

Chapter 18

Ecological Restoration of the Boreal Forest in Fennoscandia



Joakim Hjältén, Jari Kouki, Anne Tolvanen, Jörgen Sjögren, and Martijn Versluijs

Abstract Mixed-severity disturbances have historically shaped boreal forests, creating a dynamic mosaic landscape. In Fennoscandia, however, intensive even-aged forest management has simplified the forest landscape, threatening biodiversity. To safeguard this biodiversity, we therefore need to restore structural complexity in hitherto managed forests. Knowledge generated from relevant case studies on natural disturbance emulation-based ecological restoration suggests that prescribed burning positively affects many early-successional organisms. Gap cutting benefits some insects and wood fungi but has a limited effect on birds, bryophytes, and vascular plants. Restoration of deciduous forests appears to benefit light- and deciduous tree-associated insect species and some forest birds.

J. Hjältén (✉) · J. Sjögren
Department of Wildlife, Fish, and Environmental Studies, Swedish University of Agricultural Sciences, 901 83 Umeå, Sweden
e-mail: joakim.hjalten@slu.se

J. Sjögren
e-mail: jorgen.sjogren@slu.se

J. Kouki
School of Forest Sciences, University of Eastern Finland, P.O. Box 111, 80101 Joensuu, Finland
e-mail: jari.kouki@uef.fi

A. Tolvanen
Natural Resources Institute Finland (Luke), Paavo Havaksen tie 3, 90570 Oulu, Finland
e-mail: anne.tolvanen@luke.fi

M. Versluijs
The Helsinki Lab of Ornithology, Finnish Museum of Natural History, University of Helsinki, 00014 Helsinki, Finland
e-mail: martijnversluijs@hotmail.com

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18.1 Background

18.1.1 *Natural Disturbance*

Both large-scale and small-scale disturbances have shaped boreal forests. Large-scale disturbances include, for example, fire, windstorms, and insect outbreaks, all believed to be important forces structuring the boreal forest (Attiwill, 1994; Bonan & Shugart, 1989; Kuuluvainen & Aakala, 2011). Small-scale disturbances, such as gap dynamics, local flooding events, smaller windthrow events, and localized insect and fungi damage, contribute to creating a dynamic mosaic boreal landscape with many ecological niches (Berglund & Kuuluvainen, 2021). This spatiotemporal variability has structured boreal communities and maintains the typical biodiversity of these ecosystems (see Chap. 19 for details).

18.1.2 *Forestry*

Current forestry practices in boreal Fennoscandia are highly mechanized and dominated by even-aged forest management where the typical management unit, the forest stand, is most often a few hectares in size (Fig. 18.1). Active management that promotes conifers and actively removes deciduous trees during thinning has created homogeneous stands with reduced tree species diversity and has led to the loss of ancient trees. Changes in forest structure and dynamics can be seen as transforming formerly complex forest ecosystems characterized by considerable variations in habitat type, including vertical structure, tree species composition, age distribution, and deadwood dynamics, into simplified forest habitats (Esseen et al., 1997; Kuuluvainen, 2009). Commercially managed forests are also denser, have less variation in tree height, and are less permeable to sunlight than natural forests. For example, stand-level timber volumes in Sweden have increased 40%–80% since the 1950s (SLU, 2012), and this increase has led to an impoverished flora and fauna of species associated with sun-exposed conditions and deciduous broadleaf trees (Berg et al., 1994; Bernes, 2011).

Fire was the predominant large-scale disturbance in boreal forests; however, as observed in most areas of Fennoscandia, fire frequency has dropped dramatically during the past century because of effective fire-suppression measures (Zackrisson, 1977). For example, less than 0.02% of the forest area burns each year in Sweden compared with approximately 1% before CE 1900 (Granström, 2001; Zackrisson, 1977). Many boreal species are strongly favored by fire or prefer charred substrates (Granström & Schimmel, 1993), and some fire-associated species reproduce almost exclusively in burned forest, including many invertebrate species and fungi (Heikkala et al., 2017; Kouki & Salo, 2020).

The reduced habitat diversity is considered a key factor behind the species' decline in managed boreal forest ecosystems (Buddle et al., 2006; Hjäältén et al., 2012;



Fig. 18.1 Forest stand subjected to clear-felling and stump harvest. *Photo credit* Jon Andersson

Jonsson et al., 2005; Kouki & Salo, 2020; Kuuluvainen, 2009; Paillet et al., 2010; Siitonen, 2001; Stenbacka et al., 2010). Forests are the most important habitat for red-listed and threatened species in Sweden and Finland. In Finland, 32% (2,133 species) of red-listed species are forest dwelling (Hyvärinen et al., 2019). Similarly, 43% (2,041 species) of the red-listed species in Sweden are forest dwelling (Artdatabanken, 2020). The species most negatively affected by silviculture are old-growth specialists dependent on a long forest continuity and old trees and species associated with deciduous trees (Artdatabanken, 2020; Bernes, 2011; Hyvärinen et al., 2019). Efforts to mitigate these adverse effects on biodiversity have been introduced to limit the harmful effects of the prevailing forestry practices on species and habitats.

18.1.3 Mitigation Strategies

Over the last three decades, Fennoscandia has experienced an increased interest in a forest management approach that aims to mitigate the negative effects of forestry on biodiversity. This change has come about through a combination of updated legislation, e.g., the Finnish Forest Act updated in 2014 and the Swedish Forestry Act updated in 1993, revised management recommendations in forestry, and higher consumer awareness that demands products from environmentally certified forestry, such as the Forest Stewardship Council (FSC) and the Programme for the Endorsement of Forest Certification (PEFC). Currently, the forest industry is required to apply a variety of conservation measures to improve conditions for biodiversity to fulfill certification demands and legal requirements (Johansson et al., 2013). In boreal

regions, these measures include setting forest stands aside from ordinary forestry, leaving buffer zones of trees alongside wetlands and water bodies, leaving snags and logs on clear-cuts, and also actively creating deadwood in connection to final harvesting (Gustafsson et al., 2012; Johansson et al., 2013); the latter measure often occurs in the form of artificially created high stumps of trees. The prescribed burning of clear-cuts and, to some extent, standing forests are also included in the Swedish FSC standard (FSC, 2020). Although these efforts may increase the availability of vital forest habitat structures, they are likely insufficient to sustain viable populations of all forest-dwelling species (Johansson et al., 2013). Moreover, formally protected forests have increased in area in both Sweden and Finland (Hohti et al., 2019), albeit very slowly. Despite these efforts, the Swedish environmental objectives of “a rich diversity of plant and animal life” and “a living forest” are not being fulfilled, as shown by, for example, the high number of threatened species in the forest landscape (Naturvårdsverket, 2019). One reason for the lack of progress in biodiversity conservation may be that a large part of the currently protected forest areas was managed before becoming established as reserves. Consequently, they do not contain forest habitats or forest legacies that would prevail in a corresponding truly natural forest. For example, in Finland, about half of the protected forests in the southern part of the country are young, often less than 100 years old, and were intensively managed—including clear-cutting in many cases—before being established as reserves.

18.1.3.1 Why Restoration?

Since very few unmanaged forest habitats remain globally, including in Fennoscandia, conserving biodiversity can no longer rely on passive conservation measures, i.e., setting aside conservation areas under a free-development philosophy to reach conservation goals (Aronson & Alexander, 2013; Millennium Ecosystem Assessment, 2005). To achieve conservation goals, we require methods for restoring hitherto managed forest and applying an active management of forest reserves.

18.1.3.2 How to Restore?

It has been argued that reintroducing natural disturbances, referred to as *natural disturbance emulation* (NDE), is an ideal management approach when restoring natural systems (Attiwill, 1994; Kuuluvainen, 2002; Lindenmayer et al., 2006). In Fennoscandian boreal forests, appropriate NDE restoration efforts should include both large- and small-scale disturbances, e.g., introducing fire through prescribed burning and emulating gap dynamics by creating gaps in the canopy and generating coarse woody debris (CWD; Kuuluvainen, 2002). Both restoration methods accelerate the production and structural variability of CWD (Hekkala et al., 2016;

Kuuluvainen, 2002; Laarmann et al., 2013) and create more diversified forest habitats. The conceptual and practical aspects of NDE in the boreal forest are elaborated further in Chap 19.

A major challenge in forest restoration is that identifying and emulating natural disturbances is not always straightforward. These co-occur at different spatial and temporal scales, and it appears evident that natural disturbances per se can experience shifts in disturbance regimes, e.g., because of climate effects, or can present context-specific patterns related to soil or topographical factors. If specific natural disturbance processes have almost completely disappeared from managed forests, then restoring any of such features should be beneficial. Fire is an excellent example in this context for situations where fires have been completely suppressed from managed forests. Although it may be challenging to fully restore fire disturbances or fire regimes over large landscapes and at different time scales, the reintroduction of fire, even within small areas or in young forests (Hägglund et al., 2015; Hekkala et al., 2014a; Hjältén et al., 2017), can have rapid and beneficial effects on species. However, it is also clear that the benefits differ depending on the regional and local conditions (Kouki et al., 2012).

Additionally, as NDE is often introduced into landscapes containing both managed and protected areas, the actual restoration method may need to be adjusted accordingly. In situations where land-sharing prevails, a gradient of restoration methods can be implemented so that full NDE is likely only in the protected areas, whereas more nuanced measures may be more applicable to the managed parts of the landscape where timber production may continue to be the dominant land use. Overall, the difficulty of having a realistic NDE model (but see Chap. 19) and incorporating any existing limitations associated with prevailing land-use patterns and land-use history is that this quickly leads to applying a low- to high-intensity NDE gradient among the various landscapes. It is clear, however, that there are no general ecological principles or practical guidelines on how to achieve the optimal combination of different NDE methods in such a landscape mosaic. Achieving this requires a better understanding of specific case studies that can highlight how restoration can occur in an ecologically effective manner.

18.2 NDE of Large-Scale Disturbances: Prescribed Burning

Wildfires are major natural disturbances across the boreal region (Bonan & Shugart, 1989; Kouki et al., 2012; Kuuluvainen & Aakala, 2011). Because fires have been suppressed in many intensively managed landscapes, the reintroduction of fire is a promising method for NDE, and prescribed burning is required by the Swedish and Finnish FSC certification standards (FSC, 2020). Relative to many other restoration methods, prescribed burning is generally technically more challenging to apply. For example, prescribed restoration burns require large numbers of skilled fire managers and for the fires to be set during specific weather conditions. Furthermore, prescribed

fires always involve a safety risk, and it is also not exactly certain how prescribed burns should be conducted to mimic natural disturbance conditions.

Prescribed burning of clear-cut areas is a traditional management method in forestry in Fennoscandia (Fig. 18.2). Its primary purpose is to modify soil properties and promote the establishment of a new tree cohort; however, the method was abandoned because of pest- and pathogen-related damage and high labor costs. Therefore, this technique was replaced by mechanical site preparation methods (Löf et al., 2015). Methods of prescribed burning for ecological restoration vary and involve different levels of tree retention. A few recent experiments have explored the effects of prescribed burning on biodiversity patterns. Most of these studies have included various types or intensities of tree harvests combined with prescribed burns; however, some studies also included comparisons with other restoration methods. The consequences of prescribed burns have been monitored, at least, for birds, beetles and other invertebrates, wood-associated and other macrofungi, vascular plants, bryophytes and lichens, and tree seedlings. The treated forest stands typically cover 2 to 25 ha and can be regarded as large-scale experiments in a Fennoscandian context.



Fig. 18.2 Prescribed burn of a forest stand as part of an ecological restoration experiment in Sweden (see e.g., Hägglund et al., 2020; Hjältén et al., 2017; Versluijs et al., 2017) *Photo credit* Joakim Hjältén

18.2.1 *Response of Insects and Fungi*

The effect of fire on biodiversity patterns and forest dynamics is generally always strong and immediate. For example, beetle assemblages are altered dramatically when a forest is burned. This change is evident regardless of the level of harvesting (Hyvärinen et al., 2005) or the amount of fuelwood created (Hekkala et al., 2014a). Notably, the use of fire appears to favor rare and threatened coleopteran species. For example, Hyvärinen et al. (2006) found that a forest stand burned in Finland immediately harbored about four times more rare or threatened beetle species than comparable unburned forest stands. Thus, fire has a significant biodiversity conservation effect, as these species are usually the rarest of all threatened species and are in the most urgent need of conservation actions. Hekkala et al. (2014a) observed, however, that the initial and rapid increase in the richness of saproxylic and fire-dependent beetle species declined to pretreatment levels only a few years after a prescribed burn. Thus, they suggest that fire should be introduced into neighboring areas at five-year intervals to maintain populations of the most fire-dependent pyrophilous species (Hekkala et al., 2014a).

The prescribed burning of spruce-dominated forests in Sweden also revealed a strong short-term effect on saproxylic assemblages and an increase in species richness and abundance of several functional groups of beetles and flat bugs (Hägglund et al., 2015, 2020; Hjältén et al., 2017). Fire-favoring and fire-dependent beetles and flat bugs benefit in particular from prescribed burns (Hägglund et al., 2015, 2020). Contrary to the results from Finland, however, no strong short-term effect on red-listed species has been detected. A possible explanation for these differing outcomes is that the effects of prescribed burns depend on landscape quality. In landscapes with a long history of intensive management and fire suppression, the insect community may be impoverished, making it more difficult for threatened fire-dependent species to find and colonize burned sites (Johansson et al., 2013; Kouki et al., 2012). This underlines the importance of considering both temporal aspects and landscape in restoration planning.

Prescribed burns of coniferous stands affect tree mortality and thus modify the dynamics of resources available for species (Hämäläinen et al., 2016; Heikkala et al., 2014). A decadal follow-up study of the same sites of Hyvärinen et al. (2006) showed that beetle assemblages remained more diverse on burned sites (Heikkala et al., 2016). However, several obligate fire-associated species were very ephemeral in their occurrence within the burned stands. Flat bugs are good examples of this phenomenon. They were observed to efficiently colonize the burned forests (Hägglund et al., 2015; Heikkala et al., 2017), but they also disappeared only a few years after the fire (Fig. 18.3; Heikkala et al., 2017).

Macrofungi also presented several similar fire-associated species taxa that colonized quickly after a fire but then also disappeared rapidly from the assemblages, and several soil fungi were noted during the initial years after a wildfire or prescribed burn (Salo & Kouki, 2018; Salo et al., 2019). Contrary to soil fungi, wood-associated fungi responded to fire over a much more extended period and typically required a

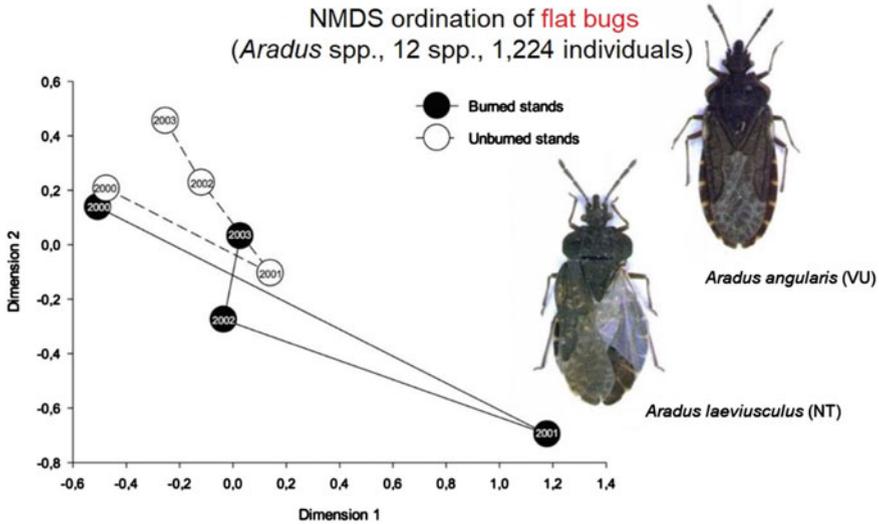


Fig. 18.3 Assemblage dynamics of fire-associated flat bugs (*Aradus* spp.) after forest harvests with burning (black circles) and after harvests without burning (white circles). Analysis is based on nonmetric multidimensional scaling (NMDS); assemblages sharing a similar composition are clustered together. Circles also include survey years: pretreatment (2000) of harvests and burning) and post-treatment survey years (2001–2003). Fire-associated species quickly colonized the burned areas in 2001; however, these species also disappeared quickly in 2002–2003, and the assemblage became similar to unburned sites. Modified with permission from John Wiley and Sons from Heikkala et al. (2017). Photo credits Petri Martikainen

decade or longer to become established (Junninen et al., 2008; Salo & Kouki, 2018; Suominen et al., 2015). The effect of fire was nevertheless very evident for these species. For example, even the stumps of harvested trees maintained a higher species richness for wood-associated fungi when the stumps were burned (Suominen et al., 2018).

18.2.2 Response of Vegetation and Pollinators

Boreal forest vegetation, dominated by coniferous trees (*Picea abies* (L.) H. Karst. and *Pinus sylvestris* L.) and dwarf shrubs such as *Calluna* spp., *Vaccinium vitis-idaea* L., and *V. myrtillus* L., is highly resilient and adapted to recurrent natural disturbances (Rydgren et al., 2004; Zackrisson, 1977). Depending on their intensity and magnitude, disturbances can affect the composition of the vegetation so that it resembles earlier stages along the successional path. Fire is the most intense natural disturbance, which may remove late-successional dwarf shrubs, mosses, lichens, and trees and replace them with seed-dispersing birch and other pioneer species (Schimmel & Granström, 1996). Restoration experiments of varying fire intensity confirm this

pattern and show that severe prescribed burning is most effective at initiating natural vegetation succession, whereas tree felling varies in its impact on the vegetation composition depending on the number of felled trees (Espinosa del Alba et al., 2021; Hekkala et al., 2014b; Johnson et al., 2014; Tatsumi et al., 2020). The effect of fire appears very organism dependent, and the time for recovery after disturbance can vary accordingly. Espinosa del Alba et al. (2021) show that ground-living bryophytes are severely adversely affected by prescribed burning and that the bryophyte community had yet to recover eight years after a fire. In contrast, after an initial decrease, the species richness of vascular plants was greater eight years postfire than pretreatment richness. However, epiphytic lichens also appear to be very sensitive to a fire's direct heat and burn effects (Hämäläinen et al., 2016). If such species groups occur in an area planned for fire restoration, special attention must be paid to the design and execution of this intervention to avoid risks to rare and threatened species. Unlike invertebrates, few plant species depend on fire in Fennoscandian boreal forests, although given the absence of natural fires, these species are increasingly threatened. Examples include the annual herbs *Geranium bohemicum* L. and *G. lanuginosum* Lam., which require high temperatures for their seeds to germinate.

Pollinators are expected to respond to vegetational changes due to fire or other disturbances (Rodríguez & Kouki, 2017). In a Finnish study, parasitoids—potential regulators of eruptive species—and pollinators of major forest dwarf shrubs bilberry (*Vaccinium myrtillus*) and lingonberry (*V. vitis-idaea*) were more diverse after a prescribed burn (Rodríguez et al., 2019). Prescribed burns expose mineral soils that provide sites for pollinators' nests. In addition, leaving dead trees or producing deadwood during prescribed burns provides nesting sites for pollinators. Prescribed burning can therefore be important for maintaining forest ecosystem functioning and providing ecosystem services continuously.

18.2.3 *Response of Birds*

The presence and distribution of forest birds are largely associated with stand-scale habitat structures, such as tree species diversity, the quantity of deciduous trees, the quantity of deadwood, and understory density (Hurlbert, 2004). Forest fires create various vital structures because there is a postfire shift toward an early-successional stage of the vegetation (Schimmel & Granström, 1996), the creation of deadwood, and an enhanced regeneration of deciduous trees, particularly aspen (*Populus tremula* L.) (Hekkala et al., 2014b). Nevertheless, changes in bird assemblages after prescribed burns have rarely been studied, possibly because burned areas tend to be small relative to the general habitat requirements of birds and other vertebrates. One of these rare prescribed burn–bird studies investigated bird assemblage changes after a prescribed burn in northern Sweden (Versluijs et al., 2017). Prescribed burning created habitat for long-distance migrants, ground breeders, and species preferring early-successional habitats. Moreover, Versluijs et al. (2020) showed that prescribed burns represent an effective means of fostering a rapid and long-lasting enrichment of important forest

structures for woodpeckers. This benefit to woodpeckers is caused mainly by the large numbers of killed and weakened trees, which facilitates their colonization by saproxylic insect populations (Kärvemo et al., 2017; Morissette et al., 2002). Phloem sap from fire-damaged Scots pine has also been shown to provide instant foraging opportunities for Three-toed Woodpeckers (*Picoides tridactylus*) (Pakkala et al., 2017). In the short-term, fire decreases the abundance of healthy trees and reduces understory density. These stands normally constitute important breeding and feeding habitats for birds preferring early-successional habitat; thus, off-ground breeders and species closely connected with mature forest occurred in lower numbers (Versluijs et al., 2017).

Most other studies on this topic have only explored the responses of birds to wild-fire. A study from northern Sweden found that wildfire positively affected ground-feeding insectivorous species (Edenius, 2011). Similarly, several studies from other forest systems showed that fire clearly benefits numerous bird species (Clavero et al., 2011; Hutto, 1995; Lowe et al., 2012). Although prescribed burns should mimic wildfire, it is unknown whether prescribed fires provoke the same response in bird assemblages as natural fires. The main difference is that, in most cases, mixed-severity wildfires produce a mosaic of variably burned areas (Salo & Kouki, 2018), whereas prescribed burns often result in low-intensity fires. Several studies have shown that fire intensity is also an important variable affecting bird responses to fire (Hutto & Patterson, 2016; Lindenmayer et al., 2014).

18.2.4 Management Considerations

Fire severity is important to consider when targeting expected biodiversity responses. Fire in the NDE of managed landscapes is often applied in a spectrum of severity so that the amount of timber left on the burned areas varies across a given site. In nature conservation areas where timber is not typically removed, the abundance of cut trees can be altered to modify the quantity of burning load and, subsequently, the amount of burned wood (Hekkala et al., 2014a, 2016). Although the use of fire represents an effective tool for restoring lost properties of a boreal stand, it is also evident that all aspects of wildfires are hard to emulate in a controlled fashion. Above all, if too few trees are left, there is unlikely a local continuity to the structures created by fire (Hämäläinen et al., 2016; Heikkala et al., 2014; Hyvärinen et al., 2005). Second, wildfires vary in severity, and the local variation in fire severity has significant consequences on biodiversity (Salo & Kouki, 2018; Salo et al., 2019;). In prescribed burns, fire severity often remains or is actively kept at a low level because of the risks associated with high-severity fires, which are typically canopy-destroying or stand-replacing fires. Despite these shortcomings, prescribed burns effectively restore lost forest properties and enhance biodiversity across landscapes that include both managed and protected sites.

18.3 NDE of Small-Scale Disturbances: Gap Cuttings and Deadwood Creation

18.3.1 *Response of Insect and Fungi*

Gap cuttings have been implemented to reduce the adverse effects of clear-felling on biodiversity and ecological processes by reducing clear-cut size. However, they also serve as a direct ecological restoration method that mimics gap dynamics and small-scale disturbances, e.g., windthrow and localized insect outbreaks (Fig. 18.4). Pasanen et al. (2016) found that gaps and the deadwood in gaps diversified wood-associated fungi five years after gap creation. On the other hand, Hägglund et al. (2020) found that ecological restoration involving the creation of small gaps (20 m in diameter) and deadwood had no significant effect on the overall stand-level species richness of beetles; however, gap-cut stands had a higher species richness for cambivores and known fire-favoring species than observed within reference stands. Moreover, coleopteran species composition differed significantly between stand types. A marginal increase of flat bugs has also been observed after gap cutting (Hägglund et al., 2015). Joelsson et al. (2018) confirmed the importance of stand heterogeneity for insect diversity by showing that harvest trails supported a different beetle assemblage than the surrounding intact forest. A likely explanation for these patterns is that the degree of sun exposure on deadwood has a strong effect on the saproxylic assemblage colonizing the deadwood (Hjältén et al., 2012; Lindhe et al., 2005; Seibold et al., 2016). This effect is potentially mediated by changes in the fungal community, as sun exposure also strongly determines the fungal composition and fungal growth rate in deadwood (Bouget & Duelli, 2004). Consistent with these observations, deadwood created in gaps favors numerous saproxylic beetles, including some fire-favored and fire-dependent species (Hägglund & Hjältén, 2018), suggesting these gaps attract species associated with more open-forest habitats. However, Hägglund and Hjältén (2018) also found significant differences in beetle assemblages in deadwood because of tree species and stature (standing or downed logs), consistent with earlier findings (Hjältén et al., 2012; Seibold et al., 2016). Pasanen et al. (2014) also observed that although wood fungi diversity was enhanced by gaps, red-listed wood fungi did not occur in gaps, most likely because of the lack of qualitatively suitable deadwood in the gaps during the five years of the study. These observations suggest that a high diversity of deadwood forms and quality must be available within the landscape to maintain saproxylic biodiversity (Penttilä et al., 2004; Similä et al., 2003).

18.3.2 *Response of Birds*

A bird study in the same stands in Sweden did not support the prediction that gaps attract species found in more open-forest habitats (Versluijs et al., 2017). They found that gap cutting did not affect bird assemblages; this pattern likely relates to the



Fig. 18.4 Gap cutting includes creating deadwood as part of an ecological restoration experiment in Sweden (see e.g., Hägglund et al., 2020; Hjältén et al., 2017; Versluijs et al., 2017) *Photo credit* Joakim Hjältén

combined effect of too-small gaps to attract open-area or edge specialists and a lack of response in the understory vegetation. Forsman et al. (2013), studying larger gaps, also did not find any general effect of gap disturbance on the overall abundance and richness of boreal-forest bird species. This could suggest that organisms such as birds that have larger home ranges, a larger spatial scale must be considered for restoration efforts and subsequent assessment (Hof & Hjältén, 2018).

18.3.3 Response of Vegetation

The documented effects of gap cutting on vascular plants provide ample theoretical support for this intervention being beneficial for species diversity per the intermediate disturbance hypothesis (Connell, 1978), which states that disturbances of intermediate frequency and severity maintain higher levels of diversity. Gap cutting could, in this sense, be viewed as an intermediate severity disturbance. However, the scientific literature is rather scarce for empirical studies on this topic (Eckert et al., 2019). When gaps are formed in the canopy following tree felling or natural disturbances, light penetration is increased on the forest floor. In North American studies, thinning or partial cutting increases the total cover of vegetation and understory species diversity (Burke et al., 2008; Thomas et al., 1999). One of the few studies from Fennoscandia demonstrated that felling 20%–40% of the initial stand volume does not affect the understory vegetation up to seven years after treatment (Hekkala et al.,

2014b). However, the uprooting of trees—to simulate storm felling—increased the species richness of vascular plants (Hekkala et al., 2014b). The authors conclude that the exposure of soil from the uprooting increases microsite heterogeneity and, therefore, greater habitat availability for pioneer seeds. The effects on vegetation have also been studied in the abovementioned Swedish experiment (Hägglund et al., 2020). However, Espinosa del Alba et al. (2021) found that 20 m diameter gaps had no significant impact on species richness or the composition of vascular plant assemblages or ground-living bryophyte assemblages up to eight years post-treatment.

In principle, canopy gaps also provide sites for tree-seedling regeneration and, thus, maintain continuous cover forests that appear as typical natural boreal landscapes. However, canopy gaps alone may be insufficient to facilitate regeneration unless the soils are also disturbed (Pasanen et al., 2016). Seed germination and seedling establishment in boreal forests generally require exposing the mineral soil to alleviate competition with the dense understory vegetation (Eriksson & Fröberg, 1996; Hautala et al., 2001, 2008). Moreover, restoration studies indicate that simulated storms that expose the soil through tree uprooting increase species diversity and the number of tree seedlings more than restoration by only cutting trees (Hekkala et al., 2014b). Pasanen et al. (2016) reported a low overall establishment of pine trees in canopy gaps despite a good initial regeneration rate. The lack of long-term success may have been caused by intensified root competition even though the soil was slightly modified in this experiment. Therefore, the use of fire in combination with small gap creation may enhance recruitment (Pasanen et al., 2015).

18.4 NDE: Restoration of Deciduous Forest Stands

In Sweden, stand-level timber volumes have increased 40%–80% since the 1950s (SLU 2012) owing to an increased production of conifers at the expense of broadleaf trees that are disfavored by modern forestry, e.g., during thinning. Commercial forests are therefore denser and less permeable to sunlight. Broadleaf trees are also disadvantaged when natural disturbance regimes, such as recurrent wildfires in upland forests and seasonal floods in riparian environments, are suppressed or altered (Hellberg, 2004; Johansson & Nilsson, 2002; Linder et al., 1997). These changes have led to an impoverished fauna of species associated with sun-exposed conditions and broadleaf trees (Bernes, 2011). Additionally, the abundance of large deciduous trees may also decline in protected areas, probably because these areas in Fennoscandia are often too small to sustain natural disturbance regimes (Hardenbol et al., 2020). Restoring broadleaf stands is therefore instrumental for biodiversity conservation.

During the last decades, large areas (much greater than 10,000 ha) have been restored in Sweden to benefit the White-backed Woodpecker (*Dendrocopos leucotos*), a critically endangered species with a population consisting of only a handful of breeding pairs. This species was once widespread throughout most of Sweden but declined rapidly during the past century because of intensified forest

management (Aulén, 1988; Stighäll et al., 2011). To restore habitats for the White-backed Woodpecker, forest managers in Sweden and Finland have created deadwood from broadleaf trees and selectively harvested spruce trees to open up forests and make deciduous trees more competitive (Blicharska et al., 2014; Hämäläinen et al., 2020). The White-backed Woodpecker has not yet recovered, but other less area-demanding and fast-responding species having similar habitat requirements have benefited from these restoration actions. Bell et al. (2015) found that the species richness of saproxylic beetles associated with deciduous deadwood and greater sun exposure was higher in the restored stands than unrestored ones, as were red-listed saproxylic beetle species. In addition, the availability of suitable insect food for White-backed Woodpeckers increased in restored areas, suggesting that when a sufficient area has been restored, the area-demanding White-backed Woodpecker can recover (Hof & Hjältén, 2018); nonetheless, the response at lower trophic levels are stronger indicators of ecosystem recovery (Fig. 18.5).

For a wide range of bird species, the occurrence of large-diameter deciduous trees is a critical habitat component. Although there is not much known about how restoring broadleaf stands influences bird assemblages, habitat specialists such as the White-backed Woodpecker are favored by an increased availability of deciduous trees. Aspen (*Populus tremula* L.) is particularly preferred as a nesting tree (Angelstam & Mikusiński, 1994) and is frequently used for foraging by the White-backed Woodpecker (Stenberg & Hogstad, 2004). Additionally, the presence of this woodpecker indicates a high species richness for forest birds, red-listed cryptogams, and

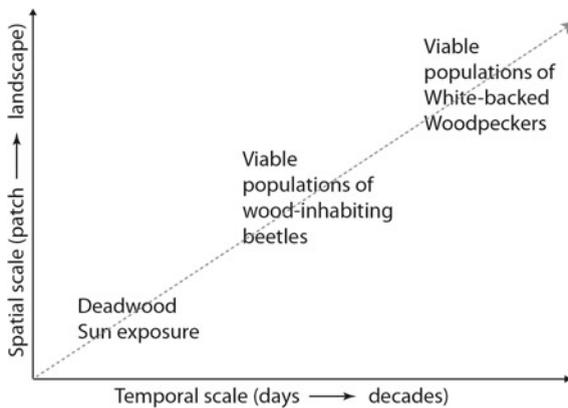


Fig. 18.5 Hypothetical example of the spatiotemporal-scaled response of organism groups, differing in their spatial requirements and reproduction rates, to the restoration of deciduous stands. Many species are resource and process limited, albeit at different spatial and temporal scales. Local restoration will not necessarily fulfill the habitat requirements of top predators, such as the White-backed Woodpecker; however, less area-demanding species, e.g., many saproxylic beetles, respond more rapidly. Forest restoration likely produces a bottom-up effect on top predators within saproxylic food webs. Under such circumstances, the recovery of umbrella species could testify to a full ecosystem recovery. The recovery of species at lower levels in the food chain could provide robust indicators of the onset of ecosystem recovery. Modified from Bell et al. (2015), CC BY 3.0 license

saproxyllic beetles (Bell et al., 2015; Mikusiński et al., 2001; Roberge et al., 2008). Different species of deciduous trees also contribute to a high variability in saproxyllic beetles, as beetle composition differs between aspen and birch stands. High variation in deciduous tree species, age, and deadwood at different decay stages will positively influence other bird species, especially bark-feeding and secondary cavity nesters. Eggers and Low (2014) observed that 83% of Willow Tits (*Poecile montanus*) excavate cavities mainly in birch and that the diameter of the nesting tree at nest height has a positive relationship with nest survival. Restoring the diversity and abundance of deciduous trees in boreal forests is thus likely crucial for the conservation of boreal-forest birds, in particular as deciduous trees improve foraging and breeding opportunities.

18.5 Risks Associated with Ecological Restoration

Prescribed burns in spruce-dominated forests in southern Finland have increased attacks by bark beetles (*Ips typographus*, *Pityogenes chalcographus*), although the harmful effects on tree survival in neighboring forests have generally been low (Eriksson et al., 2006). This observation suggests that restored areas do not provide significant refugia for the bark beetle populations unless restoration actions are repeated over consecutive years within a small area, allowing for bark beetle populations to build over time (Toivanen et al., 2009). Prescribed burns in Swedish spruce forests produced similar results, with a marked but short-lived increase in bark beetle abundance. Bark beetle densities had already decreased dramatically in the second year postfire, and five years after burning, the bark beetle densities were lower than those in the control areas, although the abundance of the natural predators of bark beetles was greater than in the controls (Hekkala et al., 2021; Kärvmö et al., 2017).

Tomicus spp., pine shoot beetles, are potentially harmful pests that may reduce the growth of Scots pine, although they usually do not kill healthy trees. In small gaps within pine forests, restoring deadwood increased *Tomicus* bark beetle numbers; however, these Coleoptera did not spread into adjacent forests, showing less than a few tens of meters of incursion into these neighboring sites. Thus, the effect was highly localized to the immediate neighborhood of restored sites. Additionally, the eruptive phase of *Tomicus* and the effects on adjacent trees typically last only a couple of years (Komonen & Kouki, 2008; Komonen et al., 2009; Martikainen et al., 2006). These observations suggest that restoring deadwood in pine forests does not increase the risk of bark beetle-related damage.

Besides the potential risk of pest outbreaks, there is also a risk of adverse effects on nontarget species. There is ample evidence that prescribed burns can harm species associated with old-growth forests and long forest continuity. For some species groups, such as epiphytic lichens and bryophytes, it is clear that they are susceptible to the direct heat and burn effects of fire (Hämäläinen et al., 2014). However, species from many other groups are disfavored by postfire conditions, and the adverse effects on some beetle groups may be transitional (Hyvärinen et al., 2009). Particular attention should be paid to the design and execution of prescribed burns so that rare and threatened species are not disfavored.

18.6 Conclusions

Ample evidence exists that ecological restoration within a NDE framework benefits biodiversity. However, there remain considerable gaps in our knowledge regarding the effect of different restoration methods on specific taxa and the duration of restoration benefits. Furthermore, most studies assessing the effects of NDE incorporating large-scale disturbances such as fire have been conducted at the plot or stand scale, whereas our knowledge of landscape-scale effects remains very limited. Thus, there is an urgent need to study the landscape-scale effect of ecological restoration (but see Kouki et al., 2012). Most studies have investigated the effects of large-scale disturbances associated with NDE—generally how prescribed burning affects biodiversity—whereas our knowledge of the impact of NDE on small-scale disturbances and the restoration of deciduous forest stands is more limited. Prescribed burns benefit many fire-adapted species; however, the restoration outcome depends on fire severity and landscape properties, including management history. The more limited number of assessments of deciduous forest stands suggests that restoration benefits light-demanding species associated with deciduous trees. However, more studies assessing this type of restoration and the response of different taxa are needed. The effect of gap cutting on biodiversity appears weak, and outcomes vary among studies and taxa. Moreover, the number of studies that have evaluated the impacts of gap cutting remains low, and the applied restoration methods differ among these studies, highlighting the need for additional and more comparative studies. Overall, the active restoration of critical habitats and substrates appears to be the only feasible way of alleviating and reducing the ongoing and projected biodiversity loss in degraded forest landscapes. Relying on passive restoration, i.e., waiting for natural structures to reappear through natural successional processes, is a painfully slow means of mitigating the rapidly advancing threat to forest biodiversity.

References

- Angelstam, P., & Mikusiński, G. (1994). Woodpecker assemblages in natural and managed boreal and hemiboreal forest—a review. *Annales Zoologici Fennici*, *31*, 157–172.
- Aronson, J., & Alexander, S. (2013). Ecosystem restoration is now a global priority: Time to roll up our sleeves. *Restoration Ecology*, *21*(3), 293–296. <https://doi.org/10.1111/rec.12011>.
- Art databanken. (2020). *The Swedish redlist*. Rodlistade arter i Sverige. Uppsala: ArtDatabanken SLU
- Attiwill, P. M. (1994). The disturbance of forest ecosystems: The ecological basis for conservative management. *Forest Ecology and Management*, *63*, 247–300. [https://doi.org/10.1016/0378-1127\(94\)90114-7](https://doi.org/10.1016/0378-1127(94)90114-7).
- Bell, D., Hjalten, J., Nilsson, C., et al. (2015). Forest restoration to attract a putative umbrella species, the white-backed woodpecker, benefited saproxylic beetles. *Ecosphere*, *6*(12), 278. <https://doi.org/10.1890/es14-00551.1>.
- Berg, Å., Ehnström, B., Gustafsson, L., et al. (1994). Threatened plant, animal, and fungus species in Swedish forests: Distribution and habitat associations. *Conservation Biology*, *8*(3), 718–731. <https://doi.org/10.1046/j.1523-1739.1994.08030718.x>.
- Berglund, H., & Kuuluvainen, T. (2021). Representative boreal forest habitats in northern Europe, and a revised model for ecosystem management and biodiversity conservation. *Ambio*, *50*, 1003–1017. <https://doi.org/10.1007/s13280-020-01444-3>.
- Bernes, C. (2011). *Biodiversity in Sweden. Monitor 22*. Stockholm: Swedish Environmental Protection Agency.
- Blicharska, M., Baxter, P., & Mikusiński, G. (2014). Practical implementation of species' recovery plans—lessons from the White-backed Woodpecker Action Plan in Sweden. *Ornis Fennica*, *91*(2), 108–128.
- Bonan, G. B., & Shugart, H. H. (1989). Environmental-factors and ecological processes in boreal forests. *Annual Review of Ecology and Systematics*, *20*, 1–28. <https://doi.org/10.1146/annurev.es.20.110189.000245>.
- Bouget, C., & Duelli, P. (2004). The effects of windthrow on forest insect communities: A literature review. *Biological Conservation*, *118*, 281–299. <https://doi.org/10.1016/j.biocon.2003.09.009>.
- Buddle, C. M., Langor, D. W., Pohl, G. R., et al. (2006). Arthropod responses to harvesting and wildfire: Implications for emulation of natural disturbance in forest management. *Biological Conservation*, *128*(3), 346–357. <https://doi.org/10.1016/j.biocon.2005.10.002>.
- Burke, D. A., Elliott, K. A., Holmes, S. B., et al. (2008). The effects of partial harvest on the understory vegetation of southern Ontario woodlands. *Forest Ecology and Management*, *255*(7), 2204–2212. <https://doi.org/10.1016/j.foreco.2007.12.032>.
- Clavero, M., Brotons, L., & Herrando, S. (2011). Bird community specialization, bird conservation and disturbance: The role of wildfires. *Journal of Animal Ecology*, *80*(1), 128–136. <https://doi.org/10.1111/j.1365-2656.2010.01748.x>.
- Connell, J. H. (1978). Diversity in tropical rain forests and coral reefs. *Science*, *199*, 1302–1310. <https://doi.org/10.1126/science.199.4335.1302>.
- Eckerter, T., Buse, J., Forschler, M., et al. (2019). Additive positive effects of canopy openness on European bilberry (*Vaccinium myrtillus*) fruit quantity and quality. *Forest Ecology and Management*, *433*, 122–130. <https://doi.org/10.1016/j.foreco.2018.10.059>.
- Edenius, L. (2011). Short-term effects of wildfire on bird assemblages in old pine- and spruce-dominated forests in northern Sweden. *Ornis Fennica*, *88*, 71–79.
- Eggers, S., & Low, M. (2014). Differential demographic responses of sympatric Parids to vegetation management in boreal forest. *Forest Ecology and Management*, *319*, 169–175. <https://doi.org/10.1016/j.foreco.2014.02.019>.
- Eriksson, M., Lilja, S., & Roininen, H. (2006). Dead wood creation and restoration burning: Implications for bark beetles and beetle induced tree deaths. *Forest Ecology and Management*, *231*(1–3), 205–213. <https://doi.org/10.1016/j.foreco.2006.05.050>.

- Eriksson, O., & Fröberg, H. (1996). "Windows of opportunity" for recruitment in long-lived clonal plants: Experimental studies of seedling establishment in *Vaccinium* shrubs. *Canadian Journal of Botany*, 74(9), 1369–1374. <https://doi.org/10.1139/b96-166>.
- Espinosa del Alba, C., Hjäältén, J., & Sjögren, J. (2021). Restoration strategies in boreal forests: Differing field and ground layer response to ecological restoration by burning and gap cutting. *Forest Ecology and Management*, 494, 119357. <https://doi.org/10.1016/j.foreco.2021.119357>.
- Esseen, P.-A., Ehnström, B., Ericson, L., et al. (1997). Boreal forests. *Ecological Bulletins*, 46, 16–47.
- Forest Stewardship Council. (2020). *The FSC National Forest Stewardship Standard of Sweden FSC-STD-SWE-03-2019*. Bonn: Forest Stewardship Council.
- Forsman, J. T., Reunanen, P., Jokimäki, J., et al. (2013). Effects of canopy gap disturbance on forest birds in boreal forests. *Annales Zoologici Fennici*, 50(5), 316–326. <https://doi.org/10.5735/085.050.0506>.
- Granström, A. (2001). Fire management for biodiversity in the European boreal forest. *Scandinavian Journal of Forest Research*, 16(sup003), 62–69. <https://doi.org/10.1080/028275801300090627>.
- Granström, A., & Schimmel, J. (1993). Heat effects on seeds and rhizomes of a selection of boreal forest plants and potential reaction to fire. *Oecologia*, 94(3), 307–313. <https://doi.org/10.1007/BF00317103>.
- Gustafsson, L., Baker, S. C., Bauhus, J., et al. (2012). Retention forestry to maintain multifunctional forests: A world perspective. *BioScience*, 62(7), 633–645. <https://doi.org/10.1525/bio.2012.62.7.6>.
- Häggglund, R., & Hjäältén, J. (2018). Substrate specific restoration promotes saproxylic beetle diversity in boreal forest set-asides. *Forest Ecology and Management*, 425, 45–58. <https://doi.org/10.1016/j.foreco.2018.05.019>.
- Häggglund, R., Hekkala, A. M., Hjäältén, J., et al. (2015). Positive effects of ecological restoration on rare and threatened flat bugs (Heteroptera: Aradidae). *Journal of Insect Conservation*, 19(6), 1089–1099. <https://doi.org/10.1007/s10841-015-9824-z>.
- Häggglund, R., Dynesius, M., Löfroth, T., et al. (2020). Restoration measures emulating natural disturbances alter beetle assemblages in boreal forest. *Forest Ecology and Management*, 462, 117934. <https://doi.org/10.1016/j.foreco.2020.117934>.
- Hämäläinen, A., Kouki, J., & Löhmus, P. (2014). The value of retained Scots pines and their dead wood legacies for lichen diversity in clear-cut forests: The effects of retention level and prescribed burning. *Forest Ecology and Management*, 324, 89–100. <https://doi.org/10.1016/j.foreco.2014.04.016>.
- Hämäläinen, A., Hujo, M., Heikkala, O., et al. (2016). Retention tree characteristics have major influence on the post-harvest tree mortality and availability of coarse woody debris in clear-cut areas. *Forest Ecology and Management*, 369, 66–73. <https://doi.org/10.1016/j.foreco.2016.03.037>.
- Hämäläinen, K., Junninen, K., Halme, P., et al. (2020). Managing conservation values of protected sites: How to maintain deciduous trees in white-backed woodpecker territories. *Forest Ecology and Management*, 461, 117946. <https://doi.org/10.1016/j.foreco.2020.117946>.
- Hardenbol, A. A., Junninen, K., & Kouki, J. (2020). A key tree species for forest biodiversity, European aspen (*Populus tremula*), is rapidly declining in boreal old-growth forest reserves. *Forest Ecology and Management*, 462, 118009. <https://doi.org/10.1016/j.foreco.2020.118009>.
- Hautala, H., Tolvanen, A., & Nuortila, C. (2001). Regeneration strategies of dominant boreal forest dwarf shrubs in response to selective removal of understorey layers. *Journal of Vegetation Science*, 12(4), 503–510. <https://doi.org/10.2307/3237002>.
- Hautala, H., Tolvanen, A., & Nuortila, C. (2008). Recovery of pristine boreal forest floor community after selective removal of understorey, ground and humus layers. *Plant Ecology*, 194(2), 273–282. <https://doi.org/10.1007/s11258-007-9290-0>.
- Heikkala, O., Suominen, M., Junninen, K., et al. (2014). Effects of retention level and fire on retention tree dynamics in boreal forests. *Forest Ecology and Management*, 328, 193–201. <https://doi.org/10.1016/j.foreco.2014.05.022>.

- Heikkala, O., Martikainen, P., & Kouki, J. (2016). Decadal effects of emulating natural disturbances in forest management on saproxylic beetle assemblages. *Biological Conservation*, 194, 39–47. <https://doi.org/10.1016/j.biocon.2015.12.002>.
- Heikkala, O., Martikainen, P., & Kouki, J. (2017). Prescribed burning is an effective and quick method to conserve rare pyrophilous forest-dwelling flat bugs. *Insect Conservation Diversity*, 10(1), 32–41. <https://doi.org/10.1111/icad.12195>.
- Hekkala, A. M., Paatalo, M. L., Tarvainen, O., et al. (2014a). Restoration of young forests in eastern Finland: Benefits for saproxylic beetles (Coleoptera). *Restoration Ecology*, 22(2), 151–159. <https://doi.org/10.1111/rec.12050>.
- Hekkala, A. M., Tarvainen, O., & Tolvanen, A. (2014b). Dynamics of understory vegetation after restoration of natural characteristics in the boreal forests in Finland. *Forest Ecology and Management*, 330, 55–66. <https://doi.org/10.1016/j.foreco.2014.07.001>.
- Hekkala, A. M., Ahtikoski, A., Paatalo, M. L., et al. (2016). Restoring volume, diversity and continuity of deadwood in boreal forests. *Biodiversity and Conservation*, 25(6), 1107–1132. <https://doi.org/10.1007/s10531-016-1112-z>.
- Hekkala, A. M., Kärvelo, S., Versluijs, M., et al. (2021). Ecological restoration for biodiversity conservation triggers response of bark beetle pests and their natural predators. *Forestry*, 94(1), 115–126. <https://doi.org/10.1093/forestry/cpaa016>.
- Hellberg, E. (2004). *Historical variability of deciduous trees and deciduous forests in northern Sweden. Effects of forest fires, land-use and climate*. Ph.D. thesis, Swedish University of Agricultural Sciences.
- Hjältén, J., Stenbacka, F., Pettersson, R. B., et al. (2012). Micro and macro-habitat associations in saproxylic beetles: Implications for biodiversity management. *PLoS ONE*, 7(7), e41100. <https://doi.org/10.1371/journal.pone.0041100>.
- Hjältén, J., Häggglund, R., Löfroth, T., et al. (2017). Forest restoration by burning and gap cutting of voluntary set-asides yield distinct immediate effects on saproxylic beetles. *Biodiversity and Conservation*, 26(7), 1623–1640. <https://doi.org/10.1007/s10531-017-1321-0>.
- Hof, A. R., & Hjältén, J. (2018). Are we restoring enough? Simulating impacts of restoration efforts on the suitability of forest landscapes for a locally critically endangered umbrella species. *Restoration Ecology*, 26(4), 740–750. <https://doi.org/10.1111/rec.12628>.
- Hohti, J., Halme, P., & Hjelt, M., et al. (2019). *Ten years of METSO—An interim review of the first decade of the Forest Biodiversity Programme for Southern Finland*. Helsinki: Publications of the Ministry of Environment
- Hurlbert, A. H. (2004). Species–energy relationships and habitat complexity in bird communities. *Ecology Letters*, 7(8), 714–720. <https://doi.org/10.1111/j.1461-0248.2004.00630.x>.
- Hutto, R. L. (1995). Composition of bird communities following stand-replacement fires in northern Rocky Mountain (U.S.A.) conifer forests. *Conservation Biology*, 9(5), 1041–1058. <https://doi.org/10.1046/j.1523-1739.1995.9051033.x-i1>.
- Hutto, R. L., & Patterson, D. A. (2016). Positive effects of fire on birds may appear only under narrow combinations of fire severity and time-since-fire. *International Journal of Wildland Fire*, 25(10), 1074–1085. <https://doi.org/10.1071/WF15228>.
- Hyvärinen, E., Kouki, J., & Martikainen, P. (2006). Fire and green-tree retention in conservation of red-listed and rare deadwood-dependent beetles in Finnish boreal forests. *Conservation Biology*, 20(6), 1711–1719. <https://doi.org/10.1111/j.1523-1739.2006.00511.x>.
- Hyvärinen, E., Kouki, J., Martikainen, P., et al. (2005). Short-term effects of controlled burning and green-tree retention on beetle (Coleoptera) assemblages in managed boreal forests. *Forest Ecology and Management*, 212(1–3), 315–332. <https://doi.org/10.1016/j.foreco.2005.03.029>.
- Hyvärinen, E., Kouki, J., & Martikainen, P. (2009). Prescribed fires and retention trees help to conserve beetle diversity in managed boreal forests despite their transient negative effects on some beetle groups. *Insect Conservation and Diversity*, 2(2), 93–105. <https://doi.org/10.1111/j.1752-4598.2009.00048.x>.

- Hyvärinen, E., Juslén, A., & Kemppainen, E., et al. (2019). *Suomen lajien uhanalaisuus—Punainen kirja 2019/The 2019 Red List of Finnish species*. Ympäristöministeriö and Suomen ympäristökeskus/Ministry of the Environment and Finnish Environment Institute.
- Joelsson, K., Hjäältén, J., & Work, T. (2018). Uneven-aged silviculture can enhance within stand heterogeneity and beetle diversity. *Journal of Environmental Management*, 205, 1–8. <https://doi.org/10.1016/j.jenvman.2017.09.054>.
- Johansson, M. E., & Nilsson, C. (2002). Responses of riparian plants to flooding in free-flowing and regulated boreal rivers: An experimental study. *Journal of Applied Ecology*, 39(6), 971–986. <https://doi.org/10.1046/j.1365-2664.2002.00770.x>.
- Johansson, T., Hjäältén, J., de Jong, J., et al. (2013). Environmental considerations from legislation and certification in managed forest stands: A review of their importance for biodiversity. *Forest Ecology and Management*, 303, 98–112. <https://doi.org/10.1016/j.foreco.2013.04.012>.
- Johnson, S., Strengbom, J., & Kouki, J. (2014). Low levels of tree retention do not mitigate the effects of clearcutting on ground vegetation dynamics. *Forest Ecology and Management*, 330, 67–74. <https://doi.org/10.1016/j.foreco.2014.06.031>.
- Jonsson, B. G., Kruys, N., & Ranius, T. (2005). Ecology of species living on dead wood—lessons for dead wood management. *Silva Fennica*, 39(2), 289–309. <https://doi.org/10.14214/sf.390>.
- Junninen, K., Kouki, J., & Renvall, P. (2008). Restoration of natural legacies of fire in European boreal forests: An experimental approach to the effects on wood-decaying fungi. *Canadian Journal of Forest Research*, 38(2), 202–215. <https://doi.org/10.1139/X07-145>.
- Kärvemo, S., Björkman, C., Johansson, T., et al. (2017). Forest restoration as a double-edged sword: The conflict between biodiversity conservation and pest control. *Journal of Applied Ecology*, 54(6), 1658–1668. <https://doi.org/10.1111/1365-2664.12905>.
- Komonen, A., & Kouki, J. (2008). Do restoration fellings in protected forests increase the risk of bark beetle damages in adjacent forests? A case study from Fennoscandian boreal forest. *Forest Ecology and Management*, 255(11), 3736–3743. <https://doi.org/10.1016/j.foreco.2008.03.029>.
- Komonen, A., Laatikainen, A., & Similä, M., et al. (2009). *Ytimennävertäjien kasvainsyönti trombin kaataman suojelumännikön ympäristössä Höytiäisen saarella Pohjois-Karjalassa*. Metsätieteen Aikakauskirja.
- Kouki, J., Hyvärinen, E., Lappalainen, H., et al. (2012). Landscape context affects the success of habitat restoration: Large-scale colonization patterns of saproxylic and fire-associated species in boreal forests. *Diversity and Distributions*, 18(4), 348–355. <https://doi.org/10.1111/j.1472-4642.2011.00839.x>.
- Kouki, J., & Salo, K. (2020). Forest disturbances affect functional groups of macrofungi in young successional forests—harvests and fire lead to different fungal assemblages. *Forest Ecology and Management*, 463, 118039. <https://doi.org/10.1016/j.foreco.2020.118039>.
- Kuuluvainen, T. (2002). Natural variability of forests as a reference for restoring and managing biological diversity in boreal Fennoscandia. *Silva Fennica*, 26(1), 97–125. <https://doi.org/10.14214/sf.552>.
- Kuuluvainen, T. (2009). Forest management and biodiversity conservation based on natural ecosystem dynamics in northern Europe: The complexity challenge. *Ambio*, 38(6), 309–315. <https://doi.org/10.1579/08-A-490.1>.
- Kuuluvainen, T., & Aakala, T. (2011). Natural forest dynamics in boreal Fennoscandia: A review and classification. *Silva Fennica*, 45(5), 823–841. <https://doi.org/10.14214/sf.73>.
- Laarmann, D., Korjus, H., Sims, A., et al. (2013). Initial effects of restoring natural forest structures in Estonia. *Forest Ecology and Management*, 304, 303–311. <https://doi.org/10.1016/j.foreco.2013.05.022>.
- Lindenmayer, D. B., Franklin, J. F., & Fischer, J. (2006). General management principles and a checklist of strategies to guide forest biodiversity conservation. *Biological Conservation*, 131(3), 433–445. <https://doi.org/10.1016/j.biocon.2006.02.019>.
- Lindenmayer, D. B., Blanchard, W., McBurney, L., et al. (2014). Complex responses of birds to landscape-level fire extent, fire severity and environmental drivers. *Diversity and Distributions*, 20(4), 467–477. <https://doi.org/10.1111/ddi.12172>.

- Linder, P., Elfving, B., & Zackrisson, O. (1997). Stand structure and successional trends in virgin boreal forest reserves in Sweden. *Forest Ecology and Management*, 98(1), 17–33. [https://doi.org/10.1016/s0378-1127\(97\)00076-5](https://doi.org/10.1016/s0378-1127(97)00076-5).
- Lindhe, A., Lindelow, A., & Asenblad, N. (2005). Saproxylic beetles in standing dead wood density in relation to substrate sun-exposure and diameter. *Biodiversity and Conservation*, 14(12), 3033–3053. <https://doi.org/10.1007/s10531-004-0314-y>.
- Löf, M., Erson, B., & Hjäältén, J., et al. (2015). Site preparation techniques for forest restoration. In J. A. Stanturf (Ed.) *Restoration of boreal and temperate forests*. 2nd edition, (pp. 85–103). Boca Raton: CRC Press.
- Lowe, J., Pothier, D., Rompré, G., et al. (2012). Long-term changes in bird community in the unmanaged post-fire eastern Québec boreal forest. *Journal of Ornithology*, 153(4), 1113–1125. <https://doi.org/10.1007/s10336-012-0841-3>.
- Martikainen, P., Kouki, J., & Heikkala, O., et al. (2006). Effects of green tree retention and prescribed burning on the crown damage caused by the pine shoot beetles (*Tomicus* spp.) in pine-dominated timber harvest areas. *Journal of Applied Entomology*, 130(1), 37–44. <https://doi.org/10.1111/j.1439-0418.2005.01015.x>.
- Mikusiński, G., Gromadzki, M., & Chylarecki, P. (2001). Woodpeckers as indicators of forest bird diversity. *Conservation Biology*, 15(1), 208–217. <https://doi.org/10.1111/j.1523-1739.2001.99236.x>.
- Millennium Ecosystem Assessment. (2005). *Ecosystems and human well-being: Biodiversity synthesis*. World Resources Institute.
- Morissette, J. L., Cobb, T. P., Brigham, R. M., et al. (2002). The response of boreal forest songbird communities to fire and post-fire harvesting. *Canadian Journal of Forest Research*, 32(12), 2169–2183. <https://doi.org/10.1139/x02-134>.
- Naturvårdsverket. (2019). *Fördjupad utvärdering av miljömålen 2019*. Stockholm: Naturvårdsverket.
- Paillet, Y., Bergès, L., Hjäältén, J., et al. (2010). Biodiversity differences between managed and unmanaged forests: Meta-analysis of species richness in Europe. *Conservation Biology*, 24(1), 101–112. <https://doi.org/10.1111/j.1523-1739.2009.01399.x>.
- Pakkala, T., Kouki, J., & Piha, M., et al. (2017). Phloem sap in fire-damaged Scots pine trees provides instant foraging opportunities for Three-toed Woodpeckers *Picoides tridactylus*. *Ornis Svecica*, 27(2–4), 144–149. <https://doi.org/10.34080/os.v27.19568>.
- Pasanen, H., Junninen, K., & Kouki, J. (2014). Restoring dead wood in forests diversifies wood-decaying fungal assemblages but does not quickly benefit red-listed species. *Forest Ecology and Management*, 312, 92–100. <https://doi.org/10.1016/j.foreco.2013.10.018>.
- Pasanen, H., Rehu, V., Junninen, K., et al. (2015). Prescribed burning of canopy gaps facilitates tree seedling establishment in restoration of pine-dominated boreal forests. *Canadian Journal of Forest Research*, 45(9), 1225–1231. <https://doi.org/10.1139/cjfr-2014-0460>.
- Pasanen, H., Rouvinen, S., & Kouki, J. (2016). Artificial canopy gaps in the restoration of boreal conservation areas: Long-term effects on tree seedling establishment in pine-dominated forests. *European Journal of Forest Research*, 135(4), 697–706. <https://doi.org/10.1007/s10342-016-0965-8>.
- 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. <https://doi.org/10.1016/j.biocon.2003.12.007>.
- Roberge, J. M., Angelstam, P., & Villard, M. A. (2008). Specialised woodpeckers and naturalness in hemiboreal forests—Deriving quantitative targets for conservation planning. *Biological Conservation*, 141(4), 997–1012. <https://doi.org/10.1016/j.biocon.2008.01.010>.
- Rodríguez, A., & Kouki, J. (2017). Disturbance-mediated heterogeneity drives pollinator diversity in boreal managed forest ecosystems. *Ecological Applications*, 27(2), 589–602. <https://doi.org/10.1002/eap.1468>.

- Rodríguez, A., Pohjoismaki, J. L. O., & Kouki, J. (2019). Diversity of forest management promotes parasitoid functional diversity in boreal forests. *Biological Conservation*, 238, 108205. <https://doi.org/10.1016/j.biocon.2019.108205>.
- Rydgren, K., Okland, R. H., & Hestmark, G. (2004). Disturbance severity and community resilience in a boreal forest. *Ecology*, 85(7), 1906–1915. <https://doi.org/10.1890/03-0276>.
- Salo, K., & Kouki, J. (2018). Severity of forest wildfire had a major influence on early successional ectomycorrhizal macrofungi assemblages, including edible mushrooms. *Forest Ecology and Management*, 415–416, 70–84. <https://doi.org/10.1016/j.foreco.2017.12.044>.
- Salo, K., Domisch, T., & Kouki, J. (2019). Forest wildfire and 12 years of post-disturbance succession of saprotrophic macrofungi (Basidiomycota, Ascomycota). *Forest Ecology and Management*, 451, 117454. <https://doi.org/10.1016/j.foreco.2019.117454>.
- Schimmel, J., & Granström, A. (1996). Fire severity and vegetation response in the boreal Swedish forest. *Ecology*, 77(5), 1436–1450. <https://doi.org/10.2307/2265541>.
- Seibold, S., Bassler, C., Brandl, R., et al. (2016). Microclimate and habitat heterogeneity as the major drivers of beetle diversity in dead wood. *Journal of Applied Ecology*, 53(3), 934–943. <https://doi.org/10.1111/1365-2664.12607>.
- Siitonen, J. (2001). Forest management, coarse woody debris and saproxylic organisms: Fennoscandian boreal forest as an example. *Ecological Bulletins*, 49, 11–41.
- Similä, M., Kouki, J., & Martikainen, P. (2003). Saproxylic beetles in managed and seminatural Scots pine forests: Quality of dead wood matters. *Forest Ecology and Management*, 174(1–3), 365–381. [https://doi.org/10.1016/S0378-1127\(02\)00061-0](https://doi.org/10.1016/S0378-1127(02)00061-0).
- Stenbacka, F., Hjältén, J., Hilszczański, J., et al. (2010). Saproxylic and non-saproxylic beetle assemblages in boreal spruce forests of different age and forestry intensity. *Ecological Applications*, 20(8), 2310–2321. <https://doi.org/10.1890/09-0815.1>.
- Stenberg, I., & Hogstad, O. (2004). Sexual dimorphism in relation to winter foraging in the white-backed woodpecker (*Dendrocopos leucotos*). *Journal of Ornithology*, 145(4), 321–326. <https://doi.org/10.1007/s10336-004-0045-6>.
- Stighäll, K., Roberge, J.-M., Andersson, K., et al. (2011). Usefulness of biophysical proxy data for modelling habitat of an endangered forest species: The white-backed woodpecker *Dendrocopos leucotos*. *Scandinavian Journal of Forest Research*, 26(6), 576–585. <https://doi.org/10.1080/02827581.2011.599813>.
- Suominen, M., Junninen, K., Heikkala, O., et al. (2015). Combined effects of retention forestry and prescribed burning on polypore fungi. *Journal of Applied Ecology*, 52(4), 1001–1008. <https://doi.org/10.1111/1365-2664.12447>.
- Suominen, M., Junninen, K., Heikkala, O., et al. (2018). Burning harvested sites enhances polypore diversity on stumps and slash. *Forest Ecology and Management*, 414, 47–53. <https://doi.org/10.1016/j.foreco.2018.02.007>.
- Swedish University of Agricultural Sciences (SLU). (2012). *Forest statistics 2012. Official statistics of Sweden*. Umeå: Swedish University of Agricultural Sciences.
- Tatsumi, S., Strengbom, J., Čugunovs, M., et al. (2020). Partitioning the colonization and extinction components of beta diversity across disturbance gradients. *Ecology*, 101(12), e03183. <https://doi.org/10.1002/ecy.3183>.
- Thomas, S. C., Halpern, C. B., Falk, D. A., et al. (1999). Plant diversity in managed forests: Understory responses to thinning and fertilization. *Ecological Applications*, 9(3), 864–879. [https://doi.org/10.1890/1051-0761\(1999\)009\[0864:pdimfu\]2.0.co;2](https://doi.org/10.1890/1051-0761(1999)009[0864:pdimfu]2.0.co;2).
- Toivanen, T., Liikanen, V., & Kotiaho, J. S. (2009). Effects of forest restoration treatments on the abundance of bark beetles in Norway spruce forests of southern Finland. *Forest Ecology and Management*, 257(1), 117–125. <https://doi.org/10.1016/j.foreco.2008.08.025>.
- Versluijs, M., Eggers, S., Hjältén, J., et al. (2017). Ecological restoration in boreal forest modifies the structure of bird assemblages. *Forest Ecology and Management*, 401, 75–88. <https://doi.org/10.1016/j.foreco.2017.06.055>.

- Versluijs, M., Eggers, S., & Mikusiński, G., et al. (2020). Foraging behavior of the Eurasian Three-toed Woodpecker (*Picoides tridactylus*) and its implications for ecological restoration and sustainable boreal forest management. *Avian Conservation and Ecology*, 15(1):art6. <https://doi.org/10.5751/ACE-01477-150106>.
- Zackrisson, O. (1977). Influence of forest fires on the North Swedish boreal forest. *Oikos*, 29, 22–32. <https://doi.org/10.2307/3543289>.

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