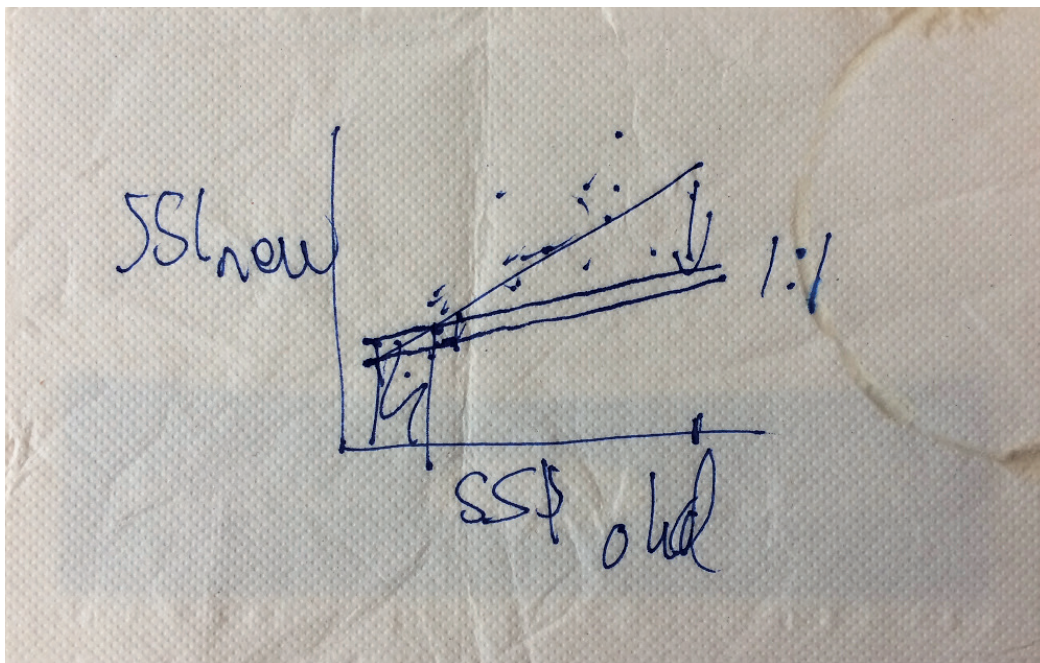


Matti Häkkilä

Biotic Homogenization of Forest Bird Communities under Human Influence



Matti Häkkilä

Biotic Homogenization of Forest Bird Communities under Human Influence

Esitetään Jyväskylän yliopiston matemaattis-luonnontieteellisen tiedekunnan suostumuksella
julkisesti tarkastettavaksi yliopiston Ambiotican salissa YAA 303
kesäkuun 1. päivänä 2018 kello 12.

Academic dissertation to be publicly discussed, by permission of
the Faculty of Mathematics and Science of the University of Jyväskylä,
in building Ambiotica, hall YAA 303, on June 1, 2018 at 12 o'clock noon.



UNIVERSITY OF JYVÄSKYLÄ

JYVÄSKYLÄ 2018

Biotic Homogenization of Forest Bird Communities under Human Influence

JYVÄSKYLÄ STUDIES IN BIOLOGICAL AND ENVIRONMENTAL SCIENCE 348

Matti Häkkilä

Biotic Homogenization of Forest Bird Communities under Human Influence



UNIVERSITY OF JYVÄSKYLÄ

JYVÄSKYLÄ 2018

Editors

Jari Haimi

Department of Biological and Environmental Science, University of Jyväskylä

Päivi Vuorio, Sini Tuikka

Publishing Unit, University Library of Jyväskylä

Jyväskylä Studies in Biological and Environmental Science

Editorial Board

Jari Haimi, Anssi Lensu, Timo Marjomäki, Varpu Marjomäki

Department of Biological and Environmental Science, University of Jyväskylä

Permanent link to this publication: <http://urn.fi/URN:ISBN:978-951-39-7463-3>

URN:ISBN:978-951-39-7463-3

ISBN 978-951-39-7463-3 (PDF)

ISBN 978-951-39-7462-6 (nid.)

ISSN 1456-9701

Copyright © 2018, by University of Jyväskylä

Jyväskylä University Printing House, Jyväskylä 2018

ABSTRACT

Häkkilä, Matti

Biotic homogenization of forest bird communities under human influence

Jyväskylä: University of Jyväskylä, 2018, 50 p.

(Jyväskylä Studies in Biological and Environmental Science

ISSN 1456-9701; 348)

ISBN 978-951-39-7462-6 (print)

ISBN 978-951-39-7463-3 (pdf)

Yhteenvedo: Metsien lintuyhteisöjen biologinen samankaltaistuminen ihmistoiminnan vaikutuksesta

Human actions impact biodiversity worldwide. Specialist species are particularly sensitive to environmental degradation whereas generalists may even benefit from habitat changes. As a consequence, specialists are declining while generalists are increasing and, therefore, communities become more similar. This phenomenon is known as biotic homogenization. In boreal forests logging and forest management is the most important factor changing the native habitat. In this thesis I studied if human actions are homogenizing boreal forest bird communities. I further studied if protected areas can maintain their diversity and, thus, prevent homogenization. Through the individual studies, biodiversity was measured using various metrics such as species richness, taxonomic, functional and phylogenetic diversities and Species Specialization Index. My results showed that human actions have diverse impacts on diversity in boreal forests. Intensive forest management has negative impacts on forest bird assemblages, and communities in protected areas are not sheltered from habitat changes in the surrounding areas. These negative impacts are particularly strong on forest specialists. The most important message of this thesis was that to really understand biodiversity, various diversity measures in all spatial scales should be considered. It is worth remembering that in biodiversity more is not necessarily better, but each area and patch has its own natural state of biodiversity. Human-induced changes to this baseline denote unwanted impacts on the communities and the whole ecosystems. With the growing demand and exploitation of natural resources, these complex relations in various scales and especially acknowledging them in conservation set growing demand of co-operation with scientists and conservation planners.

Keywords: Biodiversity; birds; boreal forest; conservation; environmental degradation; functionality; homogenization.

Matti Häkkilä, University of Jyväskylä, Department of Biological and Environmental Science, P.O. Box 35, FI-40014 University of Jyväskylä, Finland

Author's address Matti Häkkilä
Department of Biological and Environmental Science
P.O. Box 35
FI-40014 University of Jyväskylä
Finland
matti.i.hakkila@jyu.fi

Supervisors Professor Mikko Mönkkönen
Department of Biological and Environmental Science
P.O. Box 35
FI-40014 University of Jyväskylä
Finland

PhD Eric Le Tortorec
Department of Biological and Environmental Science
P.O. Box 35
FI-40014 University of Jyväskylä
Finland

Professor Gerald J. Niemi
Natural Resources Research Institute
University of Minnesota Duluth
NRRI-Duluth
5013 Miller Trunk Highway
Duluth, MN 55811
USA

Reviewers Research Professor Jani Heino
Finnish Environment Institute
Biodiversity Centre
P.O. Box 413, FIN-90014 University of Oulu
Finland

Professor Fiona Schmiegelow
University of Alberta
705A General Services
Edmonton, AB
Canada T6G 2H1

Opponent Docent Aleksu Lehtikoinen
Finnish Museum of Natural History
Zoology Unit
P.O. Box 17
FI-00014 University of Helsinki

CONTENTS

LIST OF ORIGINAL PUBLICATIONS

PREFACE

1	INTRODUCTION	11
1.1	Changing environment.....	11
1.2	Measuring Diversity.....	11
1.3	Biotic homogenization	13
1.4	Boreal forest.....	14
1.5	Protected areas	15
1.6	Aim of the thesis	16
2	STUDY QUESTIONS AND HYPOTHESES	17
3	MATERIAL AND METHODS	20
3.1	Bird data.....	20
3.1.1	Finland.....	20
3.1.2	Minnesota.....	20
3.2	Landscape data.....	21
3.3	Diversity measures.....	22
3.3.1	Species Specialization Index.....	22
3.3.2	Rao's quadratic entropy and taxonomic diversity	22
3.3.3	Functional diversity from traits	23
3.3.4	Phylogenetic diversity	23
3.4	Beta diversity	24
3.5	Statistical analyses	25
3.5.1	Differences in habitat specialization between Western Palearctic and Nearctic birds.....	25
3.5.2	Does human land-use lead to biotic homogenisation of forest bird communities in northern USA?	25
3.5.3	Degradation in landscape matrix has diverse impacts on diversity in protected areas	25
3.5.4	Is degradation in matrix homogenizing bird communities in protected areas?.....	26
4	RESULTS AND DISCUSSION	27
4.1	Differences in habitat specialization between Western Palearctic and Nearctic birds	27
4.2	Does human land-use lead to biotic homogenisation of forest bird communities in northern USA?	28
4.3	Degradation in landscape matrix has diverse impacts on diversity in protected areas	29
4.4	Is degradation in matrix homogenizing bird communities in protected areas?	31

5	CONCLUSIONS.....	34
	<i>Acknowledgements</i>	37
	YHTEENVETO (RÉSUMÉ IN FINNISH).....	39
	REFERENCES.....	43

LIST OF ORIGINAL PUBLICATIONS

The thesis is based on the following original papers, which will be referred to in the text by their Roman numerals I-IV.

- I Häkkilä M., Pietilä K., Kotiaho J. & Mönkkönen M. 2018. Differences in habitat specialization between Western Palearctic and Nearctic birds. Manuscript.
- II Le Tortorec E., Häkkilä M., Zlonis E., Niemi G.J. & Mönkkönen M. 2018. Does human land-use lead to biotic homogenisation of forest bird communities in northern USA? Manuscript.
- III Häkkilä M., Le Tortorec E., Brotons L., Rajasärkkä A., Tornberg R. & Mönkkönen M. 2017. Degradation in landscape matrix has diverse impacts on diversity in protected areas. *PLoS ONE*12(9): e0184792. <https://doi.org/10.1371/journal.pone.0184792>
- IV Häkkilä M., Abrego N., Ovaskainen O. & Mönkkönen M. 2018. Habitat quality is more important than matrix quality for bird communities in protected areas. *Ecology and Evolution* 8(8): 4019-4030. DOI: 10.1002/ece3.3923

The table shows the contributions of the authors of the original papers

	I	II	III	IV
Planning	MH, JK, MM	MH, MM, ELT, GJN	MH, MM, ELT	MH, MM, O2
Data	MH, KP	MH, ELT, GJN, EZ	MH, LB, AR, RT	MH, O2
Analyses	MH	ELT	ELT, MH	O2
Writing	MH, MM	ELT	MH, ELT, LB, MM	MH, NA, MM, O2

MH = MATTI HÄKKILÄ, JK = JANNE KOTIAHO, MM = MIKKO MÖNKKÖNEN, KP = KAROLIINA PIETILÄ, ELT = ERIC LE TORTOREC, GJN = GERALD J. NIEMI, EZ = EDMUND ZLONIS, LB = LLOUIS BROTONS, AR = ARI RAJASÄRKKÄ, RT = RISTO TORNBERG, O2 = OTSO OVASKAINEN, NA = NEREA ABREGO

CONCEPTS AND ABBREVIATIONS

Biodiversity	Diversity of life: reflects the variability and variation within species (genetics), between species (e.g. species richness, taxonomic diversity, functional diversity and phylogenetic diversity) or between ecosystems and how these change from one place to another and over time.
Alpha diversity	Local diversity of attributes within a site, e.g. species diversity within a habitat patch.
Gamma diversity	Total diversity of a landscape or region across local sites.
Beta diversity	Ratio or difference between regional (gamma) and local (alpha) diversity. Measures differentiation in community structure among sites.
Taxonomic diversity	Measures species diversity taking into account abundances.
Functional diversity	Measures the diversity of functional traits (e.g. feeding habit, motility, morphology etc.) in a community or population.
Phylogenetic diversity	Measures phylogenetic distances among taxa in a community, which reflect evolutionary history.
Biotic homogenization	A process where biotic assemblages become more similar to each other as a result of human actions.
Habitat	A site where species-specific resources and conditions enable occupancy.
Matrix	Non-habitat areas surrounding habitat patches and corridors.
SSI	Species Specialization Index; measures how evenly a species utilizes different habitat types.
CSI	Community Specialization Index; measures average species habitat specialization in a community.

PREFACE

Finland is known as a land of forests. It surely is one, but actually after the last Ice Age, for more than ten thousand years ago, the whole boreal region has been largely covered by forests. Minnesota, in the heart of USA, is rather similar to Finland, what it comes to nature. Large wooded areas, small lakes and ponds, and peatlands are characteristic especially in Northern parts of the state. Boreal forest is not a stable habitat, but major disturbances, like forest fires and storms have created a dynamic landscape with large stands in various successional stages.

For thousands of years these vast forests offered food and cover for a large variety of wildlife, including our nomadic ancestors. Slowly but surely things were changing, especially in Finland. With the rise of farming and permanent residences forested areas were used for slash and burn cultivation, later on for permanent fields and meadows. Timber was needed for many more things than just firewood. Still, as population density was low, major parts of the forests were untouched by humans, or used only for hunting, and forest fauna was flourishing.

Bigger changes, at least when compared to natural state dynamics, started to happen few hundred years ago. In the age of colonialization, large European sailing ships were treated with tar, distilled from wood, to prevent rotting. As forests in central Europe had largely been cleared for agriculture by the 17th century but the need for tar was massive, vast boreal forests suddenly started to have monetary value. For the next two hundred years tar was the biggest export product in Finland and human induced disturbance in boreal forests reached new dimensions. For example, in 1863 270 000 barrels (á 125 litres) of tar were exported from Finland. Additionally, first large paper mills and larger sawmills were established in the late 19th century.

Finnish people now knew how to take the most out of forest and they did not hesitate to use their special knowledge. Finnish emigrants put by large part into practise the major logging in the USA and Southern Canada in 19th and early 20th century, when growing and industrializing nations needed building material and other natural resources. In a few decades majority of mostly natural forests were logged in the eastern part of the USA.

Next big change started after the Second World War, when a young Finnish nation, recovering from heavy losses, started to rise by using the most abundant resource, timber, to gain export income. Forest industry was developing and management practices were intensifying. By building forest roads even the most remote wilderness became accessible for loggers. Simultaneously, the young Minnesotan forests were left more or less unmanaged and only natural succession was forming the woodlands.

The shrinking and vanishing forests awoke concern and pulled ahead nature conservation, which had already raised its head in the late 19th century. National parks and forest reserves were established and public awareness of dwindling natural habitats was increasing. Along with the wellbeing, nature

conservation has now become, slowly but inevitably, serious and presentable subject, but the usage of forest is not showing signs of slowing down. On the contrary, in the 2010's the term "bioeconomy" came to light. It seems that the appealing word "bio" means in this context ever intensifying exploitation of timber. With shortening rotation times and usage of stumps and harvest residues, the boreal Finnish forest is facing another era of major change that is increasing the contrast between protected natural forests and heavily managed commercial forests. The first alarming signs have already been observed, as one fifth of forest birds in Finland, the land of forests, have been added to Finnish Red List. What kind of changes will the forest bird fauna face because of the intensifying use of forest products? Only time will tell, but hopefully this thesis will be able to help in its part in predicting the future of forest bird populations, in understanding how changes do happen and most of all, help to prevent the most dramatic negative consequences.

1 INTRODUCTION

1.1 Changing environment

Human-induced changes in the environment are affecting species distributions and abundances worldwide. Degradation and destruction of habitats (Travis 2003, Devictor *et al.* 2008) and urbanization (Devictor *et al.* 2007) are affecting the composition of species communities. Climate change, pollution and invasive species are decreasing biodiversity throughout the world (Sala 2000). Even the remaining fragments of native habitats are impacted as a consequence of hindered migration and isolated populations (Cardinale *et al.* 2006, 2011, Hooper *et al.* 2012).

The consequences of human actions can be observed in all scales and with various diversity metrics. Local and global trends of reduction in taxonomic diversity have been pointed out (Newbold *et al.* 2015), but human impact is also affecting functional diversity by reducing functional redundancy (Laliberté *et al.* 2010), and also phylogenetic loss has been observed (Santos *et al.* 2010). Nevertheless, species are not equal in the face of habitat change. Available evidence (Julliard *et al.* 2003, Devictor and Robert 2009, Clavel *et al.* 2011) suggests that specialist species are more often negatively affected by environmental change than generalists. As a consequence, generalists are replacing specialists in communities resulting not only species poor but also structurally more similar species assemblages.

1.2 Measuring Diversity

For general public biodiversity usually means species richness and despite the multi-faceted nature of biodiversity (Mace *et al.* 2012). Also conservation biologists and community ecologists have only recently considered aspects of diversity other than taxonomic diversity. Taxonomic diversity accounts for

species richness and abundances, and it is the most commonly quantified component of diversity. Functional diversity describes the habitat and resource use by organisms as well as the range of ecological roles that organisms perform in their assemblages (Tilman 1997). High levels of functional diversity have positive effect on ecosystem functions, and, for example, for the productivity of ecosystems, functional diversity is of high importance (Srivastava *et al.* 2012). Phylogenetic diversity reflects evolutionary history of the present taxa (Faith 1992) and high levels of phylogenetic diversity may enhance the resilience of communities to changing environmental conditions (Lavergne *et al.* 2010). Phylogenetic diversity has also been proposed as a way to acknowledge the role of species interactions in biotic assemblages and it is suggested as the most synthetic estimate of community trait space (Wiens *et al.* 2010). Therefore, together with functional diversity, phylogenetic diversity could help in predicting how species losses or gains will likely affect ecosystem functions. (Srivastava *et al.* 2012).

Taxonomic, functional and phylogenetic diversity are all measuring different aspects of biodiversity, and incongruences and spatial asynchrony between these measures have been pointed out (Devictor *et al.* 2010b, Monnet *et al.* 2014). For example, areas with high taxonomic diversity do not necessarily have high functional diversity which causes challenges especially for biodiversity conservation. Therefore, integrative studies with all aspects of biodiversity taken into account are needed.

Specialist species effectively utilize a narrow range of available resources (Kotiaho *et al.* 2005), and therefore communities containing many specialist species may be more efficient in transforming available resources into offspring than communities dominated by generalists (Devictor *et al.* 2010b). In contrast to generalists, specialists often have characteristic functional traits and thus losing them may result in decreasing functional diversity, which is an aspect of biotic homogenization (Clavel *et al.* 2011).

Biodiversity in a landscape, gamma diversity, is determined by alpha diversity, or mean diversity of local sites or habitats, and beta diversity that describes turnover or differentiation of species among those sites or habitats. Even though the above mentioned aspects of biodiversity are considered, measuring mere alpha diversity of individual communities or protected areas does not necessary capture changes in landscape level. Beta diversity accounts for the relationship between alpha and gamma diversity, and informs about differentiation (or similarity) among communities. On the other hand, changes in alpha diversity are not necessarily reflected in beta diversity (Smart *et al.* 2006, Socolar *et al.* 2016). Indeed, human-induced changes in alpha diversity of communities may result in higher or lower beta diversity in a landscape or it may remain the same. Therefore, in biodiversity conservation, maximum level of beta diversity is not necessarily a goal (Socolar *et al.* 2016), and thus, when studying biodiversity or biodiversity conservation, all scales of diversity should be taken into account.

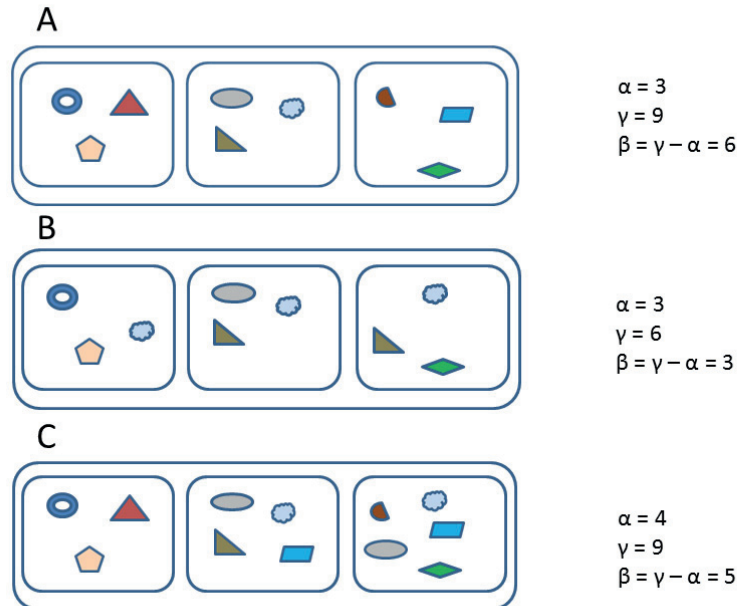


FIGURE 1 Example of different scales of diversity (different forms represent different species). In A there are three species in each community, so mean alpha diversity is 3. All species are different, so gamma diversity is 9. Additive beta-diversity (like in II) is calculated as gamma minus mean alpha, which equals 6. In B homogenization has occurred: there are still three species in each community, but some of the species are the same. Therefore gamma and beta diversities are smaller even though mean alpha is still 3. In C all species present in A are still there and, thus, gamma diversity is 9, but some species have entered into communities and mean alpha diversity is now 4, and therefore beta-diversity is lower than in A.

1.3 Biotic homogenization

Human activities cause not only extinctions but also invasions of new species as well as changes in the relative abundance of the extant species (Baiser *et al.* 2012). Cosmopolitan species are expanding their range while native endemics are losing ground in numbers and space (McKinney and Lockwood 1999). Specialist species with narrow niches are decreasing at the expense of generalists with wider dietary and habitat preferences (Clavel *et al.* 2011). Generalists are often described as species with global ranges but actually they often are native species (La Sorte and Boecklen 2005). This multifaceted human-induced process leading to decreasing beta diversity and increasingly similar

communities is known as biotic homogenization (McKinney and Lockwood 1999, Olden 2006).

Biotic homogenization does not only encompass the loss of taxonomic diversity, but also its functional component (Olden *et al.* 2004). Specialists, by definition, have specialized functions and their loss decreases functional diversity in a community. When communities become functionally more similar, it is eventually affecting ecosystem functioning (Hooper *et al.* 2005). Functional diversity is an important component of ecosystem functioning, the basis of the ecosystem services that humans depend on and, thus, of special concern for human well-being (Cardinale *et al.* 2012). It has already been shown that ongoing biodiversity loss is causing an ecosystem services debt (Isbell *et al.* 2015, Elo *et al.* 2017), which may have a negative impact on the resilience of ecosystem functions, or the ability to recover functionally after a disturbance (Oliver *et al.* 2015). Therefore, when assessing ecosystem level impacts of homogenization, it is important to take into account the functional traits of species in a community (McKinney 1997). Unlike species identities, functional traits can also inform about species' ability to adapt on particular environmental attributes (Cadotte *et al.* 2011) which increases information when analyzing community composition. Additionally, specialists have unique phylogenetic histories, and, thus, the loss of specialist species also decreases the phylogenetic diversity of communities.

1.4 Boreal forest

Boreal forest is a vast vegetation zone covering 1.890 billion hectares throughout the northern latitudes in Palearctic and Nearctic regions (Brandt *et al.* 2013). Vegetation of the boreal zone is characterized by forests with cold-tolerant tree species, but also lakes, rivers, wetlands, and in drier areas some grasslands (Brandt 2009). Even though there are similarities in avifauna and taxonomic composition of boreal forest communities between Palearctic (Europe and Asia) and Nearctic (North America) and also forest composition and disturbance dynamics are very much alike (Imbeau *et al.* 2001), there are also clear differences between these two regions.

Major disturbances modify species assemblages, and for example the ice ages in Pleistocene had drastic impacts on forests of Western Palearctic region while rest of the Northern hemisphere suffered less on glaciation (Mönkkönen and Welsh 1994). When forests were fragmented and in major parts completely lost both in breeding grounds in Eurasia as well as wintering areas in Africa, habitat generalists with good colonization abilities survived best. In Nearctic region forests remained more continuous and contact with tropical forests remained uninterrupted (Roberge *et al.* 2018), which made habitat specialism as well as migration more feasible strategy.

In addition to evolutionary history, human-induced environmental changes differ in Nearctic and Western Palearctic. While large areas of boreal

forest in North America and Russia remain unmanaged (Potapov *et al.* 2008), particularly in Fennoscandia, timber production is intense (Burton *et al.* 2010). In Finland, for instance, 91% of forests are in wood production (Kortesmaa and Jokela 2017) and the impact of habitat degradation can already be seen in declining forest bird populations (Valkama *et al.* 2011, Tiainen *et al.* 2016). By contrast, on the southern border of boreal zone, in the western Great Lakes region of North America, the natural forests experienced heavy logging 100-150 years ago, but ever since forest management has been far less intense than in Fennoscandia even though there is some commercial forestry (Schulte *et al.* 2007). Unlike Finland, most forest bird populations in the Great Lakes regions are either stable or even increasing (Niemi *et al.* 2016). Therefore, differences in community assemblages can be expected between Western Palearctic and Nearctic, and the differences should be clearest on forest specialist species.

1.5 Protected areas

The main strategy to slow and reduce the decline of biodiversity is saving small areas of land from human usage i.e. establishing protected areas. However, a growing number of scientific studies of the effectiveness of protected area networks in maintaining biodiversity is showing that the networks are not representative enough (Rodrigues *et al.* 2004, D'Amen *et al.* 2013) and biodiversity decline is continuing. There are also both theoretical (Moilanen and Hanski 1998, Lovejoy 2006) and empirical studies (Newmark 1996, Ricketts 2001, Carroll *et al.* 2004) showing that protected areas are not independent from their surroundings. Size (MacArthur and Wilson 1967) and connectivity (Hanski 1999) are important for biodiversity conservation, but in Europe most protected areas are relatively small and isolated which means that they are not able to maintain viable population sizes of species (Traill *et al.* 2007). Even though the quality and quantity of the matrix surrounding isolated areas impacts the rate of species loss (Sisk *et al.*, 1997; Prugh *et al.*, 2008), little is known about matrix effects on protected forest areas.

Matrix around protected areas is often characterized by intensive human actions and alterations. For example, protected old-growth forests are often surrounded by clear felled areas or young forests (Naughton-Treves *et al.* 2005, Mönkkönen *et al.* 2014). In boreal zone, protected forests situated in a matrix of young regeneration foster less species-rich communities but higher total bird density than those embedded in old-growth forest dominated landscapes (Mönkkönen *et al.* 2014) supporting the idea that matrix may provide additional resources even for patch-dependent species (Driscoll *et al.* 2013) even though all species are not able to utilize matrix resources. However, it has remained less studied how the matrix impacts the capacity of protected areas in maintaining functional and phylogenetic diversity or community specialization. And further, it is not well known what kinds of characteristics of protected areas promote specialized species or their functions, even though it has been

proposed that for the persistence of populations (Fahrig 2001) and the integrity of communities larger areas (Mönkkönen *et al.* 2014, Kotiaho and Mönkkönen 2017) are needed.

1.6 Aim of the thesis

Conservation ecology is a flourishing branch of science trying to inform conservationists how to slow down the 6th mass extinction wave. There is increasing amount of scientific literature about human-induced habitat change and its impacts on biodiversity. However, the number of studies how protected areas are able to maintain diversity and prevent homogenization has remained low, especially in boreal forest habitat. This information is important when the usage of forest products and logging are rapidly increasing in the era of bioeconomy.

In this thesis I study how human land use is affecting one group of living creatures, forest birds and their communities, in one part of the world, the boreal zone. I study if there are differences in species habitat specialization between two biogeographical regions in boreal zone. If no major differences can be found, the results of the studies put into practice in different regions can be generalized. However, if differences in specialization are clear, that may provide interesting results of the impacts of logging on specialist species and, thus, biotic homogenization, since there are differences in logging intensity and history between the two regions. I also study if the increasing human induced land use change causes forest bird communities to become more similar to each other, or in other words causes homogenization. Attention is paid on protected forests in northern Finland and their ability to maintain bird community composition under varying intensity of logging in the surrounding areas. I also study if the responses of functional and phylogenetic diversity and community habitat specialization on environmental change are different from the response of most commonly used taxonomic diversity. I also address if human activities have caused biotic homogenization i.e. losses in beta-diversity, in boreal forest bird communities which tells clearly how protected area network is working.

Hopefully this thesis will, in its part, provide important new knowledge that will help to understand the mechanisms of species population change and biotic homogenization and eventually slow down the decreasing trend of biodiversity.

2 STUDY QUESTIONS AND HYPOTHESES

This thesis is comprised of four individual studies providing insights to different diversity aspects in boreal forests. All studies are performed using bird data collected with standardized survey methods, and the background and part of the methods are shared with all studies. However, individual papers view diversity and human impact on natural communities from different angles and provide comprehensive outlook on human impacts on biodiversity and discuss the possible consequences of habitat degradation on boreal forest bird communities.

The first study focuses on habitat specialization, an important trait when studying biotic homogenization, and possible reasons why there are differences in specialization level of communities between two biogeographical zones, Western Palearctic and Nearctic, both within boreal ecosystem. Measuring specialization is also discussed and an improved method is suggested and developed. The main question is:

1. Are there differences in habitat specialization between biogeographical regions (I)?

Because the tree species diversity and environmental heterogeneity originating from deep history of forest biomes is higher in Nearctic region, the overall specialization rate will be higher than in Palearctic region. This difference is expected especially in forest species, whereas in non-forest species the expectation is not as clear.

Studying specialization and especially the impact of biogeographical history and characteristics helps to understand and solve challenges faced by conservation biologists all around the world. The degree of species habitat specialization (measured with Species Specialization Index, SSI) is a consequence of the evolutionary history and may be different in regions with different land-use histories and, thus, environmental characteristics. Differences in specialization may have an impact on the sensitivity of species communities on disturbance and habitat degradation. Indeed, habitat filtering in human

altered landscapes may induce changes in community composition (measured with Community Specialization Index, CSI), and that needs to be taken into account in conservation planning.

Chapters II, III and IV are empirical studies focusing on the responses of bird communities on human induced land-use changes. In all studies, I use several measures of diversity. Table 1 in the end of Results chapter summarizes the methods used in these studies.

In the second study the aim is to reveal if human impact in general homogenizes bird communities. Biotic homogenization is a worldwide phenomenon where scarce and specialized species are supposedly declining and abundant generalist species populations are increasing and expanding their ranges which results ever more similar communities. The precise mechanisms causing biotic homogenisation are still unclear, and while taxonomic homogenization has been studied a fair bit, phylogenetic and functional homogenisation have received less attention. In this study, the main questions are:

2. Does increased human impact and forest loss lead to decreased beta diversity (II)?
3. Do taxonomic, functional and phylogenetic diversity show similar responses to human impact intensity (II)?

Degradation and destruction of habitats are affecting species diversity (Travis 2003). However, changes in alpha diversity are not always reflected by changes in beta diversity (Smart *et al.* 2006, Socolar *et al.* 2016). Nevertheless, the hypothesis is that increased human footprint and forest loss will lead to decreased beta diversity.

Protected areas are currently the primary strategy to protect species and their diversity, but protected areas are not independent from their surroundings. The matrix surrounding protected areas can impact habitat quality (Sisk *et al.* 1997), dispersal ability of species and population persistence (Ricketts 2001). Habitat quality in the matrix can affect movement and dispersal of individuals and, thus, the colonization-extinction dynamics (Moilanen and Hanski 1998) and individuals may also use alternative resources available in the matrix (Dunning *et al.* 1992). The third study brings in different aspects of alpha diversity and their response to habitat structures in protected areas and to human land use in the surrounding matrix.

4. How the characteristic of protected areas and the surrounding matrix impact the community composition of forest birds within the protected areas (III)?

Because human land-use intensification tends to have negative effects on diversity (Flynn *et al.* 2009) the hypothesis is that forest bird communities will be negatively affected by intensive logging in the matrix. Large areas have

lower edge-to-area ratio, so they should be better buffered against matrix effects, whereas in small areas matrix effects will be relatively greater. As area, productivity and habitat diversity all have positive effects on species richness (Honkanen *et al.* 2010, Kahilainen *et al.* 2014), taxonomic diversity is expected to be the highest in large protected areas with high productivity and habitat heterogeneity. There are little studies about matrix effects on functional or phylogenetic diversity in protected areas and the relationship between area or productivity and functional and phylogenetic diversities or community specialization have remained less studied. Therefore, other diversity metrics are expected to show similar responses to taxonomic diversity.

In the fourth chapter I still focus on the bird communities of protected areas but the viewpoint to biodiversity is changing again to matrix quality effects on taxonomic composition, functional trait composition and beta diversity. In other words, I focus on differentiation in bird community structures among protected areas. In the study, the aim is to determine whether the bird communities from the Finnish protected area network are being subject of biotic homogenization due to the lowered quality of the matrix. To achieve this I ask:

5. Does matrix quality have impact on the taxonomical community composition of birds in the protected area network (IV)?
6. Does matrix quality have impact on functional trait composition of birds in the protected area network (IV)?
7. Does matrix quality have impact on community similarity (beta-diversity) of birds within protected areas differing in size and habitat quality (IV)?

The first hypothesis is that because of biotic homogenization processes, protected areas embedded in matrices with higher disturbance will have lower beta-diversity than the protected areas embedded in matrix with lower disturbance. The effect should be strongest in protected areas where differences in habitat composition between the protected areas and the surrounding matrix are the greatest. Further hypothesis is that large protected areas are better in maintaining their integrity whereas matrix effects are relatively greater on small protected areas. If so, conservation efforts should be focused on large undisturbed areas, and in case of small areas, on managing the surrounding matrix to minimize contrast to the protected areas in landscape structure. Using traits in the analyses makes it possible to reveal the mechanisms of biotic homogenization by studying which characteristics are particularly sensitive to environmental change. Changes in species morphological traits describing their behaviors (functions) are expected with changes in habitat quality in the protected areas and in the surrounding matrix.

3 MATERIAL AND METHODS

3.1 Bird data

3.1.1 Finland

The Finnish bird data (III, IV) were collected from protected forests in Northern Finland by Metsähallitus, Parks & Wildlife Finland during years 1988 - 1999 using Finnish line transect count method (Järvinen and Väisänen 1976). As a one-visit census the line transect count method is suitable for counting birds over large areas (Järvinen and Väisänen 1981). The survey unit is breeding pairs which are counted on average 5-6 km transects early in the breeding season.

Because I was especially interested in the impacts of forest management on bird communities, the species pool was restricted only to species that use forest as their primary breeding habitat (Väisänen *et al.* 1998). Of these, Crossbill species (*Loxia* spp.) were excluded since their breeding season is mostly over during the counts and outside breeding season all crossbills are highly irruptive.

As a second data set of Finnish birds, Finnish national level data originating from the common bird monitoring project (CBMP) point counts conducted between 1984 and 2015 (Laaksonen and Lehtikoinen 2013) was used. In this method, each point count station is located in a uniform habitat within 50 m of the station and habitat type is categorized into 17 classes. Habitat type is defined by the person conducting the survey. These data, independent from the line transect census data, were used to calculate Species Specialization Index (Julliard *et al.* 2006) for studies (I), (III) and (IV).

3.1.2 Minnesota

Minnesota Breeding Bird Atlas (MNBBA), which was conducted 2009-2014 in the state of Minnesota, was used as a third bird data set. The method used in

MNBBA is similar to Finnish point counts, but in Minnesota the approach is more systematic and covers the whole state of Minnesota, USA. In MNBBA there are 25 habitat classes. For all these data only observations made inside 50m radius from the point were used.

The state of Minnesota is split into 2775 6 by 6 mile squares, called townships. Each township is divided into four sub-quarters of which the north-eastern corner was randomly selected to be used in the censuses. Three 10 minute point counts were conducted in each of the 3 by 3 mile squares. In the study design points were selected in a way that one point was in the most common habitat of that township, second in second most common and third was randomly selected. The habitat was determined by the habitat of 50 m radius surrounding the point, where over 50% must be of uniform habitat. All the counts in Minnesota were roadside counts, so each point was moved to nearest public road.

3.2 Landscape data

Land use and cover data from the 8th National Forest Inventory of Finland, collected 1986-1994 (Tomppo 1993) was used to characterize landscape around Finnish protected areas (III, IV). In these data forests were classified by timber volume and dominant tree species into nine cover types (see Brotons et al. 2003). Variables describing the habitat composition within the protected areas and in the surrounding landscape were calculated from this classification. The sum of spruce-deciduous habitat types was used to describe productivity because in the study area, spruce-deciduous forests only grow on fertile soil whereas less fertile soils are usually pine-dominated. In northern Finnish conditions forests with more than 100m³/ha timber can be considered mature (Mönkkönen *et al.* 1997) so the sum of the three cover types with more than 100m³/ha was used to describe the proportion of old-growth forest even though forest age was not directly measured. Habitat diversity within protected areas was estimated using Shannon's diversity index from the proportions of the nine cover types in each area.

The landscape around the protected areas was characterized from a 5 km buffer around the outer border of each area. I selected this radius to make sure that the matrix effects could also be studied with larger birds with large home ranges, e.g. Golden Eagle (*Aquila chrysaetos*) and larger buffers would have overlapped.

In study (II) combined data from different databases to characterize landscape around each of the points in Minnesota Breeding Bird Atlas point counts was used. Detailed information about habitat types was obtained from Landfire program, precipitation and mean temperature from the database of PRISM Climate group, human population data from US population census and Ecological provinces, sections and subsections and conservation status of forest stands from the database of Minnesota Department of Natural Resources.

3.3 Diversity measures

3.3.1 Species Specialization Index

Species specialization index; SSI (Julliard *et al.* 2006) was used in studies (I), (III) and (IV) as a tool to study community structure. SSI is relatively simple but sensitive tool for studying community level homogenization. SSI is the coefficient of variation (standard deviation/average) of species densities among habitat classes. The more specialized the species are in their habitat, the larger the SSI value will they have. For calculation of SSI we used independent Finnish national level data originating from the common bird monitoring project (CBMP) point count censuses described in 2.1.1. For each habitat class I derived average density for the 69 forest species, and then calculated sample size bias corrected species specialization index, SSIC (Julliard *et al.* 2006). Finally, a weighted average SSIC of species present in a given site, i.e. the community specialization index, CSI (Devictor *et al.* 2010a) was calculated.

However, SSI does not take into account the potential variation in densities of each species among sampling units within habitat classes, but it assumes even distribution of individuals among all sampling units within the habitat class. That means that if the habitat categorization does not capture the finer level environmental variation potentially associated with densities of each species, SSI may underestimate the species specialization level. Therefore, an improved method for calculating SSI taking into account the variance within habitat categories is developed in paper I. Improved method is based on first calculating sample size bias corrected SSI (Devictor *et al.* 2008), which is then further corrected by multiplying it by a coefficient of within habitat class variation (see I for further details).

3.3.2 Rao's quadratic entropy and taxonomic diversity

In the (III) study species richness or number of species in each protected area was first calculated. Further, taxonomic, functional and phylogenetic α -diversities based on Rao's quadratic entropy (Rao 1982) using R functions developed by De Bello *et al.* (De Bello *et al.* 2010) were calculated for each of the protected areas, as well as the Community Specialization Index (Julliard *et al.* 2006). In Rao's quadratic entropy the α -diversity of each community is representing the expected dissimilarity between two random individuals, thus it is taking the relative abundance of each species into account. When calculating taxonomic diversity, the dissimilarity has a value of 1 if two individuals represent two different species and otherwise 0. Thus, a community with one abundant species and nine uncommon species will get lower values than community with 10 equally abundant species. Thus, for species level taxonomic diversity, α -Rao equals the Simpson diversity index (Pavoine *et al.* 2004, Ricotta 2005). For functional and phylogenetic diversity measures

dissimilarity takes into account functional or phylogenetic distances among species (Pavoine *et al.* 2004, De Bello *et al.* 2010) and unlike in taxonomic diversity, the dissimilarity values between individuals varies continuously between 0 (the two individuals are functionally totally dissimilar/belong to very distantly related species) and 1 (functionally identical/same species).

3.3.3 Functional diversity from traits

Functional diversity is often measured by using ecological traits (Petchey and Gaston 2002) and for functional diversity of forest birds in Minnesota (II) numerical data from the dataset (Belmaker and Jetz 2015) including diet composition, foraging stratum, activity time and body size was used for the calculation. Functional distances for species found in the study data were calculated using the daisy function in the R package cluster with Euclidean distances. Functional distances were then scaled between 0 and 1 to be used as a distance matrix in the calculation of diversity metrics.

In study (III) a method based merely on morphological traits was used. The functionality of a species refers to the way it uses the habitat for foraging, nesting, avoiding predators, etc. This is reflected in the morphology of a species (Miles and Ricklefs 1984). Morphological traits (wing, tail, tarsus and bill length, bill width and bill height) were measured from at least five individuals per species from museum samples in the Museum of Natural History in Helsinki, Finland and the Museum of Natural history in Oulu, Finland. As all of these measures mainly reflect the size of the bird, the original morphological variables were transformed into indices linking morphology with ecological functions of the species. First, body mass was used as an indicator of overall body size, which is an important driver of both habitat use and diet, and two species with different body size but equal shape tend use food items of different size and different habitats. Second, to describe functions related to the type of food used we used a ratio bill length/(bill width + bill height). Species with long bills relative to bill width and height tend to be more insectivorous than short-billed species (Lederer 1975). Third, we calculated three further ratios (wing length/ $\sqrt[3]{\text{body mass}}$, tarsus length/ $\sqrt[3]{\text{body mass}}$) and tail length/ $\sqrt[3]{\text{body mass}}$) to represent differences in locomotion and habitat use. The lengths were divided by the cubic root of body mass to scale these one-dimensional variables by a one-dimensional measure of body size (body mass is volume related). These five uncorrelated morphological variables were then used to calculate pairwise Euclidean distances in a morphological hyperspace among individuals in a community. This distance, scaled between 0 and 1, was then used as a measure of morphological dissimilarity when calculating functional diversity.

3.3.4 Phylogenetic diversity

To study phylogenetic diversity of forest birds a set of 1000 randomly chosen phylogenetic trees of the study species was downloaded from the database

birdtree.org that contains a phylogenetic tree of 9993 bird species (Jetz *et al.* 2012, 2014). Of the 1000 trees a single, unrooted, 50% majority rule (extended) consensus tree was constructed using the Consense function (phylip package v.3.695). In the extended majority rule, any set of species that appears in more than 50% of the trees is included. We used the distance between the two end nodes (i.e. species) in the consensus tree, scaled between 0 and 1, as a measure of phylogenetic dissimilarity in calculating phylogenetic diversity (II, III).

3.4 Beta diversity

Variation in biodiversity in space is measured with beta diversity. Unlike alpha and gamma diversities, beta diversity cannot be measured directly but it is derived from the gamma and alpha diversities. It is describing how much regional (gamma) diversity exceeds the mean alpha diversity of sites within the region. If all local sites would be similar, then gamma diversity would equal alpha, but as there are usually changes in species composition, beta diversity is actually describing the degree of species composition change between sites (Baselga 2010). The changes in species composition may stem from two phenomena. First concept, spatial turnover, means replacement of species by other species. The other is nestedness, which describes a pattern where the most species-poor site is a subset of the richest site. So the site with most species has unique species that are not present in the poorest site, but there is no species replacement (Baselga 2010).

Beta diversity can be measured using many different protocols (Anderson *et al.* 2011). In (II) beta diversity was calculated as in its additive form: gamma diversity minus the mean alpha diversity of a region, reflecting how many local sites there would be if none of the sites shared common species. In (IV) the approach to study community similarities with increasing human impact was carried out by focusing on the amount of variation of bird communities within different scenarios after which the amount of variation among the scenarios was compared (see paper IV for details of this rather complicated approach).

Higher variation between communities or beta diversity in a given region indicates that the composition of local sites is more different from each other compared to a region with lower beta diversity. Thus, even though locally there are no changes in diversity, the total diversity of a region could show decrease if the individual sites became more similar (Fig. 1). However, maximising beta diversity is not necessarily the goal in biodiversity conservation (Socolar *et al.* 2016) because local extinctions may reduce alpha diversity which increases differences between communities leading to higher beta diversity. Colonization of new species into communities, on the other hand, may increase the similarity and, thus, decrease beta diversity.

3.5 Statistical analyses

3.5.1 Differences in habitat specialization between Western Palearctic and Nearctic birds

In the first study (I), differences in species habitat specialization were compared between two geographical areas: Minnesota, USA and Finland. In the analysis, I used General Linear Model to analyse differences in SSI and CSI of both forest and non-forest birds. I also analysed if there are differences in specialization between different migration strategies. The analyses were completed using IBM SPSS Statistics 24 program.

3.5.2 Does human land-use lead to biotic homogenisation of forest bird communities in northern USA?

Linear models were used to study the effects of human land use on taxonomic beta diversity of forest bird communities. Human footprint (based on population density, land transformation, accessibility, and electrical power infrastructure), forest loss, habitat diversity, net primary production and mean temperature were used as explanatory variables describing human impact. The explanatory variables were chosen so that the variance inflation factors (VIF) were under 3 (Zuur *et al.* 2007). All analyses were performed with R version 3.4.0.

Functional beta diversity was analysed using generalized linear model because the residuals of the model explaining functional beta diversity were not normally distributed. The explanatory variables were the same as in taxonomic beta diversity.

In phylogenetic diversity there was special autocorrelation in the residuals and for that reason spatial regression error models were used in the analyses. Since a GLM with spatial regression cannot be constructed the independent variable was natural log-transformed to get normally distributed residuals.

3.5.3 Degradation in landscape matrix has diverse impacts on diversity in protected areas

Linear models with the R (version 3.4.0) were constructed to analyse the impacts of the characteristics of the protected areas and their surrounding landscape matrix on each diversity metric of the bird communities in the protected areas. The analyses was implemented using a two- step modelling approach, where the most important variables inside the protected areas were first selected, after which these variables were forced in the model and the most important variables in the surrounding matrix were then selected. N-coordinate was included as a covariate in all models to control for well-known decline in diversity with increasing latitude. Because variables describing the composition

of matrix were entered into the models after within-area variables, they describe the additional effects of the surrounding matrix.

Following Richards et al. (2011) Akaike Information Criteria with small sample size correction (AICc) was used to select the variables to retain at each step. In cases of two or more alternative models we used model averaging to create one best model (Burnham and Anderson 2002). All variables were entered as fixed effects.

3.5.4 Is degradation in matrix homogenizing bird communities in protected areas?

This study was completed using the same data as (III). To get comparable sampling units, the counts of every species were randomly assorted within transects by dividing transects in 1 km sub-transect segments. The data was then transformed to presence-absence data within segments. For this data, a joint species distribution model was fitted with the HMSC Matlab-package (Ovaskainen *et al.* 2017). Explanatory variables included in the model were log-transformed area of the protected areas, the proportion of more productive forest types within areas describing productivity, the proportion of old-growth forests and proportion of shrubs in the matrix describing clear-cuts.

To study how patch area and patch and matrix quality affect species density and community composition scenario simulations were used. For that purpose, eight hypothetical scenarios of protected areas varying systematically in size and habitat quality as well as matrix quality and the occurrence probabilities of species/transect segment were predicted. The predicted community composition within large area with high quality habitat and high quality matrix was considered as a baseline scenario.

To assess the influence of the quality of the protected area on the community composition, the posterior probabilities that 1) the community in a high quality area is more similar to the natural reference community than a community in low quality area separately for the four cases corresponding to a small vs. large protected area, and low vs. high quality matrix were computed. For 2) the size of the protected area the occurrence probabilities were calculated similarly: community in large area is more similar to the reference community than in small area (four cases corresponding to a low vs. high quality protected area and low vs. high quality matrix). Finally, 3) to assess impacts of matrix quality, the occurrence probabilities were calculated for the following cases: the community in a protected area surrounded by high quality matrix is more similar to the reference community than a community surrounded by low quality matrix (separately for the four cases corresponding small vs. large protected area, and low vs. high quality protected area).

4 RESULTS AND DISCUSSION

4.1 Differences in habitat specialization between Western Palearctic and Nearctic birds

I found that traditional SSI tended to underestimate the true level of specialization and this underestimation was bigger in more specialized species (I). Thus, species that are unevenly distributed among habitat classes also tended to be unevenly distributed among sampling units within a habitat class. This suggests that traditional SSI-index may be a severe underestimation of specialization level, because birds respond to fine level habitat variation that is not captured with habitat classification. Therefore within-habitat variation should be taken into account when estimating species habitat specialization.

Counter to my hypothesis, forest birds in Finland were more specialized than non-forest birds whereas in Minnesota the pattern was the opposite (I). I hypothesize that reduced historical habitat availability and large scale fragmentation of remaining habitats are associated with high level of habitat specialization. During Pleistocene glaciation forests were highly fragmented in Palearctic, whereas in Nearctic Ice Age conditions favoured forests, but natural grasslands were fragmented.

I found no significant differences between in habitat specialization between resident, short-distance and long-distance migrants, thus the results provide no support for the hypothesis of resident species being more specialized.

In both regions CSI values were lower than SSI values in birds in general, and in all ecological groups suggesting that generalists are dominating the regional bird assemblages. In Finland CSI value of forest birds was clearly lower than relatively high average SSI, whereas in Minnesota the differences between CSI and SSI were moderate. This suggests that forest bird assemblages in Finland are a non-random sample of the regional avifauna. I hypothesize that habitat filtering (Keddy 1992) in intensively managed landscape is favoring generalists and forest specialists are declining.

4.2 Does human land-use lead to biotic homogenisation of forest bird communities in northern USA?

Taxonomic beta diversity was not impacted by human impact (II) nor by net primary production or mean temperature. Habitat diversity was the only variable clearly influencing taxonomic beta diversity having a strong positive impact. Habitat diversity had a positive impact also on gamma diversity, but alpha diversity showed no significant response. This is a sign of species turnover; species entering the region are replacing some species originally present.

In contrast to taxonomic beta diversity, functional beta diversity was impacted by human influence (II). Human footprint had a strong positive impact on functional beta diversity (heterogenization), even when natural variation caused by mean annual temperature, net primary production and habitat diversity were taken into account. Interestingly, forest change did not appear to influence functional beta diversity. Both net primary production and mean annual temperature had a negative impact on functional beta diversity.

Phylogenetic beta diversity showed no response to human footprint index, or forest change, even though there was negative but non-significant impact on phylogenetic gamma diversity and no association with alpha diversity. There was a negative association of forest change with both phylogenetic alpha and gamma diversities but no impact on beta diversity. Like with functional beta diversity, net primary productivity and mean annual temperature both had a negative impact on phylogenetic beta diversity.

The results appear to be contradictory to many previous studies that have shown increasing human actions such as urbanization (McKinney 2006, Sol *et al.* 2017), agricultural intensification (Gordon *et al.* 2009, Rodrigues *et al.* 2013) and forest management to induce biotic homogenization, i.e. loss of beta-diversity (Mori *et al.* 2015, Ibarra and Martin 2015). However, there are also studies where human pressure has not induced homogenization (Lee-Cruz *et al.* 2013) and in some cases even an increase in beta diversity has been observed (Catterall *et al.* 2010).

Increasing functional diversity with increasing human impact was surprising and, compared to many previous studies, contradictory (McKinney 2006). One explanation for this could be that with increasing human activity environmental heterogeneity in the region was increasing and these novel habitats were occupied by new species, which would result in increased between-site diversity. Another, very potential explanation lies in the fundamental characteristics of beta diversity. In this study, beta diversity was calculated as regional (gamma) diversity minus mean local diversity of individual sites (alpha). Therefore increasing beta diversity may stem from

increase in gamma diversity or decrease in alpha diversity. In the results no statistically significant impact of human footprint on neither alpha nor gamma diversity could not be found, but the negative estimate for alpha diversity was clearly stronger than for gamma, which could have caused the positive impact on beta diversity.

Another potential reason for the positive impact of human impact on functional diversity can be subtractive heterogenization (Socolar *et al.* 2016). In this conceptual trajectory, beta diversity is first increasing by declines of native species, in addition with increasing invasive species (additive heterogenization), but with higher disturbance levels rare species are disappearing and invasive species start dominating and, thus, beta diversity is decreasing. In this study of forest bird communities only relatively forested units were used and human impact in these units was lower compared to the units that were left out of the analyses. Therefore, it is possible that the relatively low human impact in the study increased differences between sites.

Interestingly and in contrast with previous studies (Kitching *et al.* 2013, Ibarra and Martin 2015), in my study forest change (% loss in mature forest cover) did not have homogenizing impact on any of the studied responses. This may be because forest change measures the change in the age structure of the forest due to harvesting or forest fires and not permanent disappearance of habitat. For some species this means lowered quality of habitat, but as boreal forest is dynamic, most species are adapted to disturbances. However, forest change had negative impact on functional and phylogenetic alpha and gamma diversities even though taxonomic diversity showed no response. This suggests that intensifying forest use may lead to decreased functions and lower evolutionary adaptation potential, which may have impacts also for human e.g. in the form of degraded ecosystem services.

4.3 Degradation in landscape matrix has diverse impacts on diversity in protected areas

In protected areas, characteristics of the areas (total forest area, habitat diversity and productivity) all had positive impact on species richness (III). Also matrix quality affected species richness, and surprisingly both good quality (high proportion of old-growth forest) and low quality (high proportion of shrub) had positive impact on species richness. However, the effect of shrub seems to weaken with increasing reserve area and where the effect was clearly positive in small areas, in large areas there was no effect. Based on the positive interaction with area, the impact of old-growth forest in the matrix increased with increasing total area, but plotting this matrix effect separately for small and large areas suggested that species richness increased with matrix quality more strongly in small protected areas than in large ones where there was no effect.

Productivity and habitat diversity inside the protected areas had positive impact on taxonomic alpha diversity (III), but no matrix effects on taxonomic diversity were found. Similarly, phylogenetic diversity was positively impacted by productivity and habitat diversity, but matrix effects were not found. This pattern is supporting earlier studies (Honkanen *et al.* 2010) and the hypothesis of the positive impact of habitat diversity (heterogeneity) and productivity on species diversity. Even though large forest areas hosted more species, they did not have increased taxonomic nor phylogenetic diversities. This suggests that the additional bird species that occupy large protected areas are low in abundance and not phylogenetically distinct.

On functional diversity, in contrast with taxonomic and phylogenetic diversities, productivity inside protected areas showed a strong negative influence (III). Similarly to productivity, habitat diversity had negative impact on functional diversity. These results could be explained by species interactions and by the properties of Rao's quadratic entropy. Both species abundance-based diversity and functional differences among species are influencing functional diversity (Zoltan 2005, Petchey and Gaston 2006). If one species from a group or community of functionally similar species becomes lower in abundance or goes extinct, functional diversity increases with increasing average functional dissimilarity. The introduction of new functionally similar species will increase species abundance-based diversity, but it will decrease the average functional dissimilarity among species, but if colonizing species is functionally distinct the average functional dissimilarity will increase.

Of the matrix characteristics, high percentage of old-growth forest had a negative impact on functional diversity, but the negative impact of high percentage of shrub was strong only on small areas. This suggests that functional diversity is decreasing with increasing shrub in the matrix on small protected areas, but is increasing with increasing proportion of old-growth forest independent of the size of the area. Thus, large protected areas seem to be better buffered against matrix effects because the impacts of shrub decrease with increasing total forest area. Again, explanation can be found in the diversity index: functional diversity is decreasing with increasing functional similarity among species. Protected areas with higher levels of old-growth forest in the matrix had high species richness of functionally reminiscent species (III). However, also an increased proportion of shrub in the matrix had a positive association with species richness in smaller protected areas. Increasing species richness with increasing shrub (indicating recent logging intensity) in small protected areas thus reduces the average functional distance of species and resulting in decreased functional diversity. The reason for this may be spill-over of generalist species from the matrix. In conclusion, logging in the matrix will result in a loss of ecological functions and lead to biotic homogenization particularly in small protected areas.

Finally, productivity and habitat diversity, as well as high percentage of old-growth forest in the matrix all had positive impact on community specialization (III). Thus, bird communities in areas of high productivity and habitat diversity are more specialized, in particular when there is high

proportion of old-growth forest in the surrounding areas. The positive effect of habitat diversity inside protected areas on community specialization index may first sound counterintuitive because uniform habitats allow larger population sizes which should benefit specialist species by decreasing the likelihood of stochastic extinctions. The effect of habitat diversity on specialists' habitat availability is likely scale-dependent (Allouche *et al.* 2012). At small spatial scales, specialist species should be negatively impacted by habitat diversity because the amount of area available for individual species in a given area decreases with increasing habitat heterogeneity which is increasing the likelihood of extinctions (Kahilainen *et al.* 2014). If total habitat area is large, the negative effect is balanced by the positive effects of colonization by new specialist species.

The proportion of old-growth forest in the matrix impacting positively on community specialization is supporting the hypothesis of protected areas embedded in intensively managed matrix fostering more homogenous bird communities than those in less managed matrix. This is explained by the replacement of old-growth forest specialists by generalist species (McKinney and Lockwood 1999). These results support the idea of the flow of generalists from the matrix into the protected areas being an important mechanism of homogenization. However, matrix effect should be area-dependent and small protected areas would be more vulnerable to generalists' invasion. In my results about community specialization index, however, there was no evidence for this.

4.4 Is degradation in matrix homogenizing bird communities in protected areas?

The proportion of old-growth forest within the protected areas strongly influenced the bird community composition (IV), but unlike in many earlier studies (Devictor *et al.* 2008, Stouffer *et al.* 2009, Kennedy *et al.* 2010) the bird communities showed only moderate responses to the quality of the matrix (IV).

Large part of the variation in bird community composition in the protected areas varying on habitat and matrix quality was explained by the species' functional traits (IV). There was a clear pattern in the variation of morphological traits. Protected areas with low proportion of old-growth forest were occupied by species with larger body size and longer relative wing length but shorter relative tarsus. This can be explained by higher abundances of, for example, raptor species (Rayner 1988). There was also larger bill ratio in small, forested areas with little shrub in the matrix. This could be an outcome of increasing abundance of small-sized insectivorous birds, e.g. warblers and tits (Miles and Ricklefs 1984), in small protected areas with high percentage of old-growth forest cover and high quality matrix.

Protected areas with high proportion of old-growth forest host higher abundances of specialist species (high average SSI-index) than those with low proportion of old-growth forest cover. This suggests that habitat quality within the protected areas affects the relative abundances of generalist and specialist species. This is in line with earlier studies where habitat disturbance has been found to favour generalists at the expense of habitat specialists (Marvier *et al.* 2004, Clavel *et al.* 2011). In protected areas recent human disturbance is usually low, but low proportion of old-growth forest may stem from human actions before area was protected.

In protected areas with high proportion of old-growth forest but low quality matrix the abundance of species with nationally large population size was higher than in forested areas with high quality matrix. This is a sign of homogenization: if scarce and rare species are the first to disappear with increased logging in the matrix, as earlier literature shows (Henle *et al.* 2004), the result would be a community with more abundant species.

There is some support in the results for the hypothesis that matrix quality is associated with higher community similarity, or homogenization, within protected areas because the highest community variability (beta-diversity) values were found in both small and large high quality protected areas embedded in high quality matrix. High quality areas in low quality matrix had beta-diversity values that were among the lowest ones. Thus, supporting the biotic homogenization hypothesis, communities in protected areas embedded in low quality matrix are more similar to each other than those in high quality matrix.

In high quality protected areas surrounded by low quality matrix the average population size of species was higher and there was no statistically supported difference in species specialization compared to the reference scenario. The results suggest that homogenization is likely originating from more common, abundant species becoming more dominant in the reserves embedded in low quality matrix. This may also originate from landscape supplementation effect (*sensu* Dunning *et al.* 1992), i.e. a spill-over of abundant species from the surrounding areas into the protected areas. There was little evidence for the prediction of small protected areas being particularly sensitive to a decrease in community variability. Thus, even large size protected areas may not be buffered against negative matrix effects, and that maintaining high matrix quality may be important irrespectively of the size of the protected area.

TABLE 1 The impacts of Human footprint (II) and human land use intensity in the matrix (III, IV) on different diversity metrics. + and - indicate the responses of a diversity index on increased human impact, 0 indicates no response and empty cells indicate that the particular diversity metric was not used in the study.

		Alpha	Beta	Gamma	
Human land use intensity	II	Taxonomic	0	0	0
		Functional	0	+	0
		Phylogenetic	(-)	0	0
	III	Taxonomic	0		
		Functional	+		
		Phylogenetic	0		
		CSI	-		
	IV	Taxonomic		0	
		Functional		-	
		Phylogenetic			
		CSI		0	

5 CONCLUSIONS

This thesis shows that measuring biodiversity is not straightforward, but multiple metrics should always be taken into account especially when new protected areas are evaluated. Human impact via land-use and forestry on bird communities is evident but complex (I, II, III, IV). There were signals of negative impacts of intensive forest management on specialist species (I, III) and of high proportion of old-growth forest benefiting specialist species (IV). It is worth remembering that in (III) and (IV) I used traditional method of calculating SSI, even though it is suggested to be an underestimation of true level of specialization (I). Therefore, the responses of specialist species can actually be stronger than those I observed.

There was no evidence for biotic homogenization, declines in beta-diversity, because of human land-use intensity in taxonomic and phylogenetic diversity in general landscape (II) but there were clear signs of increasing similarity of bird communities in protected areas due to human actions (IV). On functional beta diversity the responses on human land-use intensity were interesting; in protected areas (IV) logging intensity in the matrix had negative impact on functional diversity suggesting functional homogenization as hypothesized, but in general landscape level (II) the human impact on functional diversity was positive, so human activities seem to increase differences between communities. However, this can be explained in reduced functional alpha diversity or increased habitat heterogeneity and new species in human-altered landscape, which both would increase beta diversity, and therefore, from conservation point of view, human impact is still considered negative.

Even though decline in old-growth forest cover did not cause homogenization in general landscape (II), it had negative impacts on functional and phylogenetic alpha and gamma diversities (II). Additionally, forest management in matrix had negative impact on community specialization in protected areas (III), which indicates that species that are declining due to human actions are specialists, but the impact was not found when comparing the variation in specialization between protected areas (IV). In protected areas,

homogenization most probably originates from the common and more abundant species entering the area (IV) because of spill-over effect from the matrix. But because forest bird communities are already dominated by generalists (I), it could be that the declines of specialists due to human actions are hard to observe, even though they may have strong impact on functioning of the ecosystems. Therefore, for preventing biodiversity loss further conservation efforts are needed.

Although it is well known that larger areas harbour more species, all biodiversity aspects, such as high phylogenetic, functional nor even taxonomic diversity may not be secured if conservation is based only on protecting large areas with high species richness. The characteristics of protected areas are the most important factor explaining diversity irrespective of the size (III, IV) and productive areas with high habitat heterogeneity seem to secure at least taxonomic and phylogenetic diversity and specialist species (III). However, traditionally protected areas are established in areas where productivity is low and possibilities for exploitation or resources are poor (Scott *et al.* 2001). And even if areas themselves are of good quality, degraded matrix will have impact on bird communities, which can be seen in increasing similarity of bird communities, thus, homogenization (III, IV). Furthermore, the response of functional diversity to environment seems to be much more complex than of taxonomic and phylogenetic diversities (II, III) even though part of this complexity can be explained by calculation and fundamental properties of diversity indexes.

Interestingly, the results suggest that for maintaining all diversity aspects of forest bird communities in boreal zone, the conservation efforts should be targeted on good quality habitats with large proportion of old-growth forest, and maintaining or improving the habitat quality within the protected areas rather than enlarging the size of current protected areas (III, IV). Nevertheless, the quality of the surrounding matrix plays important role, too (III, IV). There were some signals of matrix impacting community homogenization when matrix quality was low. Thus, the ability of protected area network to maintain regional species pool may be reduced in low quality matrix. Therefore more protected area or improved quality is needed for the same conservation effect when the protected areas are embedded in low quality matrix. However, this thesis concentrates only on birds that have relatively good dispersal ability, and in other species groups the responses could be different.

In conclusion, the most important message of this thesis is, that to really understand biodiversity or how protected area network is able to maintain diversity, various aspects of biodiversity in all spatial scales should be considered. It is also of great importance to understand that in biodiversity more is not necessarily better, but each area and patch has its own natural state of diversity, and human-induced declines, but also increases, to this baseline denote unwanted changes in the communities and the whole ecosystems. With the global change and growing demand and exploitation of natural resources, these complex relations with different diversity metrics and scales and

36

especially applying them in conservation sets growing demand of co-operation with scientists and conservation planners.

Acknowledgements

First of all, I want to thank my supervisors Mikko Mönkkönen, Eric Le Tortorec and Gerald J. Niemi for all the guidance and patience during this project. Mikko, your ability to turn everything good for example when results change during revision and when I was very close to mental breakdown, is something I envy. Eric, your peacefulness and almost unbelievable ability to organize your work is truly a gift and it really helped me in the dark moments with the manuscripts. Jerry, you were the original reason why I decided to start this PhD project, and it seems it paid off! Thank you for your support.

I also want to thank current and past members of the Boreal Ecosystems Research Group: Daniel Burgas, Merja Elo, Kyle Eyvindson, Tero Heinonen, Adriano Mazziotta, Maiju Peura, Dmitry Podkopaev, Tähti Pohjanmies, Anna Repo and Maria Triviño for all the help and support, great discussions and also fun over the years. BERG rocks! I have shared offices with almost all of you and it has been a pleasure. Special thanks to Maiju who kept me sane during the last, stressful year of my project! I also owe thanks to my collaborators involved in my studies, especially Otso Ovaskainen, Nerea Abrego and Edmund Zlonis.

I was fortunate to have a follow-up group with two excellent scientists, Mar Cabeza and Janne Kotiaho. I remember that our meetings were mostly filled with uncertainty from my side, but your common sense and expertise helped and encouraged me a lot and surely I am more confident with my skills and study subject, not the least because of you.

This project would not have succeeded without a nice working community. I have enjoyed the atmosphere of the Department of Biological and Environmental Science since I started my basic studies almost eighteen years ago and I have to say that it has been an adventure. Special thanks to Panu Halme, Esa Koskela, Leena Lindström, Jari Haimi, Emily Knott, Katja Kuitunen, Johanna and Tapio Mappes, Kalevi Viipale and many others for uncountable memorable moments and occasions during the years. Big thanks also to current and past members our early lunch posse: Atte, Mikael, Lauri, Aapo, Ilkka, Tarmo, Santtu, Marko and Merja. It is surprising how refreshing and healing daily dose of bad (and I mean bad) humour can be.

Working would not be possible without good quality free time. Special thanks to master chef Teppo, whose onions I have been chopping during our cooking nights for more than fifteen years. Birding has always been my retreat. Jyrki, Tero and Heikki have shared many pleasant and also unpleasant moments inside and outside the bird void of Central Finland. Big thanks also to other co-birders: Ossi, Kyltsi, Harri, Kuhno, Kilppari, Linjama, Esko, Keke, Tuomas, Aki, Tuomo, Marjo, Tomi, Kristiina, Hanski, Jussi, Asseri, Miia K and last but definitely not least the one and only Syde. I have many friends to thank for the fun moments during the years: Kaisa, Jyrki, Sari, Jari, Carita, Santtu, Miia R, Kalle, Nina, Arto, Tiina, Anna, Klasu, Elina, Suvi, Henri, Anni, Teppo, Johanna, Lauri, Heli, Pekka, Tarmo, Känkänen and many others!

Viimeiseksi haluan kiittää sukulaisia ja perhettäni loppumattomasta tuesta, kannustuksesta ja johdatuksesta luonnon ihmeiden pariin. Isä ja äiti, kiitos tuesta ja avusta, jota vielä 42-vuotiaana opiskeleva poikanne ei välttämättä olisi aina ansainnut. Jaakko, Medeia ja Iisa, olette minulle tärkeitä! Väinö, pieni luontomies, olet isille kaikkein tärkein. Sinun kanssasi vietetty aika ja lintu-, kala-, ötökkä- ja sieniretket ovat auttaneet unohtamaan kaikki huolet ja murheet, ja laittaneet asiat oikeaan tärkeysjärjestykseen. Inka, en osaa kertoa kuinka monella eri tavalla olet minua auttanut; tämä kirja ei olisi tässä ilman sinua. Kiitos tuesta ja terveestä järjestä, joka minulta aina välillä unohtuu.

YHTEENVETO (RÉSUMÉ IN FINNISH)

Metsien lintuyhteisöjen biologinen samankaltaistuminen ihmistoiminnan vaikutuksesta

Kasvavan ihmiskunnan vaikutukset alkuperäisluonnon monimuotoisuudelle ovat mittavia. Ilmastonmuutos, saasteet, elinympäristöjen tuhoutuminen ja niiden laadun heikkeneminen sekä ihmisen mukana leviävät vieraslajit vaikuttavat kaikki osaltaan monimuotoisuutta alentavasti. Luonnon monimuotoisuuden mittaaminen ei kuitenkaan aina ole yksiselitteistä. Yksinkertaisimmillaan monimuotoisuuden mittana voi olla lajimäärä tai kunkin lajin runsauden huomioon ottava taksonominen monimuotoisuus. Keskityttäessä pelkästään lajeihin ja niiden runsauteen on kuitenkin vaarana kerättävän tiedon puutteellisuus ja yksipuolisuus, ja vertailtaessa esimerkiksi lajiston säilymistä metsäalueella tietyllä aikajaksolla virhetulkintojen mahdollisuus voi kasvaa. Mikäli tarkastelun kohteena on vain lajimäärä, voivat vaikkapa jotkin vanhaan metsään erikoistuneet lajit hävitä alueelta ja tilalle voi tulla elinympäristövaatimuksiltaan väljempiä generalisteja. Tällöin lajimäärä säilyy samana, vaikka lajiyhteisön muutos olisi todellisuudessa merkittävä.

Lajimäärän ja taksonomisen monimuotoisuuden lisäksi onkin kehitetty useita monimuotoisuuden mittareita. Funktionaalinen eli toiminnallinen monimuotoisuus puolestaan kuvaa eliöyhteisön lajien resurssien käytön kirjoa ja tehokkuutta, ja korkean toiminnallisen monimuotoisuuden on todettu lisäävän ekosysteemien tuottavuutta. Fylogeneettinen monimuotoisuus perustuu lajien sukulaisuussuhteisiin ja siihen kuinka etäistä sukua lajit toisilleen ovat. Fylogeneettinen monimuotoisuus heijastaa nykyisen yhteisön evolutiivista historiaa, mutta fylogeneettisesti monimuotoinen yhteisö voi myös parantaa yhteisön sietokykyä ympäristönmuutoksille. Nämä monimuotoisuutta kuvaavat mitat ovat usein keskenään korreloituneita, mutta kertovat kuitenkin eri asioista. Esimerkiksi kahden yhteisön taksonominen monimuotoisuus voi olla sama, mutta lajiston fylogeneettinen historia tai toisaalta toiminnallisuus voivat olla tyystin erilaisia.

Muutokset lajien erikoistumisasteessa voivat myös kertoa yhteisössä tapahtuvista muutoksista. Erikoistuneiden lajien ekolokero on yleensä kapea, eli ne hyödyntävät vain pientä osaa tarjolla olevista resursseista. Niiden käytössä erikoistuneet lajit ovat kuitenkin yleensä tehokkaita, ja usein erikoistuneet lajit ovat toiminnallisesti erityisiä. Siten erikoistuneiden lajien väheneminen voi johtaa alentuneeseen toiminnalliseen monimuotoisuuteen, mikä puolestaan voi johtaa yhteisöjen samankaltaistumiseen. Toisaalta toiminnallinen monimuotoisuus voi säilyä muuttumattomana, vaikka hävinneiden erikoistuneiden lajien tilalle tulisi generalisteja. Siten yhteisön toiminnallisuus säilyy, mutta resurssien käytön tehokkuus voi alentua merkittävästi. Erikoistumisasteen tutkiminen voikin oleellisesti täydentää muilla monimuotoisuuden mittareilla saatua tietoa.

Tässä väitöskirjatyössä selvitin aluksi onko lajien erikoistumisasteella eroa eri eliömaantieteellisten alueiden välillä, ja ovatko metsälinnut keskimäärin erikoistuneempia kuin toisenlaisia elinympäristöjä käyttävät lajit. Työssä selvitin myös ovatko paikkalinnut keskimäärin erikoistuneempia kuin muuttolinnut. Nämä tiedot ovat tärkeitä lajiston uhanalaistumisen riskiä arvioitaessa ja suojelualueita perustettaessa. Seuraavaksi selvitin ihmistoiminnan, erityisesti metsien hakkuiden, vaikutuksia boreaalisen vyöhykkeen metsien lintuyhteisöihin. Tutkimuksen erityisenä kohteena olivat monimuotoisuuden eri muodot ja mittarit, ja erityishuomiota kiinnitetään elinympäristöönsä erikoistuneisiin lajeihin. Ihmisen aiheuttamasta elinympäristömuutoksesta ja sen vaikutuksista luonnon monimuotoisuuteen on julkaistu valtava määrä tutkimuksia, mutta suojelualueiden kyvystä ylläpitää monimuotoisuutta julkaisuja on vähän. Erityisen vähälle huomiolle ovat jääneet boreaalisen vyöhykkeen suojelualueet. Paine metsien ja niistä saatavien jalosteiden ja hyödykkeiden käytön lisäämiselle on viime aikoina lisääntynyt, joten suojelualueiden merkitys metsäluonnon suojelussa korostuu. Tutkimuksissa selvitin myös eroavatko eri monimuotoisuusmittojen vasteet ympäristömuutoksiin yleisimmin käytetyn taksonomisen monimuotoisuuden vasteesta. Beta-diversiteetti kuvaa tietyn alueen lajijyhteisöjen eroavaisuuksia. Tutkimalla ihmisen aiheuttaman ympäristömuutoksen vaikutuksia yhteisöjen välisiin eroihin voidaan tehdä päätelmiä biologisesta samankaltaistumisesta. Tämän tutkimuksen tarjoamalle tiedolle ihmisen toiminnan vaikutuksista monimuotoisuudelle ja toisaalta eri monimuotoisuusmittareiden välisistä suhteista on varmasti käyttöä monimuotoisuuden suojelussa, kun paine luonnon tarjoamien resurssien hyväksikäyttämiseksi kasvaa.

Ensimmäisessä osatutkimuksessa perehdyin kahden metsienkäsittelyhistorialtaan erilaisen boreaalisella vyöhykkeellä sijaitsevan alueen, Suomen ja Minnesotan linnuston erikoistumistason eroihin ja yhtäläisyyksiin. Tutkimuksissa havaitsin, että lintujen erikoistumisessa elinympäristöönsä on eroa näiden kahden alueen välillä. Kuitenkin hypoteesien vastaisesti Suomen metsälinnut osoittautuivat keskimäärin erikoistuneemmiksi ei-metsälintuihin verrattuna, kun taas Minnesotan ei-metsälinnut olivat selvästi erikoistuneempia. Tämä selittyy alueiden erilaisella historialla. Jääkauden aikaan Euroopan metsät olivat pirstoutuneita, jolloin voimakas valinta on johtanut lajien sopeutumiseen, eli siis erikoistumiseen, kuhunkin metsäfragmenttiin, ja metsien jälleen levitessä laajemmalle lajit ovat säilyttäneet oman ekolokeronsa. Pohjois-Amerikan ruohostomaiden lajit ovat kokeneet samanlaisen valintapaineen jääkauden aikana, jolloin metsät yleistyivät ja laajat ruohostomaat pirstoutuivat.

Suomen metsälajisto oli erikoistuneempaa myös yhteisötasolla, eli lajien yksilörunsaudet huomioiden, mutta Suomessa lajien ja yhteisöjen keskimääräisen erikoistumisen ero oli melko suuri, mikä viittaa siihen, että Suomessa erikoistuneiden lajien yksilömäärät ovat pieniä. Tämä puolestaan viittaa siihen, että metsien käsittelyllä on vaikutusta erityisesti metsiin erikoistuneiden lajien esiintymiseen ja runsauteen.

Toisessa osatutkimuksessa havaitsin, että lisääntynyt ihmisvaikutus vaikuttaa Minnesotan metsälintujen monimuotoisuuteen, mutta hieman toisin kuin odotettiin. Yhteisöt eivät samankaltaistuneet taksonomista, toiminnallista tai fylogeneettista monimuotoisuutta tarkastellessa, vaan toiminnallinen monimuotoisuus näytti jopa lisääntyvän ihmisvaikutuksen kasvaessa. Syy voi kuitenkin piillä beta-diversiteetin laskentatavassa, sillä sen voidaan olettaa kasvavan paikallisen monimuotoisuuden aletessa tai alueellisen diversiteetin kasvaessa. Koska myöskään metsien väheneminen ei tulosten mukaan aiheuta yhteisöjen samankaltaistumista, voi selitys löytyä historiasta. Alueen luonnonmetsät hävitettiin lähes tyystin 100–150 vuotta sitten, ja onkin todennäköistä, että lintuyhteisöt ovat jo aiemmin kokeneet niin suuria muutoksia, ettei nykyinen, aiempaan verrattuna maltillinen ihmisvaikutus aiheuta lisämuutoksia yhteisöihin. Kuitenkin metsien väheneminen alensi paikallisesti sekä toiminnallista että fylogeneettista monimuotoisuutta, ja vaikutus näkyi heikkona myös alueellisessa monimuotoisuudessa. Tarkasteltaessa jälleen beta-diversiteetin laskentatapaa, huomataan, että sekä alueellisen että paikallisen monimuotoisuuden vähetessä yhteisöjen väliset erot eivät välttämättä muutu, jolloin beta-diversiteettikin säilyy muuttumattomana.

Suojelualueet on perustettu säilyttämään alkuperäistä luontoa ja suojelemaan sitä ihmisvaikutukselta. Kuitenkin monissa tutkimuksissa on todettu, että suojelualueet eivät ole itsenäisiä yksiköitä, vaan jatkuvassa vuorovaikutuksessa ympäristönsä kanssa. Kolmas ja neljäs osatyö keskittyivätkin tutkimaan, miten metsien käsittelyn intensiteetti vaikuttaa metsiensuojelualueiden kykyyn ylläpitää erikoistuneita ja toiminnallisesti monimuotoisia lintuyhteisöjä. Kolmannessa osatutkimuksessa havaittiin, että metsiin erikoistuneet lajit olivat vähälukuisempia niillä suojelualueilla, joiden ympäristössä metsien käsittely oli ollut voimakasta. Suojelualueita ympäröivien metsien käsittely näkyi myös toiminnallisesti samankaltaisten lajien vähenemisenä, mikä voi haitata ekosysteemin toimintaa. Kuitenkin tärkein lajimäärään vaikuttava tekijä oli suojelualueen laatu. Neljäs osatutkimus tuki tätä tulosta, sillä alueen laatu, eli vanhan metsän määrä, oli tärkein lintuyhteisön koostumusta muokkaavista tekijöistä. Vähän vanhaa metsää sisältävillä alueilla yhteisön erikoistumisaste oli myös alhainen. Sen sijaan suojelualueen ympäristön laadulla ei ollut suoraa vaikutusta lintuyhteisöihin. Tutkimuksessa kuitenkin havaittiin selviä viitteitä ympäristön vaikutuksesta yhteisöjen samankaltaistumiseen: lintuyhteisöt, jotka elivät nuoren metsän ja hakkuualueiden ympäröimillä suojelualueilla, olivat keskenään samankaltaisempia verrattuna yhteisöihin, joita ympäröivillä alueilla oli paljon vanhaa metsää. Lisäksi huonolaatuisessa ympäristössä olevien alueiden yhteisössä runsaslukuiset lajit olivat runsaampia kuin hyvälaatuisessa ympäristössä sijaitsevilla alueilla.

Tutkimusten perusteella voidaan sanoa, että ihmisen toiminnalla ja metsien käsittelyllä on monenlaisia vaikutuksia metsälintuihin ja niiden yhteisöjen koostumukseen. Monimuotoisuuden mittaaminen ei kuitenkaan ole aivan yksiselitteistä, ja erityisesti toiminnallisen monimuotoisuuden muutokset ja niiden tul-

kinta vaativat huolellisuutta. Lisäksi beta-diversiteettiä laskettaessa ja sen muutoksia tulkittaessa tulee huomioida myös muut monimuotoisuuden tasot, joiden vaikutus beta-diversiteettiin saattaa olla merkittävä.

REFERENCES

- Allouche O., Kalyuzhny M., Moreno-Rueda G., Pizarro M. & Kadmon R. 2012. Area-heterogeneity tradeoff and the diversity of ecological communities. *Proc. Natl. Acad. Sci. U. S. A.* 109: 17495–17500.
- Anderson M.J., Crist T.O., Chase J.M., Vellend M., Inouye B.D., Freestone A.L., Sanders N.J., Cornell H. V, Comita L.S., Davies K.F., Harrison S.P., Kraft N.J.B., Stegen J.C. & Swenson N.G. 2011. Navigating the multiple meanings of β diversity: a roadmap for the practicing ecologist. *Ecol. Lett.* 14: 19–28.
- Baiser B., Olden J.D., Record S., Lockwood J.L. & McKinney M.L. 2012. Pattern and process of biotic homogenization in the New Pangaea. *Proc. Biol. Sci.* 279: 4772–4777.
- Baselga A. 2010. Partitioning the turnover and nestedness components of beta diversity. *Glob. Ecol. Biogeogr.* 19: 134–143.
- Bello F. De, Lavergne S., Meynard C.N., Lepš J. & Thuiller W. 2010. The partitioning of diversity: showing Theseus a way out of the labyrinth. *J. Veg. Sci.* 21: 992–1000.
- Belmaker J. & Jetz W. 2015. Relative roles of ecological and energetic constraints, diversification rates and region history on global species richness gradients Arita H. (ed.). *Ecol. Lett.* 18: 563–571.
- Brandt J.P. 2009. The extent of the North American boreal zone. *Environ. Rev.* 17: 101–161.
- Brandt J.P., Flannigan M.D., Maynard D.G., Thompson I.D. & Volney W.J.A. 2013. An introduction to Canada's boreal zone: ecosystem processes, health, sustainability, and environmental issues. *Environ. Rev.* 21: 207–226.
- Burnham K. & Anderson D. 2002. *Model selection and multimodel inference. A practical Information-Theoretic Approach*. Springer-Verlag, New York, USA.
- Burton P.J., Bergeron Y., Bogdanski B.E., Juday G.P., Kuuluvainen T., MacAfee B.J., Ogden A. & Teplyakov V. 2010. Sustainability of Boreal Forests and Forestry in a Changing Environment. In: *Forests and Society - Responding to Global Drivers of Change*, International Union of Forest Research Organizations (IUFRO).
- Cadotte M.W., Carscadden K. & Mirotnick N. 2011. Beyond species: functional diversity and the maintenance of ecological processes and services. *J. Appl. Ecol.* 48: 1079–1087.
- Cardinale B.J., Duffy J.E., Gonzalez A., Hooper D.U., Perrings C., Venail P., Narwani A., Mace G.M., Tilman D., Wardle D.A., Kinzig A.P., Daily G.C., Loreau M., Grace J.B., Larigauderie A., Srivastava D.S. & Naeem S. 2012. Corrigendum: Biodiversity loss and its impact on humanity. *Nature* 489: 326–326.
- Cardinale B.J., Matulich K.L., Hooper D.U., Byrnes J.E., Duffy J.E., Gamfeldt L., Balvanera P., O'Connor M.I. & Gonzalez A. 2011. The functional role of producer diversity in ecosystems. *Am. J. Bot.* 98: 572–592.
- Cardinale B.J., Srivastava D.S., Duffy J.E., Wright J.P., Downing A.L., Sankaran M. & Jouseau C. 2006. Effects of biodiversity on the functioning of trophic

- groups and ecosystems. *Nature* 443: 989–992.
- Carroll C., Noss R.F., Paquet P.C. & Schumaker N.H. 2004. Extinction Debt of Protected Areas in Developing Landscapes. *Conserv. Biol.* 18: 1110–1120.
- Catterall C.P., Cousin J.A., Piper S. & Johnson G. 2010. Long-term dynamics of bird diversity in forest and suburb: decay, turnover or homogenization? *Divers. Distrib.* 16: 559–570.
- Clavel J., Julliard R. & Devictor V. 2011. Worldwide decline of specialist species: toward a global functional homogenization? *Front. Ecol. Environ.* 9: 222–228.
- D'Amen M., Bombi P., Campanaro a., Zapponi L., Bologna M. a. & Mason F. 2013. Protected areas and insect conservation: questioning the effectiveness of Natura 2000 network for saproxylic beetles in Italy. *Anim. Conserv.* 16: 370–378.
- Devictor V., Clavel J., Julliard R., Lavergne S., Mouillot D., Thuiller W., Venail P., Villéger S. & Mouquet N. 2010a. Defining and measuring ecological specialization. *J. Appl. Ecol.* 47: 15–25.
- Devictor V., Julliard R., Clavel J., Jiguet F., Lee A. & Couvet D. 2008. Functional biotic homogenization of bird communities in disturbed landscapes. *Glob. Ecol. Biogeogr.* 17: 252–261.
- Devictor V., Julliard R., Couvet D., Lee A. & Jiguet F. 2007. Functional homogenization effect of urbanization on bird communities. *Conserv. Biol.* 21: 741–751.
- Devictor V., Mouillot D., Meynard C., Jiguet F., Thuiller W. & Mouquet N. 2010b. Spatial mismatch and congruence between taxonomic, phylogenetic and functional diversity: the need for integrative conservation strategies in a changing world. *Ecol. Lett.* 13: 1030–1040.
- Devictor V. & Robert A. 2009. Measuring community responses to large-scale disturbance in conservation biogeography. *Divers. Distrib.* 15: 122–130.
- Driscoll D.A., Banks S.C., Barton P.S., Lindenmayer D.B. & Smith A.L. 2013. Conceptual domain of the matrix in fragmented landscapes. *Trends Ecol. Evol.* 28: 605–613.
- Dunning J.B., Danielson B. & Pullian H.R. 1992. Ecological processes that affect populations in complex landscapes. *Oikos* 65: 169–175.
- Elo M., Haapalehto T., Kareksela S. & Kotiaho J. 2017. What does the recovery debt really measure? *Rethink. Ecol.* 2: 41–45.
- Fahrig L. 2001. How much habitat is enough? *Biol. Conserv.* 100: 65–74.
- Faith D.P. 1992. Conservation evaluation and phylogenetic diversity. *Biol. Conserv.*: 1–10.
- Flynn D.F.B., Gogol-Prokurat M., Nogeire T., Molinari N., Richers B.T., Lin B.B., Simpson N., Mayfield M.M. & DeClerck F. 2009. Loss of functional diversity under land use intensification across multiple taxa. *Ecol. Lett.* 12: 22–33.
- Gordon C.E., McGill B., Ibarra-Núñez G., Greenberg R. & Perfecto I. 2009. Simplification of a coffee foliage-dwelling beetle community under low-shade management. *Basic Appl. Ecol.* 10: 246–254.
- Hanski I. 1999. Habitat Connectivity, Habitat Continuity, and Metapopulations

- in Dynamic Landscapes. *Oikos* 87: 209.
- Henle K., Davies K.F., Kleyer M., Margules C. & Settele J. 2004. Predictors of Species Sensitivity to Fragmentation. *Biodivers. Conserv.* 13: 207–251.
- Honkanen M., Roberge J.-M., Rajasärkkä A. & Mönkkönen M. 2010. Disentangling the effects of area, energy and habitat heterogeneity on boreal forest bird species richness in protected areas. *Glob. Ecol. Biogeogr.* 19: 61–71.
- Hooper D.U., Adair E.C., Cardinale B.J., Byrnes J.E.K., Hungate B. a., Matulich K.L., Gonzalez A., Duffy J.E., Gamfeldt L. & O'Connor M.I. 2012. A global synthesis reveals biodiversity loss as a major driver of ecosystem change. *Nature* 486: 105–108.
- Hooper D.U., Chapin F.S., Ewel J.J., Hector A., Inchausti P., Lavorel S., Lawton J.H., Lodge D.M., Loreau M., Naeem S., Schmid B., Setälä H., Symstad A.J., Vandermeer J. & Wardle D.A. 2005. Effects of Biodiversity on Ecosystem Functioning: A Consensus of Current Knowledge. *Ecol. Monogr.* 75: 3–35.
- Ibarra J.T. & Martin K. 2015. Biotic homogenization: Loss of avian functional richness and habitat specialists in disturbed Andean temperate forests. *Biol. Conserv.* 192: 418–427.
- Imbeau L., Mönkkönen M. & Desrochers A. 2001. Long-Term Effects of Forestry on Birds of the Eastern Canadian Boreal Forests: a Comparison with Fennoscandia. *Conserv. Biol.* 15: 1151–1162.
- Isbell F., Tilman D., Polasky S. & Loreau M. 2015. The biodiversity-dependent ecosystem service debt Bardgett R. (ed.). *Ecol. Lett.* 18: 119–134.
- Järvinen O. & Väisänen R.A. 1976. Finnish line transect censuses. *Ornis Fenn.* 53: 115–118.
- Järvinen O. & Väisänen R.A. 1981. Methodology for censusing land bird faunas in large regions. *Stud. Avian Biol.* 6: 146–151.
- Jetz W., Thomas G.H., Joy J.B., Hartmann K. & Mooers A.O. 2012. The global diversity of birds in space and time. *Nature* 491: 444–448.
- Jetz W., Thomas G.H., Joy J.B., Redding D.W., Hartmann K. & Mooers A.O. 2014. Global distribution and conservation of evolutionary distinctness in birds. *Curr. Biol.* 24: 919–930.
- Julliard R., Clavel J., Devictor V., Jiguet F. & Couvet D. 2006. Spatial segregation of specialists and generalists in bird communities. *Ecol. Lett.* 9: 1237–1244.
- Julliard R., Jiguet F. & Couvet D. 2003. Common birds facing global changes: what makes a species at risk? *Glob. Chang. Biol.* 10: 148–154.
- Kahilainen A., Puurtinen M. & Kotiaho J.S. 2014. Conservation implications of species–genetic diversity correlations. *Glob. Ecol. Conserv.* 2: 315–323.
- Keddy P.A. 1992. Assembly and response rules: two goals for predictive community ecology. *J. Veg. Sci.* 3: 157–164.
- Kennedy C.M., Marra P.P., Fagan W.F. & Neel M.C. 2010. Landscape matrix and species traits mediate responses of Neotropical resident birds to forest fragmentation in Jamaica. *Ecol. Monogr.* 80: 651–669.
- Kitching R.L., Ashton L.A., Nakamura A., Whitaker T. & Khen C.V. 2013. Distance-driven species turnover in Bornean rainforests: homogeneity and heterogeneity in primary and post-logging forests. *Ecography (Cop.)*. 36:

- 675–682.
- Kortesmaa T. & Jokela A. (eds.). 2017. *E-yearbook of food and natural resource statistics for 2016: Statistical facts on agriculture, forestry, fisheries and hunting in Finland*.
- Kotiaho J.S., Kaitala V., Komonen A. & Päävinen J. 2005. Predicting the risk of extinction from shared ecological characteristics. *Proc. Natl. Acad. Sci.* 102: 1963–1967.
- Kotiaho J.S. & Mönkkönen M. 2017. From a Crisis Discipline Towards Prognostic Conservation Practise: An Argument for Setting Aside Degraded Habitats. *Ann. Zool. Fennici* 54: 27–37.
- Laaksonen T. & Lehtikoinen A. 2013. Population trends in boreal birds: Continuing declines in agricultural, northern, and long-distance migrant species. *Biol. Conserv.* 168: 99–107.
- Laliberté E., Wells J.A., Declerck F., Metcalfe D.J., Catterall C.P., Queiroz C., Aubin I., Bonser S.P., Ding Y., Fraterrigo J.M., McNamara S., Morgan J.W., Merlos D.S., Vesik P.A. & Mayfield M.M. 2010. Land-use intensification reduces functional redundancy and response diversity in plant communities. *Ecol. Lett.* 13: 76–86.
- Lavergne S., Mouquet N., Thuiller W. & Ronce O. 2010. Biodiversity and Climate Change: Integrating Evolutionary and Ecological Responses of Species and Communities. *Annu. Rev. Ecol. Evol. Syst.* 41: 321–350.
- Lederer R. 1975. Bill size, food size and jaw forces of insectivorous birds. *Auk* 92: 385–387.
- Lee-Cruz L., Edwards D.P., Tripathi B.M. & Adams J.M. 2013. Impact of logging and forest conversion to oil palm plantations on soil bacterial communities in Borneo. *Appl. Environ. Microbiol.* 79: 7290–7297.
- Lovejoy T.E. 2006. Protected areas: a prism for a changing world. *Trends Ecol. Evol.* 21: 329–333.
- MacArthur R.H. & Wilson E.O. 1967. *The Theory of Island Biogeography*.
- Mace G.M., Norris K. & Fitter A.H. 2012. Biodiversity and ecosystem services: a multilayered relationship. *Trends Ecol. Evol.* 27: 19–26.
- Marvier M., Kareiva P. & Neubert M.G. 2004. Habitat Destruction, Fragmentation, and Disturbance Promote Invasion by Habitat Generalists in a Multispecies Metapopulation. *Risk Anal.* 24: 869–878.
- McKinney M.L. 1997. Extinction vulnerability and selectivity: Combining ecological and paleontological views. *Annu. Rev. Ecol. Systeem.* 28: 495–516.
- McKinney M.L. 2006. Urbanization as a major cause of biotic homogenization. *Biol. Conserv.* 127: 247–260.
- McKinney M. & Lockwood J. 1999. Biotic homogenization: a few winners replacing many losers in the next mass extinction. *Trends Ecol. Evol.* 14: 450–453.
- Miles D.B. & Ricklefs R.E. 1984. The Correlation Between Ecology and Morphology in Deciduous Forest Passerine Birds. *Ecology*: 1629–1640.
- Moilanen A. & Hanski I. 1998. Metapopulation dynamics: Effects of habitat quality and landscape structure. *Ecology* 79: 2503–2515.
- Mönkkönen M., Rajasärkkä A. & Lampila P. 2014. Isolation, patch size and

- matrix effects on bird assemblages in forest reserves. *Biodivers. Conserv.* 23: 3287–3300.
- Mönkkönen M., Reunanen P., Nikula A., Inkeroinen J. & Forsman J.T. 1997. Landscape characteristics associated with the occurrence of the flying squirrel *Pteromys volans* in old-growth forests of northern Finland. *Ecography (Cop.)*. 20: 634–642.
- Mönkkönen M. & Welsh D.A. 1994. A biogeographical hypothesis on the effects of human caused landscape changes on the bird communities of Europe and North America. *Ann. Zool. Fennici* 31: 61–70.
- Monnet A.-C., Jiguet F., Meynard C.N., Mouillot D., Mouquet N., Thuiller W. & Devictor V. 2014. Asynchrony of taxonomic, functional and phylogenetic diversity in birds. *Glob. Ecol. Biogeogr.* 23: 780–788.
- Mori A.S., Ota A.T., Fujii S., Seino T., Kabeya D., Okamoto T., Ito M.T., Kaneko N. & Hasegawa M. 2015. Biotic homogenization and differentiation of soil faunal communities in the production forest landscape: taxonomic and functional perspectives. *Oecologia* 177: 533–544.
- Naughton-Treves L., Holland M.B. & Brandon K. 2005. The Role of Protected Areas in Conserving Biodiversity and Sustaining Local Livelihoods. *Annu. Rev. Environ. Resour.* 30: 219–252.
- Newbold T., Hudson L.N., Hill S.L.L., Contu S., Lysenko I., Senior R.A., Börger L., Bennett D.J., Choimes A., Collen B., Day J., Palma A. De, Díaz S., Echeverria-Londoño S., Edgar M.J., Feldman A., Garon M., Harrison M.L.K., Alhousseini T., Ingram D.J., Itescu Y., Kattge J., Kemp V., Kirkpatrick L., Kleyer M., Correia D.L.P., Martin C.D., Meiri S., Novosolov M., Pan Y., Phillips H.R.P., Purves D.W., Robinson A., Simpson J., Tuck S.L., Weiher E., White H.J., Ewers R.M., Mace G.M., Scharlemann J.P.W. & Purvis A. 2015. Global effects of land use on local terrestrial biodiversity. *Nature* 520: 45–50.
- Newmark W.D. 1996. Insularization of Tanzanian Parks and the Local Extinction of Large Mammals. *Conserv. Biol.* 10: 1549–1556.
- Niemi G.J., Howe R.W., Sturtevant B.R., Parker L.R., Grinde A.R., Danz N.P., Nelson M.D., Zlonis E.J., Walton N.G., Gnass Giese E.E. & Lietz S.M. 2016. Analysis of Long-term Forest Bird Monitoring Data from National Forests of the Western Great Lakes Region. Gen.Tech.Rep. NRS-159. : 322.
- Olden J.D. 2006. Biotic homogenization: a new research agenda for conservation biogeography. *J. Biogeogr.* 33: 2027–2039.
- Olden J.D., Leroy Poff N., Douglas M.R., Douglas M.E. & Fausch K.D. 2004. Ecological and evolutionary consequences of biotic homogenization. *Trends Ecol. Evol.* 19: 18–24.
- Oliver T.H., Heard M.S., Isaac N.J.B., Roy D.B., Procter D., Eigenbrod F., Freckleton R., Hector A., Orme C.D.L., Petchey O.L., Proença V., Raffaelli D., Suttle K.B., Mace G.M., Martín-López B., Woodcock B.A. & Bullock J.M. 2015. Biodiversity and Resilience of Ecosystem Functions. *Trends Ecol. Evol.* 30: 673–684.
- Ovaskainen O., Tikhonov G., Norberg A., Guillaume Blanchet F., Duan L., Dunson D., Roslin T. & Abrego N. 2017. How to make more out of

- community data? A conceptual framework and its implementation as models and software Chave J. (ed.). *Ecol. Lett.* 20: 561–576.
- Pavoine S., Dufour A.-B. & Chessel D. 2004. From dissimilarities among species to dissimilarities among communities: a double principal coordinate analysis. *J. Theor. Biol.* 228: 523–537.
- Petchey O.L. & Gaston K.J. 2002. Functional diversity (FD), species richness and community composition. *Ecol. Lett.* 5: 402–411.
- Petchey O.L. & Gaston K.J. 2006. Functional diversity: back to basics and looking forward. *Ecol. Lett.* 9: 741–758.
- Potapov P., Yaroshenko A., Turubanova S., Dubinin M., Laestadius L., Thies C., Aksenov D., Egorov A., Yesipova Y., Glushkov I., Karpachevskiy M., Kostikova A., Manisha A., Tsybikova E. & Zhuravleva I. 2008. Mapping the World's Intact Forest Landscapes by Remote Sensing. *Ecol. Soc.* 13: art51.
- Rao C.R. 1982. Diversity and dissimilarity coefficients: A unified approach. *Theor. Popul. Biol.* 21: 24–43.
- Rayner J. 1988. Form and function in avian flight. In: Johnston R. (ed.), *Current Ornithology*, Springer, New York, pp. 1–66.
- Ricketts T.H. 2001. The matrix matters: effective isolation in fragmented landscapes. *Am. Nat.* 158: 87–99.
- Ricotta C. 2005. A note on functional diversity measures. *Basic Appl. Ecol.* 6: 479–486.
- Roberge J.-M., Virkkala R. & Mönkkönen M. 2018. Boreal forest bird assemblages and their conservation. In: Mikusiński G., Roberge J.-M. & Fuller R. (eds.), *Ecology and Conservation of Forest Birds*, Cambridge University Press.
- Rodrigues A.S.L., Andelman S.J., Bakarr M.I., Boitani L., Brooks T.M., Cowling R.M., Fishpool L.D.C., Fonseca G.A.B. da, Gaston K.J., Hoffmann M., Long J.S., Marquet P.A., Pilgrim J.D., Pressey R.L., Schipper J., Sechrest W., Stuart S.N., Underhill L.G., Waller R.W., Watts M.E.J. & Yan X. 2004. Effectiveness of the global protected area network in representing species diversity. *Nature* 428: 9–12.
- Rodrigues J.L.M., Pellizari V.H., Mueller R., Baek K., Jesus E. da C., Paula F.S., Mirza B., Hamaoui G.S., Tsai S.M., Feigl B., Tiedje J.M., Bohannan B.J.M. & Nüsslein K. 2013. Conversion of the Amazon rainforest to agriculture results in biotic homogenization of soil bacterial communities. *Proc. Natl. Acad. Sci. U. S. A.* 110: 988–993.
- Sala O.E. 2000. Global Biodiversity Scenarios for the Year 2100. *Science* (80-.). 287: 1770–1774.
- Santos B.A., Arroyo-Rodríguez V., Moreno C.E. & Tabarelli M. 2010. Edge-related loss of tree phylogenetic diversity in the severely fragmented Brazilian Atlantic forest. *PLoS One* 5: e12625.
- Schulte L.A., Mladenoff D.J., Crow T.R., Merrick L.C. & Cleland D.T. 2007. Homogenization of northern U.S. Great Lakes forests due to land use. *Landsc. Ecol.* 22: 1089–1103.
- Scott J.M., Davis F.W., Mcghee R.G., Wright R.G., Groves C. & Estes J. 2001. Nature reserves: Do they capture the full range of America's biological

- diversity? *Ecol. Appl.* 11: 999–1007.
- Sisk T.D., Haddad N.M. & Ehrlich P.R. 1997. Bird Assemblages in Patchy Woodlands: Modeling the Effects of Edge and Matrix Habitats. *Ecol. Appl.*: 1170–1180.
- Smart S.M., Thompson K., Marrs R.H., Duc M.G. Le, Maskell L.C. & Firbank L.G. 2006. Biotic homogenization and changes in species diversity across human-modified ecosystems. *Proc. Biol. Sci.* 273: 2659–2665.
- Socolar J.B., Gilroy J.J., Kunin W.E. & Edwards D.P. 2016. How Should Beta-Diversity Inform Biodiversity Conservation? Conservation Targets at Multiple Spatial Scales. *Trends Ecol. Evol.* 31: 67–80.
- Sol D., Bartomeus I, González-Lagos C. & Pavoine S. 2017. Urbanisation and the loss of phylogenetic diversity in birds Haddad N. (ed.). *Ecol. Lett.* 20: 721–729.
- Sorte F.A. La & Boecklen W.J. 2005. Temporal turnover of common species in avian assemblages in North America. *J. Biogeogr.* 32: 1151–1160.
- Srivastava D.S., Cadotte M.W., MacDonald A.A.M., Marushia R.G. & Mirotchnick N. 2012. Phylogenetic diversity and the functioning of ecosystems. *Ecol. Lett.* 15: 637–648.
- Stouffer P.C., Strong C. & Naka L.N. 2009. Twenty years of understorey bird extinctions from Amazonian rain forest fragments: consistent trends and landscape-mediated dynamics. *Divers. Distrib.* 15: 88–97.
- Tiainen J., Mikkola-Roos M., Below A., Jukarainen A., Lehtikoinen A., Lehtiniemi T., Pessa J., Rajasärkkä A., Rintala J., Sirkiä P. & Valkama J. 2016. *Suomen Lintujen Uhanalaisuus 2015 - The Red List of Finnish Bird Species.*
- Tilman D. 1997. The Influence of Functional Diversity and Composition on Ecosystem Processes. *Science (80-)*. 277: 1300–1302.
- Tomppo E. 1993. Multi-source national forest inventory of Finland. In: *Nyyssönen A, Poso S, Rautala J (Eds.) Proceedings of Ilvessalo symposium on national forest inventories. The Finnish Forest Research Institute, Research Papers*, pp. 53–61.
- Traill L.W., Bradshaw C.J.A. & Brook B.W. 2007. Minimum viable population size: A meta-analysis of 30 years of published estimates. *Biol. Conserv.* 139: 159–166.
- Travis J.M.J. 2003. Climate change and habitat destruction: a deadly anthropogenic cocktail. *Proc. Biol. Sci.* 270: 467–473.
- Väisänen R.A., Lammi E. & Koskimies P. 1998. *Muuttuva Pesimälinnusto*. Otava, Keuruu.
- Valkama J., Vepsäläinen V. & Lehtikoinen A. 2011. *The Third Finnish Breeding Bird Atlas*.
- Wiens J.J., Ackerly D.D., Allen A.P., Anacker B.L., Buckley L.B., Cornell H. V., Damschen E.I., Jonathan Davies T., Grytnes J.-A., Harrison S.P., Hawkins B.A., Holt R.D., McCain C.M. & Stephens P.R. 2010. Niche conservatism as an emerging principle in ecology and conservation biology. *Ecol. Lett.* 13: 1310–1324.
- Zoltan B.-D. 2005. Rao's quadratic entropy as a measure of functional diversity based on multiple traits. *J. Veg. Sci.* 16: 533–540.

Zuur A.F., Ieno E.N. & Smith G.M. 2007. *Analyzing ecological data*. Springer.

ORIGINAL PAPERS

I

**DIFFERENCES IN HABITAT SPECIALIZATION BETWEEN
WESTERN PALEARCTIC AND NEARCTIC BIRDS**

by

Matti Häkkilä, Karoliina Pietilä, Janne Kotiaho & Mikko Mönkkönen 2018

Manuscript

Differences in habitat specialization between Western Palearctic and Nearctic birds

Matti Häkkilä¹, Karoliina Pietilä¹, Janne S Kotiaho¹ & Mikko Mönkkönen¹

¹ Department of Biological and Environmental Science, University of Jyväskylä, Jyväskylä, Finland

Abstract

Species assemblages are reflecting the changes in deep history, as major environmental changes have had different impacts on species traits. The circumpolar boreal forest biome is dominated by forests, and similarities in forest dynamics as well as in species assemblages have been observed. In Palearctic region, during Pleistocene glaciation forest habitat was severely fragmented. In Nearctic, the Ice Age was more favorable for forests, but the grasslands have become more abundant ever since. These differences in species evolutionary history are expected to be reflected in the level of species habitat specialization.

Human induced changes in the environment modify species assemblages. Specialist species are efficient in resource use, and important for the functioning of the ecosystems. However, they are often sensitive for environmental degradation and worldwide decline of specialist species has been observed. In forest habitat, logging is the most important driver of habitat degradation, and its impacts are expected to be observed in specialization level of forest bird communities.

In this paper, we introduce an improved species specialization index (SSI) for calculating species habitat specialization. Using this method, we studied differences in the level of species habitat specialization between Nearctic and Palearctic bird species. We also studied average level of specialization in extant bird assemblages in the two biogeographical regions. We used point count data from Finland and Minnesota, USA to address if between-region differences in their deep evolutionary history and in current level of forest management intensity is reflected into species and assemblage level habitat specialization.

We showed that traditional method of calculating species habitat specialization (SSI) is underestimating the true level of specialization and we therefore recommend acknowledging within-habitat variation in species abundances when estimating habitat

specialization. We did not find major differences in general specialization level of bird species. We found that forest birds in Palearctic are more specialized in their habitat than non-forest birds, whereas in Nearctic non-forest birds tend to be more specialized. We suggest that this is a reflection of the environmental changes in deep history, especially during the Pleistocene glaciation. We also found support for our hypothesis of the degrading impact of forest management on the level of specialization of forest bird communities and, thus, for biotic homogenization.

Introduction

Specialization of species has gained a lot of attention for a hundred years (Grinnel 1917; Levins 1968; Julliard et al. 2006; Belmaker et al. 2012). It is an increasingly timely topic because biotic homogenization, originating from the decline of specialist species, is a worldwide phenomenon with severe and partly unpredictable consequences (Clavel et al. 2011). It has been suggested that specialism is a result of a long lasting evolutionary process of which generalists are still underway (Julliard et al. 2006). Stable environment benefits specialist species, and for long it has been suggested that species niches are widening with latitude, or species on average are increasingly more specialized when moving towards tropics (MacArthur 1972). But even if specialists are masters of using a particular resource or habitat, they are not very good competitors, and in communities where generalists are abundant, the number of individuals of specialist species is usually low (Julliard et al. 2006). Specialist species are also often considered poor in dispersal (Devictor et al. 2008b) even though intuitively in areas where resources vary between seasons and years dispersal must be essential for specialist species to survive.

In addition to being a species trait, the level of specialization is also a characteristic of species assemblages. The way an assemblage functions is influenced by the relative amount of specialist and generalist species. Even though specialist species are not very abundant in most cases, for the functioning of ecosystem they are of great importance. Their functions often complement each other in the use of resources in a community. Specialists are efficient in the use of the resources they are specialized on whereas generalists are less efficient, i.e. "jack-of-all-trades but master of none" (MacArthur 1972). It has been shown that decrease in functional diversity resulting from the decline of specialist species is impairing the functioning of whole ecosystems (Clavel et al.

2011). Increasing level of specialization facilitates species richness by allowing a larger number of species to co-exist because niches of specialists are usually narrow (Chase & Leibold 2003). Studying specialization may help to understand how global environmental changes affect community dynamics (Barnagaud et al. 2011). Therefore, studying the degree to which species and their communities are specialized and preventing the decline of specialist species is of great importance.

Evolutionary history is reflected in present regional species assemblages. Regions where the impacts of major historical disturbances have been more severe have likely changed the most and species that survived best through the major disturbances are now dominating. For example, taxonomic diversity of tree species as well as forest-associated birds and mammals is smaller in the western Palearctic region than in the eastern Palearctic or in the Nearctic region (North America) (Mönkkönen & Viro 1997). These differences trace back to the long-term history of forest biomes in these regions (Latham & Ricklefs 1993). For example the effects of the Ice Age on forests have been more drastic in the western Palearctic region than elsewhere on the northern Hemisphere (Mönkkönen & Welsh 1994). During the Pleistocene glaciations, continuous forests were completely eliminated from the Western Palearctic region. The remaining forests together with their bird assemblages were even more effectively isolated from Afrotropical biomes than today because drier climate enlarged the Saharan desert and shrunk tropical forests during glaciations. Among forest birds, Pleistocene conditions in Europe obviously selected for habitat generalism (low habitat availability), good colonization ability (large-scale forest fragmentation) and residency (shortage of wintering habitats in the Afrotropics). In the Nearctic region, both the temperate and boreal forest biomes remained far more extensive than the European forests. Moreover, closer contact with the tropical forests to the south was uninterrupted throughout the Pleistocene in these regions (Roberge et al. 2018) making habitat specialism and migration more feasible strategies among Nearctic birds. For species associated with non-forested habitats the historical conditions can be hypothesized to have favored opposite patterns, i.e. higher level of habitat specialism among the Palearctic than among the Nearctic birds.

Human induced loss and degradation of habitats together with climate change and pollution are considered the most severe threat to biodiversity (Sala 2000; Travis 2003; Hooper et al. 2012). Specialist species are often considered more sensitive to human-

induced environmental changes than generalists, and it has been shown that specialists are declining in all taxonomic groups as a consequence of habitat degradation (Devictor & Robert 2009; Clavel et al. 2011). Simultaneously, generalists are increasing and replacing specialists. This phenomenon is known as biotic homogenization (McKinney & Lockwood 1999). Mechanistically, biotic homogenization results from habitat filtering (Keddy 1992), where individuals and species whose traits are suitable for given habitats are selected from the regional pool. Therefore, areas where human impact is strong habitat filtering favors less specialized species and results in more homogeneous local and regional species assemblages (Häkkinen et al. 2017).

Boreal forests in the Nearctic and Palearctic regions differ not only in terms of deep evolutionary history but also in terms of human-induced environmental changes. Large areas of boreal forest in the Nearctic and eastern Palearctic areas remain unmanaged (Potapov et al. 2008) but particularly in Fennoscandia, the westernmost end of the Palearctic, forest management for timber production has been intense (Burton et al. 2010). For example, in Finland 91% of forests are in wood production (Kortesmaa & Jokela 2017). Consequently, the impact of forest habitat degradation can already be seen, as bird populations are declining and as much as 20% of forest birds are in the Finnish Red List (Tiainen et al. 2016). By contrast, in western Great Lakes region of North America, on the southern border of boreal zone, commercial forestry exists but forestry is far less intense than in Fennoscandia. Most forest bird populations in the Great Lakes regions are either stable or even increasing (Niemi et al. 2016). Thus, we may assume that habitat filtering selects for different traits in the intensively managed Fennoscandian forests than in less managed Great Lakes region of the Nearctic.

In this paper, we address if habitat specialization at the level of species traits and in regional bird assemblages differ between two biogeographical regions with different evolutionary history and different current land-use. Because of reasons in deep evolutionary history of the northern hemisphere biomes, at the species trait level, one may expect Nearctic forest bird species to show higher average levels of habitat specialization than Palearctic forest birds. We contrast forest birds with non-forest birds because of non-forest birds should show the opposite pattern. We also study if there are differences in specialization between different migratory groups. It has been suggested that resident birds are more specialized than migratory species because they

live all year round in their breeding grounds (Imbeau et al. 2001). Evolutionary history has likely favored migratory strategy more in the Nearctic than in the Palearctic region, and thus, this may affect overall level of specialization between the regions. At the regional assemblage level, the effects of habitat filtering are further rendering specialist strategy less favorable in Fennoscandian boreal landscapes than in the Great Lakes region, and therefore, we may expect an increase in dominance of generalists in intensively managed Fennoscandian landscapes and thereby a lower level of specialization in the regional species assemblages.

This information is important both in conservation planning and in scientific studies that use large data sets from different regions. Studying the possible differences between areas differing in logging intensity and history will help to understand the complex effects of environmental change on biodiversity. If there are differences in habitat specialization of bird fauna between biogeographical regions, it may affect the sensitivity of species on habitat degradation and disturbance. Further, if there are differences in abundances of specialists between two regions our study may show the impacts of long-term disturbances and reveal the mechanisms of biotic homogenization. That gives new insights on protection of species and should also be taken into account in conservation planning.

Material and methods

Bird data

For this study we use point count data of breeding birds in two continents. First, point count data from the common bird monitoring project (CBMP) conducted between 1984 and 2016 (Koskimies & Väisänen 1991; Laaksonen & Lehikoinen 2013) in the whole of Finland was used to calculate the level of habitat specialism of individual species (Julliard et al. 2006) and in the regional assemblage (Devictor et al. 2008a). CBMP is based on voluntary point count routes, each established by a birdwatcher who is conducting the counts. The route has 20 points which are counted in one morning, preferably around the same time each year by the same observer. To avoid pseudoreplication we used only the data from the first year in which a route was censused. In CBMP, each station is located in a uniform habitat within 50 m of the station. Habitat type is classified into 17 classes (Appendix 1).

Second, we used Minnesota Breeding Bird Atlas (MNBBA) data conducted 2009-2014 in the state of Minnesota. The method used in MNBBA is similar to Finnish CBMP, but the approach is more systematic and more or less evenly covers the whole state of Minnesota. In MNBBA, the state is divided into 2775 townships, which is a 6 by 6 mile square. Further, each township is divided into four quarters of which the northeastern corner was systematically selected for survey. In each 3 by 3 mile square, three 10 minute point counts were conducted. The points were selected so that one point was in the most common habitat of that township, second on second most common and third was randomly selected. Within the 50 m radius surrounding the point over 50% of area must be of uniform habitat. In MNBBA, there are 25 habitat classes (Appendix 2). For both data we used only observations made inside 50m radius from the point.

We grouped the bird species used in this study into two habitat association groups, forest birds and non-forest birds, based on their primary breeding habitat obtained from literature (Alderfer 2006; Svensson et al. 2010). We also grouped the birds based on their migration strategies into three migratory habit groups: residents, short-distance migrants and long-distance migrants (Alderfer 2006; Svensson et al. 2010). A species was considered resident if at least part of the population is present on breeding grounds all year round. Species overwintering in the tropics (sub-Saharan Africa or SE Asia for Finnish birds; south from the conterminous USA for MN birds) were considered as long-distance migrants and the rest as short-distance migrants.

Species Specialization Index

In the last decade one of the most popular way to study specialization is Species Specialization Index, SSI (Julliard et al. 2006). SSI is an easy and useful tool for studying specialization even for large data sets such as bird point count data (Devictor et al. 2008a). It describes species' habitat specialization by comparing densities of individuals in different habitat classes. SSI is calculated by dividing the standard deviation of densities among habitat classes with the average density across habitat classes. SSI yields low values for habitat generalist species that show little variation in densities among habitat classes whereas high specialists' densities concentrate on one or very few habitat classes. Habitat specialization can also be applied for community scale studies by using Community Specialization Index (CSI), which is abundance

weighted average of SSI of species in a given community (Julliard et al. 2006; Devictor et al. 2008a).

However, SSI does not take into account variation in densities within habitat classes, i.e. it assumes even distribution of individuals among sampling units within a class. This creates a potential bias because species may not perceive the environmental variation corresponding to human-created habitat categories. Therefore, SSI may severely underestimate the level of species specialization particularly for truly specialized species, which show marked variation in densities within a habitat class according to finer level environmental variation. Naturally, the problem would be solved with more detailed habitat categorization. However, when large and long term data sets have been collected for decades, it may not be feasible to change the common practices very radically especially if the data are collected by volunteers as, for example, bird data often are. Therefore, we suggest a supplementary method for calculating SSI, which takes into account the variation in abundance within a given habitat category.

For each habitat class we derived average densities, and then calculated sample size bias corrected species specialization index, SSIC (from this on SSI_OLD) (Devictor et al. 2008a). We suggest that in addition to sample size bias there is another source of bias in SSI originating from within habitat variation in densities. Therefore, we further corrected SSI_OLD for variation within habitat classes by first dividing total variance in densities among sampling units (point count stations) into among-habitat and within-habitat components. Subsequently, we used the within-habitat variance to derive a correction coefficient:

$$1 + \left(\frac{\sqrt{\delta_{within}^2}}{average} - S/n \right)$$

where δ_{within}^2 is the variance in densities within habitat class and average is the average density among habitat classes, S is the number of sampling units and n is the number of observed individuals. The correction coefficient equals 1 if individuals of a species are evenly distributed across all sampling units in all habitat classes; high values denote marked within-habitat variation. In summary, the corrected SSIC-index (SSI_NEW) yields low values for species that is evenly distributed among habitats and among sampling units within a habitat (generalists), and high values for species whose

individuals are concentrated in one or few habitat classes, and unevenly distributed to sampling units within a habitat class (specialists). The original SSI was corrected for bias caused by small sample size (Devictor et al. 2008a) and therefore also our correction coefficient was further corrected for small sample size bias. To implement this, a ratio of the number of sampling units and the number of observed individuals is subtracted. However, if S/n is smaller than one, the correction factor will still be one, not to make the original SSI smaller. We calculated this bias to all species found in our data. The correction factors ranged from 0 to 36.6 in Finland and in Minnesota from 0 to 67.4 while SSI_OLD varied less (0.42-3.41 in Finland; 0.50-2.37 in Minnesota). SSI_OLD and SSI_NEW were only moderately correlated (Finland $R^2 = 0.116$, $n=75$; Minnesota $R^2 = 0.201$, $n = 78$), so actually some 80% or more of the variation in NEW_SSI was induced by the bias from within habitat variation. When plotting the values (Fig 1), it can be seen that SSI_OLD tended to underestimate the true level of specialization. This underestimation was bigger the more specialized the species is, i.e. species that are unevenly distributed among habitat classes also tended to be unevenly distributed among sampling units within a habitat class.

We calculated average SSI_NEW values for the total avifauna in Finnish and Minnesotan data, and separately for forest birds vs. non-forest birds and for different migratory groups. Finally, we calculated Community Specialization Index as abundance weighted averages of the SSI_NEW values (Julliard et al. 2006) for all birds as well as forest and non-forest birds and different migratory groups in Finland and Minnesota.

Statistical analyses

We used General Linear Model to analyze differences in Species Specialization Index of forest and non-forest birds between two geographical areas. To analyze differences in Community Specialization Index we used the same analyses weighted with abundances. We also analyzed if there are differences in specialization between different migration strategies. The analyses were completed using IBM SPSS Statistics 24 program.

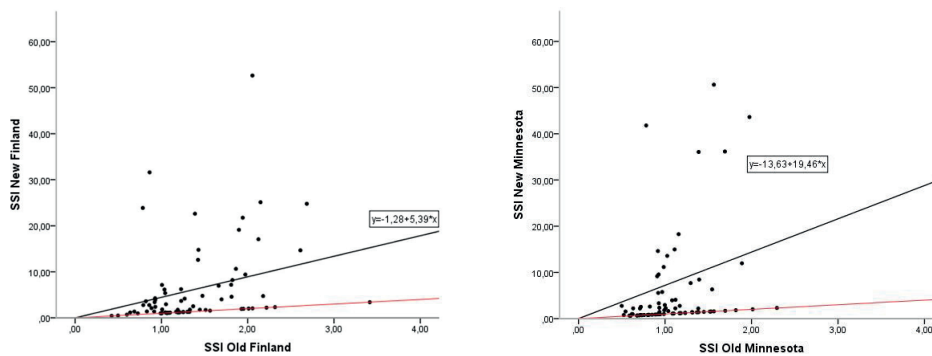


Fig. 1. Relationship between old and new SSI values. The red lines represent 1:1 line, i.e. the situation where the species are equally distributed among all points within habitats and the correction factor is 1, and, thus, both indexes have the same value. Black line represents OLS regression between old and new SSI values.

Results

We found no statistically significant differences in the overall habitat specialization between Minnesota and Finland (region effect in Table 1). There was no significant main effect of habitat association on habitat specialization (Table 1), but non-forest birds (average SSI= 8.70; sd= 16.88) tended to be more specialized than forest birds (average SSI= 4.70; sd= 8,62). There was a significant interaction effect between region and habitat association on species specialization (Table 1). In Minnesota non-forest bird were more specialized in their habitat use than forest birds; in Finland there was no difference between forest and non-forest birds in their level of specialization. (Table 2). However, we did not find support for our hypothesis that forest birds in Minnesota would be more specialized than forest birds in Finland, but the pattern is the opposite (Table 1, Table 2). We found no effect of migratory habit on species habitat specialization (Table 1).

We found no statistically significant differences in the overall community specialization between Minnesota and Finland (region effect in Table 1) even though community specialization indices were higher in all ecological groups in Minnesota than in Finland except in forest birds and resident species (Table 2). The interaction effect between region and habitat association, which was significant on species specialization index, ceased to exist on community specialization (Table 1). We found no effect of migratory habit on community specialization (Table 1).

Discussion

We found that species that are unevenly distributed among habitat classes also tended to be unevenly distributed among sampling units within a habitat class, and that most variation in species abundances stems from within-habitat rather than from between-habitat variation. Thus, traditional SSI-index - even if corrected for sample size bias - may severely underestimate the level of habitat specialization. It seems birds in general respond to fine level habitat variation that is not captured by coarse habitat classification. Applying a more refined habitat classification may not be possible or even sensible in most studies. We therefore recommend acknowledging within-habitat variation when estimating species habitat specialization.

We acknowledge that SSI-indices between Minnesota and Finland cannot be directly compared because of slightly different habitat classification systems (Appendix 1, Appendix 2.) but comparisons within region can be used to address the hypotheses we presented in the introduction. In non-forest habitat classes there is some mismatch between Finland and Minnesota, but in forested habitats the classifications are more alike, which justifies the use of the comparisons in this paper concentrating on forest birds.

We found that forest birds in Finland were more specialized than non-forest bird species but in Minnesota the pattern was the opposite. This does not support the hypothesis derived from biogeographic history, that forest birds in the Nearctic region would be more specialized with respect to their habitats than forest birds in the western Palearctic region. Actually, Nearctic forest birds showed the lowest SSI-values, i.e. showed the highest level of habitat generalism of all ecological groups. We should therefore reject the hypothesis that more extensive forest biomes and closer contact with the tropical forests to the south through the Pleistocene glaciations has favoured higher level of habitat specialism among Nearctic forest birds.

Rather it seems that reduced historical habitat availability, large scale fragmentation of remaining forests and isolation from tropical wintering grounds - characteristics of the Western Palearctic region - are associated with high level of habitat specialization. We hypothesize that the fragmented Pleistocene refuges of extant western Palearctic species may have favoured specialism via at least two mechanisms. First, it is likely that the fragmented Pleistocene forest habitat conditions has selected against poor

dispersal ability. For example, Niebuhr et al. (2015) suggested that even a low level of fragmentation yields drastic changes in the survival for species with poor dispersal ability. Good dispersal ability may then have favoured specialization because good dispersers may more readily find their favoured resources than poor dispersers. There is no research to test if western Palearctic forest birds have better dispersal ability than Nearctic birds, and thus, this possibility remains a question for further studies.

Secondly, fragmented and species-poor forest refugia during the latest glacial maximum in the western Palearctic region may have favoured specialization to certain forest types if major forest tree species were restricted to non-overlapping refugia during the glacial periods. In this scenario, isolated forest fragments composed of few tree species facilitated specialization in forest birds restricted to them. Unfortunately, exact location of refugia during the latest glacial maximum still remains elusive for most plant and animal species (Willis & van Andel 2004) and different lines of evidence are at odds with respect to hypothesis of isolated and non-overlapping refugia of tree and bird species. Svenning et al. (2008) suggest that climatic conditions during the latest glacial maximum have been favourable for many boreal tree across large areas in Central and Eastern Europe and into the Russian Plain (Svenning et al. 2008). In contrast, there is strong phylogeographic signal suggesting isolated and non-overlapping glacial refugia for many tree and animal taxa (Taberlet et al. 1998; Brito 2005).

We found that non-forest birds in Minnesota were the most specialized group of species but in Finland non-forest birds were the least specialized group. We suggest that the reason is again in deep history: whereas in the western Palearctic specialism was favored in glacial refugia of forests, in Nearctic the climatic conditions during the Pleistocene were more favorable to forests, and grasslands were replaced by spruce and jack pine forests (Delcourt & Delcourt 1981; Anderson 2006). Therefore we hypothesize that the fragmented Pleistocene refuges of grasslands of the Nearctic may have favoured specialism similarly to forest species in Western Palearctic. After glaciation, grasslands were abundant across North American continent and only after European settlement the grassland habitats have degraded in such a magnitude that grassland species have declined heavily in the past 50 years (Samson & Knopf 1994; Sauer et al. 2017).

Counter to our hypothesis there were no significant differences in habitat specialization between resident, short-distance and long-distance migrants. Our results provide no support for the idea that resident birds would more specialized than migratory species because they live all year round in their breeding grounds (Imbeau et al. 2001).

We also observed that in both regions CSI values were lower than SSI values in birds in general, and in all ecological groups. This suggests that generalists are more abundant than specialists in the regional bird assemblages in both regions. In Finnish forest birds CSI value were clearly lower than relatively high average SSI, whereas in Minnesota the differences were moderate. Therefore, Finnish forest bird assemblages are clearly a non-random sample of the regional avifauna. We hypothesize that this is a result of strong habitat filtering (Keddy 1992) in intensively managed forest landscape favoring generalists. Long-term monitoring data from Finland shows that specialist species associated with forests tend to be declining (Valkama et al. 2011; Tiainen et al. 2016). This is a clear indication of habitat filtering favoring generalist species. It is a recurrent finding in literature that generalists are replacing specialists in disturbed and fragmented landscapes (Clavel et al. 2011). In Minnesota, where forest management is less intensive, habitat filtering is likely less severe than in Finnish forest landscapes. This is supported by long-term trends in forest bird populations, which are mostly stable or increasing in Minnesota (Niemi et al. 2016).

Conclusions

Our results show that despite large scale differences in deep history of forest biomes, there are no major general differences in average habitat specialization of birds and bird communities between two biogeographical regions. However, habitat fragmentation during Pleistocene glaciation favored habitat specialization, and the impacts of the Ice Age can be seen as more specialized communities in those habitats that experienced most severe changes: forests in Palearctic and grasslands in Nearctic. Forest birds in Finland are, on average, more specialized, but habitat filtering induced by intensive forest management is modifying community composition and it has stronger impacts on Finnish forest bird communities, whereas in less managed Minnesota birds show only moderate response. In conclusion, boreal forest specialists

that survived the large scale habitat changes of the Ice Age are now declining because of human induced forest habitat degradation. This study gives support for the many previous studies where rapid environmental change is shown to be the fundamental reason for biotic homogenization.

References

- Alderfer, J., editor. 2006. Complete birds of North America. National Geographic Society, Washington, D.C.
- Anderson, R. C. 2006. Evolution and origin of the Central Grassland of North America: climate, fire, and mammalian grazers. Source: The Journal of the Torrey Botanical Society **133**:1596-262. Available from <http://www.bioone.org/doi/> (accessed March 19, 2018).
- Barnagaud, J. Y., V. Devictor, F. Jiguet, and F. Archaux. 2011. When species become generalists: on-going large-scale changes in bird habitat specialization. *Global Ecology and Biogeography* **20**:630-640. Available from <http://doi.wiley.com/10.1111/j.1466-8238.2010.00629.x> (accessed January 22, 2014).
- Belmaker, J., C. H. Sekercioglu, and W. Jetz. 2012. Global patterns of specialization and coexistence in bird assemblages. *Journal of Biogeography* **39**:193-203. Blackwell Publishing Ltd. Available from <http://doi.wiley.com/10.1111/j.1365-2699.2011.02591.x> (accessed April 24, 2017).
- Brito, P. H. 2005. The influence of Pleistocene glacial refugia on tawny owl genetic diversity and phylogeography in western Europe. *Molecular Ecology* **14**:3077-3094. Wiley/Blackwell (10.1111). Available from <http://doi.wiley.com/10.1111/j.1365-294X.2005.02663.x> (accessed March 20, 2018).
- Burton, P. J., Y. Bergeron, B. E. Bogdanski, G. P. Juday, T. Kuuluvainen, B. J. MacAfee, A. Ogden, and V. Teplyakov. 2010. Sustainability of Boreal Forests and Forestry in a Changing Environment. *Page Forests and Society - Responding to Global*

Drivers of Change. International Union of Forest Research Organizations (IUFRO).

Chase, J. M., and M. A. Leibold. 2003. *Ecological Niches*. University of Chicago Press. Available from <http://www.bibliovault.org/BV.landing.epl?ISBN=9780226101804> (accessed May 19, 2017).

Clavel, J., R. Julliard, and V. Devictor. 2011. Worldwide decline of specialist species: toward a global functional homogenization? *Frontiers in Ecology and the Environment* **9**:222–228. Available from <http://www.esajournals.org/doi/abs/10.1890/080216> (accessed January 22, 2014).

Delcourt, P., and H. Delcourt. 1981. Vegetation maps for eastern North America: 40,000 BP to present. Pages 123–165 in R. Roman, editor. *Geobotany II*. Plenum, New York, NY.

Devictor, V., R. Julliard, J. Clavel, F. Jiguet, A. Lee, and D. Couvet. 2008a. Functional biotic homogenization of bird communities in disturbed landscapes. *Global Ecology and Biogeography* **17**:252–261. Available from <http://doi.wiley.com/10.1111/j.1466-8238.2007.00364.x> (accessed January 21, 2014).

Devictor, V., R. Julliard, D. Couvet, and F. Jiguet. 2008b. Birds are tracking climate warming, but not fast enough. *Proceedings. Biological sciences / The Royal Society* **275**:2743–8. Available from <http://www.pubmedcentral.nih.gov/articlerender.fcgi?artid=2605823&tool=pmc-entrez&rendertype=abstract> (accessed January 21, 2014).

Devictor, V., and A. Robert. 2009. Measuring community responses to large-scale disturbance in conservation biogeography. *Diversity and Distributions* **15**:122–130. Available from <http://doi.wiley.com/10.1111/j.1472-4642.2008.00510.x> (accessed January 22, 2014).

Grinnel, J. 1917. The Niche-relationships of the California Trasher. *Auk* **34**:427–433.

Hooper, D. U., E. C. Adair, B. J. Cardinale, J. E. K. Byrnes, B. a. Hungate, K. L.

- Matulich, A. Gonzalez, J. E. Duffy, L. Gamfeldt, and M. I. O'Connor. 2012. A global synthesis reveals biodiversity loss as a major driver of ecosystem change. *Nature* **486**:105–8. Nature Publishing Group. Available from <http://www.ncbi.nlm.nih.gov/pubmed/22678289> (accessed January 22, 2014).
- Häkkilä, M., E. Le Tortorec, L. Brotons, A. Rajasärkkä, R. Tornberg, and M. Mönkkönen. 2017. Degradation in landscape matrix has diverse impacts on diversity in protected areas. *PLoS ONE* **12**.
- Imbeau, L., M. Mönkkönen, and A. Desrochers. 2001. Long-Term Effects of Forestry on Birds of the Eastern Canadian Boreal Forests: a Comparison with Fennoscandia. *Conservation Biology* **15**:1151–1162. Blackwell Science Inc. Available from <http://doi.wiley.com/10.1046/j.1523-1739.2001.0150041151.x> (accessed March 17, 2017).
- Julliard, R., J. Clavel, V. Devictor, F. Jiguet, and D. Couvet. 2006. Spatial segregation of specialists and generalists in bird communities. *Ecology letters* **9**:1237–44. Available from <http://www.ncbi.nlm.nih.gov/pubmed/17040326> (accessed January 22, 2014).
- Keddy, P. A. 1992. Assembly and response rules: two goals for predictive community ecology. *Journal of Vegetation Science* **3**:157–164. Blackwell Publishing Ltd. Available from <http://doi.wiley.com/10.2307/3235676> (accessed December 13, 2017).
- Kortesmaa, T., and A. Jokela, editors. 2017. E-yearbook of food and natural resource statistics for 2016 : Statistical facts on agriculture, forestry, fisheries and hunting in Finland. Available from <http://urn.fi/URN:ISBN:978-952-326-407-6>.
- Koskimies, P., and R. Väisänen. 1991. Monitoring bird populations. Zoological Museum, Finnish Museum of Natural History.
- Laaksonen, T., and A. Lehikoinen. 2013. Population trends in boreal birds: Continuing declines in agricultural, northern, and long-distance migrant species. *Biological Conservation* **168**:99–107. Elsevier Ltd. Available from <http://linkinghub.elsevier.com/retrieve/pii/S0006320713003169> (accessed April 29, 2014).

- Latham, R. E., and R. E. Ricklefs. 1993. Continental Comparisons of Temperate-Zone Tree Species Diversity. Page in R. Ricklefs and D. Schluter, editors. *Species Diversity in Ecological Communities*. University of Chicago Press, Chicago.
- Levins, R. 1968. *Evolution in changing environments: some theoretical explorations*. Princeton University Press.
- MacArthur, R. H. 1972. *Geographical ecology: patterns in the distribution of species*. Harper & Row. New York. Available from https://books.google.fi/books?hl=fi&lr=&id=3NAYEKc--WAC&oi=fnd&pg=PR11&dq=MacArthur+R.H.+1972.+Geographical+ecology:+p+atterns+in+the+distribution+of+species.+Princeton+University+Press.&ots=Mr1L4UqQPv&sig=OqmlKgEAWCuJfAoc3vJ1RfRklSI&redir_esc=y#v=onepage& (accessed May 19, 2017).
- McKinney, M., and J. Lockwood. 1999. Biotic homogenization: a few winners replacing many losers in the next mass extinction. *Trends in ecology & evolution* **14**:450-453. Available from <http://www.ncbi.nlm.nih.gov/pubmed/10511724>.
- Mönkkönen, M., and P. Viro. 1997. Taxonomic diversity of the terrestrial bird and mammal fauna in temperate and boreal biomes of the northern hemisphere. *Journal of Biogeography* **24**:603-612. Blackwell Publishing Ltd. Available from <http://doi.wiley.com/10.1111/j.1365-2699.1997.tb00072.x> (accessed May 22, 2017).
- Mönkkönen, M., and D. A. Welsh. 1994. A biogeographical hypothesis on the effects of human caused landscape changes on the bird communities of Europe and North America. *Annales Zoologici Fennici* **31**:61-70.
- Niebuhr, B. B. S., M. E. Wosniack, M. C. Santos, E. P. Raposo, G. M. Viswanathan, M. G. E. da Luz, and M. R. Pie. 2015. Survival in patchy landscapes: the interplay between dispersal, habitat loss and fragmentation. *Scientific Reports* **5**:11898. Nature Publishing Group. Available from <http://www.nature.com/articles/srep11898> (accessed March 20, 2018).
- Niemi, G. J. et al. 2016. Analysis of Long-term Forest Bird Monitoring Data from National Forests of the Western Great Lakes Region. Gen.Tech.Rep. NRS-159. U.S. Department of Agriculture, Forest Service, Northern Research Station.

- Potapov, P. et al. 2008. Mapping the World's Intact Forest Landscapes by Remote Sensing. *Ecology and Society* **13**:art51. The Resilience Alliance. Available from <http://www.ecologyandsociety.org/vol13/iss2/art51/> (accessed November 28, 2017).
- Roberge, J.-M., R. Virkkala, and M. Mönkkönen. 2018. Boreal forest bird assemblages and their conservation. Page in G. Mikusiński, J.-M. Roberge, and R. Fuller, editors. *Ecology and Conservation of Forest Birds*. Cambridge University Press.
- Sala, O. E. 2000. Global Biodiversity Scenarios for the Year 2100 . *Science* **287**:1770–1774. Available from <http://www.sciencemag.org/cgi/doi/10.1126/science.287.5459.1770> (accessed January 21, 2014).
- Samson, F., and F. Knopf. 1994. *Prairie Conservation in North America*. BioScience **44**:418–421. Oxford University Press. Available from <https://academic.oup.com/bioscience/article-lookup/doi/10.2307/1312365> (accessed May 31, 2017).
- Sauer, J. R., D. K. Niven, J. E. Hines, D. J. Ziolkowski, K. L. Pardieck, J. E. Fallon, and W. A. Link. 2017. *The North American Breeding Bird Survey, Results and Analysis 1966-2015*. Version 2.07.2017. USGS Patuxent Wildlife Research Center, Laurel, MD.
- Svenning, J.-C., S. Normand, and M. Kageyama. 2008. Glacial refugia of temperate trees in Europe: insights from species distribution modelling. *Journal of Ecology* **96**:1117–1127. Wiley/Blackwell (10.1111). Available from <http://doi.wiley.com/10.1111/j.1365-2745.2008.01422.x> (accessed March 20, 2018).
- Svensson, L., P. J. Grant, K. Mullarney, and D. Zetterström. 2010. *Collins Bird Guide*. The most complete guide to the birds of Britain and Europe., 2nd edition. Collins, London.
- Taberlet, P., L. Fumagalli, A.-G. Wust-Saucy, and J.-F. Cosson. 1998. Comparative phylogeography and postglacial colonization routes in Europe. *Molecular Ecology* **7**:453–464. Wiley/Blackwell (10.1111). Available from <http://doi.wiley.com/10.1046/j.1365-294x.1998.00289.x> (accessed March 20, 2018).

- Tiainen, J. et al. 2016. Suomen Lintujen Uhanalaisuus 2015 - The Red List of Finnish Bird Species.
- Travis, J. M. J. 2003. Climate change and habitat destruction: a deadly anthropogenic cocktail. *Proceedings. Biological sciences / The Royal Society* **270**:467–73. Available from <http://rspb.royalsocietypublishing.org/content/270/1514/467.abstract> (accessed September 4, 2015).
- Valkama, J., V. Vepsäläinen, and A. Lehikoinen. 2011. The Third Finnish Breeding Bird Atlas. Available from <http://atlas3.lintuatlas.fi/english>.
- Willis, K. J., and T. H. van Andel. 2004. Trees or no trees? The environments of central and eastern Europe during the Last Glaciation. *Quaternary Science Reviews* **23**:2369–2387. Pergamon. Available from <https://www.sciencedirect.com/science/article/pii/S0277379104001623?via%3Dihub> (accessed March 20, 2018).

Table 1. Results of General Linear Model explaining differences in Species Specialization Index of forest and non-forest birds and between different migration strategies between Finland and Minnesota.

	SSI			CSI		
	df	F	Sig	df	F	Sig
Intercept	1	23.194	0.000	1	11.484	0.001
Region	1	0.000	0.994	1	0.007	0.934
Migratory habit	2	0.009	0.991	2	0.081	0.922
Habitat association	1	1.355	0.246	1	0.988	0.322
Region*Migratory habit	2	1.825	0.165	2	0.772	0.464
Region*Habitat association	1	6.068	0.015	1	2.026	0.157
Migratory habit*Habitat association	2	2.537	0.083	2	1.315	0.272
Region*Migratory habit*Habitat association	2	0.132	0.877	2	0.140	0.869

Table 2. Average Species Specialization Index and Community Specialization Index (CSI) of forest and non-forest birds and different migratory groups in Finland and Minnesota. Standard deviations in parenthesis.

	SSI Finland	SSI Minnesota	CSI Finland	CSI Minnesota
All birds	6.11 (8.88)	8.00 (17.94)	3.16 (5.14)	6.10 (13.56)
Forest birds	8.35 (11.63)	1.48 (0.78)	2.66 (4.92)	1.19 (0.69)
Non-forest birds	4.71 (6.35)	12.78 (22.53)	3.80 (5.34)	8.37 (15.86)
Resident birds	10.01 (8.88)	2.25 (2.95)	4.99 (7.46)	2.12 (2.18)
Short-distance migrants	4.67 (5.38)	11.07 (23.02)	2.81 (3.61)	7.30 (15.34)
Long-distance migrants	4.54 (7.08)	6.29 (12.91)	2.57 (4.81)	4.90 (11.02)

Appendix 1. Habitat classes of point counts in Finland

Boreal spruce dominated forest
Boreal Scots pine dominated forest
Boreal deciduous forest
Mixed forest
Shrub (Deciduous, less than 5m tall)
Conifer saplings (less than 5m tall)
Clear cut (trees and shrubs less than 1m tall)
Pine bog
Open peatland
Grassland
Cropland
Rural inhabitation (farmsteads, buildings, orchards)
Parks
Urban areas (mainly buildings)
Mountain birch forest
Open tundra
Other

Appendix 2. Habitat classes of point counts in Minnesota

Boreal Coniferous Forest
Boreal Deciduous Forest
Boreal Lowland Grassland
Boreal Shrub Swamp
Cropland
Developed-High Intensity
Developed-Low Intensity
Developed-Medium Intensity
Lowland Coniferous Forest
Lowland Deciduous Forest
Lowland Herbaceous
Northern Hardwoods
Oak Forest
Oak Savannah
Open Water
Parkland Deciduous Forest
Pine Forest
Pine-Oak Barrens
Quarries-Strip Mines-Gravel Pits
Rural Developed Forest
Shrub Swamp
Upland Grassland
Upland Native Grassland
Upland Shrub
Urban Developed Forest

II

DOES HUMAN LAND-USE LEAD TO BIOTIC HOMOGENISATION OF FOREST BIRD COMMUNITIES IN NORTHERN USA?

by

Eric Le Tortorec, Matti Häkkilä, Edmund Zlonis, Gerald J. Niemi & Mikko
Mönkkönen 2018

Manuscript

Does human land-use lead to biotic homogenisation of forest bird communities in northern USA?

Eric Le Tortorec¹, Matti Häkkinen¹, Edmund Zlonis², Gerald Niemi², Mikko Mönkkönen¹

¹ Department of Biological and Environmental Science, University of Jyväskylä, Jyväskylä, Finland

² Department of Biology, University of Minnesota, Duluth, USA

Abstract

Studies have shown negative impacts of increased human pressures on biodiversity at both local (alpha diversity) and regional (gamma diversity) scales. However, the diversity between local sites (beta diversity) has received less attention. This is an important shortcoming since beta diversity acts as a linkage between trends at the local and regional scales. Decreased beta diversity means that local sites lose their distinctiveness, becoming more similar to each other. This process is known as biotic homogenisation and it is predicted to arise through the replacement specialised native specialists with non-native generalists. However, the mechanisms causing biotic homogenisation are still not clear and its impacts on different facets of biodiversity have not been fully studied. In this study, we studied how land-use change due to human actions causes biotic homogenisation of taxonomic, functional and phylogenetic diversity in bird communities of forested habitats in the state of Minnesota, USA. Our aim was to study if increased human pressure, which included human population density, land transformation, transport infrastructure, and electrical power infrastructure, was associated with increased similarity of bird point count sites. Our results showed that elevated human pressure did not appear to be related with increased biotic homogenisation

in our study region. Interestingly, we found that increased human pressure appeared to increase the between-site functional diversity of bird communities. This association was driven by a decrease in local diversity, which, due to the nature of beta diversity, led to an increase in between-site diversity. This study highlights the importance of taking multiple facets of biodiversity into consideration and critically considering the use of beta diversity in a conservation setting.

Introduction

Global studies have shown that human-caused land-use changes and their associated pressures have led to strong, consistent and accumulating negative impacts on biodiversity (Haddad et al. 2015). Human pressures that contribute to land use change such as agriculture, timber harvesting, and urbanisation have significantly modified ecosystems worldwide (Foley et al. 2005). Of these, forest ecosystems have been especially heavily impacted by human activities, showing a decrease in area of over 3% during just the last 25 years (FAO 2016). There are signs that the rate of forest loss is decreasing but the proportion of managed forests is increasing at the expense of natural forest cover (FAO 2016). In addition, an increasing threat to forests worldwide is harvesting forests for bioenergy (Sheppard et al. 2011). Natural forests harbour high levels of productivity, biomass, and biodiversity (Foley et al. 2005) and decreases in their cover have the potential to have significant negative impacts on biodiversity and ecosystem services.

Human activities appear to impact different scales of biodiversity in different ways (McGill et al. 2015). Studies have shown that biodiversity at the local scale (alpha diversity) has not changed significantly through time, whereas biodiversity at the global scale has decreased. For example, Vellend et al. (2013) showed that local-scale plant species diversity has not significantly changed through time, and that

species increases are as common as species decreases. Similarly, Dornelas et al. (2014) showed that time series of local species richness did not show a systematic loss, although community composition did change. However, Newbold et al. (2015) inferred from models based on empirical data that at a global scale, local assemblages have lost over 13% of their species richness due to human pressures. The discrepancy between trends in local and global biodiversity can be explained by a spatial measure of biodiversity – beta diversity.

Beta diversity measures variation in biodiversity in space and, since it cannot be measured directly, is derived from the total diversity of a region (gamma diversity) and the local diversities of sampled sites. Beta diversity, in its additive form, is calculated as gamma diversity minus the mean alpha diversity of a region (Tuomisto 2010). In this form, beta diversity reflects absolute effective species turnover by quantifying how much the effective species richness of an entire region exceeds that of an average single location. A higher level of beta diversity in a region indicates that the composition of local sites is different from each other than in a region with a lower level of beta diversity. Thus, even though local diversity might not show a decrease, the total diversity of a region could decrease if the individual sites became more similar in composition. For example, uneven losses in species between sites can lead to decreased mean alpha diversity, which will increase the beta diversity of a region. On the other hand, the colonisation of specialists into new sites can increase mean alpha diversity (McCune and Vellend 2013), leading to a decrease in the beta diversity of a region. This holds for both the additive and multiplicative forms of beta diversity. Thus, in a conservation setting, maximising beta diversity could lead to negative impacts on local biodiversity (Socolar et al. 2016).

Increasing similarity between local sites (decreased beta diversity), is a process known as biotic homogenisation (Olden 2006). Biotic homogenisation has been shown to be a global phenomenon, occurring in almost all taxonomic groups

(Baiser et al. 2012) and resulting from human land-use intensification, including urbanisation (McKinney 2006) and intensive agriculture (Ekroos et al. 2010). Human activities causing the introduction of exotic and invasive species and extinctions of native species have the potential to cause species composition in different sites to become more similar (Baiser et al. 2012). Local species extinctions often involve specialists with narrow dietary and habitat preferences, and they are often replaced by generalists that can withstand fluctuating environmental conditions and human-built environments (McKinney and Lockwood 1999, Clavel et al. 2011). These generalists have often been described as species with global ranges but there is evidence that they are often native species (La Sorte and Boecklen 2005). Since specialists, by definition, possess specialised functions, their loss in a community decreases functional diversity. Functional diversity is of special concern for human well-being as it is an important component of ecosystem functioning, which is the basis of the ecosystem services that humans depend on (Cardinale et al. 2012). There is already evidence that the loss of biodiversity is creating an ecosystem services debt that will be exacerbated by continuing biodiversity loss (Isbell et al. 2015), with potential decrease in the resilience of ecosystem functions (Oliver et al. 2015). In addition, specialised species often have unique phylogenetic histories, the loss of which decreases the phylogenetic diversity of communities. Since biotic homogenisation, and many other phenomena related to biodiversity, has been studied mainly from the aspect of the number of species (taxonomic diversity) we still have a limited understanding of how different facets of biodiversity respond to human activities.

We studied how land-use change due to human actions causes biotic homogenisation in bird communities of forested habitats in the state of Minnesota, USA. Our aim was to study if an increasing human footprint, which includes human population density, land transformation, transport infrastructure, and electrical power infrastructure, causes bird communities to become more similar to

each other (decreased beta diversity) as predicted by biotic homogenisation theory. We also addressed if biotic homogenization is associated with changes in regional forest cover, which would be expected based on the overall negative effects that habitat loss has on biodiversity. We controlled for factors known to impact biodiversity, including habitat diversity, net primary productivity, and temperature (Qian 2010). We studied this phenomenon from the taxonomic, functional and phylogenetic viewpoints. We predicted that increased human footprint and forest change would lead to decreased diversity between bird count sites, visible as decreased beta diversity. We also expected taxonomic, functional, and phylogenetic diversity to show different sensitivities to human influence (Devictor et al. 2010).

Methods

Study design

Bird point count data were collected between 2009 and 2014 as part of the Minnesota Breeding Bird Atlas (MNBBA; Pfanmuller et al. (2017)). The goal of the MNBBA was to systematically sample breeding birds across the state by collecting data in each township of the state. Townships measure approximately 93 km² (6 x 6 miles) and were developed by the Public Land Survey System (PLSS). Within each township, three point locations were selected. The first point was placed in a random land use class, the second point represented the most common land use class in the township, and the last point was placed in the second most common land use class in the township. Land use data were derived from the 2001 National Land Cover Database (Homer et al. 2004). Counts were conducted primarily on secondary roads; large, paved roads such as state or federal highways were avoided. Townships in roadless areas such as the Boundary Waters Canoe Area Wilderness, Voyageurs National Park, and the Red Lake Peatland were sampled from trails, portages, and water by hiking, biking, boat, or canoe. For the purposes

of this study, the townships in Minnesota were combined into 617 units, each comprising four townships and measuring roughly 19.3 x 19.3 km (12 x 12 miles). Each unit formed a square, except for a few specific areas where irregular units constructed from one to four townships were used. Units were developed by selecting a random township, which was used as the north-eastern square of the first unit. Subsequent units were then formed using the first unit as a reference point until the entire state was covered.

The primary objective of the MNBBA point counts was to insure equal and consistent sampling of the bird community across the state of Minnesota. This included a random sampling approach and standardization of effort in gathering data within each township. Individuals participating in the gathering of point counts were required to pass a test of 86 bird species songs or have more than 5 years of field experience in counting birds with point counts in Minnesota. Those gathering data on point counts were also tested by audiologists to insure their hearing ability was in normal ranges and they participated in three days of "standardisation" in point count data gathering with an experienced field ornithologist.

During a 10-minute point count, all birds seen or heard were recorded (i.e., unlimited distance) but distances from the point were estimated to allow habitat-specific data to be used (observations within 25, 50, 100 m, and > 100 m of the census point). Point counts were completed from the last week of May (in southern MN) to the second week of July (northern MN) from 2009 to 2014. Most counts were completed in June. Point counts were gathered from approximately 0.5 hour before to four hours after sunrise on days with little wind (< 15 km/hr) and little or no precipitation. Extensions from sunrise to 6 hours were allowed for counts in western MN due to the high proportion of windy days and based on the experience of ornithologists in that region. All points were located and marked

with a GPS device, cover type of vegetation visually estimated, and pictures taken in the two directions perpendicular to the road.

A total of 7070 MNBBA counts were performed between May 2009 and June 2014. Abundances of birds identified to the species level within 100m of the MNBBA point were used since the habitat classification was conducted at the same spatial scale (see below). For the analyses in this study we used MNBBA points located in forested land cover classes. To ensure that the dominant habitat being sampled was forest, we first calculated the proportion of landcover types within 100m of each MNBBA count location using the 'isectpolyrst' tool in Geospatial Modelling Environment version 0.7.3.0 (Beyer 2012). Landcover classes were derived from the LANDFIRE dataset (Rollins et al. 2006). One hundred and fifteen cover types in the LANDFIRE Existing Vegetation Type database were consolidated and reclassified into 25 classes representing the land-use and habitat available in Minnesota. Each count location was characterized by the dominant (highest proportion) landcover type. All counts with any of the following dominant landcover classes were considered forested; lowland deciduous forest, northern hardwoods, pine forest, boreal deciduous, oak forest, parkland deciduous forest, boreal coniferous, lowland coniferous, rural and urban developed forest, pine-oak barrens and oak savannah. For those MNBBA points that had been counted more than once we selected the earlier observation. We used MNBBA points located at least 200m from each other (twice the distance of the bird count radius) to avoid overlap between bird counts. From pairs of MNBBA points located under 200m from each other we selected the earlier observation, and if both points had the same date one was chosen randomly. For calculating bird community diversities, we only used units that had at least 3 MNBBA points located in a forested land use class (2217 forested MNBBA points in 287 units). We determined 3 points to be the minimum number of communities to reliably estimate beta diversity.

Calculation of beta diversities

Within each unit we calculated taxonomic, functional, and phylogenetic beta (β) diversities with Rao's quadratic entropy using R functions developed by de Bello et al. (2010). The Rao index measures dissimilarity by summing total dissimilarity and weighting it by species proportions. In addition, the Rao index makes it easy to incorporate alternative measures of biodiversity by taking into account distances (e.g. functional or phylogenetic) between pairs of species (de Bello et al. 2010).

We calculated β_{eqv} as the total diversity of a unit (γ_{eqv}) minus the average diversity of MNBBA points (α_{eqv}) within a unit. We then calculated β_{prop} as the proportion of γ_{eqv} explained by β_{eqv} . By taking the number of forested bird count points into account, we were able to compare the proportion of γ_{eqv} explained by β_{eqv} between units with differing numbers of points. In addition, using a proportional measure of β_{eqv} enabled us to directly compare the proportion explained by different facets of biodiversity (taxonomic, functional, and phylogenetic).

Taxonomic diversity measures were calculated using species abundance data collected from MNBBA bird count locations. We calculated functional diversity by using numerical data on the diet composition, foraging stratum, activity time and body size from the dataset produced by Belmaker and Jetz (2015). Bird species were limited to those species found in our data, and functional distances were calculated with the daisy function in the R package cluster using Euclidean distances. Functional distances were scaled between 0 and 1 and used as a distance matrix in the calculation of diversity metrics. For the calculation of phylogenetic diversity, we downloaded a set of 1000 randomly chosen phylogenetic trees from the BirdTree database (Jetz et al. 2012), limited to the bird species found in our data. We used the consense function from the PHYLIP package (v.3.695) to create a single unrooted consensus tree using the 50% majority rule. This included all species that appeared in more than 50% of the trees. A phylogenetic distance matrix for all species in our data was calculated with the distTips function from the

adephylo R package, using the sums of branch lengths. These distances were then scaled between 0 and 1 and used to calculate phylogenetic diversities.

Calculation of explanatory variables

Human influence was estimated using the human footprint index (HFI) developed by the Wildlife Conservation Society and the Center for International Earth Science Information Network (2005). The HFI uses nine datasets describing four proxies of human influence measured between 1995 and 2004: population density, land transformation, accessibility, and electrical power infrastructure (Sanderson et al. 2002). Each 1km² grid cell in the global dataset was given a value ranging from 0 (low level) to 10 (high level) for each dataset. The nine values for each grid cell were summed and for each biome, the cell with the lowest value got a value of 0, and the cell with the largest value got a value of 100. The HFI data was clipped to the state of Minnesota, and the average HFI value for each unit was calculated. HFI values in our study area summarised human influence well, as seen in the correlation coefficients between HFI and total population, road density, and cover of human land-use classes (Appendix 1).

In addition to studying the impact of general human influence we also wanted to study how changes in forest cover influence biodiversity. In the state of Minnesota, areas experiencing forest change and those with high human influence are clearly separate (Appendix 1, Appendix 2a & b). We quantified forest change from the global forest change dataset developed by Hansen et al. (2013). The dataset uses Landsat data to identify stand-replacing disturbances or the total removal of tree canopy cover within each pixel. Using these data, we were able to quantify gross forest loss and gain at an annual frequency between 2000 and 2014. For each unit, we calculated the percent cover of forest change between 2000 and 2014. However, there was no reliable way of systematically separating forest change caused by humans from change caused by natural events such as forest fires and storms. There were four units that had been significantly impacted by three large forest

fires (Cavity Lake (2006), Ham Lake (2007), and Pagami Creek (2011) fires). Since the results from models run with and without the affected units did not change significantly, we decided to keep these units in the analyses.

In addition to variables describing human-caused changes in the environment, we also took into account abiotic variables known to impact biological diversity (Qian 2010). Habitat diversity for each unit was quantified by calculating the mean alpha diversity of habitat classes within units. Habitat classes were derived from the LANDFIRE reclassification described above. Temperature and precipitation are both known to impact biodiversity but due to high variance inflation (Zuur 2007) in the models where both variables were included we decided to include only temperature. For each unit, we calculated the mean temperature measured between 1980 and 2010 from data created by the PRISM Climate Group (PRISM Climate Group, Oregon State University in press). Information about net primary production (NPP) was obtained from remotely sensed data collected by the MODIS instrument at a 1km resolution. The algorithm that produces NPP values takes into account vegetation characteristics, meteorological measurements and land cover class and estimates NPP as kg of carbon sequestered in the form of biomass per square metre per year (Zhao et al. 2005). For each unit, we averaged NPP values between 2004 and 2014.

Statistical models

We constructed linear models to analyse the influence of human footprint, forest change, habitat diversity, temperature, NPP, and the number of forested MNBBA count locations on taxonomic, functional, and phylogenetic beta diversity. In addition, to aid in interpreting the results, we also analysed the influence of the explanatory variables on alpha and gamma diversity of the three facets of biodiversity. The results for alpha and gamma diversities can be found in Appendix 3. We checked all models to ensure that the variance inflation factors (VIF) of the explanatory variables were under 3 (Zuur 2007). Correlations between

explanatory variables can be found in Appendix 4 and VIF values for all models can be found in Appendix 5.

We visually inspected the residuals of all models to ensure that they were normally distributed, and tested residuals for spatial autocorrelation. Spatial autocorrelation of residuals was tested with a permutation test for the Moran's I statistic using 1000 permutations. All of the residuals from models explaining taxonomic diversity and models explaining alpha and gamma diversity for functional and phylogenetic diversity were normally distributed. The residuals for functional and phylogenetic beta diversity were right skewed and were thus modelled appropriately. In the case of functional beta diversity, we used a generalised linear model with Gamma family and an identity link. In the case of phylogenetic beta diversity, we detected spatial autocorrelation and we had to log-transform the response variable since the spatially autoregressive model that we used was not able to utilise the generalised linear model framework. The log-transformed values have been back-transformed in the results table. We also detected spatial autocorrelation in the residuals of the models explaining alpha and gamma diversity of all facets of biodiversity studied here. The residuals from these models were normally distributed. For cases where residuals were spatially autocorrelated, we utilised spatial error models, which is a type of autoregressive model. Spatial error models assume that spatial autocorrelation is due to missing spatial covariates (Bivand and Piras 2015). We did not detect spatial autocorrelation in any of the residuals from the spatial error models. All analyses were performed with R version 3.4.3 (2017-11-30). A list of used R packages and their versions can be found in Appendix 6.

Results

Summary statistics

The range of taxonomic beta diversity values (Table 1) was substantially larger than functional and phylogenetic beta diversity, reflecting the more limited set of ecological functions and phylogenetic backgrounds in comparison to the number of species present.

All three beta diversity measures were clearly correlated with each other, especially the correlation between functional and phylogenetic beta diversity (Figure 1). On the other hand, none of the response variables was strongly correlated with the total number of forest bird species, confirming that the patterns seen in this paper are relatively independent of local species richness.

Taxonomic beta diversity

Taxonomic beta diversity was not impacted by human footprint index (HFI), nor forest change. Instead, taxonomic beta diversity was positively associated with habitat diversity. Along the range of habitat diversity values (Table 2), taxonomic beta diversity increased by 6.9 units, which is a modest increase in biological terms (12.7%). This positive association was most likely caused by the positive influence of habitat diversity on taxonomic gamma diversity (Appendix 3b) and the lack of an association with taxonomic alpha diversity (Appendix 3a).

Functional beta diversity

Functional beta diversity had a statistically significant positive association with HFI. Along the gradient of HFI values in our data (Table 2), functional beta diversity increased by 3.1 units, which was a fairly strong biological impact (19.9%). HFI did not have a clear impact on functional alpha or gamma diversity but the negative estimate for functional alpha diversity was almost 30 times larger than the positive estimate for functional gamma diversity (Appendix 3c). This might have caused the positive association of HFI and functional beta diversity

(see discussion). Forest change did not appear to influence functional beta diversity. This was likely caused by forest change negatively impacting both functional alpha and gamma diversity, which cancelled out the impact on functional beta diversity.

Net primary (NPP) had a strong negative impact on functional beta diversity. Along the range of NPP values, functional beta diversity decreased by 3.3 units (-21.2%), which was even stronger than the impact of HFI. Similarly, mean annual temperature had a negative impact, decreasing functional beta diversity by 2.2 units (-14.1%). Interestingly, both the impacts of NPP and temperature on functional beta diversity were not accompanied by straightforward associations on functional alpha and gamma diversity (Appendix 3c & d). NPP appeared to have a positive but non-significant impact on alpha diversity but no impact on gamma diversity, which might be expected to decrease beta diversity. On the other hand, mean temperature had a positive and similarly strong influence on both functional alpha and gamma diversity, which would be expected to result in no apparent impact on beta diversity.

Phylogenetic beta diversity

Similar to taxonomic beta diversity, phylogenetic beta diversity was not impacted by HFI, nor forest change. This was despite the negative but non-significant influence of HFI on phylogenetic gamma diversity and no association with alpha diversity (Appendix 3e & f). However, the estimate of HFI's influence on phylogenetic alpha diversity was only two times as large as the estimate for phylogenetic gamma diversity, compared with the very large difference in estimates in the case of functional beta diversity. As was the case with functional diversity, forest change had a negative association with both phylogenetic alpha and gamma diversity, which likely cancelled each other out. Phylogenetic beta diversity was negatively associated with NPP and mean temperature. The biological impacts of both variables were very strong. Along the range of NPP

values (Table 2), phylogenetic beta diversity decreased by 6.7 units (-31%). Along the range of mean annual temperature values, phylogenetic beta diversity decreased by 6.5 units (-30.4%). NPP was not associated with either phylogenetic alpha or gamma diversity. Mean temperature had a positive impact on alpha diversity, which was likely behind the negative impact of temperature on beta diversity.

Discussion

Elevated human pressure did not appear to be related with increased biotic homogenisation in our study region. An increase in the human footprint index, which measured the impact of increased population density, land transformation, accessibility, and electrical power infrastructure, did not cause biotic homogenisation in taxonomic, functional or phylogenetic diversity. Instead, increased human footprint appeared to cause functional heterogenisation by increasing functional diversity between sites. Forest change did not appear to cause biotic homogenisation in any of the response variables. As such, our results appear to be at odds with previous studies that have shown homogenising impacts of increased human pressure. For example, urbanisation has been shown to homogenise environments and, consequently, biological communities (McKinney 2006, Sol et al. 2017), and agricultural expansion and intensification have been shown to homogenise bacterial (Rodrigues et al. 2013) and beetle communities (Gordon et al. 2009). Forest management has also been shown to cause biotic homogenisation of forest communities, although the impacts have often been subtle (Kitching et al. 2013, Mori et al. 2015, Ibarra and Martin 2015). Häkkinen et al. (2018) found signs of homogenization in protected areas surrounded by intensively managed forest, although the quality of the reserves played a more substantial role in determining species composition. However, it is important to note that some studies have shown no biotic homogenisation in response to increased human

pressure (Lee-Cruz et al. 2013) or, similar to this study, even an increase in between-site diversity (Catterall et al. 2010).

The result that increased human footprint appeared to increase functional diversity between sites is contrary to the results of many previous studies (McKinney 2006). Human footprint clearly summarised human pressures well since it was strongly correlated with total population, density of roads and human land-use cover (Appendix 1). A potential reason that beta diversity increases in response to increased human impact is likely related to the very nature of beta diversity. Between-site diversity (beta diversity), in both its additive and multiplicative forms, is derived from total regional diversity (gamma diversity) and mean local diversity (mean alpha diversity). In this study we calculated beta diversity as gamma diversity minus mean alpha diversity. Thus, beta diversity could increase in response to an increase in gamma diversity or a decrease in alpha diversity. Human footprint did not have a statistically significant impact on functional gamma or alpha diversity (Appendix 3c & d) but the negative estimate for local diversity was more than an order of magnitude stronger than that for regional diversity, which may have been related to the positive impact on between-site diversity. The negative estimate for the impact of human footprint on functional alpha diversity suggests that increased human footprint has led to a loss of functionally distinct species from local communities. If this loss occurred randomly, impacting some areas but not others, this could lead to MNBB count locations being more different from each other. This loss of species from local communities with increasing human footprint indicates that functional beta diversity was primarily affected by the nestedness component of beta diversity, although impacts on turnover resulting from species replacement along the human footprint gradient cannot be ruled out (Baselga 2010).

The positive response of beta diversity to increasing human pressure is supported by the conceptual trajectory outlined in Socolar et al. (2016). In this model, beta

diversity increases in response to subtractive heterogenisation caused by some native species becoming rarer and invasive species beginning to establish themselves (additive heterogenisation). Beta diversity then begins to decrease as rarer species begin to disappear and invasive species start to dominate. Since we only used relatively forested units in our analyse the level of human pressure in these units was clearly lower than that of units left out of analyses (Appendix 7). Therefore, it is possible that human pressure in our study was so low that it increased diversity between MNBBA sites.

Forest change and human footprint were clearly spatially segregated in the state of Minnesota (Appendix 2a & b), and thus captured different facets of human pressure in the state (Appendix 1). However, similar to human footprint, forest change did not appear to cause biotic homogenisation in any of the responses studied here even though it has been shown to homogenise biological communities, especially in the tropics (Lôbo et al. 2011, Kitching et al. 2013, Ibarra and Martin 2015). It is possible that the forests in this region, which have experienced heavy logging of natural forests over the past 100-150 years (Schulte et al. 2007), have already been homogenised in terms of species composition and forest structure to such an extent that current forest management activities occurring have limited impact on the composition of bird communities. Indeed, forests in the area still bear a clear signature of previous land use change (Schulte et al. 2007). A loss in mature forest cover did, however, appear to decrease functional and phylogenetic diversity at the local and regional scales, although the impact on regional functional diversity was not statistically significant. Since forest change had a negative impact at both local and regional scales, the method of calculating between-site diversity would have cancelled out the impact of forest change on between-site diversity, meaning that no homogenising impact could be seen. This suggests that even though units lost local and regional diversity in response to forest change, MNBBA sites did not become more alike. Interestingly,

forestry could potentially increase differences between sites since the amount of forest that has been logged in two large national forests has been steadily decreasing since at least 1990 (Niemi et al. 2016). Indeed, early successional species such as the Chestnut-sided Warbler, Mourning Warbler, and Veery have shown clear declines, possible due to the lack in availability of early successional forest stands and higher abundance cover of middle-aged forests in the portions of the state (Pfanmuller et al. 2017).

In addition to studying the impacts of variables that captured human pressures on beta diversities, we also took into account three environmental variables known to influence patterns of biodiversity: habitat diversity, net primary production and average temperature (Qian 2010). Habitat diversity had a clear positive relation with taxonomic beta diversity, meaning that units with a higher diversity of land classes tended to have bird communities that were different from each other. This influence was due to an increase in total taxonomic diversity (Appendix 3b). Net primary productivity and average temperature did not influence taxonomic beta diversity, but both had a negative association with functional and phylogenetic beta diversity. In the case of functional beta diversity, both variables appeared to negatively influence beta diversity by increasing the diversity within MNBBA sites, which would lead to a decrease in beta diversity. In the case of phylogenetic diversity these variables did not appear to be associated with an increase in diversity within MNBBA sites but the relatively strong correlation between functional and phylogenetic beta diversity (Figure 1) suggests that the same cause was behind the negative influence of productivity and temperature on phylogenetic beta diversity.

Ultimately, conservation actions aim at maintaining global and regional diversity. High regional diversity can be achieved either by consistently high local diversities or by high between-site diversity. From a conservation viewpoint, the maximising of beta diversity, i.e. increasing differences in diversity between sites, is not

necessarily desirable. Ensuring that local communities host different species could actually minimize species persistence in the long run because each species would be represented by a single or only a few local populations, resulting in higher rates of regional extinctions. In addition, it would be difficult to argue for increasing between-site diversity at the expense of decreasing local diversity (Socolar et al. 2016) because targeting high average local diversity is a cost-efficient conservation strategy particularly when nestedness in community composition is marked. Our results indeed suggest that increasing functional beta-diversity with increasing human footprint can be due to a loss of functional diversity from local communities, i.e. nestedness. This highlights the importance of critically considering the use of beta diversity in a conservation setting.

Conclusion

Our study supports earlier findings (e.g. Devictor et al. (2010); Häkkinen et al. (2017)) that it is important to consider multiple facets of biodiversity. The positive influence of increase in human footprint on biodiversity in our study region would have been missed had we only focussed on taxonomic diversity, as has often previously been the case. Similarly, impacts on between-site and regional diversity would have been missed if we had only studied local diversity. Our results suggest that increased human footprint and forest change are not a cause of biotic homogenisation in our study site.

References

- Baiser, B. et al. 2012. Pattern and process of biotic homogenization in the New Pangaea. - *Proceedings of the Royal Society B: Biological Sciences* 279: 4772–4777.
- Baselga, A. 2010. Partitioning the turnover and nestedness components of beta diversity: Partitioning beta diversity. - *Global Ecology and Biogeography* 19: 134–143.
- Belmaker, J. and Jetz, W. 2015. Relative roles of ecological and energetic constraints, diversification rates and region history on global species richness gradients (H Arita, Ed.). - *Ecology Letters* 18: 563–571.
- Beyer, H. L. 2012. Geospatial modelling environment (Version 0.7.3.0). in press.
- Bivand, R. and Piras, G. 2015. Comparing implementations of estimation methods for spatial econometrics. - *Journal of Statistical Software* 63: 1–36.
- Cardinale, B. J. et al. 2012. Biodiversity loss and its impact on humanity. - *Nature* 486: 59–67.
- Catterall, C. P. et al. 2010. Long-term dynamics of bird diversity in forest and suburb: Decay, turnover or homogenization?: Long-term urban bird community dynamics. - *Diversity and Distributions* 16: 559–570.
- Clavel, J. et al. 2011. Worldwide decline of specialist species: Toward a global functional homogenization? - *Frontiers in Ecology and the Environment* 9: 222–228.
- de Bello, F. et al. 2010. The partitioning of diversity: Showing Theseus a way out of the labyrinth: Theseus and the partitioning of diversity. - *Journal of Vegetation Science* 21: 992–1000.
- Devictor, V. et al. 2010. Spatial mismatch and congruence between taxonomic, phylogenetic and functional diversity: The need for integrative conservation strategies in a changing world: Spatial mismatch between diversity facets. - *Ecology Letters*: 1030–1040.
- Dornelas, M. et al. 2014. Assemblage Time Series Reveal Biodiversity Change but Not Systematic Loss. - *Science* 344: 296–299.
- Ekroos, J. et al. 2010. Homogenization of lepidopteran communities in intensively cultivated agricultural landscapes. - *Journal of Applied Ecology* 47: 459–467.
- FAO 2016. Global forest resources assessment 2015: How are the world's forests changing?
- Foley, J. A. et al. 2005. Global Consequences of Land Use. - *Science* 309: 570–574.

- Gordon, C. E. et al. 2009. Simplification of a coffee foliage-dwelling beetle community under low-shade management. - *Basic and Applied Ecology* 10: 246–254.
- Haddad, N. M. et al. 2015. Habitat fragmentation and its lasting impact on Earth's ecosystems. - *Science Advances* 1: e1500052–e1500052.
- Hansen, M. C. et al. 2013. High-Resolution Global Maps of 21st-Century Forest Cover Change. - *Science* 342: 850–853.
- Häkkinä, M. et al. 2017. Degradation in landscape matrix has diverse impacts on diversity in protected areas (L-F Bersier, Ed.). - *PLOS ONE* 12: e0184792.
- Häkkinä, M. et al. 2018. Habitat quality is more important than matrix quality for bird communities in protected areas. - *Ecology and Evolution* in press.
- Homer, C. et al. 2004. Development of a 2001 national land-cover database for the United States. - *Photogrammetric Engineering & Remote Sensing* 70: 829–840.
- Ibarra, J. T. and Martin, K. 2015. Biotic homogenization: Loss of avian functional richness and habitat specialists in disturbed Andean temperate forests. - *Biological Conservation* 192: 418–427.
- Isbell, F. et al. 2015. The biodiversity-dependent ecosystem service debt (R Bardgett, Ed.). - *Ecology Letters* 18: 119–134.
- Jetz, W. et al. 2012. The global diversity of birds in space and time. - *Nature* 491: 444–448.
- Kitching, R. L. et al. 2013. Distance-driven species turnover in Bornean rainforests: Homogeneity and heterogeneity in primary and post-logging forests. - *Ecography* 36: 675–682.
- La Sorte, F. A. and Boecklen, W. J. 2005. Temporal turnover of common species in avian assemblages in North America: Turnover of common species. - *Journal of Biogeography* 32: 1151–1160.
- Lee-Cruz, L. et al. 2013. Impact of Logging and Forest Conversion to Oil Palm Plantations on Soil Bacterial Communities in Borneo. - *Applied and Environmental Microbiology* 79: 7290–7297.
- Lôbo, D. et al. 2011. Forest fragmentation drives Atlantic forest of northeastern Brazil to biotic homogenization: Biotic homogenization of Atlantic forest. - *Diversity and Distributions* 17: 287–296.

- McCune, J. L. and Vellend, M. 2013. Gains in native species promote biotic homogenization over four decades in a human-dominated landscape (J Fridley, Ed.). - *Journal of Ecology* 101: 1542-1551.
- McGill, B. J. et al. 2015. Fifteen forms of biodiversity trend in the Anthropocene. - *Trends in Ecology & Evolution* 30: 104-113.
- McKinney, M. L. 2006. Urbanization as a major cause of biotic homogenization. - *Biological Conservation* 127: 247-260.
- McKinney, M. L. and Lockwood, J. L. 1999. Biotic homogenization: A few winners replacing many losers in the next mass extinction. - *Trends in Ecology & Evolution* 14: 450-453.
- Mori, A. S. et al. 2015. Biotic homogenization and differentiation of soil faunal communities in the production forest landscape: Taxonomic and functional perspectives. - *Oecologia* 177: 533-544.
- Newbold, T. et al. 2015. Global effects of land use on local terrestrial biodiversity. - *Nature* 520: 45-50.
- Niemi, G. et al. 2016. Analysis of long-term forest bird monitoring data from national forests of the western Great Lakes Region.
- Olden, J. D. 2006. Biotic homogenization: A new research agenda for conservation biogeography. - *Journal of Biogeography* 33: 2027-2039.
- Oliver, T. H. et al. 2015. Biodiversity and Resilience of Ecosystem Functions. - *Trends in Ecology & Evolution* 30: 673-684.
- Pfannmuller, L. et al. 2017. The First Minnesota Breeding Bird Atlas (2009-2013).
- PRISM Climate Group, Oregon State University
- Qian, H. 2010. Environmentrichness relationships for mammals, birds, reptiles, and amphibians at global and regional scales. - *Ecological Research* 25: 629-637.
- Rodrigues, J. L. M. et al. 2013. Conversion of the Amazon rainforest to agriculture results in biotic homogenization of soil bacterial communities. - *Proceedings of the National Academy of Sciences* 110: 988-993.
- Rollins, M. G. et al. 2006. An overview of the LANDFIRE Prototype Project. - In: Rollins, M. G. and Frame, C. K. (eds), *The LANDFIRE Prototype Project: Nationally consistent and locally relevant geospatial data for wildland fire management*. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, ppp. 5-43.

- Sanderson, E. W. et al. 2002. The human footprint and the last of the wild. - *BioScience* 52: 891-904.
- Schulte, L. A. et al. 2007. Homogenization of northern U.S. Great Lakes forests due to land use. - *Landscape Ecology* 22: 1089-1103.
- Sheppard, A. W. et al. 2011. Biosecurity and sustainability within the growing global bioeconomy. - *Current Opinion in Environmental Sustainability* 3: 4-10.
- Socolar, J. B. et al. 2016. How Should Beta-Diversity Inform Biodiversity Conservation? - *Trends in Ecology & Evolution* 31: 67-80.
- Sol, D. et al. 2017. Urbanisation and the loss of phylogenetic diversity in birds (N Haddad, Ed.). - *Ecology Letters* 20: 721-729.
- Tuomisto, H. 2010. A diversity of beta diversities: Straightening up a concept gone awry. Part 1. Defining beta diversity as a function of alpha and gamma diversity. - *Ecography* 33: 2-22.
- Vellend, M. et al. 2013. Global meta-analysis reveals no net change in local-scale plant biodiversity over time. - *Proceedings of the National Academy of Sciences* 110: 19456-19459.
- Wildlife Conservation Society-WCS and Center For International Earth Science Information Network-CIESIN-Columbia University 2005. Last of the Wild Project, Version 2, 2005 (LWP-2): Global Human Footprint Dataset (IGHP).
- Zhao, M. et al. 2005. Improvements of the MODIS terrestrial gross and net primary production global data set. - *Remote Sensing of Environment* 95: 164-176.
- Zuur, A. F. 2007. *Analysing ecological data*. - Springer.

Table 1: Summary statistics of forest bird species richness and response variables per unit

	Species richness	Taxonomic β	Functional β	Phylogenetic β
Min	16	26.8	2.08	2.57
Median	57.5	59.6	6.44	7.93
Mean	60.4	58.8	6.73	8.3
Max	155	81	17.6	24.1
SD	26.4	9.29	2.66	3.04

Table 2: Summary statistics of explanatory variables used in models (continued below)

	Human footprint	Forest change (%)	Net primary production (kg C/m ² /Year)	Habitat diversity	Mean temperature (°C)	Number forested points
Min	1.64	0.0106	0.319	1.65	2.51	3
Median	17.9	3.33	0.473	5.43	4.08	7
Mean	21.7	4.26	0.472	5.69	4.34	7.21
Max	67.1	44.9	0.656	12.1	8	18
SD	12.5	4.5	0.0551	2.03	1.15	2.96

Table 3: Summary of linear model explaining taxonomic beta diversity

	Estimate	Std. Error	t value	p value
Intercept	50.8	6.16	8.25	6.31e-15
Human footprint	0.0877	0.0565	1.55	0.122
Forest change (%)	-0.0397	0.118	-0.337	0.737
Net primary production (kg C/m²/Year)	-13.2	9.18	-1.44	0.151
Habitat diversity	0.661	0.257	2.57	0.0106
Mean temperature (°C)	-0.866	0.604	-1.44	0.152
Number forested points	1.73	0.181	9.57	6.07e-19

Table 4: Summary of generalised linear model explaining functional beta diversity

	Estimate	Std. Error	t value	p value
Intercept	10.5	2.02	5.23	3.33e-07
Human footprint	0.0472	0.0199	2.38	0.0181
Forest change (%)	0.0068	0.0382	0.178	0.859

Net primary production (kg C/m²/Year)	-9.72	3.02	-3.22	0.00144
Habitat diversity	0.0161	0.0858	0.188	0.851
Mean temperature (°C)	-0.406	0.19	-2.13	0.0337
Number forested points	0.194	0.0609	3.18	0.00164

Table 5: Summary of spatial error model explaining phylogenetic beta diversity

	Estimate	Std. Error	z value	p value
Intercept	2.53	0.297	8.51	0
Human footprint	0.00381	0.00259	1.47	0.141
Forest change (%)	-0.00249	0.00526	-0.473	0.636
Net primary production (kg C/m²/Year)	-1.1	0.453	-2.42	0.0155
Habitat diversity	0.00344	0.0121	0.284	0.776
Mean temperature (°C)	-0.0659	0.03	-2.2	0.0281
Number forested points	0.0328	0.00815	4.02	5.74e-05

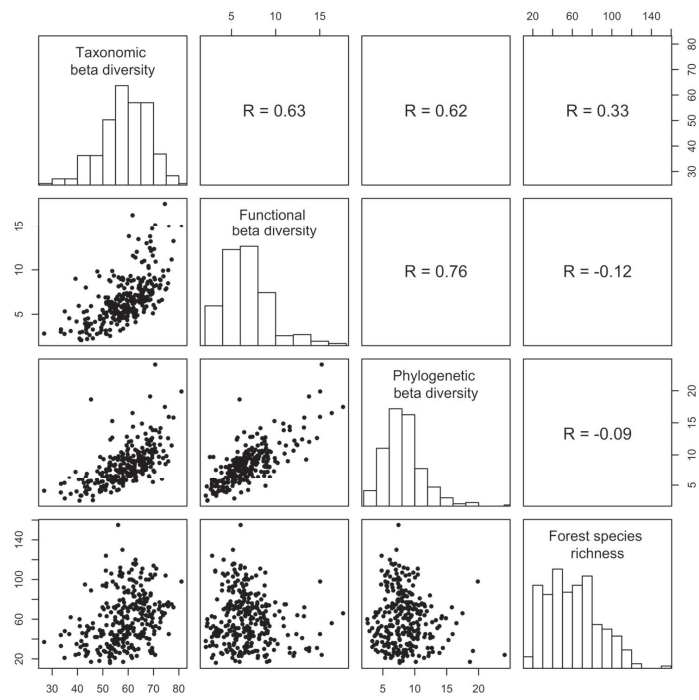


Figure 1: Distributions of taxonomic, functional and phylogenetic beta diversity, and forest species richness, and Pearson correlations between the diversity measures

Appendices

1. Correlations between human footprint and variables describing human influence

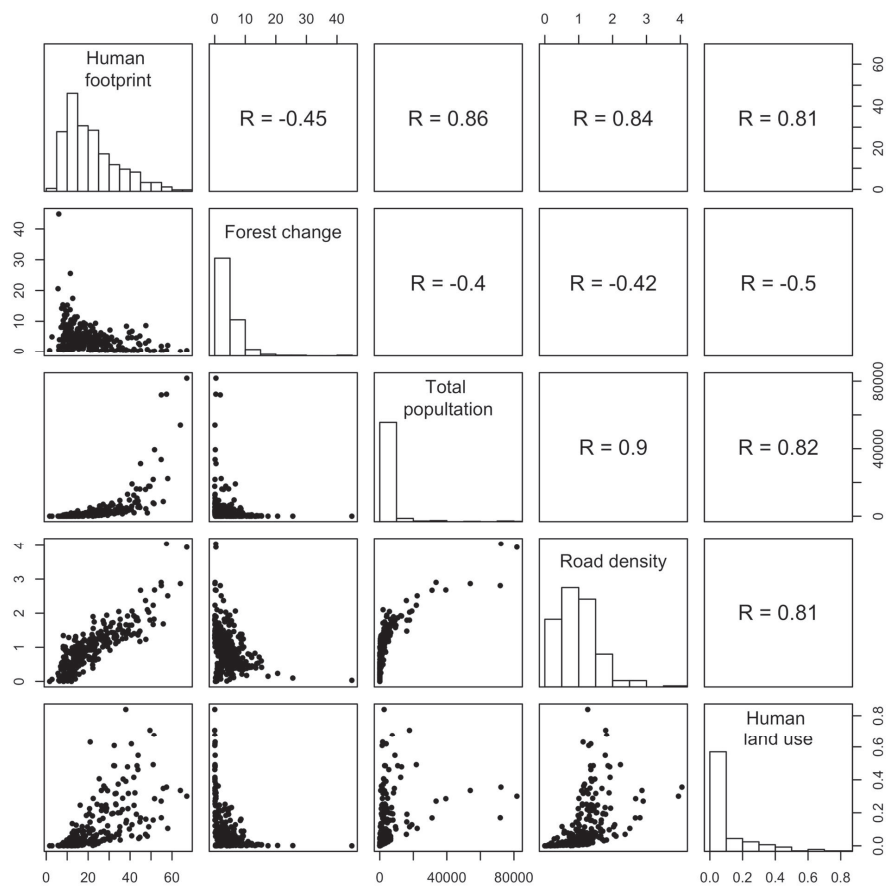


Figure 1A1: Distributions of human footprint and other variables describing human influence, and Spearman's rank correlations between variables

2. Spatial distribution of explanatory variables

a) Human footprint

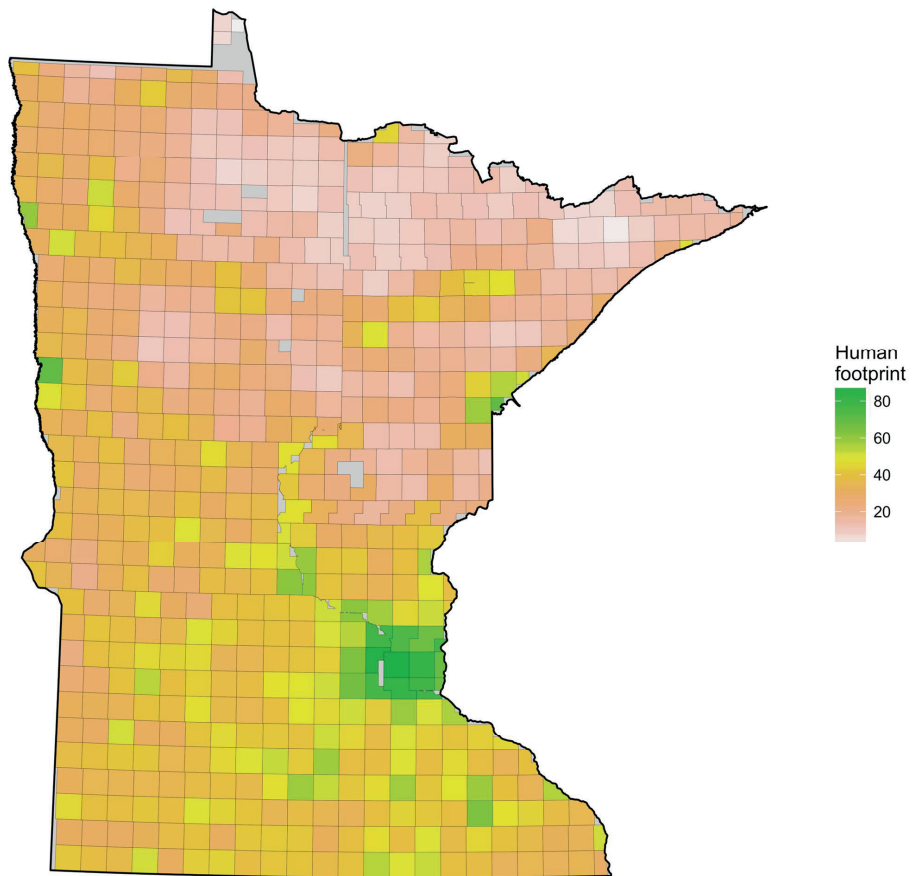


Figure 2A1: Map showing the spatial distribution of human footprint values in the state of Minnesota

b) Forest change

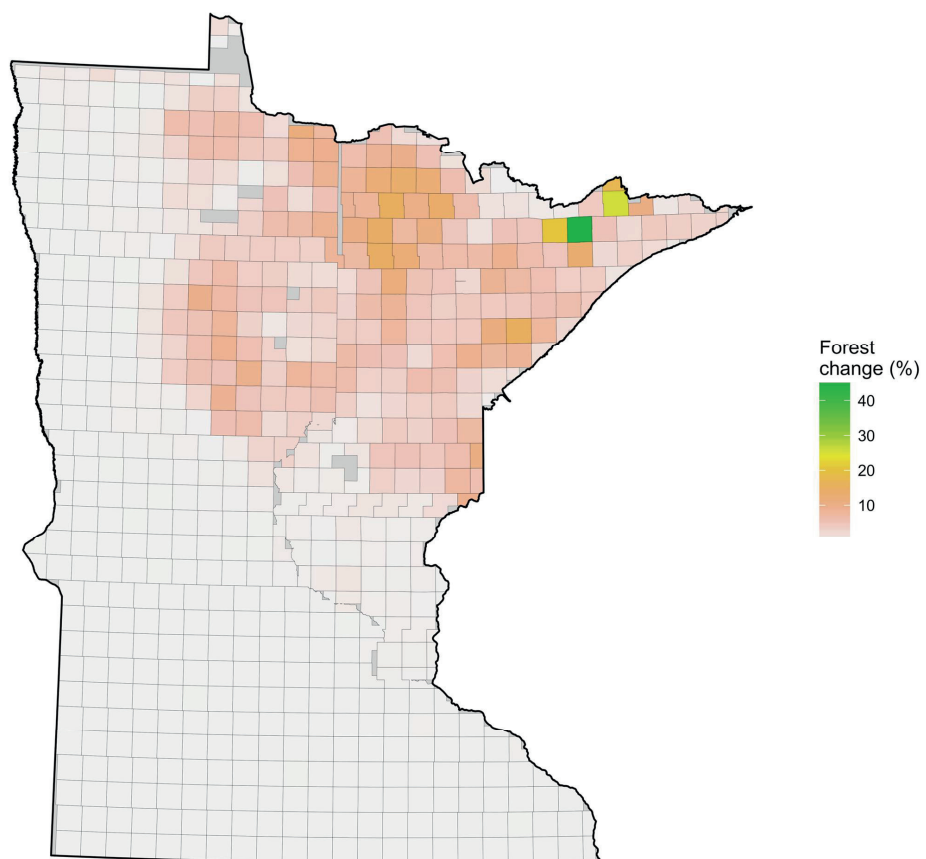


Figure 2A2: Map showing the spatial distribution of forest change values in the state of Minnesota

c) Habitat diversity

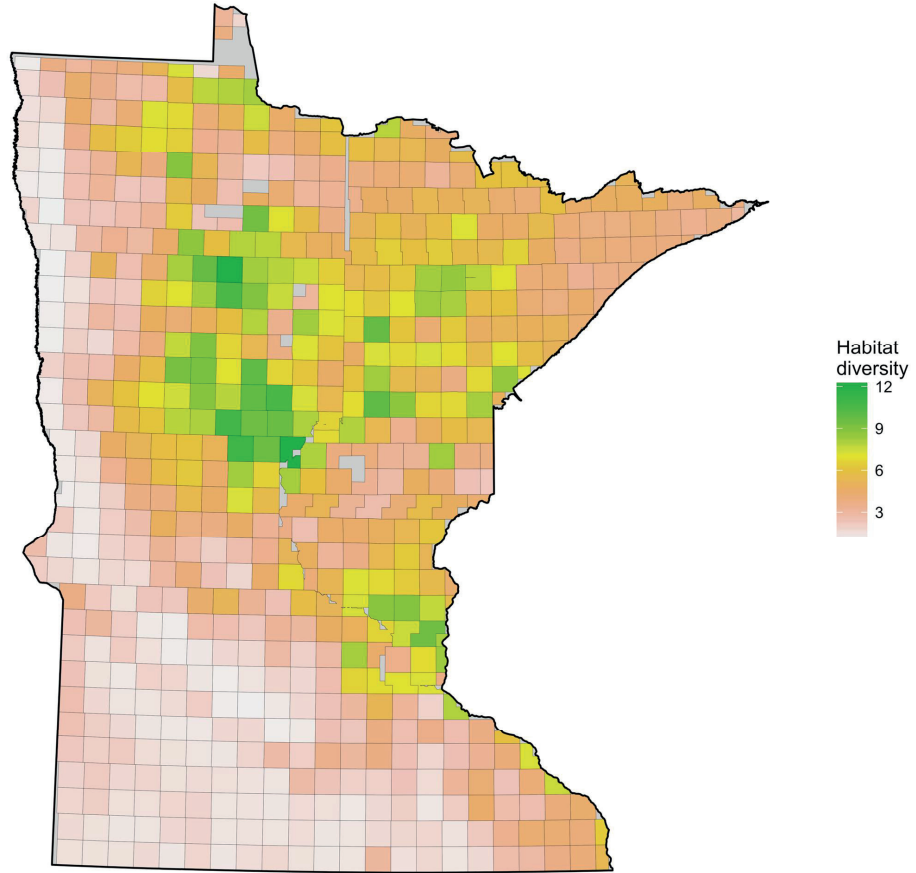


Figure 2A3: Map showing the spatial distribution of habitat diversity values in the state of Minnesota

d) Net primary production

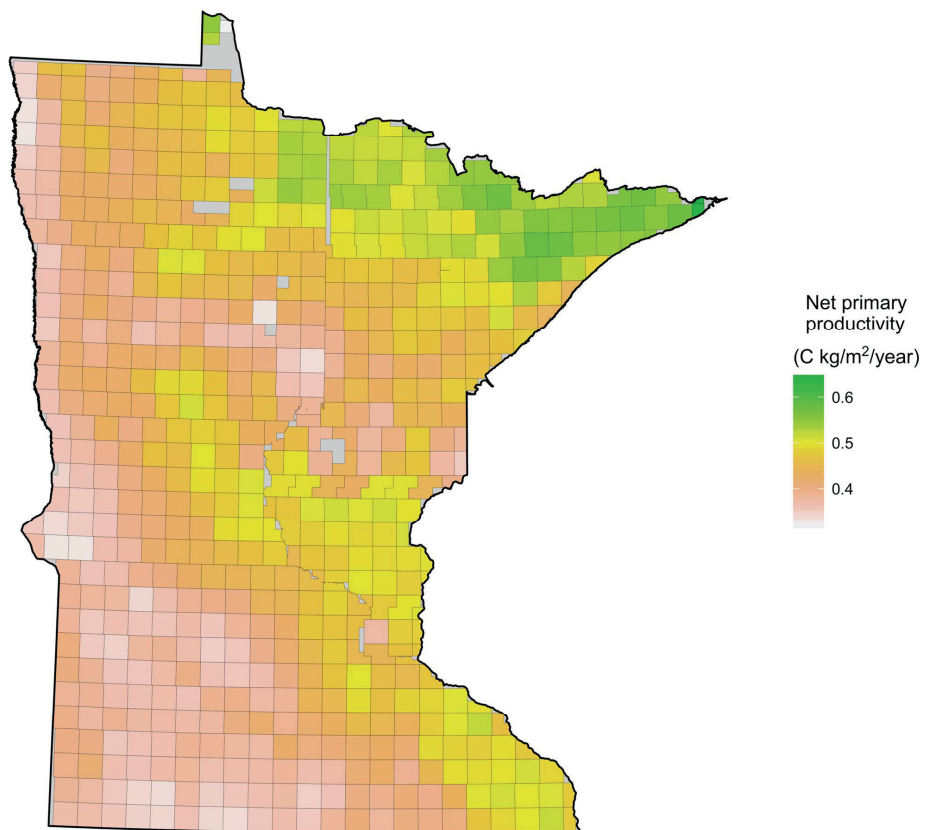


Figure 2A4: Map showing the spatial distribution of net primary productivity values in the state of Minnesota

e) Mean temperature

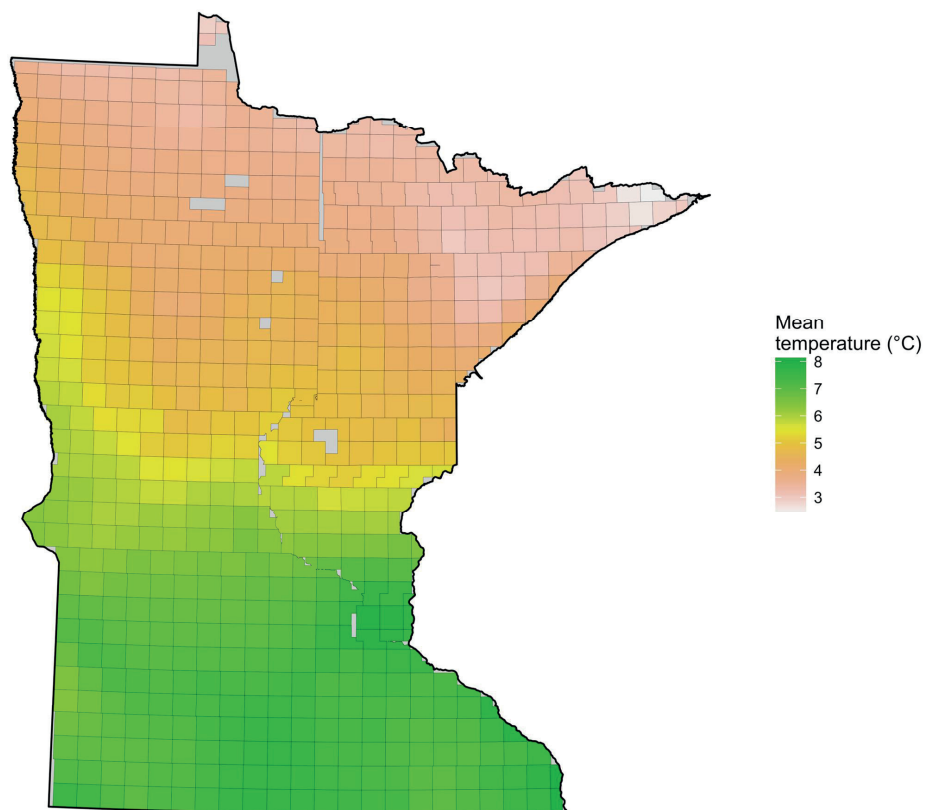


Figure 2A5: Map showing the spatial distribution of mean temperature values in the state of Minnesota

3. Results of alpha and gamma diversities

a) Taxonomic alpha diversity results

Table 3A1: Summary of spatial error model explaining taxonomic alpha diversity

	Estimate	Std. Error	z value	p value
Intercept	5.04	1.52	3.32	0.000909
Human footprint	-0.00751	0.0126	-0.598	0.55
Forest change (%)	-0.0121	0.0248	-0.489	0.625
Net primary production (kg C/m²/Year)	3.01	2.36	1.27	0.203
Habitat diversity	0.041	0.0602	0.681	0.496
Mean temperature (°C)	0.115	0.16	0.716	0.474
Number forested points	-0.0806	0.0386	-2.09	0.0368

b) Taxonomic gamma diversity results

Table 3A2: Summary of spatial error model explaining taxonomic gamma diversity

	Estimate	Std. Error	z value	p value
Intercept	8.98	3.28	2.74	0.00619
Human footprint	0.0256	0.0274	0.935	0.35
Forest change (%)	0.00485	0.0543	0.0894	0.929
Net primary production (kg C/m²/Year)	2.97	5.09	0.584	0.559
Habitat diversity	0.297	0.131	2.27	0.023
Mean temperature (°C)	-0.0755	0.342	-0.221	0.825
Number forested points	0.493	0.0845	5.83	5.45e-09

c) Functional alpha diversity results

Table 3A3: Summary of spatial error model explaining functional alpha diversity

	Estimate	Std. Error	z value	p value
Intercept	1.45	0.0591	24.5	0
Human footprint	-0.000612	0.000492	-1.24	0.214
Forest change (%)	-0.00246	0.000974	-2.53	0.0115
Net primary production (kg C/m²/Year)	0.176	0.0917	1.92	0.0548
Habitat diversity	0.00323	0.00235	1.37	0.17
Mean temperature (°C)	0.0183	0.00618	2.97	0.00301
Number forested points	-0.00534	0.00152	-3.52	0.00043

d) Functional gamma diversity results

Table 3A4: Summary of spatial error model explaining functional gamma diversity

	Estimate	Std. Error	z value	p value
Intercept	1.6	0.0567	28.2	0
Human footprint	2.17e-05	0.000478	0.0455	0.964
Forest change (%)	-0.00196	0.000952	-2.05	0.0399
Net primary production (kg C/m²/Year)	0.0409	0.0876	0.467	0.641
Habitat diversity	0.00355	0.00227	1.56	0.118
Mean temperature (°C)	0.015	0.00587	2.56	0.0105
Number forested points	-0.00234	0.00148	-1.58	0.115

e) Phylogenetic alpha diversity results

Table 3A5: Summary of spatial error model explaining phylogenetic alpha diversity

	Estimate	Std. Error	z value	p value
Intercept	1.6	0.0945	16.9	0
Human footprint	-0.00153	0.000806	-1.9	0.0578
Forest change (%)	-0.00335	0.00161	-2.07	0.0381
Net primary production (kg C/m²/Year)	0.151	0.145	1.04	0.3
Habitat diversity	0.00361	0.0038	0.948	0.343
Mean temperature (°C)	0.0137	0.00969	1.41	0.158
Number forested points	-0.00147	0.00251	-0.588	0.557

f) Phylogenetic gamma diversity results

Table 3A6: Summary of spatial error model explaining phylogenetic gamma diversity

	Estimate	Std. Error	z value	p value
Intercept	1.85	0.0964	19.2	0
Human footprint	-0.000785	0.000842	-0.932	0.351
Forest change (%)	-0.00386	0.00171	-2.26	0.0238
Net primary production (kg C/m²/Year)	-0.0392	0.147	-0.267	0.79
Habitat diversity	0.00362	0.00393	0.921	0.357
Mean temperature (°C)	0.00224	0.00972	0.23	0.818
Number forested points	0.00233	0.00265	0.88	0.379

4. Correlations between explanatory variables, and their distributions

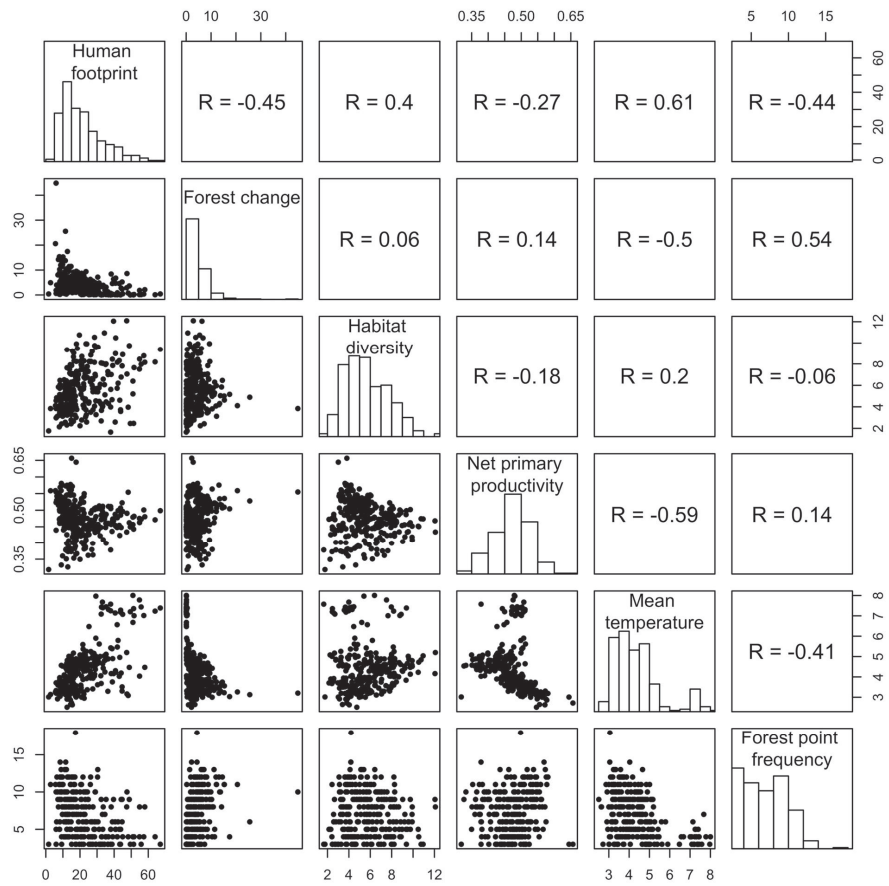


Figure 4A1: Distributions of explanatory variables, and Spearman's rank correlations between variables

5. Variance inflation factors from models

Table 5A1: Variance inflation factors of explanatory variables in models explaining taxonomic, functional, and phylogenetic beta diversity (continued below)

	Human footprint	Forest change (%)	Net primary production (kg C/m ² /Year)	Habitat diversity	Mean temperature (°C)
Taxonomic	2.37	1.34	1.21	1.29	2.29
Functional	2.64	1.35	1.21	1.28	2.54
Phylogenetic	2.37	1.34	1.21	1.29	2.29
	Number forested points				
Taxonomic	1.36				
Functional	1.36				
Phylogenetic	1.36				

6. List of used R packages and their versions

ade4 1.7.6
 adephylo 1.1.10
 ape 4.1
 base 3.4.3
 car 2.1.4
 cluster 2.0.6
 datasets 3.4.3
 dplyr 0.5.0
 ggplot2 2.2.1
 graphics 3.4.3

grDevices 3.4.3
gstat 1.1.5
knitr 1.17
lattice 0.20.35
maptools 0.9.2
Matrix 1.2.12
methods 3.4.3
nlme 3.1.131
pander 0.6.1
printr 0.1
psych 1.7.5
raster 2.5.8
readxl 1.0.0
reshape2 1.4.2
rgdal 1.2.16
rgeos 0.3.23
sp 1.2.4
spdep 0.6.13
stats 3.4.3
tidyr 0.6.3
utils 3.4.3

7. Comparison of human footprint index values in units used in analyses and units not used in analyses

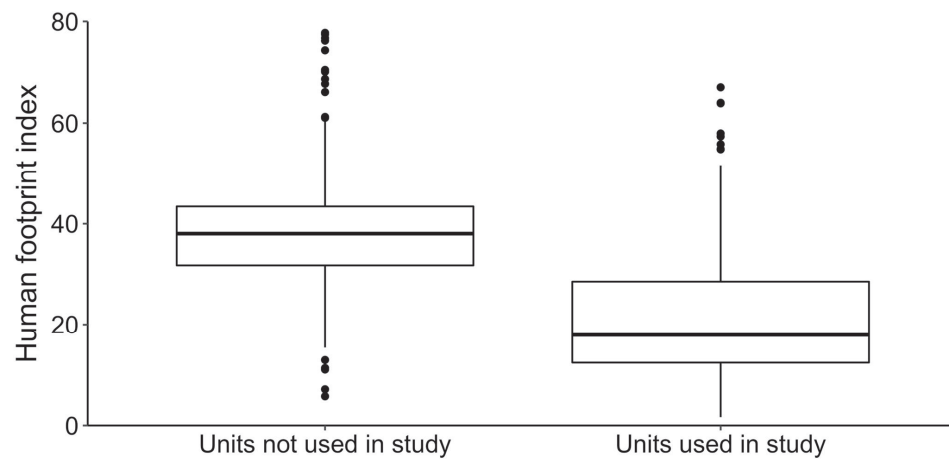


Figure 7A1: Comparison of human footprint index values in units used in analyses and units not used in analyses

III

DEGRADATION IN LANDSCAPE MATRIX HAS DIVERSE IMPACTS ON DIVERSITY IN PROTECTED AREAS

by

Matti Häkkilä, Eric Le Tortorec, Lluís Brotons, Ari Rajasärkkä, Risto Tornberg &
Mikko Mönkkönen 2017

PLoS ONE 12(9): e0184792.

RESEARCH ARTICLE

Degradation in landscape matrix has diverse impacts on diversity in protected areas

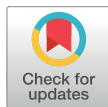
Matti Häkkilä^{1*}, Eric Le Tortorec¹, Lluís Brotons^{2‡}, Ari Rajasärkkä^{3‡}, Risto Tornberg^{4‡}, Mikko Mönkkönen¹

1 Department of Biological and Environmental Science, University of Jyväskylä, Jyväskylä, Finland, **2** Center for Mediterranean Forest Research, Centre Tecnològic Forestal de Catalunya, InForest JRU, Solsona, Spain, **3** Metsähallitus, Parks & Wildlife Finland, Oulu, Finland, **4** University of Oulu, Oulu, Finland

☉ These authors contributed equally to this work.

‡ These authors also contributed equally to this work.

* matti.i.hakkila@jyu.fi



Abstract

Introduction

A main goal of protected areas is to maintain species diversity and the integrity of biological assemblages. Intensifying land use in the matrix surrounding protected areas creates a challenge for biodiversity conservation. Earlier studies have mainly focused on taxonomic diversity within protected areas. However, functional and especially phylogenetic diversities are less studied phenomena, especially with respect to the impacts of the matrix that surrounds protected areas. Phylogenetic diversity refers to the range of evolutionary lineages, the maintenance of which ensures that future evolutionary potential is safeguarded. Functional diversity refers to the range of ecological roles that members of a community perform. For ecosystem functioning and long-term resilience, they are at least as important as taxonomic diversity.

Aim

We studied how the characteristics of protected areas and land use intensity in the surrounding matrix affect the diversity of bird communities in protected boreal forests. We used line-transect count and land-cover data from 91 forest reserves in Northern Finland, and land-cover data from buffer zones surrounding these reserves. We studied if habitat diversity and productivity inside protected areas, and intensity of forest management in the matrix have consistent effects on taxonomic, functional and phylogenetic diversities, and community specialization.

Results

We found that habitat diversity and productivity inside protected areas have strong effects on all diversity metrics, but matrix effects were inconsistent. The proportion of old forest in the matrix, reflecting low intensity forest management, had positive effects on community specialization. Interestingly, functional diversity increased with increasing logging intensity in the matrix.

OPEN ACCESS

Citation: Häkkilä M, Le Tortorec E, Brotons L, Rajasärkkä A, Tornberg R, Mönkkönen M (2017) Degradation in landscape matrix has diverse impacts on diversity in protected areas. PLoS ONE 12(9): e0184792. <https://doi.org/10.1371/journal.pone.0184792>

Editor: Louis-Felix Bersier, University of Fribourg, SWITZERLAND

Received: February 13, 2017

Accepted: August 31, 2017

Published: September 26, 2017

Copyright: © 2017 Häkkilä et al. This is an open access article distributed under the terms of the [Creative Commons Attribution License](https://creativecommons.org/licenses/by/4.0/), which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited.

Data Availability Statement: All relevant data are within the paper and its Supporting Information files.

Funding: This work was supported by Koneen Säätiö/Kone Foundation (<http://www.koneensaatio.fi/en/>), application number: 33-3492 (MH); and Suomen Akatemia / Academy of Finland (<http://www.aka.fi/en/>), Project number #275329 (MM). The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

Competing interests: The authors have declared that no competing interests exist.

Conclusions

Our results indicate that boreal forest reserves are not able to maintain their species composition and abundances if embedded in a severely degraded matrix. Our study also highlights the importance of focusing on different aspects of biodiversity.

Introduction

Human activities are a major threat to all aspects of biodiversity. A cocktail of climate change and destruction of habitats [1] mixed together with pollution and invasive species are decreasing biological diversity throughout the world [2]. The remaining fragments of native habitats are affected as a consequence of hindered migration and isolated populations [3], [4], [5].

Despite the multi-faceted nature of biodiversity [6], community ecologists and conservation biologists have only recently considered aspects of biodiversity other than taxonomic diversity. Taxonomic diversity is the most commonly quantified component of diversity, accounting for species richness and abundances. Phylogenetic diversity reflects evolutionary history of the present taxa [7], and measuring it has been proposed as a way to acknowledge the role of species interactions in biotic assemblages [8]. High levels of phylogenetic diversity may enhance the resilience of communities to changing environmental conditions [9]. Functional diversity describes the range of ecological roles that organisms perform, as well as how they use their habitat and resources [10]. For the productivity of ecosystems, functional diversity is of high importance [11]. Taxonomic, phylogenetic and functional diversity in communities tend to be positively correlated across spatial scales [12], but they reflect complementary components of biodiversity. Two communities may possess equal levels of taxonomic diversity, yet be composed of species with different phylogenetic histories or set of functional traits.

Specialist species, by definition, effectively utilize a narrow range of available resources, and communities containing many specialist species may therefore be more efficient in transforming available resources into offspring than communities with predominance of generalists [12]. Unlike generalists, specialists often have specific functional traits; losing them may result in decreased functional diversity, which is an aspect of biotic homogenization [13]. Nevertheless, functional diversity may remain unchanged when specialist species are lost if new generalist species occupy the empty niches. Thus, all ecosystem functions are retained but overall effectiveness of resource use may be considerably reduced. Therefore, quantifying changes in the level of specialization may be a useful additional indicator of important changes in communities.

Landscapes have traditionally been considered as a network of habitat patches in a non-habitable matrix [14]. However, more recent research has shown that the matrix surrounding patches can affect habitat quality [15], dispersal ability of species and population persistence [16], [17] and thus colonization-extinction dynamics [18]. Individuals moving between patches may use alternative resources outside the fragment they occupy [19]. Protected areas are often located in landscapes where land use intensity around them is high and matrix habitats are of poor quality compared to natural habitat. In forested landscapes, for example, protected old-growth forests are often surrounded by clear-cuts or young forests [20], [21]. Protected boreal forest areas embedded in a matrix of young regeneration forests foster less species-rich communities with higher total bird density than areas situated in continuous, old forest dominated landscapes [21]. This supports the idea that the matrix provides additional resources even for patch-dependent species [22], while only a limited set of species are able to

utilize resources in the matrix. However, little is known about the matrix effects on the capacity of protected areas to maintain functional and phylogenetic diversity or on community specialization in protected areas. Further, characteristics of protected areas that promote specialized species and their functions have hardly gained any interest (but see [23]). It has been proposed that larger protected areas are needed for the persistence of populations [24] and the integrity of communities [21]. The relationship between functional and phylogenetic diversity, community specialization and habitat area or productivity has remained unclear.

In this research, we studied how characteristics of protected areas and the surrounding matrix impact the community composition of forest birds within the protected areas. Increasing human land-use intensity has negative effects on diversity [25], so we hypothesize that forest bird communities will be negatively affected by intensive forestry in the matrix. Moreover, we hypothesize that matrix effects will be particularly strong in small protected areas, whereas large areas should be better buffered against matrix effects, e.g. due to their lower edge-to-area ratio. Total forest area, productivity and habitat diversity all have positive effects on species richness [26]. Therefore, we expect taxonomic diversity to be the highest in large protected areas with high habitat heterogeneity and high productivity inside the areas and that other diversity metrics will show similar responses. Correlations between different diversity measures are often positive, but there are also areas of clear incongruence [14]. Therefore, we also studied if there are correlations between different diversity measures.

Material and methods

Study area

The study area is in the boreal zone in sparsely populated Northern Finland (Fig 1) where forests are mainly dominated by coniferous forests. Open bogs, mires, small lakes and ponds are characteristic of the landscape. Most of the forests are in active commercial use and, in the Kainuu area where most of the studied forest reserves are situated, only 5.2% of forest area is protected from logging [27]. This study focuses on 91 protected areas with a total surface of approximately 3100 km². The areas differ in size, from ca. 150 to 28000 ha (mean area = 3400 ha, S.D. = 4676 ha).

Bird data

Bird species abundance was measured using the Finnish line transect census method [28] by Metsähallitus Parks & Wildlife Finland. Finnish line transect count is based on observational data with minimum disturbance to animals. It can be accomplished under Finnish Every man's right, which allows free access without separate permit to all forests, protected areas and National parks included. The line transect census method is a one-visit census and is suitable for counting birds over large areas [29]. The survey is completed early in the breeding season and all observations of breeding pairs in 5 to 6 km transects on average are counted. See [S1 Text](#) for further information.

We focused on forest species and of all the 129 bird species observed, we retained 69 species that use forest as their main breeding habitat [30] (S2 Text). The bird censuses were conducted between 1988 and 1999 for a total of 3323 km of transects. On average, 1 km of transect per km² of land within the protected areas was surveyed. Transect length correlated negatively with land area, suggesting that small areas were surveyed with higher per-unit-area effort. In large areas, all the line transect counts could not be conducted during the same breeding season. We combined data across years following Brotons et al. [31] who found that species richness and abundance of forest species in these data did not differ among years.

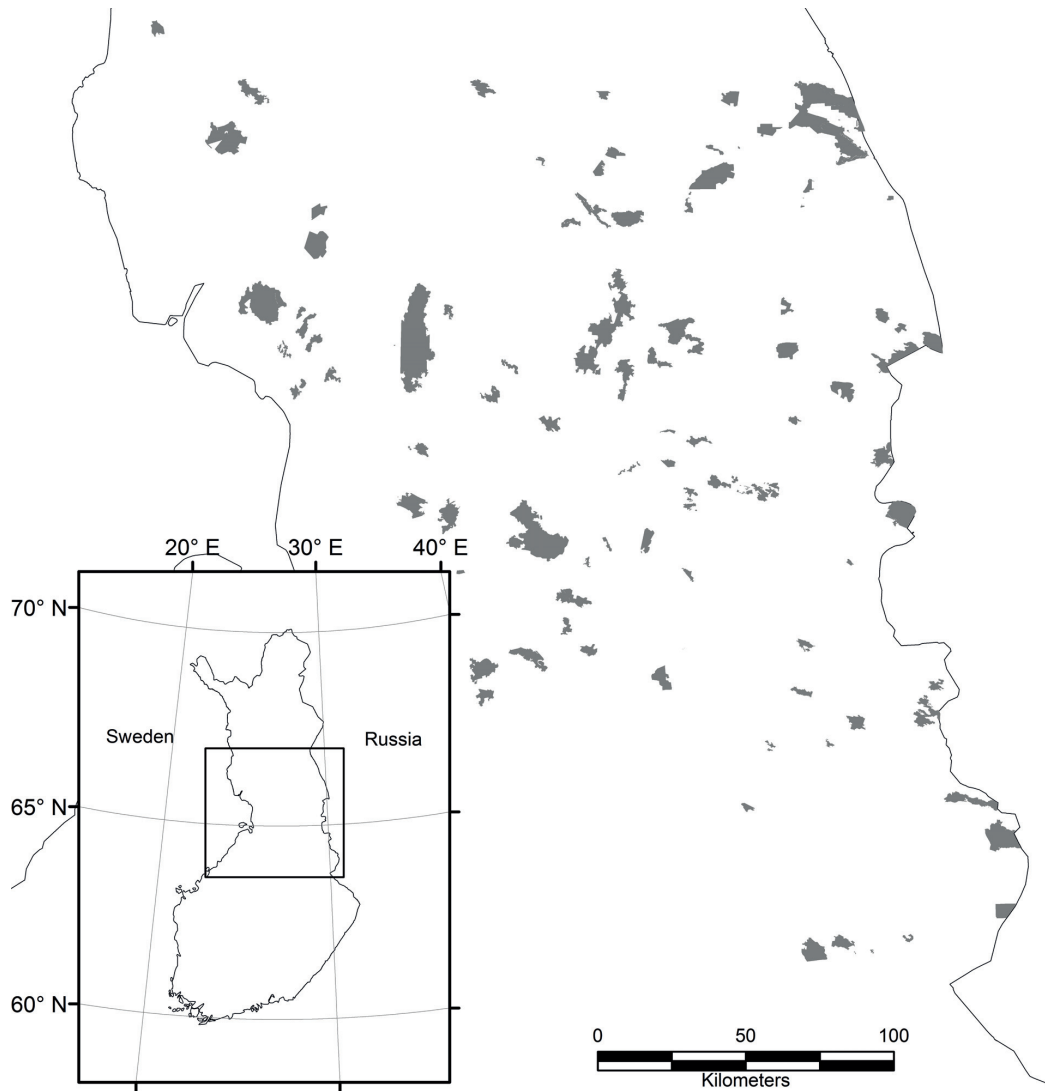


Fig 1. Map of the study area and the location of the protected areas in Northern Finland.

<https://doi.org/10.1371/journal.pone.0184792.g001>

Diversity measures

We first calculated species richness in each site. Further, for each of the protected areas, we calculated taxonomic, functional, and phylogenetic α -diversities based on Rao's quadratic entropy [32] using R functions developed by De Bello et al. [33], as well as the Community Specialization Index [34]. The α -diversity of a community represents the expected dissimilarity between two randomly selected individuals, taking the relative abundance of each species into account. For taxonomic diversity, the dissimilarity has a value of 1 if two individuals represent two different species and 0 otherwise. For functional and phylogenetic diversity measures, dissimilarity takes into account functional or phylogenetic distances among species [35], [33] (see below). For species level taxonomic diversity, α -Rao equals the Simpson diversity index [35], [36]. Thus, a community with few species and one dominant species will get a low value.

Functional diversity is often measured by using ecological traits [37], but in this study we are proposing a method based on morphological traits. The functionality of a species refers to the way it uses the habitat for foraging, nesting, avoiding predators, etc. [38], which is largely reflected in the morphology of a species. We measured morphological traits (wing, tail, tarsus and bill length, bill width and bill height) from at least five individuals per species from permanent museum samples available for scientific use at the Museum of Natural History in Helsinki, Finland, and the Museum of Natural history in Oulu, Finland. Body mass was available from museum databases (weighed when individuals were collected). In the few cases where specimens originating from Finland were not available, we chose the ones collected as close to the study area as possible. As all of these measures mainly are correlated with the size of the bird, we transformed original morphological variables into indices that link morphology with ecological functions of the species. First, we used body mass as an indicator of overall body size. Body size is an important driver of both habitat use and diet, and two species with different body size but equal shape tend to use different size food items and different habitats. Second, to describe functions related to the type of food used, we computed the ratio bill length/(bill width + bill height). Species with long bills relative to bill width and height tend to be more insectivorous than short-billed species [39]. Third, we calculated three additional ratios (wing length/ $\sqrt[3]{\text{body mass}}$, tarsus length/ $\sqrt[3]{\text{body mass}}$ and tail length/ $\sqrt[3]{\text{body mass}}$) to represent differences in locomotion and habitat use. The lengths were divided by the cubic root of body mass to scale these one-dimensional variables by a one-dimensional measure of body size. These five uncorrelated (see [S4 Text](#)) morphological variables were then used to calculate pairwise Euclidean distances in a morphological hyperspace among individuals in a community. This distance, scaled between 0 and 1, was then used as a measure of morphological dissimilarity when calculating functional diversity.

To study phylogenetic diversity in our study area a set of 1000 randomly chosen phylogenetic trees of the study species was chosen from a phylogenetic tree database of 9993 bird species that is available on [birdtree.org](#) [40],[41]. Using a large sample is better than using few trees since there can be some uncertainty in phylogeny reconstruction. Of the 1000 trees, a single, unrooted, 50% majority rule (extended) consensus tree was constructed using the Consense function (phylip package v.3.695). In the extended majority rule, any set of species that appears in more than 50% of the trees is included. To calculate phylogenetic diversity, we used the distance between the two end nodes (i.e. species) in the consensus tree, scaled between 0 and 1, as a measure of phylogenetic dissimilarity.

The species specialization index, SSI, [32] is a simple and sensitive tool for studying homogenization at the community level. SSI is the coefficient of variation (standard deviation/average) of species densities among habitat classes. The larger the SSI value, the more specialized the species is with respect to habitats. We used independent Finnish national level data

originating from the common bird monitoring project (CBMP) point count censuses, conducted between 1984 and 2011 [42], to calculate the SSI for each species. In the CBMP, each station is located in a uniform habitat within at least 50 m to the station. Habitat type is classified into 17 classes (S9 Text). For each habitat class we derived average density for the 69 species, and calculated sample-size bias corrected species specialization index, SSIC [32]. Finally, we calculated a weighted average SSIC, which takes species density into account, of species present in a given site, i.e. the community specialization index, CSI [43].

Landscape analysis

The land-use and cover data originated from the 8th National Forest Inventory of Finland and were collected between 1986 and 1994 [44]. In these data, forests were classified by timber volume and dominant tree species into nine cover types (see [31]; Table 1). From this classification, we calculated variables describing the habitat composition within the protected areas and in the surrounding landscape. We used the sum of spruce-deciduous cover types (habitat classes 3 and 6; Table 1) to describe productivity because, in our study area, spruce-deciduous forests only grow on fertile soil while less fertile sand and peat soils are usually pine-dominated. Forests with more timber than 100m³/ha can be considered mature old forests in northern Finnish conditions [45]. Consequently, we used the sum of the three cover types with more than 100m³/ha (habitat classes 1–3; Table 1) to describe the proportion of old forest, even though we did not directly measure forest age. We estimated habitat diversity within reserves using Shannon’s diversity index from the proportions of the nine cover types in each area.

The forested landscape around the reserves (the matrix) was characterized from a 5 km buffer around the outer border of each reserve. This radius was selected to make sure that the matrix could have impact on birds with large home ranges. Since clear cutting, which results in an even-age structure of trees within a stand, is the most common way to regenerate forests in the region, timber volume was considered the best estimate of forest age and forestry intensity.

Table 1. Average, minimum, and maximum percentages of the nine cover types inside the protected areas and in the matrix, and total area and habitat diversity inside the areas (HDIV_In).

Class Number	Habitat class	Inside			Matrix		
		\bar{x}	min	max	\bar{x}	min	max
1	Pine-spruce >100 m ³ /ha %	16.9	0.8	56.2	7.2	0.9	25.1
2	Pine >100 m ³ /ha %	3.3	0.1	19.0	2.6	0.3	8.6
3	Spruce-Deciduous >100 m ³ /ha %	6.8	0.2	38.6	3.2	0.5	10.0
4	Spruce 25–100 m ³ /ha %	12.4	1.4	34.6	9.9	2.5	21.2
5	Pine 25–100 m ³ /ha %	10.9	0.4	27.3	13.1	3.9	25.0
6	Spruce-Deciduous 25–100 m ³ /ha %	10.7	1.9	45.0	14.4	5.4	33.9
7	Pine bogs %	20.0	0.3	50.9	18.6	7.3	33.2
8	Shrubs <25 m ³ /ha %	5.7	0.7	17.9	15.1	5.4	32.9
9	Other open areas %	13.3	0	35.9	15.8	7.1	26.4
	Total area (ha)	3406	141	27884			
	HDIV_In	1.85	1.47	2.12			

<https://doi.org/10.1371/journal.pone.0184792.t001>

Statistical analysis

We constructed linear models with the R (version 3.4.0) to analyze the impacts that the characteristics of protected areas and their surrounding landscape matrix have on each diversity metric of the bird communities in the protected areas. Species richness, which is a count variable, was analysed with generalized linear model using a Poisson distribution with a log link function. We used a two-step modeling approach, where the most important variables inside the protected areas were first selected, after which these variables were kept in the model and the most important variables in the surrounding matrix were then selected. In all models, we included N-coordinate as a covariate to control for the well-known decline in diversity with increasing latitude. In the first step, we included and selected the most important variables describing landscape structure within protected areas, assuming that avian community composition is primarily affected by the characteristics of the area itself. The selected variables were the log-transformed total forest area (TFA; the summed area of habitat classes 1–6 in [Table 1](#)), the percentage of both young and old spruce-deciduous forests (PROD_In; percentage sum of habitat classes 3 and 6) to describe productivity, and habitat diversity (HDIV_In). In the second step, we selected the most important variables describing landscape structure in the matrix surrounding the protected areas, in addition to keeping the previously selected variables describing the protected areas. These variables were the percentage of old forest (OF_Matrix; Habitat classes 1–3), and the percentage of shrub (SHRUB_Matrix; habitat class 8). The percentage of old forest described long-term logging history in the matrix surrounding the protected areas: the more old forest in the matrix, the lower the overall logging intensity in the past. High values in the percentage of shrub in the matrix indicate high recent logging activity. To assess if the responses were different in large and small protected areas, we also included the interactions between total forest area and the percentage of old forest in the matrix, as well as total forest area and the percentage of shrub in the matrix.

We used Akaike Information Criteria with small sample size correction (AICc) to select the variables to retain at each step, and included only models that were inside 6 AIC units, which gives a 95% chance of retaining the most parsimonious model [46]. According to nesting rule [46], we discarded all models for which a nested version had a lower AICc value. In cases where we had two or more alternative models, we used model averaging to create one best model [47]. Because variables describing the composition of the matrix were entered into the models after within-area variables, they describe the additional effects of the surrounding matrix. All variables were entered as fixed effects, and correlations among the landscape variables were not particularly strong ([S3 Text](#)).

Results

We found that total forest area and productivity inside the protected areas had positive effects on species richness ([Table 2](#), [Fig 2](#)). No matrix effects on species richness were found. The percentage of spruce-deciduous forest (PROD_In) had a strong positive effect on taxonomic diversity, with an increase of 20% along the entire productivity gradient ([Table 2](#), [Fig 2](#)). There was also a strong positive impact of habitat diversity (HDIV_In) on taxonomic diversity, with an increase of 30% along the entire gradient of increasing habitat diversity ([Table 2](#), [Fig 2](#)). We found no matrix effects on taxonomic diversity. The results for phylogenetic diversity showed very similar patterns as for taxonomic diversity ([Table 2](#), [Fig 2](#)).

In contrast to taxonomic and phylogenetic diversity, there was a strong negative influence of the percentage of spruce-deciduous forest within protected areas (PROD_In) on functional diversity ([Table 2](#), [Fig 2](#)), with functional diversity monotonically decreasing by approximately 20% along the entire gradient of PROD_In ([Fig 2](#)). Also, habitat diversity (HDIV_In) had a

Table 2. Results of two-step regression models best explaining the diversity of Finnish protected forests. Empty cells indicate variables that were not included in the models. For further information about the models, see [S6 Text](#).

	Species richness			Taxonomic Diversity			Functional Diversity			Phylogenetic Diversity			Community Specialization Index		
	Estimate	Std. Error	p	Estimate	Std. Error	p	Estimate	Std. Error	p	Estimate	Std. Error	p	Estimate	Std. Error	p
Inside															
(Intercept)	11.17	1.84	<0.000***	106.79	15.24	<0.000***	2.56	0.61	<0.000***	5.203	0.846	<0.000***	0.96	0.67	0.157
N-coordinate	-0.001	0.04	<0.000***	-0.015	0.0021	<0.000***	-1.53E-04	8.26E-05	<0.000***	-0.0005	0.0001	<0.000***	-0.0001	0.0001	0.328
Total Forest Area	0.486	0.039	<0.000*				0.07	0.04	0.046*						
Productivity (PROD_in)	0.007	0.002	<0.000***	0.069	0.014	<0.000***	-2.70E-03	5.58E-04	<0.000***	0.003**	0.0008	0.0003***	0.0002	0.0006	0.007**
Habitat Diversity (HDIV_in)				2.73	0.88	0.0025**	-0.090	0.38	0.0266*	0.183	0.049	0.0001***	0.187	0.039	<0.000***
Forest Area*Shrub in area and matrix							-5.092E-03	2.568E-03	0.034*						
Matrix							-3.40E-03	1.20E-03	0.005**				0.033	0.0013	0.015*
Old Forest (OF_matrix)							-1.41E-03	6.12E-03	0.818						
Shrub (Shrub_matrix)															

*p>0.05
 ** p>0.01
 *** p>0.001

<https://doi.org/10.1371/journal.pone.0184792.t002>

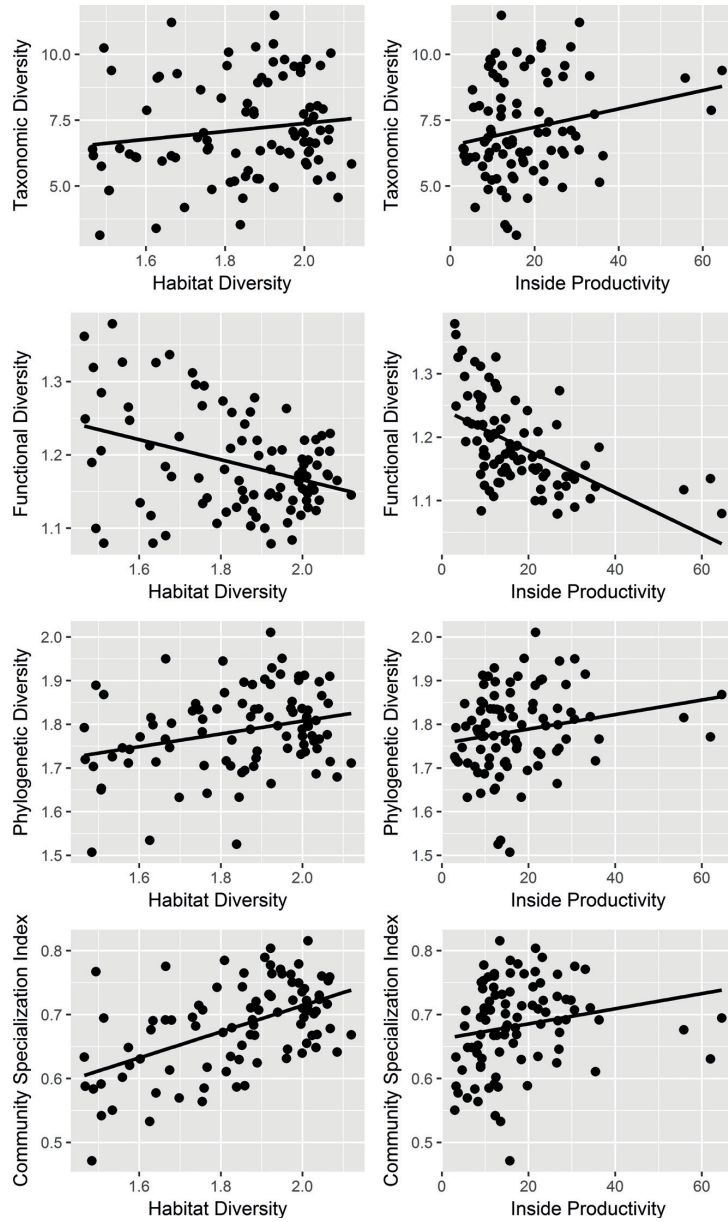


Fig 2. The effects of inside habitat diversity and inside productivity on different diversity metrics.

<https://doi.org/10.1371/journal.pone.0184792.g002>

negative impact on functional diversity, with a decrease of approximately 10% along the gradient. The effect of total forest area on functional diversity was positive but weak. Of the matrix effects, the percentage of old forest (OF_Matrix) had a negative impact, resulting in a roughly 10% decrease in functional diversity over the gradient of old forest cover (Table 2, Fig 3). The main effect of percentage of shrub was not significant, but the negative interaction between total forest area and percentage of shrub suggested that the effect of recent logging activity was stronger in small protected areas.

Community specialization was positively associated with PROD_In and HDIV_In, showing a roughly 12% increase along the increasing gradients (Table 2, Fig 2). Of the matrix effects, OF_Matrix showed a strong positive impact on community specialization, with a nearly 25% increase along the gradient of increasing old forest (Table 2, Fig 3). Thus, protected areas with high productivity foster more specialized bird communities, especially if they have a high proportion of old forest in the matrix.

Concerning the relationships between the response variables, taxonomic diversity was strongly correlated with phylogenetic diversity (Table 3). There was also a relatively strong correlation between the community specialization index and phylogenetic diversity. Functional diversity was weakly negatively correlated with all other diversity metrics.

Discussion

In this study, matrix effects were found for functional diversity, and community specialization, but not for species richness, taxonomic and phylogenetic diversity. The amount of old forest in the matrix had a positive influence on community specialization but a negative influence on functional diversity. Inside protected areas, the impacts of productivity and total forest area on species richness were positive, as expected.

The productivity and habitat diversity within protected areas had a strong positive effect on both taxonomic and phylogenetic diversity, as well as on community specialization (Table 2). The pattern supports our hypothesis, as well as earlier literature, that habitat diversity and productivity have a positive effect on species diversity [26]. There were more species in large areas, but larger forest areas did not have increased taxonomic nor phylogenetic diversities. Thus, it seems that the additional species that are occupying large areas are low in abundance and not phylogenetically distinct.

Taxonomic diversity was strongly positively correlated with phylogenetic diversity (Table 3). Thus, increasing taxonomic diversity was associated with an increased phylogenetic distance among species, i.e. with the addition of phylogenetically unique species. Community specialization was relatively strongly correlated with taxonomic and phylogenetic diversity (Table 3). This suggests that increasing taxonomic diversity is associated with an increasing number of specialist species in a community, and that specialist species tend to represent distinct phyletic lineages. In earlier research, overall positive covariation has been found between different facets of biodiversity, but some incongruence has also been found [12]. For example, in their study on spatial distribution and abundance of birds in France, Devictor et al. [12] found that regions with high versus low functional diversity do not necessarily spatially overlap with high vs low taxonomic or phylogenetic diversity. Even though in the French bird data different facets of biodiversity were positively associated, variation in taxonomic diversity explained only a very small proportion of variation (6%) in functional diversity. We found that functional diversity was negatively correlated, although weakly, with all other diversity metrics (Table 3), suggesting that different aspects of species diversity may respond in dissimilar fashion to environmental variation and change.

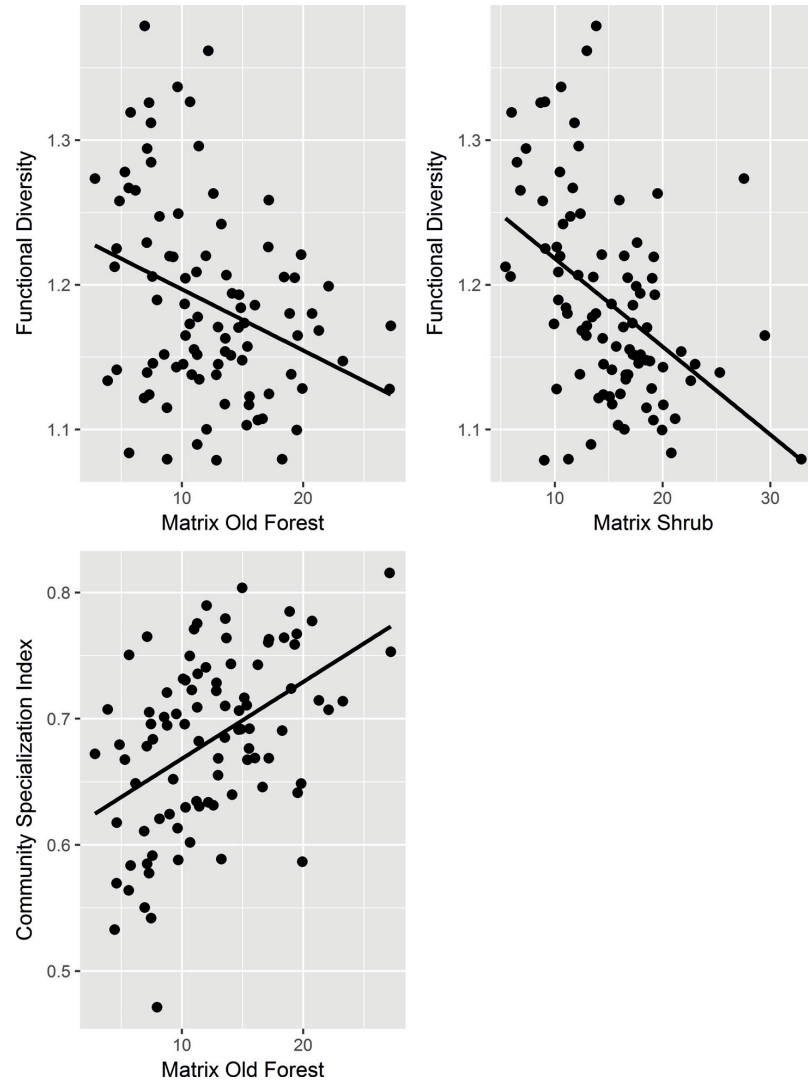


Fig 3. Matrix effects on different diversity metrics.

<https://doi.org/10.1371/journal.pone.0184792.g003>

Functional diversity showed the opposite responses to other diversity measures, with negative impacts of productivity and habitat diversity inside protected areas (Table 2, Fig 2). We

Table 3. Correlation matrix of different diversity metrics.

	Species Richness	Taxonomic Diversity	Functional Diversity	Phylogenetic Diversity	Community Specialization Index
Species Richness	1				
Taxonomic Diversity	0.417	1			
Functional Diversity	-0.170	-0.186	1		
Phylogenetic Diversity	0.355	0.910	-0.170	1	
Community Specialization Index	0.416	0.683	-0.518	0.789	1

<https://doi.org/10.1371/journal.pone.0184792.t003>

suggest that the mechanism for this phenomenon could be explained by species interactions and the properties of Rao's quadratic entropy in measuring functional diversity. Functional diversity is influenced both by species abundance-based diversity and by functional differences among species [48] [49]. Thus, if one species from a functionally similar group of species becomes less abundant or goes extinct, functional diversity increases. Likewise, the introduction of new species will increase species abundance-based diversity, but it may decrease the average functional dissimilarity among species. On the other hand, the colonization of functionally distinct species will increase average functional dissimilarity between species. A similar effect may stem from an increase in abundance of originally rare but functionally distinct species. The response of functional diversity also depends on the way it has been calculated. Counter to our results, Petchey et al. [50] found that functional diversity increased with increasing species richness. However, unlike in our study, branch lengths of the dendrogram of species (based on functional differences) are summed in their approach: when new species are added into the community the number of branches increases, leading to higher functional diversity.

Our observation that functional diversity decreases with increasing productivity is in line with the Physiological Tolerance Hypothesis [51], postulating that diversity varies according to the tolerances of individual species for different sets of climatic conditions. Accordingly, in less favorable conditions species do not share physiological traits and combinations of traits, and their overlap increases with increasing suitability of ambient conditions. Interestingly, functional diversity was positively influenced by total forest area (Table 2). Because species richness also increased with forest area, it seems that the species that occupy larger areas are also functionally distinct.

The matrix effects that explained functional diversity were the percentage of old forest and, in small areas, shrub in matrix; both had negative effects on functional diversity (Table 2, Fig 3). Thus, functional diversity decreases with increasing recent logging intensity (i.e. shrub) on small areas, but increases with increasing proportion of old forest, i.e. with decreasing overall logging intensity, independent of the size of the area. Thus, large protected areas seem to be better buffered against matrix effects because the effects of recent logging intensity decrease with increasing total forest area. The explanation can be found again in the diversity index, as functional diversity decreases with increasing functional similarity among species. Here, increasing recent logging intensity reduces the average functional distance among species, and thereby results in decreased functional diversity. This may be because of spill-over of generalist species from the matrix. In summary, logging activity in the matrix results in a loss of ecological functions and in

biotic homogenization, particularly in small protected areas and in the short-term but not in the long-term.

Community specialization was positively correlated with taxonomic and phylogenetic diversities (Table 3), and was likewise positively associated with habitat diversity and productivity inside protected areas (Table 2, Fig 2). Thus, bird communities in areas with productive forests and a wide variety of habitats have more specialized lineages but, as discussed earlier, less species with similar functions. The positive influence of habitat diversity inside protected areas on community specialization index may first sound counterintuitive because specialist species should benefit from uniform habitats allowing larger population sizes, which decreases the likelihood of stochastic extinctions. We suggest that the effect of habitat diversity on specialist species' habitat availability is scale-dependent [52]. At small spatial extents, habitat diversity should have a negative effect on specialist species, because for a given area, the amount of area available for individual species decreases with increasing habitat heterogeneity, thereby increasing the likelihood of stochastic extinctions. When total habitat area is large, the negative effect of increasing habitat heterogeneity is balanced by the positive effects of colonization by new specialist species.

The proportion of old forest in the matrix had a positive impact on community specialization (Table 2, Fig 3). This supports our hypothesis that protected areas embedded in an intensively managed matrix foster more homogeneous, less specialized bird communities than those embedded in a less managed matrix. This is caused by the replacement of old forest specialists by generalist species [53]. Our results support the idea that the flow of generalists from the matrix into the protected areas may be an important mechanism of homogenization. However, one could expect this matrix effect to be area-dependent, i.e. small protected areas would be more vulnerable to generalists' invasion, but we did not find evidence for this with the community specialization index.

Conclusions

To conclude, our results highlight how different measures of diversity may show different responses to environmental change, which emphasizes the importance of considering multiple aspects when analyzing biodiversity. Our results show that by concentrating only on the conservation of species richness, taxonomic diversity or specialist species, all functions are not necessarily safe-guarded. Even if we manage to maintain ecosystem functions, we may lose unique specialists.

Our results provide insights when establishing new protected areas. If large areas with high species richness are favored, this may not necessarily ensure high taxonomic or phylogenetic diversities, and a focus on species-rich sites may in fact minimize functional diversity. Taxonomic and phylogenetic diversities seem to be secured as long as the area is productive and has high habitat diversity. From a conservation perspective, this is challenging since traditionally protected areas are established in areas where productivity is low and possibilities for exploitation are poor [54]. On the other hand, the response of functional diversity to landscape structure is much more complex than in the case of taxonomic and phylogenetic diversity. For the protection of functional diversity in communities, the matrix is important in addition to the properties of the protected area itself. It seems that uniform areas with low habitat diversity embedded in a matrix with little disturbance have the highest functional diversity. Finally, specialist species benefit from protected areas with high productivity and habitat diversity, and from matrices with a large proportion of old forest. Thus, for specialist species and to prevent biotic homogenization, the matrix quality is of great importance.

Supporting information

S1 Text. Line transect count method.
(DOCX)

S2 Text. Species list.
(DOCX)

S3 Text. Correlations between landscape variables.
(DOCX)

S4 Text. Correlations between morphological indices.
(DOCX)

S5 Text. VIF values of model variables.
(DOCX)

S6 Text. Model rankings.
(DOCX)

S7 Text. R packages.
(DOCX)

S8 Text. Phylogenetic tree.
(TRE)

S9 Text. Habitat categories of Finnish Point Counts.
(DOCX)

S1 Table. Bird and landscape data.
(XLSX)

Acknowledgments

E. Knott helped us putting together the consensus phylogenetic tree. We also want to thank A. Nikula for his work with the landscape data. Gerald. J. Niemi, Anna Repo and two anonymous reviewers gave valuable comments on manuscript.

Author Contributions

Conceptualization: Eric Le Tortorec, Mikko Mönkkönen.

Data curation: Eric Le Tortorec, Lluís Brotons, Ari Rajasärkkä, Risto Tornberg, Mikko Mönkkönen.

Formal analysis: Matti Häkkilä, Eric Le Tortorec, Lluís Brotons.

Investigation: Matti Häkkilä, Lluís Brotons, Ari Rajasärkkä, Risto Tornberg, Mikko Mönkkönen.

Methodology: Eric Le Tortorec, Mikko Mönkkönen.

Project administration: Mikko Mönkkönen.

Supervision: Eric Le Tortorec, Mikko Mönkkönen.

Validation: Mikko Mönkkönen.

Visualization: Matti Häkkilä.

Writing – original draft: Matti Häkkinen, Mikko Mönkkönen.

Writing – review & editing: Matti Häkkinen, Eric Le Tortorec, Lluís Brotons, Ari Rajasärkkä, Risto Tornberg, Mikko Mönkkönen.

References

1. Travis JMJ. Climate change and habitat destruction: a deadly anthropogenic cocktail. *Proceedings. Biological sciences / The Royal Society* 2003; 270:467–73.
2. Sala OE. Global Biodiversity Scenarios for the Year 2100. *Science* 2000; 287:1770–1774. PMID: [10710299](https://doi.org/10.1029/10710299)
3. Hooper DU, Adair EC, Cardinale BJ, Byrnes JEK, Hungate BA, Matulich KL, et al. A global synthesis reveals biodiversity loss as a major driver of ecosystem change. *Nature* 2012; 486:105–8. <https://doi.org/10.1038/nature11118> PMID: [22678289](https://pubmed.ncbi.nlm.nih.gov/22678289/)
4. Cardinale BJ, Srivastava DS, Duffy JE, Wright JP, Downing AL, Sankaran M, Jouseau C. Effects of biodiversity on the functioning of trophic groups and ecosystems. *Nature* 2006; 443:989–92. <https://doi.org/10.1038/nature05202> PMID: [17066035](https://pubmed.ncbi.nlm.nih.gov/17066035/)
5. Cardinale BJ, Matulich KL, Hooper DU, Byrnes JE, Duffy E, Gamfeldt L, Balvanera P, O'Connor MI, Gonzalez A. The functional role of producer diversity in ecosystems. *American journal of botany* 2011; 98:572–92. <https://doi.org/10.3732/ajb.1000364> PMID: [21613148](https://pubmed.ncbi.nlm.nih.gov/21613148/)
6. Mace GM, Norris K, Fitter AH. Biodiversity and ecosystem services: a multilayered relationship. *Trends in ecology & evolution* 2012; 27:19–26.
7. Faith DP. Conservation evaluation and phylogenetic diversity. *Biological Conservation* 1992; 61:1–10.
8. Srivastava DS, Cadotte MW, MacDonald AAM, Marushia RG, Mirochnik N. Phylogenetic diversity and the functioning of ecosystems. *Ecology Letters* 2012; 15:637–648. <https://doi.org/10.1111/j.1461-0248.2012.01795.x> PMID: [22583836](https://pubmed.ncbi.nlm.nih.gov/22583836/)
9. Lavergne S, Mouquet N, Thuiller W, Ronce O. Biodiversity and Climate Change: Integrating Evolutionary and Ecological Responses of Species and Communities. *Annual Review of Ecology, Evolution, and Systematics* 2010; 41:321–350.
10. Tilman D. The Influence of Functional Diversity and Composition on Ecosystem Processes. *Science* 1997; 277:1300–1302.
11. Cadotte MW, Dinnage R, Tilman D. Phylogenetic diversity promotes ecosystem stability. *Ecology* 2012; 93:223–233.
12. Devictor V, Moullot D, Meynard C, Jiguet F, Thuiller W, Mouquet N. Spatial mismatch and congruence between taxonomic, phylogenetic and functional diversity: the need for integrative conservation strategies in a changing world. *Ecology letters* 2010; 13:1030–40. <https://doi.org/10.1111/j.1461-0248.2010.01493.x> PMID: [20545796](https://pubmed.ncbi.nlm.nih.gov/20545796/)
13. Clavel J, Julliard R, Devictor V. Worldwide decline of specialist species: toward a global functional homogenization? *Frontiers in Ecology and the Environment* 2011; 9:222–228.
14. Haila Y. A Conceptual Genealogy of Fragmentation Research: From Island Biogeography to Landscape Ecology. *Ecological Applications* 2002; 12:321.
15. Watling JI, Nowakowski AJ, Donnelly MA, Orrock JL. Meta-analysis reveals the importance of matrix composition for animals in fragmented habitat. *Global Ecology and Biogeography* 2011; 20:209–217.
16. Ricketts TH. The matrix matters: effective isolation in fragmented landscapes. *The American naturalist* 2001; 158:87–99. <https://doi.org/10.1086/320863> PMID: [18707317](https://pubmed.ncbi.nlm.nih.gov/18707317/)
17. Prugh LR, Hodges KE, Sinclair ARE, Brashares JS. Effect of habitat area and isolation on fragmented animal populations. *Proceedings of the National Academy of Sciences of the United States of America* 2008; 105:20770–5. <https://doi.org/10.1073/pnas.0806080105> PMID: [19073931](https://pubmed.ncbi.nlm.nih.gov/19073931/)
18. Moilanen A, Hanski I. Metapopulation dynamics: Effects of habitat quality and landscape structure. *Ecology* 1998; 79:2503–2515.
19. Dunning JB, Danielson BJ, Pulliam HR. Ecological Processes That Affect Populations in Complex Landscapes. *Oikos* 1992; 65:169–175.
20. Naughton-Treves L, Holland MB, Brandon K. The Role of Protected Areas in Conserving Biodiversity and Sustaining Local Livelihoods. *Annual Review of Environment and Resources* 2005; 30:219–252.
21. Mönkkönen M, Rajasärkkä A, Lampila P. Isolation, patch size and matrix effects on bird assemblages in forest reserves. *Biodiversity and Conservation* 2014; 23:3287–3300.
22. Driscoll DA, Banks SC, Barton PS, Lindenmayer DB, Smith AL. Conceptual domain of the matrix in fragmented landscapes. *Trends in ecology & evolution* 2013; 28:605–13.

23. Cottee-Jones HEW, Matthews TJ, Bregman TP, Barua M, Tamuly J, Whittaker R. Are Protected Areas Required to Maintain Functional Diversity in Human-Modified Landscapes? PLoS ONE 2015; 10(5).
24. Fahrig L. How much habitat is enough? *Biological Conservation* 2001; 100:65–74.
25. Flynn DFB, Gogol-Prokurat M, Nogeire T, Molinari N, Richers BT, Lin BB, et al. Loss of functional diversity under land use intensification across multiple taxa. *Ecology letters* 2009; 12:22–33. <https://doi.org/10.1111/j.1461-0248.2008.01255.x> PMID: 19087109
26. Honkanen M, Roberge J-M, Rajasärkkä A, Mönkkönen M. Disentangling the effects of area, energy and habitat heterogeneity on boreal forest bird species richness in protected areas. *Global Ecology and Biogeography* 2010; 19:61–71.
27. Peltola, A. (Ed. 2014. Finnish Statistical Yearbook of Forestry 2014.—Finnish Forest Research Institute.
28. Järvinen O, Väisänen RA. Finnish line transect censuses. *Ornis Fennica* 1976; 53:115–118.
29. Järvinen O, Väisänen RA. Methodology for censusing land bird faunas in large regions. *Studies in Avian Biology* 1981; 6:146–151.
30. Väisänen RA, Lammi E, Koskimies P. Muuttuva Pesimälinnusto. Otava, Keuruu; 1998.
31. Brotons L, Mönkkönen M, Huhta E, Nikula A, Rajasärkkä A. Effects of landscape structure and forest reserve location on old-growth forest bird species in Northern Finland. *Landscape Ecology* 2003; 18:377–393.
32. Rao CR. Diversity and dissimilarity coefficients: A unified approach. *Theoretical Population Biology* 1982; 21:24–43.
33. De Bello F, Lavergne S, Meynard CN, Lepš J, Thuiller W. The partitioning of diversity: showing Theseus a way out of the labyrinth. *Journal of Vegetation Science* 2010; 21:992–1000.
34. Julliard R, Clavel J, Devictor V, Jiguet F, Couvet D. Spatial segregation of specialists and generalists in bird communities. *Ecology letters* 2006; 9:1237–44. <https://doi.org/10.1111/j.1461-0248.2006.00977.x> PMID: 17040326
35. Pavoine S, Dufour AB, Chessel D. From dissimilarities among species to dissimilarities among communities: a double principal coordinate analysis. *Journal of Theoretical Biology* 2004; 228:523–537. <https://doi.org/10.1016/j.jtbi.2004.02.014> PMID: 15178200
36. Ricotta C. A note on functional diversity measures. *Basic and Applied Ecology* 2005; 6:479–486.
37. Petchey OL, Gaston KJ. Functional diversity (FD), species richness and community composition. *Ecology Letters* 2002; 5:402–411.
38. Miles DB, Ricklefs RE. The Correlation Between Ecology and Morphology in Deciduous Forest Passerine Birds. *Ecology* 1984; 65: 1629–1640.
39. Lederer RJ. Bill size, food size and jaw forces of insectivorous birds. *Auk* 1975; 92:385–387.
40. Jetz W, Thomas GH, Joy JB, Hartmann K, Mooers AO. The global diversity of birds in space and time. *Nature* 2012; 491:444–8. <https://doi.org/10.1038/nature11631> PMID: 23123857
41. Jetz W, Thomas GH, Joy JB, Redding DW, Hartmann K, Mooers AO. Global distribution and conservation of evolutionary distinctness in birds. *Current biology* 2014; 24:919–30. <https://doi.org/10.1016/j.cub.2014.03.011> PMID: 24726155
42. Laaksonen T, Lehtikoinen A. Population trends in boreal birds: Continuing declines in agricultural, northern, and long-distance migrant species. *Biol. Cons.* 2013; 168:99–107.
43. Devictor V, Clavel J, Julliard R, Lavergne S, Mouillot D, Thuiller W et al. Defining and measuring ecological specialization. *Journal of Applied Ecology* 2010; 47:15–25.
44. Tomppo E. Multi-source national forest inventory of Finland. In: Nyyssönen A, Poso S, Rautala J (Eds.). Proceedings of Ilvesalo symposium on national forest inventories. The Finnish Forest Research Institute, Research Papers 444; 1993, pp. 53–61.
45. Mönkkönen M, Reunanen P, Nikula A, Inkeröinen J, Forsman J. Landscape characteristics associated with the occurrence of the flying squirrel *Pteromys volans* in old-growth forests of northern Finland. *Ecography* 1997; 20:634–642.
46. Richards SA, Whittingham MJ, Stephens PA. Model selection and model averaging in behavioural ecology: the utility of the IT-AIC framework. *Behavioral Ecology and Sociobiology* 2011; 65:77–89.
47. Burnham KP, Anderson DR. Model selection and multimodel inference. A practical Information-Theoretic Approach, 2nd edn. Springer-Verlag, New York, USA; 2002.
48. Botta-Dukat Z. Rao's quadratic entropy as a measure of functional diversity based on multiple traits. *Journal of Vegetation Science* 2005; 16: 533–540.
49. Petchey OL, Gaston KJ. Functional diversity: back to basics and looking forward. *Ecology Letters* 2006; 9: 741–758. <https://doi.org/10.1111/j.1461-0248.2006.00924.x> PMID: 16706917

50. Petchey OL, Gaston KJ. Functional diversity (FD), species richness and community composition. *Ecology Letters* 2002; 5: 402–411.
51. Currie DJ, Mittelbach GG, Cornell HW, Field R, Guégan JF, Hawkins BA et al. Predictions and tests of climate-based hypotheses of broad-scale variation in taxonomic richness. *Ecology Letters* 2004; 7:1121–1134.
52. Allouche O, Kalyuzhny M, Moreno-Rueda G, Pizarro M, Kadmon R. Area-heterogeneity tradeoff and the diversity of ecological communities. *Proceedings of the National Academy of Sciences of the United States of America* 2012; 109:17495–500. <https://doi.org/10.1073/pnas.1208652109> PMID: 23045670
53. McKinney M, Lockwood J. Biotic homogenization: a few winners replacing many losers in the next mass extinction. *Trends in ecology & evolution* 1999; 14:450–453.
54. Scott J, Davis F, McGhie R, Wright R, Groves C, Estes J. Nature reserves: do they capture the full range of America's biological diversity? *Ecological Applications* 2001; 11:999–1007.

IV

**HABITAT QUALITY IS MORE IMPORTANT THAN
MATRIX QUALITY FOR BIRD
COMMUNITIES IN PROTECTED AREAS**

by

Matti Häkkilä, Nerea Abrego, Otso Ovaskainen & Mikko Mönkkönen 2018

Ecol Evol. 8(8): 4019-4030.

Habitat quality is more important than matrix quality for bird communities in protected areas

Matti Häkkilä¹  | Nerea Abrego^{2,3} | Otso Ovaskainen⁴ | Mikko Mönkkönen¹

¹Department of Biological and Environmental Sciences, University of Jyväskylä, Jyväskylä, Finland

²Department of Agricultural Sciences, University of Helsinki, Helsinki, Finland

³Department of Biology, Centre for Biodiversity Dynamics, Norwegian University of Science and Technology, Trondheim, Norway

⁴Department of Biosciences, University of Helsinki, Helsinki, Finland

Correspondence

Matti Häkkilä, Department of Biological and Environmental Sciences, University of Jyväskylä, Jyväskylä, Finland.
Email: matti.i.hakkila@jyu.fi

Funding information

Suomen Akatemia, Grant/Award Number: 275329 and 284601; Koneen Säätiö, Grant/Award Number: 44-7217

Abstract

Protected areas are meant to preserve native local communities within their boundaries, but they are not independent from their surroundings. Impoverished habitat quality in the matrix might influence the species composition within the protected areas through biotic homogenization. The aim of this study was to determine the impacts of matrix quality on species richness and trait composition of bird communities from the Finnish reserve area network and whether the communities are being subject of biotic homogenization due to the lowered quality of the landscape matrix. We used joint species distribution modeling to study how characteristics of the Finnish forest reserves and the quality of their surrounding matrix alter species and trait compositions of forest birds. The proportion of old forest within the reserves was the main factor in explaining the bird community composition, and the bird communities within the reserves did not strongly depend on the quality of the matrix. Yet, in line with the homogenization theory, the beta-diversity within reserves embedded in low-quality matrix was lower than that in high-quality matrix, and the average abundance of regionally abundant species was higher. Influence of habitat quality on bird community composition was largely explained by the species' functional traits. Most importantly, the community specialization index was low, and average body size was high in areas with low proportion of old forest. We conclude that for conserving local bird communities in northern Finnish protected forests, it is currently more important to improve or maintain habitat quality within the reserves than in the surrounding matrix. Nevertheless, we found signals of bird community homogenization, and thus, activities that decrease the quality of the matrix are a threat for bird communities.

KEYWORDS

beta-diversity, biotic homogenization, bird community, boreal forest, community composition, protected areas

1 | INTRODUCTION

Both theoretical (Lovejoy, 2006; Moilanen & Hanski, 1998) and empirical studies (Carroll, Noss, Paquet, & Schumaker, 2004; Newmark,

1996; Ricketts, 2001) support that protected areas are not independent from their surrounding matrix. The quality and quantity of the matrix surrounding isolated areas influence the rate of species loss (Prugh, Hodges, Sinclair, & Brashares, 2008; Sisk, Haddad, & Ehrlich,

This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

© 2018 The Authors. *Ecology and Evolution* published by John Wiley & Sons Ltd.

1997), but we still know little about matrix effects on protected forest areas. Large areas can better maintain their species diversity because on small areas, the edge effect to area ratio is larger and the impact of the edge falls upon larger proportion of the area (e.g., Ries, Fletcher, Battlin, & Sisk, 2004). Rayner, Lindenmayer, Wood, Gibbons, and Manning (2014) demonstrated that species diversity within protected areas is highly sensitive to the quality of the matrix in which they are embedded. Correspondingly, Häkkilä et al. (2017) showed that in boreal bird communities, intensification of forest management in the matrix is associated with lowered species specialization, but increased functional diversity within the forest reserves.

The knowledge about the effects of matrix quality on the community differentiation (i.e., beta-diversity) within protected areas is even more limited, albeit this knowledge is critical in conservation planning. Changes in beta-diversity are not always reflected by changes in alpha diversity (Smart et al., 2006; Socolar, Gilroy, Kunin, & Edwards, 2016). Indeed, the quality of the matrix may affect the beta-diversity within protected areas even if the alpha diversity remains unchanged. In such a case, conservation planning should take into account the structure of the landscape surrounding the protected areas.

Biotic homogenization refers to increasing similarity of biotic communities over space and time, and it is caused by nonrandom species extinctions and invasions due to human activities. Human land-use intensification and changes such as urbanization (McKinney, 2006) and intensive agriculture (Ekroos, Heliölä, & Kuussaari, 2010) contribute to the homogenization process by diminishing rare and specialist species and promoting abundant and generalist species which are better able to cope in human-altered environments (Clavel, Julliard, & Devictor, 2011; McKinney & Lockwood, 1999). This process is usually asymmetrical: few abundant and generalist species replacing a larger number of rare and specialist species (Devictor, Julliard, & Jiguet, 2008; McKinney & Lockwood, 1999; Morris & Heidinga, 1997). Consequently, biotic homogenization decreases both taxonomical and functional diversity over space and time (Clavel et al., 2011). Forest ecosystems are highly altered due to human activities (Secretariat of the Convention on Biological Diversity, 2010), yet little is known about whether and how forest-dwelling communities suffer from biotic homogenization (but see Rooney, Wiegmann, Rogers, & Waller, 2004; Solar et al., 2015). In particular, boreal forests have been poorly studied, even if they represent 26% of the world's total forest area (Bryant et al., 1997) and are highly impacted by timber harvesting actions (Lundmark, Josefsson, & Östlund, 2013; Pohjanmies et al., 2017; Vanha-Majamaa et al., 2007).

Biotic homogenization is a process that encompasses the loss of not only taxonomic diversity, but also its functional component (Olden et al. 2004). Due to biotic homogenization, communities become functionally more similar, ultimately affecting ecosystem functioning (Hooper et al., 2005). Furthermore, analyzing community composition in terms of functional traits can be more informative than focusing on species identities, as they can inform about the ability of the species to adapt to particular environmental characteristics (Cadotte, Carscadden, & Mirotnick, 2011). In the case of birds,

it has been shown that resident species are more vulnerable to anthropogenic changes than migratory species (Imbeau, Mönkkönen, & Desrochers, 2001), because resident birds are dependent on habitat resources all year round, whereas migratory birds only visit when the resources are most abundant (Mönkkönen & Welsh, 1994). Morphological traits of birds are well known to be associated with their diet, and movement and foraging behavior (Carrascal, Moreno, & Telleria, 1990; Jönsson, Lessard, & Ricklefs, 2015; Miles & Ricklefs, 1984). For instance, body size is associated with extinction risk, because larger species tend to have lower fecundity, and thereby higher sensitivity to habitat disturbances (Bennett & Owens, 1997). Using traits in our analyses, it is possible to study which characteristics are particularly sensitive to environmental change and thereby to reveal the mechanisms of biotic homogenization.

In intensively managed Fennoscandian boreal forests, protected areas are surrounded by young, fast-growing forests. Some forest-dependent bird species benefit from logging in the matrix by foraging in the matrix (Jokimäki & Huhta, 1996), whereas others are strictly confined to old-growth forests. The managed forest matrix may thus alter the community composition within protected areas by benefitting the occurrences of more generalist species that make use of the resources in the matrix. Correspondingly, Mönkkönen, Rajasärkkä, and Lampila (2014) found that the number of specialist bird species is lower in old-growth forest patches surrounded by managed forests than in continuous old-growth forests. The effects of the matrix quality may additionally differ in relation to the size of the protected areas. The effects of the matrix quality may be particularly acute in small protected areas (Carroll et al., 2004) because small area renders it difficult to maintain viable populations (Gaston, Jackson, Cantú-Salazar, & Cruz-Piñón, 2008).

The aim of this study was to determine whether the matrix quality impacts the species richness and trait composition bird communities and whether the Finnish protected area network suffers from biotic homogenization due to matrix effects. To address these aims, we use an extensive dataset of bird occurrence data comprising 69 species in 91 nature reserves in northern Finland. We apply a hierarchical joint species distribution model to simulate bird community scenarios in forest reserves of different sizes, habitat quality, and matrix quality. Specifically, we ask whether the matrix quality affects (1) the taxonomical community composition, (2) functional trait composition, and (3) community similarities (beta-diversity) within forest reserves when these differ in size, habitat, and matrix quality.

If homogenization occurs, reserves embedded in matrices with high level of disturbance (high proportion of shrubs and saplings) will have lower beta-diversity than those embedded in less disturbed matrix. Homogenization effects will be strongest in reserves where differences in habitat composition between reserves and the surrounding matrix are the greatest. We further hypothesize that the matrix effects will be strongest on small reserves, whereas large reserves are better able to maintain their integrity. If so, conservation efforts should be focused on large areas, and in case of small areas, on managing the surrounding matrix to minimize contrast to the protected areas in landscape structure. We also expect changes in species traits with changes in habitat quality

in the reserves and in their surrounding matrix. In particular, we hypothesize that resident species, specialist species as well as species with large body size will be especially susceptible to disturbance in matrix.

2 | METHODS

2.1 | Study area

The study area is in the boreal zone in northern Finland (Figure 1) where forests are mainly coniferous (Table 1). The area is sparsely populated and dominated by forest land, but open bogs, mires, small lakes, and ponds are characteristics of the landscape. Most forests are intensively managed. This study focuses on 91 unmanaged nature reserves with a total area of approximately 3,100 km². Reserves vary in size from 200 to 28,000 ha (mean area = 3,400 ha, SD = 4,676 ha), and their average distance to nearest neighbor area was 13,047 m.

2.2 | Data description

2.2.1 | Environmental data

Land use and cover data were acquired from the 8th National Forest Inventory of Finland (NFI) for which the data were collected

1986–1994 (Tomppo, 1993). These multisource data are based on satellite images and their interpretation, and entirely cover the protected areas and their matrices. Data resolution is 25 m × 25 m. For each pixel of forested land, NFI produces an estimate of growing stock volume separately for *Pinus sylvestris*, *Picea abies*, *Betula spp.*, and all other species as a combined class. Digital maps of nonforest (peatland, water, agricultural land, roads, and settlements) lands are used to separate nonforest areas from forest. Using these data, land cover of the study area was classified into nine classes according to vegetation structure (see Brotons, Mönkkönen, Huhta, Nikula, & Rajasärkkä, 2003; Table 1). From this classification, we calculated variables describing the habitat composition within the reserves and in the surrounding landscape. We used the sum of spruce-deciduous cover types (habitat classes 3 and 6; Table 1) to describe productivity. In the study area, spruce-deciduous forests only grow on fertile soil while less fertile sites are usually pine-dominated. To describe the proportion of old forest, we used the sum of the three cover types with more than 100 m³/ha (habitat classes 1–3; Table 1). On advanced thinning stands, where most trees have reached saw timber size, the average stock volume in northern Finland is 118 m³/ha, but in southern Lapland only 99 m³/ha (Peltola, 2014). Therefore, we chose 100 m³ as a limit above which we consider forest old. We assume that the proportion of forests with saw timber stock within reserves is related to their

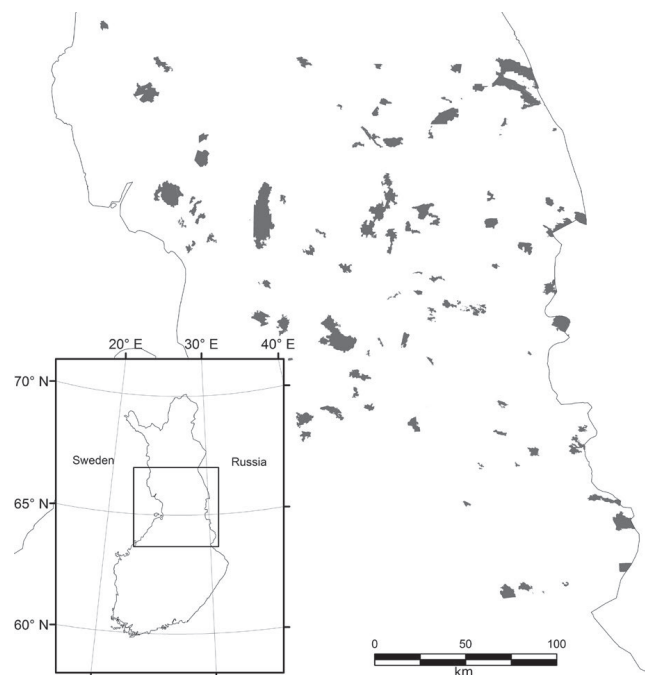


FIGURE 1 Map of the study area and the location of the forest reserves in northern Finland

Cover type	Abbreviation of habitat type	Inside			Matrix		
		\bar{x}	Min	Max	\bar{x}	Min	Max
Pine-spruce >100 m ³ /ha %	1	16.9	0.8	56.2	7.2	0.9	25.1
Pine >100 m ³ /ha %	2	3.3	0.1	19.0	2.6	0.3	8.6
Spruce-Deciduous >100 m ³ /ha %	3	6.8	0.2	38.6	3.2	0.5	10.0
Spruce 25–100 m ³ /ha %	4	12.4	1.4	34.6	9.9	2.5	21.2
Pine 25–100 m ³ /ha %	5	10.9	0.4	27.3	13.1	3.9	25.0
Spruce-Deciduous 25–100 m ³ /ha %	6	10.7	1.9	45.0	14.4	5.4	33.9
Pine bogs %	7	20.0	0.3	50.9	18.6	7.3	33.2
Shrubs <25 m ³ /ha %	8	5.7	0.7	17.9	15.1	5.4	32.9
Other open areas %	9	13.3	0	35.9	15.8	7.1	26.4

TABLE 1 Percentages of the cover types inside the protected areas and their matrices. The average, minimum and maximum percentages are shown

habitat quality because we focus on forest birds. We analyzed matrix quality within 5 km radius around the reserves. 5 km radius was selected to make sure that the matrix could have impact on species with large home ranges such as large raptors. Larger radii could have resulted in an excessive overlap in matrices of neighboring areas. A portion of the matrices around reserves adjacent to or near the Russian border fell outside the Finnish land-cover data, and comparable data from Russia were not available. In such cases, landscape structure in the buffer zone was estimated assuming that undisturbed areas along the Russian border have identical landscape composition compared with the reserve itself. This assumption is reasonable because Finnish forest reserves represent natural, undisturbed areas corresponding to the state of forests along the Russian side of the border. As indicator for low quality, we used the proportion of shrubs and saplings (habitat class 8; Table 1), because intense clear-cutting activities result in landscapes dominated by young trees.

2.2.2 | Bird data

The bird species abundance was measured with the Finnish line transect census method (Järvinen & Väisänen, 1976) by Metsähallitus Parks & Wildlife Finland. Because the basic idea was to study whether species living in protected areas are safeguarded from the impacts of logging we focused on forest species, and thus of the 129 species in the original data, including wetland species, we selected 69 species known to use forest as their main breeding habitat (Väisänen, Lammi, & Koskimies, 1998). The bird censuses were conducted between 1988 and 1999 for a total of 3,323 km of transects. On average, 1 km of transect per km² of land area was surveyed; small areas being surveyed with higher per-unit-area effort. We combined data across years as earlier analyses showed that species richness and abundance of forest species in these data did not differ significantly among years (Brotons et al., 2003).

2.2.3 | Trait data

We compiled data on morphological traits, migratory patterns, habitat requirements, and population characteristics (Table 2). We made morphological measurements (wing, tail, tarsus and bill length, bill width, bill height, and body mass) of museum samples of a minimum of five individuals per species. As all of these morphological

TABLE 2 Description of the traits included in the analyses

Trait	Description	Units
Morphological traits		
Log-transformed body size	Body mass (g)	Continuous
Bill ratio	Bill length/(bill width + bill height)	Continuous
Wing length	Wing length/(body mass ^{1/3})	Continuous
Tarsus length	Tarsus length/(body mass ^{1/3})	Continuous
Tail length	Tail length/(body mass ^{1/3})	Continuous
Migratory patterns		
Resident, migratory	Whether the species are resident or migratory (either long- or short-distance)	Categorical, two levels
Habitat requirements		
SSI	Species (habitat) specialization index	Continuous
Population characteristics		
Population size	Minimum count of breeding bird pairs in Finland	Continuous
Population trend	Whether the bird populations have increased, decreased, or remained stable during the last 20–30 years in Finland.	Categorical, three levels

measures are strongly correlated and reflect the body size of the bird, we transformed original morphological variables into indices that link morphology with ecological functions. First, we used body mass (log-transformed) as an indicator of overall body size. Body size is important driver of both habitat use and diet. Second, to describe functions related to the type of food, we used a ratio bill length/(bill width + bill height). Species with long bills relative to bill width and height tend to be more insectivorous than short-billed species (Lederer, 1975). Third, we calculated three further ratios (wing length/body mass^{1/3}, tarsus length/body mass^{1/3}, and tail length/body mass^{1/3}) to represent differences in locomotion and habitat use (Miles & Ricklefs, 1984). The lengths were divided by the cubic root of body mass to scale these one-dimensional variables by a one-dimensional measure of body size.

We classified the bird species as resident or migratory (either long- or short-distance) according to Svensson, Grant, Mullarney, and Zetterström (2010). We used the species specialization index (SSI) as a measure of habitat specialization (Julliard, Clavel, Devictor, Jiguet, & Couvet, 2006). For the calculation of SSI, we used Finnish point count data that were collected 1984–2011 (Laaksonen & Lehtikoinen, 2013). The observations in the data are categorized into 17 habitat classes Koskimies & Väisänen, 1991) from which we calculated the coefficient of variation (standard deviation/average among habitat classes) for each species. We used the estimated minimum count of breeding pairs in Finland as a measure of the population size (Valkama, Vepsäläinen, & Lehtikoinen, 2011). We also considered the population trends of the species in Finland. For the latter one, we used the Finnish bird atlas (Valkama et al., 2011) and classified the species as increasing, decreasing, or stable population trends.

2.3 | Statistical modeling

2.3.1 | Model fitting and assessment of model fit

The original data consist of counts of 69 bird species on transects ranging from 1 to 234 km per reserve. For getting comparable sampling units, we divided the transects into 1 km segments, the smallest length of the original transects, randomly assorted the counts of each species to the segments, and then transformed the data to presence-absence within segments (see Supporting Information for more details). The transformed dataset consisted of presence-absence data of the 69 bird species in 2,500 segments nested within the 91 reserves.

We analyzed the presence-absence of the bird species at the level of 1 km segments by fitting a joint species distribution model with the HMSC Matlab-package (Ovaskainen et al., 2017). We used probit regression to model species occurrence probabilities at each 1 km segment. As explanatory variables, we included (1) the log-transformed area of the reserves, (2) the indicator of the habitat productivity within reserves (proportion of productive forest types), (3) the proportion of old forests within reserves, and (4) the proportion of shrubs (clear-cuts) in the matrix. To examine the joint influence of matrix and habitat quality within reserves, we also included (5) the

interactions between variables 1 and 4, and (6) the interaction between variables 3 and 4. To account for the nested structure of the data (i.e., segments nested within reserves), we included the reserve id as a random effect. We incorporated into the model species traits to examine how much of the variation in species occurrences was explained by traits. As traits we included those described in Table 2.

We assessed how accurately the model predicted species occurrences at the level of segments by performing cross-validation, where we refitted the model 91 times so that each time we excluded the data from one of the 91 reserves. We used these models to predict the posterior mean occurrence probability of each species for the reserve that was excluded for model fitting. We then computed for each species the correlation (over the reserves) between the predicted occurrence probabilities and the fraction of segments in which the species was observed. We averaged the species-specific correlations over the species to obtain an overall measure of the model's predictive power. We followed the procedure of Abrego, Norberg, and Ovaskainen (2017) to partition the explained variation among the environmental covariates and random effects, and to assess how much of the variation in species occurrences is explained by their traits.









2.3.2 | Assessing the influence of reserve size, habitat quality within reserves, and matrix quality on bird community composition

We used scenario simulations to examine how reserve area, reserve quality, and matrix quality influence species density (number of species/1 km transect) and community composition. For this, we created eight scenarios for which we varied systematically the size of the reserve and its habitat quality, as well as buffer quality (Table 3), and by simulation predicted the occurrence probabilities of the species for 1 km transect segments.

We considered the predicted community composition within large reserve with high-quality habitat, surrounded by a high-quality matrix as the reference baseline scenario. We defined "small" and "large" reserve areas as the 10% and 90% quantiles of the distribution of reserve areas in the data, "low" and "high" proportions of old forest as the 10% and 90% quantiles of the distribution of proportion of old forest, and "low" and "high" proportions of shrubs as the 10% and 90% quantiles of distribution of proportion of shrubs. High-quality matrix corresponds to low proportion of shrubs, and vice versa. Productivity was set to its mean value for all simulated forests.

For each of the scenarios, we generated 100 simulated communities, for each of which we sampled the model parameters from the posterior distribution. For each of the eight scenarios, we predicted the expected species density, as well as community similarity to the reference community. We note that one of the scenarios (large high-quality reserve with high-quality buffer) is identical to that of the reference scenario (Table 3). Thus, community similarity between these two scenarios describes the amount of natural variation in community structure.

TABLE 3 Scenarios used to examine how bird community structure and trait distribution are influenced by the size of the reserves, its habitat quality and the quality of the buffer area. In the symbols, green color denotes high-quality habitat and red low-quality habitat

Scenario	Symbol	Environmental conditions
Baseline: large area, high quality inside and outside		Large reserve with high proportion of old forests and low shrub proportion in the matrix.
Small, low quality inside and high quality outside		Small reserve with low proportion of old forests and low shrub proportion in the matrix.
Small, low quality inside and low quality outside		Small reserve with low proportion of old forests and high shrub proportion in the matrix.
Small, high quality inside and high quality outside		Small reserve with high proportion of old forests and low shrub proportion in the matrix.
Small, high quality inside and low quality outside		Small reserve with high proportion of old forests and high shrub proportion in the matrix.
Large, low quality inside and high quality outside		Large reserve with low proportion of old forests and low shrub proportion in the matrix.
Large, low quality inside and low quality outside		Large reserve with low proportion of old forests and high shrub proportion in the matrix.
Large, high quality inside and low quality outside		Large reserve, with high proportion of old forests and high shrub proportion in the matrix.

We assessed the influence of (1) reserve quality, (2) reserve area, and (3) matrix quality on the community composition by computing the posterior probabilities that (1) the community in a high-quality reserve is more similar to the natural reference community than a community in low-quality reserve separately for the four cases corresponding to a small versus large reserve, and low- versus high-quality matrix, (2) the community in a large reserve is more similar to the natural reference community than a community in a small reserve, separately for the four cases corresponding to a low- versus high-quality reserve, and low versus high-quality matrix, and (3) the community in a reserve surrounded by high-quality matrix is more similar to the natural reference community than a community surrounded by low-quality matrix, separately for the four cases corresponding to a small versus large reserve, and low- versus high-quality reserve.

2.3.3 | Assessing the influence of reserve size, habitat quality within reserves, and matrix quality on functional bird community composition

To characterize the functional composition of bird communities in each simulated scenario, we converted the predicted data on

species compositions to trait compositions. We did this by averaging the values of each trait category over the species predicted in each scenario. We computed the mean trait values for 100 replicate communities in each of the eight scenarios. We then computed the posterior mean of mean trait values in each scenario and the posterior probability that the mean trait value was lower in a particular scenario than in the reference scenario.

2.3.4 | Testing the homogenization hypothesis

To address the homogenization hypothesis, that is, that similarity in community composition among reserves increases with increasing human impact in the matrix, we defined the following homogenization measure. We let p_{ij} denotes the occurrence probability of species j under a scenario i . Then $V_{ij} = p_{ij}(1 - p_{ij})$ corresponds to the variance of the Bernoulli distributed random variable which models the occurrence of the species. We define V_i as the mean value of the V_{ij} over all species, and call it the community variability under the scenario i . If $V_i = 0$, then the community compositions are deterministic: Some species are present with certainty and others absent with certainty, meaning that there is a maximal level of within-scenario homogenization. If $V_i = 0.25$, then the community

compositions are as variable as possible: Each species is present with probability 0.5, meaning that there is little homogenization. We computed the community variability V_i for all scenarios, and computed the posterior probability by which community variability was lower than for the reference scenario. In their relatively similar approach, Baeten et al. (2014) use the sum of V_{ij} instead of mean, but these two approaches give identical inference and thus the posterior probability by which community variability was lower for each scenario than for the reference scenario is identical whether it is computed for sum or mean.

When interpreting the outcomes of the models, we considered >0.95 posterior probabilities providing strong statistical support and posterior probabilities 0.90–0.95 providing support, but not strong, to our hypotheses.

3 | RESULTS

3.1 | Overall bird community composition

Based on the cross-validation, the fitted model explained 50% of the variation in bird species occurrence probabilities (averaged over the species) at the level of 1 km segments. Out of this variation, the environmental covariates explained 70%, and the random effects (i.e., reserve id) 30% (Figure S1). Most of the explained variation (56%) was attributed to the size of the reserve, the reserve quality, the matrix quality, and the interaction between the latter two. The productivity of the forests explained the remaining 14% of the variation.

3.2 | Influence of reserve area, reserve quality, and matrix quality on bird community composition

The bird communities most similar to the communities in the reference scenario were those from the scenarios which had a high-quality

habitat within the reserve, regardless of the matrix quality and the size of the reserve (Table S1). This suggests that the habitat quality within reserves is the main driving force to community composition. Accordingly, we found that the similarity between the reference community and a community in a high-quality reserve was greater than the similarity between the reference community and a community in a low-quality reserve, irrespective of the size of the reserve and matrix quality (Table 4, 1st row, Table S2). Reserve area (Table 4, 2nd row; Table S2) and matrix quality (Table 4, 3rd row; Table S2) did not have a substantial influence on the community composition, as the posterior probabilities for all comparisons related to these variables varied from 0.1 to 0.88.

We did not have strong support for matrix effects being stronger in small reserves. For example, similarity of a community in a small reserve with high-quality habitat but surrounded by low-quality matrix with the reference scenario was equal to that of a large reserve with otherwise similar characteristics (similarities 0.86 vs. 0.89, Table S1; posterior probability for difference $\ll 0.9$); were the matrix effects stronger in small reserves, we would have observed lower similarity for a small than a large reserve.

The expected species density was highest (15.8 species/1 km segment) in small high-quality reserves surrounded by high-quality matrix (Table 5). The expected species density was very similar (13.2–14.4) among all the remaining seven scenarios. We did not find any statistical support for differences in species density between the reference and other scenarios (posterior probability for differences $\ll 0.9$; Table S3).

3.3 | Functional bird community composition

The traits included in the model explained 52% of the variation explained by the environmental covariates. Compared to the reference scenario, the body size of the birds was larger in those scenarios which have low reserve quality (≥ 0.90 posterior probability for the four

TABLE 4 Effects of reserve quality, reserve area, and matrix quality on bird community composition. The effects have been measured by computing the posterior probabilities that the communities in "A" scenarios are more similar to the baseline reference scenario (i.e., large high-quality reserve surrounded by a high-quality matrix) than "B" scenarios. The cases in which the posterior probability is >0.95 are indicated by darker yellow, cases in which the posterior probability is ≥ 0.90 by lighter yellow and the cases in which the posterior probability is <0.90 are in white. The numerical values of the similarity measure for each of the scenarios are provided in Table S1, and the numerical values of the posterior probabilities used to construct the figure are provided in Table S2. The symbols are the same as in Table 3

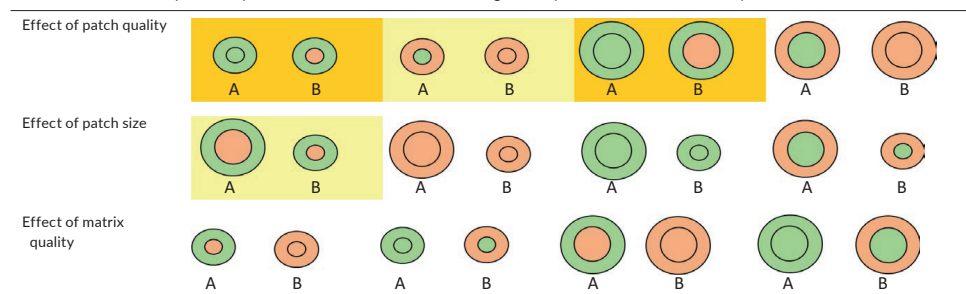


TABLE 5 Predicted species density, within-scenario variability in community composition (beta-diversity), and bird trait composition in each of the simulated scenarios. The numerical values correspond to the posterior means for the expected species density, community variability, and mean trait values in each of the scenarios. The colors of the cells indicate whether the trait value is larger (yellow color) or smaller (blue color) than in the reference scenario with >0.95 (darker color) and with ≥0.90 posterior probability (lighter color). The numerical values of the posterior probabilities are provided in Table S3. The symbols are the same as in Table 3

Scenario	Species richness	Within scenario community variability	Mean trait value									
			Resident	Body size	Bill ratio	Wing length	Tarsus length	Tail length	SSI	Population size	Increasing population	Decreasing population
1	14.4	0.076	0.12	-0.45	0.04	-0.14	0.19	0.11	0.04	0.81	0.29	0.36
2	14.8	0.073	0.15	-0.29	0.07	0.01	0.09	0.13	-0.19	0.83	0.26	0.35
3	14.2	0.070	0.13	-0.27	0.00	-0.01	0.04	0.08	-0.08	0.76	0.25	0.35
4	15.7	0.087	0.13	-0.45	0.11	-0.17	0.21	0.09	0.05	0.80	0.31	0.31
5	13.4	0.069	0.10	-0.44	0.07	-0.09	0.19	0.11	-0.05	0.89	0.30	0.34
6	13.4	0.066	0.13	-0.30	0.01	0.05	0.08	0.16	-0.20	0.83	0.24	0.39
7	14.3	0.070	0.13	-0.34	0.00	-0.03	0.07	0.11	-0.07	0.77	0.24	0.35
8	13.7	0.069	0.10	-0.48	0.08	-0.10	0.22	0.13	-0.02	0.88	0.29	0.34

scenarios with low reserve quality, Table 5). Likewise, the relative wing length was larger and the relative tarsus length smaller in those scenarios which have low reserve quality (≥ 0.90 posterior probability in all cases, Table 5).

The average specialization index for the habitat was smaller in those scenarios which have low reserve quality (≥ 0.90 posterior probability for the four scenarios with low reserve quality), but we found no support for the hypothesis that low-matrix quality is associated with low level of specialization (Table 5). The average population size of the species in the communities was highest in those scenarios of high-quality reserves surrounded by a low-quality matrix (posterior probability ≥ 0.90 , Table 5) suggesting that low-quality matrix is associated with an increased abundance of common species in high-quality reserves. Those bird species with an increasing population trend were less prevalent in scenarios with large- but low-quality reserve (posterior probability ≥ 0.90 , Table 5).

3.4 | Community homogenization

The results provide support for the hypothesis that matrix quality is associated with homogenized bird community composition within reserves. Posterior mean of community variability was highest for the scenario with a small high-quality reserve surrounded by a high-quality matrix and second highest for the reference scenario (scenarios 1 and 4 in Table 5). Lowest beta-diversity values were expected for the high-quality (small and large) reserves embedded in low-quality matrix (scenario 5 and 8 in Table 5). Even though both values (0.069) are among the smallest ones, their difference from the reference scenario did not gain strong statistical support (Table 5). The lowest value was observed for the scenario where large low-quality reserve is surrounded by a high-quality matrix, and this differed from the reference scenario with posterior probability 0.94.

4 | DISCUSSION

We observed a relatively small effect of the matrix quality on the composition of bird communities, whereas the quality of the habitat within the forest reserves strongly influenced the bird community composition. Interestingly, the variation in bird community composition in the reserves was largely explained by the species' functional traits. The community specialization index was low, and average body size was large in reserves with low proportion of old forests. Even though the matrix quality did not strongly influence the bird community composition within the reserves, we found some signals of community homogenization associated with low-quality matrix. The beta-diversity within reserves was lower (yet with low statistical support) if the reserves were embedded in low-quality matrix than in high-quality matrix. Importantly, in line with the homogenization theory, we found that in reserves situated in low-quality matrix, regionally more abundant species became more abundant.

4.1 | Community composition

As expected, the proportion of old forest within the reserves was the main factor in explaining the bird community composition. However, in contrast to results from earlier studies (Devictor, Julliard, Clavel, et al., 2008; Kennedy, Marra, Fagan, & Neel, 2010; Stouffer, Strong, & Naka, 2009), our results showed only moderate responses of bird communities to the quality of the matrix. Furthermore, the responses of bird communities were not stronger in small reserves. These results might be attributed to the design and scale of the study. First, our study units (i.e., reserves) were on average larger than in the precedent studies (our study units were 34 km² on average, whereas Devictor, Julliard, and Jiguet (2008) used 4 km² study units and Kennedy et al. (2010) worked on 1 km² study units). Thus, our results suggest that larger high-quality areas might be better buffered against the matrix effects (Carroll et al., 2004). Other plausible explanation is that the quality of the matrix in Finnish northern forest reserves is not contrasting enough. In studies in which strong matrix effects were found (Kennedy et al., 2010; McKinney, 2006), the difference in the habitat quality between the focal areas and the matrix was greater (native vs. urban habitats) than in our study. In our case, the lowest matrix quality belonged to recently logged forests, which basically represent forests in the very early successional stage. In our case, the matrix is not totally inhabitable, and even some old forest specialists are able to use resources in the matrix (Mönkkönen et al., 2014).

4.2 | Species density

We found no statistically supported differences in species density in larger areas compared with small. Thus, larger reserves do not contain more species per unit area even if total species richness increases with the area of reserves (Häkkinen et al., 2017). In contrast, we found the highest predicted species density for the scenario of small area with high proportion of old forests and low proportion of shrubs around. This may stem from the spillover effect from the surrounding matrix (landscape supplementation, *sensu* Dunning, Danielson, & Pullian, 1992). Even the highest-quality matrix contained more early and mid-successional forests than most of the reserves (Table 1), and therefore fostered more species associated with early- and mid-successional forests. Our result does not support earlier findings from the same region by Mönkkönen et al. (2014) who found no area effects on total bird species richness per standard sample size (# individuals). Mönkkönen et al. (2014) found a clear matrix effect so that for a given sample size, remnant old forest patches in human-modified landscapes foster fewer species than old forests embedded in intact forest landscapes. In summary, it seems that in these boreal settings, highest species densities are found in pristine landscapes (see also Edenius & Elmberg, 1996) but in human-dominated landscapes, small reserves may have the highest species densities due to the spillover.

4.3 | Functional composition

Our results showed that the variation in bird community composition in the forest reserves varying on habitat and matrix quality was largely explained by the species' functional traits.

First, we observed a clear pattern on the variation of morphological traits. Areas with small proportion of old forest hosted species with larger body size and longer relative wing length but shorter relative tarsus. This can be an outcome of higher abundances of raptor and grouse species (Rayner, 1988) in areas with more habitat variation and also opens areas such as bogs. We also observed larger bill ratio in small, forested areas with only little shrub habitats in the matrix. This reflects increasing abundance of small-sized insectivore birds such as warblers and tits (Miles & Ricklefs, 1984) in small reserves with high old forest cover and high-quality matrix.

Second, reserves with low old forest cover showed lower average species specialization index (SSI) values irrespective of the matrix quality. This indicates that habitat quality within the reserves affects the relative abundances of specialist and generalist species, reserves with high old forest cover harboring more specialist species than reserves with low old forest cover. This result supports previous studies showing that habitat disturbance favors generalists at the expense of habitat specialists (e.g., Clavel et al., 2011; Devictor, Julliard, & Jiguet, 2008; Marvier, Kareiva, & Neubert, 2004).

Third, the abundance of species with nationally large population size was higher in a high-quality area surrounded by low-quality matrix. Therefore, community homogenization due to low-quality matrix occurs by the increase of common or abundant bird species.

4.4 | Community similarity

The results provide some support for the hypothesis that matrix quality is associated with larger community similarity (homogenization) within reserves because we found the highest community variability (beta-diversity) values in scenarios where high-quality reserves (both small and large) were embedded in high-quality matrix. Conversely, high-quality reserves in low-quality matrix showed beta-diversity values that were among the lowest ones. Thus, communities in reserves embedded in low-quality matrix are more similar to each other than those embedded in high-quality matrix, as predicted by the biotic homogenization hypothesis. We also found that in high-quality reserves surrounded by low-quality matrix the species specialization did not differ statistically from the reference scenario and that average population size of species was higher. Homogenization likely originates from more common, abundant species becoming more pervasive in the reserves embedded in low-quality matrix. This may also result from landscape supplementation effect (sensu Dunning et al., 1992), that is, a spillover into the reserves of abundant species from the surrounding matrix. We found little evidence for the prediction that small reserves will be particularly sensitive to a decrease in community variability. Thus, large size may not buffer reserves against negative matrix effects, and maintaining high matrix effects may be important irrespective of the reserve size.

5 | CONCLUSIONS

Our results show that for conserving local bird communities in northern Finnish forest reserves, it is more important to focus on

improving or maintaining the habitat quality within the reserves than in the surrounding matrix. However, we note that this study concentrates only on birds that have relatively good dispersal ability, and the responses could be different in other species groups. Furthermore, we found signals of bird community homogenization due to impoverished matrix quality. Thus, if the quality of the matrix is not considered in conservation planning, this may compromise the ability of a conservation area network in maintaining local communities.

ACKNOWLEDGMENTS

We want to thank Dr. Eric Le Tortorec for his valuable comments. This study was funded by Kone Foundation (to MH) and Academy of Finland (project# 275329 to MM and 284601 to OO).

CONFLICT OF INTEREST

None declared.

AUTHORS' CONTRIBUTION

MH (corresponding author) involved original idea, conceptualization, writing, results interpretation; NA involved in conceptualization, analysis, visualization, results interpretation, revising; OO involved in conceptualization, analysis, result interpretation, revising; MM involved in original idea, conceptualization, revising, results interpretation. All authors contributed critically to the drafts and gave final approval for publication.

ORCID

Matti Häkkilä  <http://orcid.org/0000-0003-0583-332X>

REFERENCES

- Abrego, N., Norberg, A., & Ovaskainen, O. (2017). Measuring and predicting the influence of traits on the assembly processes of wood-inhabiting fungi. *Journal of Ecology*, 105, 1070–1081. <https://doi.org/10.1111/1365-2745.12722>
- Baeten, L., Warton, D. I., Van Calster, H., De Frenne, P., Verstraeten, G., Bonte, D., ... Verheyen, K. (2014). A model-based approach to studying changes in compositional heterogeneity. *Methods in Ecology and Evolution*, 5, 156–164. <https://doi.org/10.1111/2041-210X.12137>
- Bennett, P. M., & Owens, I. P. F. (1997). Variation in extinction risk among birds: Chance or evolutionary predisposition? *Proceedings of the Royal Society B: Biological Sciences*, 264, 401–408. <https://doi.org/10.1098/rspb.1997.0057>
- Brotons, L., Mönkkönen, M., Huhta, E., Nikula, A., & Rajasärkkä, A. (2003). Effects of landscape structure and forest reserve location on old-growth forest bird species in Northern Finland. *Landscape Ecology*, 18, 377–393. <https://doi.org/10.1023/A:1026148825138>
- Bryant, D., Nielsen, K., Tangle, L., Sizer, N., Miranda, M., Brown, P., ... Miller, K. (1997). *The last frontier forests: Ecosystems and economies on the edge*. Washington, DC: World Resources Institute.

- Cadotte, M. W., Carscadden, K., & Mirotnich, N. (2011). Beyond species: Functional diversity and the maintenance of ecological processes and services. *Journal of Applied Ecology*, 48, 1079–1087. <https://doi.org/10.1111/j.1365-2664.2011.02048.x>
- Carrascal, L. M., Moreno, E., & Telleria, J. L. (1990). Ecomorphological relationships in a group of insectivorous birds of temperate forests in winter. *Ecography*, 13, 105–111. <https://doi.org/10.1111/j.1600-0587.1990.tb00595.x>
- Carroll, C., Noss, R. F., Paquet, P. C., & Schumaker, N. H. (2004). Extinction debt of protected areas in developing landscapes. *Conservation Biology*, 18, 1110–1120. <https://doi.org/10.1111/j.1523-1739.2004.00083.x>
- Clavel, J., Julliard, R., & Devictor, V. (2011). Worldwide decline of specialist species: Toward a global functional homogenization? *Frontiers in Ecology and the Environment*, 9, 222–228. <https://doi.org/10.1890/080216>
- Devictor, V., Julliard, R., Clavel, J., Jiguet, F., Lee, A., & Couvet, D. (2008). Functional biotic homogenization of bird communities in disturbed landscapes. *Global Ecology and Biogeography*, 17, 252–261. <https://doi.org/10.1111/j.1466-8238.2007.00364.x>
- Devictor, V., Julliard, R., & Jiguet, F. (2008). Distribution of specialist and generalist species along spatial gradients of habitat disturbance and fragmentation. *Oikos*, 117, 507–514. <https://doi.org/10.1111/j.0030-1299.2008.16215.x>
- Dunning, J., Danielson, B., & Pullian, H. R. (1992). Ecological processes that affect populations in complex landscapes. *Oikos*, 65, 169–175. <https://doi.org/10.2307/3544901>
- Edenius, L., & Elmberg, J. (1996). Landscape level effects of modern forestry on bird communities in North Swedish boreal forests. *Landscape Ecology*, 11, 325–338. <https://doi.org/10.1007/BF02447520>
- Ekroos, J., Heliölä, J., & Kuussaari, M. (2010). Homogenization of lepidopteran communities in intensively cultivated agricultural landscapes. *Journal of Applied Ecology*, 47, 459–467. [https://doi.org/10.1111/\(ISSN\)1365-2664](https://doi.org/10.1111/(ISSN)1365-2664)
- Gaston, K. J., Jackson, S. F., Cantú-Salazar, L., & Cruz-Piñón, G. (2008). The ecological performance of protected areas. *Annual Review of Ecology, Evolution, and Systematics*, 39, 93–113. <https://doi.org/10.1146/annurev.ecolsys.39.110707.173529>
- Hooper, D. U., Chapin, F. S., Ewel, J. J., Hector, A., Inchausti, P., Lavorel, S., ... Wardle, D. A. (2005). Effects of biodiversity on ecosystem functioning: A consensus of current knowledge. *Ecological Monographs*, 75, 3–35. <https://doi.org/10.1890/04-0922>
- Häkkilä, M., Le Tortorec, E., Brotons, L., Rajasärkkä, A., Tornberg, R., & Mönkkönen, M. (2017). Degradation in landscape matrix has diverse impacts on diversity in protected areas. *PLoS One*, 12(9), e0184792. <https://doi.org/10.1371/journal.pone.0184792>
- Imbeau, L., Mönkkönen, M., & Desrochers, A. (2001). Long-term effects of forestry on birds of the eastern Canadian boreal forests: A comparison with fennoscandia. *Conservation Biology*, 15, 1151–1162. <https://doi.org/10.1046/j.1523-1739.2001.0150041151.x>
- Järvinen, O., & Väisänen, R. A. (1976). Finnish line transect censuses. *Ornis Fennica*, 53, 115–118.
- Jokimäki, J., & Huhta, E. (1996). Effects of landscape matrix and habitat structure on a bird community in northern Finland: A multi-scale approach. *Ornis Fennica*, 73, 97–113.
- Jönsson, K. A., Lessard, J.-P., & Ricklefs, R. E. (2015). The evolution of morphological diversity in continental assemblages of passerine birds. *Evolution*, 69, 879–889. <https://doi.org/10.1111/evo.12622>
- Julliard, R., Clavel, J., Devictor, V., Jiguet, F., & Couvet, D. (2006). Spatial segregation of specialists and generalists in bird communities. *Ecology Letters*, 9, 1237–1244. <https://doi.org/10.1111/j.1461-0248.2006.00977.x>
- Kennedy, C. M., Marra, P. P., Fagan, W. F., & Neel, M. C. (2010). Landscape matrix and species traits mediate responses of Neotropical resident birds to forest fragmentation in Jamaica. *Ecological Monographs*, 80, 651–669. <https://doi.org/10.1890/09-0904.1>
- Koskimies, P., & Väisänen, R. A. (1991). *Monitoring bird populations*. Helsinki, Finland: Zoological Museum, Finnish Museum of Natural History, University of Helsinki.
- Laaksonen, T., & Lehikoinen, A. (2013). Population trends in boreal birds: Continuing declines in agricultural, northern, and long-distance migrant species. *Biological Conservation*, 168, 99–107. <https://doi.org/10.1016/j.biocon.2013.09.007>
- Lederer, R. (1975). Bill size, food size and jaw forces of insectivorous birds. *Auk*, 92, 385–387. <https://doi.org/10.2307/4084573>
- Lovejoy, T. E. (2006). Protected areas: A prism for a changing world. *Trends in Ecology & Evolution*, 21, 329–333. <https://doi.org/10.1016/j.tree.2006.04.005>
- Lundmark, H., Josefsson, T., & Östlund, L. (2013). The history of clear-cutting in northern Sweden – Driving forces and myths in boreal silviculture. *Forest Ecology and Management*, 307, 112–122. <https://doi.org/10.1016/j.foreco.2013.07.003>
- Marvier, M., Kareiva, P., & Neubert, M. G. (2004). Habitat destruction, fragmentation, and disturbance promote invasion by habitat generalists in a multispecies metapopulation. *Risk Analysis*, 24, 869–878. <https://doi.org/10.1111/j.0272-4332.2004.00485.x>
- McKinney, M. L. (2006). Urbanization as a major cause of biotic homogenization. *Biological Conservation*, 127, 247–260. <https://doi.org/10.1016/j.biocon.2005.09.005>
- McKinney, M., & Lockwood, J. (1999). Biotic homogenization: A few winners replacing many losers in the next mass extinction. *Trends in Ecology & Evolution*, 14, 450–453. [https://doi.org/10.1016/S0169-5347\(99\)01679-1](https://doi.org/10.1016/S0169-5347(99)01679-1)
- Miles, D. B., & Ricklefs, R. E. (1984). The correlation between ecology and morphology in deciduous forest passerine birds. *Ecology*, 65, 1629–1640. <https://doi.org/10.2307/1939141>
- Moilanen, A., & Hanski, I. (1998). Metapopulation dynamics: Effects of habitat quality and landscape structure. *Ecology*, 79, 2503–2515. [https://doi.org/10.1890/0012-9658\(1998\)079\[2503:MDEOHQ\]2.0.CO;2](https://doi.org/10.1890/0012-9658(1998)079[2503:MDEOHQ]2.0.CO;2)
- Mönkkönen, M., Rajasärkkä, A., & Lampila, P. (2014). Isolation, patch size and matrix effects on bird assemblages in forest reserves. *Biodiversity and Conservation*, 23, 3287–3300. <https://doi.org/10.1007/s10531-014-0780-9>
- Mönkkönen, M., & Welsh, D. A. (1994). A biogeographical hypothesis on the effects of human caused landscape changes on the bird communities of Europe and North America. *Annales Zoologici Fennici*, 31, 61–70.
- Morris, D. W., & Heidinga, L. (1997). Balancing the books on biodiversity. *Conservation Biology*, 11, 287–289. <https://doi.org/10.1046/j.1523-1739.1997.96093.x>
- Newmark, W. D. (1996). Insularization of Tanzanian Parks and the local extinction of large mammals. *Conservation Biology*, 10, 1549–1556. <https://doi.org/10.1046/j.1523-1739.1996.10061549.x>
- Olden, J. D., Poff, N. L., Douglas, M. R., Douglas, M. E., & Fausch, K. D. (2004). Ecological and evolutionary consequences of biotic homogenization. *Trends in Ecology and Evolution*, 19, 18–24.
- Ovaskainen, O., Tikhonov, G., Norberg, A., Guillaume Blanchet, F., Duan, L., Dunson, D., ... Abrego, N. (2017). How to make more out of community data? A conceptual framework and its implementation as models and software. *Ecology Letters*, 20, 561–576. <https://doi.org/10.1111/ele.12757>
- Peltola, A. (2014). *Finnish statistical yearbook of forestry 2014*. Tampere, Finland: Finnish Forest Research Institute.
- Pohjannies, T., Triviño, M., Le Tortorec, E., Mazziotto, A., Snäll, T., & Mönkkönen, M. (2017). Impacts of forestry on boreal forests: An ecosystem services perspective. *Ambio*, 46(7), 743–755. <https://doi.org/10.1007/s13280-017-0919-5>
- Prugh, L. R., Hodges, K. E., Sinclair, A. R. E., & Brashares, J. S. (2008). Effect of habitat area and isolation on fragmented animal populations. *Proceedings of the National Academy of Sciences of the United States of America*, 105, 20770–20775. <https://doi.org/10.1073/pnas.0806080105>

- Rayner, J. (1988). Form and function in avian flight. In R. Johnston (Ed.), *Current ornithology* (pp. 1–66). New York, NY: Springer.
- Rayner, L., Lindenmayer, D. B., Wood, J. T., Gibbons, P., & Manning, A. D. (2014). Are protected areas maintaining bird diversity? *Ecography*, *37*, 43–53. <https://doi.org/10.1111/j.1600-0587.2013.00388.x>
- Ricketts, T. H. (2001). The matrix matters: Effective isolation in fragmented landscapes. *The American naturalist*, *158*, 87–99. <https://doi.org/10.1086/320863>
- Ries, L., Fletcher, R. J. Jr, Battlin, J., & Sisk, T. D. (2004). Ecological responses to habitat edges: Mechanisms, models and variability explained. *Annual Review of Ecology, Evolution and Systematics*, *35*, 491–522. <https://doi.org/10.1146/annurev.ecolsys.35.112202.130148>
- Rooney, T. P., Wiegmann, S. M., Rogers, D. A., & Waller, D. M. (2004). Biotic impoverishment and homogenization in unfragmented forest understory communities. *Conservation Biology*, *18*, 787–798. <https://doi.org/10.1111/j.1523-1739.2004.00515.x>
- Secretariat of the Convention on Biological Diversity. (2010). *Global biodiversity outlook 3*. Montreal, QC: Secretariat of the Convention on Biological Diversity.
- Sisk, T. D., Haddad, N. M., & Ehrlich, P. R. (1997). Bird assemblages in patchy woodlands: Modeling the effects of edge and matrix habitats. *Ecological Applications*, *7*, 1170–1180. [https://doi.org/10.1890/1051-0761\(1997\)007\[1170:BAIPWM\]2.0.CO;2](https://doi.org/10.1890/1051-0761(1997)007[1170:BAIPWM]2.0.CO;2)
- Smart, S. M., Thompson, K., Marrs, R. H., Le Duc, M. G., Maskell, L. C., & Firbank, L. G. (2006). Biotic homogenization and changes in species diversity across human-modified ecosystems. *Proceedings of the Royal Society of London B: Biological Sciences*, *273*, 2659–2665. <https://doi.org/10.1098/rspb.2006.3630>
- Socolar, J. B., Gilroy, J. J., Kunin, W. E., & Edwards, D. P. (2016). How should beta-diversity inform biodiversity conservation? conservation targets at multiple spatial scales. *Trends in ecology & evolution*, *31*, 67–80. <https://doi.org/10.1016/j.tree.2015.11.005>
- Solar, R. R. D. C., Barlow, J., Ferreira, J., Berenguer, E., Lees, A. C., Thomson, J. R., ... Gardner, T. A. (2015). How pervasive is biotic homogenization in human-modified tropical forest landscapes? *Ecology Letters*, *18*, 1108–1118. <https://doi.org/10.1111/ele.12494>
- Stouffer, P. C., Strong, C., & Naka, L. N. (2009). Twenty years of understory bird extinctions from Amazonian rain forest fragments: Consistent trends and landscape-mediated dynamics. *Diversity and Distributions*, *15*, 88–97. <https://doi.org/10.1111/j.1472-4642.2008.00497.x>
- Svensson, L., Grant, P. J., Mullarney, K., & Zetterström, D. (2010). *Collins bird guide. The most complete guide to the birds of Britain and Europe*. London: Collins.
- Tomppo, E. (1993) Multi-source national forest inventory of Finland. In A. Nyssönen, S. Poso & J. Rautala (Eds.), *Proceedings of Ilvessalo symposium on national forest inventories* (pp. 53–61). Helsinki, Finland: The Finnish Forest Research Institute, Research Papers.
- Väisänen, R. A., Lammi, E., & Koskimies, P. (1998). *Muuttuva Pesimälinnusto*. Otava: Keuruu.
- Valkama, J., Vepsäläinen, V., & Lehtinen, A. (2011) *The third Finnish breeding bird atlas*. Finnish Museum of Natural History and Ministry of Environment. Retrieved from <http://atlas3.lintuatlas.fi/english> (accessed 11 September 2017)
- Vanha-Majamaa, I., Liija, S., Ryömä, R., Kotiaho, J. S., Laaka-Lindberg, S., Lindberg, H., ... Kuuluvainen, T. (2007). Rehabilitating boreal forest structure and species composition in Finland through logging, dead wood creation and fire: The EVO experiment. *Forest Ecology and Management*, *250*, 77–88. <https://doi.org/10.1016/j.foreco.2007.03.012>

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

How to cite this article: Häkkilä M, Abrego N, Ovaskainen O, Mönkkönen M. Habitat quality is more important than matrix quality for bird communities in protected areas. *Ecol Evol*. 2018;00:1–12. <https://doi.org/10.1002/ece3.3923>