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The forgotten forest –

linking thinning practice, stand structural complexity, and biodiversity in boreal forest landscapes

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Introductory Research Essay
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Uppsala 2018

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Abstract

One of the world’s largest biomes, the boreal forest is the home of a great variety of life at same time as it is an important natural resource to the human society. While old growth forests, the host of high diversity, are still present in large parts of the boreal forests of North America and Russia, Fennoscandia has known a history of much more intensive forestry. These forests can now be regarded a laboratory for future forest management in Russia and North America. Research on the effects of fennoscandian forestry on biodiversity has focused mainly on the final harvest stage, clear cutting. Intermediate interventions such as forest thinning have not been in focus. Putting focus on forest thinning means investigating how the amount and dispersion of different structural elements in the boreal forest alone and interactively contribute to niche diversity. The role of deciduous trees, coniferous trees, dead wood and the bush layer for biodiversity are here discussed in the light of basic ecological mechanisms such as habitat heterogeneity and amount. Depending on the surrounding environment, pre – thinning condition, nature of the intervention and the organism group regarded, forest thinning can thus both promote and diminish diversity. Previous research on the effects of thinning on individual species and organism groups are discussed. One problem arising in this research is the characterization and quantification of the forest structural elements subject to thinning at a larger spatial scale. Here remote sensing techniques such as airborne laser scanning (ALS) is a promising tool. In fact it has shown reliable when applied to habitat suitability models. This essay further discusses how economic interests limit the structural complexity in managed boreal forests, how the identification of threshold habitat amounts are crucial here and how ALS can contribute to biodiversity retaining forest management planning.

Introduction

The boreal forest is one of earth’s largest biomes. It is estimated to be home for approximately 100 000 species of which only 20 300 are currently known to us (Ruckstuhl et al. 2008; Burton et al. 2010). Covering 11% of the landmass on earth it stores 60% of the global forest carbon stock (Kasischke 2000; Burton et al. 2010). The non – commercial ecosystem services provided across the boreal region have been estimated to be at USD 90 billion per year for the Canadian part alone (Burton et al. 2010). But the trees encompassing the boreal forest are also of great commercial value as they are the origin of 17% of all harvested round woods worldwide (Burton et al. 2010). All of the holding countries have signed both the United Nations convention on biological diversity as well as the Paris climate agreement and have thus committed to keeping commercial and non – commercial ecosystem services in balance (United Nations 1992, 2015). When it comes to biodiversity in boreal forests, old-growth stands are its most important host. These forests, characterised by large diameter trees and lots of dead wood, still exist in large parts of North America and Russia (Pan et al. 2011; Gauthier et al. 2015). Not so in Fennoscandia. This region has known a history of very intensive silviculture and as a result up to 90% of old growth forests have been removed (Östlund et al. 1997; Burton et al. 2010). Especially since the incorporation of large scale clear - cutting and replanting regimes in the 1950ies, the red list of boreal forest associated species has grown to 2260 in Sweden (2015) and 1200 in both Norway (2006) and Finland (2000; Rassi et al. 2000; Kålås et al. 2006; Sandström et al. 2015). As the need for cellulose and biofuels increases worldwide the boreal forest as a whole may face a similar destiny (Groisman and Gutman 2013; Gauthier et al. 2015). In order to prevent the red list from growing under this development research on biodiversity retaining forestry regimes has been called for (Ruckstuhl et al. 2008; Gustafsson et al. 2010).

In the boreal forest, even - aged silviculture with cycles of 80 – 100 years is dominant. Forest stands are clear-felled on areas of 1 – 100ha (The average in Sweden is 4.5ha; Skogsstyrelsen 2014). Reforestation is achieved by either retaining seed trees or by replanting. As this forest regrows, it is subject to one pre – and one to two commercial thinning stages before it reaches harvestable age. Pre – commercial thinning is the cleaning of undesired and damaged trees and occurs 10 – 20 years after the cutting. Commercial – thinning occurs 40 – 60 years after cutting and aims at reducing resource competition for the trees ultimately targeted by the forest owner. Also small trees of the forest understory are routinely removed during this process in order to facilitate machine handling. This results in a forest of even aged stands, often of the same species (Smith et al. 1997; Hedwall et al. 2013; Holm 2015). Most research in the field of biodiversity retaining forestry has focused on clear cutting, the final harvest stage. The effect on biodiversity of different levels of green and dead tree retention as well as of the area harvested have been popular topics here (Gustafsson et al. 2010). Less focus has been put on the intermediate stages of even aged forest management, i.e. thinning (but see Patriquin and Barclay 2003; Widenfalk and Weslien 2009; Griesser and Lagerberg 2012; Eggers and Low 2014). This is surprising as both the quantity and quality of the remaining forest habitat in the surrounding landscape is of crucial importance for long-term species conservation. Here, protected areas and voluntary set asides act as important source habitats (Ericsson et al. 2005; Berglund and Jonsson 2008). But whether their areal extent, dispersion and structural complexity in managed boreal forest landscapes is sufficient for playing this role is up for debate (Angelstam and Andersson 2001; Aune et al. 2005; Angelstam et al. 2013).

In fact the majority (In Sweden: 61.2% of the unprotected productive forestland; Skogsstyrelsen 2014) of stands in the managed boreal forest matrix are neither clear cuts nor protected areas but young forests (<60 years) that are subject to extensive and repeated thinning routines (Bergeron et al. 2006; Koehl and Rametsteiner 2007; Gauthier et al. 2015). The impact of forest thinning can therefore not be neglected by research. Previous research on the effects of forest thinning on both floral and faunal biodiversity has largely focused on temporal forests of North America (Verschuyl et al. 2011). It almost seems, that boreal forests subject to thinning are forgotten forests. In this introductory essay I want to shed light on these forests. I will discuss the structures that they contain and how these structures affect biodiversity at the stand and the landscape scale. I will expose knowledge gaps and argue for research questions that need to be answered should the goal of increased production and live forests be reached simultaneously.

Structural complexity affects biodiversity

If we want to understand the effect of forest thinning on biodiversity, we need to understand that the questions we ask are foremost questions about niche diversity and habitat amount. If mechanisms behind observed correlations are to be exposed, one needs to know which niches are promoted, which ones removed and about their distribution in the landscape. The habitat heterogeneity hypothesis tells us that more niches means more species (Tews et al. 2004; Stein et al. 2014). Niche diversity in the forest is equivalent to structural diversity. Structural diversity has long been regarded the essential factor shaping biodiversity and species richness in forests (MacArthur et al. 1961; Müller et al. 2010). Structural diversity refers to the variety and extent of any element present between the forest floor and the top of the canopy (MacArthur et al. 1961). The establishment of the idea that, in forests, the diversity of elements of structure is more important than the actual species composition is more important for bird diversity was made by MacArthur & MacArthur (1961). The element of structure that they looked at was foliage height diversity. Across the US and Panama in forests dominated by coniferous trees in Main to tropical forest on the American land bridge, the diversity of birds could be predicted by that parameter. The actual plant composition could not explain bird diversity any further once foliage height diversity had been considered for. The authors concluded that structural richness or niche diversity essentially shapes species diversity and that the actual plant species making up the forest only contribute if they contribute with more structure.

A linear increase in abundance of a structural element, does not necessarily result in the same increase of the species that includes that structural element in its niche, nor does species diversity necessarily increase (Venier and Fahrig 1996; Crist and Veech 2006; Fahrig 2013). The additive effect of a structural element decreases to zero at high abundances as other niche axes become limiting (Elton 1927; Boyce et al. 2016). While more structural elements of the same type can offer more feeding, predator evasion and reproduction opportunities for agile species and shady microhabitats to sessile ones to some extent, too much of it can decrease the suitability of this habitat due to low light penetration and cold microhabitats (Bartemucci et al. 2006; Niemelä et al. 2007; Nystrand et al. 2010; Nilsson and Wardle 2014). The additive effects of more of the same, indeed often connected to very productive sites, could thus not only decrease to zero but become negative at high amounts (Rosenzweig 1992; Vehviläinen et al. 2008). An optima is sometimes present (Rosenzweig 1992; Eggers et al. 2006). In a more diversified system, this rarefication and optima patterns hardly play a role. Many structural elements cannot become more abundant simultaneously, since the plants building the forest structures, themselves are subject to intra – and interspecific competition and the habitat they grow in subject to frequent disturbances (Brumelis et al. 2011).

It is reasonable to assume that some structural elements at the stand level contribute more than others to biodiversity, their biomass and frequency taken into account (Nilsson et al. 2001). Knowledge about this relative contribution and the interplay of structural abundance and its effect on biodiversity is essential in the conservation of many forest dwelling species (Schmiegelow and Mönkkönen 2002; Hottola and Siitonen 2008; Roberge et al. 2008).

Structural complexity and biodiversity at the landscape level

One actor in this interplay is the dispersion of a certain number of structural elements in the forest landscape (Andrén 1994; Aune et al. 2005). This dispersion, mostly termed habitat fragmentation has been named one of the main contributors to biodiversity losses worldwide and the managed boreal forest is no exception here (Fahrig 2003; Haddad et al. 2015). While a population can fully sustain itself in an area with certain structural abundance if the structural elements are coagulated, it might be unable to do so if that same amount appears dispersed (Andrén 1992; Doherty and Grubb 2002; Aune et al. 2005; Schmidt and Roland 2006). One reason is the fact that a coagulated habitat patch has a smaller circumference to area ratio as a dispersed one of the same area. Mortality at habitat edges caused by a predator not present within the habitat type is therefore expected to increase with increased fragmentation (Andrén 1992; Eggers et al. 2005). A further negative driver in fragmented habitats is the limited amount of suitable reproduction habitat which forces species to reuse old sites with increased risk of disease infection and parasitism (McCallum and Dobson 1995, 2002). Even if a patch of suitable habitat could support a small population at a local scale, it often does not when this habitat is very fragmented at a landscape scale. Stochastic events, genetic drift, inbreeding depression, lack of mates, and dispersal into sink habitats result in high mortality, low reproductive success, high emigration and low immigration and fall into the category of negative density dependence (Lande 1987; Tilman et al. 1994; Courchamp et al. 1999; Matthysen 2002). While these processes are among the most important drivers of the negative effect of habitat fragmentation on biodiversity, they do not stand alone (Haddad et al. 2015).

In order to alleviate negative effects of higher levels of fragmentation at the landscape level, habitat amount needs to increase at the local level (Fahrig 2003). A threshold above which a species is fairly save from the above described processes often exist for both the fragmentation and the amount of habitat (Groffman et al. 2006). As stated, is the threshold level of habitat abundance and that of fragmentation interdependent. The existence of just the right amount and dispersion of essential structural elements in the boreal forest landscape could prevent many species from falling into vicious negative density dependence cycles. Understanding the mechanisms behind the correlation between forest thinning and biodiversity, therefore means understanding the relative and combined effects of structural elements in the boreal forest as well as the threshold and optima levels of their abundance and dispersion - at different spatial and temporal scales.

Structural complexity and biodiversity at the stand level

In the boreal forest, as compared to more temperate and tropical forests, the structural diversity is poor in general (MacArthur et al. 1961; Esseen et al. 1997; Tanabe et al. 2001). The structural elements can be grouped into four categories; deciduous and coniferous trees, dead wood, and the bush layer. In the European boreal forest, the coniferous Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*) dominate at the regional scale, while the early successional deciduous trees, mainly birch (*Betula spp.*; *B. pendula* and *B. pubescens*) and aspen (*Populus tremula*) can grow in patch wise dominance (Esseen et al. 1997; Gauthier et al. 2015). This categorisation would be accordingly for the rest of the boreal forest.

Deciduous trees - Deciduous trees often appear in large numbers after fire in natural systems and clear cuts in managed ones (McCullough et al. 1998; Reich et al. 2001; Kuuluvainen 2002). Beyond their importance as dead wood habitat during late successional stages, they are the prime habitat of caterpillars, which in turn are the essential food source during the breeding season of many bird species (Neuvonen and Niemelä 1981; Schmidt and Roland 2006; Sisask et al. 2010; Vatka et al. 2011). Being bound to early successional stages, boreal deciduous trees die much earlier than their coniferous conspecifics. As dead wood in general is associated with high insect abundance, higher proportions of deciduous trees might here be the decisive factor for future passerine diversity in the boreal forest (Siitonen

2001; Roberge et al. 2008; Vatka et al. 2014). Not only as food but also as nesting resource, is aspen an essential structural element for cavity nesting birds. Among the live trees, the aspen is by far the most popular tree for primary nest excavators and consequentially also for those hole nesting birds succeeding them in using the excavations (Li and Martin 1991; Rolstad et al. 2000; Martin et al. 2004). It is Europe’s fastest growing tree species and its wood due to the high growth rate softer than that of its conspecifics, which is preferred by nest excavators (Worrell 1995; Schepps et al. 1999). In addition to avian species, deciduous trees are a key habitat for many forest floor dwelling carabids that have leaf – litter as their preferred habitat (Niemelä et al. 1992, 2007).

Coniferous trees - When it comes to coniferous trees, the dominating species, pine and spruce, are very different in their characteristics. In regions where forest fires are still frequent the fire tolerant Pine can be a key structural legacy for many species, when all other trees have died (Schimmel and Granström 1997; Angelstam 1998; Brumelis et al. 2011). Other than the spruce, it can also grow in nutritionally poor soils and thereby add a three dimensional element to sites otherwise characterised by low vegetation, e.g. mires and heathlands (Esseen et al. 1997; Nilsson and Wardle 2014). Other than pine and most deciduous trees, the spruce is shade tolerant as well as largely ignored by browsers (Snyder and Janke 1976; Messier et al. 1998; Månsson 2009). This allows the spruce to maintain a structurally rich understory in late successional stages when deciduous trees show less growth or die under the closed canopy, or after a thinning event. The spruce has more dead branches close to the ground and a much more spread vertical distribution of its live branches than both pine and the most abundant deciduous tree in boreal forests, the birch (Tahvanainen and Forss 2008). This results in a higher structural diversity per tree basal area compared to birch and pine, where the structural richness is confined mostly to the crown. Not surprisingly, was overall bird diversity higher in managed pine forests mixed with spruce compared to purely pine dominated forests (Gjerde and Saetersdal 1997). More in detail, in a recent comparative study, it was shown that the significantly lower adult - as well as nest survival probability in willow tits compared to crested tits in spruce absent pine stands was neglectable at levels above 5 spruce trees per 100 m^2 (Eggers and Low 2014). Siberian jays (*Perisoreus infaustus*) prefer feeding near a spruce tree to more open pine dominated habitats presumably as protection from their main predator, the Goshawk (*Accipiter gentilis*) (Nystrand 2006). The same species had a decreased daily nest survival rate with fewer small to medium sized spruce trees around the nest. This effect was especially strong with higher amounts of corvids present in the area as well as in years with lower temperature (Eggers et al. 2005). The predation risk was particularly high in years of low temperature presumably being associated with limited food supplies and increased exposure to visual oriented predators (Eggers et al. 2008). A higher density of younger spruce trees could thus alleviate the negative breeding conditions in very cold years. Beyond these two species that are very typical for the boreal forest of Eurasia and are well investigated in terms of their habitat requirements, there are also North American species that are closely connected to the occurrence of spruce in boreal forests. The locally threatened spruce grouse for example (*Falcipennis canadensis*) is highly dependent on black spruce (*Picea mariana*), underneath which it places its nest (Anich et al. 2013). Not only birds but also mammals, plants, lichens and insects are associated with the spruce as a critical habitat structure. Coyotes (*Canis latrans*) were more successful in killing snowshoe hare the denser the spruce (*Picea glauca*) cover was in their hunting habitats. In the case of the lynx (*Lynx canadensis*), the number of successful hunts by ambushing increased accordingly, while overall hunting success was unaffected by vegetation cover (Murray et al. 1995). While mammals and birds can move in order to find more suitable habitats, individual plants and lichens are dependent on temporal stability of their habitat. Many lichen and moss species are dependent on shade if they are to have a continuous existence in a forest stand (Gauslaa and Solhaug 1996). Here the spruce, because it has branches reaching all the way to the forest floor, can offer small scale shade refuges in an otherwise relatively light intense forest, often present after thinning (Johansson 1987). Not only its shade casting but also its high abundance of vertical structure makes the spruce an essential habitat for lichens. Arboreal lichen biomass was 1292–3669 g per tree on spruce and 742 g on pine in a sampled coniferous forest in central Finland (Liu et al. 2000). Arboreal lichen are a decisive food source for wild but also semi domesticated reindeer during the fodder bottle neck in winter (Berg et al. 2008; Rautio et al. 2016). The ability of the spruce to regrow underneath a closed canopy together with the comparatively high substrate it presents to arboreal lichen can here make the difference in reindeer winter survival. Other species of often low mobility are insects. Habitat heterogeneity at a small scale (10m) is required if carabid beetles, ants and spiders are to be found in high diversity in managed forests (Niemelä et al. 1992, 2007). Here the spruce can reestablish or maintain this requirement’s fulfillment.

Dead wood - A structural element which is diverse and abundant in the boreal forest is dead wood (Esseen et al. 1997). The high frequency of forest fire and storms results in large inputs while short growing season and the low temperature are responsible for the low decay rate (Östlund et al. 1997; Siitonen 2001; Ericsson et al. 2005). It is assumed that dead wood plays an unproportionally large role in shaping biodiversity in the boreal forest (ref). 4000 – 5000 or 20-25% of all forest dwelling species in Finland depend on Course woody debris (CWD, larger sized dead wood) habitats (Siitonen 2001). Cryptogams (Bryophytes, Lichen and Fungi) are present on dead wood in a variety far greater than in any other habitat type (ref). Many of the dead wood associated species, also termed saproxylics, are specialists for different types of CWD and their decay stages (Berglund and Jonsson 2001). Some might require recently died standing spruce logs, while others thrive in late decay stages of a grounded birch. Decaying wood is so variable in its properties that it presents microhabitats and their associated species in numbers much higher after its death than before. (Bakke and Kvamme 1993; Siitonen 2001). Following an attack of the spruce bark beetle (*Ips typographus*), 92 saproxylic beetle species, in total 10’000 individuals were collected from five trees. On alive control trees only 300 could be collected (Bakke and Kvamme 1993). Looking at invertebrates only the community associated with the spruce bark beetle was numbered to 140 species in a different study (Weslien 1992). Invertebrate diversity in general increases dramatically with an increase in dead wood (Siitonen 2001; Stenbacka et al. 2015; Joelsson et al. 2017). The same is often true for birds (Virkkala 1987; Angelstam 1998; Roberge et al. 2008). The white-backed woodpecker (*Dendrocopos leucotos*) is a species strongly interconnected with dead deciduous trees. Though not exclusively, it feeds on beetles which themselves are unique to this habitat (Martikainen et al. 2008). Undoubtedly important as a substrate of bird consumables, dead wood is essentially decisive for the presence of many hole nesting species that rely on its cavities or wood composition for breeding (Newton 1994; Buetler et al. 2004; Blancher and Wells 2005; Roberge et al. 2008; Versluijs et al. 2017). 28% of forest associate bird species in Finland belong to this group (Väisänen et al. 1998). Other vertebrates falling into the hole nesting guild of the boreal forest are pine marten (*Martes martes*), flying squirrel (*Pteromys volans*) and many bat species (Hanski 1998; Rosell and Hovde 1998; Patriquin and Barclay 2003; Holloway and Malcolm 2007).

Bush layer - A structurally rich and diverse bush layer (0 – 2m above ground) is essential for food and survival of many insects, birds and mammals feeding or breeding on or close to the ground (Virkkala 1987; Griesser et al. 2007; Nilsson and Wardle 2014; Lindberg et al. 2015). The species composition and with it the micro structures in the bush layer are governed by the soil properties and light conditions. Too little light penetration can affect the forest floor vegetation to the extent that key nutritional plants for higher trophic levels become absent (Bartemucci et al. 2006; Hedwall et al. 2013). A key forest floor species in the boreal forest ecosystem is the blueberry / bilberry (*Vaccinium spp.*). It seems that, during late summer and autumn, every non – herbivorous bird and mammal in the boreal forest relies on its sweet fruit, which can easily be seen by the suspicious blue color of their feces. The right level radiation, itself governed by overstorey structure, is essential for it to thrive. In Sweden it has decreased during the last decades, assumingly due to the decrease of average forest age and the higher forest density that comes with it. On the other end of the radiation intensity, that governing clear cuts, blueberries are as scattered in abundance (Hedwall et al. 2013). When still in their early years, the boreal forest tree species sometimes make up a major part of the bush layer. Young deciduous trees appear in very high numbers after fires or clear cuts, while spruces can sometimes be the only larger element in the bush layer in forests of low light penetration (Messier et al. 1998; Brumelis et al. 2011). Adult survival in general, due to predator evasion possibilities, and nesting success of ground nesting birds especially, due to nest concealment, can be critically dependent on these structural elements. (Haapanen 1966; Yahner and Cypher 1987; Griesser and Lagerberg 2012).

Thinning affects structural complexity

Considering that the amount of a species in a forest depends on the above described forest structures and ecological mechanisms, it is intuitive to conclude that the effects of thinning on fauna and flora must be steered by the pre – thinning condition, the environment surrounding the forest, which trees that are removed and how the trees interplay as forest structural elements. For example thinning from above, e.g. the removal of large diameter trees creates canopy gaps and promotes mid - and understory growth and with it higher tree diversity, in this case, due to higher light radiation, more deciduous trees. Thinning from below, the dominant form in the boreal forest, on the other hand removes mid - and understory trees without substantially opening up the forest canopy for diverse understory regrowth (Messier et al. 1998; Bartemucci et al. 2006; Betts et al. 2013). Depending on the nature of the intervention, forest thinning can both facilitate and deteriorate the diversity of forest interior species. Whether the former or the latter is the case depends on the nature of the disturbance and on the species guild in question. Plants tend to be promoted (Verschuyl et al. 2011; Hedwall et al. 2013). Three studies looked at how pre-commercial thinning affected plant composition at the shrub level in young Douglas fir (*Pseudotsuga menziesii*) stands in British Columbia, Oregon and Washington state (Thomas et al. 1999; Thysell and Carey 2000; Lindgren et al. 2006). Though not located in the boreal forest, high altitude coniferous stands resemble the conditions found there (Jump et al. 2009). All three found positive effects of pre-commercial thinning on plant diversity, abundance and structural richness. The strongest effects were found in the Oregon study three years after the disturbance. Weaker reactions by the plant community were found in the other two studies, 12 – 14 years post thinning. Lindgren et al. (2006) report that the plant community reacted strongly in the near disturbance period but less so later on, as the forest canopy started to close again. This is consistent with study by Widenfalk and Weslien (2009) involving 4465 100m2 permanent plots spread across the central and northern boreal forest in Sweden. They reported that pre – commercial thinning can maintain the peak in plant diversity found in the young successional stages of managed forest stands. That forest floor vegetation diversity profits from thinning and the subsequently higher radiation is further supported by the higher abundance of a boreal forest keystone species, the bilberry (*Vaccinium myrtillus*). The authors of the study suggest that the thinning intensities required for this keystone species to persist at current levels in Sweden's managed boreal forests would in fact be too high from a forestry perspective (Hedwall et al. 2013). For many species of other taxa the opposite is the case. Lichens especially, suffer from higher radiation and the lack of shade in post thinning forests (Gauslaa and Solhaug 1996). Invertebrate richness is expected to decrease as well. Although this group might profit from the higher temperatures early in the year it should decrease in numbers beyond this positive effect due to the removal of its prime niche, dying and decaying wood, during thinning operations (Pettersson et al. 1995; Siitonen 2001; Komonen 2003; Niemelä et al. 2007; Stenbacka et al. 2015). Lichen, fungi and Insect diversity have actually been shown to co - vary in diversity in the boreal forest (Pettersson et al. 1995; Komonen 2003). Whether this is due to interdependence or confounded by the amount of common habitat remains unclear.

All boreal forest interior bats and most birds depend on protein rich food during large parts of the growing season and therefore feed solely or predominantly on insects and other invertebrates (Virkkala 1991; Pettersson et al. 1995; Patriquin and Barclay 2003). Post – harvest siviculture such as clearing deciduous shrubs both mechanically and by using herbicides has here been shown to have a large effect on invertebrate food availability (Thompson et al. 2003). Research on the boreal bats’ reaction to thinning are nevertheless rare. A Canadian study on three bat species could not find any effects of thinning at either 20% or 50% tree retention levels compared with 100%, on previously untouched boreal forest stands (Patriquin and Barclay 2003). For birds, especially resident ones, the situation looks different. For instance, food reduction as a consequence of thinning white pine (*Pinus strobus*) has been reported to negatively affect the granivorous crossbills (Simard 2001). In a line of studies in the Swedish boreal forest, thinning operations were pleaded guilty for increased adult and nest predation pressure as well as the reduction in population size, nest visitation rates, juvenile and adult survival as well as feather quality (Hamilton 1982; Ekman et al. 1994; Thompson et al. 2003; Eggers et al. 2006; Griesser et al. 2007; Nystrand et al. 2010; Eggers and Low 2014). In the world of birds it is predator evasion and well-hidden nests that are often decisive for their lifetime reproductive success (Ekman et al. 1981; Jansson and Andrén 2003; Eggers et al. 2006; Chalfoun and Martin 2009). Willow tits (*Poecile montana*) for example are outcompeted by crested tits (*Lophophanes cristatus*) for both cover of predation as well as suitable nesting sites if understory vegetation is sparse (Ekman et al. 1981; Eggers and Low 2014). That an association between higher commercial thinning intensity and lower winter population indices of the willow tit was made in the Swedish boreal forest, should here not come as a surprise (Eggers and Low 2014). In accordance is the response of another strict resident bird, the Siberian jay (*Perisoreus infaustus*). In a before - after comparative study a significant reduction in nest success as well as in the number of retained offspring present in autumn was demonstrated as a consequence of commercial thinning (Griesser et al. 2007).

Characterising and quantifying structural complexity with LiDAR

Most structural elements can be quantified on a small scale, say at the extent of a passerine territory, by field measurements. This scale is sufficient to link the presence of certain structural elements in the forest with that of an associated species (e.g. Mikusiński et al. 2001). It is though not sufficient if the aim is to model the abundance of structural elements at a landscape scale or when field measurements are unable to fully grasp the structural complexity, even at a local scale (e.g. tropical forests; Drake et al. 2002). To measure the abundance of structures at this scale is often needed for habitat suitability models. Such models aim at predicting the occurrence of a species by its habitat requirements (Tattoni et al. 2012). Here, remote sensing offers great opportunities. Especially the application of active laser scanning technologies like LiDAR (Light Detection and Ranging) has here shown promising results (Martinuzzi et al. 2009; Lindberg et al. 2015; Froidevaux et al. 2016). LiDAR produces data in the form of coordinate informed 3D point clouds. The data is gathered by an airborne vessel which emits and receives laser beams that sweep across the landscape below. The position of the point of reflection on ground is informed by the coordinates, altitude, speed and the principal axes of the aircraft (roll, pitch and yaw). In addition to the coordinates and altitude of the point of reflection, information on the material of the reflector can be gathered. The three dimensionality of LiDAR is to a great extent owed to the fact that an emitted laser beam is split into several returns by incomplete reflection on the structural elements of the forest on its way to the ground. The detail richness of the 3D cloud depends on the emitting frequency and the size of the laser beam on the ground. Subtraction of a ground - or elevation model from the raw point cloud results in a vegetation only cloud. This separation facilitates the subsequent extraction of LiDAR metrics but is also the source of sometimes not unimportant bias. Low and dense vegetation as well as boulder rich landscapes can be categorised as ground. Such false categorisation can become problematic when low vegetation or the absolute height of trees are targeted as predictor variables (Lefsky et al. 2002; Monnet 2012; Davies and Asner 2014).

Many studies have successfully modelled and quantified structural elements by means of LiDAR derived point clouds, directly or in connection with empirical measurements (Lim et al. 2003; Davies and Asner 2014). Such models include metrics genuine to forestry, like tree height, above ground biomass, basal area as well as height, volume and vertical distribution of the canopy, mid – and understory topography and mean stem diameter (Thomas et al. 1999, 2008; Drake et al. 2002; Clark et al. 2004, 2011; Lindberg et al. 2012; Fieber et al. 2015). Beyond quantifying these structural elements for forestry purposes, they have been successfully correlated with the occurrence of many forest dwelling species (Davies and Asner 2014). In a mixed conifer forest in Idaho, understory density, quantified by the number of laser returns below 1.25 metres, was a successful predictor of species richness in birds (Vogeler et al. 2014). Lesak et al. (2011) could explain 15 – 20% of bird species richness in deciduous forests of North America with the help of canopy and midstorey height and density, represented by the vertical distribution and number of LiDAR returns. In addition to these more traditional metrics, structural elements specific to the habitat of forest dwelling species, such as standing dead wood of different diameters and understory shrubs have been modelled with high accuracy (Martinuzzi et al. 2009). The predictability of suitable habitat by means of LiDAR can go further than that of traditional ground data. Concerning the red-cockaded woodpecker (*Leuconotopicus borealis*), LiDAR derived habitat thresholds corresponding to open canopy structure, moderate densities of large and medium pines, and sparse hardwood midstorey trees were shown to be more specific in predicting habitat use than thresholds based on conventional measurements on the ground (Garabedian et al. 2017). Habitat and species occurrence modelling by means of LiDAR is naturally dominated by studies on birds, this owing to the strong three dimensionality of the physical side of their niches. However, LiDAR’s applicability to these kinds of models is by no means limited to this species group (Davies and Asner 2014). While studies so far have focused on habitats presents in countries with sufficient research funds to perform LiDAR measurements, there is no reason to assume that the applicability of this technology is limited to these regions. The question today is not whether structural elements and the occurrence of associated species can be modelled by LiDAR metrics but which ecologically relevant mechanisms can be exposed by its help. Whether the amount of habitat availability or the habitats fragmentation is the reason for a species’ decline might now be possible to be answered on a much larger scale. When applied to questions connected to forest thinning in the boreal forest LiDAR could help identify certain structural elements known to be relevant for a certain species or to biodiversity as a whole, both where such structures can be spared by and promoted through thinning.

Prelude – Questions in mind

The structural elements described in this text are the ingredients to a natural or natural – like boreal forest. In the managed boreal forest landscape, structural diversity is much lower, lower to the extent that some of the above mentioned elements - dead wood, deciduous trees and understory - are hardly found at all (Brumelis et al. 2011). While some essential structural elements are spared by forest managers, they often do not appear in high enough numbers to play out their positive impact on biodiversity. The amount of CWD in Finland for example has been reduced by 98% compared to pre – industrial forestry (Siitonen 2001). Larger deciduous trees have become rare due to successful fire suppression, selective thinning and herbicide application (Linder et al. 1997; Östlund et al. 1997). In northern Sweden, only 0.6% of the forest remained multi-storeyed by 1980 (Östlund et al. 1997). It seems that, even under current legislation, if biodiversity enhancing structural elements are to be spared at larger amounts they must not have a negative impact on the forest owner

(Angelstam et al. 2013). In managed boreal forest there is a clear economic objective towards coniferous trees. In these forests, mid – and understorey trees are routinely removed without always verified economic profits (Holm 2015). Questions arise from this fact. 1) Is there a minimum amount of middle – and understorey structure, still above the habitat amount and fragmentation threshold detrimental to forest interior biodiversity, that can be spared during thinning in the boreal forest without negative economic consequences? 2) Which spared structural element is most likely able to fulfil both economic and biodiversity goals? 3) Can the amount of this structural element be quantified at a landscape scale with the goal to guide thinning operations to forests where the amount of that structural element is above threshold level? Of the structural elements found in the boreal forest, the spruce is here the most promising one. Shade tolerance and low grazing pressure keeps it alive and growing under a closed canopy, later contributing also economically (Snyder and Janke 1976; Messier et al. 1998; Månsson 2009). It has most microstructure per basal area of all boreal forest tree species (Tahvanainen and Forss 2008). For two sedentary bird species, it has already been shown that 5 – 6 small and medium sized spruces per 100 meters squared is the threshold level for their well – being (Nystrand et al. 2010; Eggers and Low 2014). The same threshold levels could hold for other forest dwellers. Modelling the abundance of small and medium sized spruces at the landscape scale with the help of LiDAR could allow large scale planning of forest thinning with respect to thresholds of habitat requirements. While this insight might not help alleviate the negative consequences of intensive forestry on boreal forest specialists, it will assist in halting the negative trend found even in generalist species.

Literature

Andrén, H. 1992. Corvid Density and Nest Predation in Relation to Forest Fragmentation: A Landscape Perspective. Ecology 73:794–804.

———. 1994. Effects of Habitat Fragmentation on Birds and Mammals in Landscapes With Different Proportions of Suitable Habitat - a Review. Oikos 71:355–366.

Angelstam, P., and L. Andersson. 2001. Estimates of the needs for forest reserves in Sweden. Scandinavian Journal of Forest Research 7581:38–51.

Angelstam, P. K. 1998. Maintaining and restoring biodiversity in European boreal forests by developing natural disturbance regimes. Journal of Vegetation Science 9:593–602.

Angelstam, P., J. M. Roberge, R. Axelsson, M. Elbakidze, K. O. Bergman, A. Dahlberg, E. Degerman, et al. 2013. Evidence-based knowledge versus negotiated indicators for assessment of ecological sustainability: The swedish forest stewardship council standard as a case study. Ambio 42:229–240.

Anich, N. M., M. Worland, and K. J. Martin. 2013. Nest-site selection, nest survival, productivity, and survival of spruce grouse in Wisconsin. The Wilson Journal of Ornithology 125:570–582.

Aune, K., B. G. Jonsson, and J. Moen. 2005. Isolation and edge effects among woodland key habitats in Sweden: Is forest policy promoting fragmentation? Biological Conservation 124:89–95.

Bakke, A., and T. Kvamme. 1993. *Beetles attracted to Norway spruce under attack by Ips typographus*. Medd. Skogforsk. Norsk Institutt for Skogforskning.

Bartemucci, P., C. Messier, and C. D. Canham. 2006. Overstory influences on light attenuation patterns and understory plant community diversity and composition in southern boreal forests of Quebec. Can. J. For. Res 36:2065–2079.

Berg, A., L. Östlund, J. Moen, and J. Olofsson. 2008. A century of logging and forestry in a reindeer herding area in northern Sweden. Forest Ecology and Management 256:1009–1020.

Bergeron, Y., D. Cyr, C. R. Drever, M. Flannigan, S. Gauthier, D. Kneeshaw, È. Lauzon, et al. 2006. Past, current, and future fire frequencies in Quebec's commercial forests: implications for the cumulative effects of harvesting and fire on age-class structure and natural disturbance-based management. Canadian Journal of Forest Research 36:2737–2744.

Berglund, H., and B. G. Jonsson. 2001. Predictability of plant and fungal species richness of old-growth boreal forest islands. Journal of Vegetation Science 12:857–866.

———. 2008. Assessing the extinction vulnerability of wood-inhabiting fungal species in fragmented northern Swedish boreal forests. Biological Conservation 3029–3039.

Betts, M. G., J. Verschuyl, J. Giovanini, T. Stokely, and A. J. Kroll. 2013. Initial experimental effects of intensive forest management on avian abundance. Forest Ecology and Management 310:1036–1044.

Blancher, P., and J. Wells. 2005. The Boreal Forest Region: North America’s Bird Nursery. American Birds 30–39.

Boyce, M. S., C. J. Johnson, E. H. Merrill, S. E. Nielsen, E. J. Solberg, and B. van Moorter. 2016. Can habitat selection predict abundance? Journal of Animal Ecology 85:11–20.

Brumelis, G., B. G. Jonsson, J. Kouki, T. Kuuluvainen, and E. Shorohova. 2011. Forest naturalness in Northern Europe: Perspectives on processes, structures and species diversity. Silva Fennica 45:807–821.

Buetler, R., P. Angelstam, P. Ekelund, and R. Schlaepfer. 2004. Dead wood threshold values for the three-toed woodpecker presence in boreal and sub-Alpine forest. Biological Conservation 119:305–318.

Burton, P. J., Y. Bergeron, B. E. C. Bogdanski, G. P. Juday, T. Kuuluvainen, B. J. McAfee, A. Ogden, et al. 2010. Sustainability of boreal forests and forestry in a changing environment. Forests and society: responding to global drivers of change 247–282.

Chalfoun, A. D., and T. E. Martin. 2009. Habitat structure mediates predation risk for sedentary prey: Experimental tests of alternative hypotheses. Journal of Animal Ecology 78:497–503.

Clark, M. L., D. B. Clark, and D. A. Roberts. 2004. Small-footprint lidar estimation of sub-canopy elevation and tree height in a tropical rain forest landscape. Remote Sensing of Environment 91:68–89.

Clark, M. L., D. A. Roberts, J. J. Ewel, and D. B. Clark. 2011. Estimation of tropical rain forest aboveground biomass with small-footprint lidar and hyperspectral sensors. Remote Sensing of Environment 115:2931–2942.

Courchamp, F., T. Clutton-Brock, and B. Grenfell. 1999. Inverse density dependence and the Allee effect. Trends in Ecology and Evolution 14:405–410.

Crist, T. O., and J. A. Veech. 2006. Additive partitioning of rarefaction curves and species–area relationships: unifying α-, β- and γ-diversity with sample size and habitat area. Ecology Letters.

Davies, A. B., and G. P. Asner. 2014. Advances in animal ecology from 3D-LiDAR ecosystem mapping. Trends in Ecology and Evolution 29:681–691.

Doherty, P. F., and T. C. Grubb. 2002. Survivorship of permanent resident birds in a fragmented forested landscape. Ecology 83:844–857.

Drake, J. B., R. O. Dubayah, D. B. Clark, R. G. Knox, J. B. Blair, M. A. Hofton, R. L. Chazdon, et al. 2002. Estimation of tropical forest structural characteristics, using large-footprint lidar. Remote Sensing of Environment 79:305–319.

Eggers, S., M. Griesser, T. Andersson, and J. Ekman. 2005. Nest predation and habitat change interact to influence Siberian jay numbers. Oikos 111:150–158.

Eggers, S., M. Griesser, M. Nystrand, and J. Ekman. 2006. Predation risk induces changes in nest-site selection and clutch size in the Siberian jay. Proceedings. Biological sciences / The Royal Society 273:701–6.

Eggers, S., and M. Low. 2014. Differential demographic responses of sympatric Parids to vegetation management in boreal forest. Forest Ecology and Management 319:169–175.

Ekman, J., G. Cederholm, and C. Askenmo. 1981. Spacing and Survival in Winter Groups of Willow Tit Parus montanus and Crested Tit P. cristatus - A Removal Study. Journal of Animal Ecology 50:1–9.

Ekman, J., B. Sklepkovych, and H. Tegelstrom. 1994. Offspring retention in the Siberian jay (Perisoreus infaustus): the prolonged brood care hypothesis. Behavioral Ecology 5:245–253.

Elton, C. 1927. Animal Ecology. Animal Ecology 207.

Ericsson, T. S., H. Berglund, and L. Östlund. 2005. History and forest biodiversity of woodland key habitats in south boreal Sweden. Biological Conservation 122:289–303.

Esseen, P.-A., K. Sjöberg, B. Ehnström, L. Ericson, and K. Sjöberg. 1997. Boreal Forests. Ecological Bulletins 46:16–47.

Fahrig, L. 2003. Effects of Habitat Fragmentation on Biodiversity. Annual Review of Ecology, Evolution, and Systematics 34:487–515.

———. 2013. Rethinking patch size and isolation effects: The habitat amount hypothesis. Journal of Biogeography 40:1649–1663.

Fieber, K. D., I. J. Davenport, M. A. Tanase, J. M. Ferryman, R. J. Gurney, V. M. Becerra, J. P. Walker, et al. 2015. Validation of Canopy Height Profile methodology for small-footprint full-waveform airborne LiDAR data in a discontinuous canopy environment. ISPRS Journal of Photogrammetry and Remote Sensing 104:144–157.

Froidevaux, J. S. P., F. Zellweger, K. Bollmann, G. Jones, and M. K. Obrist. 2016. From field surveys to LiDAR: Shining a light on how bats respond to forest structure. Remote Sensing of Environment 175:242–250.

Garabedian, J. E., C. E. Moorman, M. Nils Peterson, and J. C. Kilgo. 2017. Use of LiDAR to define habitat thresholds for forest bird conservation. Forest Ecology and Management 399:24–36.

Gauslaa, Y., and K. A. Solhaug. 1996. Differences in the Susceptibility to Light Stress Between Epiphytic Lichens of Ancient and Young Boreal Forest Stands. Functional Ecology 10:344–354.

Gauthier, S., P. Bernier, T. Kuuluvainen, A. Z. Shvidenko, and D. G. Schepaschenko. 2015. Boreal forest health and global change. Science 349:819–822.

Gjerde, I., and M. Saetersdal. 1997. Effects on avian diversity of introducing spruce Picea spp. plantations in the natine pine Pinus sylvestris forests of western Norway. Biological Conservation 79:241–250.

Griesser, M., and S. Lagerberg. 2012. Long-term effects of forest management on territory occupancy and breeding success of an open-nesting boreal bird species, the Siberian jay. Forest Ecology and Management 271:58–64.

Griesser, M., M. Nystrand, S. Eggers, and J. Ekman. 2007. Impact of forestry practices on fitness correlates and population productivity in an open-nesting bird species. Conservation Biology 21:767–774.

Groffman, P. M., J. S. Baron, T. Blett, A. J. Gold, I. Goodman, L. H. Gunderson, B. M. Levinson, et al. 2006. Ecological thresholds: The key to successful environmental management or an important concept with no practical application? Ecosystems.

Groisman, P. Y., and G. Gutman. 2013. Regional environmental changes in Siberia and their global consequences. Springer.

Gustafsson, L., J. Kouki, and A. Sverdrup-Thygeson. 2010. Tree retention as a conservation measure in clear-cut forests of northern Europe: A review of ecological consequences. Scandinavian Journal of Forest Research 25:295–308.

Haapanen, A. 1966. Bird fauna of the Finnish forests in relation to forest succession. II. Annales Zoologici Fennici 3:153–196.

Haddad, N. M., L. A. Brudvig, J. Clobert, K. F. Davies, A. Gonzalez, R. D. Holt, T. E. Lovejoy, et al. 2015. Habitat fragmentation and its lasting impact on Earth’s ecosystems. Science Advances 1:1–9.

Hamilton, H. 1982. Praktisk Skogshandbok. (Sveriges Skogsvårdsförbund. Föreningen Skogen., ed.). Stockholm.

Hanski, I. K. 1998. Home ranges and habitat use in the declining flying squirrel Pteromys volans in managed forests. Wildlife Biology 4:33–46.

Hedwall, P.-O., J. Brunet, A. Nordin, and J. Bergh. 2013. Changes in the abundance of keystone forest floor species in response to changes of forest structure. Journal of Vegetation Science 24:296–306.

Holloway, G. L., and J. R. Malcolm. 2007. Northern and southern flying squirrel use of space within home ranges in central Ontario. Forest Ecology and Management 242:747–755.

Holm, S.-O. 2015. A Management Strategy for Multiple Ecosystem Services in Boreal Forests. Journal of Sustainable Forestry 34:358–379.

Hottola, J., and J. Siitonen. 2008. Significance of woodland key habitats for polypore diversity and red-listed species in boreal forests. Biodiversity and Conservation 17:2559–2577.

Jansson, G., and H. Andrén. 2003. Habitat Composition and Bird Diversity in Managed Boreal Forests. Scandinavian Journal of Forest Research 18:225–236.

Joelsson, K., J. Hjältén, T. Work, H. Gibb, J. M. Roberge, and T. Löfroth. 2017. Uneven-aged silviculture can reduce negative effects of forest management on beetles. Forest Ecology and Management 391:436–445.

Johansson, T. 1987. Irradiance in thinned Norway spruce (Picea abies) stands and the possibilities to prevent suckers of broadleaved trees. Forest Ecology and Management 20:307–319.

Jump, A. S., C. Mátyás, and J. Peñuelas. 2009. The altitude-for-latitude disparity in the range retractions of woody species. Trends in Ecology and Evolution.

Kålås, J., A. Viken, and T. Bakken. 2006. Norwegian Red List. Norwegian Biodiversity Information Centre, Trondheim.

Kasischke, E. S. 2000. Boreal ecosystems in the global carbon cycle. Pages 19–30 *in*Fire, Climate Change, and Carbon Cycling in the Boreal Forest.

Koehl, M., and E. Rametsteiner. 2007. State of Europe’s Forests 2007: The MCPFE Report on Sustainable Forest Management in Europe.

Komonen, A. 2003. Hotspots of Insect Diversity in Boreal Forests. Conservation Biology.

Kuuluvainen, T. 2002. Natural variability of forests as a reference for restoring and managing biological diversity in boreal Fennoscandia. Pages 97–125 *in*Silva Fennica (Vol. 36).

Lande, R. 1987. Extinction Thresholds in Demographic Models of Territorial Populations. The American Naturalist 130:624–635.

Lefsky, M. A., W. B. Cohen, G. G. Parker, and D. J. D. Harding. 2002. Lidar Remote Sensing for Ecosystem Studies. BioScience 52:19–30.

Lesak, A. A., V. C. Radeloff, T. J. Hawbaker, A. M. Pidgeon, T. Gobakken, and K. Contrucci. 2011. Modeling forest songbird species richness using LiDAR-derived measures of forest structure. Remote Sensing of Environment 115:2823–2835.

Li, P., and T. E. Martin. 1991. Nest-site selection and nesting success of cavity-nesting birds in high elevation forest drainages. The Auk 108:405–418.

Lim, K., P. Treitz, M. Wulder, B. St-Onge, and M. Flood. 2003. LiDAR remote sensing of forest structure. Progress in Physical Geography 27:88–106.

Lindberg, E., K. Olofsson, J. Holmgren, and H. Olsson. 2012. Estimation of 3D vegetation structure from waveform and discrete return airborne laser scanning data. Remote Sensing of Environment 118:151–161.

Lindberg, E., J.-M. J.-M. Roberge, T. Johansson, and J. Hjältén. 2015. Can Airborne Laser Scanning (ALS) and forest estimates derived from satellite images be used to predict abundance and species richness of birds and beetles in boreal forest? Remote Sensing 7:4233–4252.

Linder, P., B. Elfving, and O. Zackrisson. 1997. Stand structure and successional trends in virgin boreal forest reserves in Sweden. Forest Ecology and Management 98:17–33.

Lindgren, P. M. F., D. B. Ransome, D. S. Sullivan, and T. P. Sullivan. 2006. Plant community attributes 12 to 14 years following precommercial thinning in a young lodgepole pine forest. Canadian Journal of Forest Research 36:48–61.

Liu, C., H. Ilvesniemi, and C. J. Westman. 2000. Biomass of Arboreal Lichens and its Vertical Distribution in a Boreal Coniferous Forest in Central Finland. The Lichenologist 32:495–504.

MacArthur, R. H., J. W. MacArthur, and MacArthur. 1961. On Bird Species Diversity. Ecology 42:594–598.

Månsson, J. 2009. Environmental variation and moose (Alces alces) density as determinants of spatio-temporal heterogeneity in browsing. Ecography 32:601–612.

Martikainen, P., L. Kaila, and Y. Haila. 2008. Threatened Beetles in White-Backed Woodpecker Habitats. Conservation Biology 12:293–301.

Martin, K., K. E. H. Aitken, and K. L. Wiebe. 2004. Nest Sites and Nest Webs for Cavity-Nesting Communities in Interior British Columbia, Canada: Nest Characteristics and Niche Partitioning. The Condor 106:5.

Martinuzzi, S., L. A. Vierling, W. A. Gould, M. J. Falkowski, J. S. Evans, A. T. Hudak, and K. T. Vierling. 2009. Mapping snags and understory shrubs for a LiDAR-based assessment of wildlife habitat suitability. Remote Sensing of Environment 113:2533–2546.

Matthysen, E. 2002. Boundary effects on dispersal between habitat patches by forest birds (Parus major, P. caeruleus). Landscape Ecology 17:509–515.

McCallum, H., and A. Dobson. 1995. Detecting disease and parasite threats to endangered species and ecosystems. Trends in Ecology & Evolution 10:190–194.

———. 2002. Disease, habitat fragmentation and conservation. Proceedings. Biological sciences 269:2041–9.

McCullough, D. G., R. A. Werner, and D. Neumann. 1998. Fire and Insects in Northern and Boreal Forest Ecosystems of North America. Annual Review of Entomology 43:107–127.

Messier, C., S. Parent, Y. Bergeron, and Opulus. 1998. Effects of Overstory and Understory Vegetation on the Understory Light Environment in Mixed Boreal Forests. Journal of Vegetation Science 9:511.

Mikusiński, G., M. Gromadzki, and P. Chylarecki. 2001. Woodpeckers as indicators of forest bird diversity. Conservation Biology 15:208–217.

Monnet, J. M. 2012. *Airborne Laser Scanning for Forest Applications State - of - the - Art*. UR EMGR, Irstea.

Müller, J., J. Stadler, and R. Brandl. 2010. Composition versus physiognomy of vegetation as predictors of bird assemblages: The role of lidar. Remote Sensing of Environment 114:490–495.

Murray, D. L., S. Boutin, M. O'Donoghue, and V. O. Nams. 1995. Hunting behaviour of a sympatric felid and canid in relation to vegetative cover. Animal Behaviour 50:1203–1210.

Neuvonen, S., and P. Niemelä. 1981. Species richness of Macrolepidoptera on Finnish deciduous trees and shrubs. Oecologia 51:364–370.

Newton, I. 1994. The role of nest sites in limiting the numbers of hole-nesting birds: A review. Biological Conservation 70:265–276.

Niemelä, J., Y. Haila, E. Halme, T. Pajunen, and P. Punttila. 1992. Small-scale heterogeneity in the spatial distribution of carabid beetles in the southern Finnish taiga. J. Biogeogr. 19:173–181.

Niemelä, J., M. Koivula, and D. J. Kotze. 2007. The effects of forestry on carabid beetles (Coleoptera: Carabidae) in boreal forests. Journal of Insect Conservation 11:5–18.

Nilsson, M.-C. C., and D. A. Wardle. 2014. Understory vgetation as a forest ecosystem driver: Evidence from the Northern Swedish Boreal Forest. Frontiers in Ecology and the Environment 3:421–428.

Nilsson, S. G., J. Hedin, and M. Niklasson. 2001. Biodiversity and its Assessment in Boreal and Nemoral Forests. Scandinavian Journal of Forest Research 16:10–26.

Nystrand, M. 2006. Influence of age, kinship, and large-scale habitat quality on local foraging choices of Siberian jays. Behavioral Ecology 17:503–509.

Nystrand, M., M. Griesser, S. Eggers, and J. Ekman. 2010. Habitat-specific demography and source-sink dynamics in a population of Siberian jays. Journal of Animal Ecology 79:266–274.

Östlund, L., O. Zackrisson, and L. Axelsson. 1997. The history and transformation of a Scandinavian boreal forest landscape since the 19th century. Canadian Journal of Forest Research 27:1198–1206.

Pan, Y., R. A. Birdsey, J. Fang, R. Houghton, P. E. Kauppi, W. A. Kurz, O. L. Phillips, et al. 2011. A large and persistent carbon sink in the world's forests. Science (New York, N.Y.) 333:988–93.

Patriquin, K. J., and R. M. R. Barclay. 2003. Foraging by bats in cleared, thinned and unharvested boreal forest. Journal of Applied Ecology 40:646–657.

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

Rassi, P., A. Alanen, S. Hakalisto, I. Hanski, E. Lehikoinen, E. Ohenoja, and T. Kanerva. 2000. Suomen lajien uhanalaisuus 2000. Finnish Ministry of Environment.

Rautio, A. M., T. Josefsson, A. L. Axelsson, and L. Östlund. 2016. People and pines 1555–1910: integrating ecology, history and archaeology to assess long-term resource use in northern Fennoscandia. Landscape Ecology 31:337–349.

Reich, P. B., P. Bakken, D. Carlson, L. E. Frelich, S. K. Friedman, and D. F. Grigal. 2001. Influence of logging, fire, and forest type on biodiversity and productivity in southern boreal forests. Ecology 82:2731–2748.

Roberge, J. M., G. Mikusiński, and S. Svensson. 2008. The white-backed woodpecker: Umbrella species for forest conservation planning? Biodiversity and Conservation 17:2479–2494.

Rolstad, J., E. Rolstad, and O. Saeteren. 2000. Black woodpecker nest sites: Characteristics, selection, and reproductive success. Journal of Wildlife Management 64:1053–1066.

Rosell, F., and B. Hovde. 1998. Pine Marten, Martes martes, as a Eurasian Beaver, Castor fiber, lodge occupant and possible predator. Canadian Field-Naturalist 112:535–536.

Rosenzweig, M. L. 1992. Species Diversity Gradients: We Know More and Less Than We Thought. Journal of Mammology 73:715–730.

Ruckstuhl, K. E., E. A. Johnson, and K. Miyanishi. 2008. Introduction. The boreal forest and global change. Philosophical Transactions of the Royal Society B: Biological Sciences 363:2243–2247.

Sandström, J., U. Bjelke, T. Carlberg, and S. Sundberg. 2015. Tillstånd och trender för arter och deras livsmiljöer – rödlistade arter i Sverige 2015. ArtDatabanken Raporterar 17. ArtDatabanken SLU, Uppsala.

Schepps, J., S. Lohr, and T. E. Martin. 1999. Does Tree Hardness Influence Nest-Tree Selection by Primary Cavity Nesters? The Auk 116:658–665.

Schimmel, J., and A. Granström. 1997. Fuel succession and fire behavior in the Swedish boreal forest. Canadian Journal of Forest Research 27:1207–1216.

Schmidt, B. C., and J. Roland. 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 99:1110–1120.

Schmiegelow, F. K. A. F., and M. Mönkkönen. 2002. Habitat loss and fragmentation in dynamic landscape: avian perspectives from the boreal forest. Ecological Applications 12:375–389.

Siitonen, J. 2001. Forest management, coarse woody debris and saproxylic organisms: Fennoscandian boreal forests as an example. Ecological Bulletins 49:11–41.

Simard, J. 2001. *Habitat selection, ecological energetics and the effects of changes in white pine forests on breeding of red crossbills in Alongquin Provincial Park, Ontario*.

Sisask, E., R. Mänd, M. Mägi, and V. Tilgar. 2010. Parental provisioning behaviour in Pied Flycatchers Ficedula hypoleuca is well adjusted to local conditions in a mosaic of deciduous and coniferous habitat. Bird Study 57:447–457.

Skogsstyrelsen. 2014. Swedish Statistical Yearbook of Forestry. Skogsstyrelsen.

Smith, D. M., B. C. Larson, M. J. Kelty, and P. M. S. Ashton. 1997. The Practice of Silviculture: Applied Forest Ecology. The Practice of Silviculture Applied Forest Ecology.

Snyder, J. D., and R. A. Janke. 1976. Impact of moose browsing on boreal-type forests of Isle Royale National Park. American Midland Naturalist 95:79–92.

Stein, A., K. Gerstner, and H. Kreft. 2014. Environmental heterogeneity as a universal driver of species richness across taxa, biomes and spatial scales. Ecology Letters 17:866–880.

Stenbacka, F., J. Hjältén, J. Hilszczański, and M. Dynesius. 2015. Saproxylic and non-saproxylic beetle assemblages in boreal spruce forests of different age and forestry intensity. 20:2310–2321.

Tahvanainen, T., and E. Forss. 2008. Individual tree models for the crown biomass distribution of Scots pine, Norway spruce and birch in Finland. Forest Ecology and Management 255:455–467.

Tanabe, S. I., M. J. Toda, and A. V. Vinokurova. 2001. Tree shape, forest structure and diversity of drosophilid community: Comparison between boreal and temperate birch forests. Ecological Research 16:369–385.

Tattoni, C., F. Rizzolli, and P. Pedrini. 2012. Can LiDAR data improve bird habitat suitability models? Ecological Modelling 245:103–110.

Tews, J., U. Brose, V. Grimm, K. Tielbörger, M. C. Wichmann, M. Schwager, and F. Jeltsch. 2004. Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. Journal of Biogeography 31:79–92.

Thomas, S. C., C. B. Halpern, D. A. Falk, D. A. Liguori, and K. A. Austin. 1999. Plant diversity in managed forests: Understory responses to thinning and fertilization. Ecological Applications 9:864–879.

Thomas, V., R. D. Oliver, K. Lim, and M. Woods. 2008. LiDAR and Weibull modeling of diameter and basal area. Forestry Chronicle 84:866–875.

Thompson, I. D., J. A. Baker, and M. Ter-Mikaelian. 2003. A review of the long-term effects of post-harvest silviculture on vertebrate wildlife, and predictive models, with an emphasis on boreal forests in Ontario, Canada. Forest Ecology and Management 177:441–469.

Thysell, D. R., and A. B. Carey. 2000. *Effects of Forest Management on Understory and Overstory Vegetation: A Retrospective Study*. Pacific Northwest Research Station.

Tilman, D., R. M. May, C. L. Lehman, and M. A. Nowak. 1994. Habitat destruction and the extinction debt. Nature 371:65–66.

United Nations. 1992. Convention on biological diversity. Diversity 30.

———. 2015. Adoption of the Paris Agreement. Conference of the Parties on its twenty-first session 21932:32.

Väisänen, R. A., E. Lammi, and P. Koskimies. 1998. Distribution, numbers and population changes of Finnish breeding birds. Otava, Helsinki, Finland.

Vatka, E., M. Orell, and S. Rytkönen. 2011. Warming climate advances breeding and improves synchrony of food demand and food availability in a boreal passerine. Global Change Biology 17:3002–3009.

Vatka, E., S. Rytkönen, and M. Orell. 2014. Does the temporal mismatch hypothesis match in boreal populations? Oecologia 176:595–605.

Vehviläinen, H., J. Koricheva, and K. Ruohomäki. 2008. Effects of stand tree species composition and diversity on abundance of predatory arthropods. Oikos 117:935–943.

Venier, L. A., and L. Fahrig. 1996. Habitat availability causes the species abundance-distribution relationship. OIKOS 76:564–570.

Verschuyl, J., S. Riffell, D. Miller, and T. B. Wigley. 2011. Biodiversity response to intensive biomass production from forest thinning in North American forests - A meta-analysis. Forest Ecology and Management 261:221–232.

Versluijs, M., S. Eggers, J. Hjältén, T. Löfroth, and J. M. Roberge. 2017. Ecological restoration in boreal forest modifies the structure of bird assemblages. Forest Ecology and Management 401:75–88.

Virkkala, R. 1987. Effects of forest management on birds breeding in nothern Finland. Annales Zoologici Fennici 24:281–294.

———. 1991. Population Trends of Forest Birds in a Finnish Lapland Landscape of Large Habitat Blocks : Consequences of Stochastic Environmental Variation or Regional Habitat Alteration. Biological Conservation 56:223–240.

Vogeler, J. C., A. T. Hudak, L. A. Vierling, J. Evans, P. Green, and K. T. Vierling. 2014. Terrain and vegetation structural influences on local avian species richness in two mixed-conifer forests. Remote Sensing of Environment 147:13–22.

Weslien, J. 1992. The arthropod complex associated with Ips typographus (L) (Coleoptera, Scolytidae), species composition, phenology, and impact on bark beetle productivity. Entomologica Fennica 3:205–213.

Widenfalk, O., and J. Weslien. 2009. Plant species richness in managed boreal forests-Effects of stand succession and thinning. Forest Ecology and Management 257:1386–1394.

Worrell, R. 1995. European aspen (Populus tremula L.): A review with particular reference to Scotland I. Distribution, ecology and genetic variation. Forestry 68:93–105.

Yahner, R. H., and B. L. Cypher. 1987. Effects of nest location on depredation of artificial arboreal nests. Journal of Wildlife Management 51:178–181.