Towards repeated clear-cutting of boreal forests – a tipping point for biodiversity?

Author list: Lisa Fagerli Lunde[1], Tone Birkemoe[1], Anne Sverdrup-Thygeson[1], Johan Asplund[1], Rune Halvorsen[2], O. Janne Kjønaas[3], Jenni Nordén[4], Sundy Maurice[5], Inger Skrede[5], Line Nybakken[1] and Håvard Kauserud[5].

[1] Faculty of Environmental Sciences and Natural Resource Management, Norwegian University of Life Sciences, 1432 Ås, Norway
[2] Natural History Museum, University of Oslo, 0316 Oslo, Norway
[3] Norwegian Institute of Bioeconomy Research, 1431 Ås, Norway
[4] The Norwegian Institute for Nature Research, 0855 Oslo, Norway
[5] Section for Genetics and Evolutionary Biology, Department of Biosciences, University of Oslo, 0316 Oslo, Norway

Corresponding author: Lisa F. Lunde, lisa.fagerli@nmbu.no

Keywords (5-10): biodiversity, boreal, clear-cutting, community composition, edge effects, even-aged forest management, habitat fragmentation, old-growth forest, species richness

Abstract

Boreal forests are important carbon sinks and host a diverse array of species that provide important ecosystem functions. Boreal forests have a long history of intensive forestry, in which even-aged management with clear-cutting has been the dominating harvesting practice for the past 50–80 years. As a second cycle of clear-cutting is emerging, there is an urgent need to review the effects of repeated clear-cutting events on biodiversity. Clear-cutting has led to reduced numbers of old and large trees, decreased volumes of dead wood of varied decay stages and diameters, and altered physical and chemical compositions of soils. The old-growth boreal forest has been fragmented and considerably reduced. Here, we review short- and long-term (≥50 yrs) effects of clear-cutting on boreal forest biodiversity in four key substrates: living trees, dead wood, ground and soil. We then assess landscape-level changes (habitat fragmentation and edge effects) on this biodiversity. There is evidence for long-term community changes after clear-cutting for several taxa: epiphytic lichens; saproxylic fungi, bryophytes and insects; epigeic bryophytes; soil snails, bacteria, and ectomycorrhizal fungi. Long-term declines in species richness were found for saproxylic fungi, bryophytes and true flies. Still, for the majority of taxa, long-term effects of clear-cutting are not well understood. On the landscape level, reduced connectivity to old-growth forests has negative effects on several species of fungi, lichens, bryophytes and insects, notably among red-listed species. Furthermore, altered microclimate near clear-cut edges negatively affect epiphytic lichens and epigeic arthropods, implying complex effects of habitat fragmentation. Repeated cycles of clear-cutting might pose even stronger pressures on boreal forest biodiversity due to continued fragmentation of old-growth forests and accumulation of extinction debts. Examining the broad effects of forestry on biodiversity across the boreal biome is crucial. First, to increase our knowledge of long-term and landscape-level effects of former clear-cutting. Second, to gain a better understanding of how forestry will affect biodiversity and, subsequently, ecosystem functioning, with repeated cycles of clear-cutting.

Table of Contents

I. Introduction

Boreal forests stretch from Eurasia to North America along the northern hemisphere. This biome is home to diverse assemblages of organisms, including plants, fungi, lichens and invertebrates. In Canadian boreal forests alone, 32 000 species of insects have been described (Kayes & Mallik, 2020). The forests are dominated by coniferous trees (mainly *Pinus*, *Abies*, *Picea* and *Larix*), with varying proportions of broadleaved trees (*Populus*, *Betula*, *Alnus*, *Sorbus* and *Salix*). Boreal forests are characterized by short growing seasons, harsh winters, low annual mean temperatures, and subsequently, slow decomposition and large amounts of accumulated carbon (Burton, 2013). Indeed, around 32% of the terrestrial global carbon stock is found in boreal forests (Mayer *et al.*, 2020; Scharlemann *et al.*, 2014; Pan *et al.*, 2011), the largest stocks being located in soils (Bradshaw & Warkentin, 2015).

Boreal forests are important providers of ecosystem functions, i.e. the ecological processes that support and maintain ecosystems: primary production, water supply, climate regulation and habitat provisioning, to name a few (Brockerhoff *et al.*, 2017). Ecosystem functions are driven by environmental factors, such as climate and nutrient availability, but also by biodiversity (Tilman, Isbell & Cowles, 2014; van der Plas, 2019). For instance, both above- and belowground **species diversity** (Table 1) can have complementary positive effects on multiple ecosystem functions (Yuan *et al.*, 2020; Delgado-Baquerizo *et al.*, 2020; Li *et al.*, 2019; Sasaki *et al.*, 2022). Boreal forests' variety of species interactions, tree characteristics and disturbance dynamics maintain resilient and spatiotemporally complex ecosystems (Burton, 2013).

In this review, we summarize current knowledge and discuss how clear-cutting affects boreal forest biodiversity. We first provide an overview of boreal forest history and how clear-cutting has affected the physical forest environment. Then, we evaluate how these changes influence the forest biodiversity associated with four major substrates: living trees, dead wood, ground and soil. We then consider responses to landscape fragmentation across all substrates. In the end, we discuss future threats by evaluating how continued clear-cutting and repeated clear-cutting events may affect boreal forest biodiversity.

The review is based upon studies from the entire boreal biome, with inherent geographic bias due to uneven coverage by relevant studies; most research has been done in Fennoscandia and Canada (Table 2). Throughout this review, we address other major uncertainties, such as underrepresentation of taxa, lack of long-term studies and comparative challenges between studies with different types of forest management and histories (Table 2). We do not consider vertebrates or aquatic species groups. First, because we focus on the hyperdiverse taxa that have received less attention in forest management, and second, because they respond to forestry either indirectly or at different scales than what is relevant for this review. The literature selection has mainly been based on identifying a set of key papers in each field, then selecting relevant literature from the key paper's reference list ("backward snowballing") or literature that has cited that paper ("forward snowballing").

II. Boreal forest history

Boreal forests are historically shaped by mixed-severity disturbances acting over a range of spatial and temporal scales, thus creating a dynamic mosaic landscape. Regional and local factors of climate, soil properties, vegetation and topography determine the prevailing disturbance regime (Kuosmanen *et al.*, 2014; Shorohova *et al.*, 2011). Disturbance agents include natural large-scale events like forest fires, windstorms and insect outbreaks, as well as a continuous and complex interplay of smaller windthrow, insect outbreaks, flooding events, or other factors creating small-scale disturbances (Kuuluvainen & Aakala, 2011; Angelstam & Kuuluvainen, 2004; Schaetzl *et al.*, 1988). These disturbance dynamics result in different types of **primary forests** (Table 1) that are unequally distributed across the boreal zone (Shorohova *et al.*, 2009; Kuuluvainen & Aakala, 2011; Shorohova *et al.*, 2011):

(1) even-aged forests resulting from stand-replacing disturbances, typically crown fires or insect outbreaks, with short return intervals. These forest types characterize central and parts of western Canada, as well as nutrient-rich areas in Europe. Examples of dominating tree species in these forests are black spruce (*Picea mariana*) and jack pine (*Pinus banksiana*). Additionally, these regions contain more forest areas in early and mid successional stages with higher proportions of broadleaved trees such as birch (*Betula* sp.) and aspen (*Populus* sp.);

(2) cohort-type forests resulting from recurrent partial disturbances, leaving the older tree generation. These are found in European Scots pine (*Pinus sylvestris*) forests where surface fires prevail, central and eastern Siberia which also experience silk moth outbreaks, and sloping stands that are exposed to periodic windthrow. Cohort-type forests are, however, not catalogued in North America ; and

(3) old, multilayered forests characterized by recurrent small-scale disturbances (gap dynamics) causing mortality of individual trees. These forests are usually dominated by shade-tolerant tree species of spruce (*Picea* sp.) or fir (*Abies* sp.). They are found in western and eastern North America, northeastern Siberia and Fennoscandia. However, the old-growth stage typically arrives earlier in North America compared to Eurasia due to differences in the life span of the different tree species.

Acting over various spatial and temporal scales, these disturbance dynamics contribute to creating a heterogeneous landscape mosaic with large divergences in age and tree species distributions.

.

Boreal forests have a long history of human influence, particularly in Europe (Hjältén *et al.*, 2023; Angelstam, 1996). While early forest dwellers had local and mostly low-impact effects, growing human populations as well as technical developments in forestry led to increased impacts in the boreal biome. This included both slash-and-burn agriculture and several forms of selective logging, like harvesting of large-diameter trees. The originally fire-influenced primary forest landscape of Fennoscandia and European Russia was gradually transformed by human activities into a regulated production forest landscape (Angelstam, 1996).

Even-aged management was introduced around 1900 and, by the 1950s, clear-cutting had become the most common harvesting practice in boreal forests (Lundmark, Josefsson & Östlund, 2013; Angelstam, 1996). Practices include cycles of stand-replacing clear-cutting, usually followed by planting of tree seedlings and/or scarification to facilitate seedling establishment. The forests may be managed by thinning and nitrogen fertilization. **Rotation times** vary from 50–150 years, depending on forest type and geographical location (Gauthier *et al.*, 2023). Intensive use of the boreal forest, first by selective logging and then by clear-cutting, has led to a decrease in both primary and **old-growth forests** (Table 1).

Although clear-cutting is common also in Canada and Asian Russia, there are still large tracts of primary forests (Gauthier *et al.*, 2023), in particular in the more remote northern areas. Forest management in these regions is overall more extensive and less intensive than in Fennoscandia (Naumov, Angelstam & Elbakidze, 2016; Hytteborn *et al.*, 2005; Gauthier *et al.*, 2023). Consequently, less emphasis is put on planting and the close tending of the regenerating stands. However, even in Fennoscandian countries, the intensity of management related to clear-cutting can vary between countries and within regions.

Today, we are facing a decisive situation: the first clear-cut forests have grown to maturity and will undergo another cycle of clear-cutting in the next decades. In fact, this *repeated* clear-cutting has already begun in some areas, notably in Fennoscandia (Kuuluvainen & Gauthier, 2018). Although land-use change and direct exploitation are stated as the strongest drivers of biodiversity change by the IPBES (Díaz *et al.*, 2019), no exhaustive review has been conducted on long-term effects of the first cycle of clear-cutting on biodiversity for the whole boreal biome (but see Grove, 2002; Siitonen, 2001; Savilaakso *et al.*, 2021; Venier *et al.*, 2014; Esseen *et al.*, 1997; Niemelä, Koivula & Kotze, 2007; Tomao *et al.*, 2020 for reviews on specific boreal regions and/or species' groups). Adding fragmentation of old-growth forests and reports of extinction debts (e.g. Hanski & Ovaskainen, 2002), we may be approaching a tipping point for biodiversity (Barnosky *et al.*, 2012).

Table 1. Definition of terms used in this review (alphabetical order).

Terms	Definition
Connectivity	Measure of the proximity of a habitat or forest patch to other habitats or forest patches; the opposite of isolation.
Dead wood characteristic	A type of dead wood substrate or niche; e.g. standing, kelo, late-decay or large-diameter dead wood.

Edge effect	Abiotic and biotic processes that affect communities or species near a forest edge (Harper *et al.*, 2005); also termed *edge influence*.
Epigeic	Species growing or dwelling on the forest floor.
Epi-/endophytic	Species growing on or developing inside living plants.
Epi-/saproxylic	Species growing on or developing in dead wood.
Forest edge	A transition zone from a forest to a more open area, such as a clear-cut; experiences altered microclimate compared to the forest interior.
Kelo tree	Scots pine tree (*Pinus sylvestris*) that died standing at a very high age (300-500 yrs) and decays slowly, often standing (Niemelä, Wallenius & Kotiranta, 2002); dry, debarked dead wood with silvery stem and large proportion of heartwood; hosts niches for many specialized species.
Managed forest	Forest that is subjected to forest management or with high disturbance by human activities; managed with intensive selective logging, other harvesting and post-harvesting regimes and/or clear-cutting; specifications such as 'clear-cut' or 'previously clear-cut' are preferred in cases when this is known. However, sufficient information about forest history is sometimes lacking; general term for different management regimes if they have been grouped together for analysis.
Old-growth forest	Relatively old forest (mature or late forest succession) with only limited human disturbance (not clear-cut) in recent times (~100 yrs); characterized by high vertical and horizontal structural complexity, presence of many old and large trees, and dead wood of all decay stages (*structural old-growth* sensu Martin, Shorohova & Fenton (2023)); if management history is not described in a study, we assume some form of logging has taken place, thereby being an 'old-growth forest' and not a 'primary forest'.
Primary forest	Naturally regenerated forest of native tree species, where there are no clearly visible indications of human activities and the ecological processes are not significantly disturbed (follows EU and FAO definition). Related terms with similar definitions are *primeval, pristine* or *virgin forest*.
Retention forestry	Forest management model of retaining trees or dead wood after logging to preserve more structural complexity in the forest stand, permanently or for an extended time period; also termed *variable retention* and *tree retention*.
Rotation time	Length of time between stand-replacing harvesting cycles in a forest, for example from one clear-cutting event to the next.
Species diversity	All diversity measures based on species or species hypotheses (e.g. OTU or ASV data); includes both α- and β-diversity, richness, evenness and diversity indices combining the two (e.g. Shannon); when describing results from studies, the terms 'richness' or 'evenness' are preferred when this was tested.
Stand age	Chronological age of a forest stand, i.e. an adjoining group of trees of similar age and size. In managed forests, this represents the time since the forest stand was established, by planting or sowing.
Structural element	Substrates or habitats of high importance to forest species; provides niches for species; includes the term 'key habitat'.

III. Clear-cutting effects on the physical forest environment

To assess the physical changes that occur after clear-cutting, we would ideally compare it to a forest untouched by human activities ("primary forest"; Table 1), which correspond to the landscapes the species have adapted to. However, as boreal primary forests are very rare, especially in Europe, effects of clear-cutting are also compared to forests with minimal human disturbance ("old-growth forest"; Table 1; Figure 1C); they have never been clear-cut, but may have been subjected to selective logging of varying intensity in the past. These primary and old-growth forests are characterized by high structural complexity, with the presence of many old and large trees and high amounts of dead wood in all decay stages (Martin *et al.*, 2023). Under natural conditions, stand-replacing disturbances such as forest fires occur intermittently. Unlike clear-cutting, which involves *removal* of all or almost all trees (Figure 1A), stand-replacing natural disturbances create large and diverse amounts of sun-exposed dead wood, which contributes to the structural complexity of the regenerating stand (Swanson *et al.*, 2011; Winter *et al.*, 2015). Furthermore, a number of **structural elements** that provide niches for specialized species need centuries to develop, such as old trees, **kelo trees**, large-diameter or late-decay dead wood (Siitonen, 2001). These elements are normally absent in **managed forests** (e.g. mature clear-cut; Figure 1B).

Clear-cutting alters the physical environment of boreal forests in ways that inherently affect the organisms living there. In addition to altering the microclimate and the distribution of habitats, at both the local and landscape scale, clear-cutting has a distinct impact on each of the four major substrates of forest species: living trees, dead wood, ground and soil (Nordén *et al.*, 2014).

Figure 1. Scots pine (*Pinus sylvestris*)-dominated forests with different management histories: A) recent clear-cut, northern Sweden, B) mature clear-cut, southern Norway, and C) old-growth forest, southern Norway. In this review, recent clear-cuts represent short-term effects and mature clear-cuts (≥ 50 yrs) represent long-term effects of clear-cutting, as compared to old-growth forests. Photos by Anne Sverdrup-Thygeson.

(1) Living trees

Clear-cutting is characterized by removal of most of the living trees in the forest stand. After cutting, eventual remaining trees in the clear-cut, but also trees on the **edges** between the clear-cut and the forest, suffer high mortality due to exposure to wind and drought (Jönsson *et al.*, 2007; Stokland, Siitonen & Jonsson, 2012). Planting or natural regeneration is typically followed by a young forest phase with high tree density. Thinning, that is, removal of some trees to increase growth of remaining trees, is often carried out during this phase. Succession (i.e. reforestation) usually happens much faster in recent clear-cuts compared to early successional habitats after natural disturbances (Swanson *et al.*, 2011).

With increasing **stand age**, a canopy with more or less uniform vertical and horizontal vegetation develops, with less variation in light availability at the ground level than in old-growth forests (Messier *et al.*, 2009; Asplund et al. in preparation). The result is a homogeneous forest, in which both the average and variation of tree age, height and diameter are low compared to old-growth forests (Bouchard & Pothier, 2011; Esseen *et al.*, 1997; Hämäläinen *et al.*, 2023).

Forests that originate after clear-cutting often resemble monocultures, especially in Fennoscandia where post-harvest sowing or planting of seedlings is common (Solvin & Fløistad, 2023). One of the most pronounced differences between managed and old-growth forests is the much lower frequency of large-diameter trees in the former, as was shown in a forest landscape in Sweden: over 100 years, the number of large trees declined by 90% after the introduction of clear-cutting (Linder & Östlund, 1998). A subsequent increase in large-diameter trees was reported over the last 30 years in southern Sweden, but not in the north where the history of intensive logging is shorter (Kyaschenko *et al.*, 2022). Across the boreal biome, the clear-cutting regime has resulted in fragmentation and loss of trees that are both large and old (Lindenmayer, Laurance & Franklin, 2012; Henttonen *et al.*, 2019), and of the species-rich microhabitats associated with such trees (e.g. Michel & Winter, 2009).

(2) Dead wood

After clear-cutting, both standing and downed dead wood are sparse. New input is halted as living trees have been harvested and smaller dead wood residues are decomposed within a few years. With short rotation times, low volumes of dead wood will be a persistent feature of formerly clear-cut forests (Stokland *et al.*, 2012; Jonsson *et al.*, 2016). In Fennoscandia, dead wood volume in intensively managed forests is about 2–10 % of the volume in old-growth forests (Siitonen, 2001; Stokland *et al.*, 2012)

In addition to reduced quantity of dead wood, former clear-cut forests host a lower *quality* of dead wood, i.e. low variation of **dead wood characteristics**. Studies show that intensively selective logging greatly reduces mid- and late-decay stages of dead wood (Siitonen *et al.*, 2000; Storaunet *et al.*, 2005). Large-diameter dead wood is also rare in managed forests, both from mid- (Jönsson, Fraver & Jonsson, 2009) and late-decay (Siitonen *et al.*, 2000) stages. In particular, this is the case for large-diameter standing dead wood (Linder & Östlund, 1998). Dead wood characteristics common to primary boreal forests are almost completely lacking in forests subjected to clear-cutting. An example of such rare habitats are kelo trees, which probably depend on natural disturbances (fire) and need centuries to develop (Rouvinen, Kuuluvainen & Siitonen, 2002; Niemelä *et al.*, 2002).

(3) Ground and soil

Trees supply most of the photosynthates that are allocated belowground to support roots, mycorrhizal associations and soil microbial food webs (Prescott & Grayston, 2023; Gill & Finzi, 2016). Mycorrhizal and saprotrophic fungi drive the biological stability of soil organic carbon (SOC) through various processes (Clemmensen *et al.*, 2013; Ekblad *et al.*, 2013).

Clear-cutting breaks, to a large extent, the supply chain of photosynthates from the trees to the root-associated fungi (Prescott & Grayston, 2023). The inputs of harvest residues trigger an immediate pulse of carbon enrichment to the soil and forest floor. This leads to a fungal community shift and increased decomposition, which together with reduced photosynthate input from trees, is expected to result in a significant reduction of soil carbon (James & Harrison, 2016; Bödeker *et al.*, 2016). Studies on SOC changes following harvesting show, however, contrasting results. Podosols, one of the most common soil types in boreal forests, were among the soils with the greatest SOC losses both from the forest floor and the mineral soil in a global meta-analysis (James & Harrison, 2016). Other studies suggest that reductions in SOC stocks from logging mainly relate to removal of harvest residues (Mäkipää *et al.*, 2023; Clarke *et al.*, 2021). Harvesting impacts on

SOC stocks are most likely context-dependent (Nave *et al.*, 2024). Estimates of the recovery time of the carbon balance after clear-cutting can be highly variable according to site characteristics, climate and productivity (Peichl *et al.*, 2023b; Peichl *et al.*, 2023a). The amount of forest floor carbon is expected to slowly build up and return to pre-harvest levels during the first century (Nave *et al.*, 2010), in parallel with the tree-layer regrowth. Other immediate responses to harvesting may include reductions in soil nitrogen content, water-holding capacity and soil compaction (Jurgensen *et al.*, 1997; Bock & van Rees, 2002).

The stability of SOC is also mediated by a broad set of environmental drivers, in particular temperature and soil moisture content (Soucémarianadin *et al.*, 2018). Like natural large-scale disturbances, the open patches created by clear-cutting alter the climate at a microscale, as the ground level warms, and also potentially dries up (Stoutjesdijk & Barkman, 1992). This results in warmer days with higher temperatures above ground level in clear-cut relative to primary forests (Blumroeder *et al.*, 2019). Densely planted production forests may, on the other hand, potentially give lower soil temperatures relative to more open forest systems (e.g. Kjønaas *et al.*, 2021).

(4) Landscape patterns

Extensive clear-cutting has led to loss and fragmentation of old forests in boreal landscapes (Kuuluvainen & Gauthier, 2018; Boucher & Grondin, 2012). Concomitantly, the percentage of young forest has increased, especially in cohort- and gap dynamic-type forests (Kuuluvainen & Gauthier, 2018). These early successional forests are, furthermore, more homogeneous than those that occur after natural disturbances (Swanson *et al.*, 2011). In eastern Canada, the proportion of forests older than 100 years was reduced from 75% in 1930 to 15% in 2000 (Boucher *et al.*, 2009). Forest age has reduced also in central Sweden, with a notable shift towards more even-aged Scots pine forests (Axelsson & Östlund, 2001; Linder & Östlund, 1998). The remaining old-growth forest is mostly small and isolated (Axelsson & Östlund, 2001). Such fragmentation also increases the length of forest edges which in turn may alter microclimatic conditions (Lindenmayer & Fischer, 2013; Harper *et al.*, 2005).

Forest landscapes are typically polarized, with large contrasts between forests that have been clear-cut and old-growth forests. Still, old-growth forests are poor representations of natural conditions because (1) they might bear traces of former forestry, (2) the most productive sites are underrepresented, and (3) forest fires are supressed (Siitonen, 2001; Jönsson *et al.*, 2009). Further, early successional forests resulting from natural disturbances, which are more structurally complex than clear-cuts, are lacking in the landscape (Swanson *et al.*, 2011; Kuuluvainen & Gauthier, 2018).

IV. Clear-cutting effects on forest biodiversity

The transition to clear-cutting forestry has brought physical changes to the boreal forest, such as reduced structural complexity and **connectivity** of old-growth forests. This, in turn, impacts biodiversity. Almost half of all species on the national red lists in Fennoscandia live in boreal forests, and the majority of these are associated with old-growth forests and/or are threatened by clear-cutting (Junninen & Komonen, 2011; Larsson *et al.*, 2011; Artsdatabanken, 2021; Tikkanen *et al.*, 2006). A meta-analysis by Savilaakso *et al.* (2021) revealed an overall negative effect of even-aged forest management on species richness in European boreal forests.

Ideally, *long-term effects of clear-cutting* should be studied with permanent plots, established before the first clear-cutting and maintained for at least one tree generation (BACI; Smith, 2002). However, such infrastructure is largely absent. Further, clear-cutting has only been in regular use for 50–80 years and these forests have therefore only recently reached maturity (Table 2). Some comparative studies on the biodiversity of mature clear-cut and old-growth forests with similar site conditions have been conducted (Table 3). Short-term studies are more common. Additionally, studies on other intensive forestry operations, for example **retention forestry**, are sometimes relevant for understanding species' responses to clear-cutting. Numerous reviews have addressed how tree retention impacts boreal forest biodiversity (e.g. Koivula & Vanha-Majamaa, 2020; Seibold *et al.*, 2015; Beese *et al.*, 2019). On the landscape level, forestry-induced habitat fragmentation may impact boreal forest biodiversity.

In the following, we review how different species groups associated with living trees, dead wood, ground and soil (Figure 2) are affected by clear-cutting and landscape-level habitat fragmentation, including **edge effects**. Short- and long-term effects of clear-cutting, i.e. responses observed before or after 50 years (Figure 1), will be distinguished in the text and summarized in Table 3. We will discuss responses to the observed changes in the physical forest environment (reviewed above) where it is relevant. In a few cases, where studies on effects of clear-cutting are scarce, we discuss responses to other intensive logging methods.

Table 2. Major knowledge gaps and uncertainties identified with regards to impacts that clear-cutting have on boreal forest biodiversity.

Knowledge gaps	Explanation
Geographic bias	• The direction and severity of the changes we observe differ with boreal regions. Considering whole regions, very little data exist from Asian boreal forests, and relevant studies may exist in non-English languages. • Some forest types are underrepresented, namely early successional stages following natural disturbances and high-productivity old-growth forests.
Underrepresented taxa/functional groups	• Almost no data exist on the following groups' responses to forest management: archaea, bacteria, protists – invertebrates other than beetles and spiders – microfungi (e.g. endophytes) – epiphytic bryophytes
Long-term responses to clear-cutting	• Long-term (≥ 50 yrs) studies of clear-cutting are lacking because it has only been common for 50–80 years and absence of BACI designs. • Community-level recovery potential from natural and anthropogenic disturbances are poorly understood, including how recovery potential differs after clear-cutting and natural stand-replacing disturbances. • Responses seem to differ across species groups. Long-term data is missing or scarce for most groups.
Management regimes and forest history	• Effects of clear-cutting depend on former management history, thereby impeding interpretations. Further, this information is lacking from many studies. • 'Clear-cutting' is done differently across countries, including degree of retention, site preparation, fertilization, regeneration and thinning.
Landscape-level responses to clear-cutting	• Species' abilities to avoid regional extirpation are not well understood, nor how these responses differ across taxa. • Edge effects are complex and not well understood (Harper *et al.*, 2005).

Diversity metrics	- Most studies have looked at the effect of forestry on species richness. However, it is also important to investigate species evenness, beta diversity, gamma diversity, genetic diversity and functional diversity.
Publication bias	- Studies of no effect are rarely reported.

(1) Living trees

(a) Lichens

Several studies, as well as national red-list assessments, indicate that **epiphytic** lichens (Table 1) are currently facing severe population declines (Esseen *et al.*, 2022; Lommi *et al.*, 2010). Using data from comprehensive field surveys over 10 years, Esseen *et al.* (2022) reported annual loss rates of pendulous lichens across managed Norway spruce (*Picea abies*) forests in Sweden. The rates ranged from 1.7% in the genus *Alectoria* to 0.5% in *Bryoria*. Declines are driven by logging of forests with long continuity of tree cover, short rotation times, substrate limitation and low light availability in dense forests (Esseen *et al.*, 2022; Dettki & Esseen, 2003).

Clear-cutting ultimately removes the host trees of epiphytic lichens. Their recovery is thus dependent on dispersal and reestablishment of lichen propagules, dictated by the substrate availability and microclimatic suitability throughout succession. Few studies, however, have investigated the effects of clear-cutting on epiphytic lichen diversity. In one exception, lichen species were surveyed in hemiboreal forests of Estonia on any substrate, where old-growth were compared with mature (65–95 yrs) and young (4–19 yrs) clear-cut forests (Lõhmus & Lõhmus, 2019). Overall community composition differed between all forest types. Old-growth forests had similar richness of management-tolerant species, slightly higher richness of management-sensitive species, and significantly higher richness of old growth-dependent species, compared to mature clear-cut forests. In another study, red-listed lichens showed reduced species richness in mature (30–70 yrs) clear-cut compared to old-growth Norway spruce forests (Rudolphi & Gustafsson, 2011). However, the effect was only significant in forests with south-facing edges, and no difference was observed when accounting for the number of broadleaved trees.

Old trees are particularly important for the epiphytic lichens because of their long lifespan and high diversity of microhabitats, such as rough bark with furrows (Holien, 1996). Accordingly, tree age is a strong predictor of lichen species richness (Lie *et al.*, 2009; Uliczka & Angelstam, 1999). In his review on epiphytic lichens in boreal forests, Johansson (2008) revealed that old-growth forests host more species than younger, clear-cut forests. As much as 150-300 years are needed for recovery of the epiphytic lichen diversity, especially of rare species.

Retention of host trees after clear-cutting may serve as lifeboats for epiphytic lichen species (Johansson, 2008; Lundström *et al.*, 2013; Hedenås & Hedström, 2007; Ranlund *et al.*, 2018; Nirhamo *et al.*, 2024). Lundström *et al.* (2013) showed that the total lichen species richness on retained European aspen (*Populus tremula*) trees increased with time since clear-cutting with retention, including forest that were cut 0–16 years before. However, whether these responses to tree retention prevail in dense production forests (30–40 yrs after cutting) are not known.

(b) Bryophytes and fungi

Epiphytic bryophytes (mosses and liverworts) are also removed during clear-cutting. Little is known about the reestablishment of this group during forest succession. In a study from Canada, no differences were found in neither species richness nor composition between 35–45 year old forests regenerating after clear-cutting, forest fire and insect outbreak, and mature managed (>75 yrs old) forests (Schmalholz, Hylander & Frego, 2011). In another study from Canada, bryophyte richness increased with higher levels of canopy retention and was positively correlated with local abundance of coniferous trees (Caners, Macdonald & Belland, 2010; Bartels *et al.*, 2018). The sparse results may suggest that clear-cutting with tree retention may function as lifeboats to some epiphytic bryophytes.

A myriad of **endophytic** fungi (Table 1) live inside plants (Porras-Alfaro & Bayman, 2011), but how this largely hidden diversity is affected by forest management is scarcely addressed. Helander *et al.* (2006) compared endophytic fungi associated with silver birch (*Betula pendula*) in Finland. They observed that endophyte abundance and species composition significantly differed among leaves from seedling stands, mature managed (90-130 yrs) and old-growth (122-184 yrs) forests. Species richness was similar between the forest types.

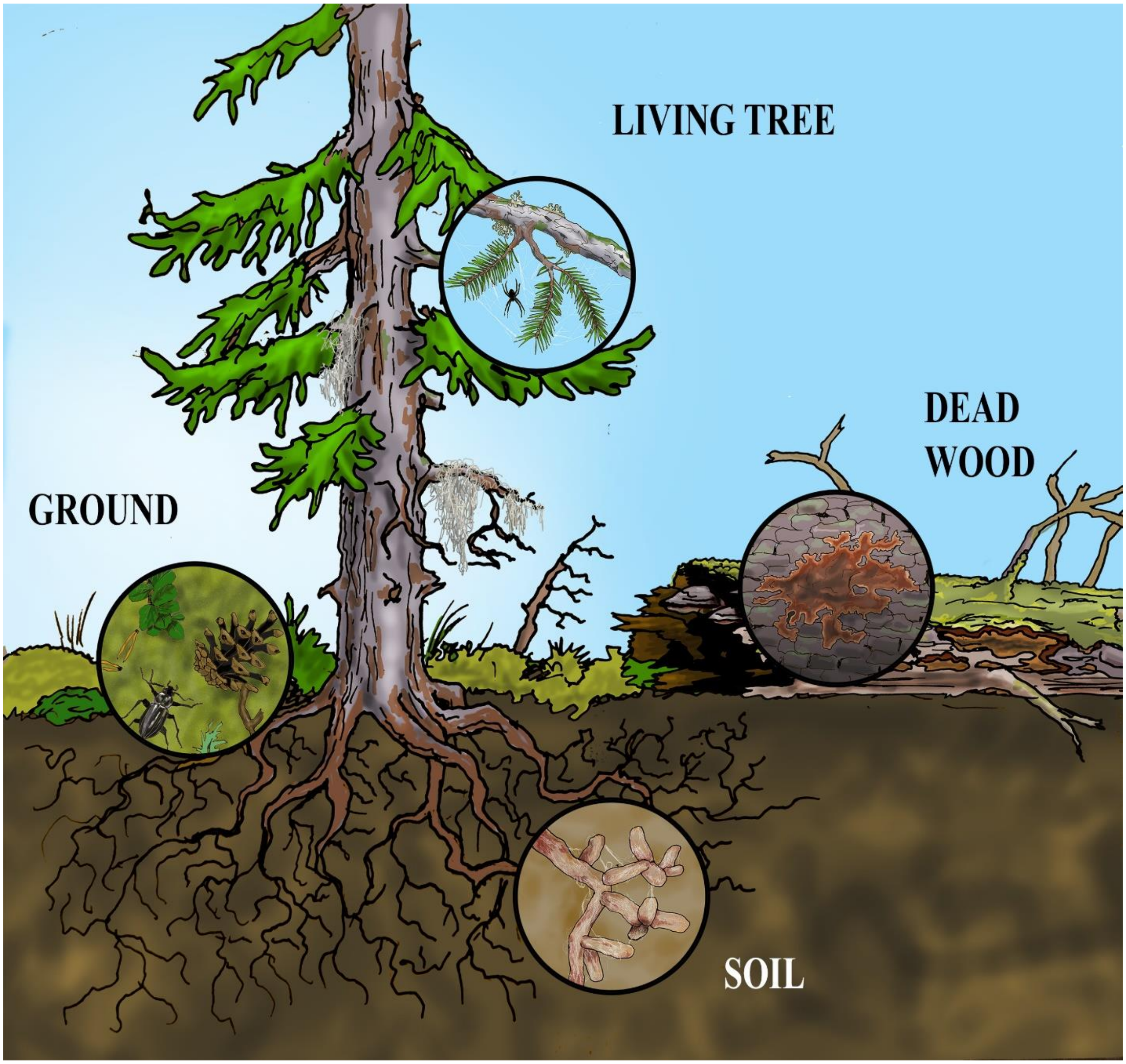


Figure 2. We focus on boreal forest biodiversity in four major substrates: living trees, dead wood, ground and soil. Some species groups that are reviewed in regards to their responses to clear-cutting are highlighted – epiphytic lichens, canopy spiders, saproxylic fungi and epixylic bryophytes, epigeic beetles and ectomycorrhizal fungi.

(c) Arthropods

Clear-cutting has an immediate effect on arthropods in tree canopies, e.g. mites, spiders and herbivorous insects, by direct removal of their habitat. However, the ability of arthropod communities to reestablish during forest succession has rarely been studied. In mixedwood forests, spider communities did not differ nine years after clear-cutting with 20% tree retention compared to primary forests (Pinzon, Spence & Langor, 2011). In western Canada, Behan-Pelletier & Winchester (1998) collected oribatid mites from the forest floor and trees of six-year-old clear-cuts and old-growth Sitka spruce (*Picea sitchensis*)-dominated forests. Only 16 out of 34 recorded species were found both in the old-growth canopy and the clear-cut. Furthermore, the old-growth forest had higher oribatid species richness compared to the clear-cuts.

No study of long-term effects of clear-cutting on canopy arthropods is known to us. However, old trees of high naturalness seem to be important. Pettersson *et al.* (1995) found five times as many arthropod individuals per Norway spruce branch in the primary than old-growth forests (80-128 yrs) subjected to selective loggings and thinning in northern Sweden. This was attributed to differences in epiphytic lichen abundance, which provide shelter, food and hunting grounds for arthropods. Indeed, larger and more web-building spiders were found in the lichen-rich primary forests (Pettersson, 1996). In coastal boreal forests in Norway with a history of selective logging, Thunes, Skarveit & Gjerde (2003) found large differences in species composition of canopy arthropods from old (>250 yrs old) and mature (60-120 yrs old) Scots pine trees. No difference was found in species richness.

As many caterpillars (Lepidoptera) feed on tree foliage, their communities are structured by the identity of the dominating tree species (Franklin *et al.*, 2003). In a review, Summerville & Crist (2008) found strong effects of clear-cutting on moth communities and declines in species richness in northeastern North America. Although most reviewed studies were from temperate forests, one found decreased species richness and altered compositions of geometrid moths in clear-cut compared to unlogged red spruce (*Picea rubens*)-dominated forests (Thomas, 2002).

(2) Dead wood

(a) General patterns

Dead wood is a substrate with a high number of associated species, mainly due to the many niches that it provides (Stokland *et al.*, 2012). Essentially, the dead wood characteristics which provide different habitats for species and that have been addressed in different studies include: tree species, decay stage, wood diameter, cause of tree death, whether the logs are standing or downed, bark cover and moisture content (Hagge *et al.*, 2019; Löfroth *et al.*, 2023; e.g. Langor *et al.*, 2008; Stokland *et al.*, 2012).

Since the volume and the variation in dead wood characteristics differ between old-growth and managed forests, we can expect a difference in the diversity of **saproxylic** and **epixylic** (Table 1) species (Stokland *et al.*, 2012; Siitonen, 2001; Hekkala *et al.*, 2023; Löfroth *et al.*, 2023; Hagge *et al.*, 2019). This is supported by Siitonen (2001), who found that 8 of 13 reviewed studies reported 18-75% higher richness in old-growth than in mature managed forests, while two studies showed no difference.

(b) Fungi

Along with beetles, fungi are the most diverse and well-studied groups of saproxylic species. In a synthesis combining 76 studies of saproxylic fungi, 72-100% more species were found in old-growth than in mature managed forests, a pattern that was even more pronounced for red-listed fungi (Junninen & Komonen, 2011). Indeed, results from fruit body surveys in Finland and northern Russia have shown lower fungal richness in mature managed or younger clear-cut forests, compared to old-growth forests (Juutilainen *et al.*, 2014; Nordén *et al.*, 2013; Purhonen *et al.*, 2021; Ylisirniö *et al.*, 2012; Penttilä, Siitonen & Kuusinen, 2004). Fungal communities differed both between formerly clear-cut (up to 44 yrs old) and old-growth forests (Ylisirniö *et al.*, 2012; Juutilainen *et al.*, 2014). In other studies, community composition was driven by management intensity (number of cut stumps) (Penttilä *et al.*, 2004; Purhonen *et al.*, 2021). Runnel & Lõhmus (2017) studied saproxylic fungal communities in hemiboreal forests of Estonia that had been clear-cut 65-95 years ago, then naturally regenerated and supplied with dead wood. Mature clear-cut forests could host old-forest species if dead wood volumes were high. Despite this, fungal species richness was lower (except dry oligotrophic *Vaccinium idaea*-type sites), and community composition altered, in formerly clear-cut compared to old-growth forests (Runnel & Lõhmus, 2017).

Suominen, Junninen & Kouki (2019) observed that dead wood harvest residues in clear-cuts could host species-rich assemblages of fungi. Indeed, dead wood volume is a strong predictor of species richness of saproxylic fungi in boreal forests (e.g. Hottola, Ovaskainen & Hanski, 2009; Juutilainen *et al.*, 2014). Moreover, variation in dead wood decay stages, sizes and tree species are also drivers of saproxylic fungal diversity (Tomao *et al.*, 2020; Küffer & Senn-Irlet, 2005; Hart *et al.*, 2023; Nordén *et al.*, 2013). Rare and red-listed fungi respond particularly strongly to the abundance of large dead wood logs (Hottola *et al.*, 2009; Nordén *et al.*, 2013). Species that are specialized to grow on rare structural elements, such as kelo trees (Niemelä *et al.*, 2002), are declining along with their substrate.

(c) Beetles

Clear-cutting also affects saproxylic beetle communities. Several studies have observed different species compositions between old-growth and clear-cut forests, both in the short- (Stenbacka *et al.*, 2010; Sippola, Siitonen & Punttila, 2002; Jacobsen *et al.*, 2020) and long-term (Jacobsen *et al.*, 2020; Stenbacka *et al.*, 2010; Bishop, 1998) after cutting (Table 3).

Red-listed saproxylic beetle species are more common in old-growth than in former clear-cut forests (Jacobsen *et al.*, 2020; e.g. Stenbacka *et al.*, 2010). The effect of clear-cutting on overall saproxylic beetle richness, however, is inconclusive, and this might reflect limitations in sampling methods. Relative to traps in old-growth forests, Jacobsen *et al.* (2020) found higher species richness in traps on recent clear-cuts and lower richness in traps in mature clear-cuts. Stenbacka *et al.* (2010) observed a richness decrease 30 years after clear-cutting in unthinned forests relative to old-growths, but no effect after 53 years in thinned forests. Two other studies found no change in species richness after clear-cutting (Bishop, 1998; Sippola *et al.*, 2002). Overall, responses to forestry may be especially difficult to detect for beetles, as a coverage of 400 species per sample may be necessary to represent rare species (Martikainen & Kouki, 2003). Sampling of saproxylic beetles is usually done by window traps, a sampling method influenced by ambient temperature and ease of flight of adult beetles. Thus, a higher species richness in the warmer and more open clear-cuts does not necessarily represent breeding populations in the stand, nor larvae in their main habitats. It will likely include species searching for dead wood units that might not be present.

Saproxylic beetles from window traps show marked differences in species composition between sun-exposed and shaded dead wood habitats (Seibold *et al.*, 2016; Hjältén *et al.*, 2012; Vindstad *et al.*, 2020). Many species are adapted to open areas with high volumes of dead wood, mimicking the early successional habitats that appear after natural disturbances (Vindstad *et al.*, 2020; Jonsell, Weslien & Ehnström, 1998).

Dead wood volume increases the species richness of saproxylic beetles (Stenbacka *et al.*, 2010; Gibb *et al.*, 2013; Martikainen *et al.*, 2000), but dead wood characteristics are as important. For instance, beetle richness differs strongly between dead wood from coniferous and broadleaved trees (Seibold *et al.*, 2016; Langor *et al.*, 2008). The importance of tree species decreases later in the decay process, thus variation in decay stage, diameter and type (standing vs downed) are other important drivers of saproxylic beetle richness (Ehnström & Axelsson, 2002; Stokland *et al.*, 2012; Hjältén *et al.*, 2012; Lee, Spence & Langor, 2014). Saproxylic beetle communities also depend on the fungal community composition (Weslien *et al.*, 2011; Birkemoe *et al.*, 2018).

(d) True flies and wasps

While wasps (Hymenoptera) and true flies (Diptera) are extremely abundant and important in the dead wood ecosystems, their responses to forest management have been poorly addressed. In one notable exception, Økland (1994) found altered species assemblages of fungus gnats (Diptera: Sciaroidea) in old-growth Norway spruce forests to forests that were clear-cut 70-120 years earlier. He observed lower richness of saproxylic, as well as soil-dwelling, species of fungus gnats, both in mature and in recent clear-cut forests. Fungus gnat richness increased with continuous presence of tree cover and dead wood over the whole range of decay stages (Økland, 1996).

For saproxylic parasitoid wasps, species richness increases with increasing dead wood volume (Gibb *et al.*, 2008; Hilszczański, 2018; Jonsell *et al.*, 2023). While species richness does not seem to be affected by management history, species composition is structured by this factor (Hilszczański, 2018), reflecting that different parasitoid assemblages have different developmental strategies.

Many species of hoverflies (Diptera: Syrphidae), bees and stinging wasps (Hymenoptera: Aculeata) use dead wood holes and crevices as nesting sites (Bogusch & Horák, 2018). Suitable nest holes appear 9–13 years after logging (Westerfelt *et al.*, 2015). In a Finnish field experiment in which forest complexity was manipulated, both bee and hoverfly richness increased with a higher variation of dead wood and floral food resources 13 years after harvesting (Rodríguez & Kouki, 2017). Interestingly, richness was higher in harvested sites compared to old-growth controls. Species richness of wood-dwelling hoverflies was also higher in recent clear-cuts and retention plots than in unharvested controls in Canada (Deans *et al.*, 2007). Early successional forest with high flower abundance may benefit wood-dwelling pollinating insect species as long as dead wood is available.

(e) Lichens and bryophytes

Numerous lichen species are found exclusively on dead wood, named **epixylic** lichens, each with preferences for specific dead wood characteristics (Spribille *et al.*, 2008). Three studies indicate long-term changes in community composition of this group due to logging, though the trajectory of these changes remains uncertain (Lommi *et al.*, 2010; Söderström, 1988; Bell-Doyon *et al.*, 2024). Söderström (1988), studying epixylic bryophytes and lichens of Norway spruce forests in northern Sweden, found that the lichen species were divided according to their preferences for either old-growth forests or an adjacent site that was clear-cut 50–60 years earlier and then thinned on several occasions. While only one species preferred the old-growth, eight (mainly *Cladonia* spp.) preferred the formerly clear-cut forest. Söderström (1988) attributes this to the preference of most epixylic lichens for drier, more open forests. Bunnell *et al.* (2008), studying epixylic lichens in mixedwood forests of western Canada, observed a shift in community composition towards crustose lichen species in old-growth compared to 20– to 30–year-old formerly clear-cut forests. No difference in species richness was found. These results suggest that clear-cutting has different effects on epixylic lichens in open, drier pine forests than in more closed, mesic spruce forests.

For epixylic bryophytes, several studies have found reduced species richness and/or altered community composition 35–70 years after clear-cutting as compared to old-growth forests (Dynesius *et al.*, 2021; Andersson & Hytteborn, 1991; Schmalholz *et al.*, 2011; Söderström, 1988; Rudolphi & Gustafsson, 2011; Dynesius, 2015; Bell-Doyon *et al.*, 2024). However, the differences may weaken when dead wood volume is taken into account (Rudolphi & Gustafsson, 2011). A comparison between 28 coniferous forests (1 ha) in northern Sweden, of which one half was old-growth and the other half formerly clear-cut (40–60 yrs ago), revealed higher epixylic bryophyte richness and cover in the old-growth forests (Dynesius et al. 2021). The difference was attributed to the availability of dead wood habitats. In his study of spruce forests in the same region, Söderström (1988) found that six liverwort species clearly preferred or were confined to old-growth forests while none preferred the mature clear-cut forests. For mosses, no clear difference was found. Studies of epixylic bryophytes clearly indicate that several species are disfavoured by clear-cutting, in particular drought-sensitive liverworts.

(3) Ground

(a) Vascular plants, bryophytes, lichens and fungi

Epigeic vascular plants (Table 1), bryophytes and lichens form the understory vegetation of boreal forests that varies regionally and locally along several environmental gradients (Halvorsen *et al.*, 2020; Tuhkanen, 1984). Vascular plant richness increases from dry-and-poor pine forests to mesic-and-rich spruce (and broadleaved) forests (Esseen *et al.*, 1997). Bryophytes are replaced by lichens as the dominating group in drought-exposed sites. Successional patterns of boreal forest plant communities after clear-cutting are well known: vascular plant richness increases in the short term after cutting and peaks during mid-succession (Hart & Chen, 2006).

Long-term effects of clear-cutting on vegetation have been addressed in very few studies. Økland *et al.* (2003) investigated the understory vegetation in Norwegian boreal forests with different forest histories (clear-cut 60 yrs ago, selectively logged, primary). Weak differences in the responses of vascular plants, bryophytes and lichens were observed. The authors concluded that former logging had a very weak long-term impact on vegetation, operating mainly via effects on tree-layer structure during forest regrowth. Interestingly, a recent resurvey of the south-facing plots revealed that the vegetation community composition had converged to the primary forest state 86 years after clear-cutting (Knapstad, 2024). In the eastern part of European Russia, Likhanova *et al.* (2023) compared the vegetation of primary Siberian spruce (*Picea obovata*)-dominated forests to areas that were clear-cut 2, 18 and 50 years earlier (winter clear-cutting). Their sparse material indicate that the richness of understory vascular plants recovered rapidly after clear-cutting while the richness of bryophytes and lichens were still lower in the formerly clear-cut forest after 50 years of succession. The mature clear-cut communities had converged towards the primary forest state, although slight differences were still seen in community composition (Likhanova *et al.*, 2021).

Long-term effects of clear-cutting on epigeic lichens appear not to have been specifically studied. Lafleur *et al.* (2016) observed no differences between *Cladonia* lichen species 4–13 yrs after clear-cutting and fire. The slow growth of the dominating *Cladonia* lichens (e.g. Scotter, 1963) suggests locally slow recovery of the lichen cover if physically disturbed, while a more open tree layer is not expected to have a negative effect as such on epigeic lichens.

For epigeic bryophytes in particular, studies indicate long-term effects on community composition, while effects on species richness are inconclusive (Paquette *et al.*, 2016; Dynesius *et al.*, 2021; Økland *et al.*, 2003; Dynesius, 2015; Schmalholz *et al.*, 2011; Likhanova *et al.*, 2023; Bell-Doyon *et al.*, 2024). However, the abovementioned resurvey from Norway (Knapstad, 2024) show that communities could recover 86 years after clear-cutting (epigeic bryophytes constituted ⅔ of the species community). Microclimate may, furthermore, be important for bryophyte resilience to clear-cutting. In northern Sweden, Dynesius (2015) observed reduced species richness in upland, but not in streamside forests, 30–50 years after clear-cutting; bryophyte richness had still not recovered in upland forests during a resurvey 15 years later (45–65 yrs after cutting).

Davey, Kauserud & Ohlson (2014) compared fungal communities associated with a moss species (*Hylocomium splendens*) in four different successional forest age classes, ranging from clear-cut sites to old-growth forests. Fungal richness was slightly higher in the old-growth forests. Furthermore, a distinct difference in fungal community composition was observed between forest ages, indicating that mosses in different forest ages host different fungal communities (Davey *et al.*, 2014).

(b) Arthropods

Long-term effects of clear-cutting on epigeic arthropods have been addressed in several studies, in particular from Canada, where communities have been studied more than 50 years after clear-cutting (Koivula, Kukkonen & Niemelä, 2002; Belluz *et al.*, 2022; Johansson *et al.*, 2016; Le Borgne *et al.*, 2018; Venier *et al.*, 2017). The most thoroughly studied groups are spiders, ground (Carabidae) and rove (Staphylinidae) beetles, which are highly abundant predatory groups on the boreal forest floor.

Following clear-cutting, epigeic beetle and spider richness increase. Moreover, the community compositions are highly altered due to immigration of open-habitat and generalist species, and disappearance of many forest species (Niemelä *et al.*, 2007; Koivula *et al.*, 2019; Larrivée, Fahrig & Drapeau, 2005; Buddle, Spence & Langor, 2000). The successional trajectories of epigeic beetle communities follow those of the vegetation. In particular, the communities start to converge towards the predisturbance (i.e. old-growth forest) state when the canopy closes, typically two or three decades after the disturbance took place (Koivula *et al.*, 2002; Niemelä *et al.*, 2007). Several studies have documented that epigeic beetle communities continue towards recovery in the long-term (53–66 yrs after cutting; Table 3), both from Fennoscandia (Koivula *et al.*, 2002; Johansson *et al.*, 2016) and Canada (Belluz *et al.*, 2022; Le Borgne *et al.*, 2018).

Long-term responses of epigeic spider communities are less clear. In Canada, two studies of spider assemblages in trembling aspen (*Populus tremuloides*)-dominated (Buddle *et al.*, 2000) and coniferous (McIver, Parsons & Moldenke, 1992) forest floors, show signs of convergence with pre-harvest compositions 30 years after clear-cutting. In contrast, in jack pine-dominated forests, spider, ground and rove beetle communities were more similar 3 and 51 years after clear-cutting, than 92 years after a forest fire (Venier *et al.*, 2017). Successional rates might, however, depend on soil moisture content. McIver *et al.* (1992) found a higher rate of epigeic spider succession in wet than dry sites after clear-cutting.

Although the overall epigeic beetle and spider communities may recover over time, species confined to old-growth forests may not. Several ground beetle species are more commonly observed in old-growth than in previously clear-cut forests (Niemelä *et al.*, 2007; Buddle *et al.*, 2006; Johansson *et al.*, 2016). Moreover, many species of rove beetles struggle to recover after clear-cutting due to low amounts of dead wood (Venier *et al.*, 2017; Klimaszewski *et al.*, 2018). For spiders, no old-growth specialists have yet been identified, but such forests apparently host unique assemblages: more web-building spider families are found in old-growth than in managed forests (Pajunen *et al.*, 1995; Larrivée *et al.*, 2005).

Mound-building wood ants (red wood ants) are keystone species and ecosystem engineers in boreal forests (Wardle *et al.*, 2011; Stockan & Robinson, 2016). Species that build long-lived and large nests with a connected network of mounds, such as *Formica aquilonia*, have higher densities in older forests, whereas species with single and smaller nests, such as *F. lugubris*, dominate in younger forests (Punttila, 1996). Clear-cutting likely has negative short-term effects on all wood ant species (Stockan & Robinson, 2016), which may be because ants depend on large amount of honeydew from aphids in tree canopies. In central Finland, more than 50% of all *F. aquilonia* nests were abandoned four years after clear-cutting, compared to 2% in unlogged controls (Sorvari & Hakkarainen, 2007).

Pollinating insect occurrence is driven by the availability of flowering plants, but also by warm microclimate and availability of nesting habitat, such as dead wood (see Section IV.2.d) and exposed soil (Milberg, Eriksson & Bergman, 2021; Willmer, 2011). Clear-cutting creates early successional habitat with tilled soil, increased temperatures and high light availability which increases the growth of flowering plants. In a heavily managed Norway spruce forest landscape in southeastern Norway, Nielsen & Totland (2014) found more species of flower-visiting insects (representing several orders) in recent clear-cuts than in old-growth controls. Species richness was highest in sites that were clear-cut 15–35 years earlier. Increased richness in the short term after clear-cutting have been shown for several groups of pollinating insects: hoverflies (Deans *et al.*, 2007; Rodríguez & Kouki, 2017), bees (Rodríguez & Kouki, 2017; Andersson *et al.*, 2022; Korpela, Hyvönen & Kuussaari, 2015) and butterflies (Andersson *et al.*, 2022; Korpela *et al.*, 2015). However, we are not aware of any studies looking at long-term effects of clear-cutting on the biodiversity of pollinating insects in boreal forests.

(4) Soil

(a) Ectomycorrhizal fungi

Clear-cutting sever the symbiotic partners of ectomycorrhizal (ECM) fungi – living tree roots. Further, the following changes in soil temperature and chemistry after cutting are important drivers of ECM communities (Jones, Durall & Cairney, 2003). Several studies have documented a strong short-term effect of clear-cutting on the fungal community composition (Jones *et al.*, 2003; Rodriguez-Ramos *et al.*, 2021) and declines in species diversity (Wilhelm *et al.*, 2017; Rodriguez-Ramos *et al.*, 2021; Sterkenburg *et al.*, 2019). Survival, biomass and relative abundance of ECM fungi are also reduced (Kyaschenko *et al.*, 2017; Parladé *et al.*, 2019; Bååth, 1980). Some fungi may, however, survive in the soil for a few years after removal of their main hosts, either as mycelia cut off from their host plant, as dormant spores or by forming symbioses with other plants (Heinonsalo & Sen, 2007; Sterkenburg *et al.*, 2019; Jones *et al.*, 2003).

Studies of the effect of tree retention on ECM fungi indicate that the most frequent species may be retained, while more infrequent species are lost with increasing levels of tree removal (Heinonsalo & Sen, 2007). Tree retention patches with 20 m in diameter were insufficient to ensure continuity of old-growth-dependent species (Kranabetter, De Montigny & Ross, 2013). Up to ~50% tree retention, and a maximum 15 m spacing between trees, may be needed to maintain the integrity between tree roots and their ECM fungal partners (Prescott & Grayston, 2023; Sterkenburg *et al.*, 2019).

A few studies suggest that clear-cutting has long-lasting effects on ECM fungal communities. Varenius *et al.* (2016) compared ECM fungal communities in old-growth and in previously clear-cut (50 yrs ago) Scots pine forests, and found no difference in the overall species richness. However, community composition differed between the two, both when using fruit body and DNA-based data (Varenius *et al.*, 2016). In congruence, Bell-Doyon *et al.* (2022) observed altered compositions of ECM fungi in previously clear-cut (50 yrs ago) balsam fir (*Abies balsamea*)-dominated forests. Species diversity was higher than in the old-growth forest, but the effect was not significant. This suggests an effect of clear-cutting on the community composition rather than on species richness *per se*. Still, these effects might differ between forests with shorter and longer histories of intensive forestry (Mielke, 2022), as mycorrhizal species richness is positively correlated with stand age (e.g. Peter, Buée & Egli, 2013). Many ECM species have strict preferences for old-growth forests, for example several species within the genus *Cortinarius* (Hasby, 2022; Varenius *et al.*, 2016) and the iconic *Tricholoma matsutake* (Risberg, Danell & Dahlberg, 2004).

(b) Other fungi and bacteria

A few studies from North America have used DNA-based data to investigate the effects of clear-cutting on the overall soil fungal community, as well as bacteria, and one has looked at long-term effects (Bell-Doyon *et al.*, 2022). In the short term after clear-cutting, the immediate pulse of harvest residues and reduced photosynthate input from living trees, lead to a community shift of soil fungi favouring saprotrophic fungi (Rodriguez-Ramos *et al.*, 2021; Rähn *et al.*, 2023). Two studies observed stronger effects of clear-cutting on the overall fungal community compared to bacteria (Hartmann *et al.*, 2012; Leung *et al.*, 2016). Still, general reponses are difficult to infer as they clearly differ between functional groups (Rodriguez-Ramos *et al.*, 2021). Responses of these groups may also depend on the techniques used during logging, as soil compaction is known to affect both fungal and bacterial communities in the soil (e.g. Hartmann *et al.*, 2014).

In contrary to ECM fungi (reviewed above), the response of the overall soil fungal diversity to clear-cutting is inconclusive. In balsam fir forests of eastern Canada, Bell-Doyon *et al.* (2022) observed altered fungal community compositions 50 years after clear-cutting. Although they observed increased alpha diversity, the effect was not significant. Two studies compared different intensities of clear-cutting (three tiers of organic matter removal), 10–15 years after logging (Hartmann *et al.*, 2012; Wilhelm *et al.*, 2017). They found increased alpha diversity of soil fungi and altered community composition. However, Rodriguez-Ramos *et al.* (2021) did not find an effect on species richness nor composition, of saprotrophic, AM or pathogenic fungi, six years after clear-cutting.

No effect has been observed on bacterial species evenness 10–15 years after logging (Hartmann *et al.*, 2012; Leung *et al.*, 2016) or alpha diversity 50 years after logging (Bell-Doyon *et al.*, 2022). However, bacterial community compositon was signficantly altered in all cases.

(c) Invertebrates

Few studies address effects of clear-cutting on soil invertebrate diversity in boreal forests, partly due to difficulties with identification, and even less studies are available on effects more than five years after cutting. In Norway spruce forests of Finland, Siira-Pietikäinen & Haimi (2009) found strong declines in abundance, and altered species composition, of soil macroarthropods 10 years after clear-cutting; effects were not mitigated by 50% tree retention. Other studies, however, indicate that some faunal groups recover to pre-harvest levels over time (Kudrin 2023, Marshall 2000). One such group is Enchytraeidae (Annelida) that quickly increases in abundance after cutting, then recovers to pre-logging levels in the first decade of succession (Siira-Pietikäinen & Haimi, 2009; Malmström *et al.*, 2009; Kudrin *et al.*, 2023; Huhta, Nurminen & Valpas, 1969). For springtails (Collembola), both positive (Malmström *et al.*, 2009; Huhta *et al.*, 1969) and negative (Bird & Chatarpaul, 1986) short-term abundance and richness responses to clear-cutting have been reported. Like enchytraeids, the effects of clear-cutting on springtails seem to weaken or level out after ten years (Malmström *et al.*, 2009; Marshall, 2000; Siira-Pietikäinen & Haimi, 2009; Huhta *et al.*, 1969).

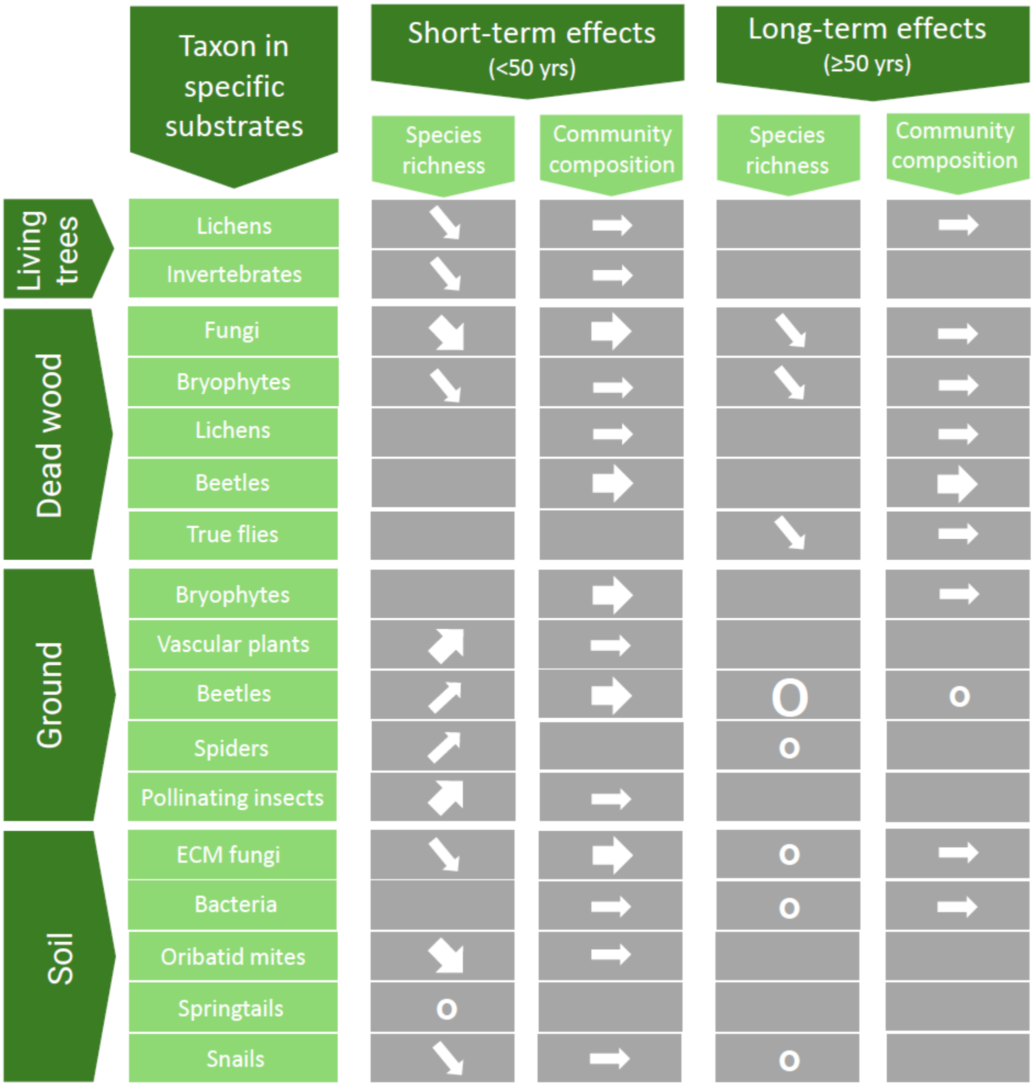
Several studies have observed negative short-term effects (≤10 yrs) of clear-cutting on oribatid mites, both when looking at the number of species and individuals (Malmström *et al.*, 2009; Marshall, 2000; Kudrin *et al.*, 2023; Huhta *et al.*, 1969; Lóšková *et al.*, 2013). Changes in microclimate have been mentioned among explanations (Marshall, 2000). A delayed response may be expected, either because oribatid mites develop slowly (Danks, 2006) or due to changes in availability of their fungal food (Marshall, 2000). Studies of Mesostigmata or Trombidiformes mites showed no effect of clear-cutting (Malmström *et al.*, 2009; Huhta *et al.*, 1969).

Results for soil nematodes are inconclusive. Combining morphological and DNA-based data, George & Lindo (2015) did not detect an effect of recent clear-cutting on richness or community composition of soil nematodes. In line with this, Sohlenius (2002) found no difference in richness

3–12 years after clear-cutting. In western Canada, Forge & Simard (2001) observed an overall increase in nematode alpha diversity after clear-cutting, but a decrease in the diversity of omnivore and predatory nematodes. Indeed, functional groups may be affected differently; low proportions of fungivores compared to bacterivores have been observed in previously clear-cut (3–12 yrs ago) forests (Sohlenius, 2002).

Land snails (Mollusca) are rarely included in soil faunal inventories, but their responses to forestry have been addressed on some occasions. While one study found no difference in species richness nine years after clear-cutting and planting in central Canada (Hawkins *et al.*, 1997), two studies found reduced richness 2–7 years after clear-cutting in Sweden (Hylander, 2011; Hylander, Nilsson & Göthner, 2004). However, snail species richness may recover in the long term (Remm & Lõhmus, 2016; Ström, Hylander & Dynesius, 2009). Ström *et al.* (2009) observed higher richness 40–60 years after clear-cutting compared to old-growth, based on 16 snail species. In hemiboreal forests, no difference was found in richness nor community composition (Remm & Lõhmus, 2016); the impact of clear-cutting on soil-dwelling snails may depend on moisture content and bryophyte cover (Hylander *et al.*, 2004; Remm & Lõhmus, 2016).

Table 3. Short- and long-term (less or more than 50 yrs) effects of clear-cutting to boreal forest species richness and community composition for species groups from four major substrates: living trees, dead wood, ground and soil. Arrows up/down = increase/decrease in alpha diversity or richness, horizontal arrow = altered community composition (beta diversity), 0 = recovery or no effect observed, and blank boxes = data missing or inconclusive evidence. Thicker symbols = stronger scientific support. Reviewed taxa not included due to lack of data: endophytic fungi, epiphytic bryophytes, epixylic lichens, epigeic lichens, ants, soil enchytraeids, soil nematodes, other soil fungi.



	Taxon in specific substrates	Short-term effects (<50 yrs) Species richness	Short-term effects (<50 yrs) Community composition	Long-term effects (≥50 yrs) Species richness	Long-term effects (≥50 yrs) Community composition
Living trees	Lichens	↘	→		→
	Invertebrates	↘	→		
Dead wood	Fungi	↘	→	↘	→
	Bryophytes	↘	→	↘	→
	Lichens		→		→
	Beetles		→		→
	True flies			↘	→
Ground	Bryophytes		→		→
	Vascular plants	↗	→		
	Beetles	↗	→	O	o
	Spiders	↗		o	
	Pollinating insects	↗	→		
Soil	ECM fungi	↘	→	o	→
	Bacteria		→	o	→
	Oribatid mites	↘	→		
	Springtails	o			
	Snails	↘	→	o	

(5) Landscape dynamics – connectivity

Clear-cutting changes the spatial distribution of habitats at the landscape scale. This fragmentation of continuous boreal forest landscapes has two main effects: reduced abundance of old-growth forest habitats and isolation of individual forest patches (see chapter II.4).

According to *metapopulation theory*, local species extinctions are frequent while regional extinctions are prevented by dispersal between habitat patches within the landscape (Levins, 1969; Hanski, 1998). Clear-cutting might hinder such recolonizations by reducing the amount of, and connectivity among, habitats.

Forest species with high dispersal abilities may persist in the landscape as long as suitable habitats are constantly present. On the other hand, species that have adapted to use relatively stable habitats, such as dead wood in late decay stages, generally have lower dispersal abilities (stability-dispersal model; Southwood, 1977; Percel, Laroche & Bouget, 2019). Consequently, these species could become dispersal-limited and face population declines.

(a) Fungi

Generalist species of saproxylic fungi are frequently present in fragmented forests and do not seem to be limited by connectivity to old-growth forests (Moor *et al.*, 2021; Nordén *et al.*, 2013). However, the opposite appears to be the case for specialist fungal species. The abundance of red-listed saproxylic fungi in Fennoscandia, in general, respond positively to increased dead wood volume, forest age and habitat connectivity, and negatively to high logging intensity (basal area of cut stumps) (Nordén *et al.*, 2018; Nordén *et al.*, 2013; Moor *et al.*, 2021; Jönsson, Edman & Jonsson, 2008; Sverdrup-Thygeson & Lindenmayer, 2003; Hottola *et al.*, 2009). Nordén *et al.* (2013) showed that the expected number of red-listed species can be more than ten times higher in well-connected than in fragmented landscapes.

The dead wood specialist, *Phlebia centrifuga*, has been shown to be dispersal-limited even within small spatial scales (Norros *et al.*, 2012; Moor *et al.*, 2021). *Phellopilus nigrolimitatus*, typically fruiting on large-diameter dead wood of late decay stages, has likely experienced a decline in population size due to a reduction in habitat quality (Stokland & Kauserud, 2004; Sønstebø *et al.*, 2022; Sverdrup-Thygeson & Lindenmayer, 2003). The occurrences of two other saproxylic species, *Phellinus ferrugineofuscus* and *P. viticola*, depend on the connectivity of old Norway spruce forests (Mair *et al.*, 2017; Nordén *et al.*, 2020). Surprisingly, the colonization rates of ten dead wood specialists were not related to landscape-scale connectivity of old growth forest in Finland (Moor *et al.*, 2021). The authors argue that low statistical power and using a metric that was too coarse to detect connectivity of dead wood habitats may have hampered the results.

(b) Lichens and bryophytes

Observations from boreal forests indicate that dispersal is a limiting factor for establishment of lichens associated with old-growth forests (Hilmo & Såstad, 2001; Sillett *et al.*, 2000; Esseen *et al.*, 2023). In northern Sweden, dispersal limited reestablishment of epiphytic lichens in previously clear-cut forests (35–78 yrs old), even when adjacent old-growth forests served as sources of propagules (Dettki, Klintberg & Esseen, 2000). Bartemucci, Lilles & Gauslaa (2022) found recolonization of *Lobaria pulmonaria* 25 years after clear-cutting in western Canada. However, overall species richness of epiphytic lichens declined with increasing distance to old-growth forests and size of the clear-cut stand. The importance of dispersal limitation for lichens is inconsistent, and clearly vary between different species and regions (e.g. Gjerde *et al.*, 2015; Bartemucci *et al.*, 2022).

Few studies have investigated the effect of fragmentation on boreal forest bryophytes. In a study on epixylic bryophytes, connectivity to old forest was positively related to the occurrence of five species (Löbel *et al.*, 2018). Furthermore, the response to connectivity depend on reproductive traits: sexually reproducing species tend to be more strongly dispersal-limited than clonal species (Löbel *et al.*, 2018; Löbel, Snäll & Rydin, 2006).

(c) Insects

Available evidence indicates that connectivity to dead wood habitat is important for insects, most notably for red-listed species (Sverdrup-Thygeson, Gustafsson & Kouki, 2014b). Species depending on early-decay dead wood, however, seem to be able to locate new resources at long distances, as predicted by ecological theory (Sverdrup-Thygeson *et al.*, 2014a).

Large-scale (> 100 km^2) landscape connectivity was found to be the main driver of 260 fungal gnat species of different functional guilds in southeastern Norway (Økland, 1996). In western Canada, moth richness was negatively affected by forest fragmentation when measured at several different spatial scales, and the effect was strongest for tree- and shrub-feeding species (Schmidt & Roland, 2006). Forest fragmentation reduces ant population size and favours single-nest species such as *F. lugubris* (Punttila, 1996).

Saproxylic insects may also differ in their responses to landscape features because they prefer different tree species (Jacobsen, Sverdrup-Thygeson & Birkemoe, 2015; Lindbladh *et al.*, 2007). For example, Jacobsen *et al.* (2015) found that while habitat amount was important for beetles in a mixedwood forest, species associated with European aspen responded to habitat at a larger scale than spruce-associated species.

Habitat fragmentation also shapes communities of insects associated with the fruit bodies of saproxylic fungi. The beetle fauna in *Fomes fomentarius* fruit bodies is negatively affected by reduced patch size and increased isolation (Rukke, 2000; Sverdrup-Thygeson & Midtgaard, 1998). Furthermore, food web length decreased with time since isolation in insect communities associated with the red-listed *Fomitopsis rosea*, irrespective of dead wood volume (Komonen *et al.*, 2000).

(6) Landscape dynamics – edge effects

Clear-cutting creates forest edges which affect biodiversity through direct or indirect effects of edge creation, for example physical damage to trees leading to a change in canopy cover, and subsequently, altered species compositions (Harper *et al.*, 2005). The magnitude of these effects on forest biodiversity depends on the contrast between the interior (old-growth) and exterior (clear-cut) end of the edge (Lindenmayer & Fischer, 2013).

(a) Fungi

Strong edge effects close to clear-cut forests have been observed on saproxylic fungi, most notably for rare and red-listed species. Snäll & Jonsson (2001) observed that polypore fungi considered to be of high nature conservation value were less frequent near clear-cut edges than in the interior old-growth forests. Differences in microclimate could account for this finding. Similarly, occupancy of logs by old-growth indicator species was negatively affected by distance to clear-cuts, while the more common species did not show such a response (Siitonen, Lehtinen & Siitonen, 2005; Ruete, Snäll & Jönsson, 2016).

An edge effect of clear-cutting has also been observed for ECM fungi. Hagerman *et al.* (1999) observed that, 2–3 years after clear-cutting, the numbers of active fine roots as well as the richness of ECM fungal species in clear-cuts were significantly reduced with distance from the forest edge.

(b) Lichens, plants and bryophytes

Epiphytic lichens respond to clear-cut edges because of altered microclimate and wind-induced physical damage, but the magnitude of this response varies significantly among species (Esseen & Renhorn, 1998; Hilmo & Holien, 2002). In their study of old-growth Norway spruce forests, Kivistö & Kuusinen (2000) found negative edge effects on species richness in sunny, south-facing edges, but not in north-facing edges. In an experimental study of *Usnea longissima* near Norway spruce forest edges to clear-cuts, Jansson, Palmqvist & Esseen (2009) found highest growth rates with intermediate edge contrast (saplings 3 m tall). They concluded that the species benefitted from the combination of better light availability and increased vegetation shelter. In central Sweden, number of lichen species of conservation concern decreased with edge contrast, while bryophytes were unaffected (Koelemeijer *et al.*, 2022).

In a study of urban forests in southern Finland, edge effects on the understory vegetation penetrated 30 m into the forest interior (Hamberg, Lehvävirta & Kotze, 2009). Hylander (2005) demonstrated reduced growth and cover of two common feathermosses along a gradient from old-growth Norway spruce forest interior to edge to adjacent clear-cuts. The magnitude of the edge effect was larger at south-facing edges.

(c) Invertebrates

Edges created from logging have been shown to influence invertebrate communities in a number of ways. The majority of the existing studies focus on epigeic arthropods, although other invertebrate groups, like soil biota, may also be sensitive to the changes in microclimate that edges produce. Some overall patterns in responses can be related to life history traits. A general review concluded that soil-dwelling and social insects were more negatively affected by anthropogenic edges, while flying species could be favoured by them (Caitano *et al.*, 2020).

Several studies have documented that assemblages of epigeic arthropods, such as spiders and ground beetles, differ between boreal forest interior and open, harvested areas (Pajunen *et al.*, 1995; Larrivée, Drapeau & Fahrig, 2008). While generalist species easily cross the edge, it acts as a filter for interior-forest species of ground beetles (Pajunen *et al.*, 1995; Niemelä, 1997). Wide buffer zones (e.g. 100 m) that reduce edge contrasts may be needed to mitigate the negative effects of edges on forest species.

Pinksen *et al.* (2021) investigated nocturnal macromoth responses to edges in mature managed forests and recent clear-cuts in Canada. The species composition of the edges was intermediate between clear-cuts and mature forests, but differed significantly from adjacent habitats and included many unique species.

V. Potential consequences of clear-cutting to forest biodiversity

The second cycle of clear-cutting in boreal forests has already started, and the area of repeatedly clear-cut forests is expected to increase rapidly over the next few years. Furthermore, old-growth forests are targeted for (first cycle) clear-cutting in many regions, leading to more forest edges and reduced connectivity on the landscape level. Although the consequences of clear-cutting for boreal forest biodiversity are not yet understood, our present knowledge suggests that the outcome may become more severe for each rotation. The basis of this assumption:

(1) Clear-cutting regimes that do not mimic natural disturbance regimes

Boreal forest systems are slow and may be affected by past events for a long time (Kuuluvainen & Aakala, 2011; Ibbe *et al.*, 2011; Bergeron *et al.*, 2017). Thus, some areas may potentially take several hundred years to reach late successional stages with species communities akin to old-growth forests. The frequency (temporal scale), intensity and extent (spatial scale) of clear-cutting is commonly far beyond the range of natural variability in boreal forests. Based on this, and the findings presented in this literature review (Table 3), rotation times of 50–150 years is likely not sufficient for recovery of most boreal species communities.

As another essential difference from natural disturbances, clear-cutting does not produce large amounts of dead wood (Swanson *et al.*, 2011). The current form of forest management will not restore the structural complexity that is characteristic of old-growth boreal forests, including a variation of dead wood characteristics. On the contrary, key structural elements – such as old trees, kelo trees or large-diameter dead wood in late-successional stages – may become even rarer with repeated clear-cutting, imposing even stronger pressures on the species that are associated with these habitats.

(2) Reduced area of old-growth/primary forests and increased area of early successional forests

In fragmented forests, remnant old-growth and primary forests are important because they might act as refugia for species that emigrate from areas where their habitat is depleted. These may include specialist species in particular, as we show for saproxylic fungi (Section IV.5.a).

Based on national databases from Fennoscandia, studies show that old-growth forest has, for the last two decades, been clear-cut, while protected areas have been further fragmented (Ahlström, Canadell & Metcalfe, 2022; Määttänen *et al.*, 2022). Ahlström *et al.* (2022) estimated an annual loss of 1.4% old-growth (here defined as pre-dating 1880) boreal forest in Sweden. In eastern Canada, primary forests have been clear-cut over the last 30 years, in particular targeting the most productive forest areas (Martin *et al.*, 2020). As we are not aware of any policy measure that aims to reduce this, and several countries have not mapped the locations of their remaining old-growth and primary forests, we do not expect these numbers to improve in the near future.

As the area of old-growth forests decreases, it will be replaced by young forest areas (Kuuluvainen & Gauthier, 2018). The impact of this shift in age class distribution may vary depending on the forest history of specific regions. In parts of Canada, where stand-replacing crown fires were historically frequent (e.g. cycles of 39–96 years depending on vegetation type in northern Alberta (Larsen, 1997)), early successional forests were common (Shorohova *et al.*, 2011). Hence, we could expect biodiversity in these regions to be more resilient to shifts in age class distributions. However, the proportion of old-growth forest in the landscape is still below historical levels (Shorohova *et al.*, 2011), making it difficult to predict the future responses of species in these areas.

Many forest species are adapted to the open and warm habitats of early forest succession. Indeed, our findings suggest increased species richness of vascular plants, epigeic arthropods and pollinating insects in the short-term after clear-cutting compared to old-growth forests (Table 3). However, the different legacies following natural disturbances and clear-cutting could mean that some species are excluded. Indeed, community composition of several taxa still differ in early successional stages after natural disturbances compared to clear-cutting (Niemelä *et al.*, 2007; Larrivée *et al.*, 2005; Johansson *et al.*, 2020; Schmalholz *et al.*, 2011). Emphasis on retaining natural legacies and variability after clear-cutting could be valuable for the conservation of species adapted to early succession (Rodríguez & Kouki, 2017).

(3) Accumulation of extinction debts

Fragmentation of habitat can, according to classical ecological models, lead to time-delayed extinction of species in remnant habitat patches – an *extinction debt*. Recurrent fragmentation in a landscape (Tilman *et al.*, 1994) and potentially, repeated clear-cutting events, can accelerate this effect. According to Hanski & Ovaskainen (2002), extinction debts can be seen by the many rare species present in fragmented old-growth forests, such as beetles in northeastern Finland. Similarly, three out of four fungal species associated with dead wood in old-growth forests showed a time-lagged negative response to landscape changes in eastern Finland (Gu, Heikkilä & Hanski, 2002). Berglund & Jonsson (2005) also found that fungal richness decreased in response to changes in forest and landscape structures in northern Sweden. Lichens associated with kelo trees may also be facing an extinction debt in central Sweden (Ekström *et al.*, 2023).

One underlying cause of these extinction debts can be a decline in genetic diversity. Habitat fragmentation will reduce the chances of sexual reproduction, increase inbreeding, and thus reduce genetic variation in populations. The saproxylic fungus *P. nigrolimitatus* was found to have the lowest levels of genetic diversity in the region with the longest history of intensive forestry (Sønstebø *et al.*, 2022).

(4) Possible aggravation of logging impacts by climate change

As boreal forests are situated at high latitudes, the impact of climate change is expected to be strong (Kausrud *et al.*, 2022). Climate models predict increases in average temperatures with large differences within the boreal biome (Constable *et al.*, 2022). Notably, large shifts in natural disturbance regimes are expected as a result of altered climate, and such shifts have already been reported (e.g. Hanes *et al.*, 2019; Safranyik *et al.*, 2010). For example, in Canada, an increase in the number and severity of natural forest fires has been observed over the last 57 years (Hanes *et al.*, 2019), and increased risk of windthrow is predicted in eastern balsam fir forests (Saad *et al.*, 2017). The effects of these changes on biodiversity, however, are unclear.

Climate change and forest management are inherently linked because the forests' resilience to natural disturbances depend on the complexity of the forest system (Filotas *et al.*, 2014). Combined homogenization of biodiversity and forest structure may have reinforcing effects on ecosystem functionality (Mori, Isbell & Seidl, 2018). Monocultural forests often have weaker resistance to natural disturbances, such as windthrow, and more unstable year-to-year productivity (Jucker *et al.*, 2014; Jactel *et al.*, 2017; Depardieu *et al.*, 2020).

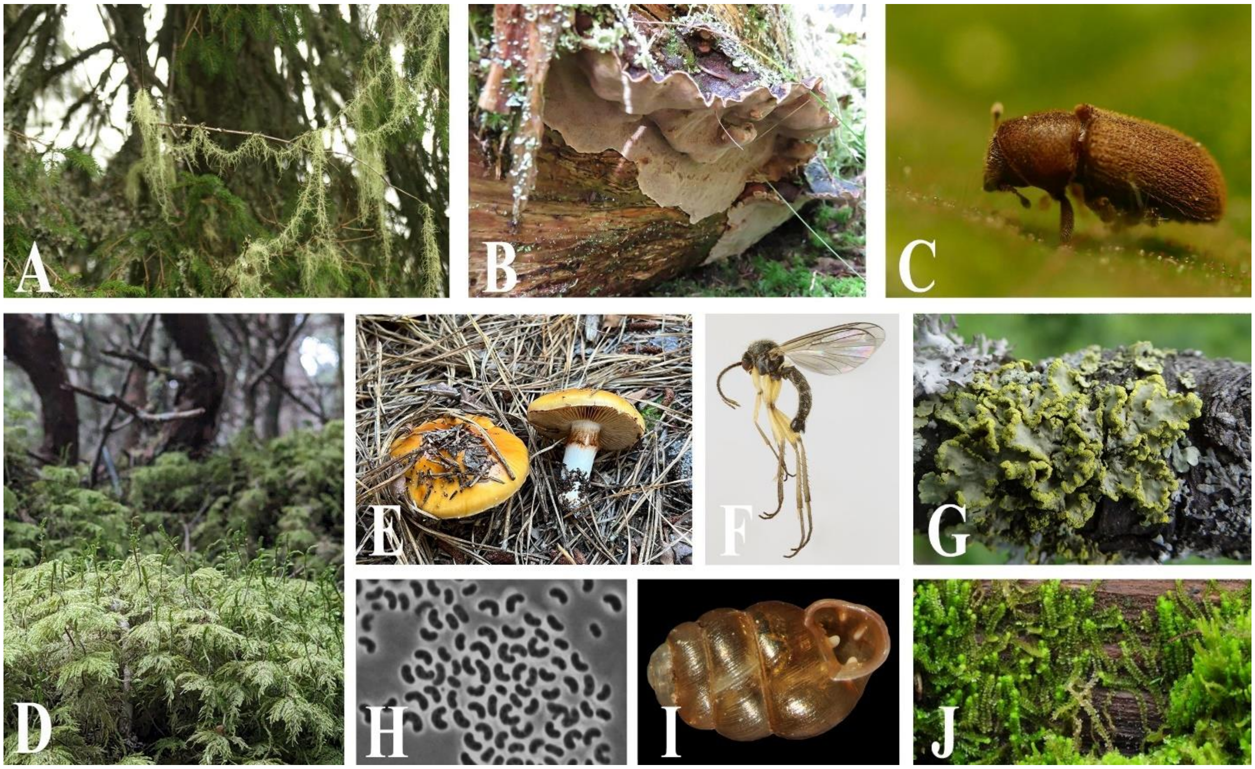


Figure 3. Species' groups with documented long-term effects of clear-cutting on community composition. Each group is represented by one species that has been disfavoured by clear-cutting in literature used in this review. A) Epiphytic lichens (*Usnea longissima* by Johan Asplund), B) saproxylic fungi (*Phellopilus nigrolimitatus* by Sandy Maurice), C) saproxylic beetles (*Xylechinus pilosus* by Alexis Orion), D) epigeic bryophytes (*Hylocomium splendens* by Portulaca), E) ectomycorrhizal fungi (*Cortinarius mucosus* by Annie Weissman), F) saproxylic fungus gnats (*Apolephthisa subincana* by Janet Graham), H) soil bacteria (*Roseiarcus fermentans* from Kulichevskaya *et al*. (2014: Fig. 1a)), I) soil snails (*Vertigo alpestris* by O. Gargominy), and J) epixylic bryophytes (*Neoorthocaulis attenuata* by Youp van den Heuvel).

VI. Conclusions

(1) The imprint of clear-cutting on boreal forest ecosystems is conspicuous. Boreal forests, particularly in Europe, have been transformed into homogeneous landscapes in which old-growth forests, rich in structural complexity and key structural elements, are isolated as small patches. These impacts have led to short- and long-term (less or more than 50 yrs) changes in the species composition and richness of many species' groups associated with four major substrates: living trees, dead wood, ground and soil.

(2) Among communities that inhabit living trees, lichen species declines have been linked to reduced numbers of old trees, reduced connectivity to old-growth forests, and edge effects. Although some short- and long-term trends have been found, more studies are needed on the effects of clear-cutting on epiphytic bryophytes, endophytic fungi and canopy invertebrates.

(3) Studies of saproxylic fungi and insects indicate long-term changes in community composition and decreased richness, in response to low volume and quality of dead

wood following clear-cutting. Specialist fungal species show dispersal limitation. Epixylic bryophytes and lichens appear to be negatively impacted by clear-cutting, also in the long-term.

(4) More research is needed to understand the long-term response of ground vegetation to clear-cutting, but some suggest long-term community changes to epigeic bryophytes. Studies on epigeic arthropods indicate that immediate increases in species richness after clear-cutting is followed by community convergence in the long-term. However, forest specialist species disappear after harvesting and have not been shown to recover, perhaps due to edge effects.

(5) Among species groups in boreal soils, ectomycorrhizal fungal communities are strongly altered in the short term after clear-cutting. Two studies report altered community composition 50 years after cutting. For soil invertebrates, studies show signs of recovery in the short-term for springtails and enchytraeids, but not for oribatid mites. Land snails may recover in the long term, but no long-term data exist on other soil invertebrates.

(6) Data on effects of clear-cutting is lacking for several abundant boreal species' groups within the protists, invertebrates (except beetles), microfungi, and some lichen and bryophyte groups.

(7) In this review, we show that many boreal forest species communities have local- and landscape-level responses to clear-cutting. Despite scarce to no data for many species groups, our observations show that rotation times up to 80 years seem not to be sufficient for the recovery of boreal forest communities. Such major changes in biodiversity are likely to affect the functioning of boreal forest ecosystems.

(8) Emphasis must be put on conserving the natural variability of boreal forests by increasing rotation times, retaining different dead wood characteristics, old trees, heterogeneous forest structures and preserving sufficient old-growth forest area in the landscape. Importantly, the most efficient management procedures to conserve biodiversity may vary geographically depending on forest type and history.

(9) Boreal forests have undergone large changes over the past century as a result of the transition to clear-cutting as the dominant harvesting regime. Available data is insufficient to paint the full picture of the effects. Our findings and discussion do, however, argue that clear-cutting may have accumulating effects on biodiversity which may, eventually, push the forest ecosystem across a tipping point with major species losses.

Acknowledgement

The Research Council of Norway is acknowledged for financial support to the EcoForest project (grant 320722).

References

Ahlström, A., Canadell, J. G. & Metcalfe, D. B. (2022). Widespread unquantified conversion of old boreal forests to plantations. *Earth's Future* **10**(11), e2022EF003221.

ANDERSSON, G. K., BOKE-OLEN, N., ROGER, F., EKROOS, J., SMITH, H. G. & CLOUGH, Y. (2022). Landscape-scale diversity of plants, bumblebees and butterflies in mixed farm-forest landscapes of Northern Europe: Clear-cuts do not compensate for the negative effects of plantation forest cover. *Biological Conservation* **274**, 109728.

ANDERSSON, L. I. & HYTTEBORN, H. (1991). Bryophytes and decaying wood–a comparison between managed and natural forest. *Ecography* **14**(2), 121-130.

ANGELSTAM, P. (1996). The ghost of forest past—natural disturbance regimes as a basis for reconstruction of biologically diverse forests in Europe. In *Conservation of faunal diversity in forested landscapes*. (pp. 287-337. Springer.

ANGELSTAM, P. & KUULUVAINEN, T. (2004). Boreal forest disturbance regimes, successional dynamics and landscape structures: a European perspective. *Ecological bulletins*, 117-136.

ARTSDATABANKEN. (2021). Status for truede arter i skog. Norsk rødliste for arter 2021. Downloaded 31.10.23.

AXELSSON, A.-L. & ÖSTLUND, L. (2001). Retrospective gap analysis in a Swedish boreal forest landscape using historical data. *Forest Ecology and Management* **147**(2-3), 109-122.

BÅÅTH, E. (1980). Soil fungal biomass after clear-cutting of a pine forest in central Sweden. *Soil Biology and Biochemistry* **12**(5), 495-500.

BARNOSKY, A. D., HADLY, E. A., BASCOMPTE, J., BERLOW, E. L., BROWN, J. H., FORTELIUS, M., GETZ, W. M., HARTE, J., HASTINGS, A. & MARQUET, P. A. (2012). Approaching a state shift in Earth's biosphere. *Nature* **486**(7401), 52-58.

BARTELS, S. F., MACDONALD, S. E., JOHNSON, D., CANERS, R. T. & SPENCE, J. R. (2018). Bryophyte abundance, diversity and composition after retention harvest in boreal mixedwood forest. *Journal of Applied Ecology* **55**(2), 947-957.

BARTEMUCCI, P., LILLES, E. & GAUSLAA, Y. (2022). Silvicultural strategies for lichen conservation: Smaller gaps and shorter distances to edges promote recolonization. *Ecosphere* **13**(1), e3898.

BEESE, W. J., DEAL, J., DUNSWORTH, B. G., MITCHELL, S. J. & PHILPOTT, T. J. (2019). Two decades of variable retention in British Columbia: a review of its implementation and effectiveness for biodiversity conservation. *Ecological Processes* **8**(1), 1-22.

BEHAN-PELLETIER, V. & WINCHESTER, N. (1998). Arboreal oribatid mite diversity: colonizing the canopy. *Applied Soil Ecology* **9**(1-3), 45-51.

BELL-DOYON, P., BELLAVANCE, V., BÉLANGER, L. & MAZEROLLE, M. J. (2022). Bacterial, fungal, and mycorrhizal communities in the soil differ between clearcuts and insect outbreaks in the boreal forest 50 years after disturbance. *Forest Ecology and Management* **523**, 120493.

BELL-DOYON, P., MAZEROLLE, M. J., BÉLANGER, L. & FENTON, N. J. (2024). Differential impact of clearcut and insect outbreak on boreal lichens and bryophytes 50 years after disturbance. *Biological Conservation* **295**, 110672.

BELLUZ, V., LANGOR, D. W., NIEMELÄ, J. K., HE, F. & SPENCE, J. R. (2022). Long-term responses of ground beetles (Coleoptera: Carabidae) to clear-cutting and wildfire in lodgepole pine stands of western Alberta, Canada. *The Canadian Entomologist* **154**(1), e41.

BERGERON, J. C., PINZON, J., ODSEN, S., BARTELS, S., MACDONALD, S. E. & SPENCE, J. R. (2017). Ecosystem memory of wildfires affects resilience of boreal mixedwood biodiversity after retention harvest. *Oikos* **126**(12), 1738-1747.

BERGLUND, H. & JONSSON, B. G. (2005). Verifying an extinction debt among lichens and fungi in northern Swedish boreal forests. *Conservation Biology* **19**(2), 338-348.

BIRD, G. & CHATARPAUL, L. (1986). Effect of whole-tree and conventional forest harvest on soil microarthropods. *Canadian Journal of Zoology* **64**(9), 1986-1993.

Birkemoe, T., Jacobsen, R. M., Sverdrup-Thygeson, A. & Biedermann, P. H. (2018). Insect-fungus interactions in dead wood systems. In *Saproxylic insects: Diversity, ecology and conservation*. (pp. 377-427. Springer, Cham, Switzerland.

Bishop, D. J. (1998). *Saproxylic beetles and deadwood structure in managed and naturally disturbed spruce forests in Nova Scotia*, Carleton University.

Blumroeder, J. S., Burova, N., Winter, S., Goroncy, A., Hobson, P. R., Shegolev, A., Dobrynin, D., Amosova, I., Ilina, O. & Parinova, T. (2019). Ecological effects of clearcutting practices in a boreal forest (Arkhangelsk Region, Russian Federation) both with and without FSC certification. *Ecological Indicators* **106**, 105461.

Bock, M. D. & van Rees, K. C. (2002). Forest harvesting impacts on soil properties and vegetation communities in the Northwest Territories. *Canadian journal of forest research* **32**(4), 713-724.

Bödeker, I. T., Lindahl, B. D., Olson, Å. & Clemmensen, K. E. (2016). Mycorrhizal and saprotrophic fungal guilds compete for the same organic substrates but affect decomposition differently. *Functional Ecology* **30**(12), 1967-1978.

Bogusch, P. & Horák, J. (2018). Saproxylic bees and wasps. *Saproxylic insects: Diversity, ecology and conservation*, 217-235.

Bouchard, M. & Pothier, D. (2011). Long-term influence of fire and harvesting on boreal forest age structure and forest composition in eastern Québec. *Forest Ecology and Management* **261**(4), 811-820.

Boucher, Y., Arseneault, D., Sirois, L. & Blais, L. (2009). Logging pattern and landscape changes over the last century at the boreal and deciduous forest transition in Eastern Canada. *Landscape Ecology* **24**, 171-184.

Boucher, Y. & Grondin, P. (2012). Impact of logging and natural stand-replacing disturbances on high-elevation boreal landscape dynamics (1950–2005) in eastern Canada. *Forest Ecology and Management* **263**, 229-239.

Bradshaw, C. J. & Warkentin, I. G. (2015). Global estimates of boreal forest carbon stocks and flux. *Global and Planetary Change* **128**, 24-30.

Brockerhoff, E. G., Barbaro, L., Castagneyrol, B., Forrester, D. I., Gardiner, B., González-Olabarria, J. R., Lyver, P. O. B., Meurisse, N., Oxbrough, A. & Taki, H. (2017). Forest biodiversity, ecosystem functioning and the provision of ecosystem services, vol. 26, pp. 3005-3035. Springer.

Buddle, C. M., Langor, D. W., Pohl, G. R. & Spence, J. R. (2006). Arthropod responses to harvesting and wildfire: implications for emulation of natural disturbance in forest management. *Biological Conservation* **128**(3), 346-357.

Buddle, C. M., Spence, J. R. & Langor, D. W. (2000). Succession of boreal forest spider assemblages following wildfire and harvesting. *Ecography* **23**(4), 424-436.

Bunnell, F. L., Spribille, T., Houde, I., Goward, T. & Björk, C. (2008). Lichens on down wood in logged and unlogged forest stands. *Canadian journal of forest research* **38**(5), 1033-1041.

Burton, P. J. (2013). Exploring complexity in boreal forests. *Managing forests as complex adaptive systems. Routledge, London*, 79-109.

Caitano, B., Chaves, T. P., Dodonov, P. & Delabie, J. H. C. (2020). Edge effects on insects depend on life history traits: a global meta-analysis. *Journal of Insect Conservation* **24**(2), 233-240.

Caners, R. T., Macdonald, S. E. & Belland, R. J. (2010). Responses of boreal epiphytic bryophytes to different levels of partial canopy harvest. *Botany* **88**(4), 315-328.

Clarke, N., Kiær, L. P., Kjønaas, O. J., Bárcena, T. G., Vesterdal, L., Stupak, I., Finér, L., Jacobson, S., Armolaitis, K. & Lazdina, D. (2021). Effects of intensive biomass harvesting on forest soils in the Nordic countries and the UK: A meta-analysis. *Forest Ecology and Management* **482**, 118877.

Clemmensen, K., Bahr, A., Ovaskainen, O., Dahlberg, A., Ekblad, A., Wallander, H., Stenlid, J., Finlay, R., Wardle, D. & Lindahl, B. (2013). Roots and associated fungi drive long-term carbon sequestration in boreal forest. *Science* **339**(6127), 1615-1618.

Constable, A. J., Harper, S., Dawson, J., Holsman, K., Mustonen, T., Piepenburg, D., Rost, B., Bokhorst, S., Boike, J. & Cunsolo, A. (2022). Cross-chapter paper 6: Polar regions. In *IPCC AR WGII*. (Cambridge University Press.

Danks, H. (2006). Short life cycles in insects and mites. *The Canadian Entomologist* **138**(4), 407-463.

Davey, M. L., Kauserud, H. & Ohlson, M. (2014). Forestry impacts on the hidden fungal biodiversity associated with bryophytes. *FEMS Microbiology Ecology* **90**(1), 313-325.

Deans, A., Smith, S., Malcolm, J., Crins, W. & Bellocq, M. (2007). Hoverfly (Syrphidae) communities respond to varying structural retention after harvesting in Canadian peatland black spruce forests. *Environmental Entomology* **36**(2), 308-318.

Delgado-Baquerizo, M., Reich, P. B., Trivedi, C., Eldridge, D. J., Abades, S., Alfaro, F. D., Bastida, F., Berhe, A. A., Cutler, N. A. & Gallardo, A. (2020). Multiple elements of soil biodiversity drive ecosystem functions across biomes. *Nature Ecology & Evolution* **4**(2), 210-220.

Depardieu, C., Girardin, M. P., Nadeau, S., Lenz, P., Bousquet, J. & Isabel, N. (2020). Adaptive genetic variation to drought in a widely distributed conifer suggests a potential for increasing forest resilience in a drying climate. *New Phytologist* **227**(2), 427-439.

Dettki, H. & Esseen, P.-A. (2003). Modelling long-term effects of forest management on epiphytic lichens in northern Sweden. *Forest Ecology and Management* **175**(1-3), 223-238.

Dettki, H., Klintberg, P. & Esseen, P.-A. (2000). Are epiphytic lichens in young forests limited by local dispersal? *Ecoscience* **7**(3), 317-325.

Díaz, S. M., Settele, J., Brondízio, E., Ngo, H., Guèze, M., Agard, J., Arneth, A., Balvanera, P., Brauman, K. & Butchart, S. (2019). The global assessment report on biodiversity and ecosystem services: Summary for policy makers.

Dynesius, M. (2015). Slow recovery of bryophyte assemblages in middle-aged boreal forests regrown after clear-cutting. *Biological Conservation* **191**, 101-109.

Dynesius, M., Olsson, J., Hjältén, J., Löfroth, T. & Roberge, J.-M. (2021). Bryophyte species composition at the stand scale (1 ha)–Differences between secondary stands half a century after clear-cutting and older semi-natural boreal forests. *Forest Ecology and Management* **482**, 118883.

Ehnström, B. & Axelsson, R. (2002). *Insektsgnag i bark och ved*. SLU Artdatabanken, Uppsala, Sweden.

Ekblad, A., Wallander, H., Godbold, D. L., Cruz, C., Johnson, D., Baldrian, P., Björk, R., Epron, D., Kieliszewska-Rokicka, B. & Kjøller, R. (2013). The production and turnover of extramatrical mycelium of ectomycorrhizal fungi in forest soils: role in carbon cycling. *Plant and Soil* **366**, 1-27.

Ekström, A. L., Sjögren, J., Djupström, L. B., Thor, G. & Löfroth, T. (2023). Reinventory of permanent plots show that kelo lichens face an extinction debt. *Biological Conservation* **288**, 110363.

Esseen, P.-A., Ehnström, B., Ericson, L. & Sjöberg, K. (1997). Boreal forests. *Ecological bulletins*, 16-47.

Esseen, P.-A., Rytterstam, J., Atrena, A. & Jonsson, B.-G. (2023). Long-term dynamics of the iconic old-forest lichen Usnea longissima in a protected landscape. *Forest Ecology and Management* **546**, 121369.

Esseen, P. A., Ekström, M., Grafström, A., Jonsson, B. G., Palmqvist, K., Westerlund, B. & Ståhl, G. (2022). Multiple drivers of large-scale lichen decline in boreal forest canopies. *Global Change Biology* **28**(10), 3293-3309.

Esseen, P. A. & Renhorn, K. E. (1998). Edge effects on an epiphytic lichen in fragmented forests. *Conservation Biology* **12**(6), 1307-1317.

Filotas, E., Parrott, L., Burton, P. J., Chazdon, R. L., Coates, K. D., Coll, L., Haeussler, S., Martin, K., Nocentini, S. & Puettmann, K. J. (2014). Viewing forests through the lens of complex systems science. *Ecosphere* **5**(1), 1-23.

Forge, T. & Simard, S. (2001). Structure of nematode communities in forest soils of southern British Columbia: relationships to nitrogen mineralization and effects of clearcut harvesting and fertilization. *Biology and fertility of soils* **34**, 170-178.

Franklin, A. J., Liebhold, A. M., Murray, K. & Donahue, C. (2003). Canopy herbivore community structure: large-scale geographical variation and relation to forest composition. *Ecological Entomology* **28**(3), 278-290.

Gauthier, S., Kuuluvainen, T., Macdonald, S. E., Shorohova, E., Shvidenko, A., Bélisle, A.-C., Vaillancourt, M.-A., Leduc, A., Grosbois, G. & Bergeron, Y. (2023). Ecosystem management of the boreal forest in the era of global change. In *Boreal Forests in the Face of Climate Change: Sustainable Management*. (pp. 3-49. Springer.

George, P. B. & Lindo, Z. (2015). Congruence of community structure between taxonomic identification and T-RFLP analyses in free-living soil nematodes. *Pedobiologia* **58**(2-3), 113-117.

Gibb, H., Hilszczański, J., Hjältén, J., Danell, K., Ball, J., Pettersson, R. & Alinvi, O. (2008). Responses of parasitoids to saproxylic hosts and habitat: a multi-scale study using experimental logs. *Oecologia* **155**, 63-74.

Gibb, H., Johansson, T., Stenbacka, F. & Hjältén, J. (2013). Functional roles affect diversity-succession relationships for boreal beetles. *PLoS One* **8**(8), e72764.

Gill, A. L. & Finzi, A. C. (2016). Belowground carbon flux links biogeochemical cycles and resource-use efficiency at the global scale. *Ecology letters* **19**(12), 1419-1428.

Gjerde, I., Blom, H. H., Heegaard, E. & Sætersdal, M. (2015). Lichen colonization patterns show minor effects of dispersal distance at landscape scale. *Ecography* **38**(9), 939-948.

Grove, S. J. (2002). Saproxylic insect ecology and the sustainable management of forests. *Annual review of ecology and systematics* **33**(1), 1-23.

Gu, W., Heikkilä, R. & Hanski, I. (2002). Estimating the consequences of habitat fragmentation on extinction risk in dynamic landscapes. *Landscape Ecology* **17**, 699-710.

Hagerman, S. M., Jones, M. D., Bradfield, G. E., Gillespie, M. & Durall, D. (1999). Effects of clear-cut logging on the diversity and persistence of ectomycorrhizae at a subalpine forest. *Canadian journal of forest research* **29**(1), 124-134.

Hagge, J., Bässler, C., Gruppe, A., Hoppe, B., Kellner, H., Krah, F.-S., Müller, J., Seibold, S., Stengel, E. & Thorn, S. (2019). Bark coverage shifts assembly processes of microbial decomposer communities in dead wood. *Proceedings of the Royal Society B* **286**(1912), 20191744.

Halvorsen, R., Skarpaas, O., Bryn, A., Bratli, H., Erikstad, L., Simensen, T. & Lieungh, E. (2020). Towards a systematics of ecodiversity: The EcoSyst framework. *Global Ecology and Biogeography* **29**(11), 1887-1906.

Hämäläinen, A., Runnel, K., Mikusiński, G., Himelbrant, D., Fenton, N. J. & Lõhmus, P. (2023). Living Trees and Biodiversity. In *Boreal Forests in the Face of Climate Change: Sustainable Management*. (pp. 145-166. Springer.

Hamberg, L., Lehvävirta, S. & Kotze, D. J. (2009). Forest edge structure as a shaping factor of understorey vegetation in urban forests in Finland. *Forest Ecology and Management* **257**(2), 712-722.

Hanes, C. C., Wang, X., Jain, P., Parisien, M.-A., Little, J. M. & Flannigan, M. D. (2019). Fire-regime changes in Canada over the last half century. *Canadian journal of forest research* **49**(3), 256-269.

Hanski, I. (1998). Metapopulation dynamics. *Nature* **396**(6706), 41-49.

Hanski, I. & Ovaskainen, O. (2002). Extinction debt at extinction threshold. *Conservation Biology* **16**(3), 666-673.

Harper, K. A., Macdonald, S. E., Burton, P. J., Chen, J., Brosofske, K. D., Saunders, S. C., Euskirchen, E. S., Roberts, D., Jaiteh, M. S. & Esseen, P. A. (2005). Edge influence on forest structure and composition in fragmented landscapes. *Conservation Biology* **19**(3), 768-782.

Hart, S. A. & Chen, H. Y. (2006). Understory vegetation dynamics of North American boreal forests. *Critical Reviews in Plant Sciences* **25**(4), 381-397.

Hart, S. C., Porter, T. M., Basiliko, N., Venier, L., Hajibabaei, M. & Morris, D. (2023). Fungal community dynamics in coarse woody debris across decay stage, tree species, and stand development stage in northern boreal forests. *Canadian journal of forest research*.

Hartmann, M., Howes, C. G., VanInsberghe, D., Yu, H., Bachar, D., Christen, R., Henrik Nilsson, R., Hallam, S. J. & Mohn, W. W. (2012). Significant and persistent impact of timber harvesting on soil microbial communities in Northern coniferous forests. *The ISME journal* **6**(12), 2199-2218.

Hartmann, M., Niklaus, P. A., Zimmermann, S., Schmutz, S., Kremer, J., Abarenkov, K., Lüscher, P., Widmer, F. & Frey, B. (2014). Resistance and resilience of the forest soil microbiome to logging-associated compaction. *The ISME journal* **8**(1), 226-244.

Hasby, F. (2022). Impacts of clear-cutting on soil fungal communities and their activities in boreal forests- A metatranscriptomic approach. *Acta Universitatis Agriculturae Sueciae* (2022: 11).

Hawkins, J. W., Lankester, M., Lautenschlager, R. & Bell, F. (1997). Effects of alternative conifer release treatments on terrestrial gastropods in northwestern Ontario. *The Forestry Chronicle* **73**(1), 91-98.

Hedenås, H. & Hedström, P. (2007). Conservation of epiphytic lichens: significance of remnant aspen (Populus tremula) trees in clear-cuts. *Biological Conservation* **135**(3), 388-395.

Heinonsalo, J. & Sen, R. (2007). Scots pine ectomycorrhizal fungal inoculum potential and dynamics in podzol-specific humus, eluvial and illuvial horizons one and four growth seasons after forest clear-cut logging. *Canadian journal of forest research* **37**(2), 404-414.

Hekkala, A.-M., Jönsson, M., Kärvemo, S., Strengbom, J. & Sjögren, J. (2023). Habitat heterogeneity is a good predictor of boreal forest biodiversity. *Ecological Indicators* **148**, 110069.

Helander, M., Wäli, P., Kuuluvainen, T. & Saikkonen, K. (2006). Birch leaf endophytes in managed and natural boreal forests. *Canadian journal of forest research* **36**(12), 3239-3245.

Henttonen, H. M., Nöjd, P., Suvanto, S., Heikkinen, J. & Mäkinen, H. (2019). Large trees have increased greatly in Finland during 1921–2013, but recent observations on old trees tell a different story. *Ecological Indicators* **99**, 118-129.

Hilmo, O. & Holien, H. (2002). Epiphytic lichen response to the edge environment in a boreal Picea abies forest in central Norway. *Bryologist*, 48-56.

Hilmo, O. & Såstad, S. M. (2001). Colonization of old-forest lichens in a young and an old boreal Picea abies forest: an experimental approach. *Biological Conservation* **102**(3), 251-259.

Hilszczański, J. (2018). Ecology, diversity and conservation of saproxylic hymenopteran parasitoids. *Saproxylic insects: Diversity, ecology and conservation*, 193-216.

Hjältén, J., Kouki, J., Tolvanen, A., Sjögren, J. & Versluijs, M. (2023). Ecological Restoration of the Boreal Forest in Fennoscandia. In *Boreal Forests in the Face of Climate Change: Sustainable Management*. (pp. 467-489. Springer.

Hjältén, J., Stenbacka, F., Pettersson, R. B., Gibb, H., Johansson, T., Danell, K., Ball, J. P. & Hilszczański, J. (2012). Micro and macro-habitat associations in saproxylic beetles: implications for biodiversity management. *PLoS One* **7**(7), e41100.

Holien, H. (1996). Influence of site and stand factors on the distribution of crustose lichens of the Caliciales in a suboceanic spruce forest area in central Norway. *The Lichenologist* **28**(4), 315-330.

Hottola, J., Ovaskainen, O. & Hanski, I. (2009). A unified measure of the number, volume and diversity of dead trees and the response of fungal communities. *Journal of Ecology* **97**(6), 1320-1328.

Huhta, V., Nurminen, M. & Valpas, A. (1969). Further notes on the effect of silvicultural practices upon the fauna of coniferous forest soil. In *Annales Zoologici Fennici*, pp. 327-334. JSTOR.

Hylander, K. (2005). Aspect modifies the magnitude of edge effects on bryophyte growth in boreal forests. *Journal of Applied Ecology* **42**(3), 518-525.

HYLANDER, K. (2011). The response of land snail assemblages below aspens to forest fire and clear-cutting in Fennoscandian boreal forests. *Forest Ecology and Management* **261**(11), 1811-1819.

HYLANDER, K., NILSSON, C. & GÖTHNER, T. (2004). Effects of buffer-strip retention and clearcutting on land snails in boreal riparian forests. *Conservation Biology* **18**(4), 1052-1062.

HYTTEBORN, H., MASLOV, A., NAZIMOVA, D. & RYSIN, L. (2005). Boreal forests of Eurasia. *Ecosystems of the World* **6**, 23-99.

IBBE, M., MILBERG, P., TUNÉR, A. & BERGMAN, K.-O. (2011). History matters: Impact of historical land use on butterfly diversity in clear-cuts in a boreal landscape. *Forest Ecology and Management* **261**(11), 1885-1891.

JACOBSEN, R. M., BURNER, R. C., OLSEN, S. L., SKARPAAS, O. & SVERDRUP-THYGESON, A. (2020). Near-natural forests harbor richer saproxylic beetle communities than those in intensively managed forests. *Forest Ecology and Management* **466**, 118124.

JACOBSEN, R. M., SVERDRUP-THYGESON, A. & BIRKEMOE, T. (2015). Scale-specific responses of saproxylic beetles: combining dead wood surveys with data from satellite imagery. *Journal of Insect Conservation* **19**, 1053-1062.

JACTEL, H., BAUHUS, J., BOBERG, J., BONAL, D., CASTAGNEYROL, B., GARDINER, B., GONZALEZ-OLABARRIA, J. R., KORICHEVA, J., MEURISSE, N. & BROCKERHOFF, E. G. (2017). Tree diversity drives forest stand resistance to natural disturbances. *Current Forestry Reports* **3**, 223-243.

JAMES, J. & HARRISON, R. (2016). The effect of harvest on forest soil carbon: A meta-analysis. *Forests* **7**(12), 308.

JANSSON, K. U., PALMQVIST, K. & ESSEEN, P.-A. (2009). Growth of the old forest lichen Usnea longissima at forest edges. *The Lichenologist* **41**(6), 663-672.

JOHANSSON, P. (2008). Consequences of disturbance on epiphytic lichens in boreal and near boreal forests. *Biological Conservation* **141**(8), 1933-1944.

JOHANSSON, T., HJÄLTÉN, J., OLSSON, J., DYNESIUS, M. & ROBERGE, J.-M. (2016). Long-term effects of clear-cutting on epigaeic beetle assemblages in boreal forests. *Forest Ecology and Management* **359**, 65-73.

JOHANSSON, V., GUSTAFSSON, L., ANDERSSON, P. & HYLANDER, K. (2020). Fewer butterflies and a different composition of bees, wasps and hoverflies on recently burned compared to unburned clear-cuts, regardless of burn severity. *Forest Ecology and Management* **463**, 118033.

JONES, M. D., DURALL, D. M. & CAIRNEY, J. W. (2003). Ectomycorrhizal fungal communities in young forest stands regenerating after clearcut logging. *New Phytologist* **157**(3), 399-422.

JONSELL, M., VÅRDAL, H., FORSHAGE, M. & STIGENBERG, J. (2023). Saproxylic Hymenoptera in dead wood retained on clear cuts, relation to wood parameters and their degree of specialisation. *Journal of Insect Conservation* **27**(2), 347-359.

JONSELL, M., WESLIEN, J. & EHNSTRÖM, B. (1998). Substrate requirements of red-listed saproxylic invertebrates in Sweden. *Biodiversity & Conservation* **7**, 749-764.

JONSSON, B. G., EKSTRÖM, M., ESSEEN, P.-A., GRAFSTRÖM, A., STÅHL, G. & WESTERLUND, B. (2016). Dead wood availability in managed Swedish forests–Policy outcomes and implications for biodiversity. *Forest Ecology and Management* **376**, 174-182.

JÖNSSON, M. T., EDMAN, M. & JONSSON, B. G. (2008). Colonization and extinction patterns of wood-decaying fungi in a boreal old-growth Picea abies forest. *Journal of Ecology* **96**(5), 1065-1075.

JÖNSSON, M. T., FRAVER, S. & JONSSON, B. G. (2009). Forest history and the development of old-growth characteristics in fragmented boreal forests. *Journal of Vegetation Science* **20**(1), 91-106.

JÖNSSON, M. T., FRAVER, S., JONSSON, B. G., DYNESIUS, M., RYDGÅRD, M. & ESSEEN, P.-A. (2007). Eighteen years of tree mortality and structural change in an experimentally fragmented Norway spruce forest. *Forest Ecology and Management* **242**(2-3), 306-313.

JUCKER, T., BOURIAUD, O., AVACARITEI, D. & COOMES, D. A. (2014). Stabilizing effects of diversity on aboveground wood production in forest ecosystems: linking patterns and processes. *Ecology letters* **17**(12), 1560-1569.

JUNNINEN, K. & KOMONEN, A. (2011). Conservation ecology of boreal polypores: a review. *Biological Conservation* **144**(1), 11-20.

JURGENSEN, M., HARVEY, A., GRAHAM, R., PAGE-DUMROESE, D., TONN, J., LARSEN, M. & JAIN, T. (1997). Impacts of timber harvesting on soil organic matter, nitrogen, productivity, and health of Inland Northwest forests. *Forest Science* **43**(2), 234-251.

JUUTILAINEN, K., MÖNKKÖNEN, M., KOTIRANTA, H. & HALME, P. (2014). The effects of forest management on wood-inhabiting fungi occupying dead wood of different diameter fractions. *Forest Ecology and Management* **313**, 283-291.

KAUSRUD, K. L., VANDVIK, V., FLØ, D., GEANGE, S. R., HEGLAND, S. J., HERMANSEN, J. S., HOLE, L. R., IMS, R. A., KAUSERUD, H. & KIRKENDALL, L. R. (2022). Impacts of climate change on the boreal forest ecosystem. Scientific Opinion of the Panel on Alien Organisms and Trade in Endangered species (CITES) of the Norwegian Scientific Committee for Food and Environment.

KAYES, I. & MALLIK, A. (2020). Boreal forests: distributions, biodiversity, and management. *Life on land*, 1-12.

KIVISTÖ, L. & KUUSINEN, M. (2000). Edge effects on the epiphytic lichen flora of Picea abies in middle boreal Finland. *The Lichenologist* **32**(4), 387-398.

KJØNAAS, O. J., BÁRCENA, T. G., HYLEN, G., NORDBAKKEN, J. F. & ØKLAND, T. (2021). Boreal tree species change as a climate mitigation strategy: impact on ecosystem C and N stocks and soil nutrient levels. *Ecosphere* **12**(11), e03826.

KLIMASZEWSKI, J., BRUNKE, A. J., WORK, T. T. & VENIER, L. (2018). Rove beetles (Coleoptera, Staphylinidae) as bioindicators of change in boreal forests and their biological control services in agroecosystems: Canadian case studies. *Biology of Rove Beetles (Staphylinidae) Life History, Evolution, Ecology and Distribution*, 161-181.

KNAPSTAD, M. H. (2024). Compositional dynamics on the forest floor - successional dynamics in the understorey after logging in a boreal coniferous forest in south-eastern Norway. *MSc thesis*. *University of Oslo, Natural History Museum and Department of Biosciences*.

KOELEMEIJER, I. A., EHRLÉN, J., JÖNSSON, M., DE FRENNE, P., BERG, P., ANDERSSON, J., WEIBULL, H. & HYLANDER, K. (2022). Interactive effects of drought and edge exposure on old-growth forest understory species. *Landscape Ecology* **37**(7), 1839-1853.

KOIVULA, M., KUKKONEN, J. & NIEMELÄ, J. (2002). Boreal carabid-beetle (Coleoptera, Carabidae) assemblages along the clear-cut originated succession gradient. *Biodiversity & Conservation* **11**, 1269-1288.

KOIVULA, M. & VANHA-MAJAMAA, I. (2020). Experimental evidence on biodiversity impacts of variable retention forestry, prescribed burning, and deadwood manipulation in Fennoscandia. *Ecological Processes* **9**(1), 11.

KOIVULA, M. J., VENN, S., HAKOLA, P. & NIEMELÄ, J. (2019). Responses of boreal ground beetles (Coleoptera, Carabidae) to different logging regimes ten years post harvest. *Forest Ecology and Management* **436**, 27-38.

KOMONEN, A., PENTTILÄ, R., LINDGREN, M. & HANSKI, I. (2000). Forest fragmentation truncates a food chain based on an old-growth forest bracket fungus. *Oikos* **90**(1), 119-126.

KORPELA, E. L., HYVÖNEN, T. & KUUSSAARI, M. (2015). Logging in boreal field-forest ecotones promotes flower-visiting insect diversity and modifies insect community composition. *Insect Conservation and Diversity* **8**(2), 152-162.

KRANABETTER, J., DE MONTIGNY, L. & ROSS, G. (2013). Effectiveness of green-tree retention in the conservation of ectomycorrhizal fungi. *Fungal Ecology* **6**(5), 430-438.

KUDRIN, A., PERMINOVA, E., TASKAEVA, A., DITTS, A. & KONAKOVA, T. (2023). A Meta-Analysis of the Effects of Harvesting on the Abundance and Richness of Soil Fauna in Boreal and Temperate Forests. *Forests* **14**(5), 923.

KÜFFER, N. & SENN-IRLET, B. (2005). Influence of forest management on the species richness and composition of wood-inhabiting basidiomycetes in Swiss forests. *Biodiversity & Conservation* **14**, 2419-2435.

KULICHEVSKAYA, I. S., DANILOVA, O. V., TERESHINA, V. M., KEVBRIN, V. V. & DEDYSH, S. N. (2014). Descriptions of Roseiarcus fermentans gen. nov., sp. nov., a bacteriochlorophyll a-containing fermentative bacterium related phylogenetically to alphaproteobacterial methanotrophs, and of the family Roseiarcaceae fam. nov. *International journal of systematic and evolutionary microbiology* **64**(Pt_8), 2558-2565.

KUOSMANEN, N., FANG, K., BRADSHAW, R. H., CLEAR, J. L. & SEPPÄ, H. (2014). Role of forest fires in Holocene stand-scale dynamics in the unmanaged taiga forest of northwestern Russia. *The Holocene* **24**(11), 1503-1514.

KUULUVAINEN, T. & AAKALA, T. (2011). Natural forest dynamics in boreal Fennoscandia: a review and classification. *Silva Fennica* **45**(5), 823-841.

KUULUVAINEN, T. & GAUTHIER, S. (2018). Young and old forest in the boreal: critical stages of ecosystem dynamics and management under global change. *Forest Ecosystems* **5**(1), 1-15.

KYASCHENKO, J., CLEMMENSEN, K. E., HAGENBO, A., KARLTUN, E. & LINDAHL, B. D. (2017). Shift in fungal communities and associated enzyme activities along an age gradient of managed Pinus sylvestris stands. *The ISME journal* **11**(4), 863-874.

KYASCHENKO, J., STRENGBOM, J., FELTON, A., AAKALA, T., STALAND, H. & RANIUS, T. (2022). Increase in dead wood, large living trees and tree diversity, yet decrease in understory vegetation cover: The effect of three decades of biodiversity-oriented forest policy in Swedish forests. *Journal of Environmental Management* **313**, 114993.

LAFLEUR, B., ZOUAOUI, S., FENTON, N. J., DRAPEAU, P. & BERGERON, Y. (2016). Short-term response of Cladonia lichen communities to logging and fire in boreal forests. *Forest Ecology and Management* **372**, 44-52.

LANGOR, D. W., HAMMOND, H. J., SPENCE, J. R., JACOBS, J. & COBB, T. P. (2008). Saproxylic insect assemblages in Canadian forests: diversity, ecology, and conservation1. *The Canadian Entomologist* **140**(4), 453-474.

LARRIVÉE, M., DRAPEAU, P. & FAHRIG, L. (2008). Edge effects created by wildfire and clear-cutting on boreal forest ground-dwelling spiders. *Forest Ecology and Management* **255**(5-6), 1434-1445.

LARRIVÉE, M., FAHRIG, L. & DRAPEAU, P. (2005). Effects of a recent wildfire and clearcuts on ground-dwelling boreal forest spider assemblages. *Canadian journal of forest research* **35**(11), 2575-2588.

LARSEN, C. P. (1997). Spatial and temporal variations in boreal forest fire frequency in northern Alberta. *Journal of Biogeography* **24**(5), 663-673.

LARSSON, A., BJELKE, U., DAHLBERG, A. & SANDSTRÖM, J. (2011). Tillståndet i skogen–rödlistade arter i ett nordiskt perspektiv. *ArtDatabanken rapporterar* **9**, 4-13.

LE BORGNE, H., HÉBERT, C., DUPUCH, A., BICHET, O., PINAUD, D. & FORTIN, D. (2018). Temporal dynamics in animal community assembly during post-logging succession in boreal forest. *PLoS One* **13**(9), e0204445.

LEE, S. I., SPENCE, J. R. & LANGOR, D. W. (2014). Succession of saproxylic beetles associated with decomposition of boreal white spruce logs. *Agricultural and Forest Entomology* **16**(4), 391-405.

LEUNG, H. T., MAAS, K. R., WILHELM, R. C. & MOHN, W. W. (2016). Long-term effects of timber harvesting on hemicellulolytic microbial populations in coniferous forest soils. *The ISME journal* **10**(2), 363-375.

LEVINS, R. (1969). Some demographic and genetic consequences of environmental heterogeneity for biological control. *American Entomologist* **15**(3), 237-240.

LI, J., DELGADO-BAQUERIZO, M., WANG, J.-T., HU, H.-W., CAI, Z.-J., ZHU, Y.-N. & SINGH, B. K. (2019). Fungal richness contributes to multifunctionality in boreal forest soil. *Soil Biology and Biochemistry* **136**, 107526.

LIE, M. H., ARUP, U., GRYTNES, J.-A. & OHLSON, M. (2009). The importance of host tree age, size and growth rate as determinants of epiphytic lichen diversity in boreal spruce forests. *Biodiversity and Conservation* **18**, 3579-3596.

LIKHANOVA, I. A., GENRIKH, E. A., PERMINOVA, E. M., ZHELEZNOVA, G. V., KHOLOPOV, Y. V. & LAPTEVA, E. M. (2023). The effects of clear cutting on the biodiversity of middle taiga blueberry spruce forests in the North-East of European Russia. In Russian: ("Влияние сплошнолесосечных рубок на биоразнообразие среднетаёжных ельников черничных Северо-Востока европейской части России"). *Theoretical and Applied Ecology* (2), 56-65.

LIKHANOVA, I. A., PERMINOVA, E. M., SHUSHPANNIKOVA, G. S., ZHELEZNOVA, G. V., PYSTINA, T. N. & KHOLOPOV, Y. V. (2021). Dynamics of vegetation after clearcutting bilberry spruce forests (middle taiga subzone of the European North-East of Russia). In Russian: ("Динамика растительности после сплошнолесосечных рубок ельников черничных (среднетаежная подзона европейского северо-востока России)."). *Vegetation of Russia* (40), 108-136.

LINDBLADH, M., ABRAHAMSSON, M., SEEDRE, M. & JONSELL, M. (2007). Saproxylic beetles in artificially created high-stumps of spruce and birch within and outside hotspot areas. *Biodiversity and Conservation* **16**, 3213-3226.

LINDENMAYER, D. B. & FISCHER, J. (2013). *Habitat fragmentation and landscape change: an ecological and conservation synthesis*. Island Press.

LINDENMAYER, D. B., LAURANCE, W. F. & FRANKLIN, J. F. (2012). Global decline in large old trees. *Science* **338**(6112), 1305-1306.

LINDER, P. & ÖSTLUND, L. (1998). Structural changes in three mid-boreal Swedish forest landscapes, 1885–1996. *Biological Conservation* **85**(1-2), 9-19.

LÖBEL, S., MAIR, L., LÖNNELL, N., SCHRÖDER, B. & SNÄLL, T. (2018). Biological traits explain bryophyte species distributions and responses to forest fragmentation and climatic variation. *Journal of Ecology* **106**(4), 1700-1713.

LÖBEL, S., SNÄLL, T. & RYDIN, H. (2006). Metapopulation processes in epiphytes inferred from patterns of regional distribution and local abundance in fragmented forest landscapes. *Journal of Ecology* **94**(4), 856-868.

LÖFROTH, T., BIRKEMOE, T., SHOROHOVA, E., DYNESIUS, M., FENTON, N. J., DRAPEAU, P. & TREMBLAY, J. A. (2023). Deadwood Biodiversity. In *Boreal Forests in the Face of Climate Change: Sustainable Management*. (pp. 167-189. Springer.

LÕHMUS, P. & LÕHMUS, A. (2019). The potential of production forests for sustaining lichen diversity: a perspective on sustainable forest management. *Forests* **10**(12), 1063.

LOMMI, S., BERGLUND, H., KUUSINEN, M. & KUULUVAINEN, T. (2010). Epiphytic lichen diversity in late-successional Pinus sylvestris forests along local and regional forest utilization gradients in eastern boreal Fennoscandia. *Forest Ecology and Management* **259**(5), 883-892.

LÓŠKOVÁ, J., ĽUPTÁČIK, P., MIKLISOVÁ, D. & KOVÁČ, Ľ. (2013). The effect of clear-cutting and wildfire on soil Oribatida (Acari) in windthrown stands of the High Tatra Mountains (Slovakia). *European Journal of Soil Biology* **55**, 131-138.

LUNDMARK, H., JOSEFSSON, T. & ÖSTLUND, L. (2013). The history of clear-cutting in northern Sweden–driving forces and myths in boreal silviculture. *Forest Ecology and Management* **307**, 112-122.

LUNDSTRÖM, J., JONSSON, F., PERHANS, K. & GUSTAFSSON, L. (2013). Lichen species richness on retained aspens increases with time since clear-cutting. *Forest Ecology and Management* **293**, 49-56.

Määttänen, A.-M., Virkkala, R., Leikola, N. & Heikkinen, R. K. (2022). Increasing loss of mature boreal forests around protected areas with red-listed forest species. *Ecological Processes* **11**(1), 17.

Mair, L., Harrison, P. J., Jönsson, M., Löbel, S., Nordén, J., Siitonen, J., Lämås, T., Lundström, A. & Snäll, T. (2017). Evaluating citizen science data for forecasting species responses to national forest management. *Ecology and Evolution* **7**(1), 368-378.

Mäkipää, R., Abramoff, R., Adamczyk, B., Baldy, V., Biryol, C., Bosela, M., Casals, P., Yuste, J. C., Dondini, M. & Filipek, S. (2023). How does management affect soil C sequestration and greenhouse gas fluxes in boreal and temperate forests?: A review. *Forest Ecology and Management*.

Malmström, A., Persson, T., Ahlström, K., Gongalsky, K. B. & Bengtsson, J. (2009). Dynamics of soil meso- and macrofauna during a 5-year period after clear-cut burning in a boreal forest. *Applied Soil Ecology* **43**(1), 61-74.

Marshall, V. (2000). Impacts of forest harvesting on biological processes in northern forest soils. *Forest Ecology and Management* **133**(1-2), 43-60.

Martikainen, P. & Kouki, J. (2003). Sampling the rarest: threatened beetles in boreal forest biodiversity inventories. *Biodiversity & Conservation* **12**, 1815-1831.

Martikainen, P., Siitonen, J., Punttila, P., Kaila, L. & Rauh, J. (2000). Species richness of Coleoptera in mature managed and old-growth boreal forests in southern Finland. *Biological Conservation* **94**(2), 199-209.

Martin, M., Boucher, Y., Fenton, N. J., Marchand, P. & Morin, H. (2020). Forest management has reduced the structural diversity of residual boreal old-growth forest landscapes in Eastern Canada. *Forest Ecology and Management* **458**, 117765.

Martin, M., Shorohova, E. & Fenton, N. J. (2023). Embracing the Complexity and the Richness of Boreal Old-Growth Forests: A Further Step Toward Their Ecosystem Management. In *Boreal Forests in the Face of Climate Change: Sustainable Management*. (pp. 191-218. Springer.

Mayer, M., Prescott, C. E., Abaker, W. E., Augusto, L., Cécillon, L., Ferreira, G. W., James, J., Jandl, R., Katzensteiner, K. & Laclau, J.-P. (2020). Tamm Review: Influence of forest management activities on soil organic carbon stocks: A knowledge synthesis. *Forest Ecology and Management* **466**, 118127.

McIver, J., Parsons, G. & Moldenke, A. R. (1992). Litter spider succession after clear-cutting in a western coniferous forest. *Canadian journal of forest research* **22**(7), 984-992.

Messier, C., Posada, J., Aubin, I. & Beaudet, M. (2009). Functional relationships between old-growth forest canopies, understorey light and vegetation dynamics. *Old-Growth Forests: Function, Fate and Value*, 115-139.

Michel, A. K. & Winter, S. (2009). Tree microhabitat structures as indicators of biodiversity in Douglas-fir forests of different stand ages and management histories in the Pacific Northwest, USA. *Forest Ecology and Management* **257**(6), 1453-1464.

Mielke, L. A. (2022). Mycorrhizal guild functions and conservation values in boreal forests. [Doctoral thesis, Swedish University of Agricultural Sciences (SLU)].

Milberg, P., Eriksson, V. & Bergman, K.-O. (2021). Assemblages of flower-visiting insects in clear-cuts are rich and dynamic. *European Journal of Entomology* **118**, 182-191.

Moor, H., Nordén, J., Penttilä, R., Siitonen, J. & Snäll, T. (2021). Long-term effects of colonization–extinction dynamics of generalist versus specialist wood-decaying fungi. *Journal of Ecology* **109**(1), 491-503.

Mori, A. S., Isbell, F. & Seidl, R. (2018). β-diversity, community assembly, and ecosystem functioning. *Trends in Ecology & Evolution* **33**(7), 549-564.

Naumov, V., Angelstam, P. & Elbakidze, M. (2016). Barriers and bridges for intensified wood production in Russia: insights from the environmental history of a regional logging frontier. *Forest Policy and Economics* **66**, 1-10.

NAVE, L. E., DELYSER, K., DOMKE, G. M., HOLUB, S. M., JANOWIAK, M. K., KELLER, A. B., PETERS, M. P., SOLARIK, K. A., WALTERS, B. F. & SWANSTON, C. W. (2024). Land use change and forest management effects on soil carbon stocks in the Northeast US. *Carbon Balance and Management* **19**(1), 5.

NAVE, L. E., VANCE, E. D., SWANSTON, C. W. & CURTIS, P. S. (2010). Harvest impacts on soil carbon storage in temperate forests. *Forest Ecology and Management* **259**(5), 857-866.

NIELSEN, A. & TOTLAND, Ø. (2014). Structural properties of mutualistic networks withstand habitat degradation while species functional roles might change. *Oikos* **123**(3), 323-333.

NIEMELÄ, J. (1997). Invertebrates and boreal forest management: Invertebrados y Manejo de Bosques Boreales. *Conservation Biology* **11**(3), 601-610.

NIEMELÄ, J., KOIVULA, M. & KOTZE, D. J. (2007). The effects of forestry on carabid beetles (Coleoptera: Carabidae) in boreal forests. *Journal of Insect Conservation* **11**, 5-18.

NIEMELÄ, T., WALLENIUS, T. & KOTIRANTA, H. (2002). The kelo tree, a vanishing substrate of specified wood-inhabiting fungi. *Polish Botanical Journal* **47**(2), 91-101.

NIRHAMO, A., HÄMÄLÄINEN, A., HÄMÄLÄINEN, K. & KOUKI, J. (2024). Retention forestry can maintain epiphytic lichens on living pine trees, but provides impoverished habitat for deadwood-associated lichens. *Journal of Applied Ecology*.

NORDÉN, B., DAHLBERG, A., BRANDRUD, T. E., FRITZ, Ö., EJRNAES, R. & OVASKAINEN, O. (2014). Effects of ecological continuity on species richness and composition in forests and woodlands: a review. *Ecoscience* **21**(1), 34-45.

NORDÉN, J., ÅSTRÖM, J., JOSEFSSON, T., BLUMENTRATH, S., OVASKAINEN, O., SVERDRUP-THYGESON, A. & NORDÉN, B. (2018). At which spatial and temporal scales can fungi indicate habitat connectivity? *Ecological Indicators* **91**, 138-148.

NORDÉN, J., HARRISON, P. J., MAIR, L., SIITONEN, J., LUNDSTRÖM, A., KINDVALL, O. & SNÄLL, T. (2020). Occupancy versus colonization–extinction models for projecting population trends at different spatial scales. *Ecology and Evolution* **10**(6), 3079-3089.

NORDÉN, J., PENTTILÄ, R., SIITONEN, J., TOMPPO, E. & OVASKAINEN, O. (2013). Specialist species of wood-inhabiting fungi struggle while generalists thrive in fragmented boreal forests. *Journal of Ecology* **101**(3), 701-712.

NORROS, V., PENTTILÄ, R., SUOMINEN, M. & OVASKAINEN, O. (2012). Dispersal may limit the occurrence of specialist wood decay fungi already at small spatial scales. *Oikos* **121**(6), 961-974.

ØKLAND, B. (1994). Mycetophilidae (Diptera), an insect group vulnerable to forestry practices? A comparison of clearcut, managed and semi-natural spruce forests in southern Norway. *Biodiversity & Conservation* **3**, 68-85.

ØKLAND, B. (1996). Unlogged forests: important sites for preserving the diversity of mycetophilids (Diptera: Sciaroidea). *Biological Conservation* **76**(3), 297-310.

ØKLAND, T., RYDGREN, K., ØKLAND, R. H., STORAUNET, K. O. & ROLSTAD, J. (2003). Variation in environmental conditions, understorey species number, abundance and composition among natural and managed Picea abies forest stands. *Forest Ecology and Management* **177**(1-3), 17-37.

PAJUNEN, T., HAILA, Y., HALME, E., NIEMELÀ, J. & PUNTTILA, P. (1995). Ground-dwelling spiders (Arachnida, Araneae) in fragmented old forests and surrounding managed forests in southern Finland. *Ecography* **18**(1), 62-72.

PAN, Y., BIRDSEY, R. A., FANG, J., HOUGHTON, R., KAUPPI, P. E., KURZ, W. A., PHILLIPS, O. L., SHVIDENKO, A., LEWIS, S. L. & CANADELL, J. G. (2011). A large and persistent carbon sink in the world's forests. *Science* **333**(6045), 988-993.

PAQUETTE, M., BOUDREAULT, C., FENTON, N., POTHIER, D. & BERGERON, Y. (2016). Bryophyte species assemblages in fire and clear-cut origin boreal forests. *Forest Ecology and Management* **359**, 99-108.

Parladé, J., Queralt, M., Pera, J., Bonet, J., Castaño, C., Martínez-Peña, F., Piñol, J., Senar, M. & De Miguel, A. (2019). Temporal dynamics of soil fungal communities after partial and total clear-cutting in a managed Pinus sylvestris stand. *Forest Ecology and Management* **449**, 117456.

Peichl, M., Martínez-García, E., Fransson, J. E., Wallerman, J., Laudon, H., Lundmark, T. & Nilsson, M. B. (2023a). Landscape-variability of the carbon balance across managed boreal forests. *Global Change Biology* **29**(4), 1119-1132.

Peichl, M., Martínez-García, E., Fransson, J. E., Wallerman, J., Laudon, H., Lundmark, T. & Nilsson, M. B. (2023b). On the uncertainty in estimates of the carbon balance recovery time after forest clear-cutting. *Global Change Biology* **29**(15), e1-e3.

Penttilä, R., Siitonen, J. & Kuusinen, M. (2004). Polypore diversity in managed and old-growth boreal Picea abies forests in southern Finland. *Biological Conservation* **117**(3), 271-283.

Percel, G., Laroche, F. & Bouget, C. (2019). The scale of saproxylic beetles response to landscape structure depends on their habitat stability. *Landscape Ecology* **34**, 1905-1918.

Peter, M., Buée, M. & Egli, S. (2013). 3.4 Biodiversity of mycorrhizal fungi as a crucial player in forest ecosystem functioning. *Integrative approaches as an opportunity for the conservation of forest biodiversity*, 170.

Pettersson, R. B. (1996). Effect of forestry on the abundance and diversity of arboreal spiders in the boreal spruce forest. *Ecography* **19**(3), 221-228.

Pettersson, R. B., Ball, J. P., Renhorn, K.-E., Esseen, P.-A. & Sjöberg, K. (1995). Invertebrate communities in boreal forest canopies as influenced by forestry and lichens with implications for passerine birds. *Biological Conservation* **74**(1), 57-63.

Pinksen, J., Moise, E. R., Sircom, J. & Bowden, J. J. (2021). Living on the edge: Effects of clear-cut created ecotones on nocturnal macromoth assemblages in the eastern boreal forest, Canada. *Forest Ecology and Management* **494**, 119309.

Pinzon, J., Spence, J. R. & Langor, D. W. (2011). Spider assemblages in the overstory, understory, and ground layers of managed stands in the western boreal mixedwood forest of Canada. *Environmental Entomology* **40**(4), 797-808.

Porras-Alfaro, A. & Bayman, P. (2011). Hidden fungi, emergent properties: endophytes and microbiomes. *Annual review of phytopathology* **49**, 291-315.

Prescott, C. E. & Grayston, S. J. (2023). TAMM review: Continuous root forestry—Living roots sustain the belowground ecosystem and soil carbon in managed forests. *Forest Ecology and Management* **532**, 120848.

Punttila, P. (1996). Succession, forest fragmentation, and the distribution of wood ants. *Oikos*, 291-298.

Purhonen, J., Abrego, N., Komonen, A., Huhtinen, S., Kotiranta, H., Læssøe, T. & Halme, P. (2021). Wood-inhabiting fungal responses to forest naturalness vary among morpho-groups. *Scientific Reports* **11**(1), 14585.

Rähn, E., Tedersoo, L., Adamson, K., Drenkhan, T., Sibul, I., Lutter, R., Anslan, S., Pritsch, K. & Drenkhan, R. (2023). Rapid shift of soil fungal community compositions after clear-cutting in hemiboreal coniferous forests. *Forest Ecology and Management* **544**, 121211.

Ranlund, Å., Hylander, K., Johansson, V., Jonsson, F., Nordin, U. & Gustafsson, L. (2018). Epiphytic lichen responses to environmental change due to clear-cutting differ among tree taxa. *Journal of Vegetation Science* **29**(6), 1065-1074.

Remm, L. & Lõhmus, A. (2016). Semi-naturally managed forests support diverse land snail assemblages in Estonia. *Forest Ecology and Management* **363**, 159-168.

Risberg, L., Danell, E. & Dahlberg, A. (2004). Is Tricholoma matsutake associated with continuity of scots pine trees?(Finns goliatmusseronen enbart i tallskogar som aldrig kalavverkats?). *Sven Bot Tidskr* **98**, 317-327.

RODRIGUEZ-RAMOS, J. C., CALE, J. A., CAHILL JR, J. F., SIMARD, S. W., KARST, J. & ERBILGIN, N. (2021). Changes in soil fungal community composition depend on functional group and forest disturbance type. *New Phytologist* **229**(2), 1105-1117.

RODRÍGUEZ, A. & KOUKI, J. (2017). Disturbance-mediated heterogeneity drives pollinator diversity in boreal managed forest ecosystems. *Ecological Applications* **27**(2), 589-602.

ROUVINEN, S., KUULUVAINEN, T. & SIITONEN, J. (2002). Tree mortality in a Pinus sylvestris dominated boreal forest landscape in Vienansalo wilderness, eastern Fennoscandia. *Disturbance dynamics in boreal forests: Defining the ecological basis of restoration and management of biodiversity*.

RUDOLPHI, J. & GUSTAFSSON, L. (2011). Forests regenerating after clear-cutting function as habitat for bryophyte and lichen species of conservation concern. *PLoS One* **6**(4), e18639.

RUETE, A., SNÄLL, T. & JÖNSSON, M. (2016). Dynamic anthropogenic edge effects on the distribution and diversity of fungi in fragmented old-growth forests. *Ecological Applications* **26**(5), 1475-1485.

RUKKE, B. A. (2000). Effects of habitat fragmentation: increased isolation and reduced habitat size reduces the incidence of dead wood fungi beetles in a fragmented forest landscape. *Ecography* **23**(4), 492-502.

RUNNEL, K. & LÕHMUS, A. (2017). Deadwood-rich managed forests provide insights into the old-forest association of wood-inhabiting fungi. *Fungal Ecology* **27**, 155-167.

SAAD, C., BOULANGER, Y., BEAUDET, M., GACHON, P., RUEL, J.-C. & GAUTHIER, S. (2017). Potential impact of climate change on the risk of windthrow in eastern Canada's forests. *Climatic Change* **143**(3), 487-501.

SAFRANYIK, L., CARROLL, A. L., RÉGNIÈRE, J., LANGOR, D., RIEL, W., SHORE, T. L., PETER, B., COOKE, B. J., NEALIS, V. & TAYLOR, S. W. (2010). Potential for range expansion of mountain pine beetle into the boreal forest of North America. *The Canadian Entomologist* **142**(5), 415-442.

SASAKI, T., ISHII, N. I., MAKISHIMA, D., SUTOU, R., GOTO, A., KAWAI, Y., TANIGUCHI, H., OKANO, K., MATSUO, A. & LOCHNER, A. (2022). Plant and microbial community composition jointly determine moorland multifunctionality. *Journal of Ecology* **110**(10), 2507-2521.

SAVILAAKSO, S., JOHANSSON, A., HÄKKILÄ, M., UUSITALO, A., SANDGREN, T., MÖNKKÖNEN, M. & PUTTONEN, P. (2021). What are the effects of even-aged and uneven-aged forest management on boreal forest biodiversity in Fennoscandia and European Russia? A systematic review. *Environmental Evidence* **10**(1), 1-38.

SCHAETZL, R. J., BURNS, S. F., JOHNSON, D. L. & SMALL, T. W. (1988). Tree uprooting: review of impacts on forest ecology. *Vegetatio* **79**, 165-176.

SCHARLEMANN, J. P., TANNER, E. V., HIEDERER, R. & KAPOS, V. (2014). Global soil carbon: understanding and managing the largest terrestrial carbon pool. *Carbon management* **5**(1), 81-91.

SCHMALHOLZ, M., HYLANDER, K. & FREGO, K. (2011). Bryophyte species richness and composition in young forests regenerated after clear-cut logging versus after wildfire and spruce budworm outbreak. *Biodiversity and Conservation* **20**, 2575-2596.

SCHMIDT, N. & ROLAND, J. (2006). Moth diversity in a fragmented habitat: importance of functional groups and landscape scale in the boreal forest. *Annals of the Entomological Society of America* **99**(6), 1110-1120.

SCOTTER, G. W. (1963). Growth rates of Cladonia alpestris, C. mitis, and C. rangiferina in the Taltson River region, NWT. *Canadian Journal of Botany* **41**(8), 1199-1202.

SEIBOLD, S., BÄSSLER, C., BRANDL, R., BÜCHE, B., SZALLIES, A., THORN, S., ULYSHEN, M. D. & MÜLLER, J. (2016). Microclimate and habitat heterogeneity as the major drivers of beetle diversity in dead wood. *Journal of Applied Ecology* **53**(3), 934-943.

SEIBOLD, S., BÄSSLER, C., BRANDL, R., GOSSNER, M. M., THORN, S., ULYSHEN, M. D. & MÜLLER, J. (2015). Experimental studies of dead-wood biodiversity—a review identifying global gaps in knowledge. *Biological Conservation* **191**, 139-149.

Shorohova, E., Kneeshaw, D., Kuuluvainen, T. & Gauthier, S. (2011). Variability and dynamics of old-growth forests in the circumbolear zone: implications for conservation, restoration and management.

Shorohova, E., Kuuluvainen, T., Kangur, A. & Jõgiste, K. (2009). Natural stand structures, disturbance regimes and successional dynamics in the Eurasian boreal forests: a review with special reference to Russian studies. *Annals of Forest Science* **66**(2), 1-20.

Siira-Pietikäinen, A. & Haimi, J. (2009). Changes in soil fauna 10 years after forest harvestings: Comparison between clear felling and green-tree retention methods. *Forest Ecology and Management* **258**(3), 332-338.

Siitonen, J. (2001). Forest management, coarse woody debris and saproxylic organisms: Fennoscandian boreal forests as an example. *Ecological bulletins*, 11-41.

Siitonen, J., Martikainen, P., Punttila, P. & Rauh, J. (2000). Coarse woody debris and stand characteristics in mature managed and old-growth boreal mesic forests in southern Finland. *Forest Ecology and Management* **128**(3), 211-225.

Siitonen, P., Lehtinen, A. & Siitonen, M. (2005). Effects of forest edges on the distribution, abundance, and regional persistence of wood-rotting fungi. *Conservation Biology* **19**(1), 250-260.

Sillett, S. C., McCune, B., Peck, J. E., Rambo, T. R. & Ruchty, A. (2000). Dispersal limitations of epiphytic lichens result in species dependent on old-growth forests. *Ecological Applications* **10**(3), 789-799.

Sippola, A.-L., Siitonen, J. & Punttila, P. (2002). Beetle diversity in timberline forests: a comparison between old-growth and regeneration areas in Finnish Lapland. In *Annales Zoologici Fennici*, pp. 69-86. JSTOR.

Smith, E. P. (2002). BACI design. *Encyclopedia of environmetrics* **1**, 141-148.

Snäll, T. & Jonsson, B. G. (2001). Edge effects on six polyporous fungi used as old-growth indicators in Swedish boreal forest. *Ecological bulletins*, 255-262.

Söderström, L. (1988). The occurrence of epixylic bryophyte and lichen species in an old natural and a managed forest stand in northeast Sweden. *Biological Conservation* **45**(3), 169-178.

Sohlenius, B. (2002). Influence of clear-cutting and forest age on the nematode fauna in a Swedish pine forest soil. *Applied Soil Ecology* **19**(3), 261-277.

Solvin, T. & Fløistad, I. S. (2023). Statistics: Forest Seeds and Plants in the Nordic Region–Version 2023.

Sønstebø, J. H., Trucchi, E., Nordén, J., Skrede, I., Miettinen, O., Haridas, S., Pangilinan, J., Grigoriev, I. V., Martin, F. & Kauserud, H. (2022). Population genomics of a forest fungus reveals high gene flow and climate adaptation signatures. *Molecular Ecology* **31**(7), 1963-1979.

Sorvari, J. & Hakkarainen, H. (2007). Wood ants are wood ants: deforestation causes population declines in the polydomous wood ant Formica aquilonia. *Ecological Entomology* **32**(6), 707-711.

Soucémarianadin, L., Cécillon, L., Chenu, C., Baudin, F., Nicolas, M., Girardin, C. & Barré, P. (2018). Is Rock-Eval 6 thermal analysis a good indicator of soil organic carbon lability?–A method-comparison study in forest soils. *Soil Biology and Biochemistry* **117**, 108-116.

Southwood, T. R. (1977). Habitat, the templet for ecological strategies? *Journal of animal ecology* **46**(2), 337-365.

Spribille, T., Thor, G., Bunnell, F. L., Goward, T. & Björk, C. R. (2008). Lichens on dead wood: species-substrate relationships in the epiphytic lichen floras of the Pacific Northwest and Fennoscandia. *Ecography* **31**(6), 741-750.

Stenbacka, F., Hjältén, J., Hilszczański, J. & Dynesius, M. (2010). Saproxylic and non-saproxylic beetle assemblages in boreal spruce forests of different age and forestry intensity. *Ecological Applications* **20**(8), 2310-2321.

STERKENBURG, E., CLEMMENSEN, K. E., LINDAHL, B. D. & DAHLBERG, A. (2019). The significance of retention trees for survival of ectomycorrhizal fungi in clear-cut Scots pine forests. *Journal of Applied Ecology* **56**(6), 1367-1378.

STOCKAN, J. A. & ROBINSON, E. J. (2016). *Wood ant ecology and conservation*. Cambridge University Press.

STOKLAND, J. & KAUSERUD, H. (2004). Phellinus nigrolimitatus—a wood-decomposing fungus highly influenced by forestry. *Forest Ecology and Management* **187**(2-3), 333-343.

STOKLAND, J. N., SIITONEN, J. & JONSSON, B. G. (2012). *Biodiversity in dead wood*. Cambridge University Press.

STORAUNET, K. O., ROLSTAD, J., GJERDE, I. & GUNDERSEN, V. S. (2005). Historical logging, productivity, and structural characteristics of boreal coniferous forests in Norway. *Silva Fennica* **39**(3), 429.

STOUTJESDIJK, P. & BARKMAN, J. (1992). Microclimate. *Vegetation and Fauna. Opulus Press, Uppsala*.

STRÖM, L., HYLANDER, K. & DYNESIUS, M. (2009). Different long-term and short-term responses of land snails to clear-cutting of boreal stream-side forests. *Biological Conservation* **142**(8), 1580-1587.

SUMMERVILLE, K. S. & CRIST, T. O. (2008). Structure and conservation of lepidopteran communities in managed forests of northeastern North America: a review1. *The Canadian Entomologist* **140**(4), 475-494.

SUOMINEN, M., JUNNINEN, K. & KOUKI, J. (2019). Diversity of fungi in harvested forests 10 years after logging and burning: Polypore assemblages on different woody substrates. *Forest Ecology and Management* **446**, 63-70.

SVERDRUP-THYGESON, A., BENDIKSEN, E., BIRKEMOE, T. & LARSSON, K. H. (2014a). Do conservation measures in forest work? A comparison of three area-based conservation tools for wood-living species in boreal forests. *Forest Ecology and Management* **330**, 8-16.

SVERDRUP-THYGESON, A., GUSTAFSSON, L. & KOUKI, J. (2014b). Spatial and temporal scales relevant for conservation of dead-wood associated species: current status and perspectives. *Biodiversity and Conservation* **23**, 513-535.

SVERDRUP-THYGESON, A. & LINDENMAYER, D. B. (2003). Ecological continuity and assumed indicator fungi in boreal forest: the importance of the landscape matrix. *Forest Ecology and Management* **174**(1-3), 353-363.

SVERDRUP-THYGESON, A. & MIDTGAARD, F. (1998). Fungus-infected trees as islands in boreal forest: spatial distribution of the fungivorous beetle Bolitophagus reticulatus (Coleoptera, Tenebrionidae). *Ecoscience* **5**(4), 486-493.

SWANSON, M. E., FRANKLIN, J. F., BESCHTA, R. L., CRISAFULLI, C. M., DELLASALA, D. A., HUTTO, R. L., LINDENMAYER, D. B. & SWANSON, F. J. (2011). The forgotten stage of forest succession: early-successional ecosystems on forest sites. *Frontiers in Ecology and the Environment* **9**(2), 117-125.

THOMAS, A. W. (2002). Moth diversity in a Northeastern, North American, red spruce forest. II. The effect of silvicultural practices on geometrid diversity (Lepidoptera: Geometridae). In *Information report M-X-213E* (ed. C. F. Service), Ottawa, Canada.

THUNES, K. H., SKARVEIT, J. & GJERDE, I. (2003). The canopy arthropods of old and mature pine Pinus sylvestris in Norway. *Ecography* **26**(4), 490-502.

TIKKANEN, O.-P., MARTIKAINEN, P., HYVÄRINEN, E., JUNNINEN, K. & KOUKI, J. (2006). Red-listed boreal forest species of Finland: associations with forest structure, tree species, and decaying wood. In *Annales zoologici fennici*, pp. 373-383. JSTOR.

TILMAN, D., ISBELL, F. & COWLES, J. M. (2014). Biodiversity and ecosystem functioning. *Annual review of ecology, evolution, and systematics* **45**, 471-493.

TILMAN, D., MAY, R. M., LEHMAN, C. L. & NOWAK, M. A. (1994). Habitat destruction and the extinction debt. *Nature* **371**(6492), 65-66.

TOMAO, A., BONET, J. A., CASTANO, C. & DE-MIGUEL, S. (2020). How does forest management affect fungal diversity and community composition? Current knowledge and future perspectives for the conservation of forest fungi. *Forest Ecology and Management* **457**, 117678.

TUHKANEN, S. (1984). Circumboreal system of climatic-phytogeographical regions.

ULICZKA, H. & ANGELSTAM, P. (1999). Occurrence of epiphytic macrolichens in relation to tree species and age in managed boreal forest. *Ecography* **22**(4), 396-405.

VAN DER PLAS, F. (2019). Biodiversity and ecosystem functioning in naturally assembled communities. *Biological Reviews* **94**(4), 1220-1245.

VARENIUS, K., KÅRÉN, O., LINDAHL, B. & DAHLBERG, A. (2016). Long-term effects of tree harvesting on ectomycorrhizal fungal communities in boreal Scots pine forests. *Forest Ecology and Management* **380**, 41-49.

VENIER, L., THOMPSON, I. D., FLEMING, R., MALCOLM, J., AUBIN, I., TROFYMOW, J., LANGOR, D., STURROCK, R., PATRY, C. & OUTERBRIDGE, R. (2014). Effects of natural resource development on the terrestrial biodiversity of Canadian boreal forests. *Environmental reviews* **22**(4), 457-490.

VENIER, L., WORK, T., KLIMASZEWSKI, J., MORRIS, D. M., BOWDEN, J., KWIATON, M. M., WEBSTER, K. & HAZLETT, P. (2017). Ground-dwelling arthropod response to fire and clearcutting in jack pine: implications for ecosystem management. *Canadian journal of forest research* **47**(12), 1614-1631.

VINDSTAD, O. P. L., BIRKEMOE, T., IMS, R. A. & SVERDRUP-THYGESON, A. (2020). Environmental conditions alter successional trajectories on an ephemeral resource: a field experiment with beetles in dead wood. *Oecologia* **194**, 205-219.

WARDLE, D. A., HYODO, F., BARDGETT, R. D., YEATES, G. W. & NILSSON, M.-C. (2011). Long-term aboveground and belowground consequences of red wood ant exclusion in boreal forest. *Ecology* **92**(3), 645-656.

WESLIEN, J., DJUPSTRÖM, L. B., SCHROEDER, M. & WIDENFALK, O. (2011). Long-term priority effects among insects and fungi colonizing decaying wood. *Journal of animal ecology* **80**(6), 1155-1162.

WESTERFELT, P., WIDENFALK, O., LINDELÖW, Å., GUSTAFSSON, L. & WESLIEN, J. (2015). Nesting of solitary wasps and bees in natural and artificial holes in dead wood in young boreal forest stands. *Insect Conservation and Diversity* **8**(6), 493-504.

WILHELM, R. C., CARDENAS, E., MAAS, K. R., LEUNG, H., MCNEIL, L., BERCH, S., CHAPMAN, W., HOPE, G., KRANABETTER, J. & DUBÉ, S. (2017). Biogeography and organic matter removal shape long-term effects of timber harvesting on forest soil microbial communities. *The ISME journal* **11**(11), 2552-2568.

WILLMER, P. (2011). *Pollination and floral ecology*. Princeton University Press.

WINTER, M.-B., AMMER, C., BAIER, R., DONATO, D. C., SEIBOLD, S. & MÜLLER, J. (2015). Multi-taxon alpha diversity following bark beetle disturbance: evaluating multi-decade persistence of a diverse early-seral phase. *Forest Ecology and Management* **338**, 32-45.

YLISIRNIÖ, A.-L., PENTTILÄ, R., BERGLUND, H., HALLIKAINEN, V., ISAEVA, L., KAUHANEN, H., KOIVULA, M. & MIKKOLA, K. (2012). Dead wood and polypore diversity in natural post-fire succession forests and managed stands–Lessons for biodiversity management in boreal forests. *Forest Ecology and Management* **286**, 16-27.

YUAN, Z., ALI, A., RUIZ-BENITO, P., JUCKER, T., MORI, A. S., WANG, S., ZHANG, X., LI, H., HAO, Z. & WANG, X. (2020). Above-and below-ground biodiversity jointly regulate temperate forest multifunctionality along a local-scale environmental gradient. *Journal of Ecology* **108**(5), 2012-2024.