Chapter 5
Living Trees and Biodiversity

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Abstract Living trees are fundamental for boreal forest biodiversity. They contribute to stand structural diversity, which determines the range of habitat niches available for forest-dwelling species. Specific characteristics of living trees, such as species, age, and presence of microhabitats, determine how species utilize trees for food, as nesting places, or as growing substrates. This chapter explores the associations between living trees and aboveground biodiversity, reviews the factors such as soil productivity, hydrological regime, stand successional stage, and forestry activities that influence the characteristics of living trees and stand structural diversity, and presents the consequences of current and future climate change on boreal biodiversity.

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5.1 Introduction

Living trees play a crucial role in supporting biodiversity and providing ecosystem functions in boreal forests. Numerous forest-dwelling species are directly dependent on living trees; for example, trees provide a substrate for epiphytic and saprotrophic species, which in boreal forests consist mainly of bryophytes, lichens, and fungi. Trees also provide shelter and nesting places for invertebrates, mammals, and birds. Trees are equally a fundamental part of forest food webs as their foliage, flowers, seeds, and bark are food sources for various species. Finally, living trees are crucial as they form the structure of forest stands, which in turn influences the number of different habitat niches available and, thus, biodiversity (Chase & Leibold, 2003).

This chapter describes the linkages between living trees and their role in developing stand structure in boreal forests and generating aboveground biodiversity. Most existing studies on these topics come from Europe (especially Fennoscandia) and North America, whereas less research has been conducted in Asian boreal forests. Although we aim to cover the entire boreal region, our main focus in this chapter will be on the regions from which a greater amount of knowledge is available. The discussion of stand structural diversity is limited to the features directly connected with living trees, such as tree species diversity, canopy structure, and tree-related microhabitats. We then explain the main natural factors that influence the structural diversity both at the tree and stand scales, such as climate, primary productivity, and stand succession. In addition, we describe anthropogenic disturbances and related changes, most importantly commercial rotation forestry, that shape the structural diversity of living trees and the associated biodiversity in the boreal region. Finally, we discuss the potential effects of future climate change.

5.2 Structural Diversity of Living Trees

The structural diversity of living trees (hereafter *structural diversity*) in a forest, as well as how it changes during forest succession, is an important driver of biodiversity. Structural diversity can be described as tree species richness, variability in tree age and size distribution, the occurrence of several canopy layers *vertical diversity*, and the presence of canopy gaps or denser patches of trees *horizontal diversity*, as well as smaller-scale variations, e.g., foliage density (Franklin & Van Pelt, 2004). Traditional successional models suggested that structural diversity was higher in old boreal forests, whereas young stands that originated naturally from a stand-replacing

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disturbance were more uniform in structure (e.g., Brassard & Chen, 2006). It is now clear, however, that in a variety of forest types, high diversity can be present at any age because of variable seedbed quality and the presence of legacy trees post-disturbance (Kuuluvainen, 2002; Lecomte et al., 2006; Martin et al., 2019). Furthermore, even when a classical succession sequence exists, the age at which structural diversification begins depends on growing conditions and differs among stand types. For example, in Canadian boreal forests, white spruce (*Picea glauca*) stands develop a high structural diversity after 160 years of age, whereas structural enrichment begins after only 80 years in balsam poplar (*Populus balsamifera*) stands (Timoney & Robinson, 1996).

In boreal forests, tree species richness is low compared with temperate or tropical regions (Esseen et al., 1997). Mid- and late-successional boreal forest stands are typically dominated by a few coniferous species; in western Europe, these dominant taxa are Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*), and in eastern Europe and Asia, they are Siberian and Yezo spruce (*Pinus obovata* and *P. jezoensis*, respectively), Siberian fir (*Abies sibirica*), Scots and Siberian pine (*Pinus sibirica*), and Siberian and Dahurian larch (*Larix sibirica* and *L. gmelinii*, respectively) (Shorohova et al., 2011). In North America, the dominant conifers are white and black spruce (*Picea glauca* and *P. mariana*, respectively) and tamarack/larch (*Larix laricina*). In central and eastern North America, balsam fir (*Abies balsamea*) and jack pine (*Pinus banksiana*) are also present, and in western North America, alpine fir (*Abies lasiocarpa*) and lodgepole pine (*Pinus contorta*) are significant components of the forest (Larsen, 1980). The most important broadleaf tree species throughout the boreal region are birches (*Betula* spp.) and aspens (*Populus* spp.). Broadleaf trees occur mainly in young stands or as an admixture in the older, conifer-dominated stands (e.g., Bergeron, 2000), although there are some exceptions, such as Erman's birch (*Betula ermanii*), which also forms stands in older successional stages in the Russian Far East.

Tree species richness is generally correlated with the other aspects of structural diversity (Juchheim et al., 2020). There is a functional feedback loop, where a horizontally diverse stand structure with canopy gaps and openings can promote the establishment of light-demanding tree species in mature stands and thus promote tree species richness (Brassard & Chen, 2006; Kuuluvainen, 1994). In turn, species-rich stands are usually structurally diverse, as tree species vary in size and physical construction. Moreover, other habitat qualities that influence forest-dwelling species, such as soil conditions and water availability, are also affected by tree species and may therefore be more heterogeneous in mixed stands than in monospecific ones (Barbier et al., 2008).

Furthermore, tree species richness is important for the diversity of forest-dwelling species, as many are associated with a particular tree species or tree species group. Reasons for these associations are various; for example, tree species–specific bark characteristics are important for epiphytes (Ellis, 2012) and bark-dwelling invertebrates (Nicolai, 1986), and the chemistry and nutritional qualities of wood, foliage, and seeds affect the species that use these resources as a food source. The strength of the associations varies from a preference to strict specialization, but in general,

species that consume foliage or other soft tissues of trees tend to be stricter in their specialization than species utilizing bark or wood (Sundberg et al., 2019). For most boreal forest trees, the total number of associated species is unknown. An exception is a recent report by Sundberg et al. (2019), which listed the number of associated species for all Swedish tree species. According to the report, the most common indigenous tree species, Norway spruce, was host to the highest number (1,100) of associated species, but note that this number includes species on both living trees and deadwood. However, less common tree species can also be important for biodiversity if they provide specific, valuable habitats for forest-dwelling species. For example, many species throughout the boreal region, particularly epiphytes and cavity-nesting birds, are associated with aspens, which provide these taxa more favorable habitats than the more common coniferous trees (e.g., Boudreault et al., 2000; Cadieux & Drapeau, 2017; Kivinen et al., 2020).

In addition to the specific tree species, the habitat value of a single tree is affected by its age and size; old and large trees are particularly important for biodiversity. Although tree age and size are often correlated, there are exceptions; on low-productivity sites, in particular, old trees can remain small but have a high biodiversity value (Cecile et al., 2013). With aging, trees develop specific characteristics and microhabitats, such as different bark structures or holes and cavities, that are important for various species (Michel & Winter, 2009); for example, rough bark typical of old trees hosts more arthropod species than smooth bark associated with younger trees (Nicolai, 1986), and certain epiphytic lichens are specifically associated with thick bark or deep bark crevices (Ranius et al., 2008). Table 5.1 presents further examples of important tree-scale microhabitats. In addition, old trees are valuable because they have been available for colonization for a longer time than young trees, which increases the chances for the establishment of dispersal-limited sessile biota (Ellis, 2012). Tree size, in turn, can be important because larger trees provide more habitat space and, in some cases, improved habitat quality; for example, many cavity-excavating birds prefer larger-diameter trees that are more stable and, because of thicker cavity walls, offer safer nesting places (Remm et al., 2006).

5.3 Factors Influencing the Structural Diversity of Living Trees

Natural key factors determining the structural diversity of living trees in unmanaged boreal forests are successional stage, disturbance history, and site productivity (Liira & Kohv, 2010; Moussaoui et al., 2016). The natural disturbance dynamics and stand successional sequence in boreal forests are explained elsewhere in this book (Chap. 3); therefore, we focus here more on the effects of productivity and its interaction with succession. For forestry purposes, productivity is usually defined as the ability to produce wood biomass per unit area over a given time (Bontemps &

Table 5.1 Important microhabitats occurring on living trees in boreal forests, with examples of associated species

Microhabitat	Occurrence and examples of species utilizing the microhabitat
Tree cavities and rot holes	Cavities are created by excavating birds (woodpeckers, in the boreal region) or, more rarely, by wood-decaying fungi. Woodpecker-excavated cavities are more prevalent on large broadleaf trees, and decay-induced cavities are more common on old trees (Andersson et al., 2018; Parsons et al., 2003). Cavities provide habitats for many insects and other invertebrates and nesting and hiding places for various birds and some mammals, such as bats (Esseen et al., 1997). Humid and shaded hollows are also colonized by some lichens, especially calicioids (Tibell, 1999)
Broken or irregular treetops	Broken or irregular tops of large trees provide nesting places for large birds of prey, e.g., Golden Eagle (*Aquila chrysaetos*) and Osprey (*Pandion haliaetus*) (Kuuluvainen, 2002)
Dead branches and treetops	Dead branches of living trees are an abundant microhabitat: they can constitute half of the total deadwood surface area in managed conifer-dominated boreal forests (Svensson et al., 2014). They serve as a substrate for saproxylic insects, fungi, and lichens (Larrieu et al., 2018), including rare species, e.g., the lichen *Erioderma pedicellatum* on dead branches of old spruces in the Russian Far East, Alaska, and eastern North America (Fig. 5.3c; Lauriault & Wiersma, 2020; Tagirdzhanova et al., 2019)
Bark pockets	Partially loose pieces of bark form a pocket between the bark and the tree trunk. These pockets are essential for many invertebrates and, if sufficiently large, can also be used as nesting places by some birds (e.g., treecreepers, Certhidae) or as day roosts by bats (Winter & Möller, 2008)
Cracks, scars, and bark loss	Cracks on the trunk provide nesting and hiding places for invertebrates, e.g., spiders and flat bugs; larger ones can also serve for birds and bats (Michel & Winter, 2009). Cracks and scars also host some crustose lichens and various fungi and microorganisms (Roll-Hansen and Roll-Hansen, 1980). Exposed wood is used by saproxylic invertebrates, fungi, and lichens (Larrieu et al., 2018)
Fire scars	Charred, exposed wood resulting from earlier forest fires occurs on fire-resistant conifers (e.g., *Pinus sylvestris*) and usually on larger trees, which are more likely to survive a fire. The fire scars serve as a substrate for species specialized on charred wood, e.g., the lichens *Carbonicola anthracophila*, *C. myrmecina*, and *Hertelidea botryosa* (Fig. 5.3d; Andersson et al., 2009; Lõhmus & Kruustük, 2010)
Resin and sap flows	Resinoses can host specialized fungi, such as *Chaenothecopsis* spp. (Titov, 2006) or the discomycetes *Sarea resinae* and *S. difformis* (Beimforde et al., 2020). Sap flows provide a food source, e.g., for several beetle species

(continued)

Table 5.1 (continued)

Microhabitat	Occurrence and examples of species utilizing the microhabitat
Cankers and burls	Cankers and burls provide substrates for epiphytic bryophytes and lichens. They are also used by certain Lepidoptera (Larrieu et al., 2018)
Witch brooms	Brooms are dense branch growths caused by pathogenic fungi, e.g., *Chrysomyxa arctostaphyli* on white and black spruce (Paragi, 2010). They provide nest sites and food sources for arthropods, birds, and small mammals, such as red squirrels (*Tamiasciurus hudsonicus*) (Tinnin et al., 1982)
Fungal fruiting bodies	Fungal fruiting bodies are used as habitat or food sources by various insects, such as beetles (Jonsell et al., 2001). They also host other fungi, e.g., calicioid fungi, such as *Phaeocalicium polyporaeum* (Titov, 2006), and lichens, e.g., *Bacidina* spp. and *Chaenotheca* spp.
Epiphytes	Epiphytic lichens and bryophytes provide habitats for various invertebrates, such as spiders, mites, and tardigrades (Ellis, 2012) and host lichenicolous fungi and epibryophytic lichens, e.g., *Mycobilimbia* spp.

Bouriaud, 2014) and combines the effects of soil conditions—nutrient availability and hydrology—and regional temperature (Fig. 5.1). The latter is an important factor in the boreal forest because in high-latitude or high-altitude regions, low temperatures can restrict the rate of cell division in trees (Rossi et al., 2007) and lead to slower tree growth. Another significant factor is paludification, i.e., the accumulation of soil organic matter, which can reduce productivity, especially in old boreal stands. In eastern Canada, for example, paludification can decrease black spruce productivity by 50% to 80%, particularly during the first centuries after a fire (Simard et al., 2007).

In general, the structural diversity of living trees increases with soil productivity in natural conditions (e.g., Boucher et al., 2006; Liira & Kohv, 2010). At higher site productivity, total stand volume is larger, and greater numbers of tree species and larger ranges of diameters and heights can co-occur. For example, in Estonian hemiboreal forests, high-productivity spruce–deciduous mixed stands have twice the stand volume, a significantly higher tree species richness, and a greater number of tree diameter classes than low-productivity Scots pine stands (Liira & Kohv, 2010; Lõhmus, 2004). Furthermore, the speed of structural development depends on productivity; trees grow faster on fertile soils, which accelerates the development toward stand complexity (Boucher et al., 2006; Larson et al., 2008). In boreal Canada, Boucher et al. (2006) found the tree size diversity of >200-year-old low-productivity black spruce stands to be low, whereas productive black spruce stands had an uneven-sized structure at a younger age. Productivity also affects the recruitment rate of new tree species, particularly for shade-tolerant coniferous species. The recruitment of these species occurs faster in more productive sites and may not happen at all at low-productivity sites (Boucher et al., 2006; Larson et al., 2008).
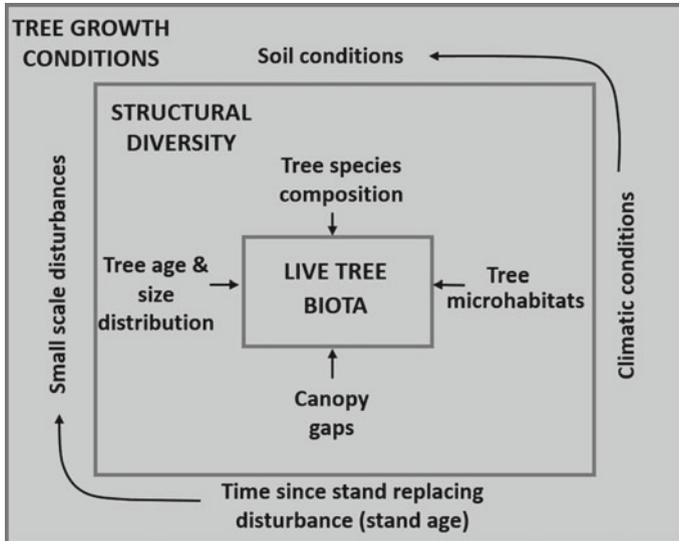
Fig. 5.1 Conceptual scheme of stand-scale predictors for the diversity of tree-dwelling biota. Some growth conditions are related to each other; all growth conditions influence the various elements of structural diversity, which in turn determine the live-tree biota

The occurrence of large or old trees is primarily determined by stand age, although large trees are also found more frequently in more productive sites. Because many tree-scale microhabitats develop with increasing age and decreasing tree vitality, their occurrence is generally correlated with that of old trees; however, various processes influence the dynamics of microhabitat development and loss (Fig. 5.2).

In addition to the processes listed above, the structural diversity of living trees and the associated biodiversity are subject to human-induced changes, particularly forest management. Management effects are often greatest in the most productive and economically valuable stand types (Martin et al., 2020). The effects vary depending on the applied practices, but typically, management simplifies the structural diversity of living trees and decreases habitat diversity.

In particular, intensely managed stands, i.e., clear-cut, reinitiated through planting, and thinned several times before final harvest, have a uniform structure lacking the multiple canopy layers, gaps, and other small-scale variations typical of natural stands (Cyr et al., 2009; Esseen et al., 1997). Because clear-cutting targets primarily old stands, a rejuvenation of the forest landscape has occurred throughout the boreal region (Bergeron et al., 2006). This rejuvenation is due to the short rotation periods used in even-aged forestry (roughly 70–120 years for conifer stands). Therefore, the number of large and old trees, and consequently the number of associated species, is low in production forests (Linder & Östlund, 1998). Even shorter rotation periods may be adopted in the future as the risk of pest and storm damage in older stands
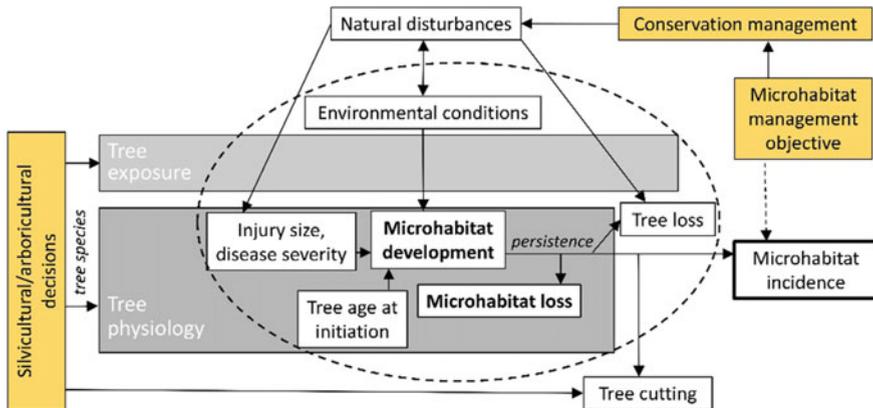
Fig. 5.2 Factors and processes contributing to the dynamics of tree-scale microhabitats. The rates of microhabitat development and loss determine the frequency of their occurrence; these processes are, in turn, influenced by tree species and physiology, environmental conditions, and disturbances, as well as forest management. Reprinted from Kõrkjas et al. (2021) with permission from Elsevier

is expected to increase because of climate change (Felton et al., 2016; Gauthier et al., 2014). Furthermore, the frequency and severity of natural disturbances such as fires, windthrow, and insect outbreaks are predicted to increase with climate change (e.g., Seidl et al., 2020). These enhanced disturbances may further decrease the proportion of old forests, especially if the frequency and intensity of salvage logging also increase (Lindenmayer et al., 2008).

Management also shapes tree species diversity because species of higher economic value are promoted by planting and thinning. In Fennoscandia, this has led to a decrease in broadleaf and mixed stands and increased conifer stands, with negative consequences for the associated biodiversity (Östlund et al., 1997). The planting of non-native or hybrid trees, such as lodgepole pine in Fennoscandia (Elfving et al., 2001), can have even more drastic effects on biodiversity because stands of non-native trees often host different communities of associated species than native stands (Bäcklund et al., 2016; Roberge & Stenbacka, 2014). The planting of non-native trees is relatively rare in the boreal region but may become more common in the future if non-native trees are deemed more profitable under a changing climate or more resilient against new pests and pathogens that will colonize the boreal region as the climate warms (Felton et al., 2016).

Climate change–related risks are also likely to affect the management of native trees. Broadleaf trees, for example, may be promoted as they are expected to be less susceptible to many climate-related risks. This scenario could have positive effects on biodiversity in regions where the number of broadleaf trees has been reduced (Felton et al., 2016). A warmer climate can also result in hemiboreal and temperate tree species migrating northward, affecting the distribution of native boreal trees (Gauthier et al., 2015).

5.4 Living Trees and the Diversity of Forest-Dwelling Species

In the previous sections, we provided an overview of how the structural diversity of living trees can affect boreal forest–dwelling species. The remainder of the chapter will illustrate these processes in more detail by presenting three groups of forest-dwelling organisms having different relationships with living trees: (1) epiphytic lichens and bryophytes, which depend on living trees as a substrate; (2) forest-dwelling birds, which utilize trees for foraging and nesting places; and (3) understory plants and epigeic lichens, which are influenced indirectly by living trees through stand microclimate, for example.

5.4.1 Epiphytic Lichens and Bryophytes

In most parts of the boreal region, epiphyte communities are formed solely by lichens and bryophytes; ferns as epiphytes are rare and occur only locally, e.g., in Norwegian boreal and boreonemoral rainforests (DellaSala et al., 2011). Lichens tend to grow on the whole tree, whereas bryophytes mostly form wefts, mats, tufts, or pendants on the lower parts of tree trunks and branches (Marmor et al., 2013; Tarasova et al., 2017). Although epiphyte biomass in boreal forests is relatively modest compared with tree foliar biomass (Botting et al., 2008), epiphytes contribute to nutrient and mineral cycling (e.g., Botting et al., 2008; Knops et al., 1991), participate in forest wood webs (e.g., Pettersson et al., 1995), and provide valuable nesting material for birds and mammals (Hayward & Rosentreter, 1994; Wesołowski & Wierzcholska, 2018).

In general, the epiphyte diversity in boreal Europe and eastern Canada is relatively well known and rich (>500 species), whereas fewer studies have examined other Canadian regions and northern Asia. Both lichens and bryophytes include obligate and facultative epiphyte species. Among macrolichens, pendulous taxa of the genera *Alectoria*, *Bryoria*, *Evernia*, *Ramalina*, and *Usnea* dominate on conifer branches (Fig. 5.3a; Esseen et al., 1997). Diverse assemblages of crustose lichens, which are often host-tree specific, inhabit both smooth and coarse bark of tree trunks (e.g., Androsova et al., 2018; Hyvärinen et al., 1992; McMullin et al., 2008). Examples of obligate epiphytic bryophytes include the mosses *Orthotrichum obtusifolium* and *Pylaisiella polyantha* and the liverworts *Frullania* spp., which all grow on aspens in the Canadian boreal forest. Tree bases and exposed roots of living trees are inhabited mainly by facultative epiphytes, e.g., *Ptilidium pulcherrimum* and *Pleurozium schreberi*, which often form a special "bryophyte sock" at the base of the tree. The bryophyte sock can house multiple species, and although most of these species can also grow on other substrates, tree bases are often the most abundant and, therefore, the most critical microhabitat.
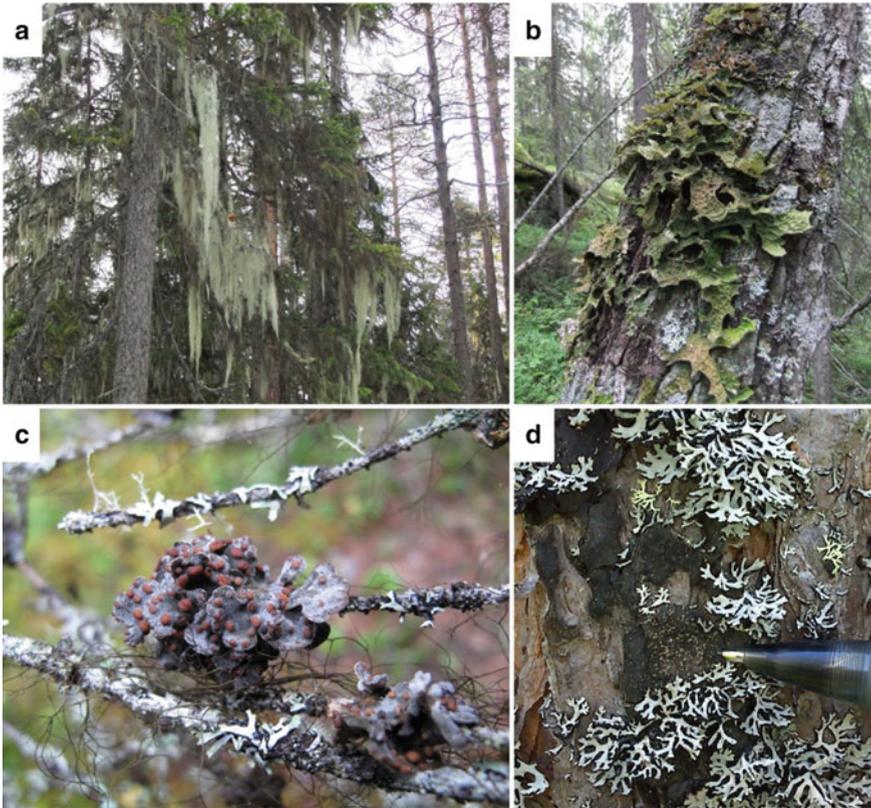
Fig. 5.3 **a** Pendulous lichens, e.g., witch's hair lichen *Alectoria sarmentosa*, dominate on conifer branches throughout the boreal region. Broadleaf trees host many specialized lichen species, e.g., **b** lungwort lichen *Lobaria pulmonaria*, here on *Salix caprea*. Certain lichen species require specific microhabitats; **c** the globally threatened boreal felt lichen *Erioderma pedicellatum* occurs on dead spruce branches, whereas **d** the small clam lichen *Carbonicola anthracophila* colonizes only burned bark or wood, here accompanied by a generalist tube lichen *Hypogymnia physodes*. *Photo credits* **a b** Aino Hämäläinen, **c** Dmitry Himelbrant, and **d** Piret Lõhmus

The quality of living trees as epiphyte habitat is determined by tree characteristics that affect the availability of light, water, and nutrients. Bark structure and chemistry are particularly important in this respect (Brodo, 1973; Gustafsson & Eriksson, 1995). Rough bark with furrows and crevices can provide a large variety of microhabitats and favors specific assemblages of epiphytes such as calicioid lichens (*pin lichens*) (Holien, 1996). Furthermore, rough bark generally has better water holding capacity, which increases the water supply for epiphytes and favors their establishment (Snäll et al., 2004). Another critical factor is bark stability; unstable, easily exfoliating bark is an unfavorable substrate for most epiphytes. In addition to the structural factors, bark pH has a strong effect on epiphytes, as most species have a specific pH range that they can tolerate (Bates, 1992; Brodo, 1973). Bark pH can influence, for

example, the availability of nutrients (Bates, 1992), the germination of bryophyte spores (Wiklund & Rydin, 2004), or the competition for space between micro- and macrolichens (Hyvärinen et al., 1992).

Bark characteristics differ among tree species, which leads to distinct epiphyte assemblages (e.g., Kuusinen, 1996). Most epiphytic species show at least some degree of preference for certain host tree species (Ellis, 2012; Kuusinen, 1996), although the association with tree species is often rather loose. Tree species differ in the total number of epiphytic species and the number of specialized species they host. In European boreal forests, for example, *Populus tremula* and *Salix caprea* are considered particularly important for epiphyte diversity, as they have a high number of specialist epiphytes (Kuusinen, 1996). Similarly, in North America, *Populus tremuloides* hosts a high epiphyte richness (Bartels & Chen, 2015). Bark characteristics are further affected by tree age; the bark of older trees is usually thicker and rougher than that of young trees. Concurrently, epiphytic communities change as the trees age. Although both young and old trees have associated epiphyte species, species richness is usually highest on old trees (e.g., Lie et al., 2009). In addition to the specific bark qualities, a longer colonization time can contribute to the high diversity on old trees (Lie et al., 2009).

Rotation forestry generally negatively affects epiphyte diversity, as it decreases the overall diversity of live-tree habitats and the amount of important substrates, such as old deciduous trees. Climate change is also expected to affect boreal forest epiphytes. Changes in temperature and precipitation can directly affect epiphyte growth and survival (e.g., Smith et al., 2018). However, the effects vary among species (Löbel et al., 2018) and forest types (Barbé et al., 2020). Furthermore, indirect effects through changes in tree species composition, disturbance regimes, or forestry practices are also likely. For example, climate change may lead to an intensification of forestry through shorter rotations or increased demand for biofuels (Felton et al., 2016), which can have negative impacts, particularly for epiphytes dependent on old-growth forest characteristics. Together, these effects and interactions can change epiphyte assemblages in complex and unexpected ways (Smith et al., 2018).

5.4.2 Forest Birds

Birds have developed many ecological adaptations to forest environments that allow them to utilize a very broad spectrum of habitats (Villard & Foppen, 2018). Moreover, because of their high mobility, birds as a group are capable of rapid responses to habitat changes in forest environments (Wesołowski & Fuller, 2012). Their ability to fly allows them to fully explore the three-dimensionality of forests created by trees, leading to an exceptionally high diversity of bird species assemblages in forests (Flade, 1994; James & Wamer, 1982; MacArthur & MacArthur, 1961).

Living trees provide birds with food, nesting sites, and shelter but are also used as a physical structure for several other activities, including perching, singing, and courting. Some boreal birds consume different vegetative parts of trees. For example,

the Eurasian Western Capercaillie (*Tetrao urogallus*) and Spruce Grouse (*Falcipennis canadensis*, Fig. 5.4) in North America are highly dependent on the needles of coniferous trees during winter. The winter diet of Hazel Grouse in Eurasia consists almost exclusively of catkins, buds, and twigs of alder, birch, and other broadleaf trees. The Great Spotted Woodpecker (*Dendrocopos major*), Eurasian Siskin (*Spinus spinus*), and several crossbill species (*Loxia* spp.) with a circumboreal distribution are specialized in eating seeds from mostly coniferous trees, and waxwings (*Bombycilla* spp.) are dependent on berries provided by trees. Furthermore, invertebrates on living trees are a key food source for many bird species. The rapidly increasing biomass of herbivorous and predatory invertebrates in the spring secures nourishment for most arboreal passerines, both resident and migratory, and provides necessary proteins for the development of their chicks. In addition, saproxylic invertebrates occurring in living trees are an important food of forest birds, especially woodpeckers (Picidae), nuthatches (Sittidae), treecreepers (Certhidae), and tits (Paridae).

Many forest birds use trees as nesting sites. This behavior encompasses common passerines like the Common Chaffinch (*Fringilla coelebs*) in Eurasia or the Least Flycatcher (*Empidonax minimus*) in North America that usually build open nests in tree canopies; however, it also includes large birds of prey such as Osprey (*Pandion haliaetus*), which often build their nests on the tops of living trees. Living trees and snags are particularly important for cavity-nesting birds, including primary excavators, i.e., woodpeckers, and species using existing cavities created by woodpeckers and decay. In boreal forests, decay-formed cavities are rare, and therefore most cavities are made by woodpeckers (Andersson et al., 2018; Cockle et al., 2011). Thus, since several dozen bird species in boreal forests are obligate secondary cavity nesters, woodpeckers can be considered keystone species. For most forest birds, living trees and shrubs also provide shelter for both day- and nighttime roosting on branches, underneath the low branches or in cavities. For example, in a Norwegian study, Finne et al. (2000) found that 90% of daytime roosting sites of capercaillie were located underneath the low branches of Norway spruce trees.

Fig. 5.4 Male Spruce Grouse (*Falcipennis canadensis*) on jack pine (*Pinus banksiana*); jack pine needles are a key food item for this species. *Photo credit* Marjorie Wilson

The intersection of the species-habitat dependencies discussed above, interspecific interactions, the regional species pool, and landscape context leads to a highly variable bird assemblage for a particular boreal forest stand. The post-disturbance successional gradient will generate a range of bird assemblages from one of open or early-succession species (often generalist and migratory species) to specialized residents dependent on old-growth stands, generally characterized by a high structural diversity (Drapeau et al., 2000; Helle & Mönkkönen, 1986; Imbeau et al., 1999; Jansson & Andrén, 2003). Structural differences, including the dominance of particular tree species, are greater and have a more marked effect on differentiating bird assemblages in the Nearctic than in the western Palearctic; this is possibly explained by the lower level of specialization in the latter (Mönkkönen, 1994).

A greater number of native tree species and a longer time since a stand-replacing disturbance generate a higher diversity of bird assemblages. In particular, the presence of broadleaf trees heightens bird species diversity, especially in boreal Europe (Jansson & Andrén, 2003). The occurrence of large and old trees provides nesting and foraging opportunities for many species, including specialized cavity nesters and large birds of prey. In addition, multilayered stands have richer bird assemblages than stands with even-aged woody vegetation (e.g., Klein et al., 2020). Thus, from a conservation and management perspective, promoting these features of structural diversity can support a higher diversity of forest bird assemblages. For example, green tree retention applied during the logging of boreal forests may positively affect several species, but it can only partially counteract the loss of mature forest (Basile et al., 2019; Price et al., 2020; Söderström, 2009; Venier et al., 2015). There is a need for more research on how different natural processes interact with human actions across landscapes and in the context of climate change (Mikusiński et al., 2018). A recent study in the boreal forests of Alberta (Cadieux et al., 2020) predicted declines in bird species associated with older coniferous forests because of climate change, and this process is expected to be accelerated by forestry. Similarly, in Finnish boreal forests, habitat alteration due to forestry compounds the negative impact of climate change on bird assemblages (Virkkala, 2016). To counteract such adverse developments, Stralberg et al. (2019) proposed large-scale recovery plans and adaptive forest management, the designation of critical habitat, and land protection. These measures are based mainly on the appropriate management of living trees at stand and landscape levels.

5.4.3   Plants and Lichens in Forest Understories

Despite not directly growing on living trees, vascular plants, bryophytes, and lichens in boreal forest understories are nevertheless influenced by the structural diversity that governs the microclimate and nutrient availability on the forest floor. In boreal forests, particularly in older conifer-dominated stands, epigeic bryophytes and lichens prevail in the forest understory rather than vascular plants (Bergeron & Fenton, 2012; Esseen et al., 1997). Bryophytes dominate the forest floor in mesic sites, whereas lichens are

more common in drier sites and in the most northern parts of the boreal region (Esseen et al., 1997). Vascular plants are more abundant in younger stands and nutrient-rich broadleaf stands.

Canopy tree species composition is an important determinant of understory diversity, and stands of different tree species typically host distinct understory assemblages. Canopy closure and, concurrently, light availability can differ notably among tree species, depending on the size and arrangement of leaves (Barbier et al., 2008). In eastern Canadian boreal forests, for example, the highest light levels are observed in *Betula* stands; the light levels then decrease in the order of *Populus*, *Pinus*, *Picea*, *Abies*, and *Thuja* stands (Messier et al., 1998). Furthermore, tree species composition affects water availability in the understory, as the amount of throughfall and water absorbed by tree roots varies among tree species. For example, throughfall is generally higher in broadleaf stands than coniferous ones and in stands of early-successional rather than late-successional tree species (Barbier et al., 2008). In addition, nutrient availability is generally greater in broadleaf and mixed stands than in coniferous stands because of the presence of nutrient-rich leaf litter (Hart & Chen, 2006). Therefore, vascular plants that benefit from higher levels of light and nutrients are usually more diverse and abundant in broadleaf and mixed stands. Bryophytes and lichens, in turn, suffer from increased competition from vascular plants and are affected by the leaf litter of broadleaf trees, which can inhibit their establishment and growth (Bartels & Chen, 2013). The cover and diversity of bryophytes and lichens are therefore generally higher in conifer-dominated stands.

In addition to tree species composition, microclimate on the forest floor is influenced by variations in canopy openness. Large canopy gaps and other openings that lead to increased light levels positively affect vascular plants and some species of lichen, e.g., *Cladonia* spp. (Boudreault et al., 2013). Bryophytes, which are generally shade tolerant, do not benefit from increased light; instead, their cover decreases in large canopy gaps because of intensified competition with vascular plants. However, since bryophytes require high moisture levels, they can benefit from small canopy gaps, which do not have notably higher light levels but rather greater water availability owing to higher throughfall and the lower transpiration by live trees (Hart & Chen, 2006; Muscolo et al., 2014). In addition, small gaps formed by tree uprooting provide an important microhabitat for bryophytes (e.g., *Schistostega pennata*) and lichens (e.g., *Chaenotheca furfuracea*) in the form of root plates and bare mineral soil (Jonsson & Esseen, 1990; Lõhmus et al., 2010).

The relationships described above make epigeic species vulnerable to changes in canopy closure and tree species composition because of, for example, forest management. In Sweden, managed forests have become denser, which has led to an increased proportion of shade-adapted plants in the understory (Hedwall et al., 2019). In North America, however, most studies have shown that the vascular plant flora of boreal forests (MacDonald et al., 2015), and to some degree epigeic lichens (Lafleur et al., 2016), are resilient in the face of most forest management regimes. Bryophytes, however, are more vulnerable (MacDonald et al., 2015; Paquette et al., 2016). Climate change is expected to affect understory species directly through altered temperature and precipitation and decreased snow cover. The latter, accompanied by frost damage,

is predicted to be one of the most significant climate change–related factors influencing boreal forest understories and could lead to altered species composition and notable decreases in the abundance of dominant species (e.g., Kreyling et al., 2012).

5.5 Conclusions

Live trees are essential for the biodiversity of boreal forests. Although forest-dwelling species groups have different relationships to live trees and therefore require different tree habitats or characteristics, the diversity of all groups generally increases with a greater structural diversity of live trees. Rotation forestry simplifies this diversity and negatively impacts the various species that depend on live trees. In the past decades, however, different restoration and management methods, such as retention harvest, have been developed to mitigate these negative impacts. Promoting habitat diversity at both the tree and stand scales (e.g., retaining trees of various species, ages, and containing different microhabitats) by creating a variable canopy structure or applying continuous cover forestry can help maintain the diversity of forest-dwelling species in managed stands. In turn, higher biodiversity can increase forest ecosystem resilience to climate change (Drever et al., 2006; Loreau, 2000).

Climate change will affect living trees and the associated biodiversity through various direct (e.g., higher disturbance severity and frequency) and indirect (e.g., changes in forest management) pathways. Although the responses of boreal tree species to climate change have been examined in various studies (e.g., Boulanger et al., 2017; Peng et al., 2011), the reaction of other forest-dwelling aboveground organism groups is less well known. With various complex effects and interactions, the overall changes in communities (e.g., species abundance, diversity, and distribution) are difficult to predict (but see Villén-Peréz et al., 2020). Finally, if forest management practices are modified because of climate change adaptation or mitigation (e.g., an increased proportion of broadleaf trees), the effects on forest-dwelling species should be assessed and compensated where necessary.

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