Emulating natural disturbances for the conservation of boreal forest birds

Martijn Versluijs
Faculty of Forest Sciences
Department of Wildlife, Fish, and Environmental Studies
Umeå

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Abstract

In the boreal biome, intensive forestry and fire suppression have led to the loss of natural disturbances regimes and changes in forest ecosystems at the landscape and local scale. A large proportion of the old-growth forests has been converted into even-aged single-species forests, with degraded understory layer and reduced availability of dead wood. This has resulted in the population decline of bird species that rely on structurally complex forest habitat. Restoring habitat structures by mimicking natural disturbance regimes can help to safeguard biodiversity. In this study I evaluated the effects of two ecological restoration measures – prescribed burning and gap cutting – on bird assemblage structure and breeding performance of the European pied flycatcher *Ficedula hypoleuca* in boreal forests. Additionally, I identified biodiversity indicators and tested how ecological restoration can affect their indicator value. Lastly, I characterized substrate preferences and foraging behavior as measured through foraging time of the Eurasian three-toed woodpecker *Picoides tridactylus* in forest stands subjected to prescribed burning and in unburned forests.

Prescribed burning increased the abundance of long-distance migrants, ground breeders, strong cavity excavators and species preferring early-successional habitat. Furthermore, fire had positive effects on the body condition of nestlings of pied flycatchers, this suggest that local habitat quality improved. Gap cutting did not influence bird assemblage structures neither the reproductive output nor nestling body condition. The three-toed woodpecker and the Siberian jay *Perisoreus infau*stus were identified as potential biodiversity indicators among birds. However, after fire, the goldcrest *Regulus regulus* became the best predictor of high species richness. The main foraging substrate for three-toed woodpeckers can be characterized as freshly dead trees with a diameter breast height (DBH) of more than 15 cm. However, data on foraging behavior suggest that substrates in the 5-15 cm DBH range and living trees are important as well.

The main conclusion from this study is that prescribed burning as a restoration treatment is an effective way to restore habitat for boreal forest birds in managed boreal forest landscapes. These results should encourage forest managers to reintroduce more fire in boreal forests as a complement to other conservation measures.

Keywords: Ecological restoration; prescribed burning; gap cutting; biodiversity indicators; breeding performance; foraging ecology

Author's address: Martijn Versluijs, SLU, Department of Wildlife, Fish, and
Environmental Studies, SE-90183 Umeå, Sweden
Email: martijn.versluijs@slu.se

Dedication

To all inspiring people who helped me to reach this goal

Look deep into nature, and then you will understand everything better
Albert Einstein

Contents

List of publications **7**

1 Introduction **9**
1.1 Dynamics within the boreal biome 9
  1.1.1 Anthropogenic influences 11
1.2 Ecological restoration 11
  1.2.1 Restoration in the boreal 12
1.3 Boreal forest birds 13

2 Aim and objectives **17**

3 Method **19**
3.1 Study Design 19
  3.1.1 Treatments 19
3.2 Data collection 21
  3.2.1 Breeding bird census (Paper I and III) 21
  3.2.2 Forest structure (Paper I and III) 21
  3.2.3 Reproductive performance (Paper II) 22
  3.2.4 Focal observations of the three-toed woodpecker (Paper IV) 22
3.3 Statistical analysis 23
  3.3.1 Responses in bird assemblages (Paper I) 23
  3.3.2 Breeding performance pied flycatcher (Paper II) 24
  3.3.3 Biodiversity indicators (Paper III) 24
  3.3.4 Foraging ecology of the three-toed woodpecker (Paper IV) 25

4 Results **27**
4.1 Forest structures 27
4.2 Assemblage responses (Paper I) 27
4.3 Breeding performance Pied Flycatcher (Paper II) 28
4.4 Biodiversity indicators (Paper III) 30
4.5 Foraging behavior of the three-toed woodpecker (Paper IV) 32
  4.5.1 Characteristics of selected foraging substrate 32
  4.5.2 Foraging behavior as measured through foraging time 33

5 Discussion 35
5.1 Evaluation of restoration outcome (paper I and II) 35
    5.1.1 Prescribed burning 35
    5.1.2 Gap cutting 37
5.2 Boreal forest bird conservation 38
    5.2.1 Biodiversity indicators (paper III) 38
    5.2.2 Three-toed woodpecker in ecological restoration (paper IV) 39

6 Conclusions 41

7 Future research 43

References 45

Popular science summary 55

Acknowledgements 57

List of publications

This thesis is based on the work contained in the following papers, referred to by Roman numerals in the text:

I Versluijs, M.,* Eggers, S., Hjältén, J., Löfroth, T., Roberge, J-M. (2017). Ecological restoration in boreal forest modifies the structure of bird assemblages. Forest Ecology and Management, vol 401, pp. 75-88

II Versluijs, M.,* Roberge, J-M., Eggers, S., Boer, J., Hjältén, J. Ecological restoration for biodiversity conservation improves habitat quality for an insectivorous passerine in boreal forests. Manuscript.

III Versluijs, M.,* Hjältén, J., Roberge, J-M. (2018). Ecological restoration modifies the value of biodiversity indicators in resident boreal forest birds. Ecological Indicators, vol 98, pp. 104-111

IV Versluijs, M.,* Eggers, S., Mikusiński, G., Roberge, J-M., Hjältén, J. Foraging ecology of Eurasian three-toed woodpecker (*Picoides tridactylus*) in burned and unburned boreal forest. Manuscript

Papers I and III are reproduced with the permission of the publishers.

* Corresponding author.

The contribution of Martijn Versluijs to the papers included in this thesis was as follows:

I Versluijs was fully responsible for planning and conducting fieldwork, all data analysis and had main responsibility for writing.

II Versluijs contributed to the study design, was fully responsible for planning and conducting fieldwork, all data analysis and had main responsibility for writing.

III Versluijs contributed forming the idea, was main responsible for planning and conducting fieldwork, all data analysis and had main responsibility for writing.

IV Versluijs contributed to the study design, was fully responsible for planning and conducting fieldwork, all data analysis and had main responsibility for writing.

1 Introduction

1.1 Dynamics within the boreal biome

The boreal zone is the second largest biome on earth making up almost 30% of the worlds' forest cover. It extends over the northern hemisphere, from Alaska and Canada, over northern Europe to Russia. The boreal biome is a conifer dominated forest system with a strong north-south climatic gradient. The climate is characterized by long cold and dry winters with a persistent snow cover and short, warm summers. In the southern, climatically milder hemi-boreal vegetation zone, conifer trees are accompanied by a significant amount of deciduous trees. Going northwards, there is a transition through the southern, middle and finally the northern boreal zone. This transition goes hand in hand with the change in climate and a significant decrease in the abundance of deciduous trees and species diversity as such. Nevertheless, there are large similarities in ecosystem dynamics over the gradient.

The structural complexity of boreal forests at the local and landscape level is shaped by continuous small-scale disturbances and large-scale disturbances occurring at varying time intervals (Angelstam 1998, Kuuluvainen 2002, 2009, Brumelis et al. 2011). Continuous small-scale dynamics mainly shape local stand structure through, for example, the death of single trees caused by insects, fungi or local wind-throw. At a larger spatial scale, natural disturbances such as fires, storms and insect outbreaks influence both the compositional (diversity of habitat types) and configurational (spatial arrangement of cover types) heterogeneity of boreal forest landscapes (Angelstam 1998, Harvey et al. 2002). Structural complexity is seen as an important factor affecting biodiversity (Smith et al. 2014, Bohn and Huth 2017).

Fire is one of the most important large-scale natural disturbance shaping boreal forest landscapes (Bradshaw et al. 2010). High intensity fires often result in stand replacing dynamics: after fire a large proportion of the trees can be killed. This contributes to shaping ideal conditions for the development of structurally complex forest stands. Fire events are often a combination of low and high intensity fires. After low intensity fires, larger individuals of the more fire resistant pine (*Pinus* sp.) will typically survive while fire intolerant species such as spruce (*Picea* sp.) have a high probability to die (Kuuluvainen 2009). In both situations, fire generates space for the germination of young trees, especially for deciduous trees (Hekkala et al. 2014b). Thus, fire creates a heterogeneous landscape of forest patches with different ages, tree species and complexity (rich vertical stratification of tree crowns). Important factors affecting fire frequency are tree species composition, soil properties, exposure and climate (Niklasson and Granstrom 2000, Bradshaw et al. 2010). Fire intervals in pine-dominated forest on sandy soils have historically been much shorter on average than in more humid forest with spruce (Tanskanen et al. 2005, Brown and Giesecke 2014). It is suggested that without fire dynamics, boreal forest systems would be spruce dominated with limited space other tree species associated with early stages of succession (Esseen et al. 1997, Hörnberg et al. 2012, Brown and Giesecke 2014).

In forest ecosystems where the impact of fire is low, small-scale forest dynamics are important determinants of stand heterogeneity. Openings in the canopy caused by the death of a tree, patches of trees killed by bark beetles or wind-fall are especially important. These small-scale canopy openings radically changes local environmental conditions on the forest floor (Greiser et al. 2018). The sudden increase in light penetration contributes to increasing the biomass of the understory and influences the demography and diversity of forest herbs and trees (Kuuluvainen 1994, Lieffers et al. 1999, McCarthy 2001). Additionally, exposition of mineral soil through uprooting of trees creates important microsites for seed germination. Fallen trees (trunk and crown) also generate shelter against browsing. Furthermore, treefall causes changes in local micro-climate and increase nutrient availability from decomposing litter. This will result in increased diversity of forest herbs and improve local conditions for the germination of trees. Another important component contributing to biodiversity is the creation of dead wood after wind-fall (Haapanen 1965, Kuuluvainen 1994, Hekkala et al. 2014b). Thus, small-scale disturbances result in a patchy distribution of trees of different ages and sizes, uneven aged stand structures and vertical forest layering. Furthermore, gap disturbance contributes to the existence of mixed species forests by facilitating the recruitment of deciduous early successional tree species. Gap-dynamics contribute to both functional and overall species diversity of the forest.

1.1.1 Anthropogenic influences

The ongoing global loss of biodiversity is one of the most critical environmental problems threatening valuable ecosystem services and human well-being. Global warming, land use changes and eutrophication are anthropogenic influences leading to habitat quality alterations, habitat fragmentation and loss of habitat structures (MacDougall et al. 2013). Intensive forestry has modified landscape and local habitat structures considerably across Fennoscandia (Esseen et al. 1997, Kuuluvainen 2009). Nowadays, a large proportion of the old-growth forests has been converted to even-aged, single species forests, with degraded understory layer and severely reduced deadwood availability. Additionally, due to modern forestry practices and fire suppression, natural disturbances have largely disappeared from the boreal forest system and have been replaced by anthropogenic disturbances, including thinning, clearcutting, soil scarification and planting of conifers (Esseen et al. 1997, Östlund et al. 1997, Linder and Östlund 1998, Wallenius 2011). As a consequence, for example forest bird species that are closely associated with fire, deciduous trees, dead wood, large-diameter trees, and a complex vertical stratification of tree vegetation are declining (Eggers and Low 2014, Virkkala 2016, Ram et al. 2017). Restoring these habitat structures has been proposed as a means to help safeguard biodiversity.

1.2 Ecological restoration

The idea of restoring natural areas came under attention when Aldo Leopold a renowned conservationist began promoting this approach in the early 20th century. With roots in community ecology and ecosystem ecology, restoration ecology is nowadays a well-established scientific field. The science and practice of ecological restoration is explicitly linked to ecological theories. Ecological restoration can therefore be used as a practical test of our ecological understanding. However, in a practical sense ecological restoration is seen as the process of assisting the recovery of an ecosystem that has been degraded, damaged or destroyed (SER 2004). Ecosystems that require restoration have been disturbed, damaged, transformed or entirely destroyed as the direct or indirect result of human activities. Traditional approaches such as the establishment of national parks, nature reserves and other types of unmanaged set-asides have proven important but insufficient to prevent population declines or extinction as well as mitigating the effects of climate change. This was already recognized more than 25 years ago by biologist E.O. Wilson:

“Here is the means to end the great extinction spasm. The next century will, I believe, be the era of restoration in ecology” (E.O. Wilson, Diversity of life (1992)).

In the boreal biome, there is a growing recognition that successful biodiversity conservation will necessitate active ecological restoration actions (Kuuluvainen 2009, Angelstam et al. 2011, Haavik and Dale 2012, Angelstam et al. 2013, Halme et al. 2013, Johansson et al. 2013).

1.2.1 Restoration in the boreal

In the boreal biome, the use of ecological restoration is still in its infancy and therefore our understanding of the effects of proposed restoration actions on local biodiversity is still very limited. Proposed restoration actions in the boreal mainly involve the emulation of natural forest dynamics (Lindenmayer et al. 2006, Kuuluvainen 2009).

Prescribed burning as restoration action is used to emulate wildfire. Fire will partially open-up of the canopy through tree death. Consequently, the vegetation structure typically shifts towards an earlier successional stage (Hekkala et al. 2014b). The newly created micro-habitats within this successional stage are expected to support a more diverse vegetation understory and at the same time it generates space for the germination of young trees. It is expected that both processes will favor flower-visiting insects and insects associated with saplings or fallen tree crowns. Furthermore, the dead wood that is created through prescribed burning is a key ecological structure important for many species. Recent research showed positive responses to prescribed burning in large numbers of species of conservation concern such as saproxylic beetles (Hekkala et al. 2014a, Ranius et al. 2014, Hägglund et al. 2015, Hjältén et al. 2017) and fungi (Ylisirniö et al. 2012). Nevertheless, our knowledge is still limited about the responses of many other organism groups such as birds.

Wind-throw can be emulated through the creation of small gaps in forest stands. As in the case of a natural small-scale wind-throw, an open space is created in forest with increased level of standing and lying dead wood. It is expected that these created gaps will create a fine-grained mosaic of different successional stages within forest stands (Hekkala et al. 2014b). Open spaces will provide early-successional habitat as well as an increase in edge habitat and favorable conditions for germination of trees which would lead to a more developed small-tree layer. Additionally, tree uprooting opens up the soil which positively influence the germination of trees (Kuuluvainen 1994, Kuuluvainen and Juntunen 1998), also providing habitat for insects, lichens, fungi and birds.

Several studies have found positive responses of saproxylic insects to gap cutting (Hägglund et al. 2015, Hjältén et al. 2017, Kärvemo et al. 2017, Hägglund and Hjältén 2018). Regarding birds, studies from North American conifer forests showed a consistent positive effect of gap creation on the total abundance of breeding forest birds, but not on their species richness (Forsman et al. 2010). In contrast, Forsman et al. (2013) studied the responses of birds to gap dynamics in European boreal forests and they did not find any consistent effects. Nevertheless, these studies did not evaluate restoration treatments as such and thus more research on restoration-induced responses in birds is of outmost importance to understand the usefulness of this restoration treatment in conservation biology. Additionally, it can help us to understand how underlying ecological processes shape bird assemblages.

1.3 Boreal forest birds

The boreal forest does not belong to the most species rich biomes on earth. Still, birds make up 75% of the occurring terrestrial vertebrate species in that biome (Mönkkönen and Viro 1997). Annually, millions of migratory birds undertake a challenging journey from their wintering and passage ranges to breed in the boreal zone. The boreal is characterized by high food availability in June-July and is therefore an important breeding area. In Eurasia, migratory passerines often tend to be generalists in their habitat preferences and common through their breeding range. Several resident bird species are more demanding in their habitat preference and can be considered forest specialists (Ram et al. 2017). This includes species that are closely associated with the occurrence of deciduous trees, dead wood, large-diameter trees, and a complex horizontal and vertical structure of the tree-layer vegetation. Some of these specialized forest bird species have been proposed as efficient tools for identifying sites with high bird species richness (Roberge and Angelstam 2006, Pakkala et al. 2014). They are often referred to as biodiversity indicators. A biodiversity indicator is a species which indicates high species richness and abundance of co-occurring organisms in or across taxonomic groups (Burger 2006, Caro 2010). Over the last decades, a large number of studies have identified potential biodiversity indicators within predefined taxonomic groups across different biomes and types of environments. In the boreal, especially woodpeckers (family *Picidae*) are considered good indicators for avian diversity (Mikusiński et al. 2001, Roberge and Angelstam 2006, Drever et al. 2008). Other potential biodiversity indicators for the boreal zone have been identified by Pakkala et al. (2014) as the red-breasted flycatcher (*Ficedula parva*) and the Eurasian pygmy owl (*Glaucidium passerinum*). Nevertheless, several studies stress the importance of using multiple biodiversity indicators representing different forest types and natural disturbance regimes (Lambeck 1997, Roberge and Angelstam 2004, Roberge and Angelstam 2006) and this knowledge is currently lacking for the boreal forest system.

Local habitat structures are important determinants affecting bird species occurrence. Complex habitats with high structural complexity profit a wider range of different niches and can sustain a wider range of species (Tews et al. 2004). This is also called niche partitioning which is described by the niche theory. Niche partitioning is influenced by many variables, including the nature and rate of supply of food resources, interspecific competition for limiting resources and natural enemies. Forestry lead to a simplification of forest structures, resulting in a smaller range of available niches, with effects on bird assemblage structures. Niche availability can be optimized by increasing the diversity of important habitat structures such as tree species diversity, age structure, dead wood and understory complexity. Bird densities on the other hand are determined by population limiting factors such as habitat fragmentation, food supply, predation and intra and inter-specific competition (MacArthur 1964, McIntyre 1995, Lee et al. 2002).

Habitat changes through for example ecological restoration may have consequences for the presence and abundance of bird species as local habitat characteristics are altered. Research from North America has shown that for example the successional development of vegetation after fire is accompanied by clear changes in boreal bird assemblages (Saab and Powel 2005, Lowe et al. 2012). However, in spite of an increasing use of prescribed burning as a restoration tool, knowledge about how the changes in habitat structures affect bird assemblages is still limited.

Evaluating the effect of ecological restoration on bird habitat quality is far from straightforward. In many studies, species population densities are used as a proxy for habitat quality. However, according to the ‘ideal free distribution’ (Fretwell and Lucas 1970), individuals should be distributed between habitats in such a way that everyone can maximize their fitness. A higher level of competition in high quality patches can lead to a reduction of individual fitness due to decreasing intake rates (Hake and Ekman 1988), and the net energy intake becomes more similar to that in lower quality patches. Competition may occur due to depletion of resources, a phenomenon called scrambling or exploitative competition (Krebs 1978), or due to interference competition, i.e. behavioral interaction between individuals (Miller 1967). In the end, individuals are distributed over patches where they can maximize their fitness. This is graphically represented in Figure 1 (Whitham 1980): increasing densities correspond with a decrease in fitness. Thus, when density in habitat 1 increases, fitness of individuals will decrease. At some point fitness equals the fitness of lower quality patch (habitat 2) and it is profitable to colonize lower quality habitat. As densities continue to increase in both habitats 1 and 2, it makes sense to colonize the lowest quality habitat, but only in lower densities.

Demographic rates are the main drivers of population dynamics. These rates can be altered by restoration or management practices, and this may occur even without an effect on species abundance. To be successful, ecological restoration should change local habitat quality in such a way that demographic rates are positively influenced. When demographic rates are negatively influenced, the restored stand may instead act as a demographic sink where reproduction is insufficient to balance local mortality (Pulliam 1988). Ideally, restored sites should function as source populations contributing to sustaining viable populations at the landscape scale.

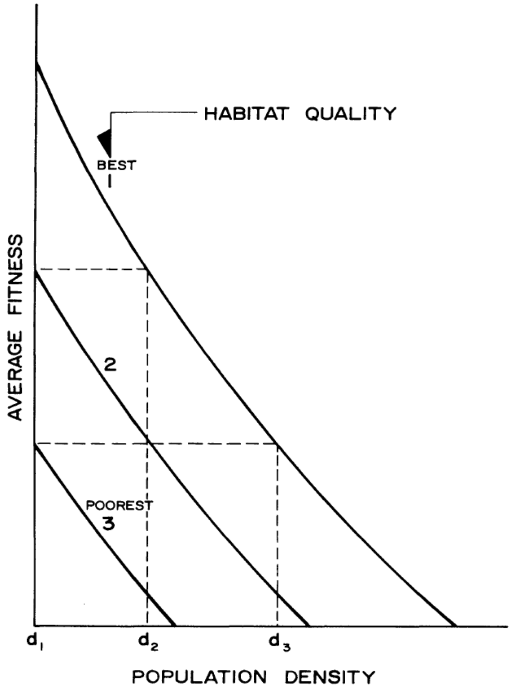


Figure 1 *Assuming that fitness is negatively correlated with competitor density, the horizontal dashed lines show that as competitor density increases in the best habitat (1), colonization of poorer habitats (2 and 3) becomes favourable, but only at reduced densities. Figure is copied from Whitham (1980).*

2 Aim and objectives

Ecological restoration is one approach for assisting the recovery of degraded ecosystem. In the boreal biome, however, our understanding of how local biodiversity responds to ecological restoration actions is very limited.

The overall purpose of this thesis is to explore to what extent ecological restoration of forest set-asides in northern Sweden is a useful tool for improving the conservation status of boreal forests birds. In paper I, I evaluated changes in bird assemblage structure after ecological restoration; this increase our understanding how ecological restoration influence the occurrence of boreal forest birds at the assemblage level. In paper II, I tested the prediction that ecological restoration will influence local habitat quality, leading not only to changes in the abundance or occurrence of species but also in reproductive performance. More precisely, I tested the consequences of ecological restoration on the breeding performance of the insectivorous pied flycatcher (*Ficedula hypoleuca*). In paper III, I identified biodiversity indicators for northern boreal forests to increase our understanding of how ecological restoration can affect their indicator value. Lastly, in paper IV I characterized substrate preferences and foraging behavior (as measured through foraging time) of the Eurasian three-toed woodpecker in forest stands subjected to prescribed burning and in unburned forests. This to better understand how ecological restoration influences prey availability and predators feeding behavior.

3 Method

3.1 Study Design

The field experiment used in this thesis is based on study stands located in the middle and northern boreal zones (Ahti et al. 1968) of northern Sweden (63°23´N to 65°02´N and 16°80´E to 21°20´E, Figure 2). In total 40 forest stands were selected, varying between 3.5 and 25 hectares, with similar forest characteristics such as age and tree species composition (see paper I, Table 1). Thirty stands were voluntary set-asides owned by forestry companies, they were initially production forest but were converted to voluntary set-asides as part of Forest Stewardship Council certification requirements (except for one burnt stand that is formally protected by the state). The remaining 10 stands were part of nature reserves. All study stands were mature forest stands (>80 years) which have never been clear-felled but historically subjected to selective felling. All stands were conifer-dominated, with a mixture of Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*) and at least 10% deciduous trees. Silver birch (*Betula pendula*), downy birch (*Betula pubescens*), European aspen (*Populus tremula*) and goat willow (*Salix caprea*) were the most common deciduous tree species. All stands belong to the mesic dwarf-shrub forest site type.

3.1.1 Treatments

Two restoration treatments were assigned to the set-asides: prescribed burning and artificial gap cutting (10 stands in each category). In addition, 10 stands served as untreated controls and 10 additional unmanaged nature reserves were included as old-growth references. Even though nature reserves cannot be considered truly pristine forest (due to the ubiquitous historical influence of

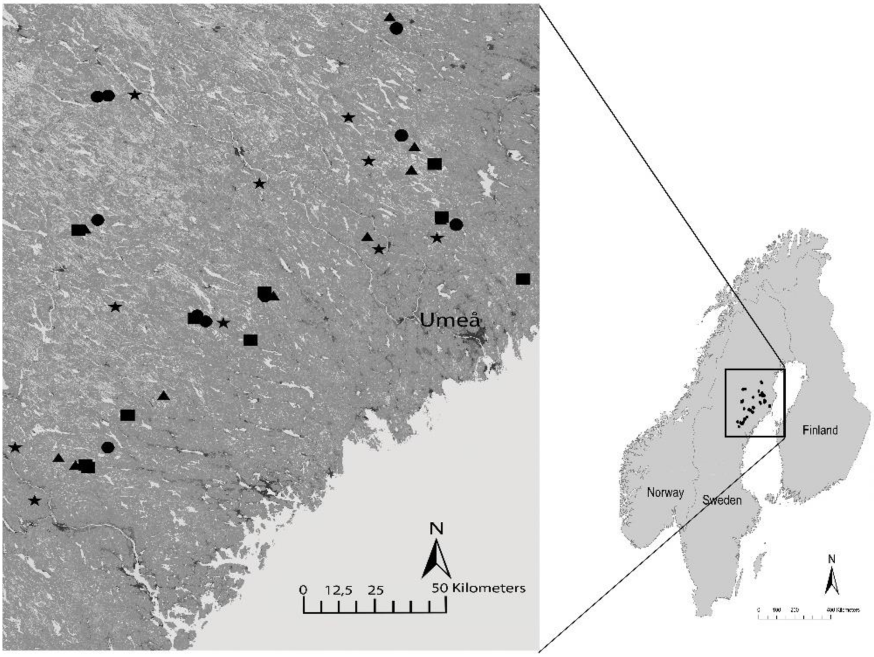


Figure 2. *Location of the experimental forest stands included in the study. Burned stands (n=10) are depicted with squares, gap-cut stands (n=10) with circles, untreated control stands (n=10) with triangles, and nature reserves (n=10) with stars. Paper I*

humans in this region), they represent the most natural-like references in the study area. The restoration treatments were implemented in the spring-summer of 2011. Prescribed burning was performed in June, July or in the first two weeks of August, depending on local conditions. Before burning in the voluntary set-asides, 5-30% of the trees were harvested in order to speed up the drying out of the ground vegetation. Of the harvested trees, approximately 2-5 m^3/ha was left on the ground as fuel.

In each of the 10 stands assigned to gap cutting, an average of six gaps per hectare were created. The gaps were well-distributed through the stand and the total area covered by the gaps was approximately 19% of stand area. Each gap had a radius of 10 m. In the center of each gap, one large tree was retained, preferably a deciduous tree. A Scots pine was retained when no deciduous tree was available. In 50% of the created gaps, the trees were either cut at the base, tipped over, cut as high stump or girdled and all were left as dead wood. In the other 50% of the gaps, the trees were cut at the base and extracted from the stand to cover the cost for the restoration treatment.

3.2 Data collection

3.2.1 Breeding bird census (Paper I and III)

Data on breeding birds were collected in 2015 and 2016 through territory mapping (Bibby et al. 2000). Each study stand was visited every 12 to 15 days (depending on weather conditions) from the beginning of April to the end of June. This resulted in six visits per stand and year. At each visit, the positions of all individual birds displaying territorial behavior, as determined through acoustic or visual cues (e.g. singing males, nests with eggs or nestlings, warning individuals), were recorded on a map. The whole territory mapping area plus a 50 m buffer in each study stand was covered by walking along fixed lines which were separated by 80 m. A predefined constant effort of 7.5 minutes of observation per hectare was used at all sites. Visits took place from a half hour before sunrise until seven hours after. In June, the starting time was fixed at 02:30 am. In case of heavy rain or strong wind, census work was cancelled and moved to the next day. In each year, the censuses were conducted by two experienced ornithologists. To minimize potential variation due to observer effects, each stand was visited 3 times by each of the two observers in a given year. The observers typically visited two stands each in a single morning. Considering that the time of day may influence bird activity, the order of the stands visited within a morning was shifted between visits.

To prepare the bird data for statistical analyses, observations from the 6 visits were clustered into territories, separately for each census year and bird species. A territory was defined on the basis of a found nest and/or spatially restricted observations of territorial individuals recorded in at least two of the 6 visits (Bibby et al. 2000).

The total area subjected to territory mapping across the 40 study stands was 374 ha (93 ha in prescribed burnings, 85 ha in gap cuttings, 96 ha in control stands and 100 ha in nature reserves)

3.2.2 Forest structure (Paper I and III)

Forest vegetation data were collected in August-September 2015 (i.e. four years after the restoration treatments) in sampling plots which were systematically distributed in the study stands. Due to differences in stand area, sampling intensity was fixed at 1 survey plot per 1.5 ha, resulting in a total of 250 sampling plots. Diameter at breast height (DBH) of all living trees was measured within a radius of 10 m from the plot's center. DBH of deciduous trees and dead trees were measured within a radius of 35 m. Only trees with a DBH ≥ 5 cm were included. Understory density was measured by counting all living tree (height >1.5 m) contributing to the understory within 1 m on either sides of four 35 m line transects starting from the center of the plot (Eggers and Low 2014). Counts of trees contributing to the understory per sampling plot were pooled and translated into densities of trees per 100 m^2.

3.2.3 Reproductive performance (Paper II)

In autumn 2015, a total of 250 identical standard wooden nest-boxes were distributed over the experimental stands. Due to the large range in stand sizes, a standard number of 1 nest-box per 1.5 ha was placed in the study stands.

From mid-May until mid-July in 2016 and 2017, all nest-boxes were visited at least once a week. In the nest-boxes occupied by pied flycatcher, laying date, clutch size, hatching success, fledgling success and breeding success were determined.

Additionally, in 2017, data on nestling quality of the pied flycatcher were also collected. The body weight and tarsus length of nestlings in occupied nest-boxes were measured. This was done only in the control, gap cutting and prescribed burnings (nature reserves were excluded). At the age of 12 days (± 2 days), nestling weight was recorded to the nearest 0.1 g by using a digital scale and tarsus length with a digital caliper to the nearest 0.01 mm.

Female pied flycatchers were caught by using mist nests, in addition, females were measured when they needed to be lifted from the nest to control the status of the nest (clutch size, nestlings). Body weight was determined to the nearest 0.1 g by using a digital scale and tarsus length with a digital caliper to the nearest 0.01 mm.

3.2.4 Focal observations of the three-toed woodpecker (Paper IV)

Fieldwork observations of the foraging behavior of the three-toed woodpecker was carried out from the beginning of April to the end of June in 2016 and 2017. Three-toed woodpeckers were located by walking slowly through the study stands; both acoustic (e.g. drumming and pecking sounds of foraging woodpeckers) and visual cues were used to detect individual birds. Observing distance was kept >10 m from the bird to avoid disturbances.

A one-minute instantaneous sampling method was used (i.e. fixed interval time point; Martin and Bateson (1993)) where we recorded for every minute if the individual was foraging or not. When the woodpecker was foraging, we recorded the following variables), *I*) foraging height, *II*) foraging site (trunk, branch or exposed roots) and *III*) substrate diameter at foraging height (estimate at nearest cm using the birds length as a reference). Foraging height was recorded in 4 classes: 1) 0-2 m, 2) 2-5 m, 3) 5-10 m and 4) >10 m. Three foraging techniques were differentiated (Villard 1994, Murphy and Lehnhausen 1998): 1) bark scaling accompanied by surface pecking, 2) excavation into sapwood and 3) sap-drinking. For each substrate selected by a three-toed woodpecker, the following variables were recorded: *I*) tree species (pine, spruce, birch, aspen and other deciduous trees); *II*) diameter at breast height (DBH) in 10 cm classes: 1) 5-15, 2) 15-25, 3) 25-35, 4) 35-45; and *III*) decay stages based on 5 classes (Thomas et al. 1979): class 1) healthy living trees, class 2) dying trees which are still alive, class 3) recently dead trees with 100% bark attached, class 4) dead trees with < 100% bark attached. All characteristics for the used tree were also noted for the nearest available tree with a DBH > 5 cm, this to determine the availability of substrates in the immediate vicinity.

3.3 Statistical analysis

3.3.1 Responses in bird assemblages (Paper I)

To test the response of bird assemblages to ecological restoration, data from the breeding bird census and forest structures measurements were used. Bird abundance data was averaged over the two census years. Owls (Strigiformes), diurnal birds of prey (Accipitriformes, Falconiformes), waders (Charadriiformes) and grouse (Galliformes) were excluded from the analyses because (daytime) territory mapping is not an appropriate survey method to obtain appropriate estimates of their abundances.

The effects of restoration on bird species richness and abundance was tested for the whole assemblage and within specific functional guilds. Therefore, individual bird species were assigned to migration guilds, foraging guilds, nesting guilds (Söderström 2009, Forsman et al. 2013, Wesołowski et al. 2015) and preferences for different successional stages of the forest vegetation (Haapanen 1965, 1966, Imbeau et al. 2003). Analyses were performed by using generalized linear models (GLM) with Poisson error distribution.

To analyze the effect of restoration on the overall structure of bird assemblages, a multivariate generalized linear model with Poisson error distribution (ManyGLM; R-package “mvabund”, Wang et al. (2012)) was used. Constrained ordination redundancy analysis (RDA) was used to visualize differences in assemblage structure.

To test for differences in forest structure among stand types (4 years after restoration) a one-way ANOVA was used.

3.3.2 Breeding performance pied flycatcher (Paper II)

The effect of stand types on clutch size, number of fledglings and number of nestlings were modelled with a generalized linear mixed model (GLMM) with penalized quasi-likelihood estimation from the "MASS" package (Venables and Ripley 2002). This was used in order to implement a quasi-Poisson distribution to account for under-dispersion. Stand types, breeding density (i.e. nest-box occupation rate), laying date and year were included as fixed effects. In all models stand-number was included as random factor. Hatching, fledging and breeding success were modelled with the same model structure as described above but here a quasi-binomial distribution was used.

A body condition index was used to investigate the difference in nestling body condition between stand types. The index reflects body mass relative to tarsus length, calculated as the residuals of a linear regression of body mass on tarsus length. Differences in body condition index between stand types were analyzed with linear mixed models (LMM).

In 2017, 63% of the breeding females within the control, gap cutting and prescribed burning treatment were caught. With this dataset, parental difference in body condition index between stand types was determined using an LMM model. Measurements were divided over three periods in the nestling phase: 1) day 1-5, 2) day 6-10 and 3) day 11-15. This was done because measurements were taken over the whole nestling period of 15 days. Sample size was too small to calculate a daily average.

3.3.3 Biodiversity indicators (Paper III)

To determine biodiversity indicators across a wider range of forest types, nestedness patterns within bird assemblages needed to be checked. Assemblages are nested when species occurring in species poor site are a subset of species assemblage of a species rich site (Patterson and Atmar 1986, Atmar and Patterson 1993). In a perfectly nested system, rare species occur only in species rich sites. Nestedness of bird assemblages within the study system is prerequisite for identifying biodiversity indicators (Roberge and Angelstam 2006). The NODF metric (Nestedness based on Overlap and Decreasing Fill), widely recognized as a robust method, was used to quantify nestedness patterns for each forest category (Almeida-Neto et al. 2008, Morrison 2013, Strona and Fattorini 2014, Matthews et al. 2015). NODF scores range from 0 (no nestedness) to 100 (perfect nestedness). To be able to determine if the observed NODF value is significantly different from values expected from a randomly selected community, 1000 null matrices were constructed based on the CE null model (proportional row and column totals). Nestedness was calculated by using the nestednodf function from the R-package "vegan" (Oksanen et al. 2016).

Relative importance of individual bird species as indicator of high species richness was calculated based on the Relative Indicator Value index (RIV; Roberge and Angelstam 2006). The following formula was used to calculate RIV for each species:

$$\mathrm{RIV} = \frac{[S + 1 - Rank(Z)] \times [S + 1 - Rank(F)]}{S^2}$$

where Rank(Z) and Rank(F) are the ranks of the species according to species-specific nestedness and frequency of occurrence, respectively. S is total species numbers observed in the study area for a given combination of stands. Species specific nestedness pattern was assessed by using a Mann-Whitney U-test (Simberloff and Martin 1991, Fleishman and Murphy 1999). The Z-scores derived from this test were used as a measure of nestedness and significance was tested by using a one-tailed test. Species were ranked according to their Z-score from highest to lowest. Indicator values were calculated for five forest categories: 1) only the continuous cover forest stands (untreated control stands and nature reserves), 2) stands subjected to prescribed burning, 3) stand subjected to gap cutting, 4) continuous cover forest stand plus prescribed burning stands and 5) continuous cover forest stands plus stands subjected to gap cutting.

It is expected that biodiversity indicators should not only reflect high species richness but also indicate high relative abundance of co-occurring species. To test this hypothesis, a generalized linear model (GLM) based on a Poisson distribution with a log link function was used. The best indicators were selected according to the RIV scores. In case of ties, the species with the highest nestedness score was selected.

The importance of habitat variables in explaining bird species abundance was tested by using a Redundancy Analysis (RDA). RDA was used as the Detrended Correspondence Analysis (DCA) showed a short gradient in all forest categories (range 1.5-2.2). Forwards model selection with 999 Monte Carlo permutations was used to select variables contributing significantly to the ordination of habitat characteristics and the abundance of the occurring bird species.

3.3.4 Foraging ecology of the three-toed woodpecker (Paper IV)

A conditional logistic regression was used to determine foraging substrate characteristics. This was done with the *clogit* function from the "survival package" in R (Therneau and Lumley 2009). Conditional logistic regression is a type of logistic regression model based on matched case-control pairs. Trees used for foraging were matched with the nearest available tree. This was done to control for local habitat differences regarding to substrate availability.

Additionally, Manly selection ratios (Manly et al. 2002) were used for each resource unit found to be the best predictor identified using conditional logistic regression. Selection ratios are based on the ratio between substrate used by three-toed woodpecker and its availability (i.e. the nearest tree available tree). The substrate type is considered ‘‘preferred’’ when the 95% confidence interval (CI) of its selection ratio was > 1; as ‘‘avoided’’ when the 95% CI was < 1; and as used proportionally to its availability when the 95% CI included 1 (Manly et al. 2002).

To examine time (number of foraging minutes per observation session) spent foraging on selected substrate, generalized linear mixed models (GLMM) with Poisson distribution were used. Here the effect of tree species, decay stage, DBH and foraging height in interaction with forest type were tested. For testing substrate thickness at foraging height, a linear mixed model (LMM) was used.

All foraging session shorter than 5 min were excluded. For graphical representation the model predictions were plotted.

4 Results

4.1 Forest structures

Four years after restoration, forest structures differed between stand types. Prescribed burning stands had lower basal areas of living conifer and deciduous trees compared to the untreated control stands ($p<0.001$ and $p=0.002$, respectively). Moreover, the basal areas of standing dead trees of all tree species and the total density of dead trees were significantly higher in prescribed burning stands compared to the untreated control stands ($p<0.001$). Gap-cut and untreated control stands contained less spruce than nature reserves ($p<0.001$) and gap-cut stands had less deciduous trees than the controls ($p=0.002$). Understory density was lower in the burned stands compared to the other three stand types ($p<0.001$). However, understory density did not differ between untreated controls and gap-cut stands. In contrast, the untreated controls had a less dense understory than nature reserves ($p<0.001$). For more detailed description of the differences in forest structure see table 2, paper I.

4.2 Assemblage responses (Paper I)

Across the two census years, we recorded a yearly average of 1145 territories of 36 bird species. Stand types did not influence overall bird species richness and abundance ($p=0.158$ and $p=0.538$, respectively). Within the specific functional guilds, prescribed burning positively influenced the abundance of long-distance migrants, ground breeding birds, strong cavity excavators and early-successional specialists, as well as the species richness of bark-feeders and strong cavity excavators. In contrast, prescribed burning negatively influenced the abundance of off-ground breeders as well as species richness of secondary cavity nesters and crown feeders. See table 3 in paper I for more details.

At the assemblage level, prescribed burning led to a significant change in the overall bird assemblage structure compared to control, nature reserves and gap-cut stands (p<0.001; Figure 3). Bird assemblage structure did not differ between gap-cut stands, control stands and nature reserves, indicating that gap cutting as a restoration treatment does not influence bird assemblage structure.

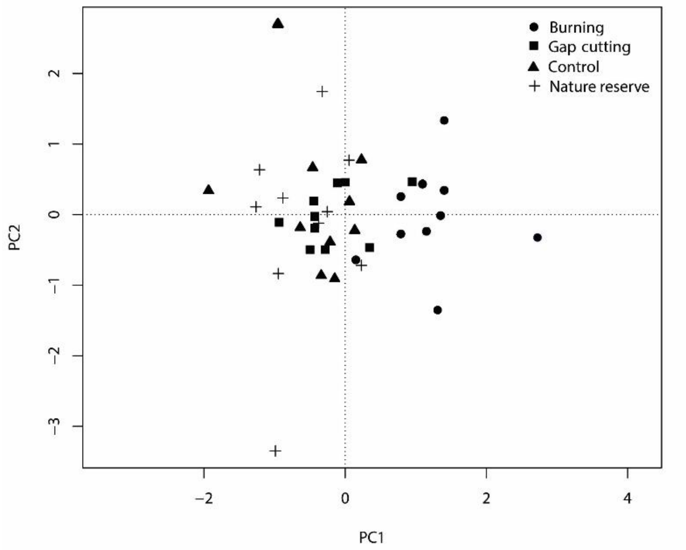


Figure 3. *Graphical representation of the constrained ordination redundancy analysis (RDA) of differences in species assemblage between four different stand types: prescribed burning, gap cutting, untreated controls and nature reserves. From Paper I.*

At the individual species level, it was found that the tree pipit (*Anthus trivialis*), redwing (*Turdus iliacus*) and brambling (*Fringilla montifringilla*) were more abundant in prescribed burning treatment than in the other stand types. The goldcrest (*Regulus regulus*) and robin (*Erithacus rubecula*) were less abundant in prescribed burning treatment. Additionally, the black woodpecker (*Dryocopus martius*) was significantly more abundant in burned stands compared with gap-cut and control stands, but no differences were found between nature reserves and the three other stand types. See table 4, paper I for more details.

4.3 Breeding performance Pied Flycatcher (Paper II)

The overall nest-box occupation rate by pied flycatchers was 39% in 2016 and 64% in 2017. Number of eggs, nestlings and fledglings did not differ between stand types (p=0.113, p=0.315 and p=0.526, respectively; Figure 4 A).

Additionally, stand types did not influence hatching success, fledging success or breeding success (p=0.455, p=0.945 and p=0.748, respectively; Figure 4 B). Average laying date (i.e. date of the first egg) was similar between stand types but differed between the two years. None of the factors discussed above was related to breeding densities.

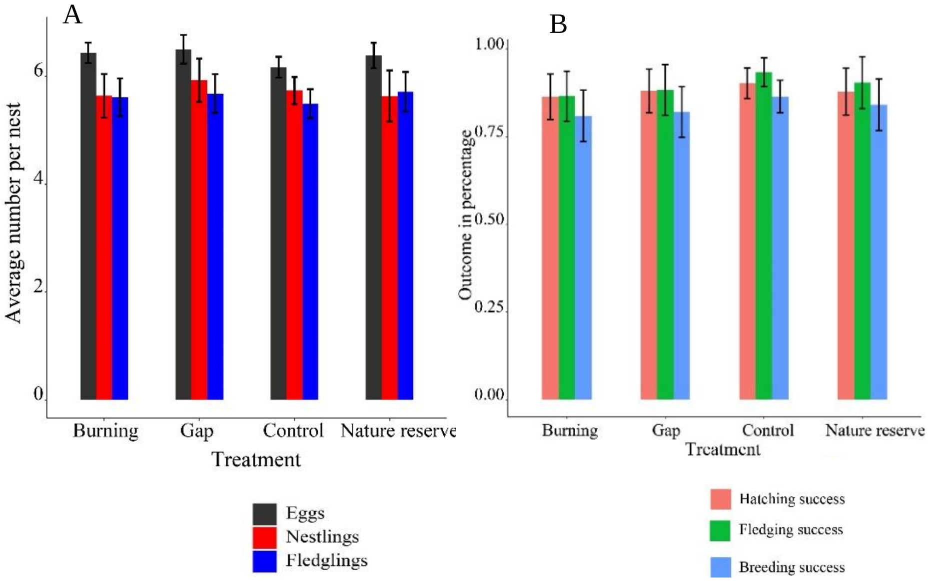


Figure 4 ***A)*** *Average number of eggs, nestlings and fledglings per nest and* ***B****) average hatching success, fledging success and breeding success between prescribed burning, gap cutting, control and nature reserve treatments (± 95% ci). From paper II*

In 2017 a total of 639 nestlings were measured over 126 nest-boxes. Nestlings in prescribed burning stands had on average a higher body condition index compared to untreated controls and gap cutting stands (p=0.017; Figure 5). The body condition index was not related to breeding densities (p=0.922).

In the control treatment, approximately 68% of the breeding females were caught. The corresponding figures for the gap cutting treatment and the prescribed burning treatments were 63% and 55%, respectively. Adult female body condition did not differ between the three periods of the nestling phase (p=0.362) or between stand types (p=0.225).

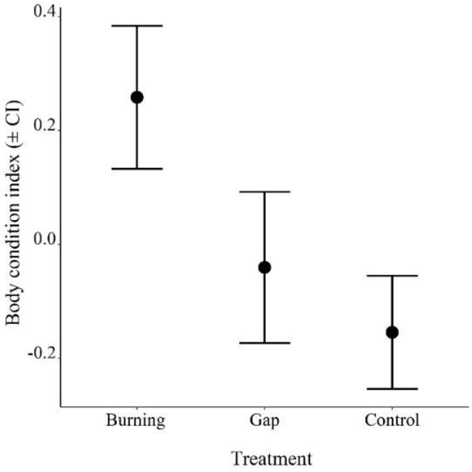


Figure 5. *Mean nestling body condition index (i.e. body mass relative to tarsus length) with ± 95% CI in the three forest stand types. From paper II.*

4.4 Biodiversity indicators (Paper III)

In total 13 resident forest bird species were recorded within the 40 study stands. In continuous cover stands (referring to untreated controls and nature reserves) a total of 12 species were found while both gap cutting and prescribed burning stands harbored 8 species, see Appendix 1 in paper III.

In continuous cover stands the three-toed woodpecker (*Picoides* tridactylus) was identified as the best biodiversity indicator. The indicator values of bird species different between restoration treatments. Gap cutting resulted in an increase in the indicator value of the Siberian jay (*Perisoreus infaustus*). In contrast, after prescribed burning the goldcrest (*Regulus regulus*) had the highest indicator value.

To understand how biodiversity indicators perform across a wider range of forest types, continuous cover stands were tested together with both restoration treatments. Results shows that when gap cutting stands were added to the continuous cover stands, the three-toed woodpecker had the highest indicator value and was thus identified as the best biodiversity indicator. To the contrary, adding prescribed burning stands to the continuous cover stands resulted in a drop in indicator value for three-toed woodpecker. Here, the Siberian jay had the highest indicator value. All results are presented in table 1.

Table 1. *Indicator values of resident forest bird based on presence-absence data. Frequency (Freq.) is the number of stands where the species occurred. Z-score test the species specific nestedness by using a one-tailed Mann-Whitney U-test. The RIV-score represent the relative indicator value of each species. Scientific species names are provided in Appendix 1, Paper III.*

	Continuous cover stands (n=20)			Prescribed burning (n=10)			Gap-cutting (n=10)			Continuous cover + prescribed burning (n=30)			Continuous cover + gap cutting (n=30)		
Species	**Freq.**	**Z-score**	**RIV**	**Freq**	**Z-score**	**RIV**	**Freq**	**Z-score**	**RIV**	**Freq.**	**Z-score**	**RIV**	**Freq.**	**Z-score**	**RIV**
Black woodpecker	2 (3)	0.321 (9)	0.278	4 (4)	0.664 (5)	0.312	NA			6 (6)	0.185 (10)	0.189	2 (3)	0.636 (10)	0.208
Great spotted woodpecke	10 (8)	1.046 (5)	0.278	10 (7)	-	-	5 (4)	1.496 (2)	0.468	20 (9)	0.089 (11)	0.088	15 (8)	1.506 (4)	0.313
Grey-headed woodpecker	NA			1 (1)	0.361 (6)	0.375	NA			1 (2)	0.824 (7)	0.497	NA		
Three-toed woodpecker	**6 (5)**	**2.116 ** (1)**	**0.667**	7 (5)	0.710 (4)	0.312	1 (1)	1.446 (3)	0.750	13 (8)	1.266 (3)	0.390	**7 (5)**	**2.791*** (1)**	**0.667**
Goldcrest	20 (12)	-	-	**3 (2)**	**2.234* (1)**	**0.875**	9 (7)	1.081 (4)	0.156	23 (11)	0.829 (5)	0.159	29 (12)	1.413 (5)	0.056
Coal tit	1 (1)	0.800 (7)	0.500	NA			NA			1 (1)	0.826 (6)	0.650	1 (1)	0.944 (7)	0.500
Crested tit	7 (7)	0.408 (8)	0.208	NA			1 (2)	0.709 (6)	0.328	7 (7)	0.579 (8)	0.248	8 (7)	0.481 (12)	0.042
Great tit	19 (11)	0.267 (11)	0.028	10 (7)	-	-	9 (8)	0.180 (8)	0.015	29 (13)	0.059 (13)	0.005	28 (11)	0.509 (11)	0.028
Willow tit	16 (9)	1.156 (3)	0.278	4 (3)	1.319 (2)	0.656	8 (6)	0.266 (7)	0.093	20 (10)	0.056 (12)	0.047	24 (10)	0.764 (8)	0.104
Treecreeper	17 (10)	1.144 (4)	0.188	9 (6)	0.723 (3)	0.281	6 (5)	0.877 (5)	0.250	26 (12)	1.320 (2)	0.142	23 (9)	1.807* (3)	0.278
Bullfinch	2 (2)	0.971 (6)	0.535	NA			NA			2 (3)	1.140 (4)	0.650	2 (2)	1.273 (6)	0.535
Siberian jay	6 (6)	1.744 * (2)	0.535	NA			**2 (3)**	**2.033* (1)**	**0.750**	**6 (5)**	**1.862* (1)**	**0.692**	8 (6)	2.626** (2)	0.535
Jay	3 (4)	0.270 (10)	0.188	NA			NA			3 (4)	0.494 (9)	0.295	3 (4)	0.707 (9)	0.250

Top biodiversity indicators in each stand type are marked in bold

Numbers in () are rank

* P < 0.05

** P < 0.01

*** P < 0.001

The relationship between the present of the biodiversity indicator and high abundance of co-occurring species was significant in four out of the five forest category combinations (i.e. the five stand category groupings presented in Table 1), suggesting that the indicators indicated high abundance of co-occurring species. When prescribed burning stands were added to the continuous cover stands, the best indicator (Siberian jay) did not represent high abundance of co-occurring resident forest birds.

The occurrence of bird species is closely correlated with local habitat characteristics. Resident forest birds in continuous cover stands and in combination with gap cutting were closely associated with the DBH of deciduous trees and the basal area of living spruce and pine. The occurrence of the three-toed woodpecker within these stands was closely associated with the occurrence of deciduous trees with larger DBH.

To the contrary, the association between woodpeckers and the DBH of living deciduous trees changed when prescribed burning stands were added. In this case a transition from the importance of DBH of living deciduous trees to a relation with dead wood quantities occurred. Habitat associations within the two restoration treatments were not tested, as the sample sizes were too small.

4.5 Foraging behavior of the three-toed woodpecker (Paper IV)

In 2016, 14 different three-toed woodpecker individuals were observed, resulting in a total of 622 observation minutes. Six of these individuals (3 males and 3 females) were observed in burned stands and 8 individuals (4 males and 4 females) in unburned stands (referring to untreated controls and nature reserves). During the spring of 2017, a total of 1301 observation minutes were recorded from 12 different individuals. Of these individuals 6 were observed in burned stands (3 males and 3 females) and 6 individuals (3 males and 3 females) in unburned stands.

4.5.1 Characteristics of selected foraging substrate

Tree species, decay stage and DBH predicted characteristics of foraging substrate in both burned and unburned forest stands (table 2, paper IV). In burned stands three-toed woodpeckers avoided pine trees while both birch and spruce were used proportionally to their availability and thus these tree species were used but not preferred (Figure 6 A). Decay class influenced substrate selection: living trees (decay stage 1) were avoided and recently dead trees (decay stage 3) were preferred (Figure 6 B). Additionally, trees in the category of DBH 15-25 cm and 35-45 cm were preferred while trees with a DBH in the category of 5-15 were avoided (Figure 6 C).

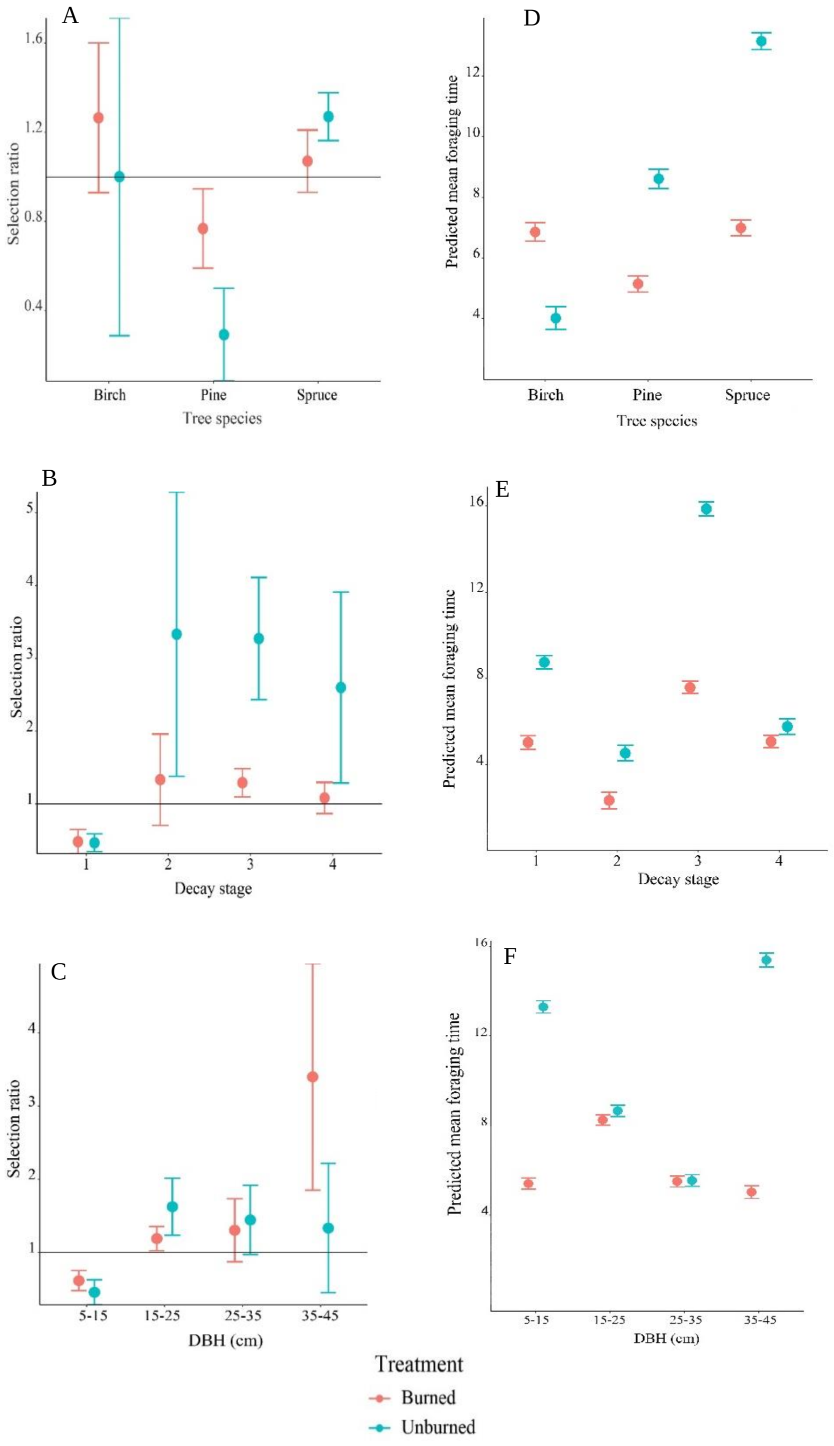
In unburned stands, three-toed woodpeckers displayed a clear selection preference for spruces while pines were avoided, birch was used proportionally to its availability (Figure 6 A). Three-toed woodpeckers preferred dying trees (decay stage 2), recently dead trees (decay stage 3) and trees dead for a longer time (decay stage 4) and trees with a DBH of 15-25 cm (Figure 6 B and C). Living trees and trees with a DBH in the category of 5-15 were avoided (Figure 6 B and C).

4.5.2 Foraging behavior as measured through foraging time

Bark scaling was the most common foraging method. This foraging method accounted for 85.3% of the foraging time in burned forest and 80.1% in unburned forest. In both forest types, the trunk was the most common foraging location, representing 96.8% of the foraging time in burned forest and 95.8% in unburned forest. We did not record any observation of three-toed woodpeckers using lying dead wood as a foraging substrate.

Forest type influenced the observed foraging time among different tree species, trees belonging to different decay stages and DBH. In burned forest, three-toed woodpeckers spent slightly more foraging time on birch and spruce compared to pine (Figure 6. D). In unburned forest, three-toed woodpeckers spent most of their foraging time on spruce (figure 6. D). This may suggest that in burned forest a homogenization of attractiveness of different tree species occurs. In both forest types, decay stage 3 had the highest mean predicted foraging time (figure 6. E), additionally a considerable amount of time was spent on living trees. Three-toed woodpeckers in burned forest spent most time foraging on trees with a DBH between 15-25 cm. In contrast, in unburned forest they spent on average most time on trees with a DBH of 5-15 and 35-45 (figure 6. F).

*Figure 6. **A-C)** Manly selection ratios with 95% confidence intervals for tree species, decay stage and DBH. Selection ratios are based on the ratio between substrate selected by three-toed woodpecker and availability (measured as the nearest tree). The line indicates the value 1, above 1 is preferred and below is avoided! **D-F)** Predicted mean foraging time (minutes) with standard error (SE) for substrates belonging to different (A) tree species, (B) decay stages and (C) DBH classes. Results derived from GLMM models with Poisson distribution and corrected for differences in sex, where forest stand and year were included as random variables. From paper IV. **Figure on next page!***


A
1.6
1.2
0.8
0.4
Selection ratio
Birch
Pine
Spruce
Tree species
D
12
10
8
6
4
Predicted mean foraging time
Birch
Pine
Spruce
Tree species
B
5
4
3
2
1
Selection ratio
1
2
3
4
Decay stage
E
16
12
8
4
Predicted mean foraging time
1
2
3
4
Decay stage
C
4
3
2
1
Selection ratio
5-15
15-25
25-35
35-45
DBH (cm)
F
16
12
8
4
Predicted mean foraging time
5-15
15-25
25-35
35-45
DBH (cm)
Treatment
Burned
Unburned

5 Discussion

With increased pressure from humanity on natural systems, it is more important than ever to develop effective tools for conserving biodiversity, maintaining ecosystem function and mitigating climate change. Ecological restoration is one way to counteract these problems and therefore it has gained much attention in the last decades. Important knowledge is still missing regarding species responses and successfulness of restoration actions. In the boreal biome, the concept of ecological restoration is based on emulating natural disturbance regimes. Within this study, the short term (4–5 years) impact of two restoration treatments - prescribed burning and gap cutting - on boreal breeding birds were evaluated.

5.1 Evaluation of restoration outcome (paper I and II)

5.1.1 Prescribed burning

This study showed clear changes in bird assemblage structure, 4-5 years after prescribed burning. The occurrence of forest bird species is largely associated with local habitat structures (Hagan and Meehan 2002, Lichstein et al. 2002, Hurlbert 2004), suggesting that habitat change through prescribed burning is the main factor leading to these changes in bird assemblage structures. Indeed, prescribed burning influenced the availability of key habitat structures, showing negative effects on the basal areas of living spruces, living deciduous trees, and understory density, as well as increased basal area of standing dead trees. The vegetation structure shifted towards an earlier successional stage, which is in line with earlier studies (Hekkala et al. 2014b). As a results of these changes in local habitat structure, prescribed burning created habitat for long-distance migrants, ground breeders, strong cavity excavators and species preferring early-successional habitat. In this study, the tree pipit, redwing and brambling responded positively to prescribed burning. Also woodpeckers – which constitute the ‘strong cavity excavator’ nesting guild and most of the ‘bark-feeder’ foraging guild – clearly benefited from burning, most probably through an increased abundance of breeding substrates and saproxylic insect prey in trees killed or weakened by the fire (Morissette et al. 2002, Rota et al. 2014, Kärvemo et al. 2017). On the contrary, the goldcrest and robin, both of which are off-ground breeders and closely connected with mature forest stands, responded negatively to prescribed burning. This may be caused by a decrease in the abundance of living spruce and understory density, which constitute important breeding and feeding habitats for these species (Haapanen 1965, 1966).

To our knowledge, this study represents the first attempt to use an experimental approach to test the response of forest bird assemblages to prescribed burning in the boreal biome. Most of the earlier studies on this topic have explored the responses of birds to wildfire. A study from northern Sweden found that wildfire had a positive effect on ground-feeding insectivorous species and they did not find negative effects (Edenius 2011). Similarly, several studies from other forest systems showed that fire clearly benefit numerous bird species (Hutto 1995, Clavero et al. 2011, Lowe et al. 2012). However, the extent to which prescribed burning and wildfire result in similar responses in bird assemblages needs further investigation. Several studies have shown that fire intensity is an important variable affecting the responses in bird assemblages (Smucker et al. 2005, Lindenmayer et al. 2014, Hutto and Patterson 2016). Wildfires often create a mosaic of areas with both low and high intensity fires while, in most cases, prescribed burning results in low intensity fire. In conclusion, habitat changes through prescribed burning positively influence the presence and abundance of several boreal forest bird species.

The ‘ideal free distribution’ suggest that bird densities are generally highest in high quality habitat patches (Fretwell and Lucas 1970). Higher bird densities lead to higher levels of competition which results in a reduction of individual fitness (Hake and Ekman 1988), consequently individual fitness becomes more similar to that in lower quality patches. Based on the lack of response in pied flycatcher abundance to restoration treatment (Paper I), the theory suggests that habitat quality did not change due to ecological restoration. Another proxy for habitat quality is reproductive performance. This study showed that prescribed burning has a positive effect on nestling body condition. Although, none of the other reproductive parameters were significantly affected by ecological restoration, improved body condition suggests that this restoration treatment enhanced local habitat quality for this species. This because it is suggested that nestling condition at the time of fledging is positively related to first-year survival (Magrath 1991, Naef-Daenzer et al. 2001, Vitz and Rodewald 2011).

Improved condition in one life stage, influencing the condition in a later stage is referred to as a carry-over effect. In this case, this indicates that the body condition of nestlings in the nestling phase may influence future survival probabilities and thus future population dynamics. Thus, observed improvement in body condition may have important implications for both the optimization of life histories and population dynamics of local pied flycatcher populations (Linden et al. 1992, Merilä and Svensson 1997, Verhulst et al. 1997, Lindström 1999).

Neither nest-box occupation rate nor female adult body condition were related to nestling body condition (or any of the other reproductive parameters). This suggest changes in local resource availability is probably the main mechanism underlying the effect of prescribed burning on nestling body condition, as lower food availability during the nestling period can limit food provision and consequently lead to a reduction in body condition of nestlings (Keller and van Noordwijk 1994, Visser et al. 1998, Naef-Daenzer et al. 2000, Tremblay et al. 2005, Sánchez et al. 2007). Unfortunately, food availability was not measured within this study. However, it has been shown that flower-visiting insects and ground-living invertebrates are positively influenced by fire (Bouget and Duelli 2004, Moretti et al. 2004, Campbell et al. 2007). It is known that pied flycatchers catch approximately 65% of their food on the ground, 20% in the air and 15% on trees (Von Haartman 1954). Thus, ground-dwelling invertebrates favored by prescribed burning may form an important food resource for pied flycatchers.

5.1.2 Gap cutting

The creation of small-scale gaps in forest stands did neither influence bird assemblage structure nor the reproductive output or nestling body condition for pied flycatchers. Gap cutting had little effect on local habitat structures. The only difference found between control stands and gap cutting stands was the amount of deciduous trees, which was lower in gap cutting stands.

The lack of responses in bird assemblage structure to the gap cutting treatment is perhaps due to the fact that gaps of 0.03 ha are too small to generate any strong edge effects. Food availability for a range of forest bird species is higher near forest edges than within undisturbed forest (Helle and Muona 1985, Jokimäki et al. 1998) but our gaps did not attract species such as tree pipits which are open or edge habitat species. Furthermore, our findings are in line with Forsman et al. (2013), who used even larger gaps (range of 0.2–1.8 ha) and yet did not find any general effect of gap disturbance on the total species richness or abundance of forest birds in Finland. A similar trend was found as regards local habitat structures: Forsman et al. (2013) did not find any significant differences in habitat structures at the stand level between control stands and gap cutting stands.

5.2 Boreal forest bird conservation

Determining the consequences of ecological restoration on birds is important, however, for successful conservation it is also important to understand how restoration action effect proposed biodiversity indicators. Biodiversity indicators can potentially be used to identify biodiversity hotspots and for the evaluation and planning of forest management or ecological restoration. However, for many proposed biodiversity indicators there remains much uncertainty about under which circumstances they are valid indicators (Lindenmayer and Likens 2011). Additionally, more knowledge about species specific responses is needed as their habitat requirements can be set as restoration or management targets (Angelstam et al. 2004).

5.2.1 Biodiversity indicators (paper III)

Biodiversity indicators for resident forest birds were determined for different forest types. Overall, the three-toed woodpecker and Siberian jay were identified as best indicators for high biodiversity and abundance of co-occurring species. Although this is the first time biodiversity indicators were identified for the middle/northern boreal zones of Europe, the results are in line with other studies from the south boreal and hemi-boreal zones. In these regions, the presence of the three-toed woodpecker is positively correlated with bird species richness and abundance of co-occurring bird species (Mikusiński et al. 2001, Roberge and Angelstam 2006, Pakkala et al. 2014). Nevertheless, the Siberian jay had not previously been identified as a potential indicator for biodiversity. An explanation for this could be that the Siberian jay occurs in too low densities at lower latitudes (Pakkala et al. 2014). In Fennoscandia, population densities of Siberian jay increases from south to north (Virkkala and Rajasärkkä 2007), this may suggest that the Siberian jay is a potential biodiversity indicator only for middle/north boreal forest systems while the three-toed woodpecker may have a high indicator value across most of boreal Fennoscandia.

Prescribed burning led to a shift in indicator values: in burned stands the goldcrest was identified as the best biodiversity indicator. Considering the large variation in spruce mortality after fire (Sidoroff et al. 2007), goldcrest occurred mainly in the stands where fire intensity was low and where spruces has survived. The goldcrest is seen as a species which is highly dependent on the occurrence of living spruces for breeding and foraging (Haapanen 1965). Based on the determined relations between the occurrence of bird species and local habitat characteristics, this study suggest that biodiversity indicators are also indicators for structural habitat complexity.

5.2.2 Three-toed woodpecker in ecological restoration (paper IV)

The three-toed woodpecker was used as focal species in this study because it is sensitive to habitat changes, it has importance as a biodiversity indicator (Mikusiński et al. 2001, Drever et al. 2008), and holds a keystone role in providing cavities for secondary cavity-nesters (Pakkala et al. 2018b). This study confirmed that in unburned forest the three-toed woodpeckers primary foraging method is bark-scaling and that its main foraging position is on the trunk (Hogstad 1977, 1991, Pechacek 2006). Similar results were found for three-toed woodpeckers foraging in burned forests. Average thickness of foraging substrate did not differ between unburned and burned forest and is comparable to what was found by Zhu et al. (2012) and Pechacek (2006) in unburned forests.

Foraging substrates for three-toed woodpeckers in burned forests can be characterized as spruce or birch, recently dead trees (decay stage 3) and trees with a DBH in the category 15-25 cm and 35-45 cm. These results are in line with those obtained in burned forests of Northern America, where the American three-toed woodpecker and black-backed woodpecker were shown to select larger snags (> 15 cm) for foraging (Murphy and Lehnhausen 1998, Nappi and Drapeau 2011).

In unburned forests, the three-toed woodpecker showed a clear preference for Norway spruce. One possible explanation for this is that their main prey, bark beetles, are relatively more abundant in spruce than in the other tree species in unburned forest compared with burned forest. Furthermore, three-toed woodpeckers preferred dying trees (decay stage 2), recently dead trees (decay stage 3) and trees dead for a longer time (decay stage 4), as well as trees with a DBH of 15-25 cm. Healthy living trees and trees with a DBH in the category of 5-15 were avoided according to the substrate selection analyses. Imbeau and Desrochers (2002) characterized foraging substrate for American three-toed woodpecker in unburned forest and found similar results, with a stronger preference for fresh larger-diameter snags over living trees, possibly an effect of prey abundance being higher in fresh large diameter snags.

Time spent on a selected foraging substrate differed in terms of tree species, decay stage and DBH. In unburned forests, three-toed woodpeckers clearly spent most of their foraging time on spruce. This is in line with other studies from Europe, which reported that three-toed woodpeckers primarily forage on

Norway spruce (Hogstad 1991, Villard 1994, Pechacek 2006). Nevertheless, such a clear difference in foraging time between tree species was not found in burned forests. Even though most time was spent on spruce and birch, a considerable amount of time was also spent on pine. This in contrast to other studies which show that in mixed burned forest stands three-toed woodpeckers mainly forage on spruce species (*Picea* spp.) (Murphy and Lehnhausen 1998, Fayt 1999). One explanation for the pattern we observed may be that saproxylic beetle distribution becomes more homogenized between tree species after prescribed burning (Wikars 2002, Toivanen and Kotiaho 2010, Hägglund and Hjältén 2018), making the woodpecker more likely to spend time foraging on different tree species.

In both burned and unburned forest, three-toed woodpeckers on average spent most of their foraging time on recently dead trees (decay stage 3). This is in line with results from earlier studies reporting that three-toed woodpeckers prefer fresh snags (Hogstad 1991, Pechacek 2006). However, we found that three-toed woodpeckers also spent a considerable amount of time on living trees, in spite of the fact that living trees were avoided in terms of substrate selection. On healthy living trees, the woodpecker spent on average 55% of their time drinking sap. These results may indicate that the woodpeckers dedicate an unproportionally large amount of time to sap drinking and hence that tree sap from living trees may be an important food source (Pakkala et al. 2018a). In unburned forest the three-toed woodpecker spent on average most time on trees with a DBH of 5-15 and 35-45. These results are partly in line with studies from unburned forest, where it has been shown that three-toed woodpeckers mainly forage on trees with a DBH larger than 10 cm (Hogstad 1977, 1991, Pechacek and d'Oleire-Oltmanns 2004, Zhu et al. 2012). However, this study suggest that, once selected, woodpeckers may spend considerable time utilize smaller diameter trees in the range of 5-15 cm as well in terms of foraging time in unburned forest. One possible explanation is that natural self-thinning in the studied old forest stands leads to the slow death of small-diameter spruces, which are colonized by bark beetles such as *Pityogenes chalcographus* (Fayt 1999). These results contribute to our understanding how the foraging ecology of the three-toed woodpeckers differ between unburned and forest subjected to prescribed burning.

6 Conclusions

The main take home message from this study is that prescribed burning as a restoration treatment constitutes an effective way to restore habitat for boreal forest birds associated with early forest successions in a managed boreal forest landscapes. In paper I, II and IV, I have shown that prescribed burning positively influences early successional species, woodpeckers and habitat for pied flycatchers and at the same time it generates foraging substrate for three-toed woodpeckers 5-6 years after fire.

Fire had a negative effect on two species that are closely associated with mature forest, namely the goldcrest and the robin. The goldcrest is a species which has lately exhibited a declining population trend in Sweden but still it is one of the most common forest birds in the country (Gärdenfors et al. 2015). In contrast, many of the species favored by fire are common species which are currently not listed as high-priority species from a conservation perspective. However, the redwing and brambling, two of the species favored by prescribed burning, have declined significantly since 1998 in Sweden (Ram et al. 2017) and may therefore gain conservation interest in the future. Although potential negative effects of fire on certain species should always be taken into consideration in restoration planning, our findings suggest that prescribed burning contributed to the conservation of beta diversity.

Moreover, I found that prescribed burning positively influenced the body condition of nestlings of the pied flycatcher. Local food provision can be an important factor influencing body condition of nestlings. My findings thus suggest that local habitat quality is improved after prescribed burning, possibly due to increased abundance of local insect populations serving food for the pied flycatchers. Furthermore, I did not find any negative effects of ecological restoration on the reproductive outcome (e.g. clutch size) of pied flycatchers. They reproduced equally well in nature reserves, forest set-asides and forests subjected to ecological restoration and the reproductive outcome in these stands was found to be similar to that in other populations of this species (Järvinen

1989, Berglund and Nyholm 2011, Strasevicius et al. 2013). However, we should be careful with generalizing these results to other bird species as they only are directly applicable to pied flycatchers. Still, they may potentially apply also to some other insectivorous bird species with similar habitat requirements.

For conservation and management purposes I identified the three-toed woodpecker (in unburned forest) and the Siberian jay (gap cutting) as potential indicators for high resident bird diversity in the middle and northern boreal forest zone. However, ecological restoration clearly affected the value of biodiversity indicators and therefore I emphasize that one must be careful about using previously identified biodiversity indicators in ecosystems subjected to ecological restoration aiming to emulate natural disturbances. This stresses the importance of using multiple biodiversity indicators representing different forest types and natural disturbance regimes. Additionally, I showed that biodiversity indicators can be used to identify potentially important areas with high habitat complexity, as the occurrence of biodiversity indicators was rather closely associated with local habitat characteristics.

This study was performed 5-6 years after fire and still the burned sites generated foraging substrates for three-toed woodpeckers. This is in contrast to wildfires, were it has been found that three-toed woodpecker densities often drop after two-four years (Fayt 2003). This suggests that the use of prescribed burning can be an efficient way for rapid and apparently long-lasting enrichment of important forest structures for woodpeckers. In unburned forests, quantity and quality of dead wood is critical for the occurrence of three-toed woodpeckers (Angelstam et al. 2003, Bütler et al. 2004, Roberge et al. 2008). Even though dead wood quantities in Swedish forests have increased by 25% since 1994, (Jonsson et al. 2016), the levels are still only about 10% of those found in old growth forest and heterogeneity of dead wood types is low in terms of species, DBH and decay classes. Additionally, Hedwall and Mikusiński (2015) showed very low levels and slow increase of dead wood in Swedish protected areas. Therefore, we suggest that the best conservation strategy for three-toed woodpeckers and other recent dead wood associated species, is to ensure the provision of more dying trees and fresh dead wood of different tree species and DBH classes in managed forests and unmanaged set-asides with a past history of management

7 Future research

Even though the results of this thesis give some insights into the consequences of ecological restoration on bird assemblage structures, many questions remain unanswered. It is known that ecosystem recovery after natural disturbances can take a long time. Within this thesis, only short-term effects were studied. Species assemblage structure is expected to change over time as local habitat characteristics continue to develop (Lowe et al. 2012). It is therefore of great importance to determine the long-term effects of the proposed restoration treatments, for example by performing follow up bird inventories every 5-10 years. In addition to this, it is essential to follow the development of the forest's structure, so that the changes in bird assemblage structure can be related to changes in habitat characteristics. This could also provide better knowledge about bird species and their relation with their habitat. This can help us understand how current forest management influence species occurrence and how resilient species are to habitat changes. The effects of the surrounding landscape on restoration outcome also deserves further investigation. Does it matter where in the landscape ecological restoration is applied? In the light of habitat fragmentation, land use changes and climate change, knowledge regarding the localization of restoration sites relative to existing populations and the influence of the landscape matrix on species occurrence can positively contribute to the development of species conservation plans and nationwide green infrastructures.

As stressed earlier, we should be careful with generalizing the result regarding the reproductive outcome of the pied flycatcher to other species with different habitat requirements. Hence, it would be desirable to also explore the reproductive response of other bird species. In this respect, habitat specialists should be prioritized as they are stricter in their habitat requirements but also open-nest and ground breeders are of interest. This would provide deeper understanding of, for example, the effects of habitat changes due to restoration on nest predation.

Lastly, the three-toed woodpecker is seen as important biodiversity indicator that requires large areas of forest rich in dead wood. In most cases, the prescribed burning stands used in this study make up only a small proportion of the individual woodpeckers’ much larger home ranges. Thus, the question remains of how three-toed woodpeckers use the current landscapes, in different seasons and how important these prescribed burning areas are for their reproductive performance. The use of individual tracking technology and more detailed study of their reproductive performance would help disentangle these questions. Additionally, it would be interesting to compare the effects of prescribed burning with wildfires.

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Popular science summary

The boreal is world's second largest biome and extends over the northern hemisphere, from Alaska to Canada, over northern Europe to Russia. Fire, wind and insect outbreaks are important natural disturbances creating a heterogenic landscape with a high diversity in tree species, forest of different ages and large volumes of deadwood. This varied forest landscape offers suitable habitat for a large number of animals and plants.

Nowadays, a large proportion of these natural forests has been subject to silviculuture and converted into even-aged, single species forests, with degraded understory layer and severely reduced deadwood availability. At the same time, modern forestry practices and fire suppression have led to the disappearance of natural disturbances from the system. Consequently, forest bird species that are closely associated with deciduous trees, dead wood and large-diameter trees are declining. To mitigate this trend, successful biodiversity conservation will necessitate active ecological restoration actions. Proposed restoration actions in the boreal mainly involves the emulation of natural forest dynamics with fire and wind-throw as the two most important natural disturbances.

In this thesis, I assessed if ecological restoration of forest set-asides in northern Sweden can be used to improve the conservation status of boreal forests birds. All data for this study was collected within a large-scale field experiment were fire and wind dynamics were emulated. More specifically, I evaluated the response in bird species occurrence and the breeding performance of the pied flycatcher *Ficedula hypoleuca* to the restoration treatments. Additionally, I identified biodiversity indicators and tested how ecological restoration can affect their indicator value. Lastly, I characterized substrate preferences and substrate use of the Eurasian three-toed woodpecker *Picoides tridactylus* in forest stands subjected to fire and in unburned forests.

The results showed that the abundance of the redwing *Turdus iliacus*, brambling *Fringilla montifringilla*, tree pipit *Anthus trivialis* and woodpeckers were positively influenced by fire. In contrast, the goldcrest and robin were found in lower abundance in burned stands compared to other stand types. Furthermore, I found that fire positively effects the body condition of nestlings of pied flycatchers. This is important as a better body condition in the nestling phase increases the survival probability in their first year. This suggest that burning improved habitat quality, possibly due to increased abundance of local insect populations serving food for the pied flycatchers. Besides the negative effects of fire on some species, our findings suggest that burning forests is an effective way to restore habitat for boreal forest birds. Lastly, I found that the creation of small-scale gaps in forest stands did not influence bird assemblage structure but also not the reproductive output or nestling body condition for pied flycatchers.

Some specialized forest bird species have been proposed to be an efficient tool for identifying sites with high bird species richness, also referred to as biodiversity indicators. I identified the three-toed woodpecker (in unburned forest) and the Siberian jay *Perisoreus infaustus* (gap-cutting) as potential biodiversity indicators. After fire, the goldcrest *Regulus regulus* became the best predictor of high species richness. This stress the importance of using multiple biodiversity indicators representing different forest types and natural disturbance regimes.

In both burned and unburned forests, the main substrate used by foraging three-toed woodpeckers can be characterized as freshly dead trees with a DBH of more than 15 cm. In unburned forest, three-toed woodpeckers mainly select spruce as foraging tree but in burned I did not find such a clear preference. Additionally, measured foraging time showed that substrates in the 5-15 cm DBH range and living trees are of importance for foraging three-toed woodpeckers as well. In conclusion, prescribed burning is an efficient method to create habitat for three-toed woodpeckers.

The main conclusion from this study is that prescribed burning as a restoration treatment is an effective way to restore habitat for boreal forest birds in managed boreal forest landscapes. Furthermore this should encourage forest managers to reintroduce more fire in boreal forests as a complement to other conservation measures.

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