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978-0-521-88873-8 — Biodiversity in Dead Wood
Jogeir N. Stokland , Juha Siitonen , Bengt Gunnar Jonsson
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1 · *Introduction*

Jogeir N. Stokland, Juha Siitonen and Bengt Gunnar Jonsson

This book is about life in dead trees. All over the world one can find a fascinating diversity of life forms in decaying wood – first and foremost a wide variety of fungi and insects. These organisms carry out the hidden but highly important work of wood decomposition.

A fundamental question frequently revisited in this book is: 'Why is the species diversity of wood-inhabiting organisms so tremendously high?' In most chapters we approach this question indirectly by highlighting the key properties of dead wood, along with the environmental factors and processes that bring about the diversity we can observe. We also discuss species richness explicitly in Chapter 11. There are at least two good reasons for addressing the biodiversity in dead wood. One is that the diversity of wood-inhabiting organisms is a multifaceted and interesting phenomenon that deserves attention for its own sake. Another reason is that this diversity is being seriously threatened due both to the loss and fragmentation of forests and because of the greatly reduced amount of dead wood in managed forests and other woodlands. Thus, we need to understand the role of dead wood for biodiversity in order to manage and maintain it while efficiently utilizing forest resources.

From the outset, the subject of this book could be presented in several different ways. One type of book could be directed at academic biologists and would discuss the subject in the context of ecological and evolutionary theories. Another type of book could focus on biodiversity-oriented management of dead wood and the associated species in forests, agricultural landscapes and urban green areas. We have chosen the middle ground, with an emphasis on describing the diversity and the underlying ecological factors, but we have also added chapters related to management. This choice is underpinned by our belief that a deeper knowledge about wood-inhabiting species has a strong applied potential, and that it is useful for people with a broad interest in forests and nature conservation.

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1.1 Biodiversity in decaying wood

Most people are completely unaware of the diversity of life that exists inside decaying trees. In fact, even the majority of biologists have a relatively limited knowledge of this diversity. Thus, we shall briefly introduce the variety of organisms that, in different ways, depend upon decaying wood.

As we have already mentioned, wood-inhabiting species primarily consist of fungi and insects. Among the fungi we find several groups that are dominated by or contain wood-inhabiting species. The most important wood-decaying species belong to the basidiomycetes (Basidiomycota), including polypore fungi or bracket fungi (a polyphyletic group with representatives in Hymenochaetales, Polyporales, Gloeophyllales and others), and corticioid fungi (another polyphyletic group represented in Hymenochaetales, Corticiales, Russulales and others). Furthermore, we find many other basidiomycete groups that are dominated by wood-decaying species such as jelly fungi (Dacrymycetales), and several different families and genera of agaric fungi (Agaricales). Large numbers of wood-inhabiting species are also found in the other main phylum of fungi, the sac fungi or ascomycetes (Ascomycota), including yeasts (Saccharomycotina) and many other groups. Even if the names of these taxa may not be informative to a non-specialist reader, the appearance of these fungi is often attractive both in shape and colour (see Figure 1.1 and book cover) and they have very interesting ways of living. Most of these fungi are wood decomposers but several of them have entirely different ecological roles.

Among insects, there are several groups where a significant proportion of the species live in decaying wood (Figure 1.2). These include four key orders that comprise the majority of wood-inhabiting insects: beetles (Coleoptera), gnats and flies (Diptera), wasps, bees and ants (Hymenoptera) and termites (Isoptera; nowadays placed in Dictyoptera). In addition, several other insect orders contain wood-inhabiting species, such as moths (Lepidoptera), bugs (Hemiptera), thrips (Thysanoptera), snakeflies (Raphidioptera) and zorapterans (Zoraptera). However, this does not complete the list of saproxylic invertebrates; for instance, mites (Acari) are well represented in decaying wood. This is a hyperdiverse group of small invertebrates belonging to the arachnids (Arachnida). The number of wood-inhabiting mite species may be as large as in the above-mentioned major insect orders, but their ecology and habitats are generally much less well known. Other invertebrate taxa such as pseudoscorpions (Pseudoscorpionida)

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Figure 1.1. Wood-inhabiting fungi representing different taxonomic groups: (a) *Fomitopsis pinicola* (photo John Munt); (b) *Pleurotus ostreatus* (© Jens H. Petersen/MycoKey); (c) *Phlebia tremellosa* (photo Atli Arnarson); (d) *Xylaria hypoxylon* (photo Mikel A. Tapia Arriada); (e) *Lachnellula subtilissima* (photo Dragiša Savić); (f) *Bisporella citrina* (photo Dragiša Savić).

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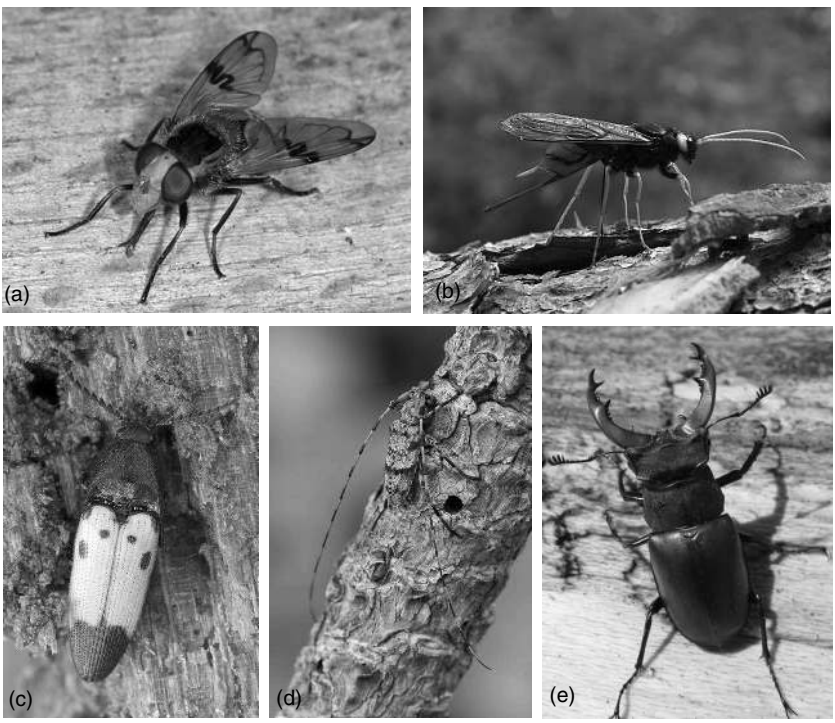

Figure 1.2. Representatives of different insect orders with numerous saproxylic species: (a) "the hoverfly" *Volucella inflata* (photo Dragiša Savić); (b) the giant woodwasp *Urocerus gigas* (photo Nikola Rahmé); (c) the click beetle *Ampedus quadrisignatus* (photo Nikola Rahmé); (d) the longhorn beetle *Acanthocinus henschi* (photo Nikola Rahmé); (e) the stag beetle *Lucanus cervus* (photographer unknown, see http://www.dreamstime.com/royalty-free-stock-photo-stag-beetle-image10207875).

and nematodes (Nematoda) are also well represented in decaying wood. In marine waters, we find both molluscs and crustaceans that bore into submerged wood. This broad taxonomic diversity is paralleled by a wide range of functional roles including those of detritivores, fungivores, predators, scavengers, parasitoids, and various types of symbiosis (commensalisms, mutualism).

Among the vertebrates there are various species with direct associations to wood, such as woodpeckers, a few mammals that eat woody materials, and there is even a group of tropical fish (catfish in the genus *Panaque*) that appear to have a specialized diet of wood.

There are also many species that live in dead and decaying trees but do not use them for their nourishment. A large number of both

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vertebrate and invertebrate species use snags, logs and cavities in living trees for breeding and other purposes.

1.2 Saproxylic species: defining the concept

In the previous section we briefly introduced various groups of species living in decaying wood. The term *saproxylic* has become well established to denote species that are dependent on dead woody material at some stage of their life cycle. It is derived from the Greek words *sapros* and *xylon*, meaning 'decayed' and 'wood', respectively. This term represents the essence of biodiversity in dead wood and we shall explore its conceptual content, especially since various authors have used it in somewhat different ways.

A term akin to saproxylic was first used by Silvestri (1913) when he described the insect order Zoraptera as new to science. Silvestri called the invertebrates living specifically in decaying wood 'saproxylophiles', in contrast with insects living in soil, dung or carcasses. Dajoz (1966) picked up and used the term saproxylic for insects living in decaying wood. Later he extended the term to include species occurring in recently dead wood (Dajoz, 2000).

It is usual to refer to Speight (1989) for a definition of saproxylic species. Speight defined saproxylic invertebrates as:

> species of invertebrates that are dependent, during some part of their life cycle, upon the dead or dying wood of moribund or dead trees (standing or fallen), or upon wood-inhabiting fungi, or upon the presence of other saproxylics.

The publication by Speight dealt mainly with saproxylic invertebrates, but he also briefly mentioned saproxylic vertebrates and fungi. A strict use of Speight's definition would exclude species confined to the bark, but typical usage includes such species as well. There are several publications that discuss alternative definitions of saproxylic species. Here we only mention Alexander (2008), who pointed out that a definition connecting saproxylic species only to dead or moribund trees may be too restrictive, because hollow trees are often healthy, or at least not moribund.

It is also relevant to mention the term *xylobiont*, which is frequently used in the German literature. Schmidl and Bussler (2004) provided the following definition for xylobiontic beetles:

> species that reproduce and spend obligatorily most of their lifespan in any kind of wood and in any kind of decay stage, including fungi living on wood.

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Thus, the meaning is close to the definition by Speight, but it also includes species living in healthy trees.

Note that the definitions above mainly concern animals. In these definitions, the wood-inhabiting fungi simply represent a habitat or medium for the animals like the wood itself. In the mycological literature it is unusual to characterize fungi as saproxylic, although it is possible to find some recent references to saproxylic fungi. Mycologists talk instead about wood-inhabiting fungi or wood-decaying fungi.

Still another related term is *epixylic*, meaning 'on wood'. This term is used for moss and lichen species that prefer to grow on the surface of dead wood. Our definition of saproxylic species in the next paragraph includes epixylic species as a functional subcategory.

In this book we adopt a broad ecological approach, and it therefore becomes essential to include fungi among the saproxylics. We use the term saproxylic based on the following definition:

> any species that depends, during some part of its life cycle, upon wounded or decaying woody material from living, weakened or dead trees.

In this context, woody material refers not only to wood, but also bark and sap (from inner bark, sapwood, or flowing from wounds) at any stage of decay. Thus, we include species living in wounds, dead branches or cavities of otherwise healthy trees. On the other hand, we do not include piercing and sucking insects (such as aphids or scale insects) that dwell on bark and feed on sap from healthy trees. Neither do we include endophytic fungi living inside living trees, unless they are active during the decomposition of the tree when it is dead. At this point we should stress that, irrespective of where one draws the line between saproxylic and non-saproxylic species, the distinction will remain somewhat arbitrary in the sense that species on either side of the boundary will be quite similar.

1.3 Structure of the book

We have written the book so that each chapter has a distinct focus and can be read separately from the others. However, many topics treated in separate chapters are closely related to each other, and we have made numerous cross-references to link such topics. When all the chapters are viewed together, they form four parts that cover different aspects of biodiversity: functional diversity (Chapters 2–4), structural diversity (Chapters 5–9), compositional diversity (Chapters 10 and 11), and finally biodiversity conservation and management (Chapters 12–17).

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In the first part we describe how different organisms are functionally associated with decaying wood and with other organisms living in this habitat. The first chapter treats the different ways in which wood-inhabiting species decompose or digest bark and wood. Next we describe how the species living in decaying wood make up a food web with a nutritional link to decaying wood. In the final chapter of this part we describe species that have a spatial link to dead wood but do not depend upon wood as a food or energy source.

The second part, on structural diversity, highlights how different types of decaying wood support various species assemblages. These are treated in separate chapters focusing on host trees, mortality factors and decomposition phases, specific microhabitats, and tree size. The last chapter in this section shows how the surrounding environment has a strong effect on the species composition inside decaying wood.

In the part dealing with compositional diversity, we focus on species diversity itself, i.e. the identity and variety of the species inhabiting decaying wood. First we describe how woody plants and wood-inhabiting organisms originated almost 400 million years ago and evolved until the present. Then we explore the saproxylic diversity that we know today and try to quantify the species richness in various organism groups.

The last part of the book represents a distinct shift in focus of interest. While we describe saproxylic species under natural conditions at a detailed (substrate) level in the first three parts, we here describe how species diversity is maintained at the landscape scale. We also adopt a conservation and management perspective and explore the ways in which we could modify land-use practices in order to maintain the diversity of saproxylic organisms in forests and other woodland types.

1.4 Knowledge, disciplines and perspectives

The knowledge about saproxylic organisms is scattered across thousands of scientific papers and hundreds of books from quite different and distinct disciplines. In addition, there are innumerable publications in national journals – mainly of a taxonomic and faunistic nature – about the species living in dead wood. Naturally, we have not been able to access all these information sources. Nevertheless, we have tried to present a broad treatment of the biology and natural history of saproxylic species. Three things have become apparent while examining various information sources.

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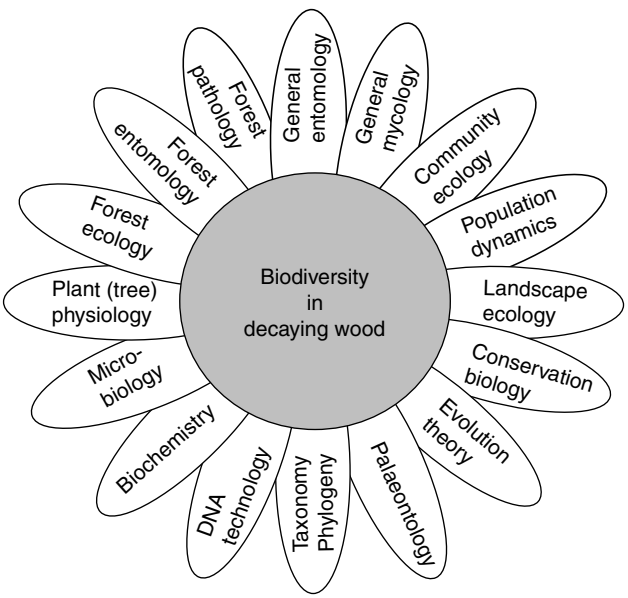

Figure 1.3. Different research disciplines that together form the basis for understanding the biodiversity in decaying wood.

First, a great deal is known about saproxylic organisms and it is quite demanding to obtain an overview of this knowledge. The main reason is that it has been developed in very different disciplines (Figure 1.3). These can be quite narrow in scope such as, for instance, the functioning of cellulose- and lignin-degrading enzymes, forest pathology and forest entomology, and tree physiology. In other cases the relevant pieces of information must be extracted from much wider disciplines such as ecology, general entomology, mycology, palaeontology, taxonomy and phylogeny, where the specific characteristics of saproxylic organisms are treated superficially or indirectly. But there are also publications that focus specifically on the diversity of wood-inhabiting species. These publications typically include keywords such as 'saproxylic', 'wood-decaying', 'wood-inhabiting', or they may contain the keywords 'woody debris', 'dead wood' or 'decaying wood' in combination with a particular taxonomic group. A classical and much cited work about the ecology of dead wood in temperate forests is the review by Harmon et al. (1986). Key books on wood-inhabiting fungi include those by Rayner and Boddy (1988) and Boddy et al. (2008). Similarly, for insects, one can find good overviews in Dajoz (2000) and Lieutier

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et al. (2004). Useful reviews on the effects of forest management on saproxylic species include those of Siitonen (2001), Grove (2002a, 2002b) and Jonsson et al. (2005). Some larger works even make the cross-over between the fungal–insect division, such as the special volume of *Ecological Bulletins* edited by Jonsson and Kruys (2001), which is devoted to the ecology of coarse woody debris in boreal forests, as well as a book about the 'afterlife of trees' by Bobiec et al. (2005).

The second thing that becomes apparent is that species living in dead wood are viewed quite differently in different disciplines. In most knowledge fields there is a neutral attitude towards saproxylic species. They are simply research objects. But in some disciplines (forest management, forest pathology, forest entomology, arboriculture) there is a strong presumption that saproxylic species are generally unwanted and should be controlled or eliminated. Here one finds terms such as pest species, disease and tree or forest damage – a vocabulary that is commonly used and appropriate when the economic value of forest resources is the primary interest. In other disciplines such as conservation biology, the attitude towards saproxylic species is positive. Here the focus is on species with declining population trends, which is considered undesirable and should be counteracted.

A third finding is that the amount of knowledge varies substantially from one organism group to another. For example, the understanding of cellulose- and especially lignin-degrading enzymes is much better for basidiomycetes than for ascomycetes. And among the basidiomycetes it is much better for initial decomposers than for decomposers that occur later in the decay succession. Similarly, the understanding is generally better for early-successional species than for late-successional species, for wood consumers as compared with predators and parasitic species, for pathogenic species rather than non-pathogenic species, etc. Even in studies of saproxylic species as such, there are big differences. Saproxylic beetles have been much more intensively studied than saproxylic gnats, flies, wasps and mites, and similarly, basidiomycete fungi are much better studied than ascomycetes.

The implication of this uneven spread of knowledge is that for some topics or organism groups we can present well-established and detailed facts, whereas in other cases the treatment is necessarily rather superficial. We have tended to be selective when a lot of knowledge exists, but present most of what we have come across on topics where little is known.

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2 · *Wood decomposition*

Jogeir N. Stokland

When you sit beside a campfire you can easily feel the energy that is tied up in woody material. As the wood burns, it is transformed to carbon dioxide, water vapour and minerals – the elements that the tree tied up through photosynthesis when it was alive and growing. The combustion of wood in the campfire takes only a few hours. In temperate and boreal forest ecosystems the equivalent degradation of a tree typically takes 50–100 years and is carried out by numerous wood decomposers working at a much lower temperature.

This chapter deals with the activity of these decomposers – how they degrade and recycle dead wood in forest ecosystems all over the globe. Fungi are the principal decomposers in terrestrial ecosystems, and especially among the basidiomycetes we find many effective wood-decaying species. Also a large number of invertebrates, such as beetles and termites, take part in the process of wood decomposition. Before we explore this fundamental ecosystem process, we shall describe some key aspects of wood structure.

2.1 Structural wood components

Wood is made up of three structural components: cellulose, hemicellulose and lignin. The chemical composition, synthesis and degradation of these economically important wood constituents have been important research topics for more than 50 years – and they still are. As a result, we have a good understanding of their biochemical properties. It is beyond the scope of this book to go into great detail about these specialized topics, which are regularly reviewed in books and scientific journals (see Buswell, 1991; Markham and Bazin, 1991; Jeffries, 1994; Schwarze et al., 2000b; Vicuña, 2000; Martínez et al., 2005; Baldrian, 2008).

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