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Dynamics of biodiversity-rich deciduous trees and microhabitats in boreal forests

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Academic dissertation
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ABSTRACT

Establishing protected areas and maintaining biodiversity in managed forests are the main methods to conserve forest habitats and their biodiversity. The habitat characteristics that affect forest biodiversity in both protected and managed forests occur on different spatial scales, with the smallest scale consisting of structures at the level of single trees and smaller. Under the influence of dynamic processes (ecological succession, natural and anthropogenic disturbances) small-scale structures may be strongly affected, altering their contribution to local biodiversity.

In this thesis, I studied two small-scale structures in northern boreal forests: deciduous trees (mainly European aspen (*Populus tremula*)) in conifer-dominated forests and woodpecker-made breeding cavities. These structures provide resources for multiple species. However, their abundance could be affected by dynamic processes, also in protected areas. I examined the temporal dynamics of these structures through long-term (16–30 years) monitoring. Specifically, I studied the recruitment of deciduous trees in managed forests, aspen demography in old-growth forests, the effect of tree- and stand-level factors on cavity persistence, and the potential to detect aspen for conservation purposes via remote sensing.

My main findings were:

1) Recruitment of deciduous trees is enhanced by prescribed burning. Mammalian herbivory impacts recruitment significantly, although its effect depends on forest age.
2) Living aspens declined by 37% in protected old-growth forests over an 18-year period and recruitment rate was low despite an abundance of saplings. Recruitment primarily occurred on forest edges.
3) Tree species, size, and condition affect the persistence of woodpecker-made cavities, with cavities lasting longer in coniferous, healthy, and larger trees. For aspen, cavities in small trees also persisted a long time.
4) Multispectral drone images can be used to detect scattered mature aspen trees in old-growth forests, most ideally in late spring.

My results emphasize that dynamic processes in forests can alter forest characteristics that are important for biodiversity quickly. Small-scale structures, that are essential to maintain local biodiversity, underwent strong changes in just a few decades. My thesis highlights the importance of continuous monitoring of biodiversity-rich habitat structures to uncover major changes in the ability of protected areas to sustain biodiversity. Remote sensing is potentially a valuable monitoring tool, also for tree-level small-scale forest structures.

Keywords: aspen, forest conservation, herbivory, old-growth forest, tree recruitment, woodpecker cavity

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Finally, I thank nature for being so astonishingly beautiful that it inspired me to pursue ecology as my field of study. Honorable mention to all the birds!

Joensuu, October 2020

Alwin Hardenbol

“Earth provides enough to satisfy every man's needs, but not every man's greed.”

— Mahatma Gandhi

LIST OF ORIGINAL ARTICLES

This thesis is a summary of the following articles, which are referred to in the text by their Roman numerals. Studies **II** and **III** are reprints of previously published articles reprinted with the permission of the publisher. Study **I** is a reprint of an article in press reprinted with the permission of the publisher. Study **IV** is a submitted manuscript.

I Hardenbol A.A., den Herder M., Kouki J. (in press). Long-term effects of prescribed burning, tree retention, and browsing on deciduous tree recruitment in European boreal forests. Canadian Journal of Forest Research. https://doi.org/10.1139/cjfr-2020-0231

II 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

III Hardenbol A.A., Pakkala T., Kouki J. (2019). Persistence of a keystone microhabitat in boreal forests: Cavities of Eurasian Three-toed Woodpeckers (*Picoides tridactylus*). Forest Ecology and Management 450: 117530. https://doi.org/10.1016/j.foreco.2019.117530

IV Hardenbol A.A., Kuzmin A., Korhonen L., Korpelainen P., Kumpula T., Maltamo M., Kouki J. (2020). Detection of aspen in conifer-dominated boreal forests with seasonal multispectral drone image point clouds. Manuscript.

The contribution of Alwin A. Hardenbol to the studies included in this thesis was as follows:

Study **I**: Performed the field sampling, analyzed the data, and wrote the manuscript together with co-authors.

Study **II**: Performed the field sampling, analyzed the data, and wrote the manuscript together with co-authors.

Study **III**: Analyzed the data and wrote the manuscript together with co-authors.

Study **IV**: Contributed to the conceptualization of the study. Participated in the field sampling and the data analysis. Wrote the manuscript together with co-authors and assisted in managing the study and its progress.

TABLE OF CONTENTS

1. INTRODUCTION

1.1 Background

Globally, 80% of the known terrestrial biodiversity is reliant on forests (Aerts and Honnay 2011). However, multiple forest-dwelling species are threatened with extinction and forest biodiversity is rapidly declining (Pimm et al. 1995; Pimm and Raven 2000; Seibold et al. 2019).

To conserve forest biodiversity, two main conservation actions are traditionally used: preserving valuable habitats in protected areas (Branquart et al. 2008) and the application of biodiversity-oriented forest management (Bhagwat et al. 2008; Puettmann et al. 2015). Forests that are protected are often old-growth or intact forests (Morales-Hidalgo et al. 2015; Sabatini et al. 2018). Despite the importance of forest protection (Betts et al. 2017; Watson et al. 2018), terrestrial protected areas cover only a small fraction of the global land area and are, at present, not considered sufficient to prevent ongoing biodiversity loss (Watson et al. 2014). Biodiversity-oriented forest management has developed to reduce the negative environmental impacts of deforestation and intensive wood production. To counter deforestation, the concept of agroforestry has developed (Bhagwat et al. 2008), and alternative silvicultural regimes (e.g. selective cutting and mixed forests) have been used to counter intensive wood production (Côté et al. 2010; Puettmann et al. 2015). While agroforestry and alternative silvicultural regimes show benefits for nature, their adoption is limited by the absence of economic incentives.

The two conservation actions outlined above fit within the framework of *land sparing* and *land sharing*, which is an important debate on how to best conserve biodiversity (Green et al. 2005; Phalan et al. 2011; Kremen and Merenlender 2018). Under land sparing, conservation relies entirely on protected areas set aside from managed areas. With land sharing, management and biodiversity conservation are aimed at, simultaneously, in managed lands. In recent years, land sparing has gained more support for biodiversity conservation (e.g. Phalan et al. 2011; Balmford et al. 2019). Empirical research has shown that land sparing results in improved maintenance of typical species (Phalan et al. 2011; Kamp et al. 2015; Dotta et al. 2016). However, the land sparing approach has also been criticized because the majority of the terrestrial land that would need to be protected has seen some form of historical anthropogenic disturbance (von Wehrden et al. 2014). While restoration of such areas has been suggested (e.g. Green et al. 2005), restoration outcomes are often uncertain, and areas may never resemble the original intact habitat, or harbor the (threatened) species characteristic of that habitat (Chazdon 2008; Kouki et al. 2012). Furthermore, currently existing protected areas in multiple countries are under intense human pressure despite official protection (Jones et al. 2018) and are not insured against policy changes resulting in protected areas regularly undergoing downgrading, downsizing, and degazettement (Mascia and Pailler 2011). This begs the question whether the land sparing approach alone is even realistic. Kremen and Merenlender (2018), as well as Grass et al. (2019), argue that land sharing, at least partly, is important, not only to complement the biodiversity conservation efforts of protected areas, but also to provide ecosystem services for humans. Extensive land use practices can provide for a more hospitable matrix in which species can persist (Mendenhall et al. 2016). Furthermore, extensive land use can improve the effectiveness of protected areas by providing protected area connectivity and buffer zones from external threats (Kennedy et al. 2011; Mendenhall et al. 2014).

The debate over land sparing *versus* land sharing often overlooks ecologically important factors that may be equally important or even more crucial. For example, which specific ecologically important features are more crucial in these two conservation types? Is it more important to conserve large landscape-scale (e.g. old-growth forest networks), stand-scale (e.g. old-growth forest stands), or small-scale structural elements (e.g. deadwood) that are considered valuable for biodiversity? In general, a multi-scale conservation approach is deemed appropriate (Lindenmayer et al. 2006; Felton et al. 2020), largely because different species have different requirements from their environment (Lindenmayer and Franklin 2002). Small-scale structural elements have garnered increasing importance for nature conservation in recent years (Winter and Möller 2008; Michel and Winter 2009; Larrieu et al. 2018) and have even been shown to be more important than larger scale elements in some cases (e.g. Regnery et al. 2013). The conservation of ecologically valuable small-scale structures can be achieved under both the land sparing and land sharing conservation approaches.

Hierarchically occurring structures in both protected areas and biodiversity-oriented silviculture are under the constant influence of dynamic processes (outlined in sections 1.2 and 1.3). These dynamic processes affect the abundance and functioning of structural elements for biodiversity. Biodiversity conservation heavily relies on maintaining specific structures, and thus the dynamic nature of structures can profoundly affect our ability to maintain biodiversity. For many structures, it has remained unclear how they are temporally and spatially affected by dynamic processes. In my thesis, I address the temporal dynamics of two biodiversity-rich small-scale structures in biodiversity-oriented silviculture and protected areas.

1.2 Ecological succession and small-scale dynamics

The structure of forests is continuously shaped by repeated disturbances and succession. These disturbance-succession dynamics occur at different spatiotemporal scales and, thus, affect the availability of structures within an area both in time and space. Structural composition and heterogeneity in turn exert a major influence on species richness and biodiversity within an area (Franklin et al. 2002; Lindenmayer et al. 2006; Gauthier et al. 2015).

The process of ecological succession is the sequential alteration of an ecological community in the same space over time following a disturbance (Clements 1916). Ecological succession based on Clements' work has traditionally been assumed to lead a community to a theoretical climax state through deterministic sequences of successional stages (Horn 1974; Connell and Slatyer 1977). However, this theory ignores the importance of stochastic processes, such as subsequent disturbances, which result in constantly changing ecosystems whereby the exact theoretical trajectory and climax state are rarely attainable or maintainable (Bormann and Likens 1979; Filotas et al. 2014). Nevertheless, certain successional patterns emerge when major subsequent disturbances are absent (Oliver 1980; Capers et al. 2005; Donato et al. 2012; Rohner et al. 2012), which can make succession predictable at the level of functional groups of species (cf. Norden et al. 2015). Successional pathways depend on several factors, defined as drivers of succession (see Meiners et al. 2015), which are grouped into three classes: (1) site conditions and history, which include soil properties, local climate, and topography (Fridley and Wright 2012; Martin et al. 2020), (2) species availability, which includes connectivity and dispersal (e.g. Noble and Slatyer 1980), and (3) species performance, which in turn affects species interactions (see Connell and Slatyer 1977). Ecological succession is a process that occurs on a rather large spatial scale (community level) as opposed to small-scale dynamics. On a temporal scale, successional shifts based on traditional habitat classification, usually take decades to centuries to become apparent, but ecological succession is nevertheless a continuously occurring but slow process similar to small-scale dynamics, such as the growth and ageing of trees.

It is often unclear how successional progression proceeds in the various types of forest habitats and how it affects the availability of specific structures in the absence of (large) disturbances, which complicates conservation efforts. This is largely a result of the stochastic processes involved in successional progression (Filotas et al. 2014). Similarly, on a smaller scale, it remains unclear as to how dynamic processes, which do not necessarily involve considerable community-level changes, affect the availability of structures (Kõrkjas et al. 2020).

1.3 Natural and anthropogenic disturbances

“A disturbance is any relatively discrete event in time that disrupts ecosystem, community, or population structure and changes resources, substrate availability, or the physical environment” (White and Pickett 1985; White and Jentsch 2001). Disturbances operate on a wide spectrum of spatiotemporal scales (see Kuuluvainen 2002) but as defined by White and Pickett (1985) exclude continuous processes. For example, fires can be of different sizes and thereby affect small to large areas, and the interval between fire events may differ between locations. Disturbances can alter successional progression or can cause it to reset, although this depends on the size and severity of the disturbance (Perera et al. 2004), and disturbances can be either natural or anthropogenic in origin.

Natural disturbances include fires, floods, insect outbreaks, and windstorms (White and Pickett 1985). As humans are increasingly dominating Earth’s ecosystems, anthropogenic disturbances are increasingly prevalent (Vitousek et al. 1997; Kareiva et al. 2007), while anthropogenic disturbances are also exacerbating natural disturbances (e.g. Seidl et al. 2017). The main anthropogenic disturbances include the logging of forests and various practices in agriculture, such as tillage and pesticide use (McLaughlin and Mineau 1995; Lambin and Meyfroidt 2011; Hansen et al. 2013; IPBES 2019). Other anthropogenic disturbances include the introduction of non-native and invasive species (Ehrenfeld 2010) and human-induced climate change (Dale et al. 2001).

Natural disturbances play an integral role in maintaining ecosystem variability on a large scale (Attiwill 1994; White and Walker 1997). At intermediate levels of regularity, disturbances also result in high species diversity, according to the intermediate disturbance hypothesis (Connell 1978). Additionally, natural disturbances create unique habitats, such as early successional forests with large amounts of deadwood (Kouki et al. 2001; Franklin et al. 2002; Swanson et al. 2011) and unique structures (e.g. Suominen et al. 2018). Conversely, anthropogenic disturbances often differ from natural disturbances in multiple aspects, resulting in a lack of unique habitats and structures (Franklin et al. 2000; Kouki et al. 2001). Moreover, anthropogenic disturbances often occur in a monotypical fashion over a large area, resulting in low ecosystem variability (e.g. clearcutting). Due to the intensity and extent of anthropogenic disturbance globally, it is considered largely negative for the environment (Rockström et al. 2009; Newbold et al. 2015; Barlow et al. 2016).

1.4 Biodiversity conservation and dynamic processes in European boreal forests

The boreal forest biome is one of the largest terrestrial biomes and represents approximately 30% of the forested area on the planet (Brandt et al. 2013). Boreal forests are not naturally homogenous across the area (Shorohova et al. 2011) but this variation is reduced by similar management practices (Kuuluvainen 2009). Management of the boreal forest is commonplace and occurs on approximately 66% of the area it encompasses, primarily for wood production (Gauthier et al. 2015). However, different degrees of management are employed in the various parts of the world where boreal forests occur. Management takes place on 90% of the forest area in Fennoscandia, 58% in Russia, and 35–40% in Canada (Gauthier et al. 2015). In addition, variations in land use history and the intensity of management practices are evident from country to country (Mönkkönen and Welsh 1994).

In this thesis, I focus on boreal forests in Europe. Nowadays, forest management in boreal Europe is primarily conducted by growing even-aged coniferous trees in stands that are thinned from below and clearcut during harvesting operations. In Finland, 91% (Vaahtera et al. 2018) and in Sweden, 80% (Swedish Forest Agency 2014) of all forest land is actively managed for wood production, while less than 10% of the forest land is protected in Finland (Vaahtera et al. 2018) and Sweden (Swedish Forest Agency 2014), most of it in the northern parts of these countries. As a result of intensive forestry in European boreal forests, anthropogenic disturbance has led to forests with low structural variability and heterogeneity (Esseen et al. 1997; Siitonen 2001), and has caused the decline in abundance of old-growth forests and early successional stage forests with pre-disturbance elements (Kouki et al. 2001; Gauthier et al. 2015). In turn, this has led to multiple European boreal forest-dwelling species being threatened and/or declining in number (Henriksen and Hilmo 2015; Westling 2015; Hyvärinen et al. 2019).

To conserve forest biodiversity in this region, some valuable forest habitats have been protected (Angelstam et al. 2011) and biodiversity-oriented silviculture is increasingly practiced. The latter includes a range of practices, such as leaving retention trees during final cutting (Gustafsson et al. 2010), uneven-aged management (Peura et al. 2018), and deadwood creation (Pasanen et al. 2019). Biodiversity conservation in practice relies heavily on the preservation of specific habitats, such as old-growth forests and structures (e.g. deadwood) that are considered important for biodiversity (e.g. Atrena et al. 2020).

In relation to land sparing and sharing, it appears appropriate and realistic to mix these two approaches in the context of European boreal forests, albeit that the role of land sharing is emphasized (Felton et al. 2020). Two models that could be considered suitable in European boreal forests are the Canadian TRIAD model (see Côté et al. 2010) and the Scandinavian ASIO-model (see Angelstam 1998). With the TRIAD model, the forest land is divided into three land use zones: (1) protected areas, (2) biodiversity-oriented silviculture, and (3) intensive silviculture. With the ASIO model, a similar division of land use can be established based on the naturally occuring fire frequencies in different forest types. There are various reasons for why such a mixed approach could be advantageous over either land sharing or sparing. In European boreal forests, most of the forest land is managed, and pristine intact forests are rare and scattered. While a large number of species can persist under the land sharing approach, there are several species that are, or are likely to be dependent on, for example, unmanaged old-growth forests (Kouki et al. 2001). Conversely, with the lack of pristine intact forests, a substantial amount of formerly managed land would need to be protected under the land sparing approach. It is unknown whether, even after restoration efforts, those forests could ever again resemble the structural properties (Similä et al. 2012) or species composition (Kouki et al. 2012) of truly intact forests. Herein, it should also be noted that, less than a decade ago, approximately 75% of the forests within protected areas in Finland showed signs of forest management and were in need of restoration efforts, such as increasing deadwood quantities and diversifying tree age distribution (Similä et al. 2012). What complicates both approaches, however, is that forestry has continued to intensify in the region, despite the increasing conservation efforts described above (Felton et al. 2020).

Further complicating nature conservation actions, dynamic processes affect the preservation of valuable habitats and structures in European boreal forests. Dynamic processes in boreal European forests follow certain general patterns. At a large scale, successional processes in European boreal forests are largely assumed to lead towards a climax state in which coniferous trees dominate (Esseen et al. 1997; Linder et al. 1997; Lilja et al. 2006). This assumes that disturbances are largely absent during the early successional stages. Natural disturbances in the boreal zone have historically been highly prevalent, especially fire, resulting in a very variable landscape (Zackrisson 1977). But nowadays, fires have been heavily suppressed in the European boreal zone (Wallenius 2011). Anthropogenic disturbances have almost entirely replaced these natural disturbances with intensively practiced forest management (Kuuluvainen et al. 2012). While clearcutting certainly resets ecological succession, it is clearly dissimilar to fire as it presents a singular intensity, and pre-disturbance forest structures are largely absent after cutting (Franklin et al. 2000; Kouki and Salo 2020). On a smaller scale, dynamic processes affect, for example, tree species composition and the amount of deadwood in protected forests as they may change over time (Lilja et al. 2006), retention trees left on clearcut areas as trees fall (Hämäläinen et al. 2016), and deadwood as it goes through various decay stages until it eventually disintegrates (Siitonen 2001).

Knowledge of these dynamic processes have recently also been applied in nature conservation actions. To better resemble natural disturbances and increase species richness and the number of threatened species in managed forests, suggestions are often made to base forest management on natural ecosystem dynamics (Attiwill 1994; Kuuluvainen 2009). In practice, this is widely applied by leaving retention trees during clearcutting operations (Gustafsson et al. 2010), as well as by carrying out various cutting methods within the managed landscape and the creation of high stumps (Pasanen 2017; Pasanen et al. 2019). Another practice is to apply prescribed burning, which has proven to be highly effective for nature conservation (e.g. Heikkala et al. 2017). To consider ecological succession and the gradual trend towards conifer dominance, management to promote deciduous trees can be applied, such as conifer removal (Hämäläinen et al. 2020) and gap creation (Similä et al. 2012).

1.5 Deciduous trees

Within the conifer-dominated boreal landscape, deciduous trees, while less abundant, host a large percentage of forest biodiversity with many associated and dependent species (e.g. Tikkanen et al. 2006). Among the various deciduous tree species that occur in European boreal forests, European aspen (*Populus tremula* L.; hereafter aspen) is considered particularly valuable for biodiversity, hosting multiple specialist species (Esseen et al. 1997; Kouki et al. 2004; Tikkanen et al. 2006).

As they are shade-intolerant, deciduous trees in boreal Europe are early successional stage species (Esseen et al. 1997) that quickly colonize newly disturbed areas (Linder et al. 1997;

Lankia et al. 2012). The successional progression theory in the European boreal zone, based on work by, for example, Lilja et al. (2006) and Linder et al. (1997) would proceed as follows after a disturbance: deciduous trees colonize the area and grow rapidly, but as succession proceeds, barring new disturbances, coniferous trees also colonize the area and eventually outgrow the deciduous trees. As the forest grows higher, canopy closure increases, and the lower vegetation layers become further shaded. The original cohort of deciduous trees in the area can persist for decades or centuries and may, therefore, also be present in the old-growth forests (e.g. Lankia et al. 2012). However, new cohorts of deciduous trees in the area may fail to become recruited due to interspecific competition and browsing (Kouki et al. 2004; Myking et al. 2011). Nevertheless, old trees eventually perish and fall, and (small-scale) canopy gaps begin to occur in old-growth forests, providing increased solar irradiation at the lower vegetation layers. This can potentially provide recruitment opportunities for trees, including deciduous trees (see Vehmas et al. 2009). Based on this successional development, disturbances are a key determinant of deciduous tree cover but their long-term occurrence in mature forest phases is uncertain (Esseen et al. 1997; Linder et al. 1997; Lankia et al. 2012).

In the absence of natural disturbances, forest management in Fennoscandia can potentially increase the abundance of shade-intolerant deciduous trees because of intense canopy removal facilitating their establishment (Edenius et al. 2011). However, as also noted by Edenius et al. (2011), deciduous trees are largely removed for economic interests. The wood industry prefers coniferous trees for economic reasons and hence, mixed and broadleaf-dominated forests constitute a minority of all managed forests in Finland (Vaahtera et al. 2018). For aspen specifically, its removal is still common, although certainly less intensive than several decades ago (see Edenius et al. 2011). This is because aspen is the intermediate host of pine-twisting rust (*Melampsora pinitorqua* Rostr.) (Kurkela 1973; Mattila 2005) and because its presence may attract moose (*Alces alces*) to browse on economically valuable tree species, such as Scots pine (*Pinus sylvestris* L.; hereafter pine) (Jalkanen 2001). Furthermore, human land-use changes have resulted in a larger moose population (see Nevalainen et al. 2016) and moose have a strong browsing preference for certain deciduous tree species, like aspen, rowan (*Sorbus aucuparia* L.), and willows (*Salix* spp.) (Månsson et al. 2007). While browsing can also cause direct mortality, it mostly results in a strong recruitment delay (Edenius and Ericsson 2015), which can indirectly lead to mortality. However, the exact effects of browsing also depend on browsing intensity (e.g. Persson et al. 2005). Herein it is important to consider that European boreal forests have large differences in moose densities, with relatively low densities in Finland compared with Sweden (see Angelstam et al. 2017).

Although deciduous trees are at a disadvantage, there has been a marked but still small increase in the overall number of deciduous trees (Vaahtera et al. 2018) and of large deciduous trees in Finnish managed forests (Henttonen et al. 2019), even aspen (Korhonen et al. 2020). However, this does not negate the importance of aspen in old-growth forests as certain species depend on this tree species in old-growth settings (e.g. Martikainen 2001; Oldén et al. 2014).

1.6 Tree-related microhabitats

Tree-related microhabitats (hereafter microhabitats) are important elements of forest structural diversity (Larrieu et al. 2018). Microhabitats consist of a wide variety of structures that include cavities, epiphytic and epixylic structures, tree injury spots, and exposed wood patches (Winter and Möller 2008; Michel and Winter 2009; Larrieu et al. 2018). Microhabitats can be used to predict the diversity of several groups of birds and bats (Regnery et al. 2013; Paillet et al. 2018). Tree cavities, specifically, are widely used for nesting and roosting purposes (review in Larrieu et al. 2018). In particular, deciduous trees are valuable for microhabitats as they generally harbor many microhabitats (Vuidot et al. 2011), and aspen is considered the most favorable tree species for cavity excavation by woodpeckers (Remm and Lõhmus 2011).

Microhabitat presence, diversity, and abundance all shift over time due to dynamic processes (Kõrkjas et al. 2020). Both natural and anthropogenic disturbances play a large role in these dynamic processes. Microhabitats are especially prone to wind-related losses (Wesołowski and Martin 2018), while relevant anthropogenic disturbances include direct effects, such as cutting (Bütler et al. 2013) and indirect effects, such as fragmentation, resulting in exposure to wind (Jönsson et al. 2007). Accurate knowledge of microhabitat dynamics in relation to both their formation and disappearance is lacking despite such knowledge being important for planning conservation actions (Kõrkjas et al. 2020) with Courbaud et al. (2017) presenting an example of how microhabitat formation probability can be modelled for trees of different species and sizes.

1.7 Aims of the thesis

In my thesis I focused on decadal temporal changes of small-scale structures that are related to the maintenance of forest biodiversity. I approached this subject from three different perspectives: (1) deciduous trees in biodiversity-oriented silviculture in study **I**, (2) aspen in old-growth forests in study **II**, and (3) woodpecker-made cavities in study **III**. In addition, I studied the use of remote sensing for aspen detection in old-growth forests as an improved methodological approach in study **IV**.

The main questions to be answered in this thesis are:

1. What are the effects of (a) biodiversity-oriented silviculture consisting of prescribed burning and retention, and (b) browsing, on deciduous tree recruitment in young forests? (**I**)
2. What are (a) the changes in aspen density, both young and old, over time, and (b) the effects of browsing on aspen recruitment in protected old-growth forests? (**II**)
3. How do tree- and stand-level characteristics affect the dynamics of a key microhabitat: cavities excavated by Three-toed Woodpeckers (*Picoides tridactylus* L.)? (**III**)
4. Can remote sensing reliably detect aspen trees in old-growth forests? (**IV**)

2. MATERIALS AND METHODS

2.1 Study sites

This thesis contains four studies for which the data was collected in two distinct parts of Finland (Figure 1). Studies **I**, **II**, and **IV** were performed in North Karelia, eastern Finland (around 63° 20′ N; 30° 30′ E). Study **III** was conducted in the Evo forest area in southern Finland (around 61° 15′ N; 25° 03′ E). The sites in study **I** were covered by 150-year-old forests dominated by pine prior to the experimental treatment. The sites in studies **II** and **IV** are protected areas of conifer-dominated secondary old-growth forest selected for these studies based on their originally high density of aspen. The site in study **III** is dominated by mostly managed, mature coniferous forests with a large population of Three-toed Woodpeckers. For more details, see the relevant studies included in this thesis.

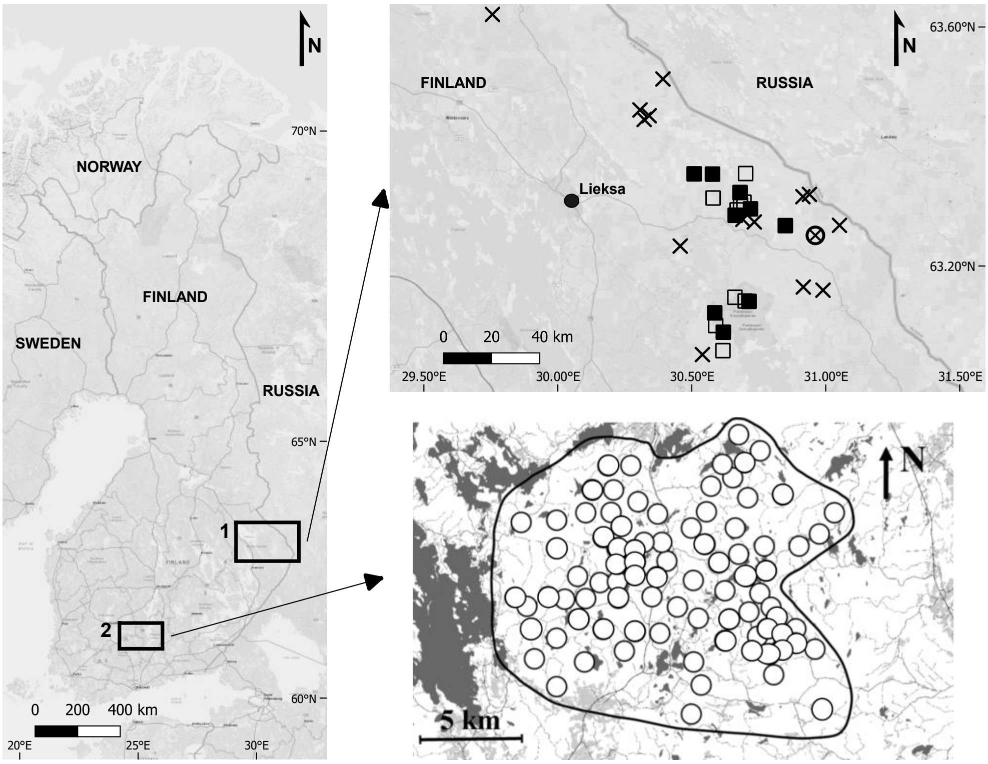

Figure 1. Left: map of Finland showing the two areas where data was collected. Top right: study sites in study **I** (burned sites: filled-in square, unburned sites: empty square), study **II** (cross and cross in circle), and study **IV** (cross in circle). Bottom right: Evo area (study **III**), showing the location of the study area and all the woodpecker territories included in the study (shown as circles).

2.2 Deciduous tree inventory (I, II, and IV)

For study **I**, I inventoried rowan, aspen, and silver birch (*Betula pendula* Roth) that were planted on 18 experimental sites. The experiment had a three-factorial design combining timber harvesting with prescribed burning and herbivore access. Of the 18 sites, six were selected to be left uncut, six to be cut with 50 m^3/ha retention, and six to be clearcut. Of these six sites per type, three were burned thereby resulting in three replicates per treatment combination. On each site, an herbivore treatment with three compartments was established (unfenced, fenced excluding moose, and fenced excluding moose and hares (*Lepus* spp.); each compartment covered 10 m x 15 m; Figure 2). In these compartments, rowan, aspen, and silver birch were planted in 2002/2003, and I inventoried these trees 17 years after planting. I measured the heights and mortality rates of the planted trees in each compartment on all sites. For more information on the methodology of the study, see study **I** (Fig. 1 specifically for the study design).

For study **II**, all living aspen in the old-growth forest parts of 15 protected areas were inventoried in 1999 and 2017 (Figure 3). In 2017, I collected GPS positions of every aspen with a diameter at breast height (DBH) $\geq$ 5 cm individually, and for aspen with DBH $<$ 5 cm at the center of sapling clusters. Furthermore, I documented signs of browsing on all aspen saplings.

Based on study **II**, a protected area was selected for study **IV** to detect aspen via remote sensing. A drone equipped with a multispectral sensor was flown over the site on five dates, spanning the thermal growing season in 2019. The resulting multispectral images were processed to generate dense photogrammetric point clouds. In addition to field-measured aspen trees, I also collected GPS locations of birches (*Betula* spp.), while Norway spruce (*Picea abies* [L.] Karst.; hereafter spruce) and pine locations were added based on visual interpretation of aerial images.

2.3 Cavity inventory (III)

Between 1987 and 2017, the study area was searched for Three-toed Woodpecker territories every breeding season. Searches for breeding cavities were carried out within these annually mapped territories. In total, 654 cavities were found and used in study **III**. When a new cavity was detected, three stand-level variables (territory occupancy patterns, forest type, and distance to nearest edge) and four tree-level variables (nest tree species, condition [healthy, weakened, and dead], and DBH, and cavity height) were measured. For a detailed account of these variables and their definitions, see study **III**. Furthermore, every previously detected cavity was inspected annually for nesting suitability and the years that a cavity persisted was thus recorded.

Figure 2. Left: Fenced compartments from study **I** with the planted seedlings behind the fence (image taken in 2020 so 18 years after planting). Top right: a heavily browsed aspen seedling from an unfenced compartment in study **I**. Bottom right: a moose (*Alces alces*). Photographs taken by the author.

2.4 Data analyses

In study **I**, a split-plot factorial Analysis of Variance (separately for each tree species) was used to analyze the effect of timber harvesting, prescribed burning, and herbivore treatment on the height and mortality rate of the planted tree species. Timber harvest and prescribed burning were used as between-group factors, herbivore treatment as a within-group factor, and two-way interactions between these factors were included.

In study **II**, the tree dataset was split into three groups for analysis; saplings ($\text{DBH} < 5$ cm), recruited trees ($5 \leq \text{DBH} < 15$ cm), and trees with a $\text{DBH} > 15$ cm. The number of recruited trees and trees with a $\text{DBH} > 15$ cm between 1999 and 2017 was compared with paired samples t-tests. With the GPS locations collected in 2017, a Mann-Whitney U test was applied to compare the median distances at which sapling clusters and recruited trees occurred.

For study **III**, the effects of the collected stand- and tree-level variables on the years of cavity persistence were analyzed with Cox proportional hazards models (Cox 1972).

For study **IV**, photogrammetric point clouds were used to create Canopy Height Models and perform Individual Tree Detection (ITD). The individual tree crown boundaries were overlaid with the field-measured trees plus spruces and pines, and for each tree, spectral and height variables were extracted. Subsequently, species classification was performed with a Linear Discriminant Analysis (LDA), using only field-measured trees and spruces and pines that were detected in the segments during ITD. LDA was performed for each of the five dates individually and was optimized once for aspen classification and once for overall tree species classification. The results are reported with user's and producer's accuracies. The former is the percentage of trees of a certain tree species that were correctly predicted as that tree species, while the latter is the percentage of correctly classified trees from all trees that were predicted to belong to a certain tree species.

All the statistical analyses were executed in R (R core team 2020) with the help of multiple R packages which have been cited in the individual studies.

Figure 3. Top left and bottom right: An old-growth forest from study **II** photographed in different settings, both showing European aspens (*Populus tremula*), either obvious from their bark structure or their leaves (especially in autumn). Bottom left: An aspen sapling in an old-growth forest from study **II**. Top right: The epiphytic lichen *Lobaria pulmonaria* [L.] Hoffm.; a species that in these parts of Finland is strongly associated with aspen. Photographs taken by the author.

3. MAIN RESULTS AND DISCUSSION

3.1 Recruitment of deciduous trees is promoted by prescribed burning over the long term (I). Browsing strongly impacts deciduous tree recruitment but its impact depends on forest age (I and II)

The admixture of deciduous trees in managed forests can potentially be improved by practices that better emulate natural disturbances in boreal forests. Such practices include prescribed burning and tree retention (Gustafsson et al. 2010; Halme et al. 2013; Kouki and Salo 2020). However, the results of these practices may also be influenced by mammalian browsing.

I found that prescribed burning significantly lowered the mortality rates of the planted silver birch and rowan seedlings on cut sites (either with or without retention) (**I**). A likely explanation is that prescribed burning can reduce allelopathic and competitive effects for deciduous trees (Nilsson and Wardle 2005) and provide various beneficial soil properties (Certini 2005). This pattern was also upheld in the unfenced compartments, which indicates that burning also reduced browsing, at least of silver birch and rowan seedlings. Burning has been found to influence the chemical composition of trees which in turn influences their palatability (Wan et al. 2014). In the absence of burning, browsing clearly increased the mortality rates of all three tree species on cut sites, as indicated by fenced versus unfenced compartments.

Tree retention over the long term did not impact the mortality and growth of the planted deciduous trees (**I**). My results therefore differ from the findings of the short-term study (see den Herder et al. 2009) and validate the importance of long-term studies on tree recruitment (Bernes et al. 2018). In the short term, den Herder et al. (2009) found that both prescribed burning and tree retention promoted deciduous tree recruitment. The legacy effects of fires have been shown to last for decades (Certini 2005) but trees fall and this may explain why retention did not promote recruitment over the long term.

The uncut forest sites (controls) showed a complete lack of deciduous tree recruitment with high, near-total tree mortality (**I**). This is a similar result to my findings in study **II** where recruitment was almost absent in the forest interior. My findings from study **I** also corroborate the conclusion from study **II** that browsing is not an important limiting factor in the forest interior, as the fenced compartments did not show different mortality patterns from unfenced compartments on uncut sites. As in study **II**, I suggest that a scarcity of resources (nutrients, light, and water) is the main limiting factor on the uncut sites in study **I**.

3.2 Overall number of aspens has strongly declined in old-growth forests and newly recruited cohorts have failed to emerge (II)

In the absence of fires, it is suggested that aspen will disappear from the old-growth forest parts of protected areas, as new cohorts are not able to establish and the aspens in the old cohort perish (Esseen et al. 1997; Linder et al. 1997; Kouki et al. 2004; Latva-Karjanmaa et al. 2007).

My findings show that previous suggestions of aspen decline are indeed accurate (**II**). In addition, I observed the severity of the decline, which amounted to, on average, 37% of the number of living aspen/ha over an 18-year period in the 15 old-growth protected forests. This decline is strongly synchronous at the landscape level (the old-growth forest network). Furthermore, I found that recruitment of new aspen cohorts is lackluster with only 0.4 recruited aspen/ha, despite a relative abundance of aspen saplings (9 saplings below 1.3 m in height/ha). Possible explanations for this lack of recruitment range from browsing, to an absence of disturbances with an ensuing deficiency of vital resources (nutrients, light, and water) (Kouki et al. 2004; Latva-Karjanmaa et al. 2007).

To uncover the exact reasons for the lack of recruitment, I analyzed the spatial occurrence of recruitment and browsing (**II**). While saplings appeared to be abundant at various distances from the forest edge, recruitment exclusively occurred at the forest edge (median distance from the edge for saplings was 34.7 m, and 5.5 m for recruited trees). This indicates that limitations for recruitment are stronger in the forest interior. I also found that browsing was greater closer to the forest edge. In the forest interior, it appears that competition for resources is the main limitation (Landhäusser et al. 2019). Nearer the forest edge, browsing is certainly a strong factor. However, resource competition is also likely to be a limiting factor near the forest edge as browsing alone does not appear to be able to explain the lack of recruitment at this distance. Recruitment appears to be possible at the old-growth forest edges despite browsing (see also Härkönen et al. 2008) and could provide a means by which aspen can persist in these forests.

My findings show that not only is the old aspen cohort disappearing, but that new cohorts have failed to emerge, with no indication of recruitment in small-scale canopy gaps. Despite the appearance that old-growth forests are stable environments, my results highlight their ever-changing conditions, which may have major consequences for biodiversity conservation in old-growth forests.

3.3 Cavities persist longer in trees with certain characteristics and in forests with high territory occupancy (III)

Cavities are considered important microhabitats for a range of species in European boreal forests (Wesołowski and Martin 2018). The majority of cavities in this biome are excavated by woodpeckers (Andersson et al. 2018) and later re-used by other species (for Three-toed Woodpecker-made cavities see Pakkala et al. 2018). Temporal patterns in cavity persistence may influence their role in providing nesting and roosting sites for species.

In my thesis, 447 cavities (out of the 654 newly excavated cavities that were found) were lost over the 30-year study period (**III**). Most of the cavities (329) were lost through tree fall or breakage, most probably caused by wind, and some to cavity damage (72) caused by, for example, other woodpeckers. A small number of the cavities (46) was lost to anthropogenic disturbance in the form of logging. The median persistence time of the studied cavities was 10 years.

At the tree-level, I found three factors that affected cavity persistence. First, cavities persisted longer in healthy and weakened trees than in dead trees. This pattern has been observed previously (e.g. Edworthy et al. 2012) and is the result of lost structural integrity in the dead trees. Second, cavities persisted longer in larger diameter trees, although this effect was not as strong in aspen, where cavities also persisted for a long time in small diameter trees. Previous research has found that trees with a large height/diameter-ratio require stronger winds to fall (Peltola 2006); so larger diameter trees can be considered more stable. Third, cavities persisted longest in pine, likely because of its deep rooting system, which gives it considerable resilience to falling (Peltola et al. 2000). At the stand-level, I found that cavities persisted longer in areas with high territory occupancy rates. The explanation for this finding remained unclear but was potentially related to unmeasured properties such as stand density.

Overall, I found that certain tree-level characteristics can be used to predict the persistence of cavities. Cavities can potentially be used as indicators of biodiversity (Cockle et al. 2010), but since their persistence time can differ, their value as indicators also varies.

3.4 Remote sensing for aspen detection shows promising results, especially in late spring when birches have leaves and aspens do not (IV)

Remote sensing has been shown to have the potential to be used for large-scale and cost-effective inventories of important structures for biodiversity (Kerr and Ostrovsky 2003; Nagendra et al. 2013). Although the identification of tree species via remote sensing would be highly relevant for ecological applications (e.g. Fassnacht et al. 2016), this is still a developing field that struggles under an increasing number of species and spectral/structural similarities between species. For aspen specifically, few attempts have been made to distinguish it from other species and when this has been attempted, it has generally led to poor outcomes as a result of spectral and structural similarities with common European boreal tree species (reviewed by Kivinen et al. 2020). In previous studies involving aspen, however, seasonal variation in canopy phenology has been ignored, which could improve classification accuracy.

I discovered that aspen classification can be reliably performed with multispectral data throughout the thermal growing season, although with clear seasonal differences (**IV**). With this data, the optimal time for aspen classification was found to occur at the start of the thermal growing season in late spring (13 May). On this date, aspen had no leaves yet, although birch did. This resulted in a user's accuracy of 91.8% and a producer's accuracy of 89.1%, likely the result of the spectral differences between bark or branches and leaves.

When the analysis was optimized for overall tree species classification, an overall classification accuracy of 87.2% was achieved in late spring (30 May). On this date, aspen was in the late leaf flush stage. The accuracy that was achieved is the highest overall accuracy (when aspen is considered as a separate species) recorded in literature thus far (see Kivinen et al. 2020; Viinikka et al. 2020).

Autumn is often suggested to be the optimal season to classify tree species in general (Hill et al. 2010; Persson et al. 2018). Between birch and aspen, there are clear phenological differences in autumn senescence coloration. Despite these autumnal patterns, the lowest classification accuracy overall, and for aspen in particular, was achieved in autumn. This is likely a result of the intraspecific variation in aspen leaf coloration on a specific date because of differences in the timing of the onset of senescence between trees (Fracheboud et al. 2009).

My findings in study **IV** are especially useful in the context of the decline in aspen that I observed in study **II**. To monitor the aspen population on a large scale, remote sensing appears a highly suitable tool. The detected trees in study **IV**, however, only included trees that had reached the canopy and, thus, further efforts are required to use remote sensing applications for complete demographic inventories.

4. CONCLUDING REMARKS

The conservation of biodiversity in European boreal forests is mainly enacted through a mixed application of land sparing and sharing with the use of both protected areas and biodiversity-oriented silviculture. However, as both protected and managed forests undergo dynamic changes, the potential of different land-use patterns in safeguarding biodiversity can also change. Within protected and managed areas, a range of small-scale structures have been shown to be of critical importance for biodiversity. My studies on the temporal dynamics of such structures show that their abundance and functioning can rapidly alter over time, both in managed and protected forests. This finding indicates that the ability of protected areas and biodiversity-oriented silviculture to conserve biodiversity can be overestimated if it does not consider spatiotemporal dynamics. This can affect the degree to which land sparing and sharing should be implemented or combined for biodiversity conservation in situations where internal dynamics and temporal changes prevail. Especially the effectivity of protected areas must be guaranteed but under current circumstances, their effectiveness appears to be dwindling for the specific structures that I studied. In both protected and managed areas, conservation actions should consider the dynamics that affect the two studied structures (deciduous trees and microhabitats) and other structures not studied here, and in turn the species that depend on them.

Regardless of the type of conservation action, small-scale structures undergo rapid and obvious temporal changes on a scale of just several decades. These rapid temporal fluctuations in small-scale structures would indicate that small-scale structures are more prone to dynamic processes than larger scale structures (e.g. an old-growth forest stand). Since small-scale structures are prone to rapid temporal changes that may also be highly synchronous, addressing the limitations of current conservation actions is an urgent issue, and multi-scale conservation approaches should intensively focus on the maintenance of small-scale structures.

In my thesis, the importance of monitoring biodiversity-rich structures for nature conservation is also highlighted. Such monitoring should be performed on a regular basis at the same locations because small-scale characteristics important to maintain biodiversity may change quickly, and exact patterns of change can only be achieved by undertaking an inventory in the same area repeatedly. As remote sensing technology continues to develop, it presents a potentially cost-effective tool for repeated monitoring at the same locations. Based on my findings, drone-based remote sensing can even be applied for the monitoring of tree-level small-scale structures present in densely forested protected areas with high accuracy.

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