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# Spatial conservation prioritization for the improvement of the national protected area network

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ACADEMIC DISSERTATION

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Omistettu Ponu-Vaarille ja muille luonnonsuojelubyrokraateille

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# Abstract

The ongoing decline of biodiversity highlights a need for smart land-use planning approaches for the development of protected area (PA) networks and their improvement by habitat restoration. As budgets are limited, conservation managers and planners commonly need to prioritize conservation and management efforts both in and outside the PA network. Spatial conservation prioritization (SCP), the methodological framework adopted in this thesis, is an approach to the synthesis of spatial data for the purpose cost-effective (spatial) conservation planning.

This thesis provides examples of three national level high-resolution SCP processes and one biodiversity value modelling. Focus was on the spatial design process, including development of an ecological model conservation value, modelling of the biodiversity surrogates, pre-processing of data for the analysis, running the spatial prioritization analyses, post-processing, and interpretation of results to support decision-making. All three analysis sets were custom-made in response to a specific real-world planning need.

First, we developed a SCP analysis for the Natura 2000 PA network (N2k), using data on the distributions, quality, and importance of 68 N2k habitats occurring in Finland. The primary purpose of this work was to assist the targeting of habitat maintenance, management, and restoration. We identified the N2k landscapes that have highest conservation value in Finland. We also studied how the priority areas for action change if the variable protection status of N2k areas is accounted for, instead of considering all areas equally protected. We identified both extensive and unfragmented high-priority areas but also small and irreplaceable areas.

Second, we describe an SCP process for the identification of candidate sites for expanded peatland protection in Finland. We coupled quantitative SCP analyses with regional targets and expert knowledge. It was possible to identify a set of peatlands, 5% of the total research area, that would bring a 39% estimated increase for the biodiversity value of the existing peatland PA network. These gains largely arise from expanded coverage for narrow-range features that are missing or insufficiently represented in the existing PA network. We found that key to a successful SCP process here was early-on, structured co-design between analysts, peatland experts, and decision-makers.

Third, we produced SCP analyses to identify unprotected forest areas that can host valuable forest biodiversity in the future. For this, we modelled stand-based dead wood potential (DWP) data as a primary surrogate for forest biodiversity. In addition, data on forestry operations that have negative impacts on biodiversity, observations of red-listed forest species, and several connectivity measures were included. Analyses addressed both the estimation of biodiversity value at the time of data extraction and biodiversity future potential following increases in connectivity. The results show that there are high conservation priority forest areas all over Finland, but in a highly fragmented distribution. A significant portion of these top-priority areas occur outside the current protected area network. Depending on analysis version, the top 10% of the landscape contains from 49% to 88% of presently remaining conservation value.

According to our results, and regardless of the scope of analysis, there are significant differences between areas in terms of biodiversity supported. Hence quantitative spatial biodiversity analysis should be integrated into land use decision-making at large.

Keywords: biodiversity, connectivity, dead wood, forests, GIS, mires, Natura 2000

# Tiivistelmä


Meneillään oleva luontokato korostaa maankäytön suunnittelun tapojen kehittämisen tärkeyttä suojelualueverkostojen kehittämisen ja elinympäristöjen tilan parantamisen tarpeisiin. Koska taloudelliset resurssit ovat niukat, tulee suojeltavia ja hoidettavia kohteita priorisoida suojelualueiden sisä- ja ulkopuolella. Tässä voidaan hyödyntää paikkatietoihin perustuvaa suojelupriorisointimentelmää (SCP), jonka avulla yhdistetään paikkatieto kustannustehokkaaseen suojelun suunnitteluun.

Tämä väitöskirja käsittelee kolmea paikkatietoihin perustuvaa valtakunnallista suuren tarkkuuden SCP-tilaustyötä ja yhtä luontoarvoaineiston mallinnusta. Väitöskirja keskittyy SCP-töiden suunnitteluun ja toteuttamiseen: priorisoinnin ekologisen mallin rakentamiseen, luonnonkirjoa kuvaavien piirteiden mallinnukseen, aineistojen esikäsittelyyn, analyysien tekemiseen sekä tulosten jälkikäsittelyyn ja käytettävyyteen.

Ensimmäisessä tutkimuksessa tunnistimme Suomen Natura 2000 (N2k) -alueverkostosta korkeimman suojeluprioriteetin alueet ja luontoarvoiltaan poikkeuksellisen suuret yhtenäiset hoitomaisemat sekä tarkastelimme alueiden suojelutason vaikutusta verkoston prioriteetteihin. Käytimme tietoja 68:n N2k-luontotyypin esiintymistä ja niiden kunnosta sekä Suomen vastuusta näiden luontotyyppien suojelusta EU:ssa. Tulostemme mukaan luontoarvoiltaan korkeita alueita esiintyy sekä hyvälaatuisina, laajoina ja yhtenäisinä kokonaisuuksina että pieninä ja korvaamattomina kohteina ja näiden välimuotoina. Joitain luontotyyppejä ei esiinny tiukimman suojelun alueilla lainkaan.

Toisessa tutkimuksessa yhdistimme SCP-analyysit alueellisiin tavoitteisiin ja asiantuntijatietoon soiden suojelualueverkoston laajentamisen tueksi. Tunnistimme joukon suojelemattomia soita, jotka kattoivat pinta-alaltaan 5 % tutkimusalueesta, mutta tuottivat 39 % lisäyksen olemassa olevan soiden suojelualueverkoston luontoarvoihin. Lisäys selittyy ensisijaisesti puuttuvien tai puutteellisesti edustettuina olleiden harvinaisten suotyyppien tai -yhdistymien esiintymillä. Havaitsimme, että avaintekijä menestyksekkäälle SCP-prosessille oli varhaisessa vaiheessa aloitettu yhteistyö analyysien tekijöiden, suoasiantuntijoiden ja päätöksentekijöiden kanssa.

Kolmannessa tutkimuksessa tunnistimme luonnonkirjon kannalta arvokkaita suojelemattomia metsäelinympäristöjä. Kehitimme metsäluonnon monimuotoisuutta kuvaavan metsätietoon pohjautuvan mallinnuksen lahopuulle, ns. lahopuupotentiaalin, joka toimi analyysimme pääaineistona. Lisäksi käytimme tietoja luonnonkirjoa heikentävistä toimenpiteistä ja tilaltaan heikentyneistä metsälajeista sekä tarkastelimme kytkeytyvyyksien vaikutuksia prioriteetteihin. Analyysiversiot esittävät metsien suojeluarvojen jakaumaa aineistojen irrotushetkellä sekä erilaisia tulevaisuuden skenaarioita kytkeytyvyyden lisäysten avulla. Tulokset osoittavat, että korkean suojeluarvon metsiä on joka puolella Suomea, mutta esiintymät eivät ole jakautuneet tasaisesti. Riippuen tarkastellusta analyysiversiota paras 10 % metsistä kattaa 49 % – 88 % kaikkein metsien yhteenlasketuista suojeluarvoista. Havaitsimme myös, että suuri osuus analyyseissä tunnistetuista arvokohteista on toistaiseksi suojelematta.

Tulostemme mukaan, riippumatta tutkimuksen aiheesta, alueiden luontoarvoissa on aina merkittäviä eroja. Sen vuoksi päätöksentekoon tulisi yhdistää tässä väitöskirjassa esiteltyjen analyysien kaltaisia määrällisiä tutkimuksia.



Avainsanat: biodiversiteetti, kytkeytyvyys, lahopuu, luonnon monimuotoisuus, luonnonsuojelu, metsät, Natura 2000, paikkatieto, suot

# List of abbreviations

| | |
|---|---|
| Complementary Mire Protection Program | A conservation programme which aimed at complementing the mire protected area network to achieve the sustainable and responsible use and protection of Finnish peatlands by end of the year 2014 |
| DWP | A modelled biodiversity surrogate for forest biodiversity, the dead wood potential, which is based on forest stand data, forest growth simulations, and forest ecology |
| Forest | Land areas growing trees |
| Forest stand | A forestry management unit with somewhat similar age and structure of trees and forest site type |
| METSO | The Forest Biodiversity Programme for Southern Finland |
| Metsähallitus Parks & Wildlife Finland | An authority that is responsible for taking care of protected areas, including both state-owned and private ones |
| Mire | A pristine or near pristine peatland environment |
| Natura 2000, N2k | Natura 2000 nature conservation area |
| PA | Protected area |
| SCP | Spatial conservation prioritization |
| Peatland | Wet soil type where decomposing of plant material is heavily prevented by the water. This causes an increase in organic matter, an accumulation of peat. Used here as a synonym for all peatland environments. |
| Woodland key habitat | Ecologically valuable natural forest environments whose structure or species would be difficult to maintain under conventional forestry, e.g., natural forest types |

# Table of Contents

# List of original publications

This thesis is based on the following publications:

I Mikkonen, N. & Moilanen, A. 2013. Identification of top priority areas and management landscapes from a national Natura 2000 network. Environmental Science & Policy 27: 11-20. https://doi.org/10.1016/j.envsci.2012.10.022

II Kareksela, S., Aapala, K., Alanen, A., Haapalehto, T., Kotiaho, J. S., Lehtomäki, J., Leikola, N., Mikkonen, N., Moilanen, A., Nieminen, E., Tuominen, S. & Virkkala, R. 2020. Combining spatial prioritization and expert knowledge facilitates effectiveness of large-scale mire protection process in Finland. Biological Conservation 241: 8. https://doi.org/10.1016/j.biocon.2019.108324

III Mikkonen, N., Leikola, N., Halme, P., Heinaro, E., Lahtinen, A. & Tanhuanpää, T. 2020. Modeling of Dead Wood Potential Based on Tree Stand Data. Forests 11(913): 21. https://doi.org/10.3390/f11090913

IV Mikkonen, N., Leikola, N., Lehtomäki, J., Halme, P. & Moilanen, A. 2023. National high-resolution conservation prioritisation of boreal forests. Forest Ecology and Management 541 (121079): 13. https://doi.org/10.1016/j.foreco.2023.121079

The publications are referred to in the text by their roman numerals.

Author contributions:

| | I | II | III | IV |
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| **Original idea** | NM, AM | AA, JSK, SK, KA, AM, TH, JL, NM, NL | NM, NL, PH | NM, NL, PH |
| **Study design** | NM, AM | SK, KA, AA, JSK, AM, TH, JL, NM, NL | NM, NL, AL, JL, PH | NM, NL, JL, PH |
| **Methods and implementation** | NM | SK, NM, NL, TH, JL, AM | NM, NL, AL, JL, PH, TT | NM, NL, JL, PH |
| **Data** | NM | NL, NM, SK, KA, AA, TH, RV, ST, EN | Model data: NL, AL; Validation data: EH, TT | NM, NL |
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# 1 Introduction

## 1.1 Land-use driving biodiversity loss

Land use is a main direct threat driving biodiversity loss (IPBES 2019). When we lose biodiversity, we lose species and genetic and ecosystem diversity, upon which life ultimately depends on. Apart from present-day human impacts, biodiversity is affected by past and present climate and geological diversity ('geodiveristy'), which contribute to substantial variation in ecosystems and promote biodiversity (Wallis et al. 2021; Tukiainen et al. 2022). Alarmingly, habitat fragmentation, loss, and degradation of ecosystems have accelerated during the recent decades and are predicted to continue in the future (Sala et al. 2000; Butchart et al. 2010; Pereira et al. 2010; IPBES 2018; 2019). This is fundamentally linked to the development of humankind to its present state (Dasgupta 2021). Furthermore, environmental conditions are changing faster than nature can adapt (Nila et al. 2019; Määttänen et al. 2023). Habitat loss also impacts geodiversity and climate, by decreasing the former and changing the latter, which probably further accelerates biodiversity loss (IPCC 2019). Some ecosystems have been assessed to be already beyond their sustainable living boundaries (Newbold et al. 2016). Recognition of global biodiversity decline has brought forth a shared global target that remaining nature should be secured and rapidly improved (European Commission 2020; CBD 2022).

## 1.2 The many ways to improve the state of biodiversity

Land use planning plays a crucial role in the attempts to halt the biodiversity crisis, because land use has major impacts on biodiversity, and it is completely in our own hands. Depending on the biodiversity target there are many potential forms of actions, including conservation, habitat management, habitat restoration, recreation of ecosystems, cleaning of environment, impact reduction, or reintroduction of species. Sometimes several of these actions can be applied to the same location which may generate interactive joint ecological benefits. However, in some cases different management actions may be in conflict with each other, or have controversial effects, for example, on species inhabiting semi-open habitats vs. those dependent on moist, shaded forest habitats. Desired outcome may also differ depending on whether the focus is on threatened or common taxa, or on habitats, simply because the effects of conservation actions may be specific to species and biotope (Baker et al. 2019; Ellison 2019; Virtanen and Moilanen 2023).

There are three major interacting factors to consider when planning conservation (Hodgson et al. 2009; Hodgson et al. 2011). These include habitat quality and habitat area, that define the carrying capacity of the area from the perspective of a species (see literature starting from Verhulst 1838; del Monte-Luna et al. 2004; Chapman and Byron 2018). The third factor is the spatial arrangement (i.e., aggregation, connectivity) of habitats, which impacts spatial (meta)population dynamics. All these factors are impacted by anthropogenic habitat loss, degradation, and fragmentation which further reduces the resilience of the species populations in the degraded landscapes (Thompson et al. 2009). This is especially true in forests, where most of the old forests that have previously experienced natural disturbances, are replaced with even-aged forests in fragmented forest landscapes (Keto-Tokoi and Kuuluvainen 2014).

## 1.3 Protected area networks

Protected area (PA) networks are a widely used conservation tool. The networks can be designed and implemented at different spatial scales, ranging from local to national scales over to the global level, and with different level of protection ranging from permanently to temporarily protected, or less intensively managed parts. In PA networks the trinity of quality, area, and aggregation becomes visible as the lack of any of the three factors can decrease the ecological functionality of the network. Changing climate increases the requirements of a functional PA network, as even protected habitats may decline due to bioclimatic changes (Nila et al. 2019; Aalto et al. 2023).

A PA network is typically spatially static. Also, the main driver for species persistence, habitat quality in the PAs, would be largely constant, although climate change or far spreading pollutants may degrade even protected areas. In contrast, the habitat matrix that surrounds the protected area network can experience significant change due to, e.g., forestry, agriculture, or urban development (Korhonen et al. 2021). Thus, the changes in the habitat matrix influences the functional connectivity of the protected areas network, affecting how species can move and disperse between individual protected areas (Mönkkönen et al. 2022). According to Baguette et al. (2013), functional connectivity is a spatiotemporal variable that is different for each species and depends on the quality of the landscape, both in and outside PA network. Landscape connectivity, including functional and structural connectivity, determines the possibilities for successful regional dispersal and migratory range shifts in the long run. Without adequate functional connectivity between (protected) areas, individual sites (habitat patches) can become into isolated populations with limited prospects of persisting under changing conditions (Rybicki and Hanski 2013). Functional connectivity is reduced by habitat degradation, which lowers the ecological quality of areas, and habitat loss, which reduces the amounts of habitats available, and ultimately, consequent fragmentation with increased distances between good-quality habitat patches and increased edge effects. Because PA networks are often very fragmented, as is the case, e.g., in southern Finland (Kuusela et al. 2022), special attention needs to be targeted to functional connectivity.

Conservation decisions are often made as political national-level decisions. Because biodiversity values are a cross-border phenomena and PA networks can span many countries, international coordination in the planning of networks would be ideal (Pouzols et al. 2014; Nila et al. 2019; Kuhmonen et al. 2022). The Natura 2000 network that stretches across the European Union countries is the largest coordinated network of protected areas in the world (EC 2023). Its intention is to ensure the long-term survival of Europe's most valuable and threatened species and habitats (EUCO 1992). Nevertheless, it has become clear that the present global, regional, or national PAs alone cannot halt the ongoing decline of biodiversity (UN 1992; Johnson et al. 2017; IPBES 2019). This is partly because many individual PAs have been established based mostly on other than biological reasons (Myers et al. 2000; Brooks et al. 2006). They are often also poorly connected to the broader PA network, which may not support connectivity and population interactions very well (Ward et al. 2020).

The conservation status of PAs may vary. In practice this means that areas with weaker protection status are intermingled with and support the more strongly protected core network together with non-protected areas that have biodiversity-friendly management practices. Certain elements of biodiversity may indeed persist under other land-use types, such as forestry, agriculture, or recreational use. This is also the case in Finland, where the PA network, covering 10% of total area (Official Statistics of Finland 2023b), is strongly biased towards the colder and less productive north (Kulju et al. 2023). Consequently, many aspects of biodiversity have declined more in southern Finland than in the north (Virkkala and Rajasärkkä 2007; Hyvärinen et al. 2019). However, this network of protected areas is complemented with areas that have been assigned to more biodiversity-friendly practises. For example, within forests, the permanent forest PA network is supported by 1 M ha (2,8% of the total area) of forests with some management restrictions (Kulju et al. 2023), such as woodland key habitats (Brumelis et al. 2011). This is a good example of how management outside strictly protected areas can play a key supportive role for biodiversity (Hansen et al. 1991). As forest industry, bioeconomy, and conservation all share an interest in the same resource (Maxwell et al. 2016; Blattert et al. 2022), these should be ideally planned together (Pressey 1994; IPBES 2019; Leclére et al. 2020; Jung et al. 2021).

## 1.4 Systematic conservation planning & spatial conservation prioritization

A methodology and process called systematic conservation planning has been developed to integrate contradicting demands of different land use (Margules and Pressey 2000). It includes computational spatial conservation prioritization (SCP) methods that utilize spatial and non-spatial data on biodiversity and land use together with ecological knowledge to plan effective conservation of biodiversity under limited resources (Margules and Pressey 2000; Moilanen et al. 2009c; Kukkala and Moilanen 2013). These SCP methods, including the Zonation approach used here (Moilanen et al. 2009a; Lehtomäki and Moilanen 2013; Moilanen et al. 2014; Moilanen et al. 2022), are powerful and highly visual decision support tools. They allow the integration of information about thousands of spatial features to be analysed and distilled into spatial maps that enhance the transparency and objectivity of large-scale land use planning. SCP methods focus on finding solutions that are cost-efficient and balanced in terms of biodiversity coverage – all features must have coverage – which makes analysis completely different from simple scoring (Moilanen et al. 2009c).

We need to understand how the most can be gained from SCP analyses and on the other hand, how the analyses can be co-produced so that the results are both relevant for the problem at hand as well as perceived legitimate by those affected. Therefore, SCP is at its best a multidisciplinary project where conservation biology, ecology, geography, statistics, applied mathematics, computation, and social science meet in broad collaboration to achieve decisions that are balanced, well-supported by argument and data, and valid in the long run (Moilanen et al. 2009c). Using SCP methods increases transparency, reduces subjectivity, and increases interaction in decision-making if process steps and decisions are developed jointly by a working group that involves stakeholders (Lehtomäki and Moilanen 2013).

As a drawback, SCP approaches are dependent on the availability of high-quality spatial data and ecological knowledge. Data used commonly for SCP include compulsory information on biodiversity which include habitats, species, and possibly ecosystem services. Optional data include information on human impacts (e.g., habitat condition, threats, pressures), costs, information on ecological dynamics (e.g., connectivity or interactions), or administrative or planning units (Kujala et al. 2018a) to name a few. Although there are abundant freely available data from various online repositories, there is often a lack of suitable and useful data for conservation planning. This may hamper the implementation of SCP analyses. Spatial data should be appropriate, up-to-date, accessible, and at the correct scale and resolution for the needs of decision-making (Arponen et al. 2012; Kukkala and Moilanen 2013). For conservation planning, there should be enough data on many species distributions and habitats so that analysis results can be treated as representative of all biodiversity. Thus, spatial modelling, remote-sensed data, and biodiversity surrogates are often needed to fill the gaps of ground-survey data (Sarkar and Margules 2002). The power of big data sets, which are typical for SCP, reduces the uncertainties in the SCP outcome that rise from uncertainties in individual input features (Kujala et al. 2018b). Additionally, using high-quality modelled data may increase the transparency and repeatability of the SCP analysis and encourage for the development of the models or techniques (Araújo et al. 2019).

## 1.5 State of biodiversity in Finland

This thesis considers improving the state of biodiversity at the national level in Finland. According to the latest assessment of threatened habitat types in Finland, 48% of habitats are threatened (classified as critically endangered, endangered, or vulnerable) and 18% near threatened (Kontula and Raunio 2019). Threatened habitats are more prevalent in the south compared to the north and declining trends have been assessed for most habitats. Habitat deterioration is also reflected at the species level. According to Hyvärinen et al. (2019), the number of threatened species is the highest for forest environments (31% of threatened species), rural biotopes and cultural habitats (24%), and alpine / fell habitats (12%). The most important reason for the threatened or near-threatened status of habitats and species is commercial forestry. A declining trend is evident also in natural forest environments, the area of which has declined to less than 4% of Finland's forested areas. Intensive forestry, including logging and other silvicultural practices, such as drainage, have impacted both forests and peatlands heavily (Gauthier et al. 2015; Kuuluvainen and Gauthier 2018; Korhonen et al. 2021).

The prevailing land use practises must change if the negative progression in the state of nature is to be halted. While knowledge about biodiversity has improved, new species for Finland and for science have been found (Juslén and Sirkiä 2013), new PAs have been established (Kulju et al. 2023), and some habitat deterioration has been reversed (Henttonen et al. 2019; Korhonen et al. 2021), biodiversity still continues to decline (Hyvärinen et al. 2019; IPBES 2019; Kontula and Raunio 2019). The high forest cutting levels have been identified as a major driver for preventing biodiversity loss and climate change mitigation (Korhonen et al. 2016; Mäkelä et al. 2023; Peltoniemi et al. 2023). To halt the negative trend, the Finnish government has committed to several international agreements such as the Kunming-Montreal Global Biodiversity Framework (CBD 2022), the European Commission Biodiversity Strategy 2030 (European Commission 2020), and the agreement to halt climate change (UN 2015). Following the implication of these agreements and all the knowledge on drivers of biodiversity loss and solutions to tackle it, it should be possible to turn the negative environmental trends to neutral or positive.

## 1.6 Objectives of this thesis

This thesis explores the possibilities that SCP offers for spatial planning of biodiversity conservation at the national scale in Finland. It consists of three studies that describe independent national SCP processes and one study that focuses on modelling of an auxiliary data set. All three SCP case studies are custom-made analyses where the broad objectives were defined by the commissioning government agency, but the technical solution of how to achieve the target was given to a group of SCP, GIS, and ecology specialists to be solved. In all cases the underlying motivation was to halt the decline of biodiversity as effectively as possible for the habitat types investigated. The results have been used for conservation, forest management, and restoration, both inside and outside protected areas. This has the potential to strengthen the national PA network, as well as improve the state of Finnish nature in general.

The focus of this thesis is on the spatial prioritization process and the usability of analysis results in supporting biodiversity conservation in Finland. Work covers the whole SCP process, which includes defining the prioritization objectives, collecting and formatting data, developing the so-called ecological model, executing the actual SCP, and interpreting the results (see, e.g., Lehtomäki and Moilanen 2013). The final part of the SCP process, the use of the results for on-the-ground conservation decisions and land-use planning is discussed only briefly, because the broad societal process of implementation is beyond the scope of this thesis.

In study (I) our aim was i) to identify priorities inside Natura 2000 network, ii) examine the impact of the PA management categories on priorities, as maintenance and utilization of these areas may depend on Natura 2000 category, and iii) identify the most important management landscapes within the permanently protected Natura 2000 area network (Mikkonen 2012; 2013; Mikkonen and Moilanen 2013). This study was done to serve the needs of Finnish Metsähallitus Parks and Wildlife, an authority that is responsible for taking care of PAs, including both state-owned and private ones.

In study (II) we examined how to identify the most effective set of unprotected peatlands for expanding the peatland protection network of Finland. These analyses were performed to support decision-making in the national Complementary Mire Protection Programme for implementing Government resolution on sustainable and responsible use and protection of peatlands by end of the year 2014 (Ministry of Agriculture and Forestry of Finland 2012; Alanen and Aapala 2015; Kareksela et al. 2020). This study was commissioned by the Finnish Ministry of the Environment that is responsible for, e.g., biodiversity and sustainable use of natural resources, and environmental protection in Finland.

Studies (III) and (IV) were developed jointly: the data modelled in study (III) were the main input for the SCP process of study (IV). These studies focus on habitat data shortage: their focus is on identifying red-listed forested habitats.

In study (III) we developed a model that describes the development of a biodiversity surrogate for natural forests, the Dead Wood Potential (Mikkonen et al. 2020).

In study (IV) we examined the distribution of high conservation value forest areas at local, regional, and national levels to support maintenance of forest biodiversity inside and outside the forest conservation network (Mikkonen et al. 2018; Mikkonen et al. 2020; Mikkonen et al. 2023b; 2023a). The prioritization results can be utilized for at least the following purposes: 1) planning the expansion of the forest PA network by suggesting new promising permanent and temporary PAs, 2) land use planning including design of regional zoning plans, green corridors, or ecological networks, and 3) directing intensive forest management to areas with comparatively low biodiversity values. These studies were commissioned by the Finnish Ministry of the Environment to support the operations of the Forest Biodiversity Programme for Southern Finland (METSO), which pays compensation for landowners who voluntarily protect ecologically valuable forest areas (The Finnish Government 2008; 2014).

# 2 Material and methods

## 2.1 Finland as a study area

The four case studies included in this thesis were conducted in Finland, a country located in Europe between latitudes 60° and 70° north and longitudes 19° and 31°, covering an area of 340,000 $km^2$ (marine areas 52,000 $km^2$ not included). Due to the post-glacial rebound Finland is divided into archipelagos and coastal lowlands, a slightly higher central lake plateau, and uplands in the north and northeast part of the country. Finland is dominated by boreal forests (74% of the total area, when marine areas are not included) with the rest of the area covered by freshwater areas (10%), as well as wetlands, including non-forested peatlands (7%), agricultural areas (7%), and built environments (3%) (Finnish Environment Institute 2018). Although the human population of Finland is rather small, 5.6 million inhabitants, and spatially aggregated to southern part of the country (Official Statistics of Finland 2023a), the nature in Finland has been exploited intensively over the past centuries (Tasanen 2004; Niemelä et al. 2005; Lindholm and Heikkilä 2006; Kontula and Raunio 2019). Most of Finland is in the boreal zone (or taiga) which is the largest land biome on earth. The boreal region is characterized by coniferous forests that are essential for the northern biota (Esseen et al. 1997). In geological terms the boreal zone has been glaciated recently, making the biota relatively young, less than 12,000 years old. The boreal climate is cold with short summers and long winters. Evaporation decreases compared to precipitation when moving towards north, which maintains moist environments, such as peatlands (Kottek et al. 2006; Peel et al. 2007).

Study (I) covers terrestrial and freshwater areas of the Natura 2000 nature PA network on government own areas (Figure 1, Panel A). Study (II) investigates peatland environments (Figure 1, Panel B) excluding the Northern Lapland, where the state of peatlands and conservation network is relatively good (Figure 1, Panel A and B.1). Studies (III) and (IV) included forested environments in Finland (Figure 1, Panel C). Marine areas and the autonomous area of Åland were not included in any of the analyses.

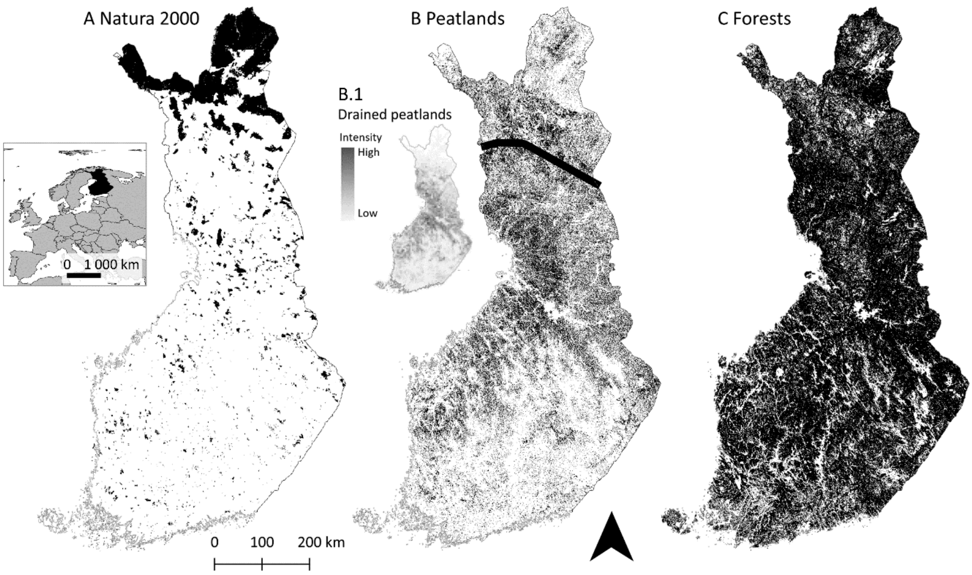


**Figure 1** Figure 1. The study areas. Panel A: The Natura 2000 habitat conservation area network on state-owned terrestrial land in Finland. Panel B: Peatlands of Finland. The border of Complementary Mire Protection Programme is marked with black. Panel B.1 the Intensity of drainage on peatlands. Panel C: Forests of Finland. In panel B and C: the darker the colour is the map, the more there are those habitats in question. © Natural Earth, Metsähallitus Parks & Wildlife Finland (2010b); Finnish Environment Institute (2011; 2018); National Land Survey of Finland (2024)

## 2.2 Spatial conservation prioritization

In studies (I), (II), and (IV) the priority areas for conservation or nature management were identified with the spatial conservation prioritization tool Zonation (Moilanen et al. 2005; Moilanen et al. 2009a; Moilanen et al. 2011a; Moilanen et al. 2022). It is a decision-support tool that utilizes mainly spatial data on species and habitat distributions, habitat condition, threats and pressures, land costs, and ecological parameters such as connectivity and spatial interactions between different biodiversity features (Lehtomäki and Moilanen 2013). For each analysis the newest available software version was used: study (I) utilized version 2.0 and 3.0 beta (Moilanen et al. 2011b) and studies (II) and (IV) version 4.0 (Moilanen et al. 2014).

Zonation requires raster format data. Therefore, all spatial data are converted before the actual prioritization to a grid system with a certain resolution. In the study (I) we used 200 x 200 metre, in study (II) 50 x 50 metre, and in study (IV) 96 x 96 metre grid cells. The grid cells included in the study landscape constitute the spatial units of the Zonation analysis. Zonation produces a nested hierarchical priority ranking of the spatial units based on data recorded for them. The analysis is an iterative process where in each iteration the relatively least important remaining spatial unit is removed from the analysis and the most important units are retained. The removal order produces a priority rank for each spatial unit and, eventually, a priority rank map that covers the full study area. Importantly, the process is based on complementarity between spatial units: Zonation tracks the decline of each input variable throughout the prioritization, and this information is used to maintain the balance between features (Kujala et al. 2018a; Kujala et al. 2018b). In study settings which include multiple analyses, possibly using different data, the greatest interest is on those areas that consistently receive high ranks – these areas are important from most or all perspectives included in analysis (Kujala et al. 2023).

In general, Zonation can be used for variable tasks (see, e.g., Lehtomäki and Moilanen 2013; Moilanen et al. 2022). In this thesis, we employed Zonation to tackle four common, essential tasks (Table xx): 1) identification of areas with the highest conservation priorities, 2) identification of areas with the lowest conservation priorities, 3) identification of areas that provide the most efficient complement when planning for protected area network expansion, and 4) assessment of an existing protected area network.

**Table 1** Zonation analysis types

| Analysis | Identify the highest priority areas | Identify the lowest priority areas (for impact avoidance) | The most efficient expansion for the protected area network | Assessment of the protected area network |
|---|---|---|---|---|
| Study (I): Natura 2000 | x | x | | x |
| Study (II): Peatland conservation network expansion | x | | x | x |
| Study (IV): Forest conservation priorities | x | x | x | |

## 2.2.1 The ecological models

In conservation planning and decision-making there are usually multiple factors that need to be considered. These vary from ecological quality-area-aggregation questions (Hodgson et al. 2011) to what is already protected and where, and land-ownership questions. In the present context, the ecological model (Figure 2) is a methodological flow for Zonation, or any other SCP approach, that describes how the challenge in question will be tackled by integrating relevant data, other ecological knowledge, and, e.g., the Zonation processing options (Lehtomäki and Moilanen 2013). Typically, in SCP analyses collating data used in the analysis is more challenging than the SCP itself. Therefore, it should be recognized that there seldom is an ecological model before the data or vice versa: they are typically developed and produced jointly in an iterative fashion.

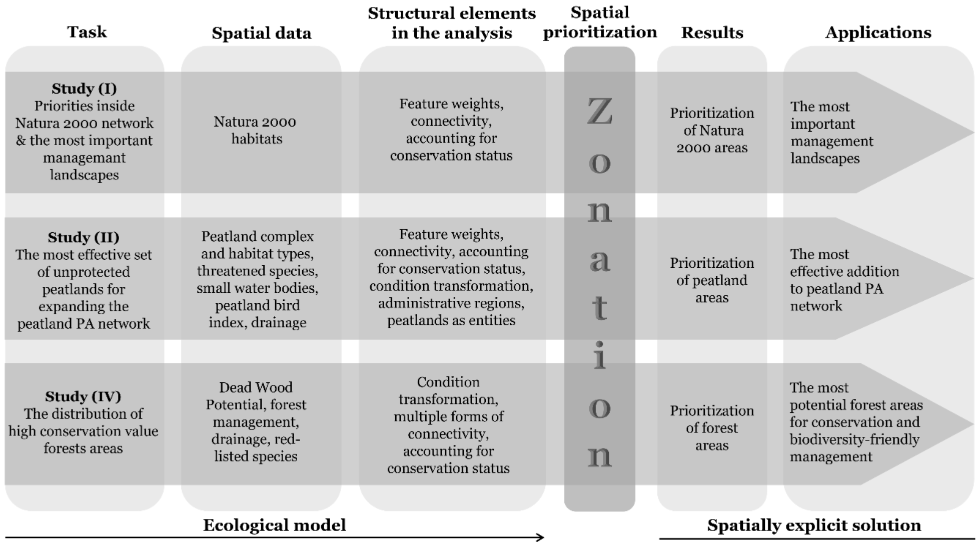


**Figure 2** Flowchart of the three Zonation analyses adapted from Kareksela et al. (2020).

Each of the SCP studies in this thesis (Figure 2) include several prioritization versions. Typically, analysis versions start from simple and develop towards more complicated versions, so that the subsequent versions include everything that has been included in the previous simpler versions. This stepwise approach helps in the verification of additional data and parameters used at each stage of model development: if multiple data and analysis elements are added simultaneously, catching data errors or errors in computational setup becomes less easy. Stepwise development of the prioritization also provides understanding about how much different sections of data and components of the ecological model influence results (Lehtomäki and Moilanen 2013; Kujala et al. 2018a; Kujala et al. 2018b).

Typical structural elements of Zonation analysis concerning this thesis are summarized in Table 2. Usually, biodiversity and habitat condition information are included first, possibly in several smaller steps, for example adding higher taxa and habitat types one by one. Then, the present PA network is applied as a constraint, followed by connectivity modifications considerations and costs (Lehtomäki and Moilanen 2013). In studies (I) and (II) the most complicated versions were considered the most eligible (realistic) ones, whereas in study (IV) there are

**Table 2** Structural elements of the three Zonation case studies, publications (I), (II) and (IV). N2k = Natura 2000

| Things to consider in nature conservation | How this is done in Zonation | How it is called in Zonation | (I) N2k | (II) Peatland | (IV) Forests | References |
|---|---|---|---|---|---|---|
| The *usability* of the results: the *spatial resolution* of the data compared to decision-making | Choose the best possible resolution for the input layers for the analyses | Grid cell resolution | 200 m | 50 m* | 96 m | (Arponen et al. 2012; Tanhuanpää et al. 2023) |
| Define *conservation value*, i.e., balancing between rare and common features | How the marginal loss of conservation value of a grid cell is calculated: emphasize cells if 1) even one species has a relatively important occurrence there or 2) the aggregate contents over all species and habitat types is high | Marginal loss rules: 1) core area zonation (CAZ) or 2) additive benefit function (ABF) | CAZ | ABF | ABF | (Moilanen et al. 2005; Moilanen 2007; Moilanen et al. 2022) |
| *Complementarity* is needed to ensure protecting balanced set of variables. | The algorithm is founded on complementarity | No specific name | x | x | x | (Moilanen et al. 2009b) |
| *What is already protected*: identification and filling the gaps in the present conservation network | Protected areas are forced to the highest priorities, thereby generating a hierarchy to the prioritization. | Hierarchical analysis | x | x | x | (Leathwick et al. 2008) |
| *Importance*: some input variables are ecologically more important than others | Specify weights that describe the importance of the input features included | Input feature weights | x | x | All equally weighted | (Arponen et al. 2005; Moilanen et al. 2005) |
| *Condition*; habitat condition: model effect of past negative anthropogenic impacts | Reduce feature occurrence levels in the impacted areas | Condition layer | | x | x | (Leathwick et al. 2010; Moilanen et al. 2011a) |

| Things to consider in nature conservation | How this is done in Zonation | How it is called in Zonation | (I) N2k | (II) Peatland | (IV) Forests | References |
|---|---|---|---|---|---|---|
| *Regional vs. national priorities*: Distribution of priorities across multiple administrative units, such as provinces. | Separate prioritization for the whole area and administrative units. | Administrative units analysis (ADMU) | (x**) | x | (x**) | (Moilanen and Arponen 2011) |
| *Connectivity type 1, planning units**: some areas should not be split into smaller parts as they function only as ecological entities, e.g., mires are hydrological entities | Prioritization is developed for spatially defined entities, not on grid cells as usual | Planning units (PLU) | | x | | (Leathwick et al. 2010; Kareksela et al. 2020) |
| *Connectivity type 2, boundary length penalty*: add aggregation to a reserve network | The prioritization includes a penalty on the structural characteristics of the reserve network to produce a more compact solution. This is a general, non-feature-specific aggregation method. | Boundary Length Penalty (BLP) | x | | | (Moilanen and Wintle 2007) |
| *Connectivity type 3, edge removal*: promote maintenance of structural habitat continuity and spare core areas from fragmentation | Remove grid cells only from edges of remaining areas: core- areas receive somewhat elevated ranks | Edge removal | x | x | x | (Moilanen et al. 2005) |
| *Connectivity type 4, semi-continuous high-quality habitats*: aggregated, ecologically partially similar, and high-quality areas support diverse ecological communities and demanding biodiversity. | Express connectivity between input variables based on their 1) (ecological) similarity, 2) local occurrence levels, and 3) distance. The closer they are to similar high value areas, the stronger the connectivity is. | Matrix connectivity | x | | x | (Lehtomäki et al. 2009) |

| Things to consider in nature conservation | How this is done in Zonation | How it is called in Zonation | (I) N2k | (II) Peatland | (IV) Forests | References |
|---|---|---|---|---|---|---|
| *Connectivity type 5, proximity to protected areas*: present PA network positively influences nature around it. Hence, placing protected area network expansion areas near the present network may be desirable to promote strong regional networks. | Some input features may have positive effects on their surroundings, or alternatively some features benefit from buffering, as defined by a connectivity interaction. The impact is expressed based on local occurrence levels of features in unprotected areas and the distance from the protected areas. The closer the areas are each other and the higher the occurrence level in unprotected site is, the stronger the connectivity is. | One-way positive interaction connectivity | | x | x | (Lehtomäki et al. 2009; Rayfield et al. 2009) |
| *Connectivity type 6, management landscapes*: identify the regional networks where management would be most effective | The conditions for landscapes that constitute an entity are defined by their ranking values and interpatch distances | Landscape identification | x | | | (Moilanen et al. 2005) |

*In study (IV) planning units (PLU) were used instead of individual grid cells as the decision-making units in SCP. The PLUs are predefined groups of grid cells, whole peatland complexes, that enable prioritization of spatially joint entities. This is important especially with peatlands, as each peatland is a connected hydrological entity and thus it is central that they are prioritized and protected as complete intact units, when at all possible (Kareksela et al. 2013).

** Not included in this thesis but included in the national reports written in Finnish (Mikkonen 2013; Mikkonen et al. 2018).

multiple analysis versions that are useful for different levels of decision-making. If costs or opportunity costs are used, then usually both analyses with and without costs are of independent interest.

In study (I) we targeted the SCP for identifying priorities inside Natura 2000 network and its most important management landscapes. The ecological model consisted of two different versions of the analysis: either ignoring or accounting for the present conservation status of habitats. The basic analysis included 68 Natura 2000 habitats with weights that were based on their threat status and importance, and connectivity that accounts for habitat quality, and ecological similarity, and distance. The impact of conservation status on spatial priorities was studied by adding a hierarchic analysis where areas with a stronger conservation status were forced to highest priorities. Doing so develops a four-level priority ranking, where the protection needs of the PA network is easy to identify and evaluate. The management landscapes were identified based on the analysis version that ignored the conservation status. This study had no previous analysis history and was developed as a completely new analysis.

In study (II) we targeted the SCP to identify the most effective set of unprotected peatlands for expanding the peatland PA network. The ecological model consisted of nine incremental analysis versions, all of which considered the already existing PA network (hierarchical analysis). The different versions included progressively 1) 31 layers of geomorphological and peatland habitat complexes, 2) the previous with weights, and 3) the state of habitat degradation measured based on peatland drainage. In the subsequent steps, all new biodiversity features added into the analysis were included with weights and their condition was adjusted using drainage information: 4) 39 layers of mapped observations of red-listed peatland habitats, 5) 3 layers of red-listed vascular plants and mosses, and 6) 17 layers for peatland indicator birds. Next, versions 7) added small freshwater bodies and 8) proximity to all other peatlands and to protected peatlands. In the final step, 9) prioritization was applied to administrative subregions by weighting jointly both scales: national and regional. Study (II) utilized up-to-date assessment and pilot SCP analysis on Finnish peatlands (Mikkonen et al. 2013; Salminen 2013). Instead of a grid cell, the decision units in this study were complete mires because they form hydrological entities.

The study (IV) focused on identifying the distribution of high conservation value forests. The environmental requirements and reasons for forest species becoming red-listed vary (Tikkanen et al. 2006) making it impossible to develop a model that would cover all of them. Therefore, the ecological model in study (IV) focused on identifying forest environments that have experienced severe threat and species that cooccur with them: herb rich forests (Kouki et al. 2018) and dead wood dependent species (Hyvärinen et al. 2019). Loss and deterioration of natural herb rich forests, which typically are multispecies, multilayered, and include a dead wood continuum, have caused the decline in species that depend on these habitats. As for dead wood dependent species, they share a significant portion of forest dwelling species (Siitonen 2001) and many of them live in herb rich forests. The ecological model consisted of seven stepwise analysis versions: 1) default: 20 Dead Wood Potential layers, 2) condition adjustment based on drainage and forest management, 3) forest connectivity, emphasizing aggregated high-quality areas, 4) red-listed forest species observations, 5) connectivity to woodland key habitats, and 6) connectivity to permanently protected areas. The final version (7) is the same as step 6, but with hierarchic structure accounting for protection status of forests. This model was developed based on earlier work by Lehtomäki et al. (2009) and Leinonen et al. (2013).

## 2.3 Summary of data

Each of the four studies aimed at achieving a national (or almost national) high resolution analysis or data for the environments in question, which imply high requirements for the initial data. Thus, only data of adequate extent and quality were accepted into the studies, as summarized by Table 3.

**Table 3** Data used in the analyses.

| Data class | Details | Variables included | Data source | Spatial or not | Studies |
|---|---|---|---|---|---|
| *Data on habitats and species* | | | | | |
| Natura 2000 habitat types | 68 habitats as individual layers | naturalness, representativeness | ground survey + interpretation of aerial photography | spatial | I |
| Geomorphological and peatland habitat complexes | 31 layers | binary presence-absence | ground survey + interpretation of aerial photography | spatial | II |
| Peatland habitat type groups: grouped by ecological similarity on site vegetation and fertility | 39 group layers | binary presence-absence | ground survey | spatial | II |
| Small freshwater bodies | 1 layer | binary presence-absence | ground survey + interpretation of aerial photography | spatial | II |
| Species data aggregates | Study (II): 3 layers<br>Study (IV): 1 layer | **Study (II):** IUCN red-listed species or otherwise important vascular plants and mosses + nesting sites of indicator bird species, **Study (IV):** forest-dependent IUCN red-listed species | observations, gridded | spatial | II, IV |
| National IUCN threat status of habitat | Used as one factor in weighting | IUCN threat status for each habitat | expert assessment | non-spatial | II |
| National report on implementation of EU Habitats Directive in Finland | Used in weighting | State of conservation status for each habitat | expert assessment | non-spatial | I |
| National IUCN threat status of species | Used in weighting | IUCN threat status for each species | expert assessment | non-spatial | I, II, IV |
| Habitats or species national responsibility status | Used in weighting | Binary priority: prioritized or not | expert assessment | non-spatial | I, II |

| Data class | Details | Variables included | Data source | Spatial or not | Studies |
|---|---|---|---|---|---|
| Stand data | Used for modelling the dead wood potential for each stand | Forest site type, tree species, mean diameter at breast height, mean volume | ground survey + modelling | spatial | III, IV |
| Dead wood potential (DWP) in forests | 20 layers | DWP value (index) for each stand, separated for 5 site types and 4 tree species combinations | modelled | spatial | IV |
| *Quantification of human disturbance* | | | | | |
| Human activities with negative impacts on biodiversity | 1 layer | Study (II): peatland drainage layer<br>Study (IV): forest management type and time since notification was done + soil drainage | mandatory forest use announcements, ground survey, and interpretation of aerial photography or satellite images | spatial | II, IV |
| Permanently protected areas | 1 layer | binary presence-absence | | spatial | I, II, IV |
| Known unprotected high biodiversity areas | 1 layer | binary presence-absence | | spatial | IV |
| *Data on regions* | | | | | |
| Vegetational zones | Used in modelling in study (IV) and as analysis regions in (II) | Zone and region identifiers | | spatial | II, IV |

### 2.3.1 Habitat data

In studies (I) & (II) we used data on existing, widely adopted habitat classifications, whereas new spatial data were produced for the specific needs of studies (III) and (IV).

The primary data in study (I) were the maps on Natura 2000 habitats on government owned areas (EUCO 1992). Thus it is important to note that private conservation areas (covering 16% of Finnish conservation areas) are not included here. The used Natura 2000 dataset provides an up-to-date assessment of Finland's Natura 2000 network, constructed by combining earlier databases, field surveys, and aerial images (Metsähallitus Parks & Wildlife Finland 2010a). It includes information on the locations where Natura 2000 habitat types have been recorded and habitat condition at these locations (naturalness). The data included information on 68 Natura 2000 habitat types, covering in total 3,6 M ha, 10% of terrestrial area of Finland. Most of the Natura 2000 habitats are rare, but the four most common habitats (alpine and boreal heaths, nordic subalpine/subarctic forests with *Betula pubescens* ssp. *Czerepanovii*, aapa mires, and western taiga) cover 79% of the study area.

Study (II) utilized data on the distribution of different peatland and geomorphological habitat types and complexes and their condition (Metsähallitus Parks & Wildlife Finland and Centres for Economic Development Transport, and the Environment 2012; Eurola et al. 2015), and of small freshwater bodies. Information gaps in the data were filled with extensive field surveys (Alanen and Aapala 2015). The data included information on 4 900 hydrologically functional peatland entities, both protected and unprotected with a total area of 929 000 hectares, 3% of terrestrial area of Finland. Data on intensively drained peatlands and peat mining areas with no known biodiversity values were excluded from analyses as was the entire northern part of Finland, where the peatland PA network was considered as sufficiently extensive already.

Studies (III) and (IV) used a forest classification based on soil fertility (Cajander 1926) and the dominant tree species, including 20 forest habitat classes in total. This classification was used to distinguish between ecologically different forest environments both in the Dead Wood Potential (DWP) modelling in study (III) and in the SCP of study (IV). These data were combined from several data sources. These stand-level data underlying the modelling differ in their data types, resolution, or information they contain, varying from 16 metre grid to vector shapes with multiple hectare polygons. This is because they have been produced and updated in different ways to serve the needs of different data owners (Finnish Forest Centre 2015a; Metsähallitus 2015; Metsähallitus Parks & Wildlife Finland and Centres for Economic Development Transport, and the Environment 2015;

Natural Resources Institute Finland 2015b; 2015a). Therefore, when available data sources overlapped, the most detailed source was utilized. Due to computational limitations the original national-scale data layers were aggregated (summed) up to 96 metres, which is close to the average size of the forest stands. The 96m data retains all quantitative information but loses track of 16m grid cell position inside the 96m grid cells. The DWP data was developed for productive forest land, poorly productive forest land, and unproductive land, 26 M ha in total, 85% of terrestrial area of Finland. The increase in coverage is explained by the aggregation to 96 metres, which attaches also some non-forested areas, such as waters close to shore, to the final data.

The DWP in study (III) predicts the potential of the forest stand to host dead wood dependent species, which are a significant fraction of all forest-dwelling species (Siitonen 2001). The modelling was needed as there is no comprehensive data on forest biodiversity available in Finland. Dead wood was chosen as it is one of the most important, and also most usable, biodiversity indicators in forests (Lassauce et al. 2011; Gao et al. 2015). The DWP modelling utilizes data about forest stand characteristics: the size and volume of the standing trees and soil fertility. This kind of information about Finnish forest resources have been extensively collected for forestry purposes for decades already (Kangas et al. 2018). The DWP process also utilized forest growth simulations made with the MOTTI 3.0 software, which has been parameterized with the field sampled plot data of the Finnish National Forest Inventory (Salminen et al. 2005; Hynynen et al. 2014; Hynynen et al. 2015). As MOTTI simulates forest growth, it also simulates the gradual accumulation of dead wood, information that we used for converting forest stand data to a spatially explicit estimate of dead wood provision at present or in the future, the DWP.

DWP estimation was done separately for each stand. The output of DWP modelling included 168 different combinations of seven tree species, six forest site types, and four vegetation zones, as presented in Figure 3. The model treats separately trees that are larger than the average commercially managed trees. This is because large trees are often also older than average trees and forest age has been identified as an important factor supporting forest biodiversity (Siitonen 2001; Hyvärinen et al. 2019).

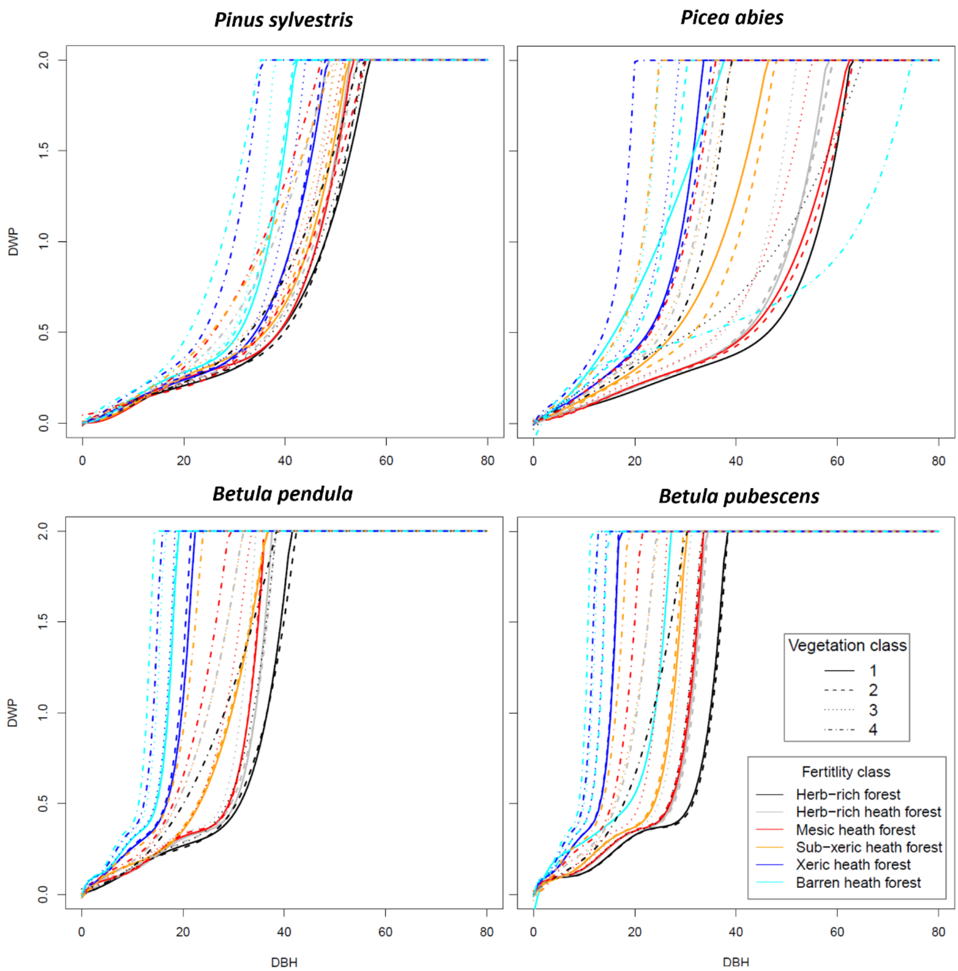


**Figure 3** The dead wood potential functions (see Mikkonen et al., 2018; Mikkonen et al., 2020) as a graph for the four most common tree species in Finland.

In studies (I) and (II), non-spatial information about habitats was used to weight them in the analysis: the national threat status of habitats was used in studies (I) (Ministry of the Environment 2007) and (II) (Raunio et al. 2008) and the national EU responsibility status for each habitat in study (I) (Ministry of the Environment 2007). This information includes EU-level expert assessment of the importance of habitats based on their history, present condition, and future prospects. At simplest, the more threatened the habitat is, the higher its weight is in the analyses. It should be noted though, that Zonation automatically accounts for the range-sizes of features, meaning that locations with relatively narrow-range species tend to get elevated priorities. Consequently, a narrow range alone is not necessarily reason for higher weighting in Zonation-based SCP.

### 2.3.2 Species data

Species observation data were used in studies (II) and (IV). In study (II) we used spatial observation data on red-listed vascular plants, mosses, birds, and other important indicator species that have peatland or forest marked as their main habitat type (Finnish Environment Institute 2014; Kareksela et al. 2020). In study (IV) we used data on all red-listed forest dwelling taxa except birds (Finnish Environment Institute 2015). The occurrences of characteristic peatland bird species were used independently in study (II) (Valkama et al. 2011). Additionally, the observations of all other taxa were used as an aggregate to minimize biases arising from small numbers of observations in studies (II) and (IV). Using species data, despite its well-known observation bias, is useful as every observation of a red-listed or otherwise important species is nevertheless an indication of known nature values at the site.

In all three SCP analyses non-spatial information about the species' national red-list threat status was used to modify weights used in analyses (Rassi et al. 2010; Hyvärinen et al. 2019). The more threatened the species was, the higher it was weighted in the analyses. This information is important in distinguishing between the importance of the habitats where the species have been observed.

### 2.3.3 Anthropogenic pressures

To complement biodiversity information, we used data on forest operations in reversed manner, effectively to develop metrics for the lack of naturalness. These data provide an estimate for the past negative human impact on biodiversity, and thereby providing information on the reduced ecological condition of a forest. For example, clear cutting causes a full-scale loss of the features typical to semi-natural forests: old trees, large trees, mixed stand structure, mixed tree species structure, and presence of old-growth forest specialist species (see, e.g., Hansen et al. 1991; Esseen et al. 1997). Drainage reduces the ecological condition of a peatland, as it starts drying and peatland species become gradually replaced by generalist forest species (see, e.g., Laine et al. 1995; Vasander et al. 2003).

In study (II) we utilized data on drainage of individual hydrological entities and in the landscape at large (Finnish Environment Institute 2011; Salminen 2013). In study (IV) we utilized data on the drainage of each pixel or site together with spatiotemporal information about commercial forest management (Finnish Environment Institute 2011; Finnish Forest Centre 2015a; 2015b; Metsähallitus 2015; Metsähallitus Parks & Wildlife Finland and Centres for Economic Development Transport, and the Environment 2015; Finnish Forest Centre 2017; Metsähallitus Forestry Ltd 2017). In both studies, data about past human activities were used for creating a spatially explicit (habitat) condition layer that was used to modify biodiversity layers in Zonation. Usage of condition layers may be critical for a well-informed analysis as is the case here with the negative effects of most forest management (see, e.g., Tikkanen et al. 2006; Hyvärinen et al. 2019).

### 2.3.4 Data on protected areas

Spatial information about protected areas was used in all SCP studies to represent existing limitations to land use imposed by the protection. These data are needed especially when planning the expansion of PA network – most interesting are the unprotected areas that would best complement the existing PA network, which was the case in studies (II) and (IV). Protected areas were used differently in study (I). There, the study area included only protected areas and the interest was in different levels of protection and how they correlate with biologically derived conservation priorities within the Natura 2000 network.

# 3 Results

The outputs from SCP analysis results include i) the ecological model, which are presented in Chapter (2). Material & methods, ii) the spatial priority ranking results, iii) the performance of each input feature, i.e., coverage of feature through the ranking, and iv) the end-products that are interpreted from the spatial maps. The latter (ii – iv) are discussed next.

## 3.1 The priorities within the Natura 2000 network

In study (I) we prioritized the Finnish Natura 2000 network using two versions of the analysis: either ignoring or accounting for the present conservation status of habitats (Figure 4, panel A and B, respectively). When conservation status is not accounted, the highest-ranked areas are those that contain a balanced set of rarest Natura 2000 habitat types in the most pristine state. Also, areas that are well connected to other Natura 2000 habitats areas are prioritized high as they provide a continuum of undisturbed environments for native species assemblages. High priority areas and their neighbourhoods are areas of high conservation relevance in terms of habitat maintenance and potential for habitat restoration. The performance curves from analysis that did not account for conservation status show that the top 25% of the Natura 2000 network includes approximately 90% of the biological values of Natura 2000 habitats, when averaged across habitats (Figure 4, panel C, red line). This is explained by the small distribution size of most of the Natura 2000 habitats. Related, areas that only host relatively widespread Natura 2000 habitats in variably degraded condition receive lowest priorities.

When conservation status is accounted for, the priority ranking is developed in stages, where a hierarchical order between protection levels forces the highest ranks to the most strictly protected areas and leaves lowest ranks areas with lowest protection levels. The most strictly protected areas cover 36% of the study area (Figure 4, Panel D, the highest priority areas before the first threshold). Forests are the only Natura 2000 habitat category with more than 50% distribution inside this protection category. Also, the performance curves of individual Natura 2000 habitats reveal that four Natura 2000 habitats only occur outside the most strictly protected areas (see Mikkonen & Moilanen 2023, S3). Less than 20% of the nature values of rocky and alpine Natura 2000 habitat categories are covered by the most strictly protected areas (Figure 4, Panel D).

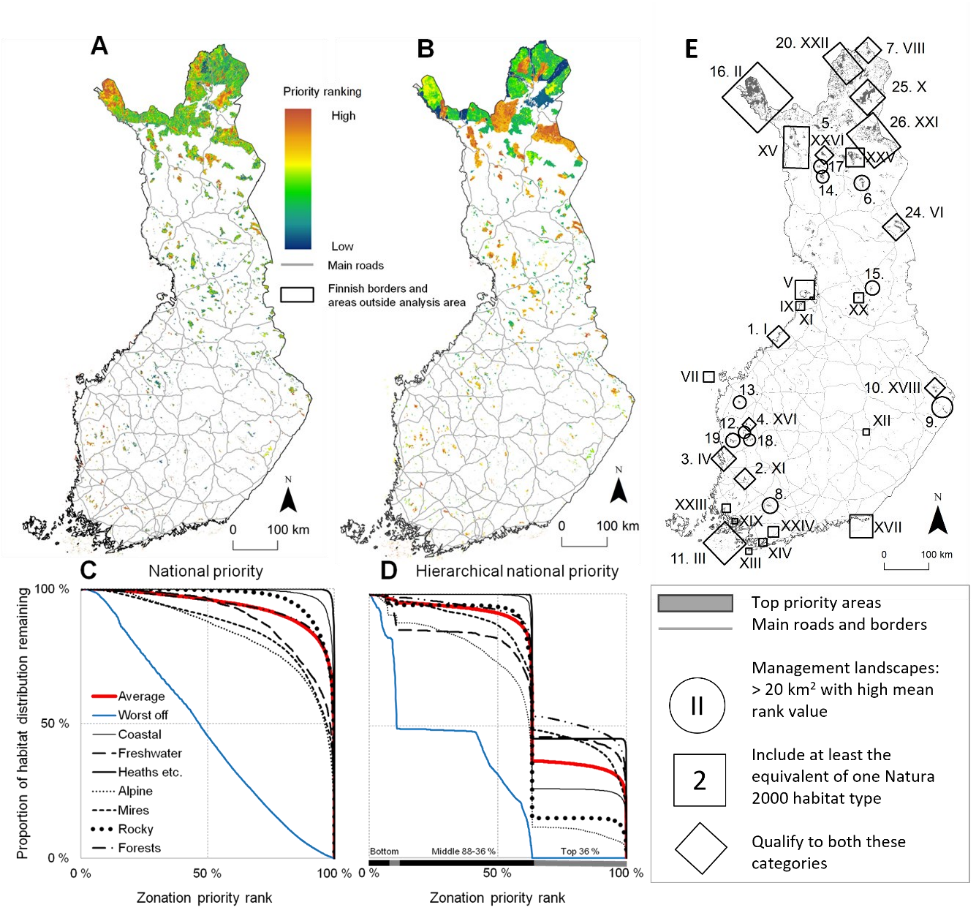


**Figure 4** Priority maps and landscapes for targeted management effort. Panel A: priority rank map of the Natura 2000 network in Finland. Colours show highest priorities in red and lowest in blue. Panel B: priority map of analysis that accounts for the conservation status of each area. Panel C: average performance curves for Natura 2000 habitat categories in prioritization where conservation status is not accounted for (map in panel A). Panel D. performance curves for prioritization where conservation status is accounted for (map in panel B). Panel E: The 36 priority landscapes identified from the analysis that did not account for conservation status (map in panel A). Landscapes indicated by squares and roman numbers each hold at least the equivalent of the full distribution of one Natura 2000 habitat type. Landscapes indicated by circles are large areas, over 20 km² in size, and were highly ranked in the analysis with mean rank over 0.87. Landscapes indicated by diamonds belong to both these categories. The numbering next to areas indicates their rank order, with highest ranked areas having smallest numbers.

Second, the final criteria were set for size, the mean rank value, and the sum of Natura 2000 habitat distributions. The count of landscapes was kept low enough to be practically useful. The final identification criteria were: 1) the landscape must be larger than 20 $km^2$ and its mean rank value must be more than 0.87, or 2) the landscape must hold at least the equivalent of the full distribution of one Natura 2000 habitat type. The criteria resulted important management landscapes that are i) large, high quality, and continuous, or ii) small with narrow-range, effectively rare habitats included. A few management landscapes met both criteria.

Two of the landscapes identified are exceptional at the national scale as they both contain habitats that are poorly represented elsewhere. At the western coast Vattajanniemi – Rahja (landscape No. I/1. in Figure 4, panel E) is a rather small region, 27 $km^2$, consisting of many distinct patches, where rare coastal and dune habitats co-occur. It includes 14 Natura 2000 habitat types with 50% + of the distributions of five Natura 2000 habitat types. The mean rank value of the region is 0.982 and the summed distribution value 11.6, both very high.

In the far north-west is Kilpisjärvi region (landscape No. II/16. in Figure 4, panel E) which is a large and spatially continuous area, 1870 $km^2$. It provides an aggregated and unfragmented continuum of high-quality environments varying from freshwater, to fell, peatlands, forests, and rocky habitats. It contains 17 Natura 2000 habitats with 50% + of the distributions of five Natura 2000 types. The mean rank value of the region is 0.954 and the summed distribution value is 11.1. It is worth noting that regions that contain widely distributed Natura 2000 habitats, like western taiga, aapa mires, alpine and boreal heaths, or nordic subalpine / subarctic forests with *Betula pubescens* ssp. *Czerepanovii*, must also contain habitats with narrow distributions to be chosen as a management landscape. This is the case in Kilpisjärvi. In comparison, e.g., the Pallas-Ylläs National Park (landscape No. XV/23, 318 $km^2$, in Figure 4, panel E), is ranked lower because while it includes occurrences of 15 Natura 2000 habitats, most of these are widely distributed ones.

## 3.2 Areas for the most effective expansion of the existing peatland protected area network

In study (II) we identified the most effective and well-balanced expansions to the Finnish peatland PA network (Figure 5), both nationally and regionally. Site selection was done hierarchically, to facilitate identification of unprotected areas that best fix gaps in and complement the existing PA network. The SCP analysis showed that a ~100 000 ha area expansion would bring major increases to nature values covered by the network (Figure 6). This 100 000 ha was eventually taken as the target for the Complementary Mire Protection Programme.

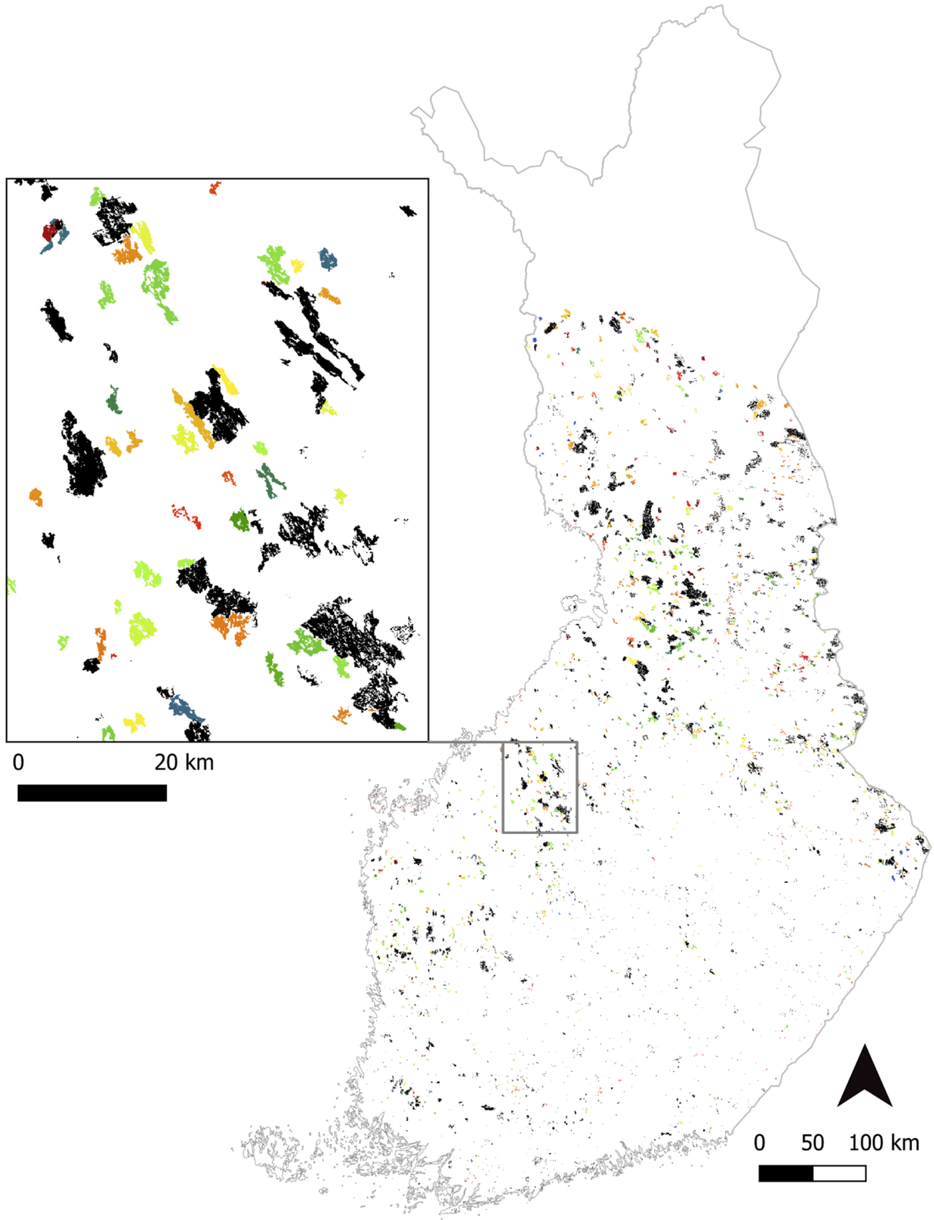


**Figure 5** Prioritization result concerning Finnish peatlands

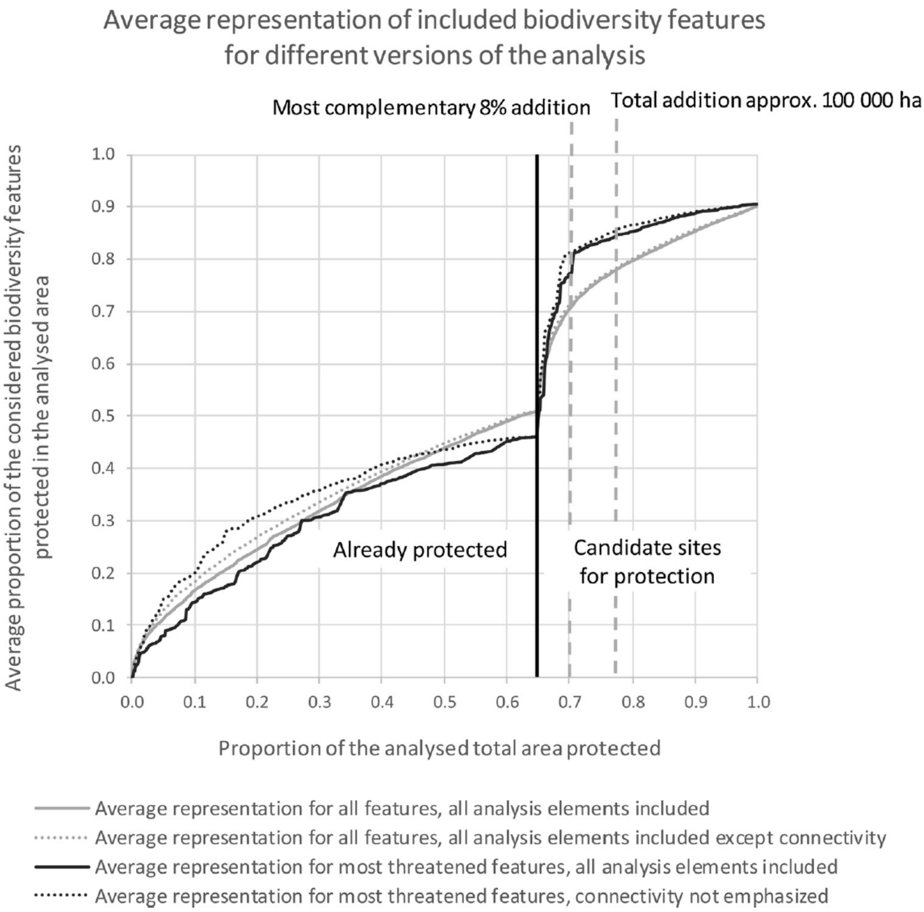


**Figure 6** The average performance of input feature groups: grey line = all features and connectivity; grey spotted line = all features, no connectivity; black line = most threatened features including their connectivity; black spotted line = most threatened features, no connectivity. Vertical lines present (from left to right): the division between presently protected and unprotected areas, the most balanced and effective 8% addition to analysis, and the 100 000 ha expansion targeted.

According to the results of study (II), the most effective and high-quality expansion corresponded to 8% of the area of the peatland PA network at the time (Figure 6, left vertical dashed line). This expansion scheme provided a significant improvement to the existing PA network: protection coverage of all biodiversity increased on average 39% and 68% for the most threatened peatland complexes and habitats. From the perspective of peatland restoration, areas with reduced hydrological condition, i.e., areas drained for forestry and agricultural purposes, were ranked high only if they hosted one or more highly weighted peatland complexes and/or habitats. In this study, up to 78% of the candidate peatland areas were considered to be in need of restoration. The candidate expansion area filled the biodiversity protection gap by adding five completely absent features and twelve features with weak representation to the peatland PA network. This complementarity-based addition increased the mean fraction of features distributions covered from 0.45 to 0.69.

The candidate area that corresponded to the optimal 8% increase based on Zonation analysis was approximately 1/3 of the proposed additions. The remaining 2/3 were chosen based on the highest points awarded by an expert-based scoring (Figure 6, right vertical dashed line). In the end, 755 peatland entities, total of 117 000 ha, were suggested to be protected by the Complementary Mire Protection Programme.

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The studies (III) and (IV) concern prioritization of forest conservation. Due to the extensive work involved, it was divided into two parts: 1) modelling of the biodiversity indicator used for in the prioritization: the Dead Wood Potential and 2) the SCP analysis itself.

## 3.3 The model for forest biodiversity value: Dead Wood Potential

The modelling of forest biodiversity produced 168 different models that were fitted to each forest in Finland, accounting for the tree species observed, the mean diameter at breast height and volume for each tree species, and forest site fertility. Analysis resolution was based on forest stands and 16 x 16 metre grid cells. The estimates of Dead Wood Potential were then used as surrogates for forest biodiversity in SCP. These index values reflect the long-term potential of forest stands to provide suitable habitats for dead wood dependent species. Importantly, the index values should not be considered as absolute-scale predictions of the amount of the dead wood and the individual DWP layers are not intended to be used independently. Rather, their full potential becomes revealed in SCP analysis, which seeks balance and representation over all input biodiversity feature layers simultaneously. Here in study (IV), the balance is sought over different types of forests and major vegetation zones.

The national Dead Wood Potential maps were calculated for 42 forest types, which were combinations of seven tree species and six soil fertility classes, for example pines growing in mesic heath forest (Figure 7). These maps were further compressed into 20 forest type layers. This was because remote sensing techniques used in forest mapping produces less detailed information about tree species occurrence and developing harmonized data across the whole country is important to avoid data-quality based biases and uncertainties in SCP analysis.


**Figure 7** A Dead Wood Potential map of pines growing in mesic heath forest (soil fertility class 3) The darker the map is the higher the DWP is. © Finnish Environmental Institute, National Land Survey of Finland

## 3.4 National high-resolution conservation prioritization for boreal forests

The results of study (IV) support expansion of the forest PA network, and land use planning and zoning, and biodiversity-friendly forest management in general. The seven versions of the national forest SCP analyses aimed at identifying forest areas that host many natural forest features (Figure 8). Such include old forests with multiple tree species, that are structurally diverse and rich in various kinds of dead wood and hence dead wood dependent species. The maps and associated information provide information about the importance of each forest patch or larger area in terms of local ecological quality and connectivity.

The results of study (IV) show that there are high conservation priority forest areas all over Finland, but their distribution is highly fragmented (Figure 8, Panel A I). Increasing connectivity requirements elevates priorities in the Northern Boreal zone, where the forest PA network coverage is higher elsewhere in Finland. Correspondingly, lack of connectivity reduces priorities in the Southern Boreal Zone (Mikkonen et al 2023, appendix F, Table F.1.). Depending on analysis version, the top 10% of the landscape contains from 49% to 88% of the conservation values recognized (Figure 8, Panel B), a significant fraction of which lie outside the current protected area network (Figure 8, Panel B, directed blue line). Areas of greatest interest are the unprotected areas that would complement the present PA network with the most effective addition. These areas correspond to the steep portion of the dashed black line in Figure 8, Panel B.

Figure (8) shows how the present PA network, and its expansion can be contrasted to what could be achieved, if the PA network was implemented from scratch. This is done by contrasting constrained (analysis version 7) and unconstrained (analyses versions 1- 6) analysis. The constrained analysis uses hierarchic analysis structure, which forces unprotected areas to lower priorities than areas already protected. The optimal PA network expansion can be identified from this analysis: observe the steep "step" in the performance curve. The unconstrained analysis does not use the hierarchic structure, meaning areas can be chosen whether or not they are protected. The constrained and unconstrained analyses are compared in terms of biodiversity coverage they achieve with selected area size. Here, to achieve the same coverage of biodiversity than available from unconstrained analysis, a 6% increase of area should be added to the present forest PA network: observe the level of the curves on the y-axis on Figure 8, Panel B, light blue dotted lines.

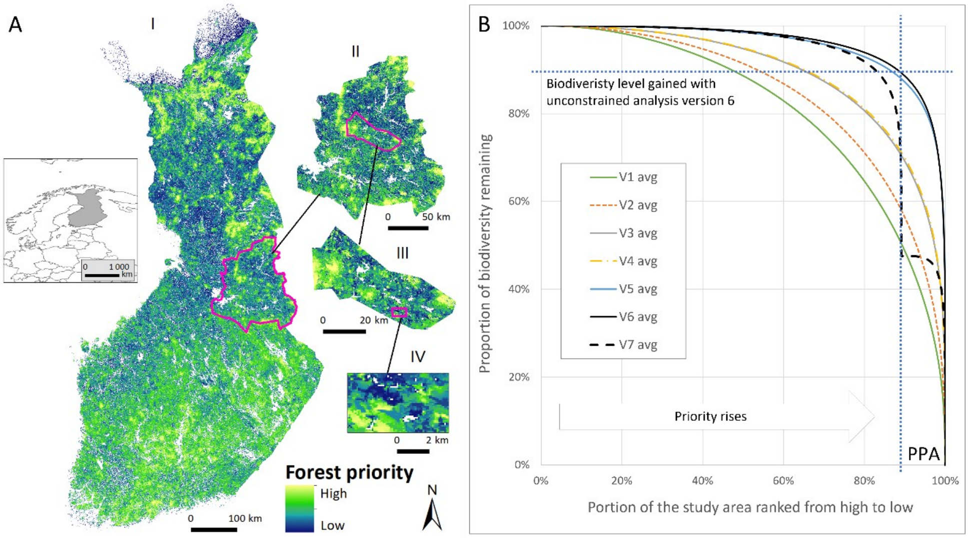


**Figure 8** Panel A: a map of forest conservation priorities across Finland, analysis version 6 including zoom-ins at the regional, communal, and local levels. Version 6 includes DWP indices, forest management with negative impacts on biodiversity, observations of red-listed forest species, connectivity within the forest landscape, and connectivity to protected areas. Panel B: the mean Zonation performance curves of analysis versions 1 – 7. PPA = area equivalent to permanently protected areas. © Natural Earth, Finnish Environment Institute, Finnish Forest Centre, Metsähallitus

The maps provided by study (IV) can be freely used by experts and decision-makers for several different purposes. The need for additional ground verification needs to be considered, as the data behind these SCP analyses is mostly modelled and the forest landscape can change rapidly due to ongoing forest management. These maps and their derivatives have since been used, e.g., to help with zoning, for the identification of new conservation areas, for identifying areas that maximize biodiversity values in forestry when leaving retention trees onto a forest stand, finding new areas for outdoor hiking during Covid -19, and the modelling of natural riverine habitats and brooks.

# 4 Discussion

This thesis illustrates three ways how to use SCP approach for combating biodiversity loss by strengthening the national PA network. We have analysed differences between areas both inside and outside the PA network, and we have identified the most efficient and balanced additions to it. To secure biodiversity requires identifying and maintaining the ecologically most valuable areas inside the PA network by, e.g., enhanced management, expanding the network, and changing land-use to more nature friendly in the network matrix (European Commission 2020; Gustafsson et al. 2020). This thesis provides useful methodologies and spatial information to support all these aims. The results, including a detailed description of the planning processes and new spatial data, provide national-level spatial information that would not have been available otherwise to help to slow down and even stop the biodiversity loss in Finland.

The results of this thesis reveal the significant differences between areas in their contribution to biodiversity. The difference can be up to many hundred-fold which is not surprising if one just compares a semi-natural forest to a recent clearcut (Siitonen 2001; Penttilä et al. 2004; Roberge et al. 2018). In this thesis, the most ecologically efficient additions to the existing PA network have been identified for peatlands (Kareksela et al. 2020) and forests (Mikkonen et al. 2023b). Additionally, the most important areas to be maintained in the long term within the Natura 2000 network (Mikkonen and Moilanen 2013) and peatlands that most urgently need restoration (Kareksela et al. 2020) were identified. As a by-product, we found high-priority areas that are poorly connected to PAs and other high-priority areas. These areas might benefit from expansion, buffering with light land use, or increased connectivity so as to maintain their biodiversity values (Mikkonen et al. 2023b). Areas with high conservation priority but with no possibility for protection identified in study (IV) provide potential locations for applying biodiversity-friendly management practises. While not the same as protection, biodiversity-friendly management would maintain or even improve the functional connectivity of the PA network with consequent biodiversity benefits (Koivula and Vanha-Majamaa 2020; Kuuluvainen et al. 2021).

This thesis provides information from fragmented to continuous landscapes and for different decision-making levels. The results underline that there is no one-size-fits-all conservation planning solution that would suit for all habitats, species, and ecosystems. The degradation, fragmentation, and loss of natural habitats have impacted biodiversity in various ways (IPBES 2018; 2019), which is especially the case within the forest and peatland environments in studies (II) and (IV). Land-use planning is always a challenging compromise, where the ecological requirements of multiple taxa and anthropogenic pressures must be considered simultaneously (Virtanen and Moilanen 2023). Consequently, different analysis versions for different levels of decision-making may be required (Henle et al. 2014).

The present work highlights the importance of addressing planning questions that arise from considering rarity, habitat quality, area, and aggregation (Hodgson et al. 2011; Kukkala and Moilanen 2013). However, sometimes individual decisions may need to be made on individual areas, such as conservation network parcels, peatland areas, or forest stands here. In such cases, consideration of local habitat quality, the main determinant of species distributions, becomes increasingly important (see, e.g., Hodgson et al. 2011). Yet, local habitat quality and other factors like connectivity, may bring contradicting priorities to the planning table. The spatial and quantitative data provided by the present SCP analyses enable conservation planners to identify the situations in which increasing connectivity is a priority action, possibly even at the expense of local quality as in study (IV). (Arponen et al. 2013).

It is important to remember that biodiversity depends also on unprotected or less protected areas (Pressey et al. 2007; IPBES 2018; Santangeli et al. 2023). This is likewise where the European Union Green Deal 2030 aims at: protecting 30% of landscape by 2030, of which 10% strictly and 20% with some restrictions to usage (European Commission 2020). This target can be achieved in many ways (Hermoso et al. 2022), and in study (IV) we identified the most important areas for forest biodiversity both with and without connectivity, as the PA matrix has a key role in maintaining biodiversity and connectivity in the network. From the biodiversity perspective we should allocate protection more evenly, because, e.g., when considering the principle of representativeness (Kukkala and Moilanen 2013), even extensive protection of the biodiversity in Northern Finland does not substitute for the highly sparce PA network in southern Finland and the species and environments with notably different ecological conditions therein (see also Kotiaho et al. 2021). Based purely on areal measures, the state of forest conservation in Finland may appear better than what it is in ecological terms. This is partly because the poorly productive and unproductive land-areas have often been counted as forest PAs (Kulju et al. 2023). At the same time, the most productive and hence ecologically more diverse areas have been subject to intensive commercial forest management (Korhonen et al. 2021). Thus, protecting forest biodiversity in Finland requires elevated attention to protection of additional forest areas with diverse tree species and layered structure, large trees, and high volume. As an example, if all provinces of Finland had equal fractions of land in forest conservation networks, the Finnish national conservation outlook would be significantly different from the present outlook (Mikkonen 2013; Mikkonen et al. 2018; Forsius et al. 2023).

## 4.1 From idea to results and their implementation

All the three SCP analyses were custom-made with different intended uses. The commitment of stakeholders has been previously identified as a key component for the results usage by, e.g., Sinclair et al. (2018). This was also recognized here: the more committed the stakeholder involvement in the project group and supervision was the more the results have typically been used. There are, however, several other factors that we have observed during these years that may influence the utilisation of SCP results (Table 4).

**Table 4** Promoting and opposing factors for the usage of SCP results. Scale: ++ strongly promoting, + promoting, - opposing, -- strongly opposing

| Factor | Explanation | Study I | Study II | Studies III + IV |
|---|---|---|---|---|
| Need | Is there an immediate need for these results? | + | ++ | ++ |
| Momentum | Are there the right people in right places that enable the effective utilization of the results? Or is someone opposing the use of the results? | +/-- | ++/-- | ++/-- |
| Funding | Is the financier favorably disposed towards the ecologically based decision-making process? If so, resources would be provided for the implementation of the prioritization results. | ++ | ++ | ++ |
| Commitment | Are the people in the project group committed to the aims of the SCP project? | ++ | ++ | ++ |
| Multisectoral cooperation | Is there multisectoral interaction, feedback, and co-operation in the planning process? | | ++ | ++ |
| Open science | Is there a common understanding about how the planning is done, who is doing it, and how one can suggest improvements in the analysis model? Are there data, that fulfills the requirements, available for doing the SCP analysis? Are model inputs and outputs adequately openly available that transparency can be ensured? | + | ++ | ++ |
| Skills | Do the end-users have some GIS skills and interest / confidence in quantitative, data-driven analysis? | -- | | ++/-- |

Study (I) was planned and done by the authors with limited supervision from the commissioning stakeholder. It was a pilot study with no a-priori agreed upon usage, which was reflected as high interest on the results per se, but with relatively low commitment to operative use of the results. Nevertheless, these analyses have paved way for later SCP studies, which have now become part of, for example, targeting of habitat restoration in PAs by Metsähallitus (Kareksela et al. 2018).

Study (II) was the opposite: the ecological model for the analysis was right from the start designed in close cooperation between the working group and experts in ecology and spatial prioritization. This work and the analysis it included is a good example of how conservation is usually implemented through a political programme that provides a framework for meeting conservation needs in the area of concern. The Complementary Mire Protection Program had a target that had been agreed in a political process, and the participants were committed to the planning process. The size and impact were impressive in the scale of Finland. Resources for executing the programme were available; for field work, SCP, and land acquisition (see Table 4). The stakeholders and working group were engaged to achieve the common target and the work was supported by operational division of responsibilities between experts, project lead, stakeholders, analysts, and field workers. Eventually, there was a clear goal to expand the PA network with 117 000 complementary peatland hectares in the following year and 31% of the proposed expansion areas were chosen following the study (II) (Alanen and Aapala 2015; Kareksela et al. 2020). Eventually, program was cancelled at the political level and turned into voluntary based (Salomaa et al. 2018), which resulted in only 1% of protection on private land compared to what the original target was. By 2021, about 63 700 ha of peatlands included in the programme still remained unprotected, and forested parts of some of the peatlands had been clearcut (Aapala et al. 2021).

Although the implementation of the Complementary Mire Protection Program was interrupted, there are various benefits that have nevertheless come from the work:

- The SCP process made stakeholders active participants by bringing everyone to the same table to decide together on the targets and details on the ecological model and how to improve the model together. The SCP process increased transparency, interaction, and communication, as expected (Luyet et al. 2012). Hence, the effort was a positive example for the future.
- Although many of the valuable peatlands were not permanently protected, the proposed peatlands on state-owned land, covering 36,000 ha, were. The rest of the peatlands were classified as high biodiversity value areas that should be saved in the future, if possible, e.g., in regional plans (Aapala et al. 2021).
- The METSO programme was updated so that also forest-peatland mosaics could subsequently be purchased with METSO funds (Koskela et al. 2016). This was not possible earlier, as METSO was at restricted to forested areas only. Later, in 2021, a voluntary HELMI habitats programme was established to, among other things, to complete the Complementary Mire Protection Program (The Finnish Government 2021).

- Following major reductions in PA network expansion, other ideas were developed for the improvement of the state of peatland biodiversity in Finland. These included i) paying attention to the hydrological state and delineations of the current PAs (Halme et al. 2013), ii) systematically diverting surface waters back to peatlands that have dried up due to forest drainage in the surrounding areas (Autio et al. 2018), iii) restoring peatlands within and outside PAs (Kareksela et al. 2021), iv) implementing additional measures in accordance with the Nature Conservation Act and Forest Act in order to secure the peatland habitats and species, and v) more careful consideration of the biodiversity of peatland environments in agriculture, forestry, and land use planning.
- In the context of the Complementary Mire Protection Program, a significant loss of conservation efficiency was demonstrated if all land use decisions are uncoordinated and voluntary (Nieminen et al. 2021). The subsequent public discussion made the lack of efficiency of voluntary conservation more widely understood.
- As usual, the SCP process showed that some relevant information was missing, and resources were later directed to correcting those deficiencies. For example, distribution data for herb-rich peatlands, which are the most productive, most species rich, and the most threatened peatland habitats have since been updated (Kokko et al. 2021).

The breadth of participatory in studies (III) and (IV) was something between the previous two: the supervisory group was actively participating in the planning of the analyses and the SCP analyst group had a stronger role compared to study (II). However, there was no clear specification of how the analyses would really be used other than by providing 'useful information for land use decision-making'. There was no jointly agreed target in hectares for conservation and no additional funding to cover forest acquisition. There was also uncertainty of who can use the maps, and how they will be used. These factors have led to divergence in the use of the results – some find them useful and use them a lot whereas others appear to not value this type of information much.

As the present studies show, there is some information about the effects and impacts the studies and their results have had on real-life decision-making, including the development, maintenance, and expansion of the national PA network and consequent effects on biodiversity (Sinclair et al. 2018). A comparison between prioritization results and new PAs or green landscape corridors in regional (zoning) plans does not provide a 100% guarantee that specifically the present results have indeed steered land use decisions. While the data and analyses were the best possible at that time, they were not able to include all potentially critical considerations such as all locally available information relevant for stakeholders (Kujala et al. 2013). And even if they would have, only data in study (I) was publicly open to everyone, delimiting the potential of the use of the results and other information that was obtained in the process. This is because not all data can be fully open, as, e.g., some threatened species are at risk of overutilization by people.

Making the most out of SCP analyses requires their integration into wider decision-making. The potential users of this thesis range from individual landowners to regional planners, the environmental administration, and national, or even global audiences. Making data openly available allows unexpected developments to happen that can increase the impact of our work significantly (Wilkinson et al. 2016).

## 4.2 Scale and resolution

All the analyses here were done at the national scale, but the results are used locally for land use decision-making. Thus, a question of the necessity of national-scale analysis arises – why is it important? First, the analyses were commissioned by the stakeholders, whose interests are at national level: Metsähallitus Parks & Wildlife and Ministry of the Environment. Second, the key issue is often the development of the ecological model. The data might be easily developed for the whole area instead of focusing on just one region, which expands the scope of results beyond one locality. Third, priorities are not a locally determined outcome. Rather, they are about the locality compared to what would be available elsewhere. Relativity can only be established if data is available from a larger area, regionally, nationally, continentally, or globally.

A broad spatial scale brings about the challenge of accounting for large-scale variation in environmental conditions and availability of comprehensive data. The former impacts habitats and species when going from the warm south to the relatively cold north. To correct for this trend, DWP was in study (III) modelled for four vegetation zones separately. There is also the issue of nationally uneven conservation coverage between south and north, which in the case of Zonation can be considered by combining regional and national priorities, as done in study (II). As a drawback to regional analyses, edge effects can appear at the borders of provinces, where connectivity may be reduced due to lack of data from outside the study area. As a solution, national scale analysis eliminates such edge effects at the borders of provinces, but edge effects may still be present at the national border.

The latter challenge has been discussed within all three Zonation-study approaches as there typically are no comprehensive data with sufficient quality. If extensive analysis need to be urgently executed, as in the analyses in this thesis, we need to combine best possible available data that are apparently similar but may differ with respect to data collection methods. In studies (I) and (IV) this included especially dealing with uncertainties that arise from remote sensed data compared to ground-surveyed information (Mikkonen et al. 2021 and Chapter 4.3). In contrast, in study (II) the uncertainties involved the dissimilarities between ground-survey instructions performed for regional planning and Complementary Mire Protection Program. If the assignment would have been restricted to cover only a certain part of Finland, or specific habitats, the data management, model development, validation, and dealing with uncertainties would have very likely been easier. However, using a spatially or biodiversity content wise narrower analysis framework would have reduced the importance of the results for the overarching nature conservation planning and knowledge development. Thus, often in SCP applications this kind of priority decisions needs to be made between using the best possible data available and analysis coverage and in case of the studies; in this thesis this decision was done by the commissioning stakeholders.

The other relevant spatial dimension is analysis resolution, which may affect the results of SCP significantly (Arponen et al. 2012; Tanhuanpää et al. 2023). This is the case especially when combining coarse resolution data with narrow distribution biodiversity features: when resolution gets coarser the priorities of areas where these features occur, decline drastically. This is simply because rare features, such as herb-rich forest types, big aspen trees (*Populus tremula* L.), or large density spots of dead wood are in Finland distributed scattered through the landscape (Kivinen et al. 2020; Korhonen et al. 2021). Averaging occupancy over a large spatial unit effectively loses track of the relevant presence of the feature. Consequently, spatial analysis resolution should be fine enough so that narrow-range features can be covered at the scale relevant for land use planning. At the time of developing the study (IV), the 96 metre analysis resolution was seen as adequate for decision making, because this resolution is close to the average size of a forest stand. This has been later seen as too coarse a resolution, because high value forest patches (woodland key habitats, etc.) can be so small, fragmented, and dispersed that 96 metre resolution analysis does not identify these areas ideally. This is the case especially in southern Finland, where land use and ownership is very fragmented (Mikkonen et. al. manuscript). It is also noteworthy, that at the time Zonation 4.0 was also not well able to analyse Finnish national data at a higher resolution higher than 1 ha, but this limitation has been lifted in Zonation 5 (Moilanen et al. 2022).

## 4.3 Managing the uncertainties in the initial data and in the SCP outputs

The SCP analysis development process should by default involve an assessment of uncertainties. These can arise from scarcity of data, assumptions of modelling, and lack of relevant ecological knowledge. In the studies included here, the most important uncertainties were recognized as missing data in all studies, uncertainties inherent in statistical modelling in study (IV), properties of the preliminary data collection method in all studies, use of surrogates instead of direct information about individual species or habitats in studies (II) and (IV), and uncertainties around different components of connectivity especially in study (IV).

The most evident missing data are species and habitat data. The species data have been collected for decades, but these data are often very biased. Therefore, species data were used as one or several aggregated and weighted data layers in studies (II) and (IV) to overcome this matter. The habitat data are more demanding as there was no open-for-all data storage outside protected area network. Natura 2000 areas were selected for study (I) as there is a general aim for gathering the information on habitats for them; even so, some data issues exist especially within data recording methods. In study (II) missing habitat data were collected from a set of focal peatlands which leaves many peatland habitats incompletely recorded.

With national scale analyses, as studies (I) – (IV) are, the quality of results are best assessed against national validation data. Independent validation cannot always be done immediately, and therefore some compromises need to be accepted, expert knowledge needs to be utilized, and field controls executed before final conclusions can be made. The good news is that the highest priorities have less uncertainty than areas with low priorities (Kujala et al. 2018a; Kujala et al. 2023), which simplifies usage from the conservation perspective. Nevertheless, we underline the importance of independent validation and openness during and after the SCP process.

Here the greatest attention to uncertainties was given in studies (III) and (IV) due to the use of forest site type fertility information and modelled biodiversity data, the DWP, and perceived lack of statistical validation (Kangas and Mehtätalo 2021; Mikkonen et al. 2021). These studies were developed based on the ecological understanding within the project group, ground survey feedback from forestry and nature conservation experts all over Finland and validated with high-quality data from the current PA network managed by Metsähallitus Parks and Wildlife Finland (Mikkonen et al. 2018). What was missing at the time of the studies were commonly acknowledged modelling method for forest biodiversity value and randomized national-scale validation data that would have allowed statistical validation for the modelling and analysis. The most fertile and rare forest site types are also the most threatened habitats and uncertain in the source data. Additionally, MOTTI algorithm had known challenges to simulate forest growth in natural forests due to the limited occurrences in Finland. Yet, had to be used in the modelling as it was seen as the most prominent option by the time of study execution. In addition, the decision to combine comprehensive forest data from multiple data sources was seen convenient as the results were thought to be meaningful and available for the landowners and administrative personnel only. Thus, although past ground surveys have commonly verified a good match between the SPC outputs and actual forest stand biodiversity values, e.g., between threatened polyphore species in spruce dominated forests in southern Finland and analysis in study (IV) that does not include information on red-listed forest species observations (Mikkonen et al. manuscript), some high-quality areas were missed, or in some cases areas with low in situ values had been given high priority ranks. A very obvious reason for such a mismatch is that some areas had been managed (clearcut) after the spatial analysis was conducted. What was also found was that the resolution of 96 x 96 metres was too coarse to be able to identify fragmented high conservation value forest parcels especially in southern Finland (Mikkonen et al. manuscript). Despite sporadic misses, the outcomes of analysis (IV) have generally been considered useful and relatively unbiased, and they have been used as reference data for forest biodiversity several times. Later, after gaining access to the 12$^{th}$ National Forest Inventory data, collected between 2014-2018 (Korhonen et al. 2021; Natural Resources Institute Finland 2022), a strong positive correlation was found between the results of study (IV) and on-the-ground observation of forest naturalness condition (Figure 9).

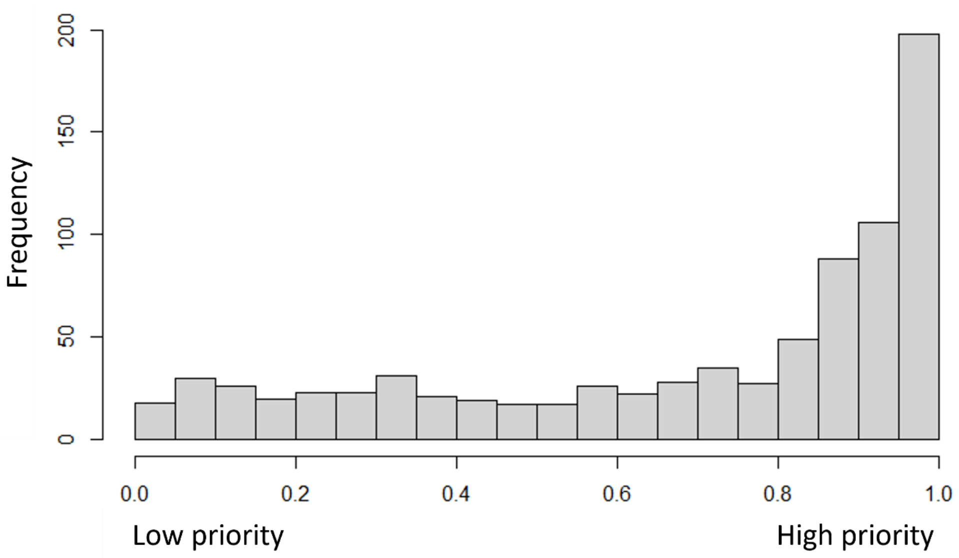


**Figure 9** Validation of results in study (IV) with ground-surveyed plot data from the Finnish National Forest Inventory No. 12 (Korhonen et al. 2021; Natural Resources Institute Finland 2022). Study (IV) is represented by version 6, which includes information on Dead Wood Potential, forest management with negative impact on biodiversity, soil drainage, observations of red-listed forest species, and connectivity within forest areas, to key forest habitats, and to permanent PAs. The validation data, National Forest Inventory data, includes one-time survey plots on forest land (annual growth > 1.0m$^2$ / year) evaluated by two naturalness criteria: naturalness of the structure of growing stock and the naturalness of the dead wood continuum. With both criteria, only locations with the classification of 'natural or almost natural' were included in the comparison. The validation shows a strong positive correlation between study (IV) and on-the-ground observation of forest naturalness, suggesting that SCP analyses can provide information valuable for planning.

## 4.4 Future directions

The SCP planning approach is likely to be used also in future, as the limits of the nature have been crossed a long time ago (IPCC 2019) and the resources for the establishment of PAs remain scarce. Updating old SCP analyses, such as studies (I), (II), and (IV), will be important, as the environments are in continuous change. The studies presented here provide a platform upon which the continued development of improved analyses for future needs can be build. Also, a wider selection of digitized biodiversity information is becoming freely available with a growing pace (Tammilehto et al. 2024 and Finnish Biodiversity Info Facility in https://laji.fi/en), which paves way for the fast updating of missing data.

Actually, the SCP approach is used in developing regional biodiversity action plans in Finland by 2028 (Metsähallitus 2023). The ecological model built in studies (I), (II), and (IV) will be sieved through to enable identification of the "regional biodiversity hotspots". The most advanced development by now is in study (IV) where new modelling method for forest biodiversity has been accomplished to avoid the challenges that came through with using MOTTI forest simulator. Issues concerning comprehensive data has not been solved but luckily there has been considerable development as regards to available and detailed open data on forest attributes. The resolution in the analysis will be higher which will serve the needs of very fragmented high biodiversity value parcels in the forest landscape.

As a global theme, SCP analyses need to be developed to consider also changing climate (Carroll et al. 2010; Jones et al. 2016) and the attempts to mitigate it (Gibson et al. 2017); in essence, the development of the PA network needs to account for ecosystems that are in rapid change (Nila et al. 2019; Määttänen et al. 2023). Relevant to the present work, adding different connectivity metrics to SCP analyses may help consider forthcoming changes in the PA network. Additionally, SCP approach can be linked with habitat restoration planning to target restoration measures into locations that most effectively mitigate the past habitat loss (Kareksela et al. 2018) that is threatening the survival of species globally (IPBES 2018).

Obvious future expansions of the present work include application to habitats and ecosystems that have not yet been studied with SCP approach, including freshwater and wetland ecosystems (excluding peatlands). Their integration to SCP analyses would be important, because these environments host many specialist species (Heino et al. 2009) and wetlands play a crucial role in climate change mitigation (Moomaw et al. 2018). Integration of major habitat types within SCP is important, as environmental impacts do not necessary limit themselves to the habitats where they occur. For example, there is also a strong connection between forest management, water quality, and biodiversity in freshwater and marine environments (Hyvärinen et al. 2019; Kontula and Raunio 2019). One can envision combining information about the Natura 2000 network (I) with the mires of study (II), forests in study (IV), and expanding further to include, e.g., marine biodiversity (Virtanen et al. 2018) and semi-natural traditional rural biotopes (Raatikainen et al. 2017). Where data allow, opportunities for habitat restoration can be built in (Kareksela et al. 2018). Societal factors including threats to the biodiversity existence can be added into the analyses, as was recently done for wind farms on marine areas (Virtanen et al. 2022). Overall, participatory processes that integrate many major habitat types and different types of conservation actions will catalyse interaction, joint understanding, and transparent argumentation between different administrative levels and various stakeholders.

As a major application area, the studies within this thesis can easily be used to support planning of ecological impact avoidance in land use zoning, urban development, and infrastructure planning. For example, in Finland, the results of studies (II) and (IV) have been used for biodiversity action plan in Pirkanmaa and Kymenlaakso regions (Kontula et al. 2021; Pirkanmaan elinkeino- liikenne- ja ympäristökeskus and Pirkanmaan maakunta 2022, Kontula et al. 2024) and previous forest SCP analyses have been used for regional zoning in the Uusimaa region (Kuusterä et al. 2015; Jalkanen et al. 2020). The key to ecological impact avoidance is: stay away from high-priority biodiversity areas and place development into low priority areas. Doing so requires high-quality data and high-quality SCP analyses to begin with (see, e.g., Kareksela et al. 2013 on peatlands), so that there is adequate confidence into the quality of the priority maps. Also, even if negative impacts cannot be fully avoided, these analyses can potentially help in finding promising candidate areas for ecological compensation (see, e.g., Moilanen et al. 2020 for forested areas), in which ecological losses from development can be are compensated by habitat restoration and new protected areas (IUCN 2016; Moilanen and Kotiaho 2018).

# 5 Conclusions

This work provides information on how we can identify areas that are important for biodiversity, and where they are. We find major differences between areas and highlight habitat quality as a primary consideration in conservation planning. We also demonstrate trade-offs between connectivity and locally high-quality areas, which is an important question as species may need to shift their distribution ranges as climate warms. Simultaneously, everyday land use decisions gradually modify our landscape. Assessments on the state of biodiversity show alarming results amplifying the need to do better decisions than previously. The SCP methods developed here can help in ecologically based land use planning including conservation and management, impact avoidance in development, and land use zoning. The crucial question is whether these methods or results are to be used or are things just getting forward with business as usual – with no comprehensive framework or joint target. Will halting biodiversity loss be a cross-cutting object in societies similarly to climate change before it is too late?

To be able to answer to the needs of the society, SCP processes would ideally utilize large amounts of different types of data and joint effort to produce the best possible models, estimations, or in this case, SCP analyses. Data has critical impacts on analysis and results. Requiring detailed ground-survey data strongly reduces the areas from which data will be available. Thus, remote sensing and modelled data will have a crucial role in developing spatially comprehensive, wall-to-wall information for studies conducted at landscape, national, continental, and global levels. In the future, we will need improved modelled data about species and habitat distributions. However, models and analyses will not be achieved without first obtaining comprehensive ground-survey data that can be used in developing the models and their validation. Open data principles are critical for future data availability and accumulation, in SCP and elsewhere, and there we will need everyone’s participation.

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