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Strengthening conservation through green infrastructure: linking protected areas, habitats and species

Ewa H. Orlikowska

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Ewa H. Orlikowska
Faculty of Forest Sciences
School for Forest Management
Skinnskatteberg

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Abstract

The green infrastructure (GI) concept was developed to mitigate habitat fragmentation. The European Union (EU) defines GI as “a strategically planned network of natural and semi-natural areas …designed and managed to deliver a wide range of ecosystem services and to improve connectivity of protected areas in order to promote multifunctional landscapes”. Natura 2000, the EU network of protected areas, constitutes the backbone of the EU’s GI. In Sweden, the “Swedish strategy for biodiversity and ecosystem services” bill incorporates GI. I analyzed GI at different spatial, habitat and species scales. These ranged from the entire EU, to Natura 2000 sites in all of Sweden, to boreal forests of northern Sweden, including forest birds and virtual species. A review of the Natura 2000 scientific literature revealed that the majority of studies were at regional or single-site scales; those from the Mediterranean region dominated. Research gaps included underrepresentation of alpine, agricultural, forest and marine habitats, as well as reptiles, amphibians, lichens, and fungi taxa. The Boreal region was also underrepresented. Analyses of the Swedish Natura 2000 network effectiveness for three forest bird species, lesser spotted woodpecker (*Dryobates minor*), Siberian jay (*Perisoreus infaustus*) and hazel grouse (*Tetrastes bonasia*), demonstrated that the majority of sites were of small size and of low functionality. The largest potential habitat increase was linked to surrounding landscapes for the smaller sites. In boreal Sweden, non-protected proxy continuity forests and forests providing Siberian jay habitat can strengthen the high conservation value forest network for GI. Sub-regional differences in functionality of spruce-, pine- and broadleaf forest types require type-specific restoration in different regions. To strengthen conservation through GI, I conclude that future Natura 2000 studies should encompass large spatial scales and modelling approaches. In Sweden, the habitat matrix surrounding the Natura 2000 sites should be carefully managed. Non-protected forest habitat networks in boreal Sweden can improve connectivity of protected areas and support functional GI over large parts of the region.

Keywords: green infrastructure, Natura 2000, protected areas, boreal forest, habitat suitability, review, modelling, forest biodiversity

Author’s address: Ewa H. Orlikowska, Swedish University of Agricultural Sciences, School for Forest Management, P.O. Box 43, 739 21 Skinnskatteberg, Sweden, Email: ewa.orlikowska@slu.se

Dedication

To my family

"Replacing "resource" with "relationship" would make nature and humanity a part of one another again. A relationship is so much more than a service provided or a resource to use. It is a mutual commitment to care."

Teri Rofkar *in* "In Search of the Canary Tree" by Lauren E. Oakes (2018)

Contents

List of publications

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

I. Ewa H. Orlikowska*, Jean-Michel Roberge, Malgorzata Blicharska, Grzegorz Mikusiński (2016). Gaps in ecological research on the world's largest internationally coordinated network of protected areas: A review of Natura 2000. Biological Conservation 200: 216-227.

II. Ewa H. Orlikowska*, Johan Svensson, Jean-Michel Roberge, Malgorzata Blicharska, Grzegorz Mikusiński (2020). Hit or miss? Evaluating the effectiveness of Natura 2000 for conservation of forest bird habitat in Sweden. Global Ecology and Conservation 22, e00939.

III. Grzegorz Mikusiński*, Ewa H. Orlikowska, Jakub W. Bubnicki, Bengt Gunnar Jonsson, Johan Svensson (2021). Strengthening the network of high conservation value forests in boreal landscapes. Frontiers in Ecology and Evolution 8, 486.

IV. Ewa H. Orlikowska,* Jean-Michel Roberge, Sönke Eggers, Johan Svensson, Grzegorz Mikusiński. Assessing green infrastructure in boreal forests of Sweden using the Siberian jay (*Perisoreus infaustus*) as an umbrella species. (Manuscript)

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*Corresponding author.

The contribution of Ewa H. Orlikowska to the papers included in this thesis was as follows:

I. Main author. Developed together with co-authors the idea of the study, collected and analyzed the data, created the figures and tables, and led the writing of the manuscript and its revision.

II. Main author. Developed together with co-authors the idea of the study, collected and analyzed the data, created the figures and tables, and led the writing of the manuscript and its revision.

III. Second author. Participated in the development of the ideas, contributed to data collection, analyses, writing and revision of the manuscript.

IV. Main author. Developed together with co-authors the idea of the study, collected and analyzed the data, created the figures and tables, and led the writing of the manuscript.

During this doctorate study, Ewa H. Orlikowska contributed to the following papers not included in the thesis:

I. Malgorzata Blicharska, Ewa H. Orlikowska, Jean-Michel Roberge, Malgorzata Grodzinska-Jurczak (2016). Contribution of social science to large scale biodiversity conservation: A review of research about the Natura 2000 network. Biological Conservation 199: 110-122.

II. Robert L. Deal, Ewa H. Orlikowska, David V. D'Amore, Paul E. Hennon (2017). Red alder-conifer stands in Alaska: an example of mixed species management to enhance structural and biological complexity. Forests 8 (4), 131.

III. Bron Taylor, Guillaume Chapron, Helen Kopnina, Ewa Orlikowska, Joe Gray, John J. Piccolo (2020). The need for ecocentrism in biodiversity conservation. Conservation Biology 34 (5): 1089–1096.

1. Introduction

As Aldo Leopold once wrote “We abuse land because we regard it as a commodity belonging to us” (Leopold, 1989). Over the past centuries, one single species, *Homo sapiens*, has seized 25–40% of the net primary production on Earth, leading to global homogenization of flora and fauna, breaking through the photosynthetic energy barrier by mining fossil fuels, and causing human-directed evolution of other species (Williams et al., 2015). The natural world has been under increasing anthropogenic pressure leading to a human-driven sixth mass extinction, an acute climatic crisis (Cafaro, 2015; Torres-Romero et al., 2020; Hardy, 2003; Büntgen et al., 2021) and ecosystem collapse, defined by Lindenmayer et al. (2016) as “long-lasting, and widespread change in ecosystem state and dynamics that has major negative impacts on biodiversity and key ecosystem services”.

New approaches to nature conservation are required to avert humankind’s transgressing of global environmental tipping points; changing conditions threaten the natural world and may slow down human progress towards more sustainable future (Barnosky et al., 2012; Saunders, 2015; Blicharska et al., 2019). According to the Protected Planet Report 2016 (UNEP-WCMC and IUCN, 2016), nearly 15% of the world’s terrestrial and inland waters, ca. 10% of the coastal and marine areas within national jurisdiction, and ca. 4% of the global ocean are under legal protection. In Sweden, 15% of the terrestrial area is formally protected as national parks, nature reserves conservation areas, habitat protection areas in forest and other land, National City Park, Natura 2000 sites, nature conservation agreements and the Swedish Fortifications Agency’s protected areas

(SCB, 2019a). However, networks of protected areas are not very effective in conserving biodiversity due often to low functionality or inadequate representativeness (e.g. Nilsson and Götmark, 1992; Rodrigues et al., 2004; Watson et al., 2014; Müller et al., 2018). Based on just area alone, disregarding representativeness and functionality, formally protected terrestrial habitat in Sweden is still below the global Aichi Target 11, which aims to conserve a minimum 17% of terrestrial and inland water areas of particular importance for biodiversity and ecosystem services by 2020 (Angelstam et al., 2020; CBD, 2021).

To address the biodiversity crisis, there are increasing voices at the global and European Union (hereafter EU) scales calling for a sharp increase in protected area coverage to safeguard at least a half of Earth's remaining ecosystems (Noss, 1992; Locke, 2013; Kopnina, 2016; Wilson, 2016; Dinerstein et al., 2017; Ripple et al., 2017; Watson and Venter, 2017; Watson et al., 2018; Dinerstein et al., 2019; Taylor et al., 2020). The European Parliament has recently endorsed this idea by proposing an ambitious and inclusive Biodiversity Strategy for 2030 setting binding targets for its member states to protect at least 30% of their terrestrial and marine areas and to restore at least 30% of degraded ecosystems by 2030. Furthermore, the strategy potentially calls for protecting half of the planet by 2050 (European Parliament, 2020). Müller et al. (2020) assessed how the EU could meet, within its territory, the 30% and 50% targets by possible enlargement of the Natura 2000 network of protected areas in its ecoregions and member states. More countries, including the U.S.A., have recently signaled similar commitments. In a new executive order, the current president of the U.S.A. set an agenda to protect 30% of country’s land and 30% of its oceans by 2030 (The White House, 2021).

In the short term, traditional designations of nature conservation, such national parks or nature reserves, have been crucial for preserving species and habitats. However, the long-term and large-scale dynamics of ecosystems as parts of dynamic landscapes or climate change are often not considered in the design and management of these areas (Bengtsson et al., 2003; Pressey et al., 2007). One of the challenges that protected areas face is intense human pressure, which affects one third of the globally protected land,

and makes smaller protected areas especially vulnerable (Jones et al., 2018). Setting aside large-scale, functional networks of protected areas is considered to be a key conservation tool for counteracting biodiversity loss and for mitigating negative impacts posed by changing climate and an anthropogenic land use (Rodrigues et al., 2004; Lehikoinen et al., 2021). During recent years, the concept of green infrastructure (see below) has been promoted as a policy intervention to address biodiversity and ecosystem services loss under land use and climate change (Sussams et al., 2015). If implemented based on scientific evidence, green infrastructure has the potential to advance biodiversity conservation (Garmendia et al., 2016; Slätmo et al., 2019).

1.1 The concept of green infrastructure and its implementation in the EU and in Sweden

The EU introduced the concept of green infrastructure in 2013, and defined it as “a strategically planned network of natural and semi-natural areas with other environmental features designed and managed to deliver a wide range of ecosystem services (e.g. water purification, air quality, space for recreation or climate mitigation) and to improve connectivity of protected areas in order to promote multifunctional landscapes” (Maes et al., 2015; EC, 2019; Slätmo et al., 2019; Hermoso et al., 2020). The main aims of the European Green Infrastructure Strategy are to mitigate fragmentation and to increase the spatial and functional connectivity between protected and non-protected areas (Maes et al., 2012). Slätmo et al. (2019) reported that EU member states had undertaken several strategic and applied green infrastructure projects and initiatives; 11 countries have planned or already developed green infrastructure-specific policies and strategies.

The “Swedish Strategy for Biodiversity and Ecosystem Services” bill encapsulated the green infrastructure initiative. The Swedish Environmental Protection Agency was commissioned by the government to elaborate green infrastructure implementation guidelines for the County Administrative Boards (Regeringskansliet, 2015). In 2018, the County Administrative Boards began developing regional action plans for green infrastructure with an objective to provide knowledge-based planning and prioritization guidelines that ensure sustainable landscape planning, taking into account ecological processes and ecosystem services delivery (SEPA, 2020). The action plans were developed in consultations with non-profit organizations, other government agencies and land users. Currently (April 2021), all counties in Sweden except one have a green infrastructure plan in completed or near-completed form.

1.2 Protected areas as an essential component of green infrastructure (Paper I and II)

The EU network of protected areas, Natura 2000, was created to preserve the most valuable and threatened species and habitats (CEC, 1992; Evans, 2012). It is considered the backbone of European green infrastructure. It provides a wide diversity of protection levels, from prohibiting most human activities to conservation of focal species or habitats combined with sustainable management of natural resources (CEC, 1992; Halada et al., 2011; Evans, 2012; Tsiafouli et al., 2013). The EU Birds Directive (CEC, 1979) and Habitats Directive (CEC, 1992) provide the foundation of the Natura 2000 network. Currently, Natura 2000 encompasses over 18% (763,986 km^2) of the EU's land area and ca 8% (441,001 km^2) of its marine territory across all 27 EU member states, and is considered as the largest coordinated network of protected areas in the world (EC, 2020).

In Sweden, work on establishing the Natura 2000 network began in 1993. There are 4539 sites covering ca. 13% of the total land area (58,000 km^2 including inland waters) and 20,000 km^2 of marine environment (SCB, 2019b). A total of 86% of the terrestrial Natura 2000 sites overlap with the nationally protected areas (SCB, 2019b), since the selection of Natura 2000 sites in Sweden was based on a network of existing protected areas under national legislation, i.e. the Environmental Code (Miljöbalk, 1998). The Swedish Natura 2000 sites include 7% (19,000 km^2) of the country's total forest area. There is a great size variation among Swedish terrestrial Natura 2000 sites; the largest site, Vindelfjällen (554,675 ha), corresponds to the combined area of the 3800 smallest sites. Due to edge effects (e.g., Maiorano et al., 2008; Svensson et al., 2019), small areas intrinsically harbor functionality risks. To secure favorable conservation status of habitats and species in particular sites, site-adjusted management strategies must be developed.

1.3 Strengthening green infrastructure in the Swedish boreal forests and forest landscapes (Paper III and IV)

Since the middle of the twentieth century the area of high-biodiversity old-growth and natural forests has decreased considerably in boreal Sweden due to anthropogenic impacts, mostly in form of intensive clear-felling forestry (Jonsson et al., 2019; Svensson et al., 2019, 2020). This has led to a highly-fragmented landscape and poor connectivity of forest patches and protected areas, posing challenges for the establishment of functional green infrastructure. To mitigate these negative consequences of landscape fragmentation, it is crucial to identify, at the landscape level, the remaining areas of intact high conservation value forests for potential protection. Moreover, it is important to identify managed and transformed forest patches in the landscape matrix that, if restored, can contribute to the functionality of the green infrastructure network. Identification can be carried out using currently available spatial data, e.g. in the form of a nationally-delineated network of high conservation value forests (HCVF, SEPA, 2016a). Parts of the remaining primary, natural or semi-natural forests have been formally protected, whereas others even those of known high conservation value, have not (Mikusiński et al., 2021). Moreover, remnants of forests with long temporal continuity are still present in Sweden. Such forests, defined as older forests that have not been clear-felled since the mid-1900s, have recently been mapped across the entire boreal biome in Sweden, and assembled in the “proxy continuity forests” database (Metria, 2016; Svensson et al., 2019). Combined, spatial analyses of the high conservation value forests and proxy continuity forests, hold great potential for evidence-based implementation of the green infrastructure in boreal forest landscape in Sweden.

1.4 Linking habitat and species – habitat suitability models (Paper II, III and IV)

In order to detect early signs of critical transitions of ecosystems towards irreversible changes, there needs to be effective biological forecasting in place that includes analyses of protected area functionality for supporting biodiversity (Barnosky et al., 2012). This is essential in particular with small and isolated protected areas surrounded by highly modified landscapes (Gaston et al., 2008). Bengtsson et al. (2003) pointed out that nature reserves have been crucial for preserving species and habitats in the short term, however, they often fail to consider the long-term and large-scale ecosystem dynamics at the landscape scale. To improve conservation planning of protected areas, Poiani et al. (2000) and Auffret et al. (2015) recommend that spatial dimensions should be considered. It is crucial that spatial analyses are applied to describe and quantify landscape structure. Moreover, such analyses must consider the conservation qualities inside the sites, as well as the restoration needs in the matrix outside the protected sites (e.g. Maiorano et al., 2008).

Land cover and vegetation data are often used as biodiversity proxies at the landscape scale to depict biodiversity values (Sinha et al., 2014). Most commonly, species' conservation statuses are used to assess conservation condition of protected areas (Brooks et al., 2004). Habitat suitability models based on expert knowledge defining species habitat requirements, often employing both vegetation cover data and the focal species approach, are considered to be effective tools for biodiversity assessment in forest management (Edenius and Mikusiński, 2006; Löhmus et al., 2020). Habitat suitability models used for assessing habitat areas for forest birds have been used in studies, e.g., by Verner et al. (1986), Van Horne and Wiens (1991), and Lauver et al. (2002) in the United States, Manton et al. (2005) and Öhman et al. (2011) in Sweden, Braunisch and Suchant (2008) in Germany, and Naumov et al. (2018) in boreal Europe. Nordström et al. (2013) applied habitat suitability models as tools in forest management in Sweden to evaluate alternative forest management strategies.

Figure 1. Study species a) lesser spotted woodpecker (*Dryobates minor*; photo: Anders Tedeholm), b) Siberian jay (*Perisoreus infaustus*; photo: Krister Melkersson) and c) hazel grouse (*Tetrastes bonasia*; photo: Thomas Österholm). Photos used with permissions of the authors.

2. Aim and Objectives

The aim of my research was to examine how green infrastructure, represented by various nature protection designations and other areas valuable for biodiversity, can strengthen conservation in Europe, Sweden and in boreal forest ecosystems. I aimed to link protected areas, habitats and species requirements. I focused in particular on the Swedish Natura 2000 protected area network, boreal forests and forest landscapes, using virtual and real forest-dwelling bird species (lesser spotted woodpecker *Dryobates minor*, Siberian jay *Perisoreus infaustus* and hazel grouse *Tetrastes bonasia*) for habitat suitability modelling.

First, I reviewed the scientific literature on the Natura 2000 and proposed future research priorities for improved conservation success at the spatial scale of the EU (Paper I). Second, I assessed effectiveness of the Swedish Natura 2000 network for three forest bird species (Paper II). Third, I investigated how non-protected high conservation value forests (HCVF) and proxy continuity forests (pCF) (Paper III), and suitable forest habitat areas for Siberian jay as an umbrella species (Paper IV) can strengthen the green infrastructure in boreal forests of northern Sweden (Papers III-IV), improving connectivity between protected areas by incorporating non-protected high value forests (Paper III).

The overall objectives of this thesis were to:

1. Evaluate peer-reviewed research publications focusing on the ecological aspects of the EU's Natura 2000 network of protected areas to identify key research gaps and to propose future research priorities for improved conservation success in the EU's member states (Paper I).

2. Quantify effective suitable habitat area in Natura 2000 sites in Sweden for three forest-dwelling bird species of conservation interest in European boreal landscapes (lesser spotted woodpecker, Siberian jay and hazel grouse): 1) with and without consideration of the surrounding landscapes, 2) along a north-south vegetation gradient, and 3) by analyzing functionality of Natura 2000 sites and by assessing how forests outside the sites influence habitat suitability inside the protected areas (Paper II).

3. Analyze how proxy continuity forests may strengthen the high conservation value forest network in the boreal biome in Sweden from a green infrastructure perspective, and to assess habitat suitability for virtual species specialized in Scots pine (*Pinus sylvestris*), Norway spruce (*Picea abies*) and broadleaf-dominated forests to provide a framework for habitat restoration in the landscape matrix (Paper III).

4. Spatially identify mature boreal forest with Norway spruce and canopy layering, using Siberian jay as an umbrella species, for the purpose of mapping opportunities to strengthen the forest green infrastructure in northern Sweden. The models incorporated recently available forest laser scanning data and satellite data with the habitat suitability index (hereafter HSI) model of the Heureka forest planning system of the Swedish University of Agricultural Sciences. I assessed the suitable habitat generated by the HSI models in comparison to the Siberian jay occurrence census data (Paper IV).

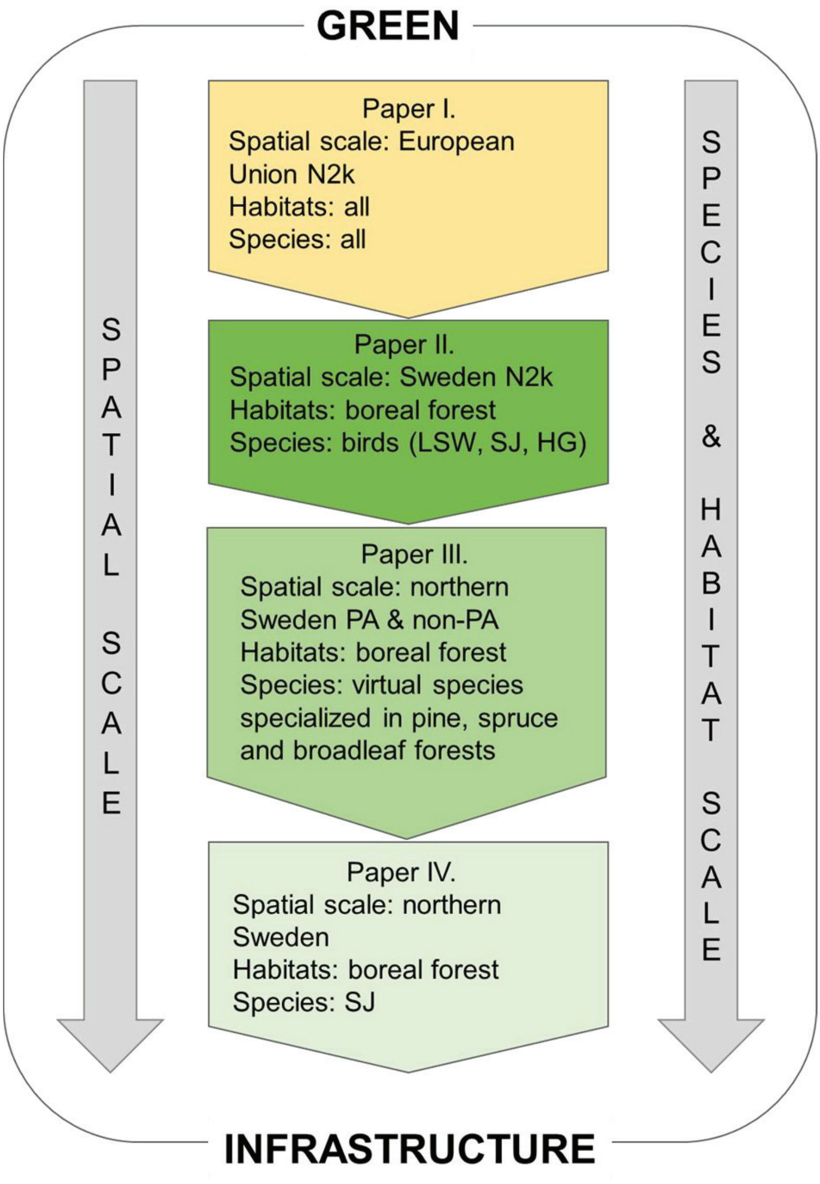

Figure 2. Conceptual framework of the thesis with green infrastructure encapsulating and interconnecting the scopes of Papers' I-IV. Abbreviations used: N2k – Natura 2000; LSW - lesser spotted woodpecker, SJ - Siberian jay, HG - hazel grouse; PA – protected area, non-PA – non-protected area.

3. Methods

3.1 Study areas

The spatial scale of the data varied from almost the entire EU to an area encompassing several counties of Sweden. For Paper I, I collected the data in the form of peer-reviewed articles covering studies across nine terrestrial and five marine biogeographical regions as defined by the EEA (2015a) for, at that time, 28 EU member states.

In Paper II, I analyzed the effectiveness of the Natura 2000 sites for lesser spotted woodpecker and hazel grouse across the entire base of Sweden, according to the Swedish Species Information Center (ArtDatabanken, 2018). These species occur throughout the whole country and in all vegetation zones (Alpine, Northern Boreal, Middle Boreal, Southern Boreal, Hemiboreal and Nemoral) as per Gustafsson and Ahlén's (1996) ecoregion classification. For Siberian jay, only Natura 2000 sites in central and northern Sweden were considered, since its range is limited to the Alpine, Northern Boreal, Middle Boreal, and Southern Boreal vegetation zones only (ArtDatabanken, 2018).

The EU Habitats Directive's 'Western Taiga' habitat type (EU-code: 9010) covers the largest proportion (21%) of the Swedish Natura 2000 sites (SEPA, 2011), and Nordic subalpine/subarctic forests with mountain birch (*Betula pubescens* ssp. *czerepanovii*; 9040) is second the most common habitat type (15%; personal communication A.-L. Maurin, and B. Olsson, SEPA, March 10, 2016).

In Papers III and IV, the study area covered northern Sweden, located between 59°51′ N and 69°3′ N and included the six most northern counties (Dalarna, Gävleborg, Jämtland, Västernorrland, Västerbotten and Norrbotten). The study area corresponded to ca. 67% of all forest land in Sweden and to around 80% of the country's boreal forests; 27.0 million ha of the terrestrial area of which forest covered 18.9 million ha (SLU, 2020; Mikusiński et al., 2021). Approximately 80% of study area's forest is considered to be productive (tree growth >1 m^3/ha/year for a management rotation period; SLU, 2020) with Scots pine-dominated forests occupying 44.0%, Norway spruce-dominated forests 19.7%, and mixed coniferous forests 12.6% (SLU, 2020). Gustafsson and Ahlén (1996) showed that pine forests are prevalent in southern and northern parts of the study area, whereas spruce forests dominate the south-eastern, central and west-central parts. The western part of the study area, located within the Scandinavian Mountains region, is dominated by open alpine areas (ca 5 million ha) and the subalpine mountain birch (*Betula pubescens* ssp. *czerepanovii*) forests forming the alpine tree line (1.1 million ha; Hedenås et al., 2016). An additional 4.4 million ha of study area consists of open mires with poor tree-growth conditions (SLU, 2020).

In Paper III, for analysis purpose the two most northern counties of Norrbotten and Västerbotten, extending from the Scandinavian Mountains to the Bothnian Sea, were divided into western and eastern parts. This division reflected the biogeographical gradient and diverse land use history. The oldest forests occur at the foothills of the Scandinavian Mountains (SLU, 2016; Jonsson et al., 2019). Below the mountain foothills region, extensive parts of the forest landscape were transformed into even-aged, single tree-species dominated stands as a result of an extensive forestry since the mid-20th century (Svensson et al., 2020).

Figure 3. Mosaic of forests and mires in the Scandinavian Mountains Green Belt (photo: G. Mikusiński used with author's permission).

3.2 Data collection

3.2.1 Selecting articles for review (Paper I)

The data for Paper I consisted of 510 peer-reviewed research publications from 1998 to 2014, focusing on the ecological aspects of the European Natura 2000 network of protected areas. Publications were selected using the Web of Science™ Core Collection (WoSCC) database (Thomson Reuters, 2014) applying the term "Natura 2000" in the topic field and "All years" timespan. This database includes only peer-reviewed literature (Falagas et al., 2008; de Winter et al., 2014; for more details, see Paper I).

Initially, the WoSCC search returned 692 English-language publications. I categorized selected publications according to their focus, defined as ecological (biotic and abiotic features of the environment, ecological processes, etc.), interdisciplinary (applying methods and approaches from more than one scientific discipline; only publications including an ecological research component were retained), social science (human- and society-related aspects), or other (no fit with any of the three categories above). The in-depth review was concentrated only on 510 publications with ecological and interdisciplinary foci (with ecological component); social science publications were reviewed in a parallel publication not included in this thesis (Blicharska et al., 2016). I further screened the initially selected 692 publications to remove those that: 1) did not present primary research, 2) were not clearly peer-reviewed, 3) were irrelevant to the Natura 2000 topic, 4) focused on areas located outside of the EU, 5) were unobtainable in full-text format, or 6) for other reasons did not meet the selection criteria. Finally, 510 publications were selected for in-depth analyses (for more details, see Paper I).

The European Environment Agency's (EEA, 2015a) shapefile (a geospatial vector data format for geographic information system (GIS) software) of ‘Biogeographical Regions’ (‘BiogeoRegions2011’) was used to calculate area for nine terrestrial biogeographical regions located in 28 EU countries. In conjunction with this shapefile, I also employed the ‘Natura 2000 End 2014’ shapefile (EEA, 2015b) to obtain the summed area and number of Natura 2000 sites located within each of the biogeographical regions (Paper I, Appendix, Table A2). In order to estimate the area of different habitat types within the Natura 2000 sites, the ‘Corine Land Cover 2006’ raster data (resolution of 250 m × 250 m; EEA, 2015c), and the ‘Digital Elevation Model’ of Europe (DEM; NOAA, 2015) were applied. In addition, to assess the various taxa’ representation in the literature in comparison to the EU Directives, I used the taxa included in the Habitats (Annexes II, IV, and V; CEC, 1992) and Birds Directives (Annexes I, II and III; CEC, 1979). If only higher taxonomic groups were listed, e.g. ‘Microchiroptera - all species’, they were counted as one ‘taxon’; all listed subspecies were collectively used as one taxon.

3.2.2 Quantifying suitable habitat area in Natura 2000 sites in Sweden for selected bird species (Paper II)

In order to calculate the effective suitable habitat area in Natura 2000 sites in Sweden for selected forest-dwelling bird species (lesser spotted woodpecker, Siberian jay and hazel grouse), I used two types of data: Natura 2000 shape-files (SEPA, 2016b, 2016c) and Swedish University of Agricultural Sciences' Forest Map (hereafter SLU Forest Map; SLU, 2016; also called in Paper IV "Satellite Data Forest Map").

Natura 2000 sites

The GIS shapefiles of non-aquatic Sites of Community Importance and Special Protection Areas (SEPA, 2016b, 2016c) were used to determine the boundaries of the Natura 2000 sites in Sweden. First, both shapefiles were spatially adjusted to each other, then combined into one file in ArcGIS (ESRI Inc., 2015). Second, the combined Natura 2000 shapefile was converted into a raster with resolution of 25 m × 25 m to match the resolution of the SLU Forest Map (SLU, 2016). Third, the Natura 2000 raster was re-classified to denote the value "1" to pixels located inside and the value "0" to pixels located outside Natura 2000 sites. Fourth, the re-classified Natura 2000 raster was used as a mask to extract habitat data generated by the models within the Natura 2000 sites. Using the classification provided by Gustafsson and Ahlén (1996), each Natura 2000 site in Sweden was assigned to a vegetation zone (Alpine, Northern Boreal, Middle Boreal, Southern Boreal, Hemiboreal and Nemoral) in order to examine regional differences in habitat amount.

Forest variables

To calculate values of model parameters describing suitable habitat, I employed the open-access SLU Forest Map data (SLU, 2016) produced by the Remote Sensing Laboratory of the Department of Forest Resource Management, SLU. It was created by integrating satellite image data and the Swedish National Forest Inventory data applying the k-Nearest Neighbors (kNN) methods (for details see Reese et al., 2003). The information about dominant tree species' age, height, and standing volume is provided in raster-based format with a 25 m × 25 m resolution (SLU, 2016).

In Paper II, using the SLU Forest map, I employed estimates of forest variables such as stand age and standing timber volume (m3 stem volume per ha) for Scots pine, Norway spruce, lodgepole pine (*Pinus contorta*), European beech (*Fagus sylvatica*), birch (*Betula* spp.), oaks (*Quercus* spp.), and all other broadleaf tree species combined. First, I calculated, in raster format (in ArcGIS; ESRI Inc., 2015), the standing volume for three groups: all tree species combined, conifers separately and broadleaf species separately. Second, I computed raster maps with proportions of coniferous species, broadleaf species, and spruce, treated separately, with 25 m × 25 m resolution. These raster maps were used for calculations of model parameters values for Siberian jay, lesser spotted woodpecker and hazel grouse, such as stand age, proportion (volume) of broadleaf trees, coniferous trees and spruce separately (see Paper II, Table 1 for more details).

3.2.3 Quantifying the high conservation value forests for low- and high- demanding virtual species in boreal landscapes (Paper III)

To spatially define forests with high conservation value four different databases were used: 1) national land cover data, NMD CadasterENV, in the form of a basic layer with a spatial resolution of 10 m × 10 m (Metria, 2015; SEPA, 2019); 2) proxy continuity forest data (pCF), delineating continuity forests in the boreal region of Sweden in a 10 m x 10 m raster resolution (Metria, 2016; Ahlcrona et al., 2017); 3) formally protected and non-protected forests of high conservation value, i.e. HCVF protected and non-protected, in the form of a polygon-based shapefile (SEPA, 2016a; Anon, 2017), and 4) clear-felled areas, in the form of a polygon-based shapefile (SFA, 2019).

The NMD CadasterENV land cover database distinguishes seven main forest types that are further divided into forest stands located on upland and on wet soils, resulting in a total of 14 classes. Using selected forest types from the NMD CadasterENV, I created three main forest categories: 1) Pine forest + Mixed coniferous forest (for virtual species using natural pine-dominated forest as a main habitat) 2) Spruce forest + Mixed coniferous forest (for virtual species using natural spruce-dominated forest as a main habitat) and 3) Broadleaf forest classes + Coniferous forest with admixture of broadleaf trees (for virtual species using natural broadleaf-dominated forest as a main habitat; for details see Paper III, Supplementary Material).

The proxy continuous forest (pCF) data was created by Metria on the commission from SEPA to delineate remnant forest patches of the boreal biome in Sweden that have not been clear-felled since the mid-1950s. In order to do this, a time series of satellite images from 1973 to 2016, as well as aerial photos from the 1950s-1960s were analyzed using an automatic change-detection method (Ahlcrona et al., 2017; Svensson et al., 2019, 2020). Forest areas smaller than 0.5 ha or narrower than 20 m were excluded. On-site validation of the conservation values of the pCF-data was not carried out, but the resulting data was validated against independent data (Ahlcrona et al., 2017) from the Swedish National Forest Inventory (SLU, 2020). However, it is important to emphasize that the relatively fine resolution of pCF-data allows identification of even small-size forest patches of potential old-growth quality.

The high conservation value forest data, HCVF, include forests delimited by the national topographic terrain (1:50,000) and road maps (1:100,000) (Anon, 2017; Bovin et al., 2017). In addition, the conservation value of the HCVF-data was partially verified by on-site surveys (e.g. within Key Habitat Survey). The protection category of the HCVF is based on a wide range of protection designations of various time spans ranging from formally protected to voluntarily set aside. In Paper III, I use the term protected primary forests for formally protected HCVFs and all primary forests for the combined set of pCF, protected HCVF and non-protected HCVF.

A shapefile with polygon-delineated recently clear-felled areas was provided by Swedish Forest Agency (2019), generated as the difference between satellite images of forest areas on a continuous basis starting from 2003. I used this data to remove clear-felled areas from the forest-type raster data prior to the landscape-level analyses. The Copernicus Land Monitoring Service data was used for calculations of the total forest area in the eight regions used in Paper III. In Paper IV, I employed the Satellite Data Forest Map (SLU, 2016) age raster as a forest proxy to compute the amount of forest for each county separately and for the entire study area (six counties). This was used to calculate proportion (%) of forest occupied by the habitat area selected by our models.

3.2.4 Quantifying suitable habitat area for Siberian jay, used as an umbrella species, in boreal Sweden (Paper IV; manuscript)

The main sources of data I employed in Paper IV, to develop and to validate habitat suitability models for Siberian jay were: 1) Laser Data Forest Map (SFA, 2017a; SFA, 2018a-c), 2) Satellite Data Forest Map (the same as the "SLU Forest Map data" in Paper II; Reese et al., 2003; SLU, 2016) called so to distinguish it from the Laser Data Forest Map used in Paper IV, 3) Clear-felled areas, in the form of a polygon-based shapefile (SFA, 2017b), and 4) Siberian jay occurrence data from the Swedish Bird Survey (Swedish Bird Survey, 2021).

The Laser Data Forest Map integrates laser-scanned forest data with the Swedish National Forest Inventory field survey data (SFA, 2018b-c). The map was produced in a raster format with a spatial resolution of 12.5 m × 12.5 m for estimated forest variables such as tree volume, basal area, basal-area weighted mean diameter, basal-area weighted mean tree height, tree biomass, tree height from laser scanning (m; 2 m × 2 m pixels), and photogrammetric tree height from aerial images (2 m × 2 m pixels). In my analyses, due to limited computing capacity, I used basal-area weighted mean tree height (dm) with a resolution of 12.5 m × 12.5 m, assuming that it was sufficient to depict forest structural characteristics (for more details see Paper IV). From the basal-area weighted mean tree height, I calculated "high variation in tree height", defined as a slope of tree height between neighboring pixels. Only slope values equal to and above the median (≥74 %) were considered as having high variation thus used as a parameter in the model (Paper IV, Appendix 1). Moreover, from the basal-area weighted mean tree height, I also computed region-specific tree heights based on the mean height of trees 70 years and older calculated as the mean on a 5 km x 5 km grid cells and reclassified into three classes: ≥ 9m, ≥ 13m and ≥17m.

The open-access Satellite Data Forest Map (SLU Forest Map data; SLU, 2016), as described in detail in section 3.2.2., was used in Paper

IV to calculate forest variables such as the proportion of volume for coniferous trees, the proportion of volume for -spruce trees and stand age variable. The age raster was employed for selection of stands 70 years and older for the region-specific tree height computations. Clear-felled areas were used to remove harvested forest area from the habitat raster before applying the landscape-level calculations, i.e. similar analyses as in Paper III but with earlier data (SFA, 2017b).

The Swedish Bird Survey data, for the period 1996-2019 (Swedish Bird Survey, 2021) was employed to validate how well the models predicted Siberian jay habitat. I used the mean number of observed adult Siberian jays per year per standard survey route lines (see paper IV) and compared this with the Siberian jay habitat amount and distribution generated by the models.

Figure 4. Multilayered conifer forest with spruce component as an example of suitable habitat for Siberian jay (*Perisoreus infaustus*), Jämtland, Sweden (photo: Jean-Michel Roberge; photo used with author's permission).

3.3 Data analyses

3.3.1 Conducting the Natura 2000 literature review (Paper I)

In Paper I, I hypothesized that the number of Natura 2000 research articles regarding a particular ecological entity should be proportional to the "size" of that entity. I tested the following predictions:

1. The number of research articles from a biogeographical region should be proportional to the region's area within the EU.
2. The number of research articles from a biogeographical region should be proportional to the region's total area of the Natura 2000 sites.
3. The number of research articles regarding taxonomic groups should be proportional to their representation in the Birds and Habitats Directives.
4. The number of research articles regarding a certain habitat type should be proportional to the combined habitat's area in the Natura 2000 network.

In the analysis, I first categorized all selected articles of ecological and interdisciplinary foci according to their spatial scale, type of research, ecological subject, taxonomic group, ecological approach, habitat, altitude, country and biogeographical region (see Paper I, Table 1). For publications that had multiple entries within a category, e.g. taxonomic groups, each entry was recorded separately, thus one paper may have been counted more than once. Next, the number of publications was summarized within each category.

To investigate how the interest in Natura 2000 research changed over time and whether it had increased relative to the general research interest in ecology and conservation, I computed a standardized whole-number index dividing the number of Natura 2000 articles by the number of articles concerning ecology or conservation published in the same three time periods and in total for 1998–2014. The spatial scale of research for Natura 2000 publications was analyzed based on their category assigned during article classification, ranging from a single Natura 2000 site to a region within a country, an entire country, multiple countries, and to the European-Union-wide scale. In order to compare the distribution of the Natura 2000 publications among the terrestrial biogeographical regions, I computed in the total areas of these regions in the EU-28 using ArcGIS (ESRI Inc., 2015) and spatial data described in section 3.2.1 (EEA, 2015a-c). The summed area of the Natura 2000 sites and their number located within each of these biogeographic regions were also calculated using the same spatial data (for more details see Paper 1, section 2.2. Data analyses). To obtain a single class called "alpine/subalpine habitat", I used an arbitrary value of 1000 m a.s.l. and merged all Corine Land Cover classes with occurrence above 1000 m a.s.l. using R software's (version 3.1.0, R Core Team, 2014) packages 'sp', 'raster', and 'rgdal'.

In addition, using cross-category analyses, I investigated the distribution of the Natura 2000 publications among taxonomic groups and habitat types within EU's nine biogeographical terrestrial regions. To assess representation of taxonomic groups in the marine Natura 2000 research, I combined all five marine regions (Marine Atlantic, Black Sea, Baltic, Macaronesian and Mediterranean) into one "region" called 'Marine' because there were fewer publications regarding marine topic. For the cross-category analyses, I selected only publications focusing on a single biogeographical region, for which I recorded: spatial scale, taxonomic groups, and habitat types. If a publication listed more than one category of a given criterion, I made one entry for each category.

Representation of taxonomic groups in the Habitats (Annexes II, IV, and V; CEC, 1992) and Birds Directives (Annexes I, II and III; CEC, 1979) was assessed using the actual number of species listed in the directives for each group (plants, birds, reptile/amphibians, fish, mammals, insects, other invertebrates, lichens, fungi) and compared with the number of Natura 2000 publications addressing species belonging to each group. I also calculated the number of publications focusing on abiotic factors, listing several taxonomic groups combined or not defining taxonomic groups.

To assess the conservation status of species, based on the IUCN European Red List categories (Least Concern, Near Threatened, Vulnerable, Endangered, Critically Endangered, and Data Deficient; IUCN, 2016) and their listing in the Habitats and Birds Directives (directive target species, non-target species; CEC, 1992; CEC, 1979), I selected a group of papers that focused only on a single species.

This was motivated by the fact that researchers purposely select species in single-species studies; moreover, computation of an "average" conservation status for species included in multiple-species studies may be difficult and moreover is not relevant given the scope of the study.

To test whether the numbers of the Natura 2000 research articles of different scopes were proportional to the biogeographical regions' size, the Natura 2000 sites' combined area, species' representation in the EU directives, and the different habitat types' coverage, I applied Chi-square tests with Monte Carlo simulation in R software (version 3.1.0, R Core Team, 2014). Moreover, I also tested if the single-species Natura 2000 research articles favored species of special conservation concern registered in the Birds and Habitat Directives or on the European Red List.

3.3.2 Calculations of effective habitat area at pixel and landscape scales using habitat suitability index models (Paper II, III and IV)

In three Papers (II-IV), I applied GIS-based habitat suitability index (HSI) models to calculate the amount of effective habitat area for 1) forest-dwelling bird species (lesser spotted woodpecker, Siberian jay and hazel grouse) within and outside the Natura 2000 sites in Sweden (Paper II), 2) virtual low- and high-demanding species specialized in pine, spruce, and broadleaf forests in northern Sweden (protected primary forests and all primary forests in the six most northern counties; Paper III), and 3) Siberian jay in northern Sweden (the six most northern counties; Paper IV). In Papers II and IV (Model 2), I applied the HSI models that are included in the biodiversity module of the SLU Heureka forest planning system (Wikström et al., 2011; Edenius and Mikusiński, 2012; SLU, 2018); however, I utilized these models in an ArcGIS environment (ESRI Inc., 2015), i.e. outside the SLU Heureka system. In Paper IV, I also constructed a new HSI model for Siberian jay (Model 1) by incorporating recently available Laser Data Forest Map (SFA, 2017a; SFA, 2018a-c) into the existing HSI Heureka model based on the Satellite Data Forest Map (the same as the "SLU Forest Map data" in Paper II; Reese et al., 2003; SLU, 2016). In Paper IV, the age parameter (based on Satellite Data Forest Map) that was used in Model 2 was replaced in Model 1 with new parameters, high variation in tree height and region-specific tree height, developed from basal-area weighted mean tree height (based on Laser Data Forest Map). HSI models in Paper III were also constructed entirely in ArcGIS environment (ESRI Inc., 2015) utilizing the NMD CadasterENV land cover database (Metria, 2015; SEPA, 2019).

In Paper III, the effective habitat area was calculated for two groups of virtual species specialized in pine, spruce, and broadleaf dominated forests (Paper III, Table A1): 1) Low-demanding species, and 2) High-demanding species representing two levels of conservation ambitions. The low-demanding species required small effective habitat area of a minimum 0.2 ha and low landscape level requirements of a minimum 5 ha within 100 ha area (5%). The high-demanding species required large effective habitat area of a minimum 2 ha and high landscape level requirements of a minimum 40 ha within 200 ha area (20%). I created six HSI-models for two different virtual species (low- and high-demanding) in three habitat types each pine-, spruce- or broadleaf forests that were later utilized using protected primary forests (HCVF protected) and all primary forests (pCF + HCVF protected + HCVF non-protected) as input data. Habitat distribution maps were produced for each scenario (12 scenarios in total). Moreover, I also estimated the number and size distribution of the habitat network components as well as habitat network's total area to assess the relative contributions of protected primary forests and all primary forests to green infrastructure assessed by virtual species requirements.

I described effective habitat area, calculated in Papers II-IV, as an area containing the habitat necessary to fulfil species' requirements as characterized by the HSI model parameters (Table 1 in Paper II and IV, Table A1 in Paper III) based on the best available knowledge provided by the species experts. I computed the effective habitat area for two habitat scores (in Paper III called habitat value HV), with 1.0 defining good conditions and 0.5 defining moderately good conditions. In the effective habitat calculations 1 ha of HS=1.0 equals to 1 ha of suitable habitat. However, to calculate the input of the

HS=0.5 stratum into the effective habitat area, I divided the HS=0.5 area by 2, as proposed by Edenius and Mikusiński (2012).

In Papers II-IV, I carried out effective habitat area calculations for each species at two spatial scales: 1) individual pixels; and 2) landscape scale. I defined the spatial scale of individual pixels as based exclusively on parameters from the spatial data used (Paper II - SLU Forest Map data; Paper III - NMD CadasterENV land cover database; Paper IV - combination of Laser Data Forest Map and Satellite Data Forest Map) and not considering the neighborhoods' habitat quality. At the landscape scale, obtained by using a landscape filter, pixels had not only to fulfill species' habitat quality requirements, but also to be located in the areas fulfilling species' landscape-level requirements (Table 1 in Paper II and IV, Table A1 in Paper III).

First (Papers II-IV), I computed pixel-scale effective habitat area at the spatial scale of individual pixels for the habitat scores 1.0 and 0.5 in the form of raster maps (Table 1 in Paper II and IV, Table A1 in Paper III). Then rasters for habitat score 1.0 and 0.5 were merged into one raster (Paper II, Fig. 1a and 1e). Second, I calculated the effective habitat at the landscape scale by using a species-specific measure of neighborhood utilizing ArcGIS Focal Statistics tool (ESRI Inc., 2016) for a circle-shaped moving window with a radius of: 1) 798 m (200 ha) for lesser spotted woodpecker, Siberian jay (Paper II for both and IV for S. jay only) and virtual high-demanding species (Paper III), and 2) 564 m (100 ha) for hazel grouse (Paper II) and virtual low-demanding species (Paper III), applied to the raster with pixel-level combined habitat scores 1.0 and 0.5 (Paper II, Fig. 1b and 1f; Wikström et al., 2011; Edenius and Mikusiński, 2012). In the output raster, computed by the Focal Statistics tool, the value for each output pixel was a sum of the input pixel values located within a species-specific circular moving window centered on that pixel (ESRI Inc., 2016). Species' habitat requirements at the landscape scale defined the sizes of moving windows and were based on the best available knowledge provided by the experts (for more details see Papers II-IV).

Third, using the raster obtained from the Focal Statistics analyses, I identified pixels summing up to effective habitat area at landscape scale that are part of habitat networks consisting of: 1) ≥5 ha within a 100 ha window for low-demanding virtual species (Paper III), 2) ≥20 ha within a 100 ha window for hazel grouse (Paper II; Fig. 1c and 1g; Åberg et al., 1995; Jansson et al., 2004; Manton et al., 2005), 3) ≥40 ha effective area within a 200 ha window for lesser spotted woodpecker (Paper II; Wiktander et al., 1992) and high-demanding virtual species (Paper III), and 4) ≥50 ha within a 200 ha window for Siberian jay (Paper II and IV; Angelstam et al., 2004).

Fourth, in order to obtain the landscape scale effective habitat area, I computed the number of pixels for habitat score 1.0 and 0.5 positioned within the habitat networks identified in step three by multiplying the raster with identified habitat networks by the step's one, pixel scale raster maps with habitat scores 1.0 and 0.5 separately (Paper II, Fig. 1d and 1h).

In Paper II, I calculated the total effective habitat area of: 1) entire forest land in Sweden at both pixel and landscape scales, 2) Natura 2000 sites at pixel scale without buffers and at landscape scale both without and with buffers, and 3) outside of Natura 2000 sites, at the pixel and landscape scales, computed as the difference between 1 and 2 (without buffers at pixel scale and with buffers at landscape scale).

3.3.3 Calculations of habitat estimates (Paper II)

In Paper II, I employed habitat estimates to evaluate: 1) average habitat functionality of the Swedish Natura 2000 sites along the north-south vegetation gradient, and 2) average habitat increase assessing how forests outside Natura 2000 sites influence habitat suitability inside the protected areas. I applied "habitat functionality" ("functional habitats") following Mikusiński and Edenius (2006), who defined this as "the degree to which a given forest environment fulfils the spatial requirements of a given species in terms of composition, quantity, configuration and temporal dynamics". Habitat functionality has been also used by several other authors for different taxonomic groups, e.g. forest birds (Angelstam et al., 2003; Lazdinis et al., 2005; Manton et al., 2005) or butterflies (Vanreusel and Van Dyck, 2007; Turlure et al., 2010). In Paper II, I defined habitat functionality as "the proportion of habitat which remains after applying a filter representing the species' landscape-scale requirements". In practice, to obtain habitat functionality of each Natura 2000 site, I divided its landscape scale effective habitat area by its pixel scale effective habitat area (for equations see Paper II, online Appendix A1 Definitions and Formulas, Eq. (A.1)).

For each bird species used as modelled species in Paper II, I also computed the average habitat functionality of Natura 2000 site, located in the different vegetation zones (Alpine, Northern Boreal, Middle Boreal, Southern Boreal, Hemiboreal and Nemoral), as an average of Natura 2000 sites' functionality within vegetation zone. Moreover, I calculated habitat functionality at the vegetation zone level for areas inside and outside Natura 2000 sites through dividing the sum of Natura 2000 sites' landscape-scale effective habitat area by the sum of Natura 2000 sites' pixel scale effective habitat area within the vegetation zone (for equations see Paper II, online Appendix A1 Definitions and Formulas, Eq. (A.2)). To estimate the habitat functionality outside Natura 2000 sites, I divided the sum of the landscape-scale effective habitat area located outside Natura 2000 sites by the sum of the pixel scale effective habitat area outside Natura 2000 sites (for equations see Paper II, online Appendix A1 Definitions and Formulas, Eq. (A.3)).

The average functionality of Natura 2000 site per forest area class (%) was computed as an average of Natura 2000 sites' functionality within forest area class (1-500 ha, 501-1000 ha, 1001-5000 ha, 5001-10,000 ha and above 10,000 ha).

To assess how forest located outside of the Natura 2000 sites influenced the habitat suitability inside the sites, I used around Natura 2000 sites, GIS-applied, species-specific buffers (Paper II, Fig. 1e) of 798 m for lesser spotted woodpecker and Siberian jay, and of 564 m for hazel grouse prior to using the landscape filter acting for the species' landscape-scale requirements (Paper II, Fig. 1e, 1f). Then, I calculated the landscape scale effective habitat area for buffered Natura 2000 sites (Paper II, Fig. 1g and 1h). Habitat increase, defined as "the increase in proportion of suitable habitat inside Natura 2000 sites after taking into account the quality of areas outside Natura 2000 (within buffers) measuring the effect of the neighborhood on the quality of habitat within Natura 2000 sites", was computed as the difference of landscape scale effective habitat area between buffered and non-buffered Natura 2000 sites, and then divided by the landscape scale effective habitat of non-buffered Natura 2000 sites (for equations see Paper II, online Appendix A1 Definitions and Formulas, Eq. (A.4)).

In addition, in Paper II, I also calculated what proportion (%) of habitat suitable for lesser spotted woodpecker, Siberian jay and hazel grouse was located within Natura 2000, dividing the species' landscape effective habitat area in the Natura 2000 sites by the total species' landscape effective habitat area in all of Sweden including Natura 2000 sites (for equations see Paper II, online Appendix A1 Definitions and Formulas, Eq. (A.5)).

3.3.4 Evaluating the spatial overlap between proxy continuity forests and high conservation value forests (Paper III)

In order to assess how pCF can contribute to known HCVF' potential for strengthening the green infrastructure in boreal forests of northern Sweden, I overlapped spatial data for these two categories. Then, I computed proportions (%) of pCF occurring within the HCVF (protected and non-protected) and outside of them within the eight regions used in this study (six northern counties: Dalarna, Gävleborg, Jämtland, Västernorrland, with Västerbotten and Norrbotten split into western and eastern parts). Moreover, I also calculated what proportion (%) of the total region's forest area is located within the pCF.

3.3.5 Assessing the large-scale structural connectivity of boreal primary forests (Paper III)

To assess the large-scale structural connectivity of boreal primary forests within our study area a connectivity model based on the circuit theory was employed (McRae et al., 2008) and implemented in the Circuitscape software v5 (http://www.circuitscape.org). Three different categories of primary forest relevant to conservation (protected primary forests; protected and non-protected HCVF; all primary forests) and a baseline scenario (all forestland) were used to examine how applying different scenarios could support the establishment of a functional forest green infrastructure in boreal region by optimizing structural connectivity.

The assessment of large-scale structural connectivity was conducted without focus on any particular species or species group and for the whole study area. Two land-cover classes were used in the Circuitscape modeling for establishing of the resistance surface raster: 1) clusters of primary forests with different combinations of their components (resistance value 1); and 2) matrix of other land-cover classes, managed forests including (resistance value 100). In the absence of empirical data, the resistance values were chosen to provide contrast between these two classes (for more details see Analyses in Paper III).

For each pixel of the resistance surface raster the connectivity was assessed using the cumulative current density calculated as the current flow between 24 pairs of focal nodes (552 combinations) evenly spaced along the outer boundary of a 50 km buffer zone surrounding the study area. In order to compare the cumulative current density output maps created for the three categories of forest conservation scenarios, and the baseline scenario, the same number and locations of focal nodes were used. Since the main purpose of this study was to detect study-area wide connectivity patterns, and in order to avoid computational limits, the resolution of the pCF raster prior to the Circuitscape modeling was recalculated step-wise from the initial 10 m × 10 m resolution to 50 m × 50 m and to 500 m × 500 m. The cumulative current density maps were made using the open source software QGIS (QGIS Development Team 2017 Ver. 2.18) and GRASS GIS software (Neteler et al., 2012; Ver. 7.4.0).

3.3.6 Assessing Siberian jay HSI models' performance using the Swedish Bird Survey data and habitat patch size distribution (Paper IV)

In Paper IV, I employed the Swedish Bird Survey data on Siberian jay occurrence (Swedish Bird Survey, 2021) to evaluate how well two different models estimated suitable habitat for Siberian jay. The Swedish Bird Survey conducts bird inventory along 2 km × 2 km fixed square-shaped survey routes (8-km-long) where visual and audio observations of birds are counted (Ottosson et al., 2012). The locations of all fixed survey routes are pre-determined and systematically spread over all of Sweden (total of 716) at 25-km intervals.

In the Paper IV analyses, I used the number of observed adult Siberian jays per year per standard survey lines for the period 1996-2019 (Swedish Bird Survey, 2021). To assess my models, I computed mean suitable habitat area for Siberian jay per fixed survey route using four spatial scales with two-sided buffers of 250 m, 1000 m, 4000 m and 8000 m applied to each fixed survey route (for details see Material and Methods, Paper IV). I then compared calculated mean suitable habitat area (ha) per fixed survey route to the mean number of observed adult Siberian jay per year and route categorized into three classes based on the number of birds observed on average per year and route (>0-1; >1-2; and >2). In order to appraise the landscape-scale habitat patch size distribution; I vectorized the rasters with Model 1 and 2 habitat area networks at the landscape scale. Then I computed size of all habitat patches and classified them based on their size into categories (<1 ha; 1-100 ha; 101-1000 ha; 1001-10K ha; >10K ha).

4. Results

4.1 How spatial scale, biogeographical regions, taxonomic groups and habitat types are represented in the publications about the Natura 2000 network? (Paper I)

The review of the research publications on the EU's Natura 2000 network (n=664), revealed that the vast majority of the publications (62.0%) focused on the ecological aspects of the network, whereas 23.2% on social sciences, and 13.4% on interdisciplinary subjects with an ecological component. For the remaining 1.4% I detected no fit to any of these categories. It was interesting to discover that from the beginning (1998–2004), there was an equal number of articles published about the ecological and social foci, however since 2005 the latter category was vastly outnumbered by the ecological publications. The standardized index of the Natura 2000 publications showed that the scientific interest increased during 1998–2014.

The analyses of the papers showed that the Mediterranean countries of Greece (14%), Italy (12%), Spain (9%) and central European Poland (7%) published the most articles within these categories. Moreover, the assessment of spatial scale applied indicated that most projects focused on relatively small areas within a country, i.e. a region (35%) or a single Natura 2000 site (25%), whereas studies encompassing the whole EU were least common (6%). The EU-wide studies investigated mostly interdisciplinary topics, whereas the studies in the other spatial scale categories had mostly ecological focus.

The most commonly applied research methods in the reviewed articles included quantitative empirical studies (57%), modelling (22%), and qualitative/analytical methods (16%). The ecosystem approach (56%) dominated over the community/guild approach (27%), and single species approaches were least common (14%). Studies carried out at low elevation sites prevailed (34%) over those from high elevation sites (19%) and sites that cover from low to high elevation (16%). Almost one third of the studies (31%) did not indicate the elevation.

At the scale of the EU's terrestrial biogeographical regions, the largest number of Natura 2000 publications were from the Mediterranean (25%) and the Continental (20%) regions. Further analyses showed that the published research was not proportionally represented either in relation to the biogeographical region's area within the EU (χ^2 = 1620.8, $p < 0.001$), or to the region's summed area of the Natura 2000 sites within it (χ^2 = 759.5, $p < 0.001$). Moreover, the smallest biogeographical regions, such as Pannonian, Steppic, terrestrial Black Sea and terrestrial Macaronesia, were overrepresented in the literature in comparison to their total area and to the summed area of the Natura 2000 sites within them. My analyses revealed that the situation was generally opposite for the EU's largest biogeographical regions, the Continental and Boreal, that were poorly represented in the Natura 2000 articles when compared to their total area and to the combined Natura 2000 sites' area within them. The Boreal region, occupying 19% of the EU's land area, was least represented, with merely 6% of the publications focusing on Natura 2000 issues.

The assessment of the taxonomic groups' representations in the Natura 2000 literature showed that vascular plants were not only most commonly represented in the EU's Habitats Directive (CEC, 1992), but also in the research articles (48%). However, the taxonomic groups' representation in the Natura 2000 literature was not proportional to their presence in the Birds and Habitats Directives (CEC, 1979; CEC, 1992; χ^2=291.1, $p < 0.001$). Some taxonomic groups, e.g. insects, were overrepresented in the published Natura 2000 research in comparison to their presence in the directives, whereas other, i.e., birds, reptiles and amphibians were underrepresented. Moreover, there were very few articles addressing lichens (9) or fungi (2), important groups from the forest conservation perspective.

Among habitat types, forests were most commonly addressed (157 articles). Representation of the habitat types in the publications was not proportional to the area occupied by them within the Natura 2000 sites ($\chi^2 = 535.5$, $p < 0.001$). Moreover, in comparison to the habitat type's total area, grasslands (14.8%), freshwater (13.5%) and wetlands (10.5%) were overrepresented, whereas agricultural crops (7.0%), alpine/subalpine habitats (2.4%), forest (23.8%) and marine habitats (8.3%) were underrepresented.

The cross-category analyses on the distribution of the Natura 2000 publications among taxonomic groups and habitat types within the nine biogeographical terrestrial and combined marine regions, revealed that the largest number of publications within most taxonomic groups was for the Mediterranean region. Vascular plants were the most common subject of research within all regions. However, insect research dominated the Pannonian, and fish and mammals the combined Marine region. Research on the different habitat types was well represented across all biogeographical regions, with some minor differences; wetlands, forest and grasslands were more commonly investigated in the Boreal and Continental regions, forests in the Macaronesian and Mediterranean regions, and grasslands in the Pannonian region.

The majority of studies conducted in the Alpine, Mediterranean and Pannonian regions encompassed a small spatial scale (a single Natura 2000 site), whereas in the Atlantic, Continental, and Macaronesian regions they were of a regional character. Natura 2000 research carried out in the Boreal region occurred at both single site-scale and regional scales. Within the Mediterranean region, many studies were at national scale or for multiple countries.

The number of red-listed species at the European level (NT, VU, EN, CR, and DD) was larger than the number of Least Concern (LC) species in the Natura 2000 publications focusing on single species. The combined number of species targeted in the Habitats or Birds

Directives was higher than the number of non-target species (Paper I, Fig. 7).

4.2 Contribution of the Natura 2000 sites in Sweden to the conservation of forest-dwelling birds (Paper II)

Effective habitat area analyses of forest-dwelling bird species revealed that the Natura 2000 sites in Sweden only partly provide a suitable habitat for the selected species. At the landscape scale, 51% (292,276 ha) of suitable habitat for lesser spotted woodpecker was located within these sites, 13% (535,520 ha) for the Siberian jay, and 10% (456,710 ha) for the hazel grouse (Paper II, Fig. 2). Comparable shares at the pixel scale were, 27% (427,176 ha), 12% (673,259 ha), and 9% (577,675 ha) (Paper II, Fig. 2). Considering the fact that the Natura 2000 sites in Sweden cover 7% (1,883,447 ha) of the total forest land area, the Natura 2000 network is successful in encapsulating habitat for lesser spotted woodpecker, to a lesser degree for Siberian jay, but not for hazel grouse. The Siberian jay distribution in Sweden is limited to the northern parts only (between 59°51′ N and 69°3′ N) where 12% (1,688,913 ha) of the Swedish forest land area occurs within the Natura 2000 sites. Since the proportion of the Siberian jay habitat within Natura 2000 is almost the same as northern Sweden's proportion of forests located within these sites, the Natura 2000 sites do not more effectively contribute with Siberian jay's habitat than the north-Swedish forests do, in general. The contribution of the forest located outside the Natura 2000 sites (within species-specific buffers applied in GIS) to the effective habitat area within the sites was relatively low when summarized on the national level (Paper II, Fig. 2a). Applying a landscape filter to the pixel-level effective habitat area produced habitat areas 32%, 20% and 21% smaller for lesser spotted woodpecker, Siberian jay and hazel grouse, respectively, than the effective habitat areas at the pixel scale (Paper II, Fig. 2b).

The nation-wide effective habitat area at the landscape scale generated by the models was assessed for the number of pairs of each bird species that it could support. Here, the results diverged slightly from the estimated population sizes reported by BirdLife

Sverige (2018) by +3% (LSW), −22% (SJ) and −4% (HG) (Paper II, Appendix Table A1).

The relative contributions to the suitable habitat varied across the northern and southern vegetation zones. Natura 2000 sites located the Northern Boreal and Alpine zones provided the largest effective habitat area for all three species, whereas the Natura 2000 sites in the Middle Boreal zone contributed with large effective habitat areas for Siberian jay and hazel grouse, but much smaller, especially at the landscape scale, for the lesser spotted woodpecker (Paper II, Fig. 3). There was no suitable habitat for lesser spotted woodpecker in the Southern Boreal zone, and very limited suitable habitat for the Siberian jay and hazel grouse. The most southern zones, Hemiboreal and Nemoral provided very limited suitable habitat area for lesser spotted woodpecker and hazel grouse.

The assessment of the average habitat functionality within the Natura 2000 sites showed that for the lesser spotted woodpecker it was the highest in the Alpine, then in the Nemoral and Northern Boreal zones (Paper II, Fig. 4). The average functionality for hazel grouse was higher in the northern than in the southern vegetation zones and for the Siberian jay in the Middle Boreal zone.

The analyses showed that the average functionality of the Natura 2000 sites was impacted by their size. This did not apply to the Natura 2000 sites with Siberian jay habitat. For lesser spotted woodpecker and hazel grouse, larger sites, located in the Alpine, Northern and Middle Boreal zones, were more functional. The majority of the Natura 2000 sites providing suitable habitat for those two species, however, occupied small areas (1-500 ha) and had low functionality (3.1% lesser spotted woodpecker and 26.1% hazel grouse (Paper II, Fig. 5a). The largest average habitat increase, defined as the increase in the proportion of suitable habitat inside Natura 2000 sites after taking into account the contribution of the forest areas outside the sites' boundaries, was found for the smallest sites (1–500 ha; Paper II, Fig. 5b).

Across all vegetation zones, areas located within the Natura 2000 sites were clearly more functional than the surrounding matrix for the lesser spotted woodpecker (Paper II, Appendix Fig. A1). The difference in habitat functionality between Natura 2000 sites and the matrix outside was less pronounced for Siberian jay and hazel grouse. For Siberian jay in the Alpine and Middle Boreal zones, habitat functionality was slightly higher inside than outside. For hazel grouse, the difference was mostly visible in the southern vegetation zones where habitat functionality was higher outside than inside Natura 2000 sites.

4.3 Assessing high conservation value primary forest network in boreal Sweden (Paper III)

The proportion of the proxy continuity forests (pCF) in the region's total forest area (%), based on the Copernicus Land Monitoring Service data, was highest for the regions of Norrbotten west (75%) and Västerbotten west (69%) and the lowest for Västernorrland and Gävleborg (ca 40% each; Paper III, Fig.2). Quantitative analyses of the spatial overlap between pCF and combined HCVF (protected and non-protected), showed that the proportion of pCF located within HCVF was higher in the western part of the study area, that is in the regions of Dalarna, Jämtland, Norrbotten west and Västerbotten west, with a clear increase northwards. The proportion of the pCF located outside the HCVF categories was higher in the eastern part of the study area and decreased northwards. The most extensive overlap between pCF and protected HCVF was found in the western part of study area, with 50% overlap within protected HCVF in Norrbotten west. The lowest proportion of pCF within protected HCVF (below 10%) was found in the eastern parts and decreases southward. The proportions of pCF overlapping with non-protected HCVF were low across all regions and lowest in the eastern parts.

The structural connectivity analyses showed diverse patterns for the applied forest conservation categories (protected HCVF, protected and not protected HCVF, protected and not protected HCVF and pCF (all primary forest), and baseline scenario, i.e. all forestland) and for the different regions (Paper III, Fig. 3). The connectivity of the protected forests analyzed alone was low, however this did not apply to the forests located at the mountain foothills. Adjoining non-protected HCVF to the protected forests did not substantially improve the connectivity. However, connectivity improved the most when applied to the all primary forests category with considerable connectivity gains in particular in the northern region of the study area. There were also visible connectivity improvements in the southwest part of the study area.

The analyses of the spatial distribution of suitable habitat for the virtual species, low- and high-demanding, conducted for protected primary forests and all primary forests) revealed that there was, in both cases, much larger habitat area for low- than for high-demanding species (Paper III, Fig. 4). All primary forests generated considerably larger suitable habitat area than the protected primary forests alone, but moreover, this pattern was especially visible for the low-demanding species. The protected primary forests and all primary forests created very different habitat networks for the two virtual species within the broadleaf-, pine- and spruce-dominated forests in terms of habitat patches' size and spatial distribution (Paper III, Fig. 4). All primary forests contributed with a considerable habitat increase for the low-demanding species, but with a much lesser increase for the high-demanding species.

The suitable habitats associated with broadleaf forests were mostly limited to the alpine region of the Scandinavian Mountains with the mountain birch forest. The suitable habitats associated with spruce-dominated forests also prevailed at the foothills region, especially for the high-demanding species. The suitable habitats associated with pine-dominated forests occurred mostly in the coastal areas as well as in north and southwestern parts of the study area (Paper III, Fig. 4).

The comparisons of the virtual species' potential suitable habitat increase, measured as an absolute area increase (ha) and a relative increase (%) for the eight subregions, revealed lower increases for the high-demanding species in most sub-regions (Paper III, Fig. 5). For the low-demanding pine species, the largest habitat area increases occurred in Norrbotten east (182,000 ha) and in Dalarna (176,000 ha); however, the proportional increase was largest in Västerbotten east (2118%) and in Västernorrland (2058%). For the low-demanding spruce species, the increase was largest in Västernorrland (2110%). For the low-demanding broadleaf species, the largest habitat increase was recorded in Norrbotten east (1989%) (Paper III, Fig. 5).

The number, area, and size distribution of the spatial components (spatially connected areas fulfilling virtual species' habitat requirements) of the habitat networks revealed great differences for the six virtual species analyzed in protected primary forest and all primary forests (Paper III, Table 1). For high-demanding species, the habitat networks' spatial components were fewer and smaller than for low-demanding species for both analyzed cases. The comparisons between low- and high-demanding species, in terms of number and size of the habitat spatial components, showed a great difference for broadleaf species located within all primary forest with >12 times as many components for low-demanding species as for high-demanding species. For pine species occurring within all primary forests the total area of the network components was >6 times larger for low-demanding species.

The analyses of the size of the habitat networks' spatial components showed that the vast majority (>94%) were larger than 100 ha (Paper III, Table 1). Spatial components larger than 1000 ha were found for the high-demanding species (48.8%) and low-demanding species (89.4%) in pine-dominated forest within all primary forests. Spatial components larger than 10 000 ha were found for high-demanding species (10.7%) and low-demanding species (77.5%) also in pine-dominated forest within all primary forests considered. The sub-regional level analyses of the number and size distribution of the habitat networks' spatial components are reported in Paper III's Appendix Tables A2–A4.

4.4 Assessing green infrastructure in boreal forests of Sweden using the Siberian jay as an umbrella species (Paper IV)

The effective habitat area for Siberian jay generated by Model 1 was 1.9 million ha, and by Model 2, 4.2 million ha; i.e. the area provided by Model 1 equaled to 44% of that of Model 2 (Paper IV, Fig. 3a and 3b). The spatially generalized (1 km × 1 km) difference in estimated effective habitat area (ha) between Model 2 and Model 1 revealed regional dissimilarities with Model 1 that resulted in estimates of larger effective habitat areas in the southern and south-eastern parts of study area (north-west Dalarna, eastern Gävleborg), central coastal area and the north-central part (Norrbotten) (Paper IV, Fig. 4). Model 2 provided larger habitat area in the majority of the region.

When compared to the total forest area, effective habitat generated by Model 1 counted for 11% and by Model 2 for 25%. For Model 1, the southern counties of Gävleborg and Dalarna (16% respectively) held the highest proportion of effective habitat whereas the northern county of Norrbotten held the lowest (6%) (Paper IV, Fig. 5). The largest effective habitat proportions (%) for Model 2 were located in central counties of Jämtland (31%) and Västernorrland (30%) and the lowest in northern Norrbotten (19%).

The comparison of the suitable habitat area with the Siberian jay's presence-absence data at the fixed survey route provided by the Swedish Bird Survey (2021), revealed that Model 2 created larger mean effective habitat area than did Model 1, at all spatial scales (i.e. with buffers of 250 m, 1000 m, 4000 m and 8000 m applied to each route) (Paper IV, Fig. 6a and 6b). This difference was especially pronounced for the Siberian jay absence and presence class >2, with Model 2 providing almost twice as much habitat and three times as much for presence classes >0-1 and >1-2.

For both models, the highest number of Siberian jays reported (>2 individuals per visit) overlapped with the greatest amount of habitat per fixed survey route at all spatial scales (Paper IV, Fig. 6a and 6b). The effective habitat area per route for absence class was larger than for the presence class >0-1 for both models, and for the presence class >1-2 for model 1. An analysis of human population within 1000-m from the survey route was also included. The mean Siberian jay presence per year was lower where humans were present (0.67) and higher where humans were absent (1.24).

Analyses of the number and size of the habitat network components showed that Model 1 generated more patches (19197) than Model 2 (11164). For both models, most of them had areas of less than 1 ha, however these were more frequent for Model 1 (10

131) than for Model 2 (4979). Model 1 also produced a higher number of large habitat patches (>1000 ha and >10 000 ha; 564 and 79, respectively) than did Model 2 (458 and 60, respectively) (Paper IV, Fig. 7).

5. Discussion and Conclusions

5.1 Research interest in Natura 2000 the backbone of European green infrastructure

Successful implementation of green infrastructure at the European, national or even regional scales requires a solid scientific evidence base. The review of research publications on the EU's Natura 2000 network, in particular focusing on the network's ecological and interdisciplinary aspects, revealed that studies encompassing the whole EU were least common (6%) and had mostly an interdisciplinary character. Since Natura 2000 is considered the backbone of the EU's green infrastructure strategy, aiming at mitigating fragmentation and increasing the spatial and functional connectivity between protected and non-protected areas (Maes et al., 2012), more EU-wide studies on how to improve the success of the green infrastructure are needed. Slätmo et al. (2019) reported that the EU member states are in the process of implementing a green infrastructure strategy and considered several EU funding opportunities appropriate for supporting studies on the implementation of green infrastructure strategy, including spatial planning tools availability and applicability, e.g., concerning geo-referenced information, zoning and biotope area factors.

The high Natura 2000-related scientific publication rate detected for Mediterranean counties Greece, Italy, Spain and central European Poland was probably not linked to secured research funding. Indeed, scientists in, e.g., Greece, may have used freely-available European-level data (e.g. EUNIS database; EEA, 2015d) regarding species and habitats protected under the EU Directives. Moreover, the Mediterranean Basin is one of the prominent biodiversity hotspots at the European and global scales (Myers et al., 2000; EC, 2009); thus the high representation of the Mediterranean region in Natura 2000 research is not surprising.

The Natura 2000 literature review revealed that research gaps included alpine, agricultural, forest and marine habitats. Underrepresented taxonomic groups were reptiles, amphibians, lichens and fungi, and among the biogeographical regions a clear underrepresentation in studies on the boreal region was found, in particular given its area coverage and rich biodiversity and ecosystem services values (Triviño et al. 2017; Mikusiński et al., 2021). The Boreal region occupies 19% of the EU's land area, but was represented in only 6% of the publications focusing on Natural 2000 network. Moreover, the "State of nature in the EU" report (EEA, 2015e) showed that the Annex I habitats in Boreal region had the highest proportion of unfavorable assessments in which habitats are deteriorating (close to 50%). Clearly, more research is needed in the boreal region, including modelling studies and both large and multiple spatial scales. For practical planning and monitoring of protected areas like Natura 2000 network, data with high resolution and high precision and accuracy are needed (Nagendra et al., 2013; Kallimanis et al., 2015; Willis, 2015).

My review was done almost seven years ago, and a currently-performed search (2021-04-23) in the Web of Science Core Collection using "Natura 2000" as a "Topic" gave 1743 hits i.e. over 1000 more than in 2014. This clearly indicates continuously high interest in performing studies related to the Natura 2000 network. These included many papers concerning forest environments with some from the boreal zone. My papers II, III and IV provide new insights to some of the detected knowledge gaps, i.e. the papers focus on the underrepresented forest habitats within Boreal biogeographical region and applied modelling methods at different spatial scales.

5.2 Protected areas

Since any boundaries are a *sensu stricto* human invention, not necessarily respected by the representatives of the wild fauna or flora, ideally the larger the spatial scale the green infrastructure is applied to, the more functional it could be. The analyses conducted in Paper III (Fig. 3) clearly demonstrate that the connectivity of forest areas increased substantially when the area of assessed forests increased. The protected forests alone had the lowest connectivity. As shown in Paper II, many terrestrial Natura 2000 sites in Sweden, especially in the southern regions, are small and isolated; moreover, they outnumber larger sites, since 94% of the sites for hazel grouse, 93% for lesser spotted woodpecker, and 83% for Siberian jay are smaller than 500 ha. The combined area of the 3800 smallest sites corresponds to the area of the largest Swedish Natura 2000 site (Vindelfjällen; 554,675 ha).

The great size variation of protected areas demands that management strategies for securing favorable conservation status of habitats and species will have to be adjusted for particular sites. The results presented in Paper II indicate that for lesser spotted woodpecker and hazel grouse the average habitat functionality was influenced by the size of the Natura 2000 sites, with larger sites located in the Alpine, Northern and Middle Boreal zones being more functional (Paper II, Fig. 4 and 5a).

Interestingly, the average functionality of the Natura 2000 sites that provided suitable habitat for Siberian jay was not influenced by their size. This can be explained by the fact that Siberian jay occurrence is limited to the northern parts of Sweden (north from ca 59°51′ N) and Natura 2000 sites there are larger than in southern part of the country. Angelstam et al. (2020), confirming earlier findings by Götmark and Nilsson (1992), indicated that there is an obvious geographical bias in the spatial distribution of the nationally designated protected areas in Sweden, since the larger, more functional sites are mostly located in the northwestern Sweden, in the Scandinavian Mountains characterized by low human population densities. These protected areas were used as a foundation for site selection when establishing Natura 2000 sites in Sweden. Presently in Sweden, there is an 86%

overlap between the terrestrial Natura 2000 sites and the nationally designated protected areas (SCB, 2019b).

The contribution of protected areas to continent-wide green infrastructures securing both biodiversity conservation and provision of vital ecosystem services is crucial. Hermoso et al. (2020) demonstrated that in the European Union, consideration of GI linkages between countries was, in addition to country-based planning, of particular importance for successful biodiversity conservation and some ecosystem services (e.g. carbon retention).

5.3 The matrix

The connectivity of protected areas is essential for meeting international and national conservation goals (Santini et al., 2016). The Aichi Target 11 of the Convention on Biological Diversity (2021) aims at covering minimum 17% of the globe by well-connected protected areas by 2020; however, Saura's et al. (2018) evaluation of countries' progress towards achieving Aichi Target 11 shows that in Sweden only 8-12% of the territory is considered to be protected connected land, far below the Achi Target 11 level or EU average of ca. 19%. At the national level, the Swedish Environmental Objective "Sustainable Forests" suggest strengthening forest connectivity precisely through the implementation of green infrastructure approach. Green infrastructure's role should be to preserve forest biological diversity and to allow species to spread in their natural distribution within all geographical regions (SEPA, 2021). From that perspective, if green infrastructure can be successfully implemented in Sweden, it can play an important role in improving the connectivity and functionality of protected areas by using the matrix between them to enhance the habitat quality within them and to provide species movement corridors. As reported in Paper II, smaller Natura 2000 sites are much less effective in providing functional habitat for forest species of conservation interest; for these species the forest areas located outside the site's boundaries, within species-specific buffers, are very important for securing favorable conditions for conservation. Moreover, due to edge effects, a small site can be influenced to a larger degree by the conditions of the outside matrix (Woodroffe and Ginsberg, 1998; Svensson et al., 2019). Thus, the management of the forests neighboring protected areas is of crucial importance for the effectiveness of smaller sites in providing habitat for conservation interest species (Lindenmayer and Franklin, 2002; Franklin and Lindenmayer, 2009). According to the EU Habitats Directive, activities outside a Natura 2000 site that adversely affect the site's integrity should not be permitted, with a few exceptions (CEC, 1992). In addition, this directive also requires that the EU Member States "endeavor to improve the ecological coherence of Natura 2000 by maintaining, and where appropriate developing, features of the landscape which are of major importance for wild fauna and flora" (CEC, 1992).

The Habitats Directive does not legally require creation of buffer zones around Natura 2000 sites. Based on the results of Paper II, however, I recommend that management outside Natura 2000 sites should focus on maintaining and possibly enhancing the protected area's value, at the same time maintaining and enhancing habitat quality within the site (Häkkilä et al., 2018). This could easily be implemented in case of smaller, forest-dominated protected sites surrounded by production forests. Several authors (e.g. Lindenmayer et al., 2006; Felton et al., 2020; Klein et al., 2020a and 2020b) provide a multitude of alternatives to clear-felling measures that can be applied in buffer zones. Buffer zone size should be guided by the spatial requirements of the key species of conservation interest at particular site. In addition to increasing the functionality, as demonstrated in Paper II, buffer zones may have additional functions important for biodiversity conservation, like lessening the negative impact of edge effect (e.g. Ruete et al., 2017), limiting the spread of invasive species, lowering the impact of generalist predators on forest vertebrates (e.g. nesting birds) or securing larger areas with forest interior conditions. As suggested in Paper II, the buffer zones are of special importance for smaller sites, however, they could also benefit larger sites, e.g. those of elongated shape or those consisting of several smaller areas or containing non-forest areas (such as mires, lakes or rivers). Because these types of sites have extensive edges, they are greatly influenced by the conditions of the outside areas.

5.4 Potential areas for fulfilling the EU Biodiversity Strategy for 2030 targets for protected area and habitat restoration

Unprotected primary forest areas located in northern Sweden, as demonstrated by the results of Papers III and IV, show a great promise for strengthening green infrastructure in the boreal region. However, the analyses in Paper III detected large regional differences. Overall, currently unprotected primary forests, located in the western part of the study area, at the foothills of the Scandinavian Mountains, have the largest potential for improving north-south, large-scale connectivity in the subalpine forests (see also Svensson et al., 2020). As Kuuluvainen et al. (2017) demonstrate, improved spatial coherence of these areas would increase their ecological resilience and potentially safeguard them in the face of climate change and other disturbances. As a result of the study described in Paper III, spatial target maps were generated providing potential areas for implementing functional green infrastructure for species with low and high demands on habitat availability and its spatial configuration, specializing in pine, spruce, and broadleaf forest. These maps could be used when planning and developing further green infrastructure areas in Sweden, to support the quest to fulfil country's obligations for the EU Biodiversity Strategy for 2030 to protect at least 30% of its terrestrial area (European Parliament, 2020).

More efforts should be undertaken to improve currently insufficient connectivity and suitable habitat availability for species of conservation concern in the eastern and coastal parts of the study area (northern Sweden; Paper III). I pinpoint that the area of habitat for low-demanding species dependent on spruce or pine forests can be largely increased by incorporating the currently unprotected primary forest (Paper III). The situation is less promising for the high-demanding species, unless additional habitat restoration efforts in the landscape matrix are implemented. Several different ways to restore boreal forest landscapes and stands have been proposed, including the use of natural disturbance regimes as a guidance (Angelstam, 1998; Kuuluvainen, 2002) and, more recently, the replacement of clear-fell forestry by continuous-cover forestry (e.g. Peura et al., 2018). The circumstances for the broadleaf-specializing species are particularly dramatic, because even including all valuable broadleaf forests available, there is not enough area to provide suitable habitat for high-demanding species. Thus, there is an acute need for landscape-scale habitat restoration of broadleaf forests. Mikusiński et al. (2003) show that most of Sweden, with the exception of forest landscapes in southernmost Sweden, have a very small broadleaf component; otherwise the distribution of broadleaf stands and trees in Sweden is highly skewed towards settlements and their boundaries outside of contiguous forests and, in the northern Sweden, to birch forests along the mountain range. The lack of a natural fire regime in boreal forest landscapes in Fennoscandia (Rolstad et al., 2017) along with the Swedish forestry oriented towards coniferous species caused a great scarcity of broadleaf-dominated forest in intensively managed production landscapes. Leaving parts of areas affected by wildfires for natural succession may be part of the restoration effort (Gustafsson et al., 2019).

There is a pressing need to further detect and map the unknown remaining areas of high conservation value. Also, extensive restoration efforts need to be carried out in areas where there are gaps in forests with high conservation value (Paper III; Angelstam et al., 2020). These actions would prepare Sweden for fulfilling its obligations to restore at least 30% of degraded ecosystems by 2030 as included in the Biodiversity Strategy for 2030 (European Parliament, 2020). Remote sensing methods combined with field-based inventories need to be employed to detect and verify the value of the last remaining high conservation value forest areas, as well as to map and assess the forest in need of restoration. In addition, a baseline connectivity map, to be used as a reference, depicting a natural fragmentation of forest habitats should be created. Jonsson et al. (2019) show that the future of the currently unprotected boreal forests of high conservation value is uncertain and is being debated, thus action is needed to improve the situation.

5.5 Conclusions

In my thesis, I attempted to encompass protected areas, habitats and species requirements as the most relevant topics as a base for successful implementation of green infrastructure for biodiversity conservation. With a focus on Europe (Paper I) and Sweden (Paper II-IV), I contributed with new knowledge concerning further research needs, effectiveness of protected areas, and the need for restoration, largely with use of spatially explicit methods.

Effective execution of a Green Infrastructure Strategy needs to be grounded on evidence-based science. My review of the Natura 2000 literature pinpointed the areas of major scientific focus, and more importantly, gaps that require further investigations. My analyses of the Natura 2000 network's effectiveness for three forest bird species in Sweden showed that the vast majority of sites were of small size (<500 ha) and of low functionality. Moreover, habitat increase linked to the surrounding landscapes was largest for smaller sites; thus, the management of the surrounding habitat matrix matters most for the smaller sites. To counterbalance this effect, I recommend the establishment of buffer zones around Natura 2000 sites, based on species-specific spatial requirements. In addition, the areas outside Natura 2000 sites should be managed in ways that maintain and possibly enhance the value of these protected areas.

In boreal Sweden, structural connectivity of the currently protected forests can be improved by including forests with long temporal continuity, as well as currently non-protected forests with known high conservation values. The habitat area for low-demanding species dependent on spruce or pine forests can be largely increased if continuity and non-protected high-conservation forests are included. However, restoration is needed in the landscape matrix for high-demanding species, and for safeguarding conditions for broadleaf-dependent species, since at present there are not enough valuable broadleaf forests available to provide suitable habitat for their associated species. Habitat suitability models are a useful tool to spatially identify mature boreal forest with Norway spruce and canopy layering that provide habitat for Siberian jay, used as an umbrella species. Such areas of suitable habitat can strengthen the effectiveness of green infrastructure in northern Sweden by covering the habitat needs of other species, thus furthering the Swedish Environmental Objective “Sustainable Forests”.

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Popular science summary

Background

The concept of green infrastructure (hereafter GI) has become more popular worldwide since the mid-1990s. It was developed as a tool to mitigate increasing habitat fragmentation due to land use change and leading to rapid loss of biological diversity. The European Union (hereafter EU) defines GI as “a strategically planned network of natural and semi-natural areas with other environmental features designed and managed to deliver a wide range of ecosystem services (e.g. water purification, air quality, space for recreation or climate mitigation) and to improve connectivity of protected areas in order to promote multifunctional landscapes”. Natura 2000, the existing EU network of nature protection areas, is considered the backbone of the EU’s GI, and currently the EU member states are in the process of implementing the GI.

In Sweden, GI was incorporated in the “Swedish Strategy for Biodiversity and Ecosystem Services” bill, and the government commissioned the Swedish Environmental Protection Agency to develop guidelines for regional GI-plans under the responsibility of the county administrative boards. These plans have been under development since 2018, in cooperation with land users, government agencies and non-profit organizations. Different GI-approaches are planned and under implementation.

Investigation

In my thesis, I analyzed GI at different spatial, habitat and species scales. These ranged from the entire EU with its' habitats and species protected by the EU Habitats and Birds Directives, to Natura 2000 sites as habitat for selected birds in all of Sweden, to boreal forests of northern Sweden as habitat for Siberian jay and for virtual species.

My first analysis was a review of published scientific literature on the ecological aspects of the EU's Natura 2000 network. This was done to identify key research gaps and to propose future research priorities for improved conservation and GI effectiveness and implementation in EU countries. I categorized the articles by spatial scale, biogeographical regions, taxonomic groups, habitat types, and the analytical methods used.

Since Natura 2000 is an essential part of the EU's GI, it has potential for improving GI's conservation efficiency. However, when establishing the Natura 2000 network, the effectiveness of the sites and the influence of the surrounding landscapes for species of interest was often not taken into consideration. In this thesis, I analyzed the effectiveness of Natura 2000 sites in Sweden for three forest bird species of conservation interest in European boreal landscapes: lesser spotted woodpecker (*Dryobates minor*), Siberian jay (*Perisoreus infaustus*) and hazel grouse (*Tetrastes bonasia*).

For the boreal region, combining the six northern counties of Sweden, one approach of strengthening GI I applied in this thesis was to analyze older forests that have not been clear-felled since the mid-1900s, called "proxy continuity forests", and "currently non-protected forests of high conservation value". I assessed how these may contribute to improving connectivity of currently protected forests and to expanding GI area. First, I assessed the spatial overlap between proxy continuity forests and high conservation value forests. Then, a large-scale connectivity analysis was conducted for four different categories including: a) protected high conservation value forest, b) combined (protected and non-protected) high conservation value forests, c) proxy continuity forests with combined high conservation value forests, and d) a baseline scenario including all forestlands of study area. In addition, the size, number, and distribution of the habitat network components were estimated for virtual species dependent on conifer forests dominated by Norway spruce (*Picea abies*) or Scots pine (*Pinus sylvestris*), or broadleaf forests located within formally protected forests of high conservation value (a). Moreover, the potential increase of habitat area was assessed for virtual species in scenarios where besides the protected high conservation value forests (a), the scenario combining proxy continuous forest with both categories of high conservation value forests (c) were used.

Another approach of strengthening GI in the boreal region is to spatially identify mature boreal forests with Norway spruce and canopy layering, using the Siberian jay as an umbrella species. I performed this analyses by developing a new habitat suitability model by incorporating recently available forest laser scanning data and adjusted parameters into existing model from the Heureka analysis and planning system created by the Swedish University of Agricultural Sciences. To validate and compare the suitable habitat generated by the two models, I used the observed Siberian jay occurrence data provided by the Swedish Bird Survey for the period 1996-2019.

Results

The review of the Natura 2000 scientific literature revealed that the vast majority of studies encompassed small spatial scales (i.e. a single Natura 2000 site or a region within a country). The southern EU's biogeographical terrestrial regions such as Mediterranean, Black Sea, Macaronesia, Pannonian and Steppic had the greatest number of publications in relation to their total area and to the area of Natura 2000 sites that they comprised. Habitats such as grasslands, freshwater and wetland habitats were overrepresented in comparison to their area within Natura 2000. Among taxonomic groups plants were the most commonly studied and quantitative empirical studies dominated among research type used.

The forests inside Natura 2000 sites in Sweden fulfilled species' habitat requirements better than those outside Natura 2000 areas for lesser spotted woodpecker in all vegetation zones, and for Siberian jay in the Alpine and Middle Boreal zones; for hazel grouse the habitat outside the sites was more functional in all zones accept the Alpine and Middle Boreal. The majority of Natura 2000 sites were smaller than 500 ha. For lesser spotted woodpecker and hazel grouse the site's size influenced its functionality; however, this trend did not apply to the Siberian jay. The habitat functionality of the smallest Natura 2000 sites (1-500 ha) was to largest degree influenced by the habitat quality of the areas outside Natura 2000 sites.

The large-scale connectivity analysis revealed that adding proxy continuity forests, located outside high conservation value forest, strongly increases the structural connectivity of the network of protected forests (a). Large regional differences in the ability to secure habitat for virtual species specialized in pine, spruce, and broadleaf forests were detected when analyzing combined non-protected proxy continuity and high conservation values forests (c). The latter forests have potential to increase habitat area for low-demanding species dependent on spruce or pine. To fulfill habitat requirements of the high-demanding species, the habitat located in the landscape matrix needs to be restored. The situation is more dramatic for species dependent on broadleaf forests, since the remaining areas are not sufficient to provide a suitable habitat for their associated species.

The suitable habitat area for Siberian jay estimated by the new habitat suitability model (incorporating forest laser scanning data) produced habitat area equal to 44% of that provided by the existing Heureka model (based on combined satellite and forest inventory data). There were regional differences in habitat areas selected by both models with the new model selecting the largest areas in the southern part of study area with older pine forests that were not accounted by the Heureka model, which gave preference to the central part of study area. The comparison of the amount of suitable habitat area for Siberian jay generated by the models at the buffered survey route of the Swedish Bird Survey, at all spatial scales, was the largest for the highest Siberian jay occurrence class (>2 birds). For both models, the amount of habitat per fixed survey route for absence was greater than amount of habitat for the lowest presence lass (>0-1 birds). Analyses of human presence showed that Siberian jay presence was greater where humans were absent the and vice versa. The Siberian jay habitat produced by both models was very fragmented with large number of small habitat areas and fewer large habitat areas.

Thesis’s contribution to research and policy

In order to improve GI at the EU scale, future Natura 2000 research should address knowledge gaps by directing more research efforts towards: 1) the Boreal region, 2) alpine, agricultural, forest and marine habitats, and 3) taxonomic groups such as reptiles, amphibians, lichens and fungi. To enhance the conservation potential of Natura 2000, more studies should encompass large spatial scales and utilize modelling approaches.

Research conducted in the remaining papers of this thesis aimed at fulfilling some of the research gaps detected in the Natura 2000 literature review by focusing on forest habitats in Boreal region, applying large spatial scale and using modelling approach.

To improve conservation efficiency of the Natura 2000 sites in Sweden, the presence and quality of forests in the outside matrix should be considered. This is especially important for smaller sites, which should be managed according to protected species’ requirements and restored when necessary.

To improve GI size and function, landscape-scale habitat restoration initiatives for high-demanding and broadleaf-dependent species should be undertaken to recreate suitable habitat. GI can be also strengthened by incorporating mature boreal forests with Norway spruce and canopy layering as required by Siberian jay. Most importantly, the results of this thesis can be used when planning and developing further GI areas in Sweden. They can provide information that will fulfil Sweden’s obligations for the EU Biodiversity Strategy for 2030 to protect at least 30% of its terrestrial area.

Populärvetenskaplig sammanfattning

Bakgrund

Begreppet grön infrastruktur introducerades som en planeringansats för att förebygga förluster och fragmentering av livsmiljöer. I början handlade grön infrastruktur mest om grönytor i urbana miljöer, men senare utvecklades begreppet till att omfatta hela naturgeografiska regioner och alla landskapstyper och naturtyper. Europeiska unionen (EU) definierar grön infrastruktur som ett strategiskt nätverk av naturliga och naturnära områden som planerats och utformats för att förvalta och bevara biologisk mångfald och ekosystemtjänster i landskap som påverkas av markanvändning och klimatförändringar. Grön infrastruktur är ett nätverk av natur som bidrar med livsmiljöer för växter och djur och till människors välbefinnande, d.v.s. säkerställer ett hållbart och multifunktionellt landskap. Det finns en tydlig betoning på att det ska vara funktionellt, i meningen ekologisk och biologiskt funktionellt med fungerande ekosystem och ekosystemprocesser. Med detta omfattar grön infrastruktur inte bara skog utan också öppna marker, våtmarker, stränder, vatten, m.m., eller för den delen också sammanhängande natur för människan att röra sig i landskapet.

Europeiska kommissionen har utarbetat en strategi för grön infrastruktur. Denna strategi syftar till att se till att skydd, återställande, skapande och förbättring av grön infrastruktur blir en integrerad del av fysisk planering och regional och lokal utveckling. Natura 2000, det befintliga EU-nätverket av skyddad natur, betraktas som utgångspunkten i grön infrastruktur, där kompletterande skyddad natur och natur där särskilda hänsyn tas ska förstärka de redan skyddade områdena.

I Sverige införlivades grön infrastruktur i propositionen ”Svensk strategi för biologisk mångfald och ekosystemtjänster” där regeringen gav Naturvårdsverket i uppdrag att utveckla riktlinjer för regionala grön infrastruktur-planer. Dessa planer har utvecklats sedan 2018 av respektive länsstyrelser i samarbete med markanvändare, övriga myndigheter och ideella organisationer.

Denna avhandling

I denna avhandling presenterar jag studier om grön infrastruktur i olika rumsliga skalor och i olika tematiska perspektiv; Natura 2000-nätverket i hela EU, Natura 2000-områden som livsmiljöer för ett antal fåglar i hela Sverige, och boreala skogar i norra Sverige som livsmiljö för lavskrika och arter och för virtuella arter som är konstruerade för ett representera olika arters olika krav på livsmiljö. Denna avhandling har alltså ett fokus på skog och skogslandskap i huvudsak i boreal miljö.

Den första studie som ingår i sammanläggningen är en granskning av de ekologiska aspekterna i Natura 2000 i vetenskapliga publikationer. Denna gjordes för att identifiera kunskapsbrister och därmed forskning som behövs för att förbättra kunskapsunderlag för ett mer effektiv bevarande av biologisk mångfald i samband med implementering av grön infrastruktur strategierna. Jag kategoriserade artiklarna efter rumslig skala, biogeografiska regioner, taxonomiska grupper, livsmiljötyper och de analysmetoder som har använts. Vid upprättandet av Natura 2000-nätverket beaktades ofta inte i vilken grad enskilda Natura 2000 områden innehåller livsmiljöer för viktiga arter eller hur stor är påverkan av det omgivande landskapet, vilket är integrerat i grön infrastruktur. I de följande studierna i sammanläggningen har jag därför analyserat hur effektiva Natura 2000-områdena är i Sverige när det gäller livsmiljöer för tre skogsfågelarter av bevarandeintresse i europeiska boreala landskap: mindre hackspett, lavskrika och järpe.

För den svenska boreala regionen, som i stort utgörs av de sex norra länen, har jag analyserat så kallade ”potentiella kontinuitetsskogar" d.v.s. äldre skogar som inte har avverkats sedan mitten av 1900-talet. Jag utvärderade hur dessa kan bidra till att minska fragmentering av livsmiljöer i befintliga formell skyddade skogar, för att på så sätt stärka konnektivitet och därmed grön infrastruktur. Först bedömde jag till vilken grad sådana skogar överlappade geografiskt med redan kända skogar med högt bevarandevärde. Sedan genomförde jag en analys på stor geografisk skala av konnektivitet för fyra olika teman: a) skyddad skog med känt högt bevarandevärde, b) skyddad och inte skyddad skog med känt högt bevarandevärde, c) potentiella kontinuitetsskogar kombinerade med skogar med känt högt bevarandevärde (skyddade och inte skyddade), och d) all skogsmark, som representerar en baslinje för referens. Dessutom uppskattade jag storlek, antal och fördelning av livsmiljöer för virtuella arter som är beroende av skog som domineras av gran, tall eller lövträd. Dessutom bedömde jag den potentiella ökningen av areal livsmiljö för virtuella arter i dessa skogar enligt flera olika scenarier. Ett annat tillvägagångssätt för att stärka grön infrastruktur i den boreala regionen är att använda lavskrika som en paraplyart för värdefulla skogar med tydlig skiktning. Jag utförde sådana analyser genom att utveckla en prediktiv modell för arter baserat på expertkunskap och de senaste tillgängliga skogsdata (bl. a. från laserskanning). Därefter validerades modellen med fältdata gällande förekomsten av lavskrika i Sverige.

Resultat

Granskningen av vetenskapliga publikationer om Natura 2000 visade att de allra flesta studierna omfattade små rumsliga skalor (d.v.s. ett enda Natura 2000-område eller en region i ett land). EU:s södra biogeografiska regioner har flest publikationer i förhållande till deras totala areal och till areal Natura 2000. Livsmiljöer som gräsmarker, sötvatten- och våtmarksmiljöer var överrepresenterade i jämförelse med deras relativa areal inom Natura 2000. Bland taxonomiska grupper var kärlväxter de mest studerade; kvantitativa empiriska studier dominerar. Dessutom konstaterade jag en generell brist på forskning om skogliga miljöer i Natura 2000 områden, och särskilt i norra Europa. Sverige är bland de europeiska länder där forsknings kring Natura 2000 är mycket begränsad.

I de därpå följande studierna visar jag att skog inom Natura 2000-områden i Sverige uppfyller livsmiljökrav bättre än skog utanför Natura 2000-områdena, för mindre hackspett i hela Sverige och för lavskrika i de alpina och mellanboreala regionerna. För järpe är livsmiljön utanför Natura 2000 mer funktionell i alla regioner utom i de alpina och den mellanboreala regionerna. För mindre hackspett och järpe är det tydligt att Natura 2000-områdens storlek påverkar dess funktionalitet, med detta gäller dock inte lavskrika. Ekologisk funktionalitet i skog som livsmiljö för dessa arter är storleksberoende och i de minsta Natura 2000-områdena (1-500 ha) finns en tydlig påverkan från omgivande landskap.

Den analys av konnektivitet på stor geografisk skala som ingår i min tredje studie visade att potentiella kontinuitetsskogar som ligger utanför skog med känt högt bevarandevärde kan utöka och därmed förbättra rumslig funktionalitet för skyddade skogar. Dock, stora regionala skillnader förekommer i möjligheterna att säkra livsmiljöer för arter som är specialiserade på tall-, gran- och lövrika skogar. Bristen är speciell stor i norra Sveriges inland och kustland. Där går det inte att uppfylla arternas krav på livsmiljö, utan storskalig restaurering av värdefulla skogar är nödvändigt. Situationen är mest allvarlig för arter som är beroende av lövrika skogar, där enbart fjällbjörkskogen framträder som tillräckligt utbredd och omfattande. Överlag erbjuder det fjällnära området bra ekologiska förutsättningar för många arter. Här har ett mindre omfattande trakthyggesbruk lämnat tillräckliga arealer av intakta skogslandskap som är ekologisk funktionellt.

Slutsatser och tillämpningar

För att förbättra kunskapsförutsättningarna för en framgångsrik tillämpning av grön infrastruktur i Europa behövs mer forskning, i synnerhet forskning som tar en utgångspunkt i Natura 2000. Mina slutsatser är att mer forskning bl.a. behövs för: 1) boreala regionen, 2) alpina områden, jordbruks- och skogsdominerade områden och havsmiljöer, och 3) taxonomiska grupper såsom kräldjur, groddjur, lavar och svampar. För att förbättra förståelsen av bevarandepotentialen i Natura 2000 bör fler studier omfatta stora rumsliga skalor och använda modellering som metod och utgångspunkt för planering. Detta var utgångspunkten för de studier som presenteras som artikel 2, 3 och 4 i min avhandling, som på olika sätt och på olika geografiska nivåer har bidragit med ny och viktigt kunskap om Natura 2000 i dagsläget och vilka möjligheter som finns att förbättra och förstärka förutsättningar för bevarande av biologisk mångfald och ekosystemtjänster inom ramen för grön infrastruktur planering.

De nuvarande Natura 2000-områdena är inte tillräckliga, i meningen storlek och livsmiljöegenskaper, för att säkra ekologisk funktionalitet för många arter. Dessa behöver förstärkas genom att skogsområden i omgivande landskap tillförs och antingen skyddas formellt eller frivilligt eller på annat sätt ges en skötsel och förvaltning som utökar bevarandeegenskaperna. Detta är särskilt viktigt för areellt små Natura 2000-områden, som dessutom utgör en stor andel av alla Natura 2000-områden i Sverige. För att möjliggöra en funktionell grön infrastruktur, måste restaurering av livsmiljöer göras i stor skala för de mer krävande arterna.

Jag rekommenderar tillämpning av arters krav för att analysera funktionalitet som verktyg i planering av grön infrastruktur. Delar av mina resultat kan användas direkt som underlag vid sådan planering, åtminstone för det boreala skogslandskapet i Sverige men också som generell princip och överlag. Jag hoppas att jag med den forskning som jag presenterar i denna avhandling bidrar till utvecklingen mot att uppfylla Sveriges skyldigheter enligt EU:s biologiska mångfaldsstrategi; att till 2030 skydda minst 30% av landets landområde.

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Green infrastructure (GI) was developed to mitigate habitat fragmentation. This thesis analysed GI for EU-wide Natura 2000 literature, Swedish Natura 2000 sites as habitat for forest-dwelling birds, and northern Sweden's boreal forest connectivity and habitat potential for real and virtual species. To strengthen conservation through GI, Natura 2000 studies should encompass large spatial scales and habitat matrices around Swedish Natura 2000 sites should be carefully managed. In boreal regions, non-protected forest networks can improve protected area connectivity and GI functionality.

Ewa H. Orlikowska received her doctoral education at the School for Forest Management, Swedish University of Agricultural Sciences (SLU), Skinnskatteberg, and her Master of Forestry degree from the Agricultural University of Poznańń (currently Poznańń University of Life Sciences), Poland.

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