Chapter 6
Deadwood Biodiversity

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Abstract Deadwood is a key component for biodiversity and ecosystem services in boreal forests; however, the abundance of this critical element is declining worldwide. In natural forests, deadwood is produced by tree death due to physical disturbances, senescence, or pathogens. Timber harvesting, fire suppression, and salvage logging reduce deadwood abundance and diversity, and climate change is expected to bring further modifications. Although the effects of these changes are not yet fully understood, restoring a continuous supply of deadwood in boreal forest ecosystems is vital to reverse the negative trends in species richness and distribution. Increasing the availability of deadwood offers a path to building resilient forest ecosystems for the future.

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6.1 Introduction

Deadwood, which includes standing dead trees, stumps, and downed logs in both terrestrial and aquatic habitats, is an important driver of biodiversity in boreal forests (Fig. 6.1; Thorn et al., 2020b). Deadwood abundance and its composition—characterized by deadwood diameter, decay class, tree species, and position—influence the diversity and abundance of a variety of organisms, including bryophytes, lichens, fungi, beetles, birds, and mammals (Fig. 6.2; Stokland et al., 2012). Saproxylic species live in and/or feed on deadwood for at least some part of their life cycle. They use deadwood as a direct or indirect food source (e.g., herbivores, detrivores, fungivores, predators, parasitoids) and/or as a nesting site or shelter. Epixylic species, such as bryophytes and lichens, live on the deadwood surface, and tree seedlings often establish on decomposing downed logs (Stokland et al., 2012). The ecosystem services that deadwood-associated organisms provide, e.g., decomposition, nutrient turnover, and pollination, make them an integral component of the boreal food web (Harmon, 2021; Müller et al., 2020). The extensive variability in deadwood-related habitats favors a high diversity of specialized species and intricate species interactions. Consequently, any anthropogenic disturbance that changes the abundance and diversity of deadwood alters this biodiversity and ecosystem functioning. The main factor currently influencing deadwood abundance in boreal forests is large-scale intensive forestry, including biofuel harvesting (Hof et al., 2018), although the influence of climate change is also growing (Cadieux et al., 2020; Tremblay et al., 2018). In this chapter, we first review deadwood characteristics and dynamics across the boreal biome. We then provide a brief overview of the various groups of organisms associated with the specific forms of deadwood in terrestrial and aquatic habitats. Finally, we examine the anthropogenic factors, including forestry and climate change, that alter deadwood forms and abundance in boreal forests.

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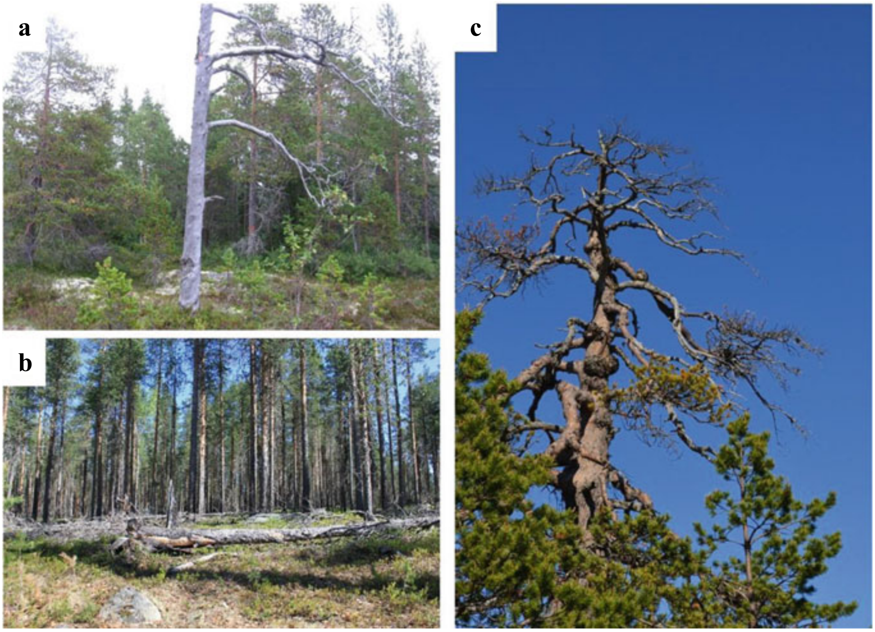


Fig. 6.1 Examples of deadwood types in boreal forests; **a** kelo tree, **b** fallen tree, **c** dead top caused by the fungus *Cronartium flaccidum* or *Peridermium pini*. *Photo credits* **a**, **c** Ekaterina Shorohova, **b** Therese Löfroth

6.2 Deadwood Composition and Dynamics in Natural Forests

The volume and diversity of deadwood vary greatly with site productivity, tree species composition, forest age, and disturbance history (Table 6.1; Martin et al., 2018; Shorohova & Kapitsa, 2015). High productivity sites, producing more and larger trees, also produce more abundant and larger deadwood (Shorohova & Kapitsa, 2015). Tree species vary in size, wood quality, and dominant mortality mode (i.e., uprooting, decline, or stem breakage), eventually resulting in different types of deadwood (Müller et al., 2020). Special deadwood qualities are formed from injured and slow-growing trees that form dense and resin-rich wood (Fig. 6.1). Deadwood dynamics include the generation and loss (e.g., through combustion, decomposition, and overgrowth by vegetation) of deadwood. The cumulative effects of these processes, adding and removing deadwood, are reflected in the deadwood volume and composition in a given area (Fig. 6.3).

Late-seral and post-disturbance forests are the two most deadwood-rich habitats in natural boreal forest landscapes (Siitonen, 2001; Stokland et al., 2012). These stands are shaped by small-scale mortality processes that provide a relatively constant recruitment of recently dead trees (Aakala et al., 2008; Boulanger & Sirois, 2006),

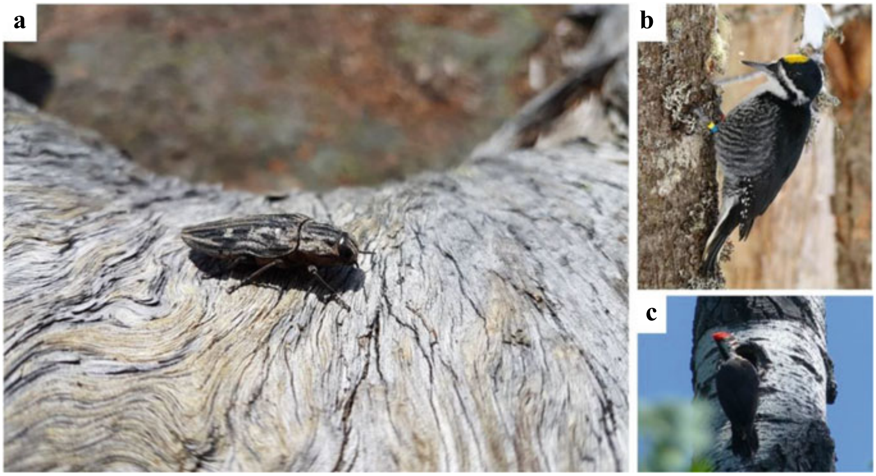


Fig. 6.2 Many species depend on deadwood for larval development, foraging, or nesting. Examples of the deadwood-dependent species include **a** the buprestid beetle (*Chalcophora mariana*) that depends on large pine trunks in sun-exposed habitats, **b** the Black-backed Woodpecker (*Picoides arcticus*), nesting in a dead tree, and **c** the Pileated Woodpecker (*Dryocopus pileatus*) nesting in a trembling aspen (*Populus tremuloides*). *Photo credits* **a** Kristina Viklund, **b** David Tremblay, **c** Réjean Deschênes

which have been identified as critical ecological attributes to many support specialist forest-related species (Martin et al., 2020, 2021). Larger-scale disturbances concentrated in time and space, such as fire, storm felling, and insect outbreaks, produce large pulses of deadwood (Bergeron et al., 2004; Taylor & MacLean, 2007). Following these pulses, deadwood volume decreases over the next 50–100 years before gradually increasing, although to a much lower level, when either these stands reach maturity (Harmon, 2021) or another disturbance occurs (Fig. 6.4). After intense disturbances in late-seral boreal forests, deadwood volumes might exceed hundreds of $m^3 \cdot ha^{-1}$ and average 210 $m^3 \cdot ha^{-1}$ (Table 6.1; Shorohova & Kapitsa, 2015). Less severe disturbances also affect deadwood quality by injuring trees; these trees later produce tar-rich deadwood that, in turn, provides critical resources for specialized fungi, wood-boring arthropods, and avian and arthropod predators (Nappi et al., 2010).

Standing dead trees (*snags*) often constitute a significant part of the basal area of trees in natural boreal forests (Nilsson et al., 2002). Tree species differ in standing times after death, leading to variable snag dynamics across boreal forests (Aakala et al., 2008; Taylor & MacLean, 2007). In eastern Canada, Angers et al. (2011) found that the standing time of snags ranged from 15 years for trembling aspen (*Populus tremuloides*) to close to 30 years for jack pine (*Pinus banksiana*). In Europe, tree species such as Scots pine (*Pinus sylvestris*) can form barkless tar-rich snags having a characteristic hard and silvery-gray surface; these snags are known as *kelo trees* (Fig. 6.1). The formation and decay of kelo trees require centuries, and these snags

Table 6.1 Examples of estimated deadwood volumes across the boreal biome for various mature unmanaged forest types experiencing different disturbance regimes

Region	Forest type	Disturbance regime	Mean (± SE) total deadwood volume ($m^3 \cdot ha^{-1}$)	Range ($m^3 \cdot ha^{-1}$)	References
Northwestern Russia	Spruce-dominated	Wind/gap dynamics	147.7 ± 10.8	–	Shorohova and Kapitsa (2015)
Northwestern Russia	Pine-dominated	Fire	74.4 ± 13.1	–	Shorohova and Kapitsa (2015)
Western Canada	Mixedwood	Fire	76.1 ± 41.5 (SD)	3–93	Work et al. (2004)
Western Canada	Coniferous	Fire	93.9 ± 18.9 (SD)	–	Work et al. (2004)
Eastern Canada	Black spruce (*Picea mariana*)	Fire		3–155	Martin et al. (2018)
Eastern Canada	Mixedwood	Fire/Postfire succession		0–708	Hély et al. (2000)
Finland/western Russia	Scots pine (*Pinus sylvestris*)–dominated	Fire		117	Rouvinen and Kouki (2002)
Fennoscandia	Coniferous	Fire/gap dynamics		20–120	Siitonen (2001)
Finland and northwestern Russia	Norway spruce (*Picea abies*)	Gap dynamics	60	41–170	Aakala (2010)
Eastern Fennoscandia	Scots pine (*Pinus sylvestris*)	–	69.5	22.2–158.7	Karjalainen and Kuuluvainen (2002)
Eastern Canada	Black spruce (*Picea mariana*)	–	71.3 ± 11.2 (>90 y) 49.5 ± 14.2 (<90 y)	–	Tremblay et al. (2009)

form a distinct habitat for specialized wood fungi and lichens (Niemelä et al., 2002; Santaniello et al., 2017). The extremely slow recruitment of kelo trees and their suitability as firewood have made them a rarity in modern landscapes, and long-term conservation and restoration strategies are needed for these unique habitats (Kuuluvainen et al., 2017).

In natural forests, deadwood is lost through consumption by fire, decomposition by fungi, bacteria, and animals, and overgrowth by ground vegetation. Although forest fires create deadwood, they also consume existing pre-fire deadwood (Hyde et al.,

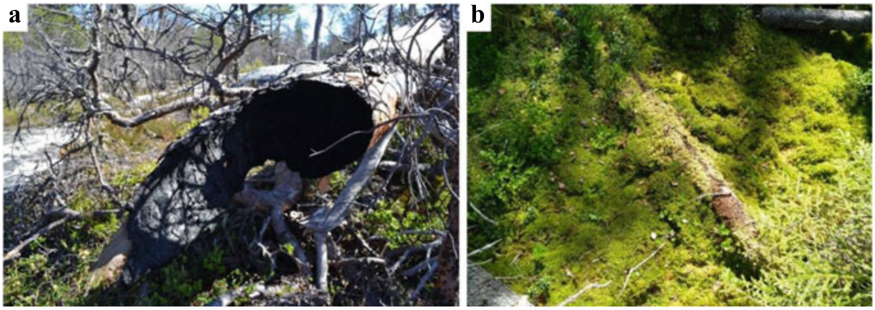
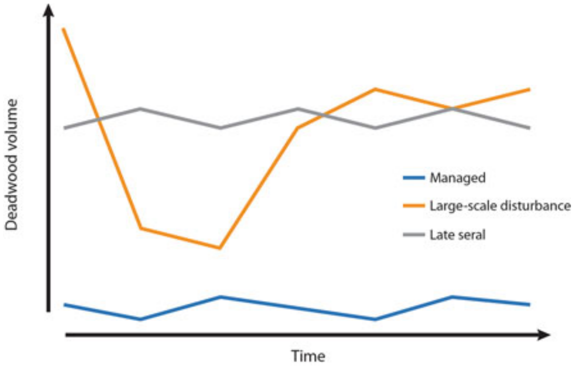


Fig. 6.3 Several natural processes impact deadwood dynamics, including wildfires, which add (by damaging living trees) and consume deadwood; **a** hollow trunk after fire, **b** overgrowth is an important process that incorporates deadwood into the soil. *Photo credits* Ekaterina Shorohova

2011). The nonfire decomposition rate of deadwood varies with climate, site conditions, tree species, deadwood size (Shorohova & Kapitsa, 2016), and the composition of the decomposer community (Bani et al., 2018). In addition, many wood attributes, including annual ring width, wood density, and chemical composition (e.g., resin content), affect the decomposition rate (Edman et al., 2006; Venäläinen et al., 2003). Finally, the burial of downed deadwood within the soil organic layer affects, for example, accessibility to deadwood for colonization by saproxylic insects and its utility as habitat for epixylic bryophytes. Burial is faster in sites with a soft organic layer, such as peat, and with fast-covering ground vegetation, such as vascular plants and *Sphagnum* mosses (Fig. 6.3; Dynesius et al., 2010). More than a quarter of the carbon originating from deadwood in boreal forests is estimated to be stored in buried, downed deadwood. Therefore, although this wood is no longer important for aboveground biodiversity, it continues to perform important ecosystem functions, such as nutrient cycling and carbon storage (Stokland et al., 2016). Deadwood burial is affected by several factors that can be altered by climate change, such as microclimate and the depth of the organic layer (Dynesius et al., 2010; Stokland et al., 2016).

Fig. 6.4 Deadwood dynamics for forests under even-aged management, after a stand-replacing fire in natural forest, and in a late-seral natural forest



Burial also interacts with decomposition, as buried deadwood typically decomposes at a much slower rate than aboveground deadwood (Stokland et al., 2016).

6.3 Deadwood Substrates and Their Associated Biodiversity

Deadwood provides numerous ecological niches, and a multitude of species interact within the deadwood food web (Fig. 6.5). Species assemblage composition and richness in deadwood are affected by tree species, sun exposure, decay stage, wood density and diameter, type of rot, cause of death, and whether the stem is standing, lying, charred, or in contact with the ground (Hägglund & Hjältén, 2018; Johansson et al., 2017; Kushnevskaya & Shorohova, 2018).

A well-known example of niche differentiation linked to deadwood diameter is bark beetles selecting wood on the basis of bark thickness. For example, the emerald ash borer (*Agrilus planipennis*) attacks ash trees that have a stem diameter within a limited range (Timms et al., 2006), and the six-toothed beetle (*Ips sexdentatus*) is restricted to the base of old large-diameter pines (Gilbert et al., 2005). Some saproxylic organisms function as keystone species, e.g., the primary spruce bark beetle (*Ips typographus*), which affects more than 100 associated species (Weslien, 1992). Several invertebrate species use deadwood primarily as nesting sites. Solitary bees and wasps dig their nest tunnels into soft decaying wood or use tunnels made by other insects. Social wasps and honeybees build their nests in hollow trees, and ants

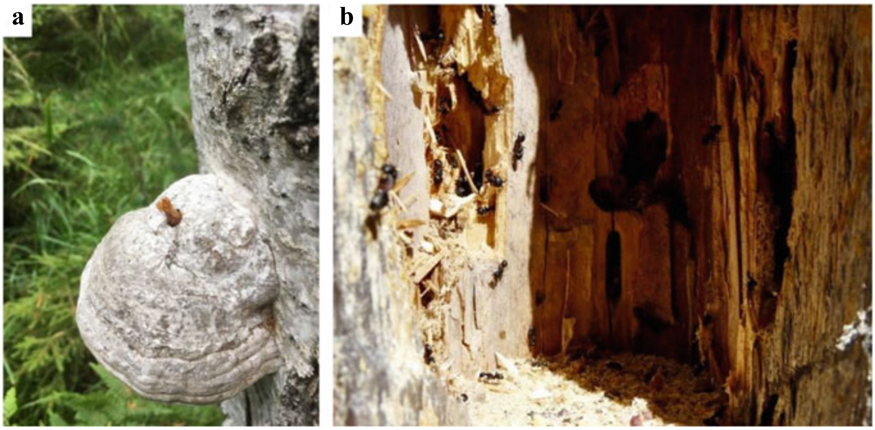


Fig. 6.5 Species interactions are an essential part of deadwood dynamics. **a** The lepidopteran *Scardia boletella* (Tineidae) seen here recently hatched from the saproxylic tinder fungus (*Fomes fomentarius*). *Scardia boletella* is vulnerable to forest management and is listed as endangered in Norway. **b** Carpenter ants (*Camponotus* sp.) in a dead balsam fir (*Abies balsamea*), here excavated by the Pileated Woodpecker (*Dryocopus pileatus*). *Photo credits* **a** Tone Birkemoe, **b** Pierre Drapeau

(e.g., *Camponotus* spp.) excavate their nests into living or dead trees (King et al., 2018; Westerfelt et al., 2015). Many dipterans use emergence holes and galleries from other insects as nest sites (Dennis et al., 2018).

Below we describe the biodiversity associated with three types of fully dead trees: snags, logs, and underwater deadwood.

6.3.1 Dead Standing Trees (Snags)

Lichens thrive on snags and often on decorticated stems, such as kelo trees. In Fennoscandia and the Pacific Northwest of North America, more than 40% of the analyzed lichen species occurred on deadwood, and 10% were found solely on deadwood (Spribille et al., 2008). The pin lichens (calicioid lichens) are the most specialized of the wood-living lichens, and for many species in this group, kelo trees constitute the main substrate (Santaniello et al., 2017). The specific lichen flora varies with snag decay, and there is a distinct shift in assemblage makeup, from species that colonized before tree death to species colonizing the barkless surface after bark loss. After bark loss, the tree species becomes less important as a factor influencing the lichen flora (Lõhmus & Lõhmus, 2001).

The decay processes of standing deadwood are intrinsically related to saproxylic insect activity (Siitonen, 2001), particularly for wood-feeding species that colonize dying and dead trees. Saint-Germain et al. (2007) found that wood-feeding insects were most abundant in black spruce at the beginning of the decay sequence on fresh snags, whereas they observed opposite wood-feeding insect patterns in aspen, as insects reached large numbers in snags at the middle- to late-decay stages. These results highlight the importance of considering the entire range of decay classes of standing deadwood for conservation planning in managed forest landscapes. In a study of the substrate requirements of red-listed saproxylic invertebrates in Sweden, Jonsell et al. (1998) found that a high proportion of these species require sun-exposed deadwood, of which snags are a significant proportion. Typically, snags are inhabited by species that thrive in drier and more exposed habitats (Hjältén et al., 2012); an example is the beetle *Peltis grossa* that thrives in snags within clear-cuts (Weslien et al., 2011). Hence, leaving standing, sun-exposed deadwood in clear-cuts could be an effective means of increasing the breeding substrates for saproxylic invertebrates; however, such retention strategies may not be adequate for species living in late-seral forests that depend on shaded sites.

Insects colonizing snags and dying trees are critical food resources for woodpeckers (Hammond & Theimer, 2020). Forest stands after natural disturbances often represent significant foraging opportunities for these bird species; this includes burned areas (Nappi et al., 2010; Versluijs et al., 2020) and forest stands affected by insect outbreaks (Rota et al., 2015). However, landscapes characterized by high amounts of late-seral forest are also important and provide snags continuously over time (Martin et al., 2021; Nappi et al., 2015). Individual woodpecker species specialize in specific decay stages of dying and dead trees (Hammond & Theimer, 2020), again underlining the importance of a continuous input of standing deadwood to ensure a steady supply of suitable foraging trees for the woodpecker community (Nappi et al., 2015).

Dying trees and snags provide cavities for nesting, roosting, and denning for 10–40% of species of birds (including the families Picidae and Sittidae and the order Stringiformes) and mammals (from the order Microchiroptera and the families Mustelidae and Sciuridae) in forest ecosystems (Kotowska et al., 2020; Parsons et al., 2003). In boreal forests, most cavities are produced by avian excavators, mostly woodpeckers, whereas few cavities originate through natural tree-decay processes (Wesołowski & Martin, 2018). At least 1878 species worldwide (18.1% of all bird species in the world) nest in tree cavities, and at least 338 of these species use cavities created by woodpeckers (Picidae) (van der Hoek et al., 2017). Cavity-using communities form interspecific hierarchical networks called nest webs (Martin & Eadie, 1999), where cavity-bearing tree species, cavity-producing agents (excavators and decay processes), and nonexcavating cavity users interact. Cavities are created every year, reused over time, change as they age (Edworthy et al., 2018), and are formed both in living trees showing signs of decay and in dead trees (Drapeau et al., 2009; Edworthy et al., 2018). Aspens (*Populus* spp.) are particularly important cavity-bearing trees—either natural or excavated cavities—in both North American and European boreal forests (Andersson et al., 2018; Parsons et al., 2003).

6.3.2 Downed Deadwood (Logs)

The characteristics of lying and standing deadwood differ. Downed deadwood is generally moister because it has more extensive ground contact and is shaded; sun-exposed logs also occur, particularly after a severe disturbance. Logs contribute to the structural diversity of the forest floor and provide nest sites, food, and cover for both mammals and amphibians (Fauteux et al., 2012). Because downed deadwood in boreal areas is hidden in winter under snow, its importance as foraging sites for woodpeckers and other birds is more limited than for snags; however, downed deadwood is still used, and its use is likely underestimated (Tremblay et al., 2010).

Large-diameter logs host a higher number of species (and specialized species) than small-diameter logs (Juutilainen et al., 2011). The larger, longer-lasting, and more varied deadwood habitat of larger logs partially explains this difference, often offering larger proportions of heartwood, an important habitat for some species. For example, the hairy pine borer beetle (*Tragosoma depsarium*) inhabits pine logs larger than 25 cm in diameter having large proportions of heartwood and a slow decay rate (Wikars, 2004). The polypore fungus *Fomitopsis rosea* also occurs more frequently in larger logs and is favored by the higher wood density of slow-growing trees (Edman et al., 2006). However, in old-growth forests having a high availability of deadwood, the total log volume per hectare rather than log size may be more critical for species diversity and composition, as demonstrated for mosses, liverworts, and lichens growing on logs (Kushnevskaya & Shorohova, 2018).

The saproxylic insects of logs include several feeding guilds that shift in dominance as the log decomposes. First, the cambium consumers and their associated predators and parasitoids colonize the freshly fallen tree, followed after a few years by wood borers, which feed on the wood, and fungivores (Gibb et al., 2013). Species feeding on the short-lived but nutritious cambium have short generation times, whereas larger wood-boring taxa have life cycles lasting 3–15 years, e.g., *Tragosoma depsarium*, *Pytho kolwensis*, and *Chalcophora mariana* (Fig. 6.2; Siitonen & Saaristo, 2000; Wikars, 2004).

Logs are essential hibernation sites for many epigeic and litter-dwelling arthropods, e.g., carabid beetles and mollusks. For wood ants and small mammals, logs can also serve as pathways when foraging (Boucher et al., 2015; Westerfelt et al., 2015).

Logs harbor a rich flora of wood-decaying fungi. There is a turnover of fungal species during log decomposition, as wood density and C:N ratios decrease and moisture and lignin contents increase (Rajala et al., 2011). In unmanaged boreal forests, Ascomycetes colonize recently fallen spruce logs, whereas Basidiomycete fungi—responsible for brown rot—peak during the intermediate decay stages. White rot fungi constitute approximately one-fifth of all fungal species in decomposing logs, except at the latest decay stages when ectomycorrhizal fungi become dominant (Rajala et al., 2012). Bark attached to logs also hosts diverse fungal communities that vary during decomposition (Kazartsev et al., 2018).

Many boreal bryophytes (i.e., mosses and liverworts) grow on fallen logs, and logs are often bryophyte biodiversity hot spots. Several ecological groups of deadwood-associated bryophytes can be distinguished (Kushnevskaya et al., 2007). *Facultative epiphytes* grow on the lowest parts of living tree trunks and also colonize other parts of fallen logs until the midstages of decay (e.g., *Ptilidium pulcherrimum*). *Epixylic specialists* grow mainly on logs and stumps. Some species (e.g., *Lophozia ciliata*) colonize the bark, whereas others colonize softened barkless logs (e.g., *Crossocalyx hellerianus*, *Riccardia palmata*, and *Lophocolea heterophylla*). *Opportunistic generalists* colonize at any stage of decay, and *epigeic species* normally cover the forest floor but overgrow the logs as they decay (Dynesius et al., 2010; Kushnevskaya & Shorohova, 2018).

6.3.3 Deadwood in Water

Deadwood has several vital ecological functions in aquatic environments. Deadwood alters river flow and serves as habitat for fish. In lakes, woody debris in the littoral zone has proven important for prey fish abundance and predatory fish growth potential (Ahrenstorff et al., 2009). Driftwood, i.e., stranded deadwood, harbors a rich fungal flora and contributes significantly to the deadwood biodiversity in coastal regions (Blanchette et al., 2016). In forest ecosystems, deadwood can link terrestrial and aquatic habitats. A key species here is the beaver, which creates substantial amounts of deadwood both directly by felling trees and indirectly by flooding forests. The deadwood in water includes rare deadwood types (e.g., aspen in Fennoscandia) in areas otherwise rarely affected by stand-replacing disturbances (Thompson et al., 2016).

6.4 Species Interactions in Deadwood

Insects and fungi are the most species-rich taxa in deadwood. Coexisting at least since the late Silurian (Misof et al., 2014; Sherwood-Pike & Gray, 1985), this tight coupling has resulted in reciprocal adaptations and intricate interactions with profound impacts on deadwood dynamics; however, relatively little is known about these interactions (Birkemoe et al., 2018), possibly because of the cryptic nature of fungi. One important and direct interaction is through feeding (Fig. 6.5a), which is likely to have a significant functional importance for biodiversity and deadwood decomposition. Fungi live on insects as parasites, pathogens, and mutualists; insects feed on various forms of fungi, including yeast cells, mycelia, and fruiting bodies. Many insect species feed directly on fungi, and adding fungi to the diet might be essential for beetles that feed primarily on wood, which has low nutritional value. For instance, it has been calculated that the longhorn beetle *Stictoleptura rubra* would require 40–85 years to reach adulthood if all its nutrients were obtained from wood, or 13–28 times longer than its maximum recorded life-cycle length (Filipiak & Weiner, 2014).

Bark and ambrosia beetles bring their mutualistic fungi to the colonized trees; however, recent studies indicate that insects also disperse nonmutualistic wood-decaying fungi (Jacobsen et al., 2018; Seibold et al., 2019). A study identifying wood-living fungi from beetles landing on recently cut wood showed that the networks between beetles and fungi were comparable in strength to seed dispersal networks (Jacobsen et al., 2018) and thus of potential importance for deadwood biodiversity. However, the study must be replicated in other systems to determine whether these findings can be generalized.

Insects also farm fungi, as observed in termites and several ambrosia beetles. Conversely, some fungi protect insects by reinforcing nest-wall structures (Schlick-Steiner et al., 2008), fighting microbial pathogens (Flórez et al., 2015), or degrading tree defenses that would otherwise be detrimental to insects. Indirect interactions, where fungi or insects modify the deadwood habitat, could also significantly affect the insect/fungal communities and their functions.

In addition to the interactions between insects and fungi, multiple interactions exist within these two highly diverse groups. Among insects, predator/prey interactions are important for regulating populations. For instance, the bark beetle *Tomicus piniperda* produces fewer offspring when predators are present in high numbers (Schroeder & Weslien, 1994). Fungi in deadwood live in constant chemical warfare with other fungi (Hiscox et al., 2018), and the war zones can be observed as dark lines in deadwood. Many fungi also feed on other fungi (Maurice et al., 2021). Insects also compete, facilitate colonization, and produce priority effects, i.e., when initially colonizing species determine what species can colonize later. Priority effects have been observed for insects and fungi in the succession and colonization of deadwood (Weslien et al., 2011).

Various other taxa also interact within deadwood. Bacteria is an often overlooked but vital part of the deadwood community. Bacteria interact with wood-decaying fungi (Johnston et al., 2016), affecting the wood decay rate and fungal species composition. Recently, nematode parasites of insects were also found to modify the wood decay rate (Davis & Prouty, 2019). Larger organisms, such as shrews, mice, and woodpeckers, forage for invertebrates in deadwood.

6.5 Forest Management Impact on the Deadwood Profile

Forest management significantly impacts the abundance and diversity of deadwood in boreal forests. Even-aged management, converting deadwood-rich, uneven-aged mature, and old forests into even-aged stands, remains the most common forestry harvesting approach. Furthermore, forest management promotes fast-growing healthy trees and reduces the abundance of slow-growing, injured, and unhealthy trees. Consequently, forest management has caused a decline of many boreal deadwood-associated species (Siitonen, 2001). Deadwood species are generally lower in managed forests than in natural ones, and harvesting intensity and time amplify these differences (Junninen et al., 2006). Consequently, regions with a long forest management history have smaller populations of specialized deadwood-associated species found in fewer sites (Müller et al., 2013; Nordén et al., 2013). For example, the amount of deadwood in intensively managed forests in Fennoscandia is considerably lower (4–10 $m^3 \cdot ha^{-1}$) than that found in natural stands (Fig. 6.4) (for volumes in natural stands, see Table 6.1). Timber harvesting by thinning and final felling has caused this decline, exacerbated by the more recent practice of extracting woody debris left after harvesting for biofuels (Hof et al., 2018). In contrast, less intensive management, in which stands are allowed to self-thin during development and smaller pieces of deadwood generated during harvest are left on-site, helps reduce declines in deadwood abundance. Thus, significant volumes of deadwood have been documented in Russian managed forests, with an average of 28.0 $m^3 \cdot ha^{-1}$ (Malysheva et al., 2019) and ranging from 1 to more than 100 $m^3 \cdot ha^{-1}$ in the Novgorod region (Shorohova & Tetioukhin, 2003). Forestry also changes the diameter and decay stage distributions of deadwood and disrupts the recruitment of new large deadwood items (Martin et al., 2021). In unmanaged forests, large stems often constitute the majority of deadwood volume. For example, in spruce-dominated boreal old-growth forest, large-diameter (>30 cm) dead trees can comprise 42–54% of the volume, whereas smaller-diameter stems (<10 cm) represent only 1.7–2.7% (Nilsson et al., 2002; Siitonen, 2001); this pattern is reversed in younger to middle-aged managed forests (Stenbacka et al., 2010).

6.6 Effects of Climate Change on Deadwood and Associated Biodiversity

Timber harvesting has disfavored deadwood-associated species for decades if not centuries, particularly in Europe (Stokland et al., 2012). More recently, climate change has put additional stress on forest ecosystems and their biodiversity, as a changing climate alters nutrient cycles and disturbance regimes (Tremblay et al., 2018; Venäläinen et al., 2020). Climate change mitigation may also impact forestry practices; for example, logging and biofuel harvesting may increase to substitute for fossil-based products.

Changes in nutrient cycles and disturbance regimes will influence deadwood abundance and diversity in various ways. In boreal areas, forests are expected to grow either faster or slower depending on site-specific conditions (Marchand et al., 2019; Miquelajauregui et al., 2019), altering the input of deadwood and deadwood quality, e.g., fast growth versus slow growth. The decomposition rate is also expected to increase in locations where temperature is currently a limiting factor (Davidson & Janssens, 2006); however, the effect on the decomposition rate will largely depend on local habitat factors (Bradford et al., 2014).

Natural disturbances (fire, windthrow, and insect outbreak) are generally expected to accelerate in the future, albeit showing large geographic variability (Chap. 3); this may limit the long-term development of deadwood in some areas, as trees may not have sufficient time to grow large before another severe disturbance strikes (Kuuluvainen & Gauthier, 2018; Seidl et al., 2020). Moreover, the projected reduction of large deadwood because of climate change will be exacerbated by forest management policies having caused a skewed age-class distribution with a low proportion of old forest (Berglund & Kuuluvainen, 2021; Lamarre & Tremblay, 2021). Shorter disturbance return intervals may accelerate the development toward higher proportions of young stands and small-diameter deadwood.

These changes in deadwood abundance, type, and diversity affect deadwood-associated species in multiple manners. First, the quantity of insects that emerge from a burned tree is proportional to tree diameter (Saint-Germain et al., 2008), resulting in cascading effects on predators that depend on this resource, e.g., the Black-backed Woodpecker (*Picoides arcticus*) (Nappi & Drapeau, 2009; Nappi et al., 2010; Tremblay et al., 2020). These effects contribute to a projected decline of up to 92% in the potential productivity of the Black-backed Woodpecker under the worst-case climate forcing scenario (RCP8.5) (Tremblay et al., 2018). Second, a lower abundance of large trees related to an increased fire frequency would reduce the area of forests housing large standing or downed deadwood stems, which are typically associated with a high species diversity of bryophytes and lichens (Dittrich et al., 2014).

Climate change will also alter the distribution and phenology of wood-inhabiting species, affecting interactions and food chains. Higher temperatures and a longer growing season will affect insect phenology. Depending on the length of the growing season, the European spruce bark beetle (*Ips typographus*) can produce one to six generations per year, and the area prone to outbreaks of this species is expanding northward (Romashkin et al., 2020). Likewise, warmer winters in western North America have contributed to continuous outbreaks of the mountain pine beetle (*Dendroctonus ponderosae*) on lodgepole pine (*Pinus contorta*) and other pine species, turning the forests from carbon sinks into carbon sources (Kurz et al., 2008). Indirect consequences of climate change also include potential effects on insect-fungus interactions. For example, phenological mismatches (i.e., relevant species life stages no longer co-occur) may emerge between insects and fungi. Insect visits of fungal fruiting bodies, and thus spore dispersal, may be disrupted given that sporulation is generally determined by environmental cues other than insect emergence and flight. Similarly, controls on populations may be disrupted if predators and their prey no longer co-occur (Ekholm et al., 2020). Such phenological mismatches will add uncertainty to the current difficulty in predicting insect outbreaks, including significant uncertainties in terms of outbreak duration, intensity, and spatial variation (Biedermann et al., 2019; Boulanger et al., 2016).

6.7 Conclusions and Future Perspectives

Deadwood profiles, the frequencies and severity of natural disturbances, and management history vary across the boreal zone. Deadwood abundance and quality have decreased dramatically in many managed areas, especially in northern Europe, and deadwood-associated biodiversity has declined accordingly. Moreover, climate change will likely affect the formation and dynamics of deadwood to produce concomitant effects on deadwood-associated organisms and the intricate interactions and networks associated with this habitat.

A means of adapting to this massive challenge is implementing new silviculture approaches that mimic natural disturbance patterns and their effects on standing and fallen deadwood. The retention and maintenance of these biological legacies is a tenet of ecosystem-based management, which proposes a diversification of forestry practices (Gauthier et al., 2009). These approaches include longer rotations, retention forestry, continuous-cover silviculture, and enhanced patch retention of living and dead trees in clear-cuts (Felton et al., 2020). When included in forest landscape planning, such approaches are likely to attenuate habitat alteration and biodiversity loss associated with conventional forest management (Fig. 6.6; Berglund & Kuuluvainen, 2021; Drapeau et al., 2016). For deadwood management, this will necessarily require incorporating baseline data on deadwood dynamics and recruitment and the biodiversity it supports (Tremblay et al., 2015). Given that deadwood dynamics—including recruitment and decay processes—are tree species–specific and support taxonomic and functional diversity, live and deadwood retention strategies will have to be flexible in regard to the dominant tree species or forest cover types under management (Angers et al., 2011). Careful and rigorous planning in managed boreal forest landscapes is thus vital to account for a wide range of tree ages and sizes, species, and deadwood decay stages to ensure a steady supply of suitable substrates for biodiversity (Drapeau et al., 2009; Edworthy et al., 2018).

In severely impoverished areas, ecological restoration is needed to maintain deadwood-associated biodiversity. Prescribed burning, tree felling, pushing over, and girdling, together with green tree retention, have already proven successful (Hägglund & Hjältén, 2018; Hägglund et al., 2020), and future research must further evaluate the effects of such efforts on biodiversity (Fig. 6.6). It is possible to restore some deadwood qualities such as intermediate size classes and early decay stages in the short term. Recent reviews (Koivula & Vanha-Majamaa, 2020; Sandström et al., 2019) show that the artificial addition of deadwood supports a wide range of saproxylic species; however, the species composition on artificially created wood differs from communities in trees that died naturally. Some species require the active creation and conservation of their specific habitats, such as thick-diameter deadwood, slow-grown wood, resin-rich wood, wood from injured trees, and wood in forests with continuous canopy cover. For substrates and qualities that require a long time to regenerate (e.g., large logs of late-decay stage, wood from old trees), it is essential to conserve what is left, but also to implement artificial aging, for example by partial bark removal.

Conflicts between deadwood restoration and pest and fire management can occur because deadwood is often regarded as a source of pest species and wildfire fuel. Salvage logging may lead to ecological traps, i.e., species are attracted to a habitat that is too degraded for their survival (Hale & Swearer, 2016), for saproxylic organisms on burned areas, and pest control can reduce the recruitment of deadwood (Thorn et al., 2020a, 2020b). More research is needed to better balance these conflicting goals in an era of climate change.

Management practices that ensure the continuous availability of deadwood in managed boreal forests require monitoring and modeling. Modeling the potential of different forest types to produce and maintain deadwood could be a means forward,

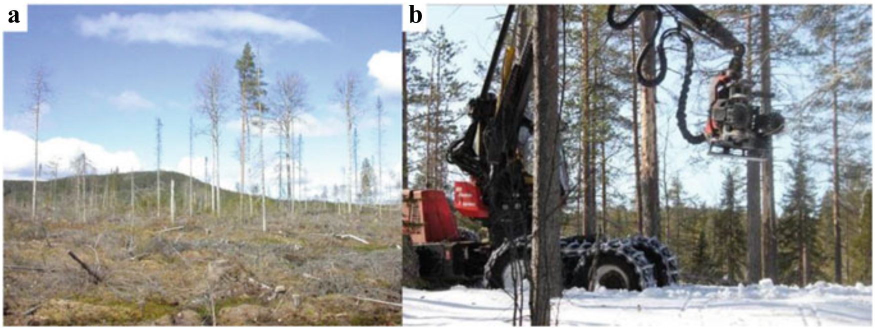


Fig. 6.6 In heavily managed landscapes, the restoration of deadwood may be necessary. Restoration examples include **a** created high stumps and retention trees at a clear-felling site and **b** the scouring of tree stems to reduce tree vitality. *Photo credits* **a** Therese Löfroth, **b** Joakim Hjältén

and accurate models are vital for reliable estimates of deadwood volume and production in both natural and managed stands (e.g., Mikkonen et al., 2020). To conclude, both forestry and climate change are interactive challenges for conserving the biodiversity of deadwood-associated species (Tremblay et al., 2018). Conservation and restoration efforts must be designed appropriately to provide a continuous supply of highly variable forms of deadwood.

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