Chapter 7
Embracing the Complexity and the Richness of Boreal Old-Growth Forests: A Further Step Toward Their Ecosystem Management

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Abstract Boreal old-growth forests are specific and often undervalued ecosystems, as they present few of the structural attributes that usually define old forests in the collective culture. Yet, these ecosystems are characterized by exceptional naturalness, integrity, complexity, resilience, as well as structural and functional diversity. They therefore serve as biodiversity hot spots and provide crucial ecosystem services. However, these forests are under significant threat from human activities, causing a rapid and large-scale reduction in their surface area and integrity. The multiple values associated with boreal old-growth forests should be therefore better acknowledged and understood to ensure the sustainable management of boreal landscapes.

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7.1 The Old-Growth Forest Concept: A General Overview

Forests considered as "natural" have an important place in our collective consciousness for cultural, ethical, spiritual, artistic, and aesthetic reasons (Frelich & Reich, 2003; Kimmins, 2003; Pesklevits et al., 2011; Satterfield, 2002). Interest in these forests has also grown continuously during the twentieth century as a source of inspiration for establishing sustainable management strategies (Puettmann et al., 2009). Theories of how to maintain forest biodiversity and ecosystem services include forest management based on natural disturbance dynamics (Gauthier et al., 2009) and managed stands containing forest-specific structural elements that are considered as natural references (Bauhus et al., 2009; Halme et al., 2013).

Many terms considered synonymous with *natural forest* have long been used, e.g., primary, primeval, pristine, old-growth, virgin, mature, natural, overmature, original, or intact forest (Wirth et al., 2009); however, each of these terms represents a different ecological concept, and further clarification of the terminology has gradually taken place over the twentieth century (Frelich & Reich, 2003; Wirth et al., 2009). The concept of *old-growth forest* was one of the most important concepts to attract the attention of the scientific community, managers, and the general public, as it relates to many important current issues related to forests: (1) intrinsic value (e.g., academic, cultural, spiritual), (2) exigencies of "closer to nature" management, conservation, and restoration strategies, and (3) their role in addressing the challenges of climate change and biodiversity loss (Frelich & Reich, 2003; Kuuluvainen et al., 2017; Pesklevits et al., 2011; Wirth et al., 2009).

Defining what an old-growth forest is, and by extension what is not, is nevertheless particularly complex. Many definitions have been proposed over time, some of which are now debated. These definitions can be grouped into seven main classes (Frelich & Reich, 2003; Issekutz, 2020; Kimmins, 2003; Kneeshaw & Gauthier, 2003; Wirth et al., 2009):

Structural a stand that has reached a certain age; the presence of many old trees with large diameters; a high volume of deadwood of all decay classes; a high vertical and horizontal complexity; the presence of trees of all ages.

Dynamic: a stand under gap dynamics; the stand has reached the final stage of succession; a stand age greater than the return interval of primary disturbances, i.e., disturbances of high severity that reinitiate forest succession; the age of trees exceeding their average life expectancy.

Scale: a continuous forest having a small human footprint over a sufficiently large area (forest track, forest massif).

Functional or *biogeochemical*: the net primary productivity is equal to or less than zero; the *climax* concept; a trophic network reaching a given threshold of complexity; the presence of all stages of deadwood degradation.

Economic: a forest that has exceeded the optimum age for harvesting; the volume of commercial timber has reached a peak and is now stable or declining.

Aesthetic: an impressive forest; invites humility and spirituality.

Other definitions: undisturbed by humans; covers a minimum area.

Each of these definitions has its specific limitations and therefore represents a different view of what can be considered *old growth*. The main criticisms generally relate to their arbitrary nature, the difficulty of integrating some of these thresholds into daily management, and the existence of counterexamples that limit their universality (Kimmins, 2003; Pesklevits et al., 2011; Wirth et al., 2009). Other definitions, such as the concept of climax defined by Odum (1969), are now generally considered too reductionist and consequently ecologically irrelevant (Wirth & Lichstein, 2009). Similarly, the degree of human footprint in a forest is more a question of naturalness rather than *old-growthness*, even if the two concepts are often linked (Frelich & Reich, 2003). Old-growth forests are not necessarily *primary*, i.e., a forest of high naturalness almost undisturbed by anthropogenic activities, and, conversely, not all primary forests are old growth. For example, a primary forest that recently burned due to a wildfire caused by lightning can still be considered primary after the disturbance, as this disturbance does not influence its naturalness. Conversely, a previously managed stand that has returned to an old-growth state is not a primary forest because of its history, although its abandonment progressively increased its naturalness. From a more philosophical perspective, the very concept of old-growth forest is arbitrary, artificially classifying forest ecosystems (Pesklevits et al., 2011). Therefore, it is now accepted that a universal definition is neither possible nor necessarily desirable. On the contrary, definitions of old-growth forests need to be adapted to the ecological context of the region under study (Frelich & Reich, 2003; Pesklevits et al., 2011). There may therefore be a diversity of definitions restricted to a local scale. Hunter and White (1997) offer a less precise but more general definition that is commonly used: an old-growth forest is relatively old and minimally disturbed by natural and anthropogenic disturbances.

Moreover, the term *old growth* actually describes a wide diversity of forests in terms of structure, tree species composition, and disturbance history, even within a restricted area (Martin et al., 2018; Meigs et al., 2017; Shorohova & Kapitsa, 2015). Combining all these attributes influences habitat characteristics markedly at the local scale (Kozák et al., 2021). It also underscores the importance of the spatial extent and continuity of old-growth forests, as small and insulated old-growth stands are not a surrogate for large old-growth areas (Moussaoui et al., 2016; Schmiegelow & Mönkkönen, 2002). For these reasons, it is crucial to consider that the forests designated as old growth often contain a diversity of structures and composition. Oliver and Larson (1996) thus proposed to distinguish *true* old-growth forests—all the trees of the first cohort have died and have been replaced by new shade-tolerant trees—from *transition* old-growth forests in which some individuals of the first cohort are still present. This approach still has its limitations, notably its relatively arbitrary nature; however, it distinguishes between different types of old-growth forest. Nevertheless, the concept of transition or true old-growth forests can group forests with very different structures and compositions (Martin et al., 2018). We therefore propose a hierarchical definition of old-growth forests, highlighting the complexity and limits of this concept while making it adaptable to different operational contexts (Table 7.1). In this chapter, we will use the general definition of old-growth forests as "relatively old and little disturbed by natural and anthropogenic disturbances" because of the great diversity of contexts covered.

The importance of old-growth forests as biodiversity hot spots is widely recognized. They contain many structural features that are absent or rare in younger and managed stands, such as deadwood of various sizes and decay stages, large trees, and high structural complexity (Franklin et al., 2002; Wirth et al., 2009). The diversity of old-growth forest attributes and structures within the same forest tract is also an essential factor in explaining their importance for biodiversity, as they provide a wide range of habitats (De Grandpré et al., 2018; Schowalter, 2017). The high degree of forest continuity (i.e., the length of time an area has been continuously wooded) that defines old-growth forests is also vital for low-dispersal and disturbance-sensitive species that can require decades or centuries to recolonize a stand after a severe

Table 7.1 Proposition for a hierarchical definition of old-growth forests, depending on the spatial scale and the research question addressed. A definition integrating several levels adapted to different contexts allows for recognizing the complexity of this ecological concept while offering the possibility of adjusting to possible particular cases

Scale	Question/Motivation	Definition
General definition (broad concept, international scale)	What do we generally consider as "old growth"?	Hunter and White (1997) definition: "Relatively old and little disturbed by natural and anthropogenic disturbances"
Intermediate-scale definition (country, continent, or biome scale)	Which forests can be considered as *old growth* in a given area?	Definition based on the most relevant ecological criteria at the level of the concerned territory, with attention to possible specific cases
Coarse small-scale definition (local scale)	How can we roughly distinguish between different old-growth forest types within the same landscape?	Distinction between *transition* and *true* old-growth forests proposed by Oliver and Larson (1996), with the possibility of adjusting the thresholds depending on the context (see, for example, Kneeshaw and Gauthier (2003) and Martin et al. (2018))
Fine small-scale definition (local scale)	How can we finely distinguish between different old-growth forest types within the same landscape?	Consideration of the range of structural characteristics and tree species composition that old-growth forests can take depending on the successional process, the action of natural disturbances, and the influence of abiotic conditions

disturbance (McMullin & Wiersma, 2019). However, many forest species are dependent on younger forests (Drapeau et al., 2003; Fenton & Bergeron, 2011), while certain attributes often associated with old-growth forests may also be abundant in young forests that have been recently disturbed, e.g., deadwood (Donato et al., 2012). Overall, primary forests generally contain stands of all ages, the proportions of which depend on the natural disturbance regime (Kneeshaw et al., 2018). Thus, old-growth forests do not necessarily host maximum species diversity.

The importance of old-growth forests is not limited to their role as habitats for biodiversity. In the context of climate change, the importance of old-growth forests for the long-term sequestration of atmospheric carbon is, for example, a concrete ecosystem service, acting for the benefit of all (Lafleur et al., 2018; Vedrova et al., 2018). Watson et al. (2018) also listed many services provided by intact forests and, by extension, old-growth forests, such as regulating local and regional weather regimes, buffering against the transmission of new diseases, and providing a source of yet unexplored scientific knowledge. The cultural value attributed to old-growth forests, whether in terms of aesthetics, intrinsic value, or spirituality, should also be considered (Kimmins, 2003; Satterfield, 2002). The tensions and conflicts regularly observed for issues related to the management and protection of old-growth forests, e.g., between economic and environmental actors, can be partly explained by the strong cultural and social values attributed to these forests (Kimmins, 2003; Pesklevits et al., 2011; Satterfield, 2002). Although this chapter focuses mainly on old-growth forests through the perspective of forest ecology and management, we also invite the reader to explore the insights from the social sciences and humanities on this subject.

7.2 Can the Distinctive Characteristics of Boreal Forests Help Us Rethink Old-Growth Forests?

Boreal old-growth forests are one of the counterexamples limiting the relevance of broad-scale old-growth definitions. Forests in this biome are generally characterized by a relatively low diversity of tree species, and many of these species are also found at the beginning or end of forest succession (Angelstam & Kuuluvainen, 2004; Harvey et al., 2002; Shorohova et al., 2011). This particularity challenges standard forest succession models, where the replacement of pioneer shade-intolerant species by shade-tolerant species is one of the conditions defining the old-growth stage (Oliver & Larson, 1996; Wirth et al., 2009). Harsh climatic conditions and low site fertility also limit tree growth and size, resulting in stands defined by a relatively simple vertical structure compared with what is commonly expected from old-growth forests (Bergeron & Harper, 2009). Martin et al. (2020b) highlighted the numerous similarities among the vertical structures of even-aged and old-growth black spruce (*Picea mariana*)–dominated stands. However, this type of structure may also partially result from a particular regeneration dynamic, where the black spruce understory remains limited as long as the canopy is not disturbed (Martin et al., 2020d). A similar pattern has also been observed in Norway spruce (*Picea abies*) forests in Finland and Russia (Shorohova et al., 2008, 2009). Moreover, the process of paludification, i.e., the gradual thickening of the organic horizon under poor drainage conditions (Fenton et al., 2005), can markedly reduce stand productivity (Bergeron and Fenton 2012). This process eventually creates forests composed of trees of very small diameter and height despite their old age. The productivity decline caused by paludification in boreal old-growth forests is nevertheless generally restricted to specific environmental conditions; old-growth forests situated on sufficiently drained sites retain their structure over the centuries (Pollock and Payette 2010; Shorohova et al., 2008).

Tree diameter and stand volume are also relatively low compared with forests of other biomes (Fig. 7.1). The presence of very large living or dead trees—generally defined by a diameter at breast height between 70 and 100 cm; (Gosselin & Larrieu, 2020; Spies & Franklin, 1991)—is often considered as one of the key attributes of old-growth forests, for either ecological or cultural reasons, e.g., because very large trees give a sense of greatness and oldness (Kimmins, 2003; Paillet et al., 2017; Wirth et al., 2009). Some types of boreal old-growth forest can contain trees of notable size (e.g., diameter at breast height >40 cm), such as Scots pine (*Pinus sylvestris*), Norway spruce, or balsam fir (*Abies balsamea*)–white birch (*Betula papyrifera*) stands (Desponts et al., 2004; Lilja & Kuuluvainen, 2005; Shorohova et al., 2009). Yet, very large trees can be rare if not completely absent from many boreal old-growth forests, as observed in eastern Canada (Bergeron & Harper, 2009). These examples illustrate that tree size is unreliable for defining old-growth forests, as this attribute can vary enormously from one boreal old-growth forest type to another (Fig. 7.1). Moreover, large trees in old boreal forests are mainly softwood species, as hardwood species are generally pioneer taxa. The value of large trees for ecological, economic, and aesthetic reasons has been often emphasized (Lindenmayer et al., 2014; Lutz et al., 2018; Paillet et al., 2019), explaining their importance in the discussions related to old-growth forests. Poplar species (e.g., *Populus tremula* in Eurasia and *Populus tremuloides* in Canada) are often the larger hardwood species than can be found in boreal landscapes, even though these fast-growing species are generally restricted to the youngest successional stages and specific abiotic conditions (Hardenbol et al., 2020; Harvey et al., 2002). It should be noted, however, that some counterexamples of multicohort *Populus tremuloides* do exist (Cumming et al., 2000). Similarly, hardwood species can sometimes be found mixed in small proportions with conifers in some old-growth boreal forests because of natural disturbances (Bergeron & Harper, 2009; Vehmas et al., 2009), thus increasing habitat diversity in these forests.

The small tree size in boreal forests thereby limits deadwood volume and large log density in boreal old-growth stands. This scarcity of deadwood can be reinforced by the rapid burial of fallen dead trees in soils dominated by moss species (Stokland et al. 2016). Boreal old-growth forests can therefore contain a large volume of almost-intact deadwood within the soil organic layer, although not immediately apparent at the surface. Hence, several studies in eastern Canada found no significant changes in visible deadwood volume in old-growth forests of different ages or differing in

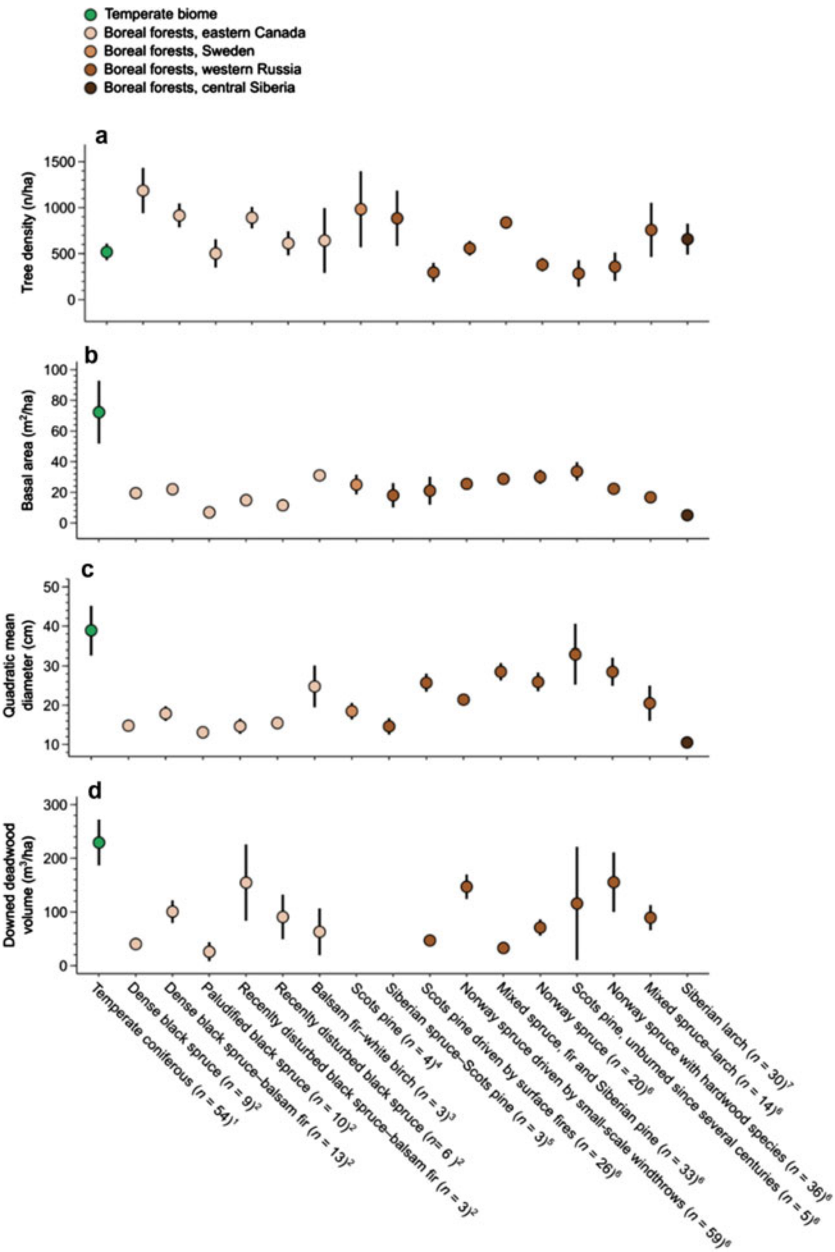


Fig. 7.1 Mean (*circles*) and 95% confidence intervals (*vertical black bars*) for **a** tree density, **b** basal area, **c** quadratic mean diameter, and **d** downed deadwood volume among temperate and coniferous old-growth forests from the literature review of Burrascano et al. (2013) and those of boreal old-growth forests differing in terms of location, tree species composition, and disturbance history. 1 Burrascano et al. (2013), 2 Martin et al. (2018), 3 Desponts et al. (2004), 4 Lundqvist et al. (2019), 5 Stavrova et al. (2020), 6 Shorohova and Kapitsa (2015), 7 Bondarev (1997). Survey methodologies, e.g., the minimum size of sampled trees, may vary between sources

the degree of first-cohort replacement (Bergeron & Harper, 2009; Martin et al., 2018). Marked variability in abiotic conditions (e.g., drainage and surficial deposits) and disturbance dynamics (e.g., disturbance agent, severity, and recurrence) also characterizes the boreal biome at the local to global scale (Kneeshaw et al., 2011; Kuuluvainen & Aakala, 2011; Shorohova et al., 2011). Deadwood dynamics, either in terms of input, decomposition, or burial, can thereby vary markedly between two different locations or periods (Aakala, 2011; Shorohova & Kapitsa, 2015; Stokland et al. 2016). Although a small volume of visible deadwood may define some boreal old-growth forests, other nearby old-growth stands can hold a substantial volume of deadwood (>150 m^3/ha) (Martin et al., 2018; Shorohova & Kapitsa, 2015), again highlighting the diverse nature of these ecosystems.

7.3 The Exceptional Ecological Value of Boreal Old-Growth Forests

7.3.1 An Important Aspect of the Last Great Tracts of Intact Forest

Primary forests continue to decline rapidly and often represent small and isolated patches within degraded areas (Potapov et al., 2017; Sabatini et al., 2018). Most of the large tracts of remnant primary forests are now in remote boreal and tropical regions (Fig. 7.2) (Achard et al., 2009; Kuuluvainen et al., 2017; Potapov et al., 2017). For the boreal zone, most of these forests are found in Canada and Russia, as forestry activities have drastically modified most northern Fennoscandian forest landscapes (Sabatini et al., 2018). Because natural disturbances are essentially defined by a low to moderate severity in northern Fennoscandia, old-growth forests were initially abundant in preindustrial landscapes (Shorohova et al., 2011). Nevertheless, forestry activities caused a rapid decline and almost complete loss of their surface area (Östlund et al., 1997; Sabatini et al., 2018). In northern Fennoscandia, the remaining old-growth forests are thus often isolated in small areas and poorly accessible territories (Sabatini et al., 2018; Svensson et al., 2020). Consequently, populations of many forest species have declined sharply through the loss and fragmentation of their habitats (Esseen et al., 1992). Restoration strategies have since been successfully implemented, but conservation remains far more effective than having to restore altered ecosystems (Halme et al., 2013). The example of the boreal forests of northern Fennoscandia is thus a warning of the ecological risks of the disappearance of old-growth forests and must therefore be considered in areas where these forests are still present.

Not all primary boreal forests are, however, old-growth forests, and their abundance may significantly vary from one region to another, depending on the characteristics of the natural disturbance regime (Shorohova et al., 2011). Because of the generally random distribution of wildfires, the main primary disturbance in boreal

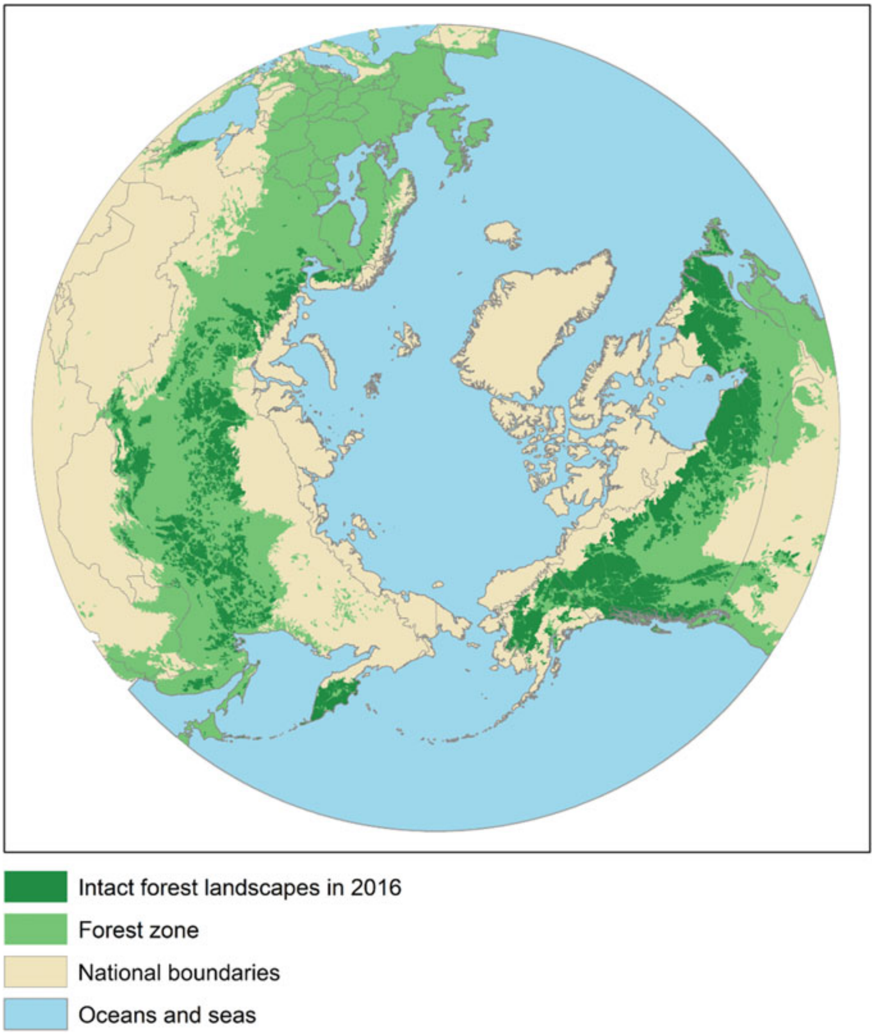


Fig. 7.2 Intact forest landscapes (*dark green*) in the forested regions (*light green*) in the Northern Hemisphere as determined by Potapov et al. (2017). Intact forest landscapes are defined as a "seamless mosaic of forests and associated natural treeless ecosystems that exhibit no remotely detected signs of human activity or habitat fragmentation and are large enough to maintain all native biological diversity, including viable populations of wide-ranging species" (Potapov et al., 2008). Most remaining intact forests are situated in the northern areas of the forested zone, hence in the boreal biome

forests, large portions of the forest can remain untouched by this disturbance for extended periods, even in landscapes with recurring fires (Kneeshaw et al., 2018). The variability in definitions of old-growth forests makes it difficult to obtain a general picture of their proportion in boreal landscapes. Using the overall natural disturbance regimes identified by Shorohova et al. (2011), we can estimate that old-growth forests are the dominant successional stage in the eastern and western parts of North America and Eurasia, as the fire cycles are relatively long. In contrast, the central parts of these continents are generally defined by a shorter fire cycle, implying a reduced presence of old-growth forests (Belleau et al., 2007). Nevertheless, this abundance of continuous and vast tracts of forests with high naturalness containing both old-growth and younger forests in the boreal biome is vital for many species (Venier et al., 2018). Woodland caribou (*Rangifer tarandus caribou*) is an example of the biological value of large natural forest areas. This subspecies of *Rangifer tarandus*, which is specific to North America, requires vast (>1,000 km^2) forest areas having a high proportion of mature and old-growth forests (Kneeshaw et al., 2018). Their populations are declining rapidly because of direct and indirect anthropogenic disturbances modifying the characteristics of their habitats, in particular the loss of old-growth forest areas and unfavorable predation dynamics (Venier et al., 2014). Similarly, Schmiegelow and Mönkkönen (2002) and Cadieux et al. (2020) highlighted that avian communities dependent on old boreal forests are vulnerable to the fragmentation of their habitats caused by the rejuvenation of the boreal landscapes. Species with low dispersal capacity, e.g., arthropods and nonvascular plants, may have difficulties adapting to new environmental conditions where the residual old-growth forest area is too small and isolated (Barbé et al., 2017).

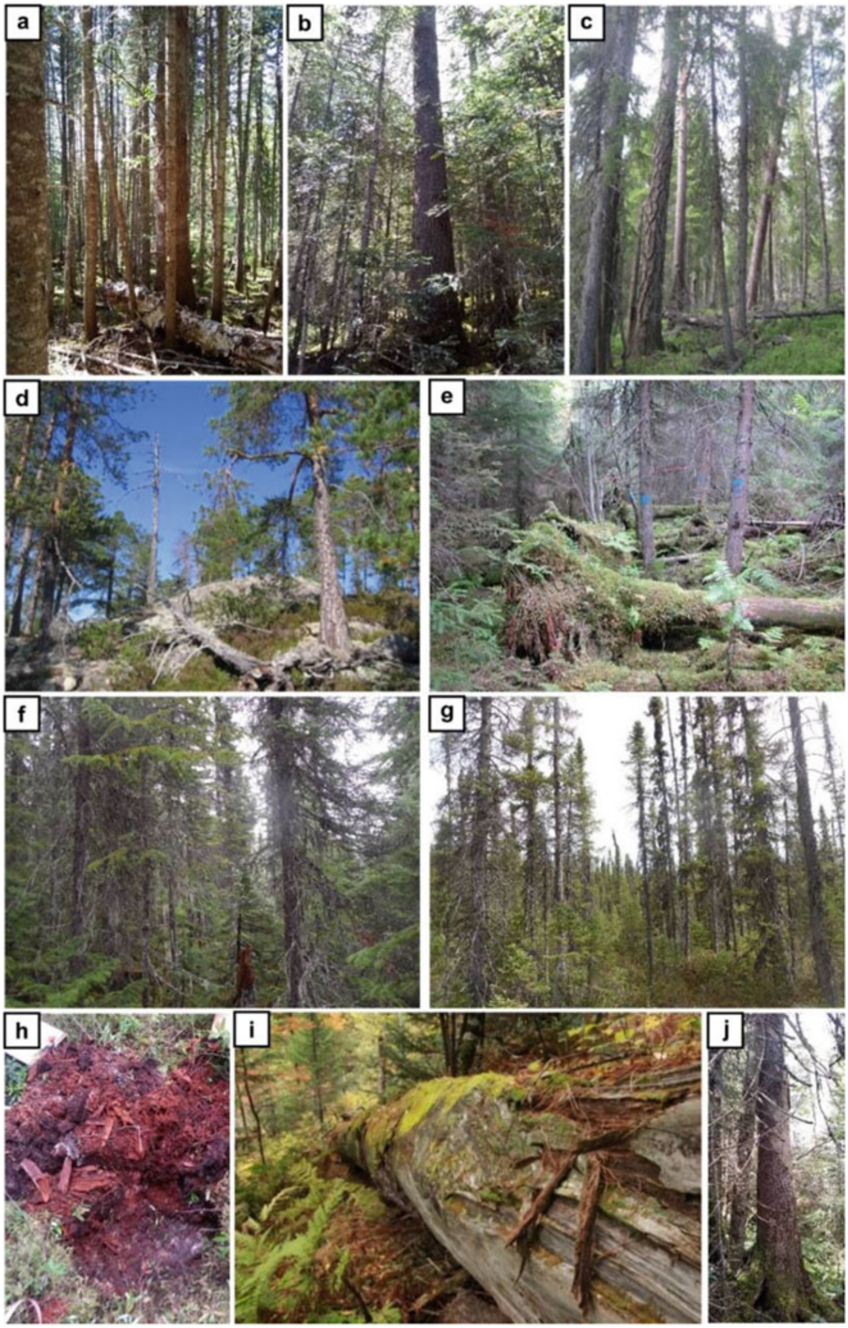
Because of their remoteness and the harsh climatic conditions, large tracts of primary boreal forests were generally spared by human activities during the Holocene. Archaeological evidence shows First Nations in North America purposely influenced forest fire dynamics long before European colonization, but this anthropogenic influence on forests was probably limited and had a similar effect on forests as wildfires (Munoz & Gajewski, 2010). In contrast, forests considered primary or highly natural in areas characterized by a continuous human presence over centuries, such as Europe or northwestern Russia, may show ancient traces of forest management, deforestation, and agricultural activity (Jaroszewicz et al., 2019; Shorohova et al., 2019a). Although not immediately visible, they can durably modify certain environmental conditions and thus the associated biodiversity (Dambrine et al., 2007).

An essential part of boreal old-growth forests therefore belongs to vast, continuous massifs of highly natural forests. This temporal and spatial continuity is critical for biodiversity (McMullin & Wiersma, 2019; Venier et al., 2018). Such forests, however, are becoming increasingly rare because of the impact of human activities, old-growth forests generally being the first stands to disappear (Aksenov et al., 1999; Cyr et al., 2009; Martin et al., 2020a). Maintaining or restoring large areas of intact forest containing a high proportion of old-growth forest in boreal landscapes must be prioritized for maintaining associated habitats (Sabatini et al., 2020; Venier et al., 2018).

7.3.2 *High Habitat Diversity Characterizes Boreal Old-Growth Forests*

Although boreal old-growth forests generally contain few large trees and few tree species, these ecosystems are characterized by a high diversity of structures (Fig. 7.3). For example, Martin et al. (2018) identified 11 different old-growth forests types within a 2,200 km^2 area, defined by specific structures, e.g., canopy cover, basal area, the volume of downed wood debris, and composition (varying proportions of black spruce and balsam fir). This diversity observed within a relatively restricted landscape resulted from different environmental conditions, e.g., surficial deposits and drainage, and disturbance history, e.g., time since the last high-severity and moderate-severity secondary disturbances (Martin et al., 2018, 2020c). These results are in line with other studies that highlighted the heterogeneity in stem diameter distribution, aboveground biomass, and tree species composition observed in the boreal old-growth forests of eastern Canada (McCarthy & Weetman, 2007; Moussaoui et al., 2019; Portier et al., 2018). A high internal diversity for these ecosystems has also been demonstrated in northern Fennoscandia and Russia, where tree species composition, disturbance regime, and abiotic composition can greatly vary among landscapes (Shorohova et al., 2009, 2011). Primary forests dominated by Norway spruce in the alpine regions of eastern Europe (Kozák et al., 2021; Meigs et al., 2017; Trotsiuk et al., 2014) also provide examples of old-growth dynamics, where such reference forests are now almost entirely absent. Boreal old-growth forests are therefore dynamic and diverse ecosystems, from the circumboreal to the local scale. The scarcity of obvious attributes, e.g., very large and tall trees, may nevertheless challenge the recognition of these ecosystems, particularly within large and remote areas where forest surveys are based mainly on remote sensing. For example, Martin et al. (2020b) highlighted that the vast majority of boreal old-growth forests in Québec, Canada, were not identified as such in provincial surveys, probably because the applied size and structure criteria, defined for use in temperate forests, are unsuitable for boreal forests.

The secondary disturbance regime of boreal forests (i.e., a disturbance of low to moderate severity that does not reinitiate forest succession) is defined by a high diversity in its nature, periodicity, spatiality, and severity from the local to the circumboreal scale (Chap. 3; De Grandpré et al., 2018; Kuuluvainen & Aakala, 2011; Shorohova et al., 2011). The characteristics of the disturbance history at the local scale characterize part of forest structural attributes, hence the habitats it contains (Martin et al., 2020c; Meigs et al., 2017) (Fig. 7.4). For example, spruce budworm (*Choristoneura fumiferana*) outbreaks in eastern Canada are top-down disturbances, first killing tall balsam fir trees and progressing toward the understory and spruce species as the outbreak increases in severity (Morin et al., 2009). Windthrow will also kill the tallest trees first. Relative to spruce budworm outbreaks, this latter disturbance is less species-specific and creates fewer snags, produces more fallen logs, and generates more tips and mounds, the latter providing habitats for many forest species (De Grandpré et al., 2018). In contrast, surface fires will generally kill the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◀**Fig. 7.3** Old-growth forests can represent a wide diversity of structures, composition, and dynamics at the local and circumboreal scales. **a** Balsam fir (*Abies balsamifera*) forest in eastern Canada that was severely disturbed 40 years ago by a spruce budworm outbreak. This disturbance produced a stand having a relatively simple diameter structure despite a multicohort age structure and a large deadwood volume; **b** a large white spruce (*Picea glauca*) surrounded by smaller balsam fir trees in eastern Canada; **c** a mixed Siberian larch (*Larix sibirica*), Scots pine (*Pinus sylvestris*), and Norway spruce (*Picea abies*) forest in western Russia; **d** a primeval northern boreal Scots pine forest driven by periodic surface fires; **e** a Norway spruce forest in eastern Russia recently disturbed by moderate-severity windthrows, creating a diversity of soil microhabitats; **f** a dense black spruce (*Picea mariana*)–balsam fir forest in eastern Canada driven by low-severity disturbances; **g** a paludified black spruce forest in eastern Canada. Trees are generally small, but their age can often exceed 250 years; **h** buried deadwood pieces at various stages of decay in a black spruce forest in eastern Canada. A very large portion of deadwood in boreal old-growth forests can be hidden in the soil organic layer; **i** a large Siberian pine (*Pinus sibirica*) log in eastern Russia. These stems may require more than 1,000 years to decompose, sequestering carbon and nutrients and providing a habitat for many wood-inhabiting species; **j** a white spruce with a large wound exposing sapwood in eastern Canada. The disturbance dynamics and the presence of trees from all ages and sizes in old-growth forests favor the development of tree-related microhabitats, necessary for many species. *Photo credits* **a b f–h j** Maxence Martin, **c–e i** Ekaterina Shorohova

understory but preserve the overstory, particularly in pine forests (Mosseler et al., 2003; Shorohova et al., 2009). Secondary disturbances, however, also greatly vary in severity, even for a same disturbance event within a restricted area (Khakimulina et al., 2016; Martin et al., 2019). This variability creates complex matrixes of old-growth forest structures (Kulha et al., 2020; Kuuluvainen et al., 2014). This complexity is also reinforced by variable local abiotic factors that may increase stand sensitivity to a certain disturbance type, e.g., windthrow and hilly topography, or favor tree species that are more susceptible to specific disturbance agents, e.g., balsam fir and spruce budworm outbreaks (De Grandpré et al., 2018). Current knowledge about the complexity of secondary disturbances is, however, still limited. Kuuluvainen and Aakala (2011) classified secondary disturbance severity into three classes of forest dynamics: gap, patch, cohort. They stressed that patch dynamics, i.e., canopy openings between 200 and 10,000 m^2, have been little studied in Scandinavian forests. Hart and Kleinman (2018) expressed a similar concern, highlighting that moderate-severity disturbances, also called intermediate-severity disturbances, have been generally overlooked in favor of low-severity (e.g., gap dynamics) or high-severity (e.g., crown fire) disturbances. The cumulative impact of disturbances over the centuries, such as recurrent insect epidemics of moderate severity, on the structure and dynamics of old-growth forests also remains to be determined (Martin et al., 2019). Similarly, the dichotomy between young/simple forests following high-severity disturbances and old/complex forests boosted by low-severity disturbances is questioned, and more elaborate successional models are now proposed (Donato et al., 2012; Meigs et al., 2017). Therefore, although there is growing interest in the complex effects of secondary disturbances in boreal landscapes, our knowledge of these dynamics is incomplete.

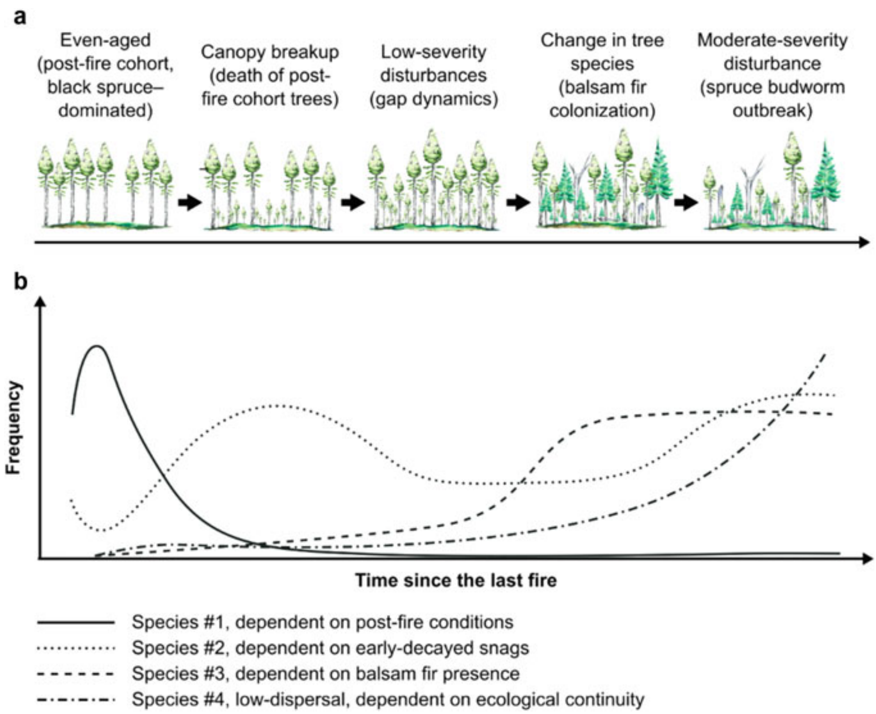

Fig. 7.4 **a** An example of the changes in structure and composition that an old-growth forest in eastern Canada may follow over time; **b** possible changes in the frequency of species defined by different ecologies in this old-growth forest as a function of its change

Overall, the diversity in stand structural attributes and forest history creates a wide variety of habitats that can differ markedly from one stand to another. A greater vertical and structural complexity favors more diversity in forest species such as invertebrates and epixylics (Desponts et al., 2004; Rheault et al., 2009; Schowalter, 2017). Deadwood-related species often depend on specific substrate characteristics, e.g., tree species, decay stage, contact with the ground, cause of death, and size (Janssen et al., 2011; McMullin et al., 2010; Stokland et al., 2012), and the high abundance and diversity of deadwood at the stand scale often results in greater deadwood-related species richness (Lassauce et al., 2011; Wagner et al., 2014). Kozák et al. (2021), for example, underscored that the characteristics of the secondary disturbance regime, e.g., severity, frequency, and time since the last disturbance, strongly influence saproxylic beetle diversity in alpine forests dominated by Norway spruce. Similarly, trees that survived a disturbance can also act as refugia for low-dispersal species, such as lichens, facilitating their recolonization of a disturbed area (Zemanová et al., 2017). However, the link between biodiversity and old-growth forest attributes can be unclear. Forest age, i.e., time since the last stand-replacing disturbance, for example, is a commonly applied indicator. Some species, e.g., birds and nonvascular plants, may be highly dependent on this variable, whereas other taxa may not (Drapeau et al., 2003; Fenton & Bergeron, 2011). This variability can be partly explained by species-specific requirements in terms of habitat, ecological continuity, and landscape. Moreover, two old-growth forests of the same age can be defined by very different structures because of local abiotic conditions and disturbance history (Martin et al., 2018), implying markedly different habitats (Martin et al., 2021a). Similarly, landscape structure around a given old-growth forest can also strongly influence its use by some forest species, e.g., birds and mammals (Faille et al., 2010; Schmiegelow & Mönkkönen, 2002; Tremblay et al., 2015). For these reasons, although forest age is a relevant indicator, it is not sufficient on its own.

Many abiotic, historical, and spatial factors can hence influence the characteristics of old-forest habitats and their attractiveness to boreal species. The complexity of the interactions between these factors can make it difficult to identify clear links between the structural/functional biodiversity and specific structural/ecological attributes (Burrascano et al. 2018; Kozák et al., 2021; Larrieu et al., 2018). Experiments in close-to-nature silvicultural practices can be effective in gaining a direct understanding of how disturbance dynamics can influence biodiversity (Fenton et al., 2013; Franklin et al., 2019; Koivula and Vanha-Majamaa 2020). Given that these are anthropogenic disturbances, e.g., use of heavy machinery, wood removal, and soil disturbance, it can be difficult to compare them with natural disturbances. Yet, certain types of old-growth forests, especially those more productive stands—and therefore of greater economic value—are more threatened by human activities than others (Martin et al., 2021b). This pattern is consistent with a general trend worldwide where the remaining intact forests are the least attractive for human use (Joppa & Pfaff, 2009). It implies that the risk of losing specific habitats, e.g., habitats observed almost exclusively in the most productive forests, could go unnoticed if boreal old-growth forests continue to be considered homogeneous ecosystems. Although the example of the boreal forests of northern Fennoscandia gives us an idea of the general consequences of old-growth forest rarefaction, it may not be sufficient to accurately understand what can be potentially lost. Therefore, a better understanding of the factors influencing the structural and habitat diversity of old forests, both at the stand and landscape scales, is necessary to maintain the associated biodiversity.

7.4 Ecosystem-Based Management of Boreal Old-Growth Forests: Where to Start?

7.4.1 Accurately Identifying Old-Growth Forests

One of the main challenges for sustainable management of old-growth forests is the need for operational definitions. Defining those stands that can be considered (or not) as *old growth* has been a recurrent issue for forest ecologists and managers

(Hendrickson, 2003; Pesklevits et al., 2011; Wirth et al., 2009). This difficulty is reinforced for boreal forests, where the scarcity of obvious old-growth attributes further complexifies this task (Bergeron & Harper, 2009; Martin et al., 2020b). Issekutz (2020), for instance, underscored that only six of the Canadian provinces (Québec excluded) have an operational definition and that there was little consistency between these definitions (e.g., variable age thresholds between and within provinces, use of different indicators of stand or landscape structure). In Québec, forests are classified as old growth if their age exceeds 80 years in the balsam fir–white birch bioclimatic domain and 100 years in the black spruce–feathermoss bioclimatic domain (MFFP 2016). This definition can be considered close to those of other provinces for boreal forests (e.g., Ontario, Saskatchewan), although some differences remain (Issekutz, 2020). Nonetheless, some stands can attain the old-growth stage well before (Cumming et al., 2000) or after (Kneeshaw & Gauthier, 2003; Martin et al., 2018) the age thresholds used by Québec. This issue mainly concerns boreal territories where primary forests are still abundant. In the case of northern Fennoscandia, where most forests are managed, detailed knowledge of these landscapes' history facilitates the identification of remnant old-growth forests.

Accurately identifying these ecosystems at a large scale is also challenging. Because of the limited longevity of some boreal species, taking core samples to determine tree age provides only limited information (Garet et al., 2012; Kneeshaw & Gauthier, 2003). The typical suppression period for trees in old-growth forests is sometimes challenging to account for, causing an underestimation of forest age (Krause and Morin 2005; Marchand & DesRochers, 2016). The remoteness and vastness of boreal landscapes nevertheless prevent exhaustive field surveys in many regions. Aerial photographic surveys can cover large areas and have often been used; however, their accuracy in identifying old-growth forests has been questioned (Martin et al., 2020b). Therefore, it remains necessary to assess whether this misclassification is an inherent limitation of this inventory method or whether it stems from the use of unsuitable criteria for boreal forests. Other techniques have been explored over the last decades for a more straightforward and more accurate classification of forest ecosystems, in particular the use of LiDAR (light detection and ranging). This technology has provided promising results in identifying old-growth structures in temperate forests (Kane et al., 2010; Torresan et al., 2016). However, related studies involving boreal forests are currently lacking, as current predictive models of forest age generally end at a relatively early age, e.g., 100 or 160 years (Maltamo et al., 2020; Wylie et al., 2019). Multispectral airborne imagery can also complement LiDAR for identifying and discriminating old-growth forests within boreal landscapes (Zhang et al., 2017). Although promising, these methods still require further studies to evaluate their ability to accurately evaluate the *old-growthness* of boreal stands and identify the structural diversity of these stands at a fine scale. Developing new innovative and effective forest survey tools able to discern the complexity of boreal landscapes at a fine scale is essential for ensuring the sustainable management of old-growth forests.

7.4.2 Reducing Anthropogenic Pressure on Old-Growth Forests

Anthropogenic activities severely degrade and fragment boreal old-growth forests, in particular by applying short-rotation, i.e., having a shorter return period than the natural primary disturbance regime, and clear-cut-based forestry (Aksenov et al., 1999; Cyr et al., 2009; Kuuluvainen & Gauthier, 2018). Other disturbances, such as mining and oil and gas extraction, can also severely damage natural boreal landscapes (Venier et al., 2014). Industrial-scale forestry is nonetheless a particularly specific disturbance, as it generally targets old-growth forests first (Bouchard and Pothier 2011; Martin et al., 2020a; Östlund et al., 1997). The scarcity of remnant old-growth forests in northern Fennoscandia provides a striking example of the possible consequences of forest management that excessively exploits old-growth forests. Without explicit constraints favoring old-growth forest protection, simulations for eastern Canadian forests show that these ecosystems will disappear in the coming decades (Bergeron et al., 2017; Didion et al., 2007). Therefore, it is urgent to decrease the logging pressure on old-growth forests in landscapes where they are still present, as it is easier to protect than to restore the systems (Halme et al., 2013).

In addition to the reduction of old-growth areas, clear-cut-based forestry also leads to changes in tree species composition (Bouchard and Pothier 2011; Boucher & Grondin, 2012; Kuuluvainen et al., 2017), landscape homogenization and fragmentation (Faille et al., 2010; Schmiegelow & Mönkkönen, 2002), and a decrease in deadwood richness (Jonsson & Siitonen, 2012; Moussaoui et al., 2016). In the context of ecosystem-based management, new management strategies are necessary to maintain the habitats and services related to boreal forests. A combination of clear-cuts having a longer rotation, careful salvage logging, active forest restoration, retention forestry, and continuous-cover forestry, coupled with an investment in disturbance suppression, are the leading proposals for achieving a balance between sustainable wood provision and environmental objectives (Bauhus et al., 2009; Eyvindson et al., 2021; Halme et al., 2013; Kuuluvainen, 2009; Leduc et al., 2015; Shorohova et al., 2019b). For example, numerous recent experiments underscore the efficacy of low-intensity continuous-cover forestry to maintain old-growth attributes and the associated biodiversity (Fenton et al., 2013; Franklin et al., 2019; Koivula and Vanha-Majamaa 2020).

However, the economic feasibility of these alternative strategies is still debated, particularly for remote boreal regions, and will undoubtedly be an important social question in the coming years (Kneeshaw et al., 2018). In regions already heavily modified by forestry practices, it has been demonstrated that economic benefits outweigh the costs (Eyvindson et al., 2021; Ruel et al., 2013). The benefits of ecosystem-based management alternatives may be significantly reinforced by targeting high-quality wood products for harvest (Rijal et al., 2018) or by including ecosystem services in the financial balance (Anielski & Wilson, 2005). Nevertheless, a certain precaution is required in developing alternative management strategies; for example, by removing deadwood, salvage logging can negatively affect species that depend on this habitat (Nappi et al., 2004; Thorn et al., 2018; Waldron et al., 2013). Continuous-cover forestry can lose its benefits if the harvest rate is too high (Fenton et al., 2013; Franklin et al., 2019). Similarly, the extension of road networks through primary forest landscapes to apply alternative methods can also accentuate problems of fragmentation and the modification of trophic networks (Venier et al., 2018). Finally, strategies for conserving intact boreal old-growth forest tracts mainly on the basis of area thresholds are insufficient, as some old-growth forest types—often those with the highest market value—can be under much greater pressure than others (Martin et al., 2020a, 2021b; Fig. 7.5).

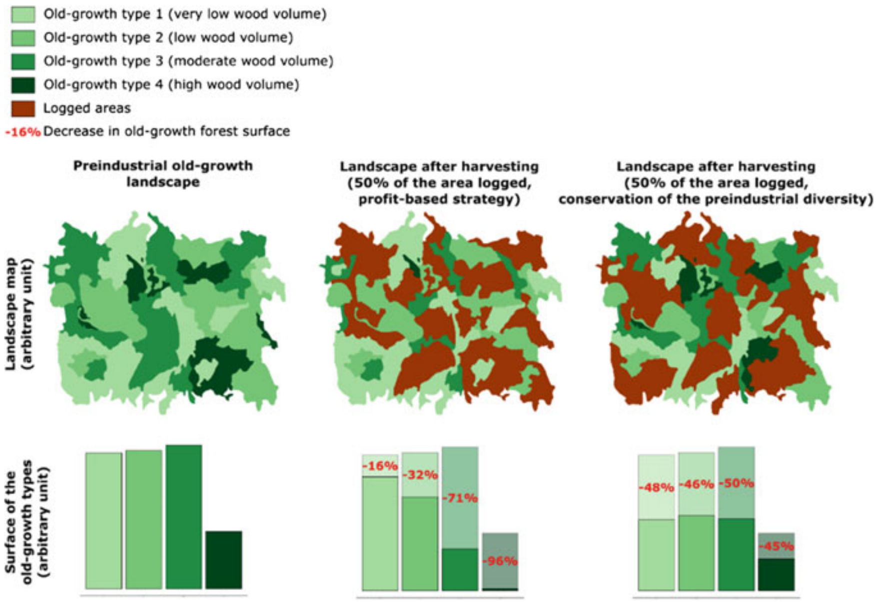

Fig. 7.5 Conceptual scheme of the impact of logging on old-growth forests if only their surface area and not their structural diversity are considered. In this example, old-growth forests can be divided into four types (e.g., different structures and/or composition) distributed along a gradient of merchantable wood volume and, therefore, a gradient of economic interest. A conservation strategy that aims to maintain 50% old-growth forest could then have a very different impact on the residual landscape depending on the criteria used to select the harvested forests: profit-based strategy (objective of maximum profitability from logging, and the more economically valuable old-growth forests are logged first) or the conservation of preindustrial diversity (the proportions of the various old-growth forest types are the same before and after logging)

7.4.3 What is the Place for Boreal Old-Growth Forests in an Uncertain Future?

Climate change will markedly modify boreal landscapes in terms of, for example, disturbance dynamics and tree species composition and hence the characteristics of the oldest forests (Bouchard et al., 2019; Gauthier et al., 2015; Seidl et al., 2017). Nonetheless, evaluating the impacts of climate change on boreal old-growth forests remains challenging, and these impacts can strongly vary between territories and periods (see Chap. 31). Overall, an increase in natural disturbance recurrence and severity is expected, which may markedly decrease the abundance and functionality of boreal old-growth forests (Kuuluvainen & Gauthier, 2018). Boreal tree species, in particular softwoods, may also become less competitive than boreal and sub-boreal hardwood species, implying significant changes in tree species composition (Bouchard et al., 2019). Yet, forest management may remain the leading cause of the loss of boreal old-growth forest surfaces in such areas as eastern Canada, for example (Bergeron et al., 2017). Moreover, it has been emphasized that these forests provide and will continue to provide precious ecosystem services, in particular carbon sequestration, which can help mitigate the impacts of climate change (Lafleur et al., 2018; Thom et al., 2019; Vedrova et al., 2018). Kalliokoski et al. (2020) also recently highlighted that maintaining a continuous forest cover was more effective for carbon sequestration and cooling than increased harvesting rates. However, some boreal regions may become a carbon source because of lower stand productivity and increased fire activity (Miquelajauregui et al., 2019; Walker et al., 2020). This scenario underscores the need to adapt management strategies to local climatic characteristics. Nevertheless, it is generally assumed that maintaining a high diversity of structures and composition in the forest landscape will increase forest resilience and facilitate the adaptation of management practices to new environmental conditions (Augustynczik et al., 2019; Gauthier et al., 2009; Seidl et al., 2017). Old-growth forests will therefore play a key role in adapting ecosystems and human societies to a changing environment (Halpin & Lorimer, 2016; Kuuluvainen & Gauthier, 2018; Leduc et al., 2015). For these reasons, it is essential to protect the remaining old-growth forests and ensure that their functionality, e.g., connectivity, productivity, and diversity, is maintained (Halme et al., 2013; Smith, 2020; Chap. 31). In areas where these ecosystems are now absent, it will be necessary to apply active policies to restore elements and dynamics related to old-growth forests (Bauhus et al., 2009; Halme et al., 2013; Kuuluvainen & Gauthier, 2018; Sabatini et al., 2020; Smith, 2020).

7.5 Conclusions

Old-growth boreal forests are complex ecosystems of high value for biodiversity and human societies. However, these ecosystems are often still described in a reductionist way that does not consider their richness. Old-growth forests are under serious threat, and many measures are urgently needed to protect these forests and their associated habitats and services. A fully effective ecosystem-based management must emphasize the size, connectivity, diversity, and functionality of old-growth forests. The operational tools to achieve this objective remain nevertheless lacking and must be developed rapidly. Similarly, the pressure exerted by human activities on these ecosystems must be significantly and urgently reduced, including in areas where old-growth forests remain abundant. Numerous alternative management practices to short-rotation clear-cuts hold promise and could fulfill this objective. Improved management and protection of old-growth forests go beyond the sphere of forest managers and ecologists alone and involves much broader socioeconomic considerations.

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