

Chapter 1

An Introduction to the Diversity, Ecology, and Conservation of Saproxylic Insects



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Thousands upon thousands of lives would cease and their races become extinct were it not for the occasional death of such a jungle giant as this.

Beebe (1925)

Abstract Much like flowering plants set the stage for an explosion of herbivore and pollinator diversity, the origin of dead wood in early Devonian forests (~400 mya) was followed by an incredible diversification of life, giving rise to some of the most successful morphological adaptations and symbioses on Earth. Approximately one third of all forest insect species worldwide depend directly or indirectly on dying or dead wood (i.e., saproxylic), with major functional groups including wood feeders, fungus feeders, saprophages, and predators. Although beetles and flies dominate saproxylic insect communities worldwide, other orders are represented by a wide variety of species as well, and the composition of these assemblages varies biogeographically. Most notably, termites (Blattodea) and the subsocial beetle family Passalidae are both largely restricted to the tropics where they play a major role in the decomposition process. The large body of European research linking declines of saproxylic insect diversity to reductions in the amount of dead wood and old trees across the landscape serves as a cautionary tale for researchers and land managers working in other parts of the world. The conservation of saproxylic insects everywhere can be promoted by efforts to provide an adequate amount and variety of dead wood and old trees across space and time. The preservation of old-growth forests is also critically important as they support relict populations of the most sensitive species. There is a strong need for research outside the boreal and temperate

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zones to develop a more global appreciation for the diversity and ecology of saproxylic insects and to inform management strategies for conserving these organisms in subtropical and tropical forests.

Although William Beebe made his observations of “the little people of bark and wood” in a South American rainforest, he could have reached this same conclusion from studying a recently fallen tree in any of the world’s forests. Indeed, approximately one third of all forest insect species are saproxylic, meaning they depend, either directly or indirectly, on dying or dead wood. Directly dependent species are those that consume parts of woody stems (i.e., bark, phloem, or wood) for food, whereas indirectly dependent species include those that feed on other wood-dependent species (e.g., wood-rotting fungi or other saproxylic organisms), require dead wood for nesting purposes, etc. In addition to the strictly dependent saproxylic species, a very large number of other invertebrates are known to benefit from the presence of dead wood in forests but do not require it. Such taxa include a wide variety of litter-dwelling invertebrates that concentrate near logs, hibernating insects that overwinter within the shelter provided by dead wood, soil feeders that encounter richer food sources underneath fallen wood, and predators that respond opportunistically to an abundance of prey in and around woody debris. While dying and dead wood represent some of the most critical resources to life in forests worldwide, only in the past few decades have researchers turned their attention to the importance of dead wood to biodiversity, with most work taking place in boreal or temperate forests. Moreover, although saproxylic insects are thought to provide some key ecosystem services, research on the value of these organisms to the resiliency and productivity of forests is only just beginning.

Early research on saproxylic insects focused primarily on the small fraction of saproxylic insects that pose a threat to forest health and reduce the marketability of timber products or are pests of wooden structures. In temperate zones, wood-boring beetles have received the most attention (Hickin 1963), whereas termites have long been the focus of study in the tropics. This difference in focus among regions reflects the uneven distribution of social insects, especially termites and ants, which generally become more abundant and diverse toward equator (King et al. 2013). Whereas termites are absent from boreal forests and are represented by just a handful of species in temperate forests, the number of species present at tropical forest locations ranges from several dozen to well over a hundred (Krishna et al. 2013). As a consequence of these patterns, the literature on the diversity and ecology of saproxylic insects is largely fragmented along taxonomic and geographic lines. Efforts to unite these bodies of knowledge are needed to achieve a more holistic understanding of saproxylic insects including how their diversity and functions may vary geographically.

This book represents an effort by researchers around the world to summarize the current state of knowledge about the diversity, ecology, and conservation of insect

life in dying and dead wood. Because a comprehensive coverage of this vast topic is not possible within the covers of a single book, our main aims here include (1) uniting bodies of literature on social and nonsocial saproxylic insects that have, until now, existed in relative isolation from one another; (2) addressing a number of neglected topics including some less-studied orders or families of saproxylic insects, insects associated with highly decomposed woody substrates, and the diversity and ecology of wood-dwelling insect assemblages in tropical forests; and (3) providing the most up-to-date coverage of topics of particular ecological importance or interest to those making forest management decisions. Before further introducing the chapters that follow, it is worth taking a moment to consider the history of insect life in dead wood. Below we briefly discuss the origins and properties of woody plants, the origins and diversification of wood-dwelling insects, and a timeline of research on saproxylic insects.

1.1 Origins and Properties of Wood

1.1.1 Origins

Fossils of a small shrub-like plant similar to the genus *Psilophyton* from the early Devonian (~407 mya) represent the earliest known records of wood (Gerrienne et al. 2011). Although the evolution of wood is thought to have initially been driven by hydraulic constraints (Gerrienne et al. 2011), wood also proved to be an effective solution to the challenge of maintaining an upright growth form arising from competition for sunlight among plants (Cichan and Taylor 1990). The earliest known arborescent plants appeared in the middle Devonian, approximately 380 million years ago (Willis and McElwain 2002). By the late Devonian and Carboniferous, much of the Earth's land surface was covered in dense forests. These early forests consisted of a mixture of spore-producing and early seed-producing tree species (Stein et al. 2007; Willis and McElwain 2002). The spore producers included lycopsids (lycophods), sphenopsids (giant horsetails), filicopsids (ferns), cladoxylopsids, and progymnosperms (extinct), whereas the early seed producers included pteridosperms (seed ferns, extinct) and *Cordaites* (extinct). Pteridosperms would later give rise to the gymnosperms (cycads, ginkgos, and conifers) and angiosperms (flowering plants) that dominate modern forests (Frohlich and Chase 2007).

Vascular cambium arose multiple times in the evolution of plants (Cichan and Taylor 1990), and the tree lineages listed above differed in how wood was arranged within their stems. Many of these early trees possessed unifacial vascular cambium and only produced small amounts of secondary xylem. One highly successful but now-extinct genus of trees from the period, for instance, was *Lepidodendron*, a lycopod that grew up to 35 m tall and over a meter in trunk diameter (Scheckler 2001; Willis and McElwain 2002). Because the stems of *Lepidodendron* possessed unifacial cambium and produced little wood, most of their support came from an extremely thickened cylinder of bark. In contrast, other early trees, like most forest

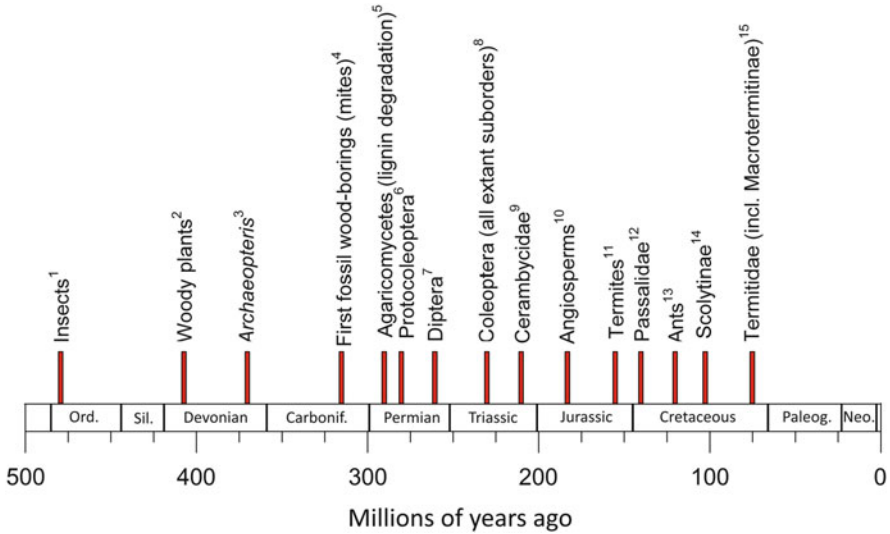


Fig. 1.1 Timeline showing major events in the history of saproxylic life (many of the dates given here represent median values from ranges reported in the literature). Superscripts refer to the following references: 1: Misof et al. (2014), 2: Gerienne et al. (2011), 3: Willis and McElwain (2002), 4: Cichan and Taylor (1982), 5: Floudas et al. (2012), 6, 8, 11, 13, 15: Grimaldi and Engel (2005), 7: Bertone and Wiegmann (2009), 9: Wang et al. (2014), 10: Bell et al. (2010), 12: Scholtz and Chown (1995), 14: Hulcr et al. (2015)

trees living today, possessed bifacial cambium which produces secondary phloem in addition to secondary xylem. Although easily taken for granted in modern forests, the appearance of trees possessing bifacial vascular cambium was a major step in the evolution of plants (Spicer and Groover 2010) as well for arthropods and other organisms. The first such trees were progymnosperms such as *Archaeopteris*. These trees grew 10–30 m in height and produced thick woody stems similar in morphology to those of modern conifers (Meyer-Berthaud et al. 1999; Scheckler 2001). Perhaps due to their perennial lateral branches, deep-rooting structures, and megaphyllous leaves, *Archaeopteris*-dominated forests of the carboniferous and their fossils can be found worldwide (Willis and McElwain 2002). Thus a plausible approximate beginning of dead wood as an abundant and widespread resource was the appearance and rapid spread of *Archaeopteris* in the late Devonian 370 million years ago (Fig. 1.1).

1.1.2 Modern Wood Producers

Trees, woody shrubs, and lianas are the principle wood-producing plants in modern ecosystems. All extant species can be categorized as gymnosperms or angiosperms

(flowering plants) depending on whether their seeds are “naked” or enclosed within ovaries. Gymnosperms are much older and consist of many fewer species than angiosperms. Tree forms include approximately 310 species of cycads, 1 ginkgo, and roughly 615 species of conifers. Although conifers such as pine, spruce, and fir still dominate forests in many regions and represent some of our most valuable timber trees, they have been largely displaced by angiosperms throughout much of the world. Angiosperms include many thousands of species and can be distinguished between monocots or dicots depending on whether their seeds contain one embryonic leaf (i.e., cotyledon) or two. Although some monocots such as palms, bamboo, and banana trees are arborescent, their stems lack vascular cambium and do not produce wood. Other nonwoody arborescent plants such as “tree ferns” also lack vascular cambium and are therefore not considered true trees (Thomas 2000).

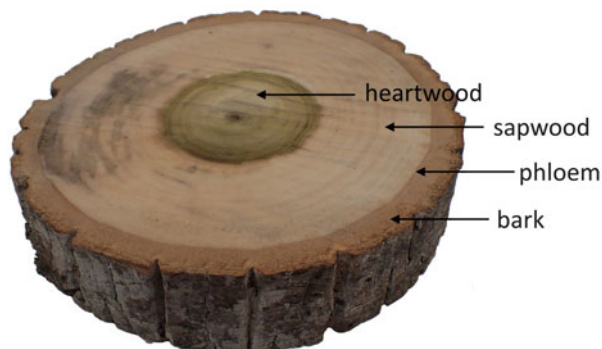
1.1.3 Basic Growth Patterns and Products of Woody Stems

All modern wood-producing plants exhibit both primary (length) and secondary (girth) growth arising from the division of undifferentiated cells in special meristematic tissues. Primary growth occurs in apical meristems located at the tips of shoots and roots, whereas secondary growth occurs in the vascular cambium, a lateral meristem, between the bark and the wood. As mentioned previously, the vascular cambium in modern plants is bifacial, producing secondary phloem to the outside (i.e., the inner bark) and secondary xylem (wood) to the inside. A third type of meristem called the cork cambium contributes to the outermost layers of bark. The cork cambium first arises from parenchyma cells in the cortex (i.e., the outer layer of the stem) and later from parenchyma cells in older, nonfunctional layers of phloem (Wilson and White 1986). The walls of cells produced by this meristem become impregnated with wax and suberin, their protoplasts die, and their lumina become air-filled (Wilson and White 1986). These resulting layers of outer bark function to prevent water loss and protect underlying tissues from various external threats such as fire.

Though essential to the life of a plant, the phloem layer is so thin as to be easily overlooked when viewed in cross section (Fig. 1.2). The youngest innermost layers, often only 0.2–0.3 mm in width (Wilson and White 1986), are responsible for distributing organic substances produced in leaves throughout the rest of the plant and are particularly rich in sugars. Not surprisingly, therefore, a wide variety of organisms target these tissues in dying or recently dead trees (see Sect. 1.2.3.1). Phloem remains active in the transport of photosynthates for just a few years in most species. Older tissues become blocked by callose or crushed by the forces of continued cambial activity (Wilson and White 1986). Old layers of phloem gradually become incorporated into the outer bark.

Wood provides support for the plant and is responsible for conducting water and minerals upward from the roots. Successive layers of secondary xylem are often visible in cross section as distinct annual rings. These reflect changes in growth rate

Fig. 1.2 Cross section of a woody stem (*Liriodendron tulipifera* L.)



and are most obvious in regions experiencing strong seasonality with respect to precipitation or temperature. In temperate regions, for instance, fast-growing wood produced early in the year (i.e., “early wood”) is typically less dense (consisting of wider cells with thinner cell walls) and usually lighter in color than slow-growing “late wood” (Panshin and de Zeeuw 1970). By contrast, in relatively stable tropical regions where conditions change little over the course of the year, it is not uncommon for trees to lack clearly visible growth rings.

Many tree species produce heartwood which is often visible in cross section as a central core of darkened wood surrounded by younger sapwood (Fig. 1.2). Heartwood differs greatly from sapwood in several physical and chemical properties. Most notably, heartwood contains greater concentrations of “extractives,” a variety of extraneous compounds including waxes, fatty acids, alcohols, steroids, higher carbon compounds, and resins which give it its dark color and have an inhibitory effect on decay (Rayner and Boddy 1988; Panshin and de Zeeuw 1970). These compounds are de novo synthesized (from materials stored in parenchyma cells) in a narrow transition zone in which ethylene levels are high and metabolic levels are increased (Rayner and Boddy 1988). In addition, tyloses often form in the heartwood of many hardwood tree species, thereby partially or completely blocking vessels. This reduces permeability (Panshin and de Zeeuw 1970) and causes heartwood to be drier and harder than sapwood and also more resistant to all kinds of decay (Cornwell et al. 2009 and references therein; Thomas 2000). Furthermore, nitrogen, phosphorus, and potassium concentrations are generally lower in the heartwood than in sapwood, although the concentrations of magnesium and calcium sometimes exhibit the opposite pattern (Meerts 2002). Although heartwood is much richer in defensive secondary metabolites compared to sapwood and its extracts have a clear inhibitory effect on most organisms (Noll et al. 2016), certain species of fungi, the “heart-rot fungi,” specialize on heartwood and can play a central role in the creation of tree cavities (Thomas 2000; Rayner and Boddy 1988).

1.1.4 *The Structure and Composition of Wood*

Cells produced by the vascular cambium are either oriented parallel (i.e., “axial elements”) or perpendicular (i.e., “radial elements”) to the stem or root (Shigo 1984). The axial elements include vessels, tracheids, fibers, parenchyma, and resin ducts (Shigo 1984). As soon as the cellular contents of vessels and tracheids die, they become functional in water transport. Fibers have heavily lignified cell walls and provide a supportive function to the stem. They too are usually, but not always, dead at maturity. Parenchyma cells remain alive in functional wood (the wood becomes heartwood once they die) and store starch along with other compounds. Some of the substances stored by parenchyma cells are converted to defensive compounds that have an inhibitory effect on decay fungi and bacteria (Shigo 1984). The radial elements of wood include ray cells (primarily parenchyma) and resin ducts. The ray cells are arranged in vertical bands that divide the stem into sections. These divisions are not complete, however, as the bands of cells are not continuous throughout the length or across the width of the stem. These cells perform an important function in the radial transfer of nutrients from the outer bark to the inner parts of the wood. They also play a key role in tylose formation.

Wood (i.e., the walls of xylem cells) mostly consists of cellulose, hemicelluloses, and lignins although a wide variety of other less common compounds are present as well. The most common organic compound on Earth is cellulose, a polysaccharide consisting of a linear chain of approximately 500–14,000 β -glucose units that accounts for 40–45% of wood weight (Wilson and White 1986; Sjoström 1993; Leschine 1995). Cellulose is an exceptionally strong molecule and plays an important role in cell wall structure. As discussed in later sections, very few organisms are capable of breaking the bonds between the β -glucose subunits, and this has given rise to numerous symbiotic relationships between saproxylic insects and microbes. Hemicelluloses are also polysaccharides, comprised of various *D*-pentose sugars forming branched polymers of up to 3000 units (Sjoström 1993), and account for 20–40% of wood weight (Wilson and White 1986). Lignin, making up 20–35% of wood weight, is a heterogeneous biopolymer lacking a well-defined structure but consisting in general of phenylpropanoid units (*p*-hydroxyphenyl, guaiacyl, syringyl, sinapyl, and others), all being aromatic cores with hydroxylated side chains linked together by C–C or ether bonds (Wilson and White 1986; Freudenberg and Nash 1968). Lignin plays a fundamental role in protecting cellulose and hemicelluloses from enzymatic attack. The large lignin molecules fill spaces between cellulose and hemicelluloses in cell walls, bonding predominantly with the latter (Jeffries 1987). Unlike cellulose and hemicellulose, lignin is hydrophobic which aids in water conduction (Wilson and White 1986). Together, cellulose, hemicelluloses, and lignin form a complex matrix generally referred to as lignocellulose.

The digestion of lignocellulose requires specialized enzymes: cellulases, hemicellulases, and ligninases. Three basic types of cellulases are needed to cleave the polymer into glucose units, and these are endo- β -glucanase (cleaving the internal bonds of cellulose), cellobiohydrolase (breaking usually two glucose units from the

chain end), and β -glucosidases (splitting the glucose oligomers into monomers) (Lo et al. 2011). These cellulases can be organized into supramolecular complexes allowing cellulose to be fully digested (Bayer et al. 1998; Brune and Ohkuma 2011). Hemicellulases are digested by a wider range of less-specialized enzymes, due to their heterogeneous chemical nature and branched molecular pattern (Jeffries 1987). Ligninases include many diverse enzymes, peroxidases, phenoloxidases, and laccases, produced by many fungi, and also some bacteria and actinomycetes (Singh and Chen 2008; Sigoillot et al. 2012). Among microorganisms, fungi are the most important and conspicuous (i.e., often forming macroscopic structures like mycelia and fruiting bodies) organisms capable of digesting lignocellulose. Filamentous fungi are particularly effective at decomposing wood as they can quickly extend deep within the wood and can translocate water and nutrients between locations through their mycelia (Jeffries 1987). Three main wood-rotting fungal types, as summarized by Rayner and Boddy (1988), are as follows: (1) white rot fungi, which cause degradation of all basic units of wood (cellulose, hemicellulose, and lignin), are common in hardwoods and have a more tropical distribution; (2) brown (or red) rot fungi, which are incapable of degrading lignin, are primarily associated with conifers and have more of a northern distribution; and (3) soft rot fungi degrade cellulose and hemicellulose but cause less extensive degradation than brown rot and give the wood a more spongy consistency. Soft rot is largely confined to situations where white rot and brown rot are inhibited, such as wood saturated with water. Bacteria also play significant role in the process of wood degradation (Kim and Singh 2000) but, due to their small size and limited mobility, are typically more active in situations where mycelial fungi are less abundant (Rayner and Boddy 1988; Kim and Singh 2000). Examples of situations favoring bacterial activity include aquatic environments, tree wounds and sap flows, highly decomposed wood, and wood comminuted or egested by insects (Kim and Singh 2000; Ausmus 1977). Three recognized forms of bacterial decay, as summarized by Kim and Singh (2000), are as follows: (1) tunneling by bacteria that penetrate cell walls and appear to be capable of metabolizing lignin in addition to cellulose and hemicellulose; (2) erosion by bacteria present in wood cells that create troughs in the cell walls; and (3) cavitation by bacteria that is less well-known and apparently restricted to certain situations but involves forming cavities within the cell walls. Interestingly, fungi can digest wood in aerobic conditions, while other wood-digesting microorganisms are more often anaerobic, due to the need of protecting their extracellular enzymes from damage by oxidation (Leschine 1995). While fungi and bacteria are the primary decomposers in all ecosystems, other organisms known to produce the enzymes necessary to break down one or more compounds comprising the lignocellulose matrix include protozoa (e.g., ciliates or metamonads; Breznak 1982; Ohkuma et al. 2005; Leschine 1995) and examples from a few groups of Metazoa including Mollusca (e.g., *Haliotis*, *Mytilus*, or *Bankia*; Suzuki et al. 2003; Xu et al. 2001; Dean 1978), Nematoda (Smant et al. 1998), crayfish (Byrne et al. 1999), termites and other cockroaches (Lo et al. 2000; Watanabe et al. 1998), beetles (Girard and Jouanin 1999), and even certain sea squirts (Dehal et al. 2002).

In addition to being so recalcitrant, and despite being rich in energy content, wood is not a very nutritious resource compared to other plant tissues (e.g., leaves, flowers, seeds, etc.) and especially compared to animal tissues (Woodwell et al. 1975; Käärik 1974). The nitrogen content of wood, for instance, is only 0.03–0.1% by dry weight compared to 1–5% for living herbaceous tissues (Käärik 1974, and reference therein). Of the three major constituents of woody stems, phloem tends to be the most rich in sugars and nutrients followed by sapwood and heartwood (Woodwell et al. 1975). Readers interested in a much more detailed description of wood anatomy are referred to major textbooks on the subject such as Panshin and de Zeeuw (1970) or Wilson and White (1986).

1.1.5 Differences Between Gymnosperms and Angiosperms

It is worth briefly reviewing some important differences in the structure and composition of wood produced by gymnosperms and angiosperms. Gymnosperm wood is generally more uniform and consistent in structure among taxa than that of angiosperms (Wilson and White 1986). This is because the wood of gymnosperms consists almost entirely of tracheids, narrow, and elongated axial elements (commonly 100 times longer than wide) with highly lignified and thickened cell walls. These cells are responsible for providing structural support in addition to the conduction of water. Some gymnosperm genera (e.g., *Pinus*, *Picea*, *Larix*, and *Pseudotsuga*) also possess resin canals which produce and carry resin for use in defense and wound response. Angiosperm wood, by contrast, contains a much more varied array of axial elements. These include tracheids, parenchyma, vessel elements, fiber tracheids, and fibers. In addition, these cell types appear in different proportions and in different arrangements among tree species (Wilson and White 1986). Unique to angiosperms, vessel elements are shorter and generally wider than tracheids. They are arranged end-to-end longitudinally to form water-conducting vessels. Vessels can be distributed uniformly within each growth ring (diffuse-porous trees), concentrated at the beginning of each tree ring (ring-porous trees) or some variation of this. Unlike the tracheids of gymnosperms, the tracheids and vessels of angiosperms provide little structural support. This function is instead performed by fibers, long needle-like cells with thick and heavily lignified walls. The mechanical strength of angiosperm wood is a function of its density which, in turn, is related to the proportion of fibers (Wilson and White 1986). Angiosperms produce a wide range of wood densities but on average produce denser wood than gymnosperms. The two categories of trees are therefore often referred to as “hardwoods” and “softwoods,” respectively. It is also relevant to mention that gymnosperm wood tends to contain more lignin than angiosperm wood (Weedon et al. 2009) and generally has lower mineral nutrient concentrations including, most notably, nitrogen, potassium, and magnesium (Meerts 2002). Such differences have important implications for relative decay rates with the wood of gymnosperms decaying more slowly than that of angiosperms (Weedon et al. 2009).

1.1.6 *Variety of Wood*

Dead wood is a highly variable resource depending on a wide variety of intrinsic and extrinsic factors, and this in large part explains why it supports so many species of insects and other organisms. The diversification of woody plants over the past 400 million years has resulted in tens of thousands of species distributed unevenly around the world. There are more than 60,000 tree species in the world (Beech et al. 2017) as well as many other woody shrubs and lianas. Tropical forests contain the highest diversity of woody plants, with as many as 283 species per hectare in Peru alone (Phillips et al. 1994), whereas many temperate or boreal forests are dominated by just one or several species. There are important physical and chemical differences in the dead wood produced by these various species. The most obvious differences concern stem diameter which exhibits a wide range of interspecific variation as well as intraspecific variation (i.e., depending on tree age) and of course decreases with distance from the ground within individual trees. In addition, the structure of wood varies considerably among species, with major differences between the wood of gymnosperms and angiosperms (see Sect. 1.1.5).

In addition to these intrinsic differences in wood properties, extrinsic factors also play a vital role in increasing the variety of dead wood in forests. The degree of sun exposure experienced by a woody substrate, for example, can result in major differences in wood temperature and moisture content (Graham 1925). Moreover, the posture (standing or fallen) and vertical position of wood relative to the forest floor also has important implications for wood conditions (Fig. 1.3). The wood of standing dead trees (i.e., snags) or of dead branches attached to living trees is typically drier and decomposes more slowly than wood lying on the forest floor or dead roots belowground. It is not uncommon for a large proportion of dead wood volume to be standing or suspended. In old-growth forests in southern Finland, for instance, Siitonen et al. (2000) found that about 63% of dead wood volume consisted of logs, with the rest consisting of intact or broken snags. Similar results were obtained in managed stands (after excluding man-made dead wood), with only about 56% of the dead wood volume consisting of logs on the forest floor (Siitonen et al. 2000). Furthermore, a considerable amount of aboveground dead wood exists within the stems of aging trees. The decomposing cores of living trees often result in the formation of hollows which form a special habitat for many organisms when they become open to the outside (Micó 2018; see Chap. 21). One of the most distinguishing features of old-growth forests is the presence of very old large-diameter “veteran” trees (Siitonen et al. 2000; Spies et al. 1988; Franklin et al. 1981). These living but declining trees are of immense ecological value due to the tree cavities they provide as well as the many dead branches they contain within their crowns.

Another process contributing to dead wood variety concerns the chemical and physical changes wood experiences as it decomposes. Although a number of decay classification systems have been developed, three are of particular relevance with respect to the succession of insects (see Sect. 1.2.4). The first and shortest of these is

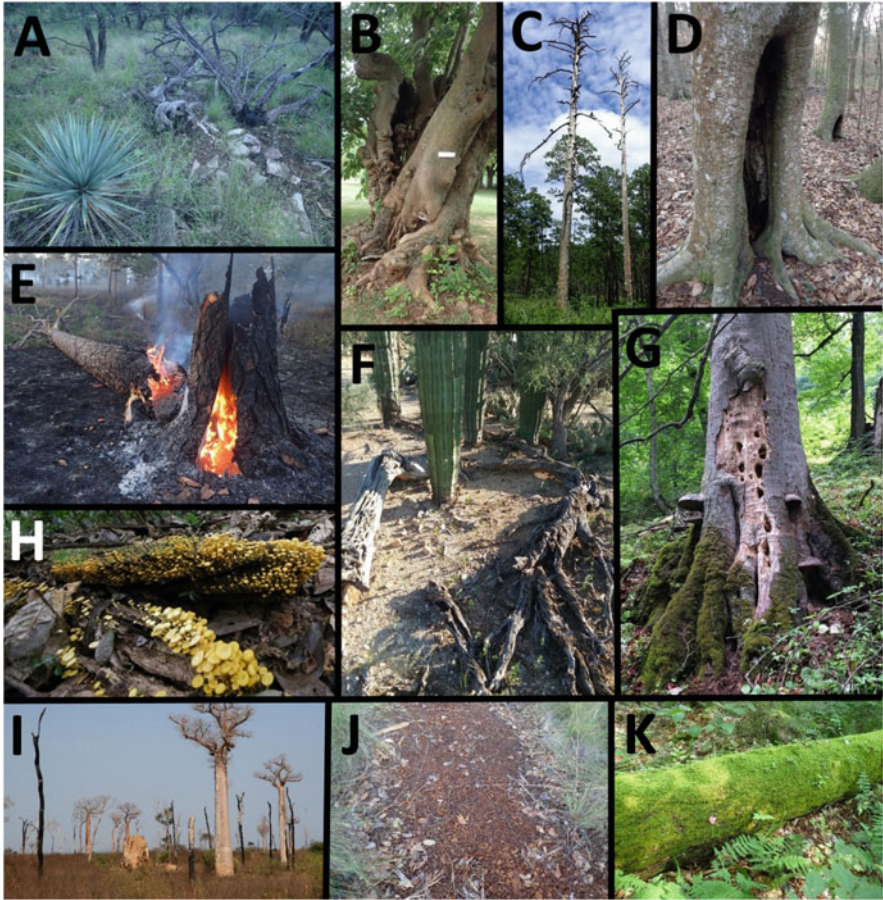


Fig. 1.3 Examples of dead wood variety. (a) Montane pine-juniper forest, Arizona; (b) veteran *Broussonetia papyrifera* (L.) L'Hér. Ex Vent. (a nonnative species) at Monticello, the historic home of Thomas Jefferson, Virginia; (c) dead *Pinus palustris* Mill. snags in old-growth longleaf pine forest, Georgia; (d) hollow-bearing *Magnolia grandiflora* L. in old-growth Beech-Magnolia forest, Florida; (e) *Pinus taeda* L. following a prescribed burn, Florida; (f) dead acacia (right) and the wood-like ribs of a saguaro cactus (left) in the Sonoran desert, Arizona; (g) dead *Fagus orientalis* Lipsky with fungal fruiting bodies in old-growth Caspian Hyrcanian forest, Iran; (h) highly decomposed wood with fungal fruiting bodies, Thailand; (i) charred wood in burned Baobab forest, western Madagascar; (j) thin layer of highly decomposed pine, Arizona; (k) moss-covered log in the Adirondacks, New York (Images (a–f), (j), and (k) by Michael Ulyshen, image (h) by Jan Šobotník, and images (g) and (i) by Martin Gossner)

the phloem phase which lasts until the nutritious phloem layer beneath the bark gets entirely degraded by insects and fungi. The second phase is the subcortical-space phase which begins as soon as the phloem layer becomes partly degraded and continues until the bark has completely fallen away from the wood. The final rot phase is the longest and does not end until the wood has become completely

humified and incorporated into the soil. At the time of death, it is common for a tree to contain a wide variety of rot holes and pockets of decay. The process of falling to the ground often results in considerable fragmentation and breakage, and these damaged areas decay more rapidly than intact portions. Moreover, portions of the tree in contact with the soil decay more quickly than elevated portions due to differences in moisture levels. Different parts of the tree are colonized by different wood-decaying fungi, which results in diverse kinds of rot, and attacks by wood-feeding arthropods or scavenging vertebrates are similarly patchy. Sapwood usually decays more rapidly than heartwood, and early wood decays more quickly than late wood. It is clear from these and other influences that wood decay is not a homogeneous process, even within the same piece of wood. Although various classification schemes have been developed for assigning a piece of wood to a particular decay class, such designations overlook the inherent variability of wood decay in nature. Because it is not uncommon for a single log to contain wood at widely varying stages of decomposition, Pyle and Brown (1999) proposed that decomposing woody substrates are best thought of as falling along a continuum of decay class variability.

1.2 Origins and Diversity of Life in Dead Wood

Much like flowering plants set the stage for an explosion of pollinator and herbivore diversity (Grimaldi and Engel 2005), the appearance of dead wood in early Devonian forests was followed by a diversification of saproxylic insect life, giving rise to some of the most successful morphological adaptations (e.g., the elytra of beetles) and symbiotic relationships on Earth. Because wood provides relatively moist conditions during times of drought, relatively warm conditions during periods of cold, protection from many kinds of irradiation, and insulation from fire (Blackman and Stage 1924; Holmquist 1926, 1928, 1931; Jabin et al. 2004; Seibold et al. 2016a), the first invertebrates to utilize dead wood in early forests likely consisted primarily of refuge seekers and opportunists that only later became specialists of this new substrate.

1.2.1 Origins

It is clear from the fossil record and phylogenetics that life was slow to utilize woody debris in early forests. For example, fungi with the ability to degrade lignin (i.e., white rot) are thought to have originated roughly 120 million years after progymnosperms like *Archaeopteris* became major components of early forests (Fig. 1.1). This lag may explain the high rate of organic carbon accumulation during the intervening Carboniferous period (Floudas et al. 2012) and underscores the recalcitrance of lignocellulose as well as the low nutritional quality of wood. The borings of insects and other arthropods provide the earliest and best fossil evidence

for animal life in dead wood. Frass-filled oribatid mite burrows in petrified *Cordaites* wood from the Lower-Middle Pennsylvanian (Carboniferous) represent the earliest records of wood-boring arthropods (Cichan and Taylor 1982). Indeed, oribatid mites appear to have been the pioneering wood-boring arthropods for millions of years until major wood-boring insect groups arose in the Permian (Kellogg and Taylor 2004; Labandeira et al. 1997). Larger diameter frass-filled galleries in petrified glossopterid wood from the Permian (Zavada and Mentis 1992) may represent the earliest fossil evidence of insect activity in dead wood, possibly attributable to beetles (Labandeira et al. 2001). The earliest beetle-like insects are thought to have originated soon after the *Agaricomycetes* [but see Toussaint et al. (2017)] and were likely wood feeders, much like modern Archostemata (e.g., Cupedidae and Micromalthidae) which belong to the basal-most suborder of extant beetles (Grimaldi and Engel 2005; Yan et al. 2017). Borings within conifer-like wood from the Middle Permian represent the first evidence of wood-boring beetles, tentatively attributed to Permocupedidae, an extinct family of beetles ancestral to Archostemata (Naugolnykh and Ponomarenko 2010). Late Permian fossil beetle galleries analogous to those of modern bark beetles, but preceding scolytines by well over 100 million years, were recently discovered in China (Feng et al. 2017). They were presumably made by an extinct early lineage of Polyphaga and represent the earliest known evidence of subsocial behavior in saproxylic insects. The first eusocial animals on Earth were termites which also originated as wood feeders in the late Jurassic (Bourguignon et al. 2015). By the time termites and ants appeared on the scene, the diversity of beetles we know today was largely in place (Grimaldi and Engel 2005). There can be little doubt that the arrival of these social insects resulted in profound changes to saproxylic food webs, however, especially in tropical forests where the highest diversity and abundance of termites and ants are found.

1.2.2 Insect Diversity

The total number of saproxylic insect species worldwide remains far from known (Stokland et al. 2012), and this is also true for most regions of the world. Progress continues to be limited by a shortage of taxonomic knowledge although molecular tools can be expected to resolve many current problem areas including the existence of cryptic species (Garrick and Bouget 2018; see Chap. 25). Estimates from the best-studied forests in developed areas (e.g., northern Europe) suggest approximately 20–30% of all forest insects are saproxylic. Recognition of this in Britain led Elton (1966) to suggest that dying and dead wood represent one of the two or three most important resources for animal life in forests. The most diverse and well-studied order of insects found in dead wood throughout the world is Coleoptera. The earliest beetle, as mentioned above, was most likely saproxylic, and 122 of all 187 extant beetle families (65%) contain saproxylic members (Gimmel and Ferro 2018; see Chap. 2). Saproxylic beetles range more widely in size (<1 mm for families like



Fig. 1.4 *Orthognathotermes gibberorum* Mathews (Termitidae: Termitinae), a wood-soil interface feeder, French Guiana (Jan Šobotník)

Ptiliidae and Ciidae to >150 mm for certain Scarabaeidae and Cerambycidae) and functional group than other orders. They also include a number of economically important groups like bark and ambrosia beetles (Curculionidae: Scolytinae, Platypodinae) and wood-boring beetles (Cerambycidae, Lymexylidae, Bostrichidae, etc.) that can be major forest pests.

Blattodea is perhaps the second most studied group of wood-dependent insects, due to the inclusion of termites into this order (Bignell 2018; see Chap. 11). Termites are primarily found in tropical and subtropical regions (Fig. 1.4) where they are by far the most dominant wood-feeding insects and also include some serious pests of wooden structures. Hymenoptera is another order which contains many saproxylic members, including parasitoids of other saproxylics that provide an important ecosystem service (Hilszczański 2018; see Chap. 6). Diptera has received surprisingly little attention from researchers considering about half of all families contain saproxylic members, and they rival beetles as the most diverse order of saproxylic insects (Ulyshen 2018b; see Chap. 5). The orders Hemiptera (Gossner and Damken 2018; see Chap. 9) and Lepidoptera (Jaworski 2018; see Chap. 10) contain relatively few saproxylic species, but those species tend to be highly specialized for life in dead wood and are sometimes sensitive to forest management activities. The fact that the term saproxylic includes species indirectly dependent on dying and dead wood, like many fungus-feeding and predatory taxa, also adds greatly to the proportion of species assigned to this category. Major functional groups of saproxylic insects are discussed briefly below.

1.2.3 Functional Groups

Saproxyllic insects can be assigned to any number of functional groups, and various classification systems have been proposed (Bouget et al. 2005; Stokland et al. 2012; Krivosheina 2006; Hövemeyer and Schauer mann 2003). For the purpose of this introduction, we limit our discussion here to four broad groupings: phloem feeders, wood feeders, fungus feeders, and predators. While these are all functions performed by saproxyllic insects, such designations are often somewhat arbitrary at the species level as it is not uncommon for a species, even at a single developmental stage, to qualify for multiple categories. Many wood-boring beetles, for instance, begin life feeding on phloem before tunneling into the wood. Within the wood the larvae often obtain some of their nutrients from microbial biomass that is ingested along with the wood, and it is not uncommon for them to prey upon other insects they happen to encounter in their tunnels. At later stages of decomposition, the wood ingested by wood feeders consists mostly of fungal biomass and other microbes, and these species are commonly considered saprophagous. These four groupings also fail to capture the entire diversity of saproxyllic insects. Species that feed on sap flows, for instance, are considered by many to be saproxyllic (Alexander 2008) and can be assigned to their own functional group. The same is true for cavity-nesting bees and wasps (Bogusch and Horák 2018; see Chap. 7) as well as aquatic insects confined to water-filled tree holes. Although incomplete, sometimes arbitrary, and overlapping, these four broad groupings, briefly introduced below, provide a simple and useful framework for categorizing the major functions performed by saproxyllic insects.

1.2.3.1 Phloem Feeders

The soft, sugary, and protein-rich layer of secondary phloem located just beneath the bark is a particularly desirable resource and ultimately gave rise to a diverse assemblage of phloem feeders (e.g., bark beetles, cerambycids, buprestids, etc.) and their predators. Host-specific defensive compounds present in these tissues are largely responsible for the high degree of host specialization observed within these groups today (Wende et al. 2017). As proposed by Graham (1925), insects that feed on phloem fall into two main groups. One consists of species, like many bark beetles, that never leave the zone between the bark and the wood, while the other group consists of species that begin feeding on the phloem but later bore into the wood. This latter group includes many species of wood-boring beetles (e.g., cerambycids, buprestids, etc.) that attack dying or recently dead trees but are not capable of colonizing wood that lacks phloem. Some beetle species are considered secondary phloem feeders. The endangered beetle *Pytho kolwensis* Sahlberg (Pythidae), for instance, colonizes large trunks of Norway spruce in the boreal regions of Europe and Russia after bark beetles and other primary phloem feeders have left (Siitonen and Saaristo 2000). Even after the phloem layer has been completely consumed, a large diversity of invertebrates can be found living or sheltering within the

subcortical space between the bark and wood. The same is true for damp-wood termites, which primarily colonize the subcortical space of freshly fallen trunks, where numerous colonies fiercely compete until most are eliminated or fused with stronger neighbors (Thorne et al. 2003).

1.2.3.2 Wood Feeders

Despite being hard to chew, difficult to digest, and characterized by very low nutrient concentrations, wood represents a very rich substrate in terms of energy content and is therefore consumed by a wide variety of wood-feeding insect taxa. These include various groups of Blattodea (*Cryptocercus* wood roaches and termites from all families except for Hodotermitidae), as well as numerous Coleoptera (Anobiidae, Bostrichidae, Brentidae, Buprestidae, Cerambycidae, Lymexylidae, Zopheridae, and many others that feed on decomposing wood), Diptera (Pantophthalmidae, Tipulidae: *Ctenophora*), Lepidoptera (Cossidae, Hepialidae, Sesiidae), and Hymenoptera (Siricidae, Xiphydriidae). Surviving on a diet of wood is largely made possible for these organisms by interactions with fungi, prokaryotes, and other microbes. Although cellulases belong to the ancestral biochemical machinery of protostomes and deuterostomes (Lo et al. 2003), they have been lost in many insect taxa. Even modern wood-feeding groups usually produce just some of the cellulases needed for cellulose digestion, most frequently β -glucosidases and sometimes also endo- β -glucanases (Lo et al. 2011). These insect cellulases are thus called incomplete, as cellulose digestion must necessarily be aided by symbiotic microorganisms (predominantly bacteria including actinomycetes and fungi including yeasts and, to a lesser extent, protists) (Breznak 1982; Dillon and Dillon 2004; Lo et al. 2011). Complete cellulases are known only from some bacteria and fungi (Tomme et al. 1995). As a consequence, virtually all wood-feeding insects benefit from endo- or ecto-symbioses with microbes capable of degrading lignocellulose (Birkemoe et al. 2018; see Chap. 12). Symbioses between insects and microbes are in some cases so specialized that insects obtain nutrition from wood without ingesting it. Thompson et al. (2014) showed that *Sirex noctilio* F. larvae extract and consume liquids from wood shavings rather than consume the wood itself. The liquid contains compounds liberated by the enzymatic activities of the insect's fungal symbiont.

In addition to the important role fungal symbionts play in digesting wood, a large proportion of the nitrogen requirements of many wood-feeding insects comes from nitrogen-fixing prokaryotic endosymbionts within their guts (Ulyshen 2015). Nitrogen fixation is an energy-demanding process and is typically only seen in insects feeding on N-poor substrates. Consistent with this pattern, rates of nitrogen fixation in termites decrease along the humification gradient, typically being higher in species that feed on sound wood compared to species feeding on more highly decomposed wood and being mostly absent from soil-feeding or fungus-growing taxa (Breznak et al. 1973; Yamada et al. 2007; Tayasu et al. 1997).

1.2.3.3 Fungus Feeders

Dead wood is quickly colonized by a variety of wood-digesting fungi, bacteria, and other microbes which collectively account for a large proportion of total biomass of rotting wood as decomposition proceeds (Jones and Worrall 1995; Noll et al. 2016). It is thus inevitable for these organisms to be consumed, whether intentionally or not, by wood-feeding insects. Fungal biomass is more nutritious than wood and therefore acts to enrich the food of many insects in addition to providing the enzymes necessary to digest the wood itself (Kukor and Martin 1986). Various termite taxa, for example, have been shown to feed preferentially on wood decayed by fungi, with documented benefits to colony size and health (Becker 1965; Smythe et al. 1971; Hendee 1935; Cornelius et al. 2002). The distinction between wood feeding and fungus feeding is unclear for many saproxylic insect species, especially within highly decayed wood. Fungi are thought to be the main source of nutrition for certain “wood-feeding” passalid (Mishima et al. 2016) and lucanid (Tanahashi et al. 2009) beetles, for example. The consumption of wood by many insects may therefore be consistent with the peanut butter and cracker analogy developed by Cummins (1974) for decomposers of coarse particulate organic matter in stream ecosystems. That is, wood consumption may represent just a strategy utilized by some saproxylic insects to obtain the more nutritious microbial biomass. Fungi also play an important role in translocating nutrients into wood from external sources, thus further reducing the nutritional limitations imposed by wood on wood-feeding insects (Filipiak 2018; see Chap. 13).

Many other insects are obligate fungus feeders. Some, such as the Hemipteran family Aradidae, feed on fungal hyphae under bark (Gossner and Damken 2018; see Chap. 9). Many others, including a large diversity of beetles and flies, feed on fungal fruiting bodies (Jonsell et al. 2001; Epps and Arnold 2010; Graf-Peters et al. 2011). Perennial fruiting bodies that provide a relatively stable resource often support a highly specialized fauna (Jonsell et al. 2001), with approximately half of the species being monophagous (Jonsell and Nordlander 2004). One of the most specialized groups of obligate fungus feeders are species that feed on symbiotic fungi they cultivate within their galleries or nests (Birkemoe et al. 2018; see Chap. 12). There are two major examples of this among saproxylic insects. The first concerns ambrosia beetles of the families Curculionidae [Scolytinae and Platypodinae, including the eusocial Australian platypodine *Austroplatypus incompertus* (Schedl)] and Lymexylidae. These insects cultivate their symbiotic fungi on the walls of their tunnels, and adults carry the symbionts within special structures on their bodies called mycangia.

The other major group of insects that cultivate symbiotic fungi is Macrotermitinae, the most basal subfamily of the crown termite family Termitidae (Fig. 1.5). Macrotermitinae are commonly referred to as the “fungus-growing termites” due to their association with ectosymbiotic fungi (Basidiomycetes: Agaricales: *Termitomyces*) (Poulsen et al. 2014; Bignell 2016). The fungus represents the principal food source for the colony, providing protein-rich asexual spores

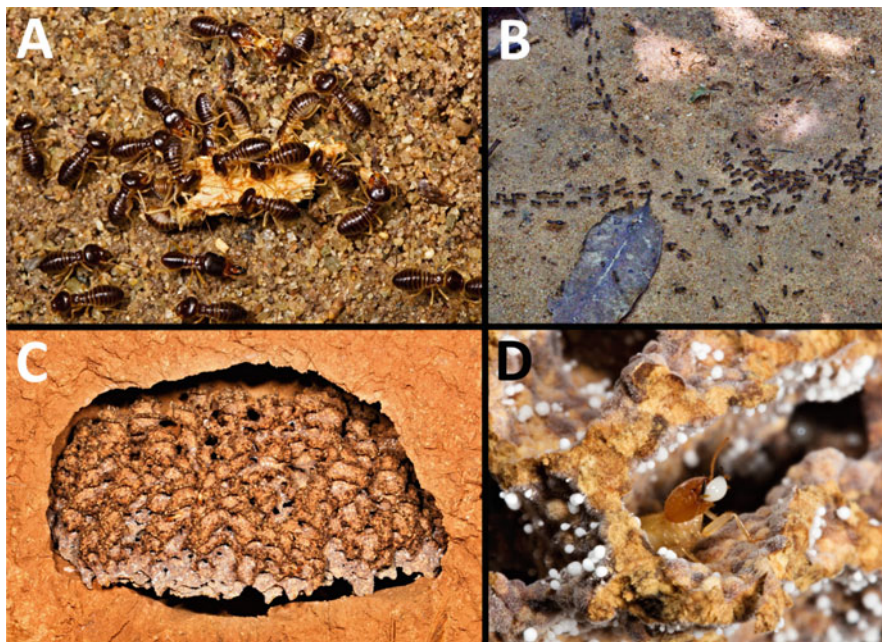


Fig. 1.5 Examples of Macrotermitinae (Termitidae), the fungus-growing termites. (a) *Macrotermes carbonarius* foraging on a small wood item on the ground, Thailand; (b) *Macrotermes carbonarius* (Hagen 1858) workers marching to the nest from a foraging trip (note trail-following behavior), Thailand; (c) fungus comb of *Odontotermes* sp., China; (d) soldier of *Odontotermes* sp. spitting the defensive labial gland secretion in response to disturbance (note the white nodules, conidia, growing from the fungus comb), China (All images by J. Šobotník)

(nodules). It also supplies the colony with cellulases that complement the innate enzymes of the host and greatly improve food digestion and detoxification (Hyodo et al. 2003; Nobre et al. 2011). Due to their symbioses with *Termitomyces*, macrotermitines are considered among the most efficient of all insects at decomposing dead wood and other plant matter (Schuurman 2005; Brune and Ohkuma 2011), processing 5–6 times more food per unit biomass than other termites (Bignell and Eggleton 2000).

1.2.3.4 Predators

Predators make up a large proportion of the insect biodiversity associated with dying and dead wood. For example, predators accounted for about 41% of all saproxylic beetle species collected in a recent study conducted in Germany (Wende et al. 2017). While some saproxylic predators opportunistically prey upon a wide range of species present in dead wood, many others exhibit a high degree of host specificity. This is especially true among parasitoids that are predatory as larvae and, unlike parasites,

ultimately kill their hosts (Godfray 1994). Most parasitoids belong to the order Hymenoptera (major saproxylic families include Braconidae, Ichneumonidae, etc.) (Hilszczński 2018; see Chap. 6) although there are some notable groups of dipteran (e.g., Tachinidae) and coleopteran parasitoids (e.g., Bothrideridae and Passandridae) as well. Parasitoids typically specialize on particular life stages, with some attacking only eggs, larvae, or pupae. An important distinction can be made between parasitoids that do (idiobionts) or do not (koinobionts) paralyze their hosts at the time of oviposition. Hosts parasitized by koinobionts continue to feed until they are ultimately killed by the larvae feeding within. Parasitoids can also be categorized as endo- or ectoparasitoids depending on whether they feed from the outside or within their hosts. Endoparasitoids tend to be more host-specific than ectoparasitoids, with some ectoparasitoids known to attack an extremely wide range of host species. The habitat associations of parasitoids are typically more narrow than those of their hosts. For example, larval parasitoids that attack hosts hidden under bark can be limited by the length of their ovipositor, being unable to penetrate thick bark (Abell et al. 2012; Berisford 2011). Although few species are strictly saproxylic, ants are often extremely abundant in dead wood, especially toward the tropics, and no doubt play an important role in structuring saproxylic insect communities (King et al. 2018; see Chap. 8).

1.2.4 *Specialization and Succession*

The huge diversity of saproxylic insects can largely be attributed to the fact that many saproxylic insect species specialize on particular species of wood, wood positions (standing/suspended or fallen), wood diameters, environmental conditions (sun exposure, temperature, and humidity), etc. There is also a predictable succession of insects as decomposition proceeds, with some species occurring only during the phloem stage or while there is bark, whereas others colonize wood only after it has become highly decomposed by fungi. Although these successional patterns have been described in multiple studies (Ulyshen and Hanula 2010; Hövemeyer and Schauer mann 2003; Muñoz-López et al. 2016; Lee et al. 2014; Grove and Forster 2011; Derksen 1941), the insects associated with the last stages of decomposition remain very poorly characterized (Ferro 2018; see Chap. 22). This highly degraded and fungus-rich substrate is known to support a unique fauna (Grove 2007), however, including some of the largest and most visually stunning species. A wide variety of Scarabaeoidea breeds only in highly decomposed wood (including the material that collects in tree hollows), for example, including lucanids (Huang 2018; see Chap. 4), passalids (Ulyshen 2018a; see Chap. 3), and the scarab subfamilies Dynastinae, Cetoniinae, and Rutelinae (Fig. 1.6). These groups appear to be especially diverse and numerous in the tropics where they process large amounts of woody material [e.g., 1.5 kg per individual in the case of *Megasoma elephas* (F.)] and are thought to strongly influence decomposition (Morón 1985; Morón and Deloya 2001). Because highly decomposed wood is slow to develop and can be

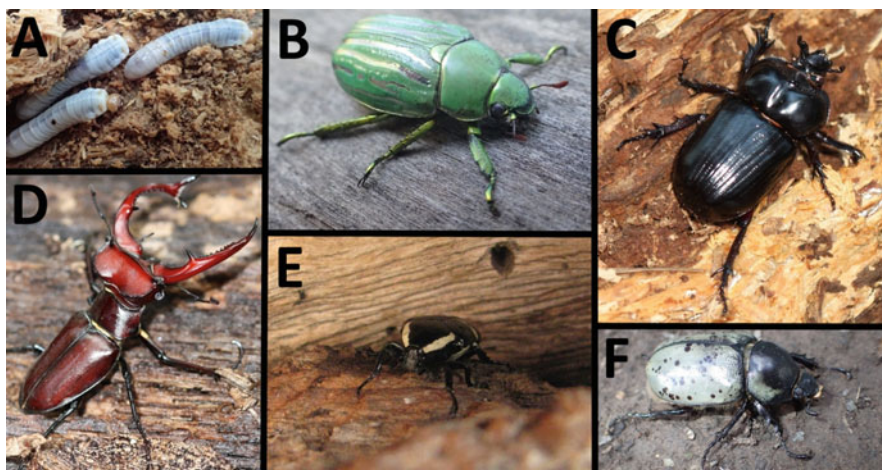


Fig. 1.6 North American examples of Scarabaeoidea associated with highly decomposed wood. (a) Passalid larvae (*Odontotaenius disjunctus* (Illiger), Georgia); (b) ruteline scarab (*Chrysina gloriosa* LeConte, Arizona); (c) dynastine scarab (*Phileurus truncatus* (Beauvois), Florida); (d) lucanid (*Lucanus elaphus* L., Mississippi); (e) cetoniine scarab (*Gymnetina cretacea* (LeConte)) emerging from oak tree hollow, Arizona; (f) dynastine scarab (*Dynastes granti* Horn, Arizona) (Images (a–d) and (f) by Michael D. Ulyshen, image (e) by Michael L. Ferro)

easily destroyed during timber operations (McCarthy and Bailey 1994), it is typically more common in older less-disturbed forests, except in the case of legacy debris from a previous stand (Carmona et al. 2002; McCarthy and Bailey 1994; Idol et al. 2001). Similar patterns have been shown for insects that depend on highly decomposed wood. Lucanids, for example, are among the insects most sensitive to forest disturbance (Lachat et al. 2012) but can persist after a harvest if an adequate amount of wood is left behind (Michaels and Bornemissza 1999).

1.2.5 Global Diversity Patterns with a Focus on Social Insects

Although the four main functional groups described above occur in all forest types, the composition of these communities varies greatly among the regions of the world as dictated by the biogeography of the different taxa. One of the biggest differences concerns the uneven distribution of eusocial groups like termites (Bignell 2018; see Chap. 11) and ants (King et al. 2018; see Chap. 8) and subsocial groups like the beetle family Passalidae (Ulyshen 2018a; see Chap. 3). These groups tend to be more diverse and abundant toward the tropics compared to more temperate regions (King et al. 2013; Schuster 1978). It remains largely unknown whether or not the diversity patterns of nonsocial saproxylic insect groups also become more diverse toward the tropics. Most organisms exhibit this pattern, however, and it seems likely to hold true for most groups of saproxylic insects considering tropical forests support a much

larger number of tree genera than temperate or boreal forests. Tropical forests also tend to be much older, especially compared to those occurring in areas that were glaciated just several thousand years ago, and this may also contribute to a higher insect diversity. Few studies have specifically focused on saproxylic insect biodiversity in tropical forests, however, although it is clear from work by Grove (2002a, c) that a high diversity of saproxylic beetles (>500 species) can be found in the rainforests of tropical Australia. An analysis of saproxylic hemipteran diversity by Gossner and Damken (2018; see Chap. 9) shows these insects are more diverse in tropical and subtropical forests. A related question concerns whether the proportion of species that is saproxylic differs among regions. Hanski and Hammond (1995) were among the first to broach this topic, noting that the proportion of beetles that are “wood-associated” is about equally as high in the rainforests of Sulawesi (33%) as in the forests of Finland (35%). Because Sulawesi has many times more beetle species overall than Finland, this suggests the number of saproxylic beetle species should be an equal degree higher in Sulawesi.

On the other hand, the tremendous abundance of social insects in tropical forests could potentially cause other saproxylic insects to be less diverse in tropical forests than expected. Due to their large colonies, for example, termites may meaningfully reduce the amount of resources available to other insects. The Sulawesi example mentioned above does not rule this out given the relatively low diversity of termites there compared to other tropical regions. Indeed, termites richness varies greatly within the tropics, firstly being more diversified at the southern hemisphere and secondly being both more diverse and abundant in the Afrotropics followed by the Neotropics, the Indomalayan region, and Australasia (Davies et al. 2003). While these patterns are probably a consequence of historical events, such as the origin of the most successful termite family, Termitidae, in the rainforests of Africa (Bourguignon et al. 2017b; Aanen and Eggleton 2005), the same pattern of abundance calls for a different, yet-unknown, explanation. If termites do negatively influence the number of saproxylic species present in a forest, the strongest effect might be seen in places like west Africa where the “higher” termites originated and termite diversity and abundance remain the highest. While this has never been formally tested, observations from Cameroon and other tropical locations suggest that fewer saproxylic insect species are encountered where termites are most active (JS, pers. obs.).

Ants are also extremely abundant on the forest floor, especially in the tropics where they have been shown to be the major agents of resource removal (Griffiths et al. 2018). Ants are among the most important predators of termites (King et al. 2018; see Chap. 8) and are likely to reduce the populations of other insects found within dead wood as well. There is limited information on this question in the literature, however. In Puerto Rico, Torres (1994) attributed the low beetle diversity in logs in part to the presence of many ant species. Stronger evidence that ants negatively influence insects in dead wood comes from Jackson et al. (2012) who showed the probability of log occupancy by a species of passalid beetle in Louisiana to be higher when ants were absent. In Portugal, by contrast, Henin and Paiva (2004) found no evidence that an aggressive species of ant reduced the ability of a bark

beetle to colonize logs. Their study found that attempts by the ants to attack the beetles were not successful and the ants were also unable to access the galleries under the bark, possibly due to the plug of dust surrounding the boring hole. Insects have been evolving in the presence of ants for a long time, and many morphological and/or behavioral adaptations may exist for surviving encounters with these predators. This certainly seems to be the case for termites which are known to often coexist in wood with ants (Shelton et al. 1999).

1.3 Wood in Human History

But who really owns the tree stump? The bark beetle that gnaws tunnels inside it? The ants that travel through the tunnels? The earwig that sleeps under its bark? Or the bear that uses it to sharpen her claws? Does it belong to the titmouse that flies down upon it? The frog that find shelter in one of its holes? Or the man who believes he owns the forest? Maybe the stump belongs to all- the beetle and the ants, the bear and the titmouse, the frog, the earwig, and even the man. All must live together.

Romanova (1985)

The quote above, translated from the Russian children's book "Чей это пенек?" (i.e., Whose stump?), nicely captures the conflict between human demand for woody resources and the importance of those resources to many other species. It also recognizes our inherent appreciation for biodiversity and desire to protect it. Throughout most of human history, however, demand drove the relationship between humans and wood, with wood playing a key role in our quality of life and technological progress. Perlin (1989) summarized this particularly well:

It may seem bold to assert wood's crucial place in the evolution of civilization. But consider: throughout the ages trees have provided the material to make fire, the heat of which has allowed our species to reshape the earth for its use. With heat from wood fires, relatively cold climates became habitable; inedible grains were changed into a major source of food; clay could be converted into pottery, serving as useful containers to store goods; people could extract metal from stone, revolutionizing the implements used in agriculture, crafts, and warfare; and builders could make durable construction materials such as brick, cement, lime, plaster, and tile for housing and storage facilities. Charcoal and wood also provided the heat necessary to evaporate brine from seawater to make salt; to melt potash and sand into glass; to bake grains into bread; and to boil mixtures into useful products such as dyes and soap. Transportation would have been unthinkable without wood. Until the nineteenth century every ship, from the Bronze Age coaster to the frigate, was built with timber. Every cart, chariot, and wagon was also made primarily of wood. Early steamboats and railroad locomotives in the United States used wood as their fuel. Wooden ships were tied up to piers and wharves made from wood; carts, chariots and wagons made of wood crossed wooden bridges; and railroad ties, of course, were wooden. Wood was also used for the beams that propped up mine shafts and formed support for every type of building. Water wheels and windmills—the major means of mechanical power before electricity was harnessed—were built of wood. The peasant could not farm without wooden tool handles or wood plows; the soldier could not throw his spear or shoot his arrows without their wooden shafts, or hold his gun without its wooden stock. What would the archer have done lacking wood for his bow; the brewer and vintner, without wood for their barrels and casks;

or the woolen industry, without wood for its looms? Wood was the foundation upon which early societies were built.

Whereas many regions were extensively forested for thousands or even millions of years prior to human colonization, most forests now growing in developed regions are just decades or centuries old and exist in scattered patches (Speight 1989). These patches are also known to contain less dead wood in terms of both abundance and variety compared to the least disturbed old-growth remnants (Stenbacka et al. 2010b). It is ironic but also encouraging to consider that the wood- and coal-fueled technological progress that gave rise to modern civilization and resulted in drastic changes in forest cover may have given us the opportunity as a species to stop and consider how our actions have affected forest ecosystems over time. As it became apparent, near the end of the twentieth century, that saproxylic organisms were being lost from intensively managed forests, the conservation of these organisms became a major research focus in places like Europe, Australia, and North America. There has been dramatic change in how foresters view dead wood in forests over the past half century or so. Spaulding and Hansbrough (1944) captured the sentiment held by many foresters in the mid-twentieth century as follows: “Those who harvest forest trees are faced with the problem of the disposal of the resulting logging slash. It has been termed the “garbage” of the woods. Because of its ubiquity in the exploited forest, however, the tendency has been to accept it as a necessary evil, one about which little or nothing can be done in a practical way.” Today, by contrast, the value of woody debris to biodiversity and nutrient cycling is widely recognized although it should be noted that there is some concern about the role woody debris can play in increasing certain pest populations. In Europe, for example, major inputs of dead wood (e.g., severe wind damage) have been shown to briefly (for 1–2 years) increase the outbreak risk of the bark beetle, *Ips typographus* L. (Schroeder and Lindelöw 2002). Examples from other parts of the world are lacking, but, because most forest-damaging pests (e.g., bark beetles and various wood borers) are associated with dying or freshly killed trees, wood at later stages of decay (i.e., after the phloem layer is gone) poses little threat in this regard.

1.4 History of Research on Saproxylic Insects

Sharp divisions exist in the saproxylic insect literature along both taxonomic and biogeographical lines. Examples include separate bodies of literature on primarily tropical groups like eusocial termites, subsocial passalid beetles, and other nonsocial insect assemblages. Although understandable, these divisions are unfortunate given the fact that many or all of these groups, depending on the region, interact extensively within their shared substrate. Moreover, progress in a number of research directions has been limited by this divided view of saproxylic insect communities. Efforts to quantify the role of insects in decomposition historically focused on termites, for example, without regard for the activities of other insects. Artificial

wooden substrates such as machined wooden blocks have been and continue to be used in these studies despite the fact that they exclude entire guilds of insects (e.g., phloem feeders and others associated with the subcortical space) known to facilitate fungal colonization and have strong but indirect effects on levels of decomposition. Indeed, it is clear from recent research that ignoring the effects of bark coverage and phloem-feeding beetles can yield highly unrealistic information on rates of wood decomposition and the contributions of insects (Ulyshen et al. 2016). As stated earlier, a major goal of this book is to take steps toward uniting the literature on nonsocial saproxylic insects and wood-dwelling social insects (including saproxylic termites as well as ants which are mostly non-saproxylic). The global diversity and ecology of saproxylic insects cannot be understood without achieving this unified perspective. As the two largest bodies of literature, brief histories of research on nonsocial saproxylic insects and research on wood-feeding termites are provided in the following sections.

1.4.1 Research on Nonsocial Saproxylic Insects

The diversity of wood borers and other species associated with freshly dead woody material was noted by many early naturalists. At a single small location over a 2-month period in Singapore, for instance, the Victorian-era naturalist Alfred Russell Wallace (1869) collected at least 700 species of beetles, including 130 distinct kinds of wood-boring cerambycids, which he attributed in large part to the felling of trees in the area. Townsend (1886) similarly reported collecting 34 species from the dead trunks of *Tilia americana* L. in North America, and Davis and Leng (1912) collected 42 species of beetles in just 2 hours from a recently felled longleaf pine in Florida. Shelford (1913) recognized the value of dead wood to animal life in his big book on temperate American zoology. Blackman and Stage (1924) were among the first researchers to consider the succession of insects throughout the decomposition process. They published an extremely detailed study of insects and other organisms associated with the bark and wood of dead hickories in New York, including information on successional patterns over a period of 6 years. The following year, Graham (1925) published an article entitled “The felled tree trunk as an ecological unit” in which he carefully described how nutrition, moisture, and temperature vary within and among dead trees and how these factors influence early insect colonists. Other notable contributions from that decade include those of Richards (1926) and Krogerus (1927). The 1930s saw the publication of a major effort by Savely (1939) on the ecology of arthropods associated with dead pine and oak in North Carolina. Several excellent papers were published in German in the 1940s on the succession of insects in decomposing wood. Derksen (1941) studied the insect communities associated with beech stumps, for example, and Eidmann (1943) investigated the succession of wood-dwelling insects in West Africa. In the 1950s, Howden and Vogt (1951) surveyed the insect communities associated with standing dead pine in

Maryland, and Wallace (1953) studied the ecology of insects in pine stumps in Britain.

This growing body of literature along with his own research in England led Elton (1966) to conclude that “dying and dead wood provides one of the two or three greatest resources for animal species in a natural forest, and if fallen timber and slightly decayed trees are removed the whole system is impoverished of perhaps more than a fifth of its fauna.” Yet it would be some time before the importance of dead wood to biodiversity would be widely recognized by the community of researchers and foresters. For example, Stubbs (1972) remarked that “many of those who manage woodlands for amenity and conservation, and many conservationists themselves, appear to be uninformed of the immense value of dead and dying wood for the conservation of a variety of wildlife.” Indeed, for many land managers, dead wood represented waste, lost revenue, or risk from pest outbreak—concerns still held by some today. Beginning in the late 1970s, researchers in the northwestern United States were among the first to fully recognize the value of dead wood to terrestrial and aquatic ecosystems. Teskey (1976) compiled a list of Diptera known to utilize dying and dead wood in North America. Thomas et al. (1979) reviewed the importance of snags to cavity-nesting birds, while Maser et al. (1979) reviewed dead and downed woody material utilization by vertebrates. Maser and Trappe (1984) reviewed the properties of dead wood and discuss their ecological importance in both forests and streams. An even more detailed treatment was provided several years later by Harmon et al. (1986). In addition to discussing forests and freshwater systems, Maser et al. (1988) also included lengthy sections on the ecology of dead wood in estuaries, in the sea, and on coastal beaches.

The modern era of research aimed specifically at conserving insect biodiversity in dead wood largely began in 1980 when the Council of Europe initiated a project aimed at using insects dependent on dead wood to compile a list of high-quality forests and to assess the health of the terrestrial decomposer community (Speight 1989). Before this effort was undertaken, as written by Speight (1989), “the plight of the saproxylics (i.e., species reliant on dead or dying wood) had not been recognized, the significance of their role in natural forest had been ignored and only a handful of European forests supporting a recognizably diverse saproxylic community had been secured for protection.” The committee began by developing a list of insect species that were thought to be associated with mature forests and highly localized in their distribution. They then sent this list to specialists across Europe, requesting information on forests likely to be important to such species. The results from the project were compiled by Speight (1989) who began his report by defining the term “saproxylic” as species “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.” Their survey efforts resulted in a list of approximately 150 forests throughout Europe with potential conservation value, some of them as little as 40 hectares in size. They were found to be largely concentrated in mountainous regions, whereas lowland and valley forests were noticeably lacking, and alluvial forests were almost totally absent from the list (Speight 1989). According to Speight (1989), these remaining high-value forests, all

hundreds or even thousands of years old and quite isolated from one another, “have effectively become islands within a sea of hostile terrain too vast for saproxylics to successfully traverse.” Perhaps more than any other previous work, Speight’s report brought attention to the challenges facing saproxylic organisms in Europe after millennia of deforestation, fragmentation, and intensive management.

The years following Speight’s publication have seen a dramatic increase of interest in the ecology of dead wood, especially regarding the conservation of saproxylic organisms. The number of papers using the keyword “saproxylic” in titles and abstracts, for instance, has been increasing at a rate of about 5 per year since the year 2000 (source: Scopus, accessed 29 October 2017). This timeline was punctuated by some major review articles and books aimed at compiling the growing body of evidence and guiding conservation-oriented management. Samuelsson et al. (1994) wrote an excellent book outlining the importance of dead and dying trees to biodiversity in both terrestrial and aquatic environments. McComb and Lindenmayer (1999) outlined spatiotemporal patterns of dead and dying trees in forests, with particular attention given to the importance of tree cavities to many species. A paper by Siitonen (2001) reviewed the state of knowledge for Northern Europe. The following year Grove (2002b) published another excellent review, also largely focused on the European case but also including some of his findings from Australia. Another review article by Bunnell and Houde (2010) focused on vertebrates associated with dead wood in the Pacific Northwest of North America. Most recently, Stokland et al. (2012) published their book on *Biodiversity in Dead Wood* which is perhaps the most ambitious effort ever undertaken to produce a comprehensive synthesis of this vast and multidisciplinary topic.

1.4.2 Research on Wood-Feeding Termites

Such however are the extraordinary circumstances attending their economy and sagacity, that it is difficult to determine, whether they are more worthy of the attention of the curious and intelligent part of mankind on these accounts, or from the ruinous consequences of their depredations, which have deservedly procured them the name of Fatalis or Destructor.

Smeathman (1781)

The above quote came from a letter written by Henry Smeathman to Sir Joseph Banks of the Royal Society in which he reported his observations of termites in and around Sierra Leone, Africa. Although termites have been written about since at least 1350 BC (Snyder 1956), Smeathman’s letter stands among the earliest efforts to accurately report on the natural history of termites, so much so that Smeathman worried about whether readers would even believe his accounts of these “wonderful insects.” The first family description, of Termitidae, took place in 1802 (Latreille 1802), and the order Isoptera (in Greek “equally winged”) was introduced by Brullé (1832). Many important early observations were summarized in a three-volume book *Monographie der Termiten* by Hagen (1855, 1858, 1860). Observations on the nesting biology of Indo-Malayan termites were introduced by Haviland (1898),

and the relationships between termites and their social parasites were described by Wasmann (1893). Pioneering work on Asian termites was published by Holmgren (1909, 1911, 1912) in his extensive descriptions of termite biology, and perhaps the first modern monograph on termites describing the biology of a single species, *Archotermopsis wroughtoni* (Desneux), was published by Imms (1919). A taxonomic survey of African termites was published by Sjöstedt in 1926. Research by Emerson and Snyder on termite evolution, biogeography, and taxonomy was especially influential in directing the progression of termite research, and Grassé and Noirot made many important pioneering observations on termite biology, nesting and feeding habits, ontogenetic patterns, and communication. Several landmark books have been published on termites in the past 50 years, including the two-volume *Biology of Termites* (Krishna and Weesner 1969, 1970) and the multivolume compendium on termite biology by Grassé (1982, 1984, 1986). More recent reviews of termite ecology include the books by Abe et al. (2000) and Bignell et al. (2011), and an excellent survey of termite systematics, including all relevant resources, was recently published by Krishna et al. (2013).

As urban pests, termites globally have an estimated annual cost of \$40 billion (Rust and Su 2012) and also greatly reduce the value of timber in forests by hollowing out the centers of living trees (Werner and Prior 2007; Apolinário and Martius 2004). According to Rust and Su (2012), about 6.1% of the ~3000 termite species globally are considered pests, and only about 2.8% (~80 species) cause severe damage to wooden structures or furniture. These most damaging urban pests have received the majority of attention from researchers, however. Among these are termites that have been introduced into new areas. According to Evans et al. (2013), there are 28 species of termites worldwide considered to be invasive outside their native ranges, all of which are wood feeders. The most serious invasive termite pests are the kalotermitids *Cryptotermes brevis* (Walker) and *C. havilandi* (Sjöstedt); the rhinotermitids *Reticulitermes flavipes* (Kollar), *Coptotermes formosanus* Shiraki, and *C. gestroi* (Wasmann); and the nasutitermitine termitid *Nasutitermes corniger* (Motschulsky) (Evans et al. 2013). The introduction of these particular invasives can have major economic consequences and may also have strong effects on native ecosystems although the latter question has received little attention to date. While the negative effects of termites have long been a primary focus of termite research, resulting in the production of books with titles like *Termites and Termite Control* (Kofoed 1934), *Our enemy the termite* (Snyder 1948), or *Termites—a world problem* (Hickin 1971), the treatment of termites and other wood-dwelling insects has expanded over time to include all aspects of their ecology and even concerns about their conservation. Termite researchers have long speculated about the key functions termites perform in nutrient cycling and in aerating and turning over the soil (Noyes 1937; Snyder 1948; Kofoed et al. 1934; Grassé 1984; Ulyshen 2016), and appreciation for the ecosystem services provided by termites has grown over time. Indeed, it is now widely acknowledged that termites are among the most important ecosystem engineers of all invertebrates (Lavelle et al. 1997; Bignell and Eggleton 2000), with the role they play in promoting decomposition and nutrient cycling being of particular interest (see Sect. 1.5).

One of the most fundamental facts and key discoveries about termites is that they can function as decomposers only in partnership with endo- or ectosymbionts. Although initially mistaken for parasites (Leidy 1881), the flagellate protists found in the guts of non-termitid termites and *Cryptocercus* cockroaches were among the first endosymbionts of wood-feeding invertebrates to be discovered by researchers. Cleveland (1923) provided the first experimental evidence that protists play a key role in the digestion of wood, showing that “lower” termites quickly die of starvation in the absence of their symbionts. The traditional distinction between “lower” (basal taxa) and “higher” (Termitidae only) termites is based on the presence of gut flagellates in the former and absence in the latter (both groups contain bacterial endosymbionts). Although this separation is artificial from a phylogenetic point of view, it is often helpful from an ecological perspective. Like *Cryptocercus*, all “lower” termites are wood feeders, with the exception of Hodotermitidae, which feed on dry grasses, and *Serritermes* (Serritermitidae), which is the sole inquiline among “lower” termites and feeds on *Cornitermes* spp. (Termitidae: Syntermitinae) nest material (Emerson and Krishna 1975). By contrast, not all termitid species are wood feeders, with some feeding instead on microepiphytes, grasses, leaf litter, highly decayed wood, upper soil layers, and bare soil and within the nests of other termites or ants. Indeed, given the diversity of Termitidae, only about 26% of termite genera overall feed on wood, 59% are soil feeders, and the rest feed on grass, leaf litter, or microepiphytes (Bignell 2016; Krishna et al. 2013).

After being assigned to their own order (Isoptera) for over 150 years, recognition that termites are in fact eusocial cockroaches (Blattodea: Termitoidae), with *Cryptocercus* wood roaches being their sister group, is another landmark finding in the history of termite research (Lo et al. 2000; Inward et al. 2007). This fact was suspected long before it was proven molecularly due to the many similarities (e.g., endosymbionts, sociality, xylophagy, etc.) between *Cryptocercus* and “lower” termites (Cleveland et al. 1934). Several important classification schemes have been developed for understanding the ecology of termites. Combined evidence from termite anatomy and gut content led Donovan et al. (2001) to recognize four distinct feeding groups, generally corresponding to wood feeders, litter feeders (including dried grass, dung, etc.), soil/wood feeders (including humus), and soil feeders (including mound walls) (Bignell 2018; see Chap. 11). More recent work utilizing carbon and nitrogen stable isotopes, however, suggests termites can be meaningfully separated into just two broad groups: wood feeders and soil feeders (Bourguignon et al. 2011). Another classification system based on where termites nest in relation to their food substrate was first developed by Abe (1987) who distinguished between termites that feed within the same piece of wood (“one-piece nesters”) and those that forage away from their nests (“separate-piece nesters”). There are also “intermediate nesters” that nest and feed within the same substrate but also forage outside the limits of that substrate. One-piece nesting is probably the ancestral condition, whereas separate-piece nesting is exemplified by mound-building termitids. An additional category, the inquilines, was introduced by Shellman-Reeve (1997) for species feeding on the nest material or stored food of a separate-piece nester host.

Working in Nigeria, Wood et al. (1977) were perhaps the first to show that termites, similar to other saproxylic taxa, are highly sensitive to land-use changes. In fact, soil-feeding termites are negatively influenced by faint changes, such as selective logging, and deforestation leads to almost immediate disappearance of the vast majority of soil-feeding taxa. Although wood-feeding guilds are in general less affected by these man-made perturbations, many specialists quickly disappear, and only the most resistant segment of the local fauna can survive habitat alterations (Bourguignon et al. 2017a). The most resilient taxa consist primarily of species capable of forming large colonies, controlling their environment by bringing water from distant sources, and building well-defined centralized nest. Examples include *Coptotermes* (Rhinotermitidae), *Odontotermes* (Termitidae: Macrotermitinae), *Microcerotermes* (Termitidae: Termitinae), or *Nasutitermes* (Termitidae: Nasutitermitinae). The ability to acquire water from air humidity is common only in several species of *Cryptotermes* (Kalotermitidae). Wood-feeding species, of course, cannot persist for long in deforested areas which are commonly colonized by specialized grass-feeding taxa from neighboring habitats (Eggleton et al. 2002; Jones et al. 2003; Krishna et al. 2013).

1.5 Valuing and Conserving Saproxylic Insects

1.5.1 Importance to Decomposition, Nutrient Cycling, and Productivity

Given their taxonomic and functional diversity as well as the abundance of many species, saproxylic insects may provide important ecosystem services in forests. One of the most commonly assumed, but rarely quantified, functions provided by these insects is accelerating wood decomposition. Wood decomposition is largely driven by fungi in most forested ecosystems, but saproxylic insects may also contribute significantly to this process (Ulyshen 2016). Termites are thought to be particularly influential in this regard, as supported by estimates of wood-processing rates and various experimental approaches. An excellent review of termite contribution to organic matter turnover, focused mostly on grasses and leaf litter, was provided by Bignell and Eggleton (2000). The importance of termites for wood mineralization has received less attention but is thought to be higher in dry habitats (but see Cheesman et al. in press), where microbial decomposition is slow. Findings from studies using a variety of estimates and experimental approaches suggest the amount of wood consumed by termites varies greatly among locations, ranging from <10% of wood consumed to nearly all of it (Ulyshen 2016). Studies in Africa have reported some of the largest effects of termites, and macrotermitines stand out as being particularly important (Buxton 1981; Collins 1981; Schuurman 2005). Despite being a topic of investigation for over 50 years, estimates of the contributions of termites to wood decomposition suffer from a number of limitations. First, studies

using a combination of field-based estimates of termite density and lab-based measurements of feeding rates may yield highly inaccurate estimates given that termites exist within complex communities of microbes and other insects that cannot be recreated under laboratory conditions and wood quality changes as decomposition proceeds. Past experimental approaches in which chemical or physical methods were used to exclude termites and other insects are also problematic because most exclusion methods are known to affect microbial activity (Ulyshen and Wagner 2013). Open-topped pans with screened bottoms may largely overcome this challenge, at least for studies primarily targeting termites (Ulyshen et al. 2016). Another shortcoming of decomposition studies is the frequent and continued use of machined wooden blocks which represent an unnecessary and misleading simplification of naturally occurring wood. Using wood without the natural bark layer, for instance, has been shown to greatly underestimate decay rates and excludes an entire guild of saproxylic insects (Ulyshen et al. 2016).

In addition, because most experimental decomposition studies have been short in duration (<3 years), thus covering only the early stages of the process, it is not currently possible to determine whether termites provide more than a short-term acceleration of wood decomposition. Termites consume large amounts of wood but are known to focus their feeding on the least dense and most nutritious parts of wood, leaving the most recalcitrant fractions behind. It thus remains possible that termites have no net accelerative effect on decomposition over the entire process (Ulyshen et al. 2014). Long-term studies that extend over almost the entire decomposition process and allow for interactions among species under field conditions are needed to adequately address this question. A related question and one of particular relevance to forest managers concerns the role saproxylic insects play in accelerating nutrient release from decomposing wood and stimulating tree growth. This question was recently tested in the southeastern United States where subterranean termites are known to significantly speed up wood decomposition, but termites were found to have no effect on tree growth after more than 4 years of decomposition in that study (Ulyshen et al. 2017).

Although much of the research addressing the value of saproxylic insects to decomposition has focused on termites, nonsocial taxa are also likely to influence the process. In addition to those that directly facilitate decomposition by consuming and digesting wood, saproxylic insects are likely to have a variety of indirect effects on decomposition. These include promoting fragmentation by scavenging vertebrates, creating tunnels that facilitate the movement of fungi into wood, and vectoring fungi and other decay organisms on or within their bodies (Ulyshen 2016). It is also important to recognize that insects can have both accelerative and inhibitory effects on the overall decomposition process. By providing a food source for woodpeckers, for example, insects can hasten the loss of bark which can greatly reduce how quickly wood decomposes (Ulyshen et al. 2016).

1.5.2 Importance as Predators

As discussed earlier, a large proportion of saproxylic insect species are predators, including parasitoids, and this guild has the potential to reduce economically damaging pest populations associated with dying or recently dead trees. The best evidence for this comes from the extensive literature on bark beetles. For example, a species of monotomid beetle, *Rhizophagus grandis* Gyllenhal, has been shown to greatly reduce numbers of *Dendroctonus micans* (Kugelann) in Europe (Fielding and Evans 1997) and *D. valens* LeConte in China (Yang et al. 2014), often below economically damaging levels. Several fly taxa are also major predators of bark beetles, with *Medetera* and *Lonchaea* (Dolichopodidae and Lonchaeidae, respectively) being particularly influential. *Medetera* was the only predator significantly associated with *Ips typographus japonicus* Nijima mortality in Japan, for example (Lawson et al. 1996). *Medetera* was also one of the two most important predators (the other being *Enoclerus sphegeus* Fab.) of *Dendroctonus* in Western North America, contributing to over 90% mortality in some trees (Hopping 1947).

Although high rates of mortality have been reported for many parasitoid species as well, parasitoids are generally expected to play a less important role than predators in reducing pest populations (Wegensteiner et al. 2015). This is because a parasitoid larva is confined to a single host, whereas a predatory larva commonly kills multiple hosts. In some cases, including some lonchaeid and pallopterid flies, predators are known to kill more hosts than they consume (Wegensteiner et al. 2015). Parasitoids have been shown to impact pest populations, however. In North America, Duan et al. (2015) showed that both introduced and native larval parasitoids played a part in significantly reducing population growth rates of the emerald ash borer, *Agrilus planipennis* Fairmaire. The effectiveness of parasitoids at reducing host populations is often limited by the lengths of their ovipositors, however, with parasitism rates decreasing with increasing bark thickness (Berisford 2011; Abell et al. 2012).

As reviewed by Wegensteiner et al. (2015), efforts to measure the overall impact of predators and parasitoids on bark beetle populations suggest a high degree of variability, with studies reporting mortality rates of between 23 and 90%. They conclude that natural enemies play an essential role in controlling forest pest populations and stress the importance of having a diversity of predatory taxa. More research is needed to understand the role predation and other interspecific interactions play in structuring saproxylic insect assemblages (Brin and Bouget 2018; see Chap. 14).

1.5.3 Conserving Saproxylic Insect Diversity in Managed Forests and Beyond

Forest clearance and degradation are the two main processes by which dead wood has been lost from many landscapes, resulting in a patchwork of forest stands of

varying size, age, and quality surrounded by a matrix of other land uses. In some parts of the world, these disturbances happened so long ago that the appearance and composition of the original forests can only be guessed (Speight 1989). Fragments of old-growth forests, for which there is no history, records, or suspicion of clearance or major disturbance, provide invaluable insights into the amount and variety of dead wood as well as the diversity and composition of saproxylic insects in the absence of human activity (Lachat and Müller 2018; see Chap. 17). Many studies indicate that old-growth forests contain a greater volume and variety of dead wood than younger managed forests from the same region (Siitonen 2001; Stenbacka et al. 2010a). In addition to containing larger volumes of dead wood, old-growth forests support a greater variety of dead wood than most managed forests. In Sweden, for example, Siitonen et al. (2000) reported the average number of dead trees greater than 40 cm in diameter to be 25 and 35 times higher in old-growth forests compared to mature managed forests for coniferous and deciduous species, respectively. Similarly, Spies et al. (1988) reported twice as many logs exceeding 60 cm in diameter in old-growth forests as compared to those of intermediate age in northwestern North America. Old-growth forests also contain more wood at advanced stages of decomposition.

Given these large differences in the amount and variety of dead wood, it is perhaps not surprising that many studies have highlighted the importance of relatively undisturbed old-growth forests to saproxylic insect communities. Indeed, numerous studies have shown a positive correlation between saproxylic insect diversity and dead wood volume (Grove 2002c; Vanderwel et al. 2006; Økland et al. 1996; Martikainen et al. 2000). Moreover, Grove (2002c) showed that the basal area of large-diameter trees can be used as an indicator of ecological integrity for saproxylic beetles in Australian rainforests. Old trees are particularly valuable because they frequently contain tree hollows which are required by some of the most vulnerable species. Floren and Schmidl (2008) estimated that approximately 86% of beetle species dependent on tree hollows in Germany are threatened, for example. Species with limited dispersal abilities or dependence upon microhabitats characteristic of old forests are often much more common at locations with a long history of forest cover. In Germany, for example, Buse (2012) showed that flightless saproxylic weevils are restricted to “ancient” forests (at least 220 years old). The relict status of these small-twig feeders is due to their inability to disperse long distances rather than a dependence on old-growth features. Other species are largely restricted to old-growth forests due to the absence or rarity of suitable microhabitats in younger forests. Tree hollows, for example, typically require a long time to develop and become more common as forests age. A number of hollow-dependent insect species are thus more common in older forests, although these species can be supported in other contexts when efforts are taken to protect veteran trees. Indeed, although old-growth forests play a central role in maintaining populations of sensitive species, second-growth forests are known to support diverse assemblages as well, including vulnerable species, provided that efforts are taken to provide an adequate abundance and continuity of critical microhabitats. How much wood is necessary remains an open question and is perhaps less critical than the variety of wood provided (Seibold and Thorn 2018; see Chap. 18). It is well-known that

different saproxylic species utilize different tree genera and also differentiate between wood that is either standing or suspended in the canopy and wood in contact with the forest floor (Berkov 2018; see Chap. 16). Fire also plays an influential role in providing resources for specialist species (Hjältén et al. 2018; see Chap. 20). In addition, species separate into groups defined by their preferences for particular stages of decomposition. Whereas some species attack only trees that are dying or recently dead, colonization by others occurs only near the end of the process. These patterns suggest that efforts to maximize the number of tree species, wood postures, and stages of decomposition will be the most successful at maintaining diverse saproxylic insect assemblages.

Another key question concerns how much spatial and temporal continuity is needed. Many studies indicate that spatial and temporal continuity of dead wood is more important than the amount or variety of dead wood at any particular time and place (Similä et al. 2003; Sverdrup-Thygeson et al. 2014; Schiegg 2000a, b). In France, for example, Brin et al. (2016) found forests >200 years old to support a higher richness of saproxylic beetles, including more large-bodied species, than younger forests despite having less volume and variety of dead wood. These patterns may be due in large part to differences in dispersal ability among species (Feldhaar and Schauer 2018; see Chap. 15), with large-bodied species being generally less capable of flying long distances (Ranius and Hedin 2001) and/or having shorter flight periods (Gillespie et al. 2017) than smaller species. The same is of course also true for flightless species (Buse 2012). Many species with the weakest dispersal abilities are associated with persistent habitats such as tree hollows, whereas species associated with ephemeral habitats such as phloem or small-diameter wood tend to be relatively strong dispersers (Nilsson and Baranowski 1997). Although site history is important (Goßner et al. 2008) and large blocks of old forest have the highest conservation value (Irmeler et al. 2010; Grove 2002a), it is important to recognize the value of smaller and younger forest patches in supporting a subset of the saproxylic fauna (i.e., the strong dispersers), especially within the context of metapopulation dynamics. One example of this comes from the wheat-farming region of western Australia where Abensperg-Traun (2000) found that even small and disturbed patches of *Eucalyptus* imbedded within an agricultural matrix supported wood-feeding termites. Termite species richness increased with tree number (patch size), but distance from other source populations had no effect, probably due to the ability of termites to disperse over long distances. Similarly, studies on the tree-hollow specialist, *Osmoderma eremita* (Scopoli), in Europe show that even scattered trees in highly managed landscapes can promote the conservation of certain species. In managed forests, strategies such as retention harvesting, where a certain number of trees are left behind either in a dispersed or aggregated arrangement, may improve spatial connectivity, thus softening the impact of harvest operations for many species (Lee et al. 2018; see Chap. 19).

The relationship between saproxylic insect diversity and canopy openness is another question of high relevance to managers. Naturalists have long recognized that many saproxylic insect groups, especially many of the large and colorful taxa most prized by collectors (e.g., cerambycids, buprestids, etc.), are more readily

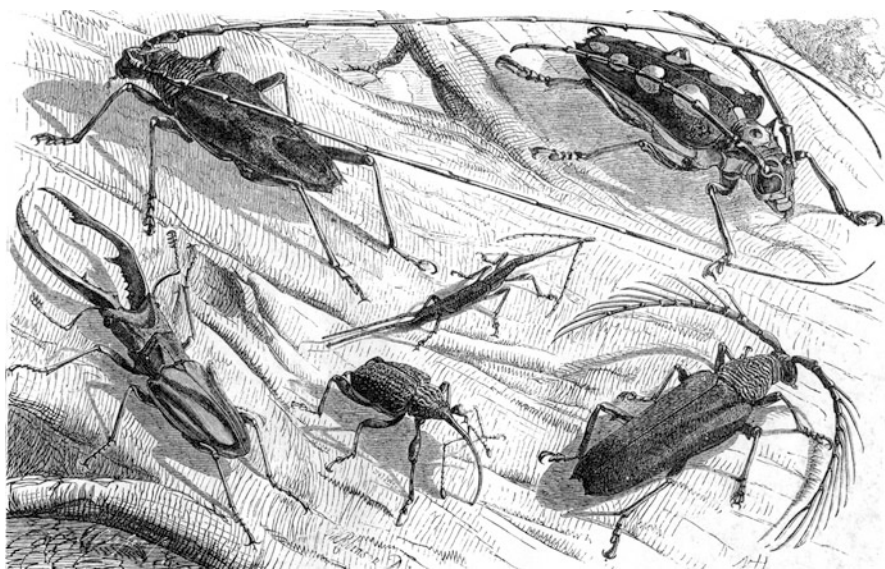


Fig. 1.7 Examples of “remarkable” saproxylic beetles collected by Alfred Russel Wallace (1869) in Borneo

collected in sunny areas. In his 12 years of collecting insects in the tropics, for example, Alfred Russel Wallace (1869) found recently cleared areas of forest to be by far the most productive, with one such place in Borneo yielding nearly 2,000 species of saproxylic beetles (Fig. 1.7). Studies using passive trapping techniques (e.g., flight intercept traps) have shown this to be true for a wide range of taxa although many others prefer shady conditions. In Germany, for example, Seibold et al. (2016b) found that 105 and 57 species of beetles collected in flight intercept and pitfall traps were significantly associated with sunny and shady plots, respectively. Lachat et al. (2016) compared saproxylic beetle assemblages present in the centers and on the edges of canopy gaps as well as under closed canopy conditions away from the gaps in an old-growth Ukrainian beech forest. They found beetle abundance to be higher and beetle composition to be different in the centers of the gaps compared to the forest but found no difference in species richness. The findings from passive trapping have the potential to exaggerate the importance of sunny conditions, however, as many insects are more active and thus more readily captured in sunny areas. Few studies have addressed this question using emergence traps although Gossner et al. (2016) reported a positive correlation between the number of beetle species emerging from dead wood and canopy openness in Germany. More emergence-trap studies are needed to better understand these patterns, and studies targeting less commonly studied insect orders would be particularly informative. Flies, for example, are dependent on moist or wet substrates, and may be particularly sensitive the drying effects of more open forest conditions (Ulyshen 2018b; see

Chap. 5). The needs of such species should be taken into consideration when developing management plans.

In addition to the effects of forest clearance and degradation, saproxylic insects are likely to be impacted by the intentional or accidental introduction of nonnative tree species into many of the remaining forested areas. Invasive trees and shrubs are a growing problem in many regions, and plantations of nonnative trees are planted over vast expanses of land that once supported native forests. The quality of these highly modified forests to saproxylic insects, especially the most vulnerable species, remains uncertain (Ulyshen et al. 2018; see Chap. 23). The value of urban environments to saproxylic insects is also an increasingly important question, representing both a challenge and opportunity for community engagement (Horák 2018; see Chap. 24). Although many questions remain about how best to conserve saproxylic insects in managed landscapes, there can be little doubt that these decisions can have important and lasting consequences for this major fraction of our biodiversity.

1.6 Aims and Scope of This Book

The 25 chapters included here are in-depth considerations of prioritized topics but are united by several broad objectives that collectively aim to provide the most global and inclusive synthesis of current knowledge possible. These objectives include (1) incorporating information from regions outside of Europe, (2) recognizing the key roles social insects (e.g., termites, ants, and passalid beetles) play in saproxylic assemblages, (3) highlighting some of the less commonly studied taxa, and (4) addressing the value of highly decomposed wood. The book is organized into four sections. The first section, titled “Diversity,” includes chapters addressing particular taxonomic groups. Insect orders are presented in decreasing order of estimated global saproxylic diversity. The three chapters on Coleoptera are thus presented first, followed by Diptera, Hymenoptera, Hemiptera, Lepidoptera, and Isoptera. The second section, titled “Ecology,” contains chapters on insect-fungal interactions, nutrient dynamics in decomposing wood, biotic interactions among saproxylic insects, dispersal of saproxylic insects, and seasonality and stratification of saproxylic beetles in tropical forests. The third section is titled “Conservation” and includes chapters on the importance of primary forests to saproxylic insects, the importance of dead wood amount and variety, saproxylic insect conservation under variable retention harvesting, saproxylic insects and fire, saproxylic insects and tree hollows, insects in highly decomposed wood, utilization of nonnative wood by saproxylic insects, and the role of urban environments for saproxylic insects. The fourth section, titled “Methodological advancements,” contains a single chapter on molecular tools for assessing saproxylic diversity.

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