes, which should be left to run their course without human intervention. The practice of cutting down snags and removing wood from existing forest reserves, including those where active conservation measures are applied, should cease. If intervention is unavoidable, only the trees intended for elimination should be killed and thereafter left in place without any further treatment.
5. The remnants of natural and semi-natural forests in Poland should be placed under a passive conservation management regime (strict protection or a hands-off approach). Natural processes do not threaten the existence of these forests!
6. Every forest should feature a network of areas of at least a few hectares that should be left to function naturally, i.e. it is permanently excluded from harvesting operations. Such a network should cover at least 5% of the area of each forest. Such areas already established in Polish forests, referred to as "reference ecosystems", "biodiversity refuges" or "areas excluded from management", fulfil this objective admirably, as do species protection zones, so long as they are treated as permanent biodiversity refuges in forests.
7. In wet forests, such as marshy coniferous forests, alder carrs and riparian forests, as well as in upper montane spruce forests, even if they are not legally protected, all coarse woody debris (fallen logs, uprooted or broken trees) should be retained, as it provides the conditions necessary for the efficient regeneration of trees and also reduces erosion in mountain regions. At the same time, care should be taken to preserve their distinctive hydrological regimes, because they act as water storage reservoirs for the catchment area.
8. Tree harvesting in managed forests should not take place during the growing season. Wood that has not been taken away within the designated harvesting period should be left in the forest until complete decomposition. Trees or snags left in the forest should not be felled, debarked or sawn into shorter sections.
9. Whenever a stand is destroyed by a natural disaster, e.g. hurricane-force wind, fire, tree disease or insect outbreak, a certain percentage of the dead trees should be left to decompose naturally, ideally fairly large swathes of them, but failing that, smaller clumps. In protected areas, e.g. national parks and nature reserves, leaving entire uncleared areas to regenerate naturally usually yields the best results. In managed forests, it is worth leaving at least some areas to regenerate naturally.
10. As much organic matter as possible should be retained in forests. When harvesting is carried out to improve forest stands (commercial thinning), wood should be extracted only if this is economically justifiable.
11. Slash should be retained to the fullest possible extent without piling or chipping. Stumps should not be debarked. Debarking should be permitted only in the case of coniferous monocultures susceptible to large-scale outbreaks of cambio- and xylophages.

12 Wherever possible, uprooted and broken trees should be retained in the forest. If the trunk of an uprooted tree is to be cut off, the elevated root plate should be secured in order to prevent it from falling into the windthrow pit.

13 The volume of dead wood (standing trees and downed woody material) in all managed stands older than 50 years should not be less than 10% of the stand volume. The species composition and size structure of the dead wood stock should correspond to the species composition and size structure of the stand; overrepresentation of admixed species and trees with thick trunks is acceptable.

14 It is important to ensure the presence of flowering plants, especially of the families *Apiaceae* (formerly *Umbelliferae*) and *Asteraceae* (formerly *Compositae*) and *Rosaceae*, near stands with dead trees, as they are food resources for the imagines (adult forms) of many saproxylic insects. This can be achieved by retaining glades (mown at the appropriate times), ensuring that these plants have sufficient insolation, and preserving herbaceous vegetation on forest roadsides.

15 It is very important to retain all trees with hollows in groves and parks; all kinds of openings and cavities in the trunk should be treated as "hollows". Hollows should never be cleared of rotting wood as the decayed material is a suitable environment for many rare stenotopic species of invertebrates. "Curing" old and weakened trees should be restricted to selected trees of cultural significance and should not interfere with the processes taking place within the rotting wood microhabitats.

16 Similar rules should be applied to all trees hosting other types of tree-related microhabitats (habitat trees). The principle of retaining habitat trees should be consistently adhered to, even when this hampers forest management operations or is otherwise inconvenient.

17 Concerns for public safety in forests should not be used to justify the removal of all "damaged" or "hazardous" trees, as many of them are habitat trees. Minimizing the risk posed by trees to people must be weighed against the ecological and aesthetic value of each individual tree, taking into account the realistic level of risk.

18 To ensure the continuity of habitat trees in commercial stands, existing ones should be left in place. However, this is not enough. At least some trees must be given the chance to reach an appropriate age, which will allow them to develop their full habitat potential. Typically, such an age is at least 50-100% longer than the harvesting ages determined in forestry for individual tree species.

19 Consequently, with all final cuttings, regardless of harvesting method, 10-25% of the initial number of trees in the logged area should be left to die and decay naturally. The trees selected should be representative of the species composition and size structure of the stand. Ideally, trees should be left in the largest possible groupings with the ground cover intact. Similar parts of the stand should also be left in the case of polycyclic harvest systems, not only in clearcuts. Whenever possible, one of the considerations for selecting the parts of the old stand to be retained should be the presence of protected plants, fungi and animals. Allowing these parts of the stand to decompose naturally will create a mosaic of micro-refuges for protected species in managed forests.

20 Fallen logs in parks should be retained, as should standing dead trees, as long as they are situated at some distance from footpaths (for safety reasons). If a tree does pose a safety hazard, it is better to cut off its upper portion, leaving the middle section of the trunk (> 3 m), rather than cut it down entirely.

21 Dead trees should not be removed from watercourses or lake shores. It is important to ensure that natural groves or forests are present in the vicinity of watercourses so that the stock of dead wood can be renewed there. If there are no such trees, introducing them as part of the regeneration process should be considered.

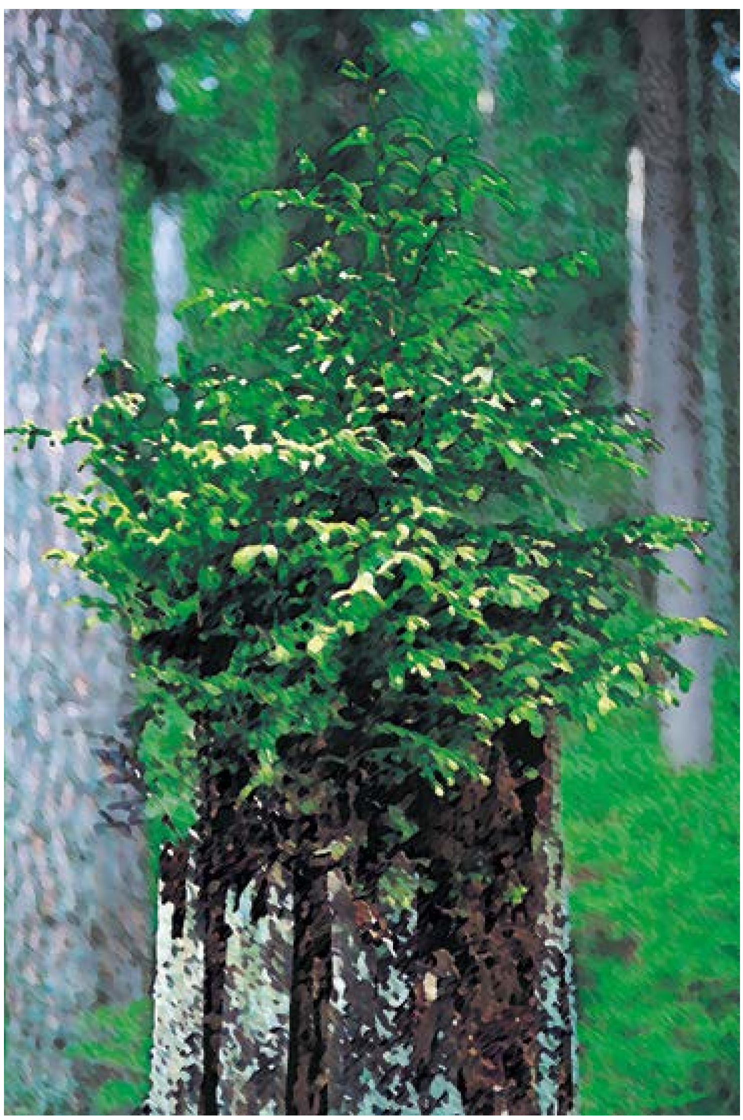
22 Educational campaigns highlighting the role and significance of dead wood should be implemented. They should target the general public, but especially children and young people, and also the various conservation services, state forestry administrations and local authorities.

23 Further research on various functions of dead wood in both forest and aquatic ecosystems is required.

Table 9 Recommended quantities of dead wood in different forest types

Forest type	Reasonable quantity and structure of dead wood
Natural and semi-natural forests in nature reserves and national parks	As much as possible; the removal of any amount of dead wood resulting from natural processes is inconsistent with the function of these forests. Most trees reach biological old age and natural death. If individual trees need to be felled for safety reasons, they should be left lying on the ground.
Artificial forests within nature reserves and national parks	As much wood as possible representing species appropriate to the ecosystems in a given site; the removal of any amount of dead wood resulting from natural processes is inconsistent with the function of these forests. If individual trees need to be felled for safety reasons, they should be left lying on the ground. At least as much dead wood of species alien to the ecosystem, so as to ensure that the total volume of dead wood is not less than 10% of the stand volume. As many trees as possible with hollows and other habitat trees. Many trees reach biological old age and natural death.
Upper montane and marshy spruce forests, alder carrs	As much as possible, because the presence of decaying logs is key to the regeneration of these forests.
Channels of woodland watercourses	As much as possible, because its presence improves the water retention capacity of these woodlands and shapes the associated biotopes.
Stands in near-natural forest complexes	As many trees with hollows and other habitat trees as possible. Most trees reach biological old age and natural death.
Forests designated by forest managers as "reference plots", "biodiversity refuges", "areas excluded from management", "refuges of saproxylic organisms"	As much as possible; the removal of any amount of dead wood arising out of natural processes is inconsistent with the function of such forests. Most trees reach biological old age and natural death. If individual trees need to be felled for safety reasons, they should be left lying on the ground.
Protected forests "constituting valuable patches of native ecosystems". Forests on steep slopes. Forests within 30 m of the edges of watercourses, water bodies and peat bogs	As many trees with hollows and other habitat trees as possible. Most trees reach biological old age and natural death.
Other forests protecting soils and waters. Forests harbouring protected and threatened species associated with dead wood	More than 20 m^3/ha. No less than 7 thick logs or entire standing trees with DBH > 30 cm per 1 ha of forest. As many trees with hollows and other habitat trees as possible. Many trees reach biological old age and natural death.
Protected habitats, e.g. beech forests (9110, 9130), oak woods (9190), oak-hornbeam forests (9160, 9170), riparian and alluvial forests (91E0, 91F0), montane coniferous forests (9410)	More than 20 m^3/ha. No less than 7 thick logs or entire standing trees with DBH > 30 cm per 1 ha of forest. As many trees with hollows and other habitat trees as possible. Many trees reach biological old age and natural death.
Forests harbouring protected and threatened species associated with dead wood	In accordance with the favourable conservation status criteria for habitats of a given species with regard to both the quantity and quality of dead wood or tree-related microhabitats. For species protected in Natura 2000 sites, favourable conservation status criteria for habitats have been proposed in methodological handbooks; for other species, similar criteria would need to be developed based on current scientific knowledge; until then, efforts should be made to maximize the density of microhabitats which, according to scientific knowledge, are suitable for them.
Other forests (multi-purpose)	More than 10 m^3/ha. At least some scattered trees with hollows and other habitat trees in the area. At least some trees (no less than 5% of the forest's surface area) reach biological old age and natural death.

Appendices



Andrzej Bobiec

Appendix 1: Methods for the qualitative and quantitative assessment of dead wood

At first glance, evaluating the quantity and quality of dead wood in the forest seems easy, but there are some aspects that rather complicate the practical side of this task. The greatest difficulty stems from the diversity of dead wood forms, its various shapes and patchy occurrence. Whatever the method, however, the results will always be approximate, but this usually suffices for research and practical purposes. True, the margin of error can be reduced, but this would entail a much more labour-intensive approach.

There are many methods of assessing the quantity of dead wood. The most accurate one requires all pieces of dead wood (both standing and fallen) to be measured directly, after which the results are worked up using appropriate geometric formulas (modified formulas for the volume of a cone). But not even this method can guarantee one hundred percent accuracy: it is hard, after all, to imagine having to measure every single twig. Because the necessary input of labour is great, even when high-tech laser instruments and a portable computer are used, the direct measurement method is employed only on relatively small, permanent plots, where a high degree of accuracy is demanded, e.g. as an aspect of detailed, long-term studies, and then usually in tandem with the simultaneous mapping of the woody debris. In the broader practical context, e.g. in forestry or nature conservation, the standard methods are based on sample plots.

Conventionally, only pieces of wood meeting minimum size criteria (DBH usually > 7-10 cm, length > 10 cm) are taken into consideration, and stumps less than 1.3 m in height are ignored. The wood of small branches and stumps is only taken into account for specific research purposes; in such cases, each piece is measured individually.

Methods based on sample plots

These methods are founded on the premise that the quantity of dead wood on specified patches of the surveyed forest (sample plots) is measured and the results extrapolated to cover the entire area or calculated per unit of surface area. If the plots are to be representative, they need to be many in number and randomly distributed. The randomness criterion can be satisfied, for example, by superimposing a grid on the map of the study area and locating the sample plots at its nodes. Sites can be selected in other ways, but this should be done before starting the fieldwork so as to avoid being influenced by the appearance of the site.

For studying a diverse forest complex, e.g. a mosaic of old and young stands, sample stratification is applied. This first involves dividing the study area into parts in which the focal characteristic, e.g. stands in nature reserves, old or younger commercial stands, are likely to be significantly differentiated, and then designing the plot grid separately for each of the identified layers.

Shape of the sample plot

Circular plots are the most common and most convenient, because it is enough to locate their centre (e.g. using GPS) and then to delineate the boundary relative to the centre with a short tape, laser rangefinder or ultrasonic rangefinder. The work in a circular plot can be carried out by one person. In flat terrain, 0.05 ha of surface area corresponds to a radius of 12.62 m, while 0.2 ha of surface area corresponds to a radius of 25.24 m. Square and rectangular plots are more difficult to set up, as measuring the necessary right angles usually requires two people. Often, very long belt transects are used and the areas extending up to 10 m, say, on either side of the central line are surveyed.

Although surveying smaller plots is easier and faster, one has to bear in mind that the smaller the grid, the more variable the results between particular plots will be. This can greatly increase the number of plots needed to achieve reasonably accurate results. If the wood in the forest is very unevenly distributed, smaller sample plots will yield values deviating significantly from the average, i.e. the accuracy of the measurements will be unsatisfactory. If the amounts of dead wood are very small, monitoring them using a grid of smaller plots becomes counterproductive (the result on most plots will be zero), so longer transects are recommended in such situations.

How many plots are needed?

Usually many more than we can manage to survey; especially when we are working on smaller plots, there has to be a lot of them. The main problem is that dead wood occurs in patches, so the results obtained from individual sample plots will be highly variable. The number of sample plots required to determine, for example, the average volume of dead wood in m^3/ha can be calculated with the desired accuracy. In order to determine the average value with a d% accuracy, assuming the required 95% confidence level, we need $N = (2 \cdot v/d)^2$ sample plots, where v is the coefficient of variation of the re-

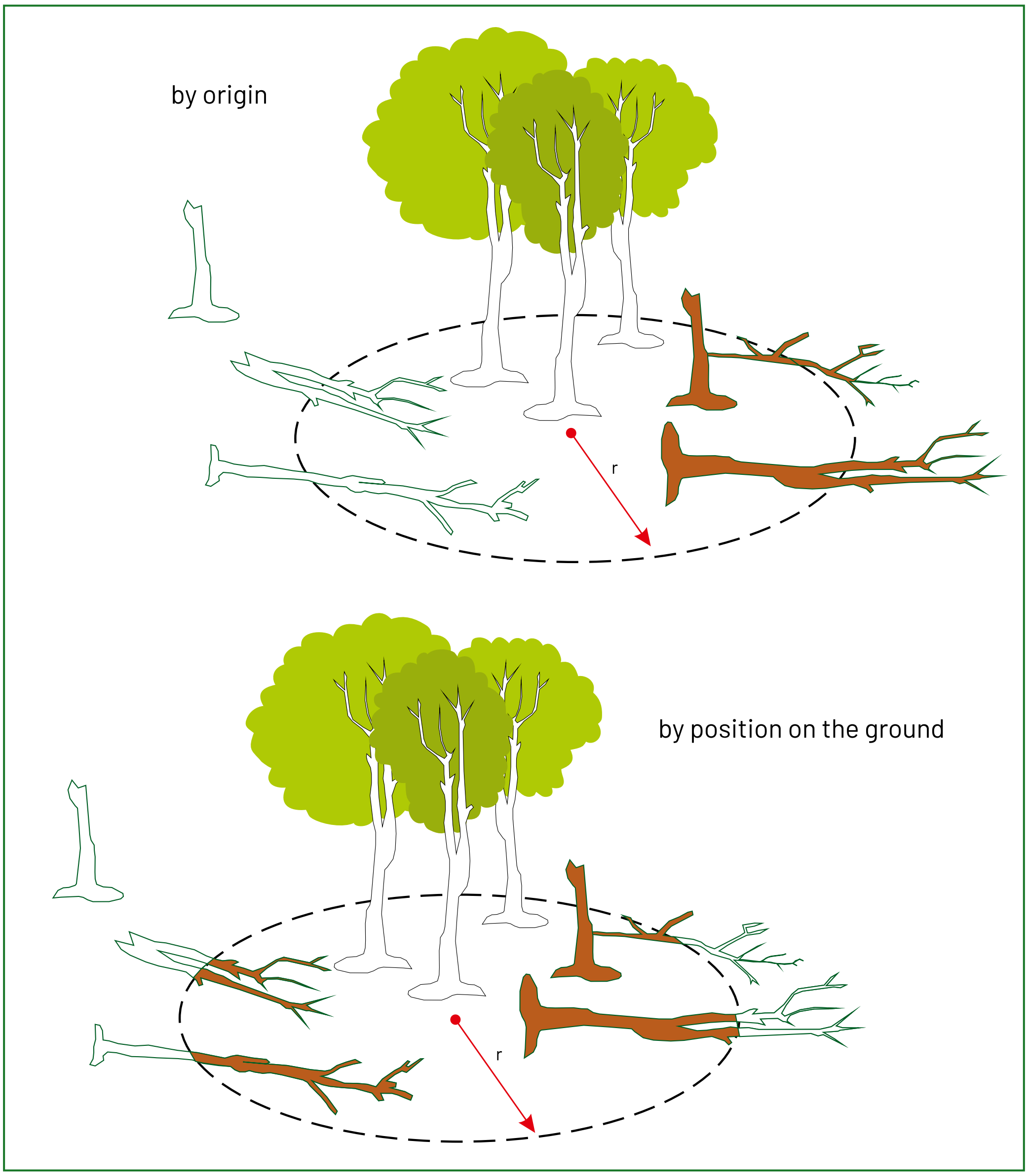


Fig. 43 Selection of woody debris "by origin" (top) and "by position on the ground" (bottom) (after Pawlaczyk 2014)

sults obtained from the samples, expressed as a percentage. Instead of the coefficient of variation of results for all samples, which can only be known once the results have been obtained, we can use the average result from 20 randomly selected preliminary samples. The smaller the sample plot, the higher the coefficient of variation of the amount of dead wood, which will necessitate setting up more sample plots. For example, if the coefficient of variation is 100% (which is quite typical for areas of 0.05 ha), as many as 100 sample plots will be needed in order to calculate the quantity of dead wood with 20% accuracy at the 95% confidence level. Optimizing the research effort requires the optimization of both the size and the number of plots, and this is generally a difficult problem to resolve.

Dead wood selection: by origin or by position on the ground?

We can record woody debris on a sample plot in one of two ways (Fig. 43):

- "By position on the ground": all woody debris within the plot boundary is recorded. But a log which straddles this boundary must be "virtually truncated", i.e. the portion beyond the boundary is not taken into account.
- "By origin": this requires the origin of each piece of dead wood to be identified. All pieces originating from trees growing within the sample plot are recorded (even if they are lying wholly or partially outside the plot), whereas pieces from trees growing outside the plot are ignored (even if they are found entirely or partially inside the plot boundary).

The former approach is more objective as it does not involve having to figure out where each fragment has come from. It is also easier to implement and probably more reliable. However, information about the actual size of individual pieces is lost (unless this is additionally recorded elsewhere). The latter approach requires guessing the history of individual trees, which can be difficult and sometimes unreliable.

The volume of an individual piece of wood

The volume of a fallen log is usually calculated as the volume of a frustum of a cone based on the length of the log and its diameter in the middle, i.e. using Huber's formula:

$$V = L \cdot \pi (d/2)^2,$$

where L – length of the log, d – mid-length diameter of the log.

Measuring the volume of a standing tree is more difficult, as measuring the mid-length diameter is not possible. The height can be measured using an altimeter or, more likely nowadays, using a smartphone or tablet application. Having measured the DBH, i.e. the diameter at 130 cm above ground level, one can estimate the volume of each tree based on the tree volume tables used in forestry. Alternatively, the following formula can be used:

$$V = f H \cdot \pi (d/2)^2,$$

where H – height of the tree, d – DBH, f – form factor.

The value of f depends on the species and age of the tree; it can be read off from the volume tables for the species dominant in the measurements. Most often, f lies between 0.55 and 0.7, so as a rule of thumb we can take the value to be 0.65. Alternatively, Denzin's formula can be used, although it is much less accurate:

$$V = 0.001\ m^3/cm^2 \cdot d^2.$$

It is exceedingly difficult to obtain a reasonable estimate of the volume of a broken tree. Here, the reference is usually the hypothetical volume of a whole standing tree of the same DBH (the height must be assumed from the ratio of DBH to tree heights in the studied stand), but the key question is what part of that volume corresponds to what part of the height. For spruce, pine, fir and alder trees, Radwański's tables can be applied. For other tree species, foresters can use relevant parameters coded into computer programs used in forest districts, but their source documentation has not been published.

In the authors' experience, empirical formulas work quite well. To give an example: for beech trees

$$v = -1.2319\alpha^2 + 2.2373\alpha - 0.0089,$$

where v – part of the total tree volume, α – part of the total tree height.

Stage of decomposition

Because the decay of wood is a continuous process, the stage of decomposition can be determined either through detailed laboratory analysis or by assigning the relevant material to arbitrary decomposition classes. However, forest ecology is concerned with large-scale phenomena and not the decay of individual pieces of dead wood, so such methods are not used because they are extremely labour-intensive and the laboratory analyses are very costly. The stage of decomposition is determined by comparing the analysed material with the adopted classification model, e.g. the dead wood decay classification system proposed by Maser et al. (1979; Chapter 3.1, Fig. 4). The five-point scale in that system seems optimal, although it is sometimes simplified to three points.

The method used in forest management in Poland

The current Instruction for Forest Management in Poland, in use since 2012, envisages the assessment of dead wood resources in forest districts during inventory work performed every 10 years within the framework of successive revisions of management plans. The decision to perform such an assessment is made by a special committee before the management work is commissioned. Usually, the assessment goes forward as planned. For this, a grid of circular sample plots is used (from 0.005 to 0.5 ha in size, depending on the age of the stand), established for the purpose of evaluating living stands. Plots are located at selected nodes of a 100×100 m grid. The required number of plots is chosen at random and takes into account sample stratification by species and age classes. Stands less than 21 years old are not taken into consideration. The volume of dead wood is measured on every tenth plot. The woody debris is recorded using the "by origin" approach and includes:

- all pieces of dead wood thicker than 10 cm at the narrower end and longer than 0.1 m, originating within the area of the transect (0.4 ha),
- standing dead trees (snags) and dead broken trees (windsnaps) with DBH > 7 cm. The height is recorded in metres (excluding the part thinner than 7 cm) and the DBH is recorded in centimetres.

This method does not envisage gathering information about the stage of decomposition of the wood. It also has significant drawbacks: sample stratification, which is valid for measuring the abundance of living stands, is unsuitable for gauging the diversity of dead wood; a very small plot size in younger age classes generates a very high variability of results; the requirement that only every tenth plot should be used for assessing dead wood renders the pool of sample plots too small to obtain reasonable accuracy. Nevertheless, the data collected do give some insight into the overall state of the dead wood resources in each forest district. The method is described in the Instruction for Forest Management (DGLP, 2012).

The method used for Large-scale Forest Inventories in Poland

Measurements are taken on more than 30,000 circular sample plots each with a surface area of 0.04 ha. L-shaped blocks of 5 areas are mapped onto a 4x4 km grid covering all Polish forests. Assessment of dead wood is based on the "by position on the ground" approach and takes into account fallen (pieces inside the sample plot boundary thicker than 10 cm at the broader end) and standing dead trees (DBH of at least 7 cm). The rate of decomposition is assessed on a 3-point scale: not decayed – partially decayed – strongly decayed. The description of the method is published in Large-scale Forest Inventory reports (e.g. BULiGL 2020).

The method used for habitat monitoring in Poland

In a forest habitat monitoring site, surveyed as part of the National Environmental Monitoring programme, the amount of dead wood is measured on a representative monitoring transect, which is also used to record other ecosystem characteristics. To ensure that monitoring is reliable, i.e. to study exactly the same area in consecutive surveys, recognizable transect points must be permanently marked or otherwise located with sub-metre accuracy. The study plot consists of two 10 m belts, one on each side of the transect line. Thus, for a typical 200 m transect, an area of 200×20 m = 0.4 ha is surveyed. The purpose of this method is not to determine the average amount of dead wood in the forest, rather to study temporal changes occurring at individual sites (transects). It makes sense to focus primarily on comparisons between results obtained from the same transect in consecutive series of monitoring observations, i.e. every few years.

Individual pieces of dead wood are selected and measured in the same way as in the forest management method (see above).

As part of the survey, tree-related microhabitats and habitat trees are also recorded on the same transect, according to a simplified classification of major microhabitat types: H – conks; Ob – significant crown breakage: Os – dead main boughs in the crown, at least one-quarter of the crown dead; Rz – broken trees with multiple splinters at least 50 cm in length; Pr – trees with lightning scars at least 3 m in length and penetrating into the sapwood; Pk – trees with cracks through the bark, at least 50 cm in length, reaching at least 2 cm into the sapwood; Dz – trees with hollows >5 cm in diameter, with no rotting material, or the presence of rotting material cannot be determined; DzP – trees with rotting wood microhabitats: large cavities or other internal hollows with significant amounts of rotting material visible; Wk – uprooted trees with elevated root plates at least 1.2 m in height; S – old trees with an estimated age of over 150 years based on size and other factors.

A description of the method, developed by Pawlaczyk (2015), has been published in the monitoring guidelines for habitat type 9130 (*Asperulo-Fagetum* beech forests).

The line intersect method

Comparative studies on the efficiency and accuracy of various methods show that assessing the volume of dead trees can be done efficiently using the method proposed by Van Wagner (1968) for calculating the amount of accumulated downed woody material in North American forests – a crucial factor in forest fire predictions – and later popularized by Brown (1974). The method is based on the relationship between the total number of times sample lines of a specified length intersect with randomly distributed horizontal elements, e.g. pieces of dead wood, and the total length of these elements. If the diameters of the intersecting elements are measured simultaneously (at the intersection points), it is possible to calculate their volume (total or in predefined size classes):

$$V = A\pi^2 \sum d^2/8L$$

where V – volume of dead wood in a given area [m^3], A – area from which the volume is estimated [m^2], d – diameter of debris at intersection [m], L – length of sample line [m].

The accuracy of the method is closely dependent on the quantity of dead wood. It has been assumed that in order to maintain a 10% statistical error, the total line length per hectare should be calculated using the exponential equation:

$$L = 5132e^{-0.04V}$$

where L – length of the line in m/ha, e – base of the natural logarithm, V – estimated volume of dead wood per ha.

This means that for a volume of downed woody material of ca 10 m^3/ha, the length of the sample line L (older managed stands) should be around 3,500 m; for 50 m^3/ha (old-growth forests where dead trees have not been cleared for several decades) it should be slightly under 750 m, and for 120 m^3/ha (the average volume in the Białowieża National Park) ca 50 m (after Warren and Olsen 1964). Given the uneven distribution of downed woody material, it is recommended to double these figures. It would be best to carry out quantitative assessments of the volume of dead wood with reference to fixed plots, enabling repeatability and the monitoring of changes in dead wood dynamics. In quarter-hectare (50×50 m) plots, it is recommended to use a grid formed by unrolling twelve 50 m sections of tape at 10 m intervals (6 in each direction). On 25 ha plots (500×500 m), the inventory can be based, for instance, on a grid of 50 m sections arranged perpendicular to each other (in a "stair" pattern) along both diagonals of the plot.

Although suitable only for lying logs, this method is highly efficient in such cases, as it has a favourable ratio of research effort to assessment accuracy. In order to cover the whole stock of dead wood, one needs to provide the volume of standing and broken dead trees measured with another method, e.g. in 10 m wide sample plots along the line used for measuring downed wood, e.g. 5 m on each side.

The method was successfully used to inventory dead wood in 25 ha plots (500×500 m) in the Białowieża Forest. It involved unrolling a linen tape along two axes with a total length of 2 km, divided into 50 m long, perpendicularly arranged sections (stair pattern). The use of a broken line instead of a straight line is necessary to meet the requirement of the random distribution of dead wood (according to previous studies, the direction of fallen trees in the Białowieża Forest is determined largely by the direction of the prevailing winds). As the method's efficiency is relatively high, especially when an electronic data logger is available, the data can be complemented with information on the diameter, species (where possible; or type – deciduous/coniferous) and the degree of decomposition of the wood piece intersecting the sample line. The accuracy of the method is proportional to the length of the line (unrolled tape), and inversely proportional to the size of the inventoried area. The data obtained can be grouped into arbitrarily selected size classes and classified by species or genus, and/or by degree of decomposition.

Relascope methods

Though ingenious, these methods are rarely used in practice. They are based on counting visible pieces of dead wood that meet certain criteria from randomly selected points. The volume of dead wood per hectare of forest is equal to the number of such pieces multiplied by an appropriate constant. These methods are only usable when dead trees are relatively abundant, i.e. at least a few can be seen from any one point in the forest. Therefore, their practical application in Polish forests is very limited.

The classic relascope method involves counting all the trees surrounding a particular sampling point with a thickness exceeding a certain angle as observed from that point, i.e. trees wider than the notch in a plate relascope (a small metal plate with a notch of a fixed width, held on a string at a fixed distance away from the eye) or a scale visible through a mirror relascope (an optical instrument showing the observed tree along with a scale of a certain width; modern phone applications offer the same functionality). The basal area of trees per hectare of the stand is equal to the number of trees optically wider than the notch or scale of the relascope, multiplied by the relascope factor. Knowing the size of this area and the average height of the stand, the stand volume can then be determined (taken from appropriate tables or calculated using a form factor). This method is mainly used to measure the volume of living stands, but it can be used just as well to measure the volume of standing dead trees.

By verifying the mid-length width of each visible log using a relascope rotated through 90° and then measuring the length of each positively verified log, the total volume of these logs per hectare of forest can be calculated in an analogous manner (using Huber's formula).

The critical length sampling method, proposed by Ståhl et al. (2010), allows for a more accurate use of the relascope to measure lying logs. Using a relascope or a plate rotated through 90°, a section of the log exceeding the scale is identified on each lying log. The length of the identified section is called the critical length. The volume of logs per hectare of forest area is determined as the sum of "critical lengths", multiplied by the appropriate relascope factor. An analogous "critical heights" method can be applied to standing trees.

The perpendicular distance sampling method, proposed by Williams and Gove (2003), does not even require a relascope, just a tape. It involves counting lying logs for which the ratio of the distance from the point of observation (measured perpendicular to the log) to the cross-sectional area of the log at the intersection with the perpendicular distance is less than a chosen constant K. In practice, a table of "limiting distances" is used for logs of a certain diameter. A person proficient at estimating log thickness and distance from the log will only occasionally need to verify these estimates using a measuring tape. The volume of logs in m^3/ha of forest area is calculated using the following formula:

$$V = n \cdot 5000\ m^3/K$$

where n – number of logs counted (the average result from many sampling points scattered across the surveyed area), K – constant.

The method is only suitable for lying trees and does not work well when there are only a few of them.

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Appendix 2: Educational workshops: "What are dead trees for?"

The first edition of the book included lesson plans of activities organized in 2001 at the Nature Education Centre of the Białowieża National Park as part of a workshop entitled "What are dead trees for?". At the time, this was a ground-breaking way of discussing issues related to dead wood in forestry education. Now, in 2021, nearly all such educational centres offer similar lessons, and along almost every nature trail there is at least one board with information on the ecological importance of dead trees. Educational tools and techniques have also developed in the past twenty years. Even so, nothing can replace actually touching a tree and wood. In this new edition, we have decided to reproduce those lesson plans as a reminder of the beginnings of this educational trend in Poland.

Lesson I Andrzej Keczyński

Trees of the Białowieża Forest – living and dead

Objective: Introduction to the common tree species of the Białowieża Forest, factors contributing to their death and rates of wood decomposition.

List of materials: Herbarium sheets with specimens of woody species (leaved twigs), paper (notebooks), pencils, sets of illustrations: profiles of tree species, diagrammatic vertical sections of forest stands (forest profiles), tape measures, guides and keys to tree identification.

Lesson/activity time: I. A – 4 hours; I. B, C – 1 hour; II – 4 hours; III – 2 hours

Number of participants: one class (up to 30 persons).

I. Preparation for field activities

A. Preparatory activity:

Participants copy leaf outlines from herbarium sheets, which will help them identify tree species by their leaves. The leaf outlines are accompanied by outline illustrations of trees and profiles illustrating the vertical structure of stands.

B. Introductory lecture:

- What is a tree, how do trees differ from shrubs, perennials and other herbaceous plants?
- Common tree species of the Białowieża Forest.
- Tree stands as forest tree communities – how diverse are they? Why are they diverse?
- Why do trees die? – biotic and abiotic factors.
- How quickly does wood decompose? What factors influence the rate of decomposition?

C. Organization of fieldwork:

Dividing the participants into groups and subgroups. Establishing the rules of group work. Explaining to the participants how to set up transects, marking trees and placing quadrats on the transects. The quadrat is the basic unit of observation along the transect.

Detailed discussion of the recording form. Definitions:

- **transect** – a research and observation area in the shape of a long rectangle cutting through the stand; in order to make the work easier, it is often divided into smaller sections of the same size;
- **small tree** – a tree with diameter < 21 cm – the shorter edge of the survey form;
- **large tree** – a tree with diameter > 21 cm;
- **dead fallen tree, fresh** – a tree which has died and fallen within the last few years; the wood is hard, often covered in bark, remnants of dried leaves, needles or buds are still attached to the branches;
- **dead fallen tree, decaying** – a tree which died a long time ago, covered by mosses; the outer layers of wood are soft, but the wood inside the log is still hard; boughs are recognizable, but smaller branches and twigs have practically all fallen off by now;
- **dead fallen tree, decayed** – a tree which has been lying on the ground for many years; covered by mosses, vascular plants, shrublets and young trees; the wood is strongly decomposed, soft, spongy and wet, and the shape of the trunk and boughs is barely discernible;
- **young generation** – trees of all species ranging from 10 cm (seedlings and 1- to 2-year-old saplings) to 3-4 m in height and < 4-5 cm in diameter.

II. Fieldwork

1. Participants divided into groups. Recording forms handed out to the groups.
2. Two transects are set up (nature reserve, managed forest). A transect can be 5 m wide, for example, but it is important that its width and length are identical in both the natural and the managed forest. The transects are

divided into quadrats, which makes it easier to count the trees and take measurements.
3. Tree species identified along the transects using leaf and bark characteristics as identification criteria; participants estimate the number of trees on the transect (species, size classes).
4. Participants look for dead trees and determine the causes of their death; they try to estimate the number of dead trees (standing, fallen) on the transect and the stage of their decomposition.
5. Participants examine the young generation of trees. How numerous are they? How do they come to be growing here and what are their chances of survival?

III. Final indoor activities and conclusions

1. Participants prepare lists of living and dead trees with their general characteristics.
2. Description of the young generation of trees (circumstances of their development and growth, chances of survival).
3. Participants discuss the final conclusions:
- What are the differences between natural and managed forests based on the results of the data collected?
- What is the significance of standing and fallen dead and dying trees for existing trees in the stand, the young generation, other plants, fungi and animals?

Recording form

		Quadrats of the transect										
		I	II	III	IV	V	VI	VII	VIII	IX	X	∑
Tree species												
Number of living trees	small											
	large											
Number of dead trees – standing												
Number of dead trees – fallen	fresh											
	decaying											
	decayed											
Young generation trees	species (which?)											
	number											

Lesson II Bogdan Jaroszewicz

Insects and other invertebrates

Objectives:
1. To explore the diversity of invertebrate organisms inhabiting dead wood and living trees.
2. To build awareness of the importance of invertebrates to the natural cycle of organic matter in the forest.
3. To compare the biological diversity of invertebrates inhabiting dead wood and living trees.

IMPORTANT! If the lesson is to take place in a nature reserve or a national park, a permit must be obtained from the appropriate authorities (e.g. Regional Directorate for Environmental Protection, national park management) to hold the lesson at a specific place and date. Details must be provided regarding methods and procedures, showing that they will not have an adverse effect on the protected site, along with a justification as to why the lesson must be held within the protected area rather than outside of it.

Both within and outside protected areas, damage to dead logs must be reduced to a minimum; all organisms and pieces of wood collected during the lesson must be put back where they were found.

Lesson/activity time: in-class activities – 30 min., field activities – 1 hour

Number of participants: 20-25.

List of materials: pencils and paper, magnifying glass 10 ×, vials with stoppers (for each participant), penknife, guides and keys to the identification of forest invertebrates, including insects.

I. Preparation for field activities

1. The participants should be prepared for the exercise beforehand by their biology teacher. They should learn:
a) general facts about invertebrates,
b) characteristics of the major groups of insects associated with dead wood,

c) characteristics of the major types of insect larvae.
2. The second part of the introductory activities covers the general characteristics of the invertebrate fauna of the Białowieża Forest:
a) ecological groups of invertebrates,
b) general characteristics of the succession of organisms occupying dead wood,
c) classification of microhabitats for invertebrates associated with dead wood.

Observing invertebrates in their natural habitat is often very difficult owing to their concealed lifestyle, and in the case of insects, the short period during which imagines (adult forms) – their most visible developmental stage – can be encountered.

II. Fieldwork

The participants should be organized into three small groups with specific tasks. Each group searches for invertebrates and evidence of their presence:
A) on living trees (in crevices in the bark, flutes, on lichens, mosses),
B) on dead trees (on the surface, under the bark, in rotting wood; participants should also look for pieces of wood lying on the ground and any organisms living underneath them);
C) in microhabitats in living and dead trees where invertebrates can live and develop.

Groups A and B work in the same plot, while group C should work on a separate one.

The groups should be divided into working groups of 2-3 participants, which should enable them to examine closely any object they may encounter in the forest: standing live, dead and dying trees, fallen logs and smaller pieces of woody debris. Each working group should receive and fill out a recording form (see below). A "+" sign should be entered into the relevant cell to record a single observation of a specific group of organisms in a given plot. For example, observations of snails on 3 different trees should be indicated by "+++". Organisms should be classified only in accordance with the systematic level specified in the form.

Participants should collect 1-2 specimens of insects or other invertebrates and place them in the vials. After the search is completed, the instructor/teacher empties the contents of each vial on to a sheet of white paper and talks about each organism, characterizing the systematic affiliation of each one, summarizing its biology and its function in the ecosystem, and providing other information about each species that seems particularly relevant or interesting.

III. Final indoor activities and conclusions

After the exercise, the results should be recorded on the summary data form. When discussing the results, it is important to cover the following topics:
a) Which groups of organisms occur exclusively in or on dead wood? Which group is more abundant in dead wood than in other environments? In a functioning and balanced forest ecosystem, it is always the case that far more species occupy dead wood than living trees.
b) Which groups of organisms occur in relatively equal numbers on both living and dead wood? This can be deceptive, because the material collected does not represent the whole spectrum of biodiversity, which might otherwise suggest entirely different species structures on the two substrates.
c) Which microhabitats are found only in living trees or only in/on dead wood?

The post-activity discussion should provide answers to the following questions:
a) What is responsible for the differences in the number and composition of invertebrates occurring on living trees and dead wood?
b) What types of microhabitats do not exist in managed forests?
c) Why are most of the invertebrates associated with dead wood rare and endangered species?
d) What is a "pest"? When does an organism qualify as a "pest"? Why is it that the concept of a "pest" is irrelevant in the context of a national park?
e) What are the ecological functions of invertebrates living in dead wood?

Recording form: Number of organisms associated with dead wood and living trees

ORGANISM / ENVIRONMENT	Earthworms	Snails	Spiders	Myriapods	Insects (developmental stages and group)	Herbivorous and saproxylic organisms	Predatory and saproxylic organisms	Organisms looking for shelter
Dead wood								
Living trees								

Lesson III Arkadiusz Szymura

Birds and other vertebrates

Objectives:

Knowledge:
- a closer look at woodpeckers, which need dead wood to survive
- definitions: tree hollow, semi-hollow, natural cavity
- explanation of the function of dead wood for other bird species
- details of field tasks and methods

Skills:
- identifying the male and female of the great spotted woodpecker in its natural habitat
- telling hollows from natural cavities and semi-hollows
- measuring the DBH
- distinguishing evidence of woodpecker foraging from other signs

Attitudes:
- developing pro-ecological thinking about forests
- raising awareness of the effects of removing dead wood from forests
- focusing on active and creative team work

Form and methods:
- indoor activities – lecture, working with a bird identification guide
- field activities – a trip to the forest, setting up sample plots, taking measurements and conducting observations

Materials: bird guides, slides, transparencies, pairs of binoculars, measuring tapes, callipers, pencils and paper

Lesson time: indoor activities – 1-2 hours, field activities – 2-3 hours

Number of participants: 12-16.

I. Indoor activities

1. **Preparatory in-class activities**

Using bird guides, slides and transparencies, discuss woodpeckers as a group of birds specialized in finding food in dead wood. Point out the following characteristics:
- bill structure
- features of the tongue (stickiness, barbs),
- how the very long tongue is used (in conjunction with the hyoid bones)
- structure of the tail feathers (rectrices)
- anatomy of the legs, toes (their number and position) and claws
- anatomical adaptations to excavating cavities and drumming

Explain the concepts of hollows and semi-hollows.

Talk about the species nesting in natural cavities, hollows and semi-hollows in dead trees, e.g. abandoned by black woodpeckers or formed as a result of tree breakage. Explain why sites associated with dead wood are important for birds (foraging, excavating hollows and their use by other species such as tits, swifts, nuthatches and owls, e.g. Eurasian pygmy-owl, Tengmalm's owl).

2. **Preparatory activities at the Nature Education Centre of the Białowieża National Park**

A systematic overview of the bird species discussed above in block I: woodpeckers (sexual dimorphism), tits, nuthatches, owls, swift.

II. Field activities

During the walk to the strictly protected zone of Białowieża National Park, participants can look and listen for birds. Binoculars and identification guides can be used to reinforce observations and identification skills.

Participants are divided into three groups. Rules of group work are explained. Each group should survey a rectangular plot (50×25 m) in the dominant type of stand in Białowieża – oak-hornbeam forest.
1. plot with dominant European hornbeam
2. plot with dominant small-leaved lime
3. plot with dominance of other species: pedunculate oak, black alder; admixture of European ash.

Each group should then measure the DBH (diameter at 1.3 m above ground) of all trees in the plot and record the species of each tree.

The trunks and boughs of all trees should be carefully scrutinized for natural cavities that could be occupied by birds and for hollows excavated by woodpeckers. Cavities and hollows should be counted.

All observations of birds feeding on standing trees or fallen wood should be recorded together with the degree of wood decay. The results are recorded in the table (see below).

III. Summary

1. **Presentation of the results and discussion:**
- How does the species composition of trees in the stand improve nesting opportunities for birds that nest in hollows or cavities?
- On which tree species do woodpeckers feed? How many species exhibited signs of foraging?
- Where is the most evidence of woodpecker feeding sites found? On living trees, standing dead trees or fallen logs? What was the degree of decomposition of the most favoured foraging site?

2. **Conclusions:**
- What is the relevance of dead wood to birds?
- Which systematic group benefits the most from the presence of dead wood?

Recording form

Plot no.						
Tree species	DBH	Tree status, i.e. living or dead	Natural cavities	Hollows excavated by woodpeckers	Signs of foraging	Stage of wood decomposition

Lesson IV Karol Zub

Fungi

Objectives:

1. To demonstrate the diversity and abundance of fungi associated with dead wood.
2. To explain the part played by fungi in wood decomposition processes in forests.
3. To compare the levels of diversity of fungi inhabiting dead wood in natural and managed forests.

List of materials: paper (notebooks), pencils, guides and keys to the identification of fungi species, measuring tape.

Lesson/activity time: in-class activities – 30 min., field activities – 3 hours

Number of participants: 20-25.

I. Introductory activities

1. The living environment, diversity of forms, feeding and reproduction of fungi.
2. Key characteristics of fungi.
3. The importance of fungi in nature and human life.

II. Preparatory activities at the Nature Education Centre of the Białowieża National Park

1. Testing the knowledge of sporocarp fungi among young people.
2. A short presentation showing the species richness and diversity of fungi in the Białowieża Forest.
3. A more detailed look at a few species (specimens, slides, posters).
4. Discussion about the potential hazards posed by fungi to forests.

III. Field activities

The activities take place by the Browska Road (Droga Browska), on the border between the strict protection zone of the Białowieża National Park and the managed forest. It takes about half an hour to reach this place from the Education Centre.

Procedure:

1. Two 50 m long transects are laid out perpendicular to the road. One transect extends into the natural forest, the other into the managed forest. The transects can be marked using tape or pegs.
2. Participants are divided into two groups.
3. Participants should be instructed in the fungus inventory method and how to fill out the recording forms.

Recording forms:

a) substrates on which fungi develop are given in the rows of the table;
b) columns differentiate the various forms of fruiting bodies:
- caps (with different types of hymenophore: gills, pores and teeth),
- brackets (hoof-shaped),
- other permanent fruiting bodies (small, spreading, protruding, flat),
- fleshy fruiting bodies of various shapes (bowl, flat, irregular),
- puffballs;

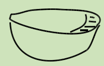
c) participants enter the number of fruiting bodies of a particular form found on a given substrate; both rows and columns contain cells where the total number of fungi specimens should be entered after the inventory;

d) the inventory should be performed on a 2 m wide belt transect (a total sampling area of 100 m^2);
e) if there are many participants, the groups can be subdivided into smaller ones tasked with investigating specific substrates, e.g. living or fallen dead trees, the ground;
f) after the inventory, the results should be entered in a summary table;
g) the instructor may demonstrate and name a few more examples of interesting fungi. Depending on the time available, participants may themselves try to identify the species of some specimens using the guides and keys they have brought with them.

IV. Summary

1. Presentation of the results. The following points should be discussed:
a. the diversity of fungi in natural forests,
b. the dominance of fungal species growing on dead wood,
c. the greater abundance of fungal species of no importance to the human economy (inedible saprophytes).
2. Further discussion and conclusions. The concept of "harmfulness" of fungi in the context of natural forests.
3. Final remarks on endangered and protected species of fungi (posters) and the importance of dead wood in preserving fungal diversity.

Recording form

Form of the fruiting body	 caps	 brackets	 other permanent forms	 fleshy	 puffballs	TOTAL
on standing live trees						
on standing dead trunks						
on fallen trunks						
on downed boughs and branches						
on the ground (except dead wood)						
TOTAL						

Lesson V The Nature Education Centre of the Białowieża National Park

An example of the practical implementation of methods for assessing dead wood volumes in environmental education

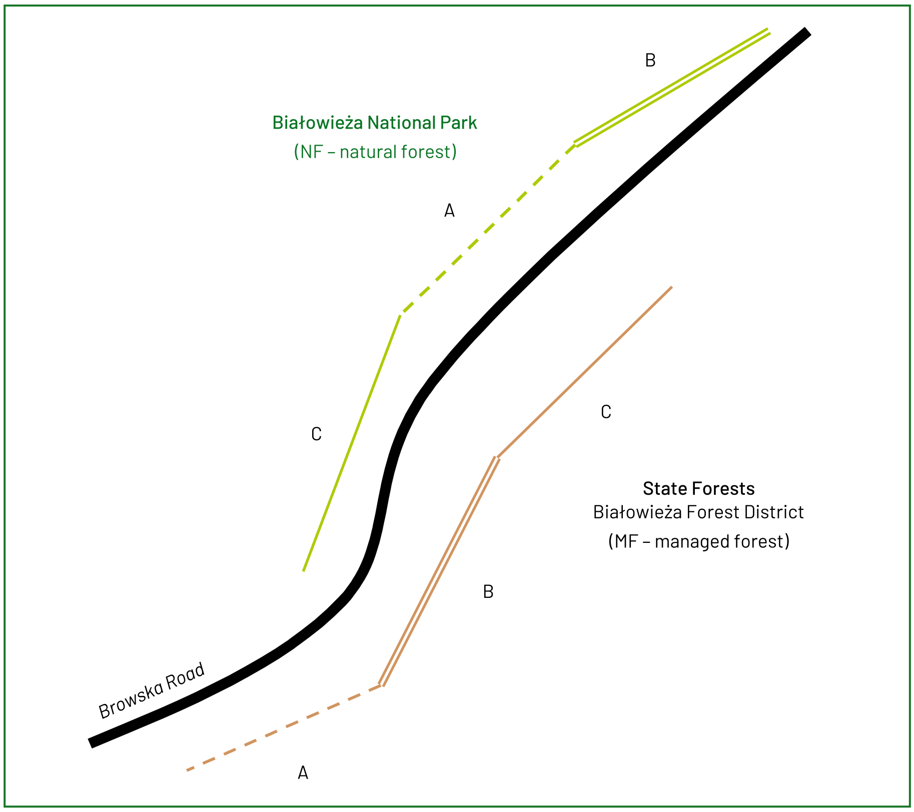
The objective of this lesson is to teach the participants how to detect certain distinguishing features of a natural forest (analytical method). The close proximity of the strictly protected zone of the Białowieża National Park to managed forests allows direct comparison of measurements and observations made under analogous habitat conditions. Special forms and data collection protocols enable the participants to compare a set of selected characteristics from one forest type with the same characteristics from the other one. During the presentation of the results, the participants verify the definition of a natural forest on the basis of their own findings.

Description of activities held during the Workshop: "Green Leaders for the Future" on 1 May 2000, organized by the Nature Education Centre of the Białowieża National Park.

Each of the three groups of participants (A, B, C) carried out observations and measurements along their assigned 150 m long sectors of sampling lines along both sides of the Browska Road: one in the strict protection zone of the Białowieża National Park (natural forest) and the other in the managed forest (see Fig. on p. 268).

The majority of the observation plots in both the natural and managed forests were oak-ho-

The area in the Białowieża Forest where the fieldwork was carried out



rnbeam forest, i.e. deciduous forest on slightly moist, sandy loam soil. Only a small (ca 50 m) section (on either side of the Browska Road) consisted of riparian forest habitat, i.e. marshy forest with alder-ash stands.

Most of the surveyed area was harvested in the first half of the 20th century. This explains why the multi-species oak-hornbeam stand typical of a natural forest has been replaced by a transition stand with dominant birches and aspens, small-seeded species known to spontaneously colonize clearcut areas. Because natural succession is taking place in the natural forest, short-lived species like birches and aspens are gradually replaced by hornbeams, limes and maples. At the same time, the managed forest is being subjected to what is known as reconstruction, which consists in felling the birches and planting oaks with an admixture of other species.

Larger specimens (in two size classes: >40 cm and >70 cm) of both standing trees and trees with hollows were counted along the 10 m wide belt (5 m on each side of the sampling line) covering an area of 4,500 m^2 (3×150×10 m) in the managed forest. The same method was applied in the natural forest. Participants also collected additional ecological information about ground layer species, animal tracks, abiotic factors (insolation, soil temperature and pH, wind speed), as well as dead wood microhabitats (e.g. uprooted trees and large decaying logs).

Van Wagner's (1968) method was used to assess the volume of downed woody debris by measuring the diameters of each piece of dead wood at the point of intersection with the sampling line. During the indoor activities, all the results were entered in a summary table and discussed.

Simplified profile of the communities observed

Stand: birch, hornbeam, lime, spruce, aspen, oak, ash (riparian), alder (riparian), pine (only in the managed forest).

Advanced regeneration and understory: hornbeam, lime, maple, oak (favoured and planted in very large numbers in the managed forest), ash (riparian), alder (riparian), hazel, spindle, field elm.

Ground layer: yellow archangel, wood anemone, European wild ginger (asarabacca), alternate-leaved golden saxifrage, woolly buttercup, liverleaf, creeping buttercup, large bittercress, wood sorrel, martagon lily, toothwort, spring pea, early dog violet, common bugle, false lily of the valley, stinging nettle, male fern, oak fern, common horsetail, ground elder, greater stitchwort, wood stitchwort, Solomon's seal, lesser celandine, herb Paris, sedge, wood millet (grass), seedlings: oak, maple, hornbeam, aspen, ash, elm.

Final results and summary

1. The measurements and observations carried out during the activities demonstrate the considerably greater complexity of natural forest ecosystems – see Tables on p. 269.
2. This complexity results from the fact that, in contrast to managed forests, natural processes in natural forests are not inhibited in any way. The ecosystem of managed forests

Fieldwork in the Białowieża Forest – summary of data and observations gathered by groups A, B and C

Characteristic	Natural forest	Managed forest
Trees with a specific DBH (number per hectare)		
over 40 cm	73	24
over 70 cm	13	2
Standing dead trees (number per hectare)	26	4
Trees with hollows (number per hectare)	19	4
Downed woody debris with a specific diameter (m^3/ha)		
10- 20 cm	7	2
21- 30 cm	46	–
31- 40 cm	20	–
41- 60 cm	27	–
TOTAL	**100**	**2**

Fieldwork in the Białowieża Forest – final results

Characteristic	Natural forest	Managed forest
Stand (+/–)	+	+
Cultivated (+/–)	–	+
Damaged caused by natural factors (+/–)	–	+
Pests (+/–)	–	+
Stand species structure is the result of		
a) targeted measures	–	+
b) unrestricted growth	+	+
Old trees (**M**any / **F**ew)	M	F
Sick and dead trees (**M**any / **F**ew)	M	F
Dead wood (**M**uch / **L**ittle)	M	L
Microhabitats (**M**any / **F**ew)	M	F

is maintained to achieve specific management goals, which is why it is deliberately regulated.

3. "Forest protection", as understood in forest management, i.e. protection against pests and fungi, is inconsistent with the definition of a functioning natural forest, which includes producers (including trees), consumers (including fungi, invertebrates and vertebrates), the biotope, as well as the mutual associations among all the forest's constituents (including European spruce bark beetle infestation of spruces, fungal parasitism, bark stripping and browsing by deer).
4. A natural forest is a constantly evolving, dynamic system. The current species composition of the stand is the resultant of the forest's response to past and present changes in the external environment.
5. Natural forests are absolutely indispensable:
   - as biological diversity banks (species richness, intraspecific variability),
   - as models of natural interrelationships (e.g. natural resistance mechanisms),
   - as natural laboratories (of evolutionary processes, natural selection).
6. Protecting a natural forest does not imply preserving the current species composition. It means guaranteeing the continuity of natural processes and abandoning any activities that may alter the ecosystem.

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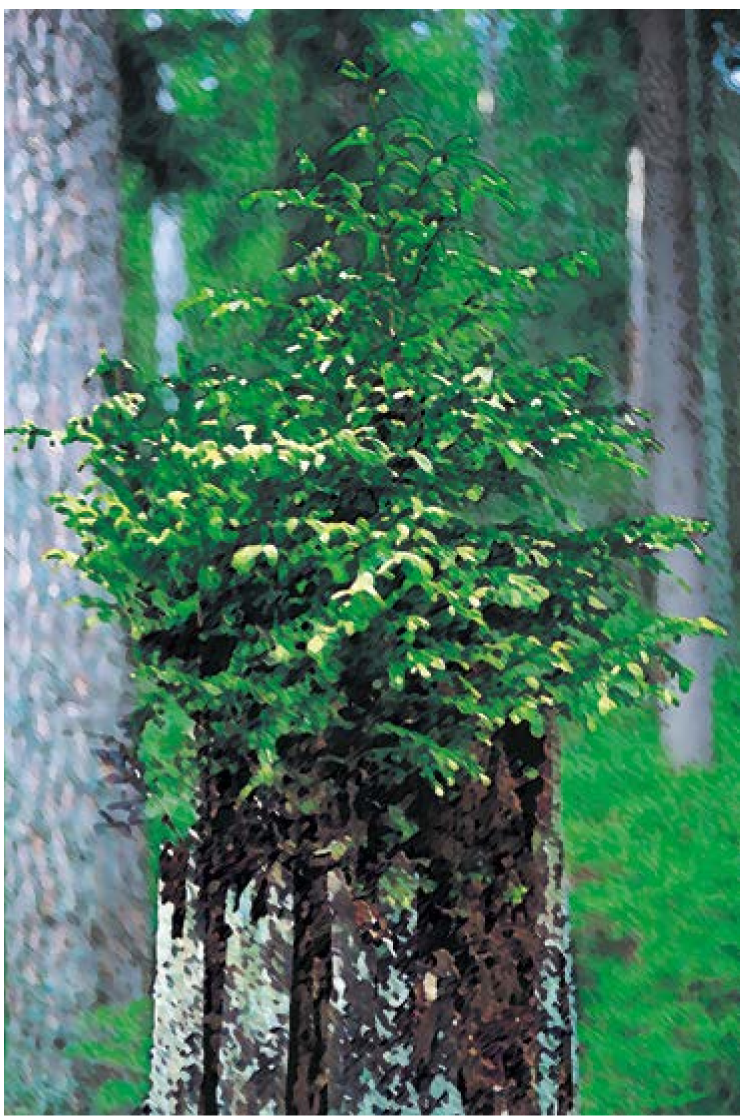

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Index of scientific names of organisms

An asterisk * indicates the page on which the taxon is illustrated

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An asterisk * indicates the page on which the taxon is illustrated

Index of English names of organisms

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Andrzej Bobiec

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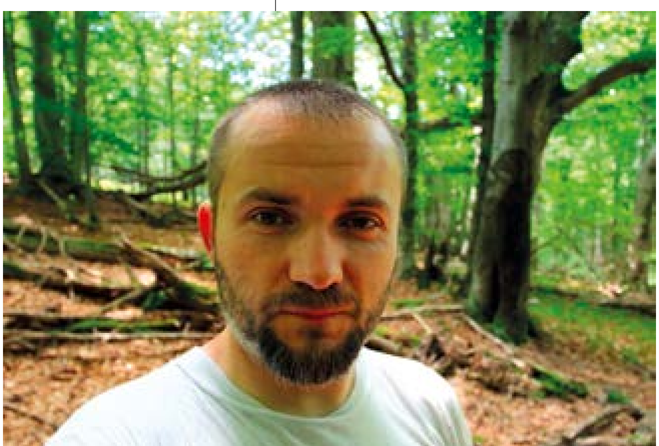
Andrzej Bobiec is a forester, biologist and a Professor of Rzeszów University. In 1995 he co-founded the Society for the Conservation of the Białowieża Forest, which promotes the conservation of natural processes (and the dead wood associated with them) in the Białowieża Forest. He has authored a dendrochronological reconstruction of the history of the oak stands in the Białowieża National Park, and researched the long-term changes in the mosaic-like structure of the ground layer vegetation in the oak-hornbeam forests of Białowieża.

He is fascinated by the non-forest lives of oak trees – faithful companions of shepherds and farmers for thousands of years. He believes that the best response on the part of Poland and Europe to current climatic and ecological challenges should be to return to the extensive, diversified management of rural landscapes, where traditional farming methods are employed, rather than simply further increase the forest cover.

Michał Ciach



A Professor of Forestry Sciences at the University of Agriculture in Kraków, Michał Ciach teaches and carries out research at the Department of Forest Biodiversity in the Faculty of Forestry. His scientific interests focus mainly on the ecology of animals. He runs courses in zoology, ecology and nature conservation. He has cooperated with international and governmental institutions, as well as with NGOs involved in environmental issues and the conservation of natural resources.

He is the author of several hundred of scientific publications and expert opinions, and has delivered lectures at conferences. His scientific experience has been enriched by stays in Canada, Venezuela and Tanzania. He is actively involved in environmental conservation and the rational management of forests.

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Jerzy M. Gutowski

Professor Jerzy M. Gutowski was awarded his PhD in the forest sciences in 1985 and the title of Professor in 2005. He is employed at the Forest Research Institute in Białowieża. For a few years he also worked at the Białystok University of Technology. His research interests lie in entomology, woodland ecology and nature conservation. He is a renowned expert on insects associated with dead wood.

He is actively involved in the conservation of the Białowieża Primeval Forest. The author of some 200 scientific and popular science publications, Professor Gutowski also gives lectures and does editorial work. He is the editor and co-author of books such as "A Catalogue of the Fauna of the Białowieża Primeval Forest" (2001), "The Afterlife of a Tree" (2004), and "Beetles (Coleoptera) of the Suwalski Landscape Park – a Monograph" (2019).

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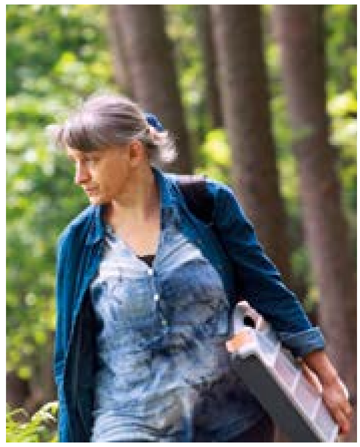
Anna Kujawa



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A botanist and mycologist, Anna Kujawa was for more than 30 years associated with the now defunct Institute of the Agricultural and Forest Environment, Polish Academy of Sciences, Poznań. Her research interests focus on the diversity and distribution of as well as the threats to fungi in Poland. She carries out her field research in national parks and in the agricultural landscape.

She has written around 200 scientific and popular science publications, as well as fungi protection appraisals for national park conservation plans in the Bieszczady Mountains, the Białowieża Primeval Forest and the Warta Mouth. She is the deputy chairperson of the Section for Diversity and Protection of Fungi at the Polish Mycological Society.

For many years she has been the content supervisor of the annual "Fungi of the Białowieża Primeval Forest" exhibition, organized since 1993 by the Białowieża National Park. She is also the co-founder and curator of the Register of protected and endangered species of fungi.

Paweł Pawlaczyk

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Paweł Pawlaczyk works in the Świebodzin Naturalists' Club, a non-governmental environmental conservation organization. He used to do research into the biology of forest trees and woodland ecology, but nowadays he is involved, among other things, in drawing up nature conservation plans for protected areas and integrating aspects of nature conservation with forestry.

He is an expert in European nature conservation law, for example, in the context of the Natura 2000 network. He takes an active part in the conservation of sites of great natural value in Poland. He has written some 200 scientific and popular science publications. He has also co-authored two books: "A Handbook for Local Nature Conservation" (4 editions, the latest one in 2008), and "Natura 2000 and other European nature conservation requirements – the forester's vademecum (2009, 2012), and has also written a series of methodologies for monitoring natural habitats in woodlands (2010-2015).

Karol Zub

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A Professor of the biological sciences at the Mammal Research Institute, Polish Academy of Sciences, Białowieża, Karol Zub is the author of numerous scientific and popular science publications on avian and mammalian ecology. His main research interests are the relationships between predators and their prey, how environmental conditions affect animal mortality, and the management of populations of invasive species.

Besides the Białowieża Primeval Forest, Professor Zub is associated professionally and emotionally with the Biebrza Marshes and the Orkney Islands (Scotland). He is the editor-in-chief of the journals "Mammal Research" and "National Parks and Nature Reserves" ("Parki Narodowe i Rezerwaty Przyrody").

WWF is an international organization that has been actively involved in wildlife conservation for more than 60 years. During that time, we have initiated, carried out or assisted in the implementation of some fifteen thousand wildlife protection projects; in doing so, we have contributed to the founding of more than 270 national parks.

Our mission is to halt the degradation of Earth's natural environment and to shape a future in which people live in harmony with nature. Experience has shown us that the good of people, nature and the environment are intimately linked, no matter where in the world we find ourselves. Our activities are innovative, rooted in cooperation and based on scientific evidence. That is why we want our activities to fully embrace and respond to the needs of the environment and the public. We believe that dialogue and openness to diversity are powerful sources from which we can draw energy and inspiration.

Since 2001, WWF has been protecting wildlife in Poland. We have been saving endangered species. We have been acting to protect not only the largest Polish predators, i.e. the wolf, lynx and bear, and Baltic Sea mammals, i.e. seals and porpoises, but also their natural habitats. Through education, as well as dialogue with business people, decision makers, local government and various interest groups, we are promoting sustainable fishery and agriculture and are acting to stop climate changes. We are tackling the illegal wildlife trade. And we are doing our utmost to ensure that the seas and rivers are full of life.

Everything we do is possible thanks to ordinary people. Without your help, we would not be able to realize our nature conservation projects. To those who have already helped us we owe an enormous debt of gratitude. We invite everybody else to support our organization.

Together we can do more!

The Afterlife of a Tree came out in 2004, as a result of a project run by WWF in the Białowieża Primeval Forest. It was published in response to the need to draw the public's attention to protecting what remained of the natural lowland forests in the Białowieża Primeval Forest and the natural processes taking place there. Ultimately, however, the book took on a more universal character, drawing attention as it did to the need to conserve biodiversity in general.

The Afterlife of a Tree was the first publication in Poland to describe in such depth the dying of trees and their "life after death". The book found a ready audience not only among professionals in science, environmental conservation and nature education, but also among amateur naturalists. After it had gone out of print, many people encouraged us to publish a new edition. And this is precisely what we have done: we hope that this important and necessary book will encourage our readers to view forests from a fresh perspective and inspire them to help protect their most valuable treasures. In conception and layout, this second edition is based largely on its predecessor, but its scope has been much broadened and the content of the earlier version updated.

Stefan Jakimiuk
WWF Poland

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