

This is a self-archived version of an original article. This version may differ from the original in pagination and typographic details.

Author(s): Mikkonen, Ninni; Leikola, Niko; Lehtomäki, Joonas; Halme, Panu; Moilanen, Atte

Title: National high-resolution conservation prioritisation of boreal forests

Year: 2023

Version: Published version

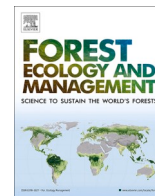
Copyright: © 2023 the Authors

Rights: CC BY 4.0

Rights url: <https://creativecommons.org/licenses/by/4.0/>

Please cite the original version:

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



National high-resolution conservation prioritisation of boreal forests

Ninni Mikkonen^{a,b,*}, Niko Leikola^a, Joonas Lehtomäki^c, Panu Halme^{d,e}, Atte Moilanen^b

^a Finnish Environment Institute, Latokartanonkaari 11, FI-00790 Helsinki, Finland

^b Faculty of Science, Department of Geosciences and Geography, P.O. Box 64, FI-00014 University of Helsinki, Helsinki, Finland

^c Department of the Natural Environment, the Ministry of the Environment, P.O. Box 35, FI-00023 Government, Helsinki, Finland

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

^e School of Resource Wisdom, P.O. Box 35, FI-40014 University of Jyväskylä, Jyväskylä, Finland

ARTICLE INFO

Keywords:

Biodiversity
Connectivity
Conservation planning
Dead wood
Ecological decision-making
Forest biodiversity
Land use planning
Zonation software

ABSTRACT

The continuous decline of forest biodiversity highlights the importance of the development of cost-effective and ecologically sustainable land-use planning approaches. Spatial conservation prioritisation (SCP) can be regarded as a useful tool for this challenge. We produced high-resolution, national scale SCP analyses to identify unprotected forest areas that host valuable forest biodiversity. We used stand-based modelled dead wood potential (DWP) data as a primary surrogate for conservation value. In addition, data on forestry operations that have negative impacts on biodiversity, connectivity between forest areas, the observations of red-listed forest species, connectivity to forest habitats of special importance for biodiversity, and connectivity to permanent protected areas were included in the analyses. Analyses addressed the estimation of present value and that of future potential following increases in connectivity. The results show that there are high conservation priority forest areas all over Finland although their distribution is highly fragmented. Depending on the version of the analyses, the best 10% of the landscape contains from 49% to 88% of the conservation values, a significant portion of which lie outside the current protected area network. Consequently, as biodiversity continues to decline in Finland and as most of the Finnish forest area is under commercial management, the current protected area network cannot be expected to halt the ongoing decline of forest biodiversity. Therefore, these analyses provide much-needed information for decision-making. They are a pragmatic tool for the planning of forest conservation networks and commercial management of forests at regional and national scales.

1. Introduction

Land use is a main direct threat driving biodiversity loss (IPBES, 2019). Habitat fragmentation, loss, and degradation due to land use changes have intensified and expanded during the recent centuries and are predicted to continue in the future (Sala et al., 2000; Butchart et al., 2010; Pereira et al., 2010; IPBES, 2018, 2019). As a consequence, some ecosystems are assessed to be already beyond their sustainable living boundaries (Newbold et al., 2016). Land loss is linked to the development of humankind to the present state. It has also brought forth a shared global target that remaining nature should be secured and rapidly improved (European Commission, 2020; CBD, 2022).

It has become clear that the present conservation network alone cannot halt the ongoing decline of biodiversity (UN, 1992; Johnson et al., 2017; IPBES, 2019). This is partly because individual conservation areas have been established partly based on other than biological

reasons (see, e.g., Myers et al., 2000; Brooks et al., 2006; Pouzols et al., 2014). They are often also poorly connected to the broader conservation area network (Ward et al., 2020). Management outside protected areas plays a key role for forest biodiversity: as forestry, bioeconomy and conservation share an interest on forests (Blattert et al., 2022), these should be planned together (Pressey, 1994; IPBES, 2019; Jung et al., 2021).

Boreal forests (or Taiga) is the largest land biome on earth. It is essential for the northern biota and has been broadly used by humans (Niemi, 2005). Today, intensive forestry, including logging and other silvicultural practices, is the major form of land use that impacts northern European boreal forests (Gauthier et al., 2015; Kuuluvainen and Gauthier, 2018). The total amount of biomass in European forests has increased due to climate change and commercial management (Kohl et al., 2015; Mäkinen et al., 2021; Kulju et al., 2023). Also, several structural forest features have turned positive (Henttonen et al., 2019;

* Corresponding author at: Finnish Environment Institute, Latokartanonkaari 11, FI-00790 Helsinki, Finland.

E-mail address: ninni.mikkonen@syke.fi (N. Mikkonen).

Korhonen et al., 2021), but forest biodiversity is still declining in many places (Kouki et al., 2018; Hyvärinen et al., 2019; IPBES, 2019). Therefore, spatial conservation planning and prioritisation is needed to effectively maintain the biodiversity of boreal forests (Moilanen et al., 2005; Jung et al., 2021).

One of the most important habitats for biodiversity are forests where anthropogenic impacts are absent or minimal, hereafter called natural forests (Watson et al., 2018). These forests were dominant in the Boreal region thousands of years ago, which is why many forest species are adapted to them (Wallenius et al., 2010). Natural forests can be up to hundreds of years old and are structurally more diverse than managed forests. This is because the disturbance-succession cycles in natural forests vary from fine scale tree mortality to large scale stand replacing disturbances (Kuuluvainen and Aakala, 2011), which promote uneven-aged, multi-layered, and spatially patchy habitats. Also, the species networks and assemblages are comparatively complex in natural forests (Hansen et al., 1991; Esseen et al., 1997). Nevertheless, natural and semi-natural forests have become globally rare (Watson et al., 2018; IPBES, 2019; Korhonen et al., 2021), and they tend to experience habitat loss, fragmentation, and habitat degradation outside conservation areas (Kouki et al., 2001; Kouki et al., 2018).

Finland, situated in the Boreal forest zone, is 75% forested (Kulju et al., 2023). According to the assessments of the present state of species and habitat types in Finland, 76% of forest habitats and 9.8% of species living in forests are threatened (Hyvärinen et al., 2019; Kontula and Raunio, 2019). The main causes for this are: 1) reduced amount of dead wood, 2) reduced cover of old natural forests and old and large trees, and 3) changes in tree species composition. These pressures are interconnected as they usually occur concurrently (Hansen et al., 1991; Mönkkönen et al., 2022). For example, only four percent of natural forests remain in Finland (Korhonen et al., 2021). Improvements for features important to biodiversity, including the number of large trees and dead wood volume, are far from the ecologically effective (Mönkkönen et al., 2022). What follows is that biodiversity loss in Finnish forests is a particularly direct consequence of the degradation of forest environments and the fragmentation of suitable forest patches (see, e.g., Haddad et al., 2015; Hyvärinen et al., 2019; Kontula and Raunio, 2019). Species and habitats are more threatened in more intensively managed regions compared to less managed regions (Hyvärinen et al., 2019; Kontula and Raunio, 2019). Additionally, 64% of the area of forested mires has experienced drainage to promote forest growth. Consequently, also mire biodiversity has been impacted as the drainage has turned 7% of them into mineral soils (Korhonen et al., 2021) and it is the main reason for mire species and habitats decline (Hyvärinen et al., 2019; Kontula and Raunio, 2019).

The core of the forest conservation toolbox is the permanently protected forest area network, where no forestry is allowed. This network covers 2.3 M ha (10%) of forests in Finland and 0.76 M ha (33%) of these areas are situated in productive forest land (forest growth more than 1 m³ per ha per year) and the remaining 1.5 M ha (66.7%) is situated on poorly productive forests (forest growth between 1 and 0.1 m³ per ha per year) and unproductive land (forest growth below 0.1 m³ per ha per year) (Kulju et al., 2023). The Finnish conservation area network is strongly biased towards the colder and less productive North (Kulju et al., 2023) and the biodiversity of southern Finland has experienced more decline than the north (Virkkala and Rajasärkkä, 2007). As an addition to permanently protected areas, there are 1 M ha (4%) areas where forestry measures are somewhat restricted (Kulju et al., 2023). Less than 0.2 M ha (0.9%) of these are small forest patches protected by the Forest Act, called key forest habitats, that are classified as “habitats of special importance to safeguard the biodiversity of forests” (Forest Act, 1996, updated 2013; Ministry of Agriculture and Forestry of Finland, 2015; Kulju et al., 2023). These key forest habitats supplement the permanent protected area network as they host similar species richness and dead wood volumes than natural forests (Häkikilä et al., 2021). However, their conservation status can change over time and

commercial forest management is allowed in some of these areas (Pykälä, 2004, 2007; Olden et al., 2019; Siitonen et al., 2021; Kulju et al., 2023). Forest certification schemes are used to promote ecological sustainability in forestry, as they define, e.g., valuable forest environments, buffer zones around watersheds that should be left unmanaged, and the amount of retention trees to be left standing in management. According to Kuuluvainen et al. (2019) and Punttila (2020), the certifications are insufficient to achieve ecological sustainability of forest management from the perspective of biodiversity. In addition to all of these, non-monetary voluntary conservation can also benefit forest biodiversity (Santangeli et al., 2012; Santangeli et al., 2016).

The information used for nature-friendly forest management planning should be appropriate, up-to-date, and at the correct scale for the needs of decision-making, as stand-level data is for forest management planning (Arponen et al., 2012; Čosović et al., 2020). This calls for utilising information and data initially collected for other purposes and also use of surrogates as there are rarely data collected solely on conservation purposes (Sarkar and Margules, 2002; Chirici et al., 2012; Vihervaara et al., 2017). Dead wood is a good surrogate variable to be used in forest conservation planning: it is a good indicator for many forest-dwelling species groups, it is easy to recognize on site (Similä et al., 2006; Lassauce et al., 2011; Gao et al., 2015), and dead wood volume is one of the most significant differences between managed and natural forests (Siitonen, 2001; Aakala, 2010; Junninen and Komonen, 2011; Korhonen et al., 2021). Dead wood, in all its forms, provides resources and microhabitat diversity that support up to 75% higher species richness of saproxylic species in natural boreal forests compared to managed forests (Siitonen, 2001; Paillet et al., 2010). A recently developed method enables the estimation of the dead wood potential (DWP) of each stand (Mikkonen et al., 2020) to be used in optimization of forest conservation.

The assessment of biodiversity for land-use planning can utilize a group of methods called spatial conservation prioritisation (SCP) (Margules and Pressey, 2000; Moilanen et al., 2009b; Kukkala and Moilanen, 2013). These methods can integrate spatial and non-spatial data on habitats, species, and possibly ecosystem services, human impacts (e.g., habitat condition, threats, pressures), costs, and information on ecological dynamics (e.g., connectivity or interactions) to identify priority areas for sustainable land use and nature conservation (Moilanen et al., 2009b; Kukkala and Moilanen, 2013; Kujala et al., 2018a). These methods, including the Zonation software used here (Moilanen et al., 2009a; Lehtomäki and Moilanen, 2013; Moilanen et al., 2014; Moilanen et al., 2022), are powerful decision support tools by which information of even thousands of spatial features can be integrated, analysed, and distilled into spatial maps to enhance the transparency and objectivity of large-scale land use planning. Overall, the approach very much relies on the availability of high-quality spatial data and ecological knowledge.

Here we utilize SCP analysis to combat further forest degradation from biodiversity perspective by identifying areas that could support threatened, near-threatened, and data deficient forest species, hereafter called red-listed forest species. We report our approach for high-resolution assessment and prioritisation of forest conservation values across a national extent. We focus on identifying high conservation value forest areas that display the elements of natural or old-growth forests such as several tree species and especially deciduous tree species, have an uneven-aged structure with plenty of decaying wood. In addition, we focused on forests that are well-connected to valuable forest landscapes. We present collation and modifying of data and modelling of new data for the computational spatial prioritisation analysis. We interpret the results, the priority rankings, and discuss their use in conservation and land use planning at different scales. The analyses were performed to help the operations of the Forest Biodiversity Programme for Southern Finland (METSO) which pays compensation for land owners who voluntarily protect areas of ecologically valuable forest (The Finnish Government, 2008, 2014).

2. Methods

2.1. Study area

The study area covered the forested land area in Finland, excluding the autonomous Åland Islands. The forested areas include productive and poorly productive forest land, and unproductive land. These have respective areas of 20 M ha, 2.6 M ha, and 3.1 M ha, altogether 26 M ha, 85% of the terrestrial land area of Finland. Of this area, 67% are mineral soils and the remaining 33% is peatland (Kulju et al., 2023).

2.2. Analysis process

The conservation values of Finnish forest were studied with a spatial conservation prioritisation (SCP) process (e.g., Lehtomäki and Moilanen, 2013).

2.2.1. Definition of the prioritisation objective

The objective for the prioritisation was to develop spatial prioritisations that can assist the METSO programme to make well-informed decisions about acquisition of forests for protection. The results are also aimed to be useful for other actors interested in forest conservation or biodiversity friendly forest management, including regional councils and cities responsible for land use zoning. We focused the prioritisation on the most threatened forest types and areas that display some or many elements of natural forests: more than one and preferably more than two tree species, forest structure that present else than even age structure or a history of clear cut harvesting, and the amount of dead wood that exceed the volume of dead tree material in managed forests (starting

from non-existing) and reach preferably quantities that can be found in natural forests (more than hundred cubic metres). From the perspective of connectivity, these areas should be situated close (varying from metres to a few kilometres) to other valuable forest areas. These kinds of forest areas represent the most threatened forest types and forest species in Finland (Hyvärinen et al., 2019; Kontula and Raunio, 2019).

2.2.2. Collecting and formatting data

Our SCP analyses were made with modelled biodiversity surrogate data based on quantitative and qualitative tree stand data, together with additional information about past forest management and loss of forests, observations of red-listed forest species, and multiple connectivity components. To represent these factors, we used 15 different datasets, including spatial and non-spatial data, openly and unopenly available, and custom-made data. Data coverage ranged from point observations to complete, national, high-resolution GIS data (Table 1. and Appendix A). Multiple datasets are needed, because there is no single high-quality data source that would fill our analytical needs (Chirici et al., 2012; Tuominen et al., 2017). National datasets are needed for national SCP analyses. To achieve adequate national coverage, we combined data from different sources (Table 1, data classes I, II, and IV). By this we wanted to 1) maximize data accuracy, 2) avoid data gaps in connectivity calculations, and 3) make sure that the analysis covers the entire country.

All of the spatial data were processed with GIS operations to the analysis resolution, which was 96 m (0.92 ha), aggregated up from 16 m grids (6x16 metres = 96 m), which is used in the Finnish National forest inventory data (Mäkisara et al., 2016) and Forest management inventory data (Kangas et al., 2018; Suomen metsäkeskus, 2021), and

Table 1
Spatial and non-spatial data used in analysis, see Appendix A for more detailed description.

Data class	Variables	No.	Name of the data	Type	Owner of the data and reference
I Stand data	Tree species, mean diameter at breast height, volume, forest site type	1	SutiGIS data on state-owned areas	vector	Metsähallitus 2015
		2	SutiGIS data on privately owned protected areas	vector	Metsähallitus Parks & Wildlife Finland, Centres for Economic Development Transport and the Environment 2015
		3	Forest Management Inventory data (FMI)	vector	Finnish Forest Centre 2015a
		4	Multisource National Forest Inventory data (MS-NFI)	raster	Natural Resources Institute Finland 2015b
		5	Multisource National Forest Inventory data on the species-specific diameter at breast height	raster	Natural Resources Institute Finland 2015a
II Forestry operations	Forestry management operations with negative impact on biodiversity: e.g., ditching and harvesting	1, 2, 6	SAKTI Protected area biotope information system: drainage of forest stands	vector	Metsähallitus 2015, Metsähallitus Parks & Wildlife Finland and Centres for Economic Development Transport and the Environment 2015, Metsähallitus Parks & Wildlife Finland, The Ministry of the Environment's Administrative Branch 2017a, 2017b
		1, 7	SILVIA forestry resource and planning system: executed forest management operations since 1997 and drainage of forest stands	vector	Metsähallitus 2015, Metsähallitus Forestry Ltd 2017
		8	Forest use notifications	vector	Finnish Forest Centre 2015b, 2017
		9	Drainage status of peatland	raster	Finnish Environment Institute 2011
		3	FMI: drainage of the stands	vector	Finnish Forest Centre 2015a
		10	Global Forest Loss	raster	Hansen et al. 2013
		11	Observations of red-listed forest species in Finland	vector	Finnish Environment Institute, 2015
IV Conservation areas	Location	3	Habitats of special importance for biodiversity (Forest Act 10 §) (considered as non-permanent conservation areas)	vector	Finnish Forest Centre 2015a
		1	SATJ protected area information system	vector	Metsähallitus Parks & Wildlife Finland, 2018
V Penalties	Negative impact on biodiversity	12	Expert assessment on the impact of forest management on biodiversity	text	Mikkonen et al., 2018
		13	Condition layer: ecological penalties due to forest management operations	raster	published here
		14	Ecological similarity matrix for connectivity calculations	text	Mikkonen et al., 2018
VI Connectivity	Ecological similarity between tree species and forest site type combinations	15	Ecological similarity matrix for connectivity calculations	text	Mikkonen et al., 2018
VII Validation	Location	12	SATJ protected area information system: herb-rich forests and old pristine forests	vector	Metsähallitus Parks & Wildlife & The Ministry of the Environment's Administrative Branch 2021

considering the average size of a forest stand (approximately 1 ha in Finland) as it is the typical decision unit in forestry. Overall, data fulfilling our analytical requirements were available for 30.8 M grid cells (28.4 M ha) but part of this is, e.g., waters due to expanding the data to 96 m resolution.

2.2.2.1. Modelling of new data. We used modelled dead wood potential (DWP) as a surrogate of the threatened forest biodiversity in Finland (Mikkonen et al., 2020). DWP is an estimation of the potential of a stand for hosting dead wood dependent species. The potential is increased when the stand can be expected to produce more dead wood and more varied dead wood in terms of size and tree species composition. For example, productive and comparatively wet forest habitats produce more dead wood than dry and low-productivity sites.

The DWP was calculated for each stand or pixel based on the forest data (data Class I): tree species and tree stock quantities (mean diameter at breast height and volume), soil fertility (Cajander, 1926), and location. The modelling is based on forest growth and increase of dead wood calculated with Motti forest simulator 3.3 (Salminen et al., 2005; Hynynen et al., 2014; Hynynen et al., 2015) for 168 combinations of seven tree species, six forest site types, and four vegetation zones. The model separates trees that are larger than average commercially managed trees, as these are often also older than average trees and the forest age has been identified as an important driver for forest biodiversity (Siitonen, 2001; Stokland et al., 2012; Hyvärinen et al., 2019; Nirhamo et al., 2023). The size information is combined with stand volume and forest site type. See Appendix B for modelling details and C for modelling behaviour.

2.2.3. Ecological model and spatial conservation prioritisation

We implemented prioritisations with the Zonation software 4.0 (Moilanen et al., 2005; Moilanen et al., 2009a; Moilanen et al., 2011), which produces a nested hierarchical priority ranking of spatial units (here 96 × 96 m grid cells) over the landscape of interest. The analysis is an iterative process where in each iteration the relatively least important remaining spatial unit is removed from the analysis and thus the most important units are retained last. The removal order produces a priority rank for each spatial unit and, eventually, a priority rank map that

covers the full area. Importantly, the process is based on complementarity of biodiversity between spatial units: Zonation tracks the decline of each input feature throughout the prioritisation, which information is used to maintain balance between features (Kujala et al., 2018a; Kujala et al., 2018b). With multiple analysis versions, the greatest interest is on those areas that repeatedly receive high ranks – these areas are important from all perspectives included in analysis. For further explanation and updated methods, we refer the reader to Moilanen et al. (2022).

The ecological model of conservation value. In the ecological model (Fig. 1) we detailed how we can identify the targeted forest areas with seven successively more complicated prioritisation versions. There are two main reasons why multiple analyses are needed. First, it enables the evaluation of the impact of every addition of new major data and / or structural analysis features (Kujala et al., 2018a; Kujala et al., 2018b). Second, some analysis variants are informative from alternative perspectives. For example, both regional and national priorities may be needed by authorities with different regional / national responsibilities.

The seven analysis versions start from a local perspective and then evolve towards regional and national levels (following Lehtomäki et al., 2009). Each new analysis version included everything that had been included in the previous simpler versions. The versions are 1) local estimation of the conservation potential of the forests based on tree stock alone, 2) local estimation with additional information about forest management and drainage, 3) landscape level (not local but not regional either) estimation with internal forest connectivity, 4) landscape level estimation with additional information about observations of red-listed forest species, 5) landscape-level estimation with added short distance connectivity to key forest habitats, 6) regional estimation with added long distance connectivity to permanently protected areas, and 7) regional estimation of the most appropriate addition to the present conservation network. The regional level analyses can be used for national inspection. Our approach to prioritisation of forest conservation values is an extension of earlier, smaller scale and less accurate SCP analyses for Finnish forests (Lehtomäki et al., 2009; Leinonen et al., 2013; Lehtomäki, 2014; Lehtomäki et al., 2015; Mikkonen et al., 2018). See Appendix B for data preparation in each step and Appendix D for detailed Zonation analysis setup.

ECOLOGICAL MODEL OF THE CONSERVATION VALUE		COMPUTATIONAL PRIORITIZATION
Analysis versions	Modelling, spatial data, GIS preprocessing, and expert assessments	Zonation Spatial conservation prioritization analysis features used
Version 1: Biodiversity value based on trees	Biodiversity features: modelled dead wood potentials of tree species and forest site types	A balanced (complementarity based) priority ranking for many biodiversity features simultaneously
Version 2: Biodiversity value with management information	Version 1 + expert assessment of forestry operations with negative impact on biodiversity	Condition layer
Version 3: Connectivity between high biodiversity value forest areas	Version 2 + ecological similarity of biodiversity features	Matrix Connectivity
Version 4: High biodiversity value forest areas with species observations	Version 3 + observations of IUCN red-listed forest species	Positive interaction connectivity
Version 5: Connectivity to key forest habitats	Version 4 + quality of habitats of special importance for biodiversity (Forest Act 10 §)	Positive interaction connectivity
Version 6: Connectivity to permanently protected areas	Version 5 + quality of permanently protected areas	Positive interaction connectivity
Version 7: The most effective addition to conservation network	Version 6 + sites of permanently protected areas	Hierarchical analysis mask

Fig. 1. Construction of analyses 1–7. Analysis versions were nested with subsequent versions containing the previous and adding data (middle column) or prioritisation operations (right column). The first meaningful version for real use is the version 2.

Analysis version 1 describes biodiversity value based on quantitative information on trees alone. There we used only the DWP for each type of stand as inputs. The DWP data were processed to 20 national input layers, which come from combinations of four tree species and five forest site type groups (Table D.1.). The principles of combining and aggregating data are described in Appendices A (reasoning for the use of the data), B.1 (technical details) and C (model details). This was a default Zonation analysis that produced a balanced, complementary based, priority ranking without any specific adjustments. This first result is useful for verification of analysis development, but should not be used for conservation planning, as several factors of ecological relevance are missing.

In version 2 biodiversity value was updated with information about past (or planned) forest management that is known to have a negative effect on biodiversity (Lehtomäki et al., 2009; Hyvärinen et al., 2019; Kontula and Raunio, 2019). Technically, this was done by using a condition layer that penalized areas that have experienced such management (Leathwick et al., 2010). We combined the spatiotemporal information on forest management with an expert assessment on the impact of forest management on biodiversity (data No. 13 in Table 1), which resulted in a penalty layer for use in the Zonation analysis (data No. 14 in Table 1). The penalty layer combines information about soil drainage, nationally tracked obligatory forestry use notifications (available since 1997), which report the location and quality of forest management to authorities, and information on forest loss based on satellite data (Data class II in Table 1). The effects of forest management actions on biodiversity were defined based on time since management and accounting for the intensity and frequency of management (Appendix B.2, Formula B.1, Table B.1.). This procedure is critical for a well-informed analysis, as most management has a clear negative impact on biodiversity (see, e.g., Hyvärinen et al., 2019). The management itself aims at increasing tree stock, which is the main interest of forestry (Skovsgaard and Vancley, 2008). Mean diameter at breast height and the volume of the trees also are two quantities utilized by the DWP modelling. Forest management actions with only positive or neutral impacts on biodiversity are rare and poorly monitored, but their impacts were nevertheless included in DWP modelling as they contribute to changing the forest structure towards uneven aged multispecies forests.

The analysis version 3 moves towards the landscape level where species are dependent also on the quality and accessibility of their surroundings, i.e., ecological connectivity. Contiguous high biodiversity value forest areas were identified across the landscape by taking into account local forest quality (the penalized DWP), ecological similarity, and the distance between forest patches. This was done by using an analytical technique called matrix connectivity, which combines a declining-by-distance connectivity response with information about the ecological similarity of forest types (Appendices A, data No. 15, and B.3, Table B.2.) (Lehtomäki et al., 2009). Overall, the priorities of semi-continuous forests of high local value become elevated compared to the rest of the landscape.

In the analysis version 4, observations of red-listed forest species were used to elevate priorities in areas where they have been observed (Appendices A, Data No. 11., and B.4). This serves two purposes. First, it elevates priorities near locations with confirmed observations of red-listed species. As a negative, an observation bias is introduced, which needs to be accounted for in the interpretation of the results, as the observation effort for species has not been even across the country. Despite the bias, a confirmed red-list observation is preferable to no observation. Second, observations of red-list species may reveal if planned management has been left undone. Information about biodiversity may reach the landowner only after making the forest use notification, which in many cases change management plans or even cancel management in some areas to reduce impacts on important species (Arnkil, 2020). The red-list observations were added as an input layer in which each observation was weighted based on the species IUCN threat status (Appendix B, Table B.3.).

In the analysis versions 5 and 6 we investigated regional and national priorities with connectivity to the key forest habitats and protected area network added (Table 1. data No. 1, 3, and 12, Appendix A). In both cases, we used positive interaction connectivity in which the quality of the site, here protected area or key habitat patch, impacts its surroundings (Rayfield et al., 2009; Arponen et al., 2012). In other words, high-quality focal sites act as positive connectivity sources. For site quality we used a standard Zonation output called *weighted range-size rarity map of inputs* (Moilanen et al., 2014). In this implementation, local occurrence levels of all input features in focal patches influence nearby connectivity. The higher biodiversity density in focal patches, the stronger the connectivity effect will be, which allows distinguishing between the importance of source areas in the connectivity calculation. A short mean connectivity decay distance of 200 m was used for key forest habitats as they are small-sized areas by definition, like springs or rivulets. Species that do not require large areas but merely high local quality such as many lichens or aspen (see, e.g., Kivinen et al., 2020; Nirhamo et al., 2023) this was seen as adequate distance. For larger permanently protected forest areas that measure in square kilometres, the mean decay distance was 2000 m (Appendix B, B.5). This refers to the requirement of species such as Siberian flying squirrel (Selonen and Hanski, 2004), Siberian Jay (Pukkala et al., 2012) or Capercaillie (Storch and Segelbacher, 2000). We highlight that species distribution capabilities vary (see, e.g., Nathan and Muller-Landau, 2000; Norros et al., 2023) and therefore there is no right answer on this.

The most balanced and efficient addition to the present Finnish conservation area network was investigated in **analysis version 7**. So-called hierarchical analysis was used to produce a two-stage hierarchy in prioritisation, in which the ranking is divided between protected areas and the rest of the landscape (Leathwick et al., 2008; Mikkonen and Moilanen, 2013). This allows gap analysis and the identification of a set of new areas that complement existing forest conservation areas in an efficient and balanced manner.

The validation of the analysis process was based on investigation of priorities in forest areas with conservation value that is known from empirical observation. Validation results demonstrate good performance of the ecological model and SCP process in finding new candidate areas for conservation. Also, the value of using the most accurate data for each site is shown. See appendix B for more details.

3. Results

The two basic Zonation results are priority rank rasters and performance curves. The priority rank rasters show the priority rank order of areas (Figs. 2 and 3 and Appendix E). Performance curves quantify how much of the biodiversity is included within each top or bottom fraction of the landscape (Fig. 4). Changes in priority rank rasters and performance curves show the effects of adding new data or analysis features into analysis.

In these analyses the high conservation value areas are typically (see Fig. 3 yellow high priority areas) less managed forests with many large trees (high DWP), many tree species (high biodiversity), and situated in a region where little forest management has taken place (low penalties and fragmentation, high internal connectivity). If these areas are located close to known high conservation value forest areas (best protected areas) or red-listed species had been observed on site, the area is ranked even higher. (See panel E as an example of this in Fig. 3). In converse, areas with low priorities are typically managed, monocultural areas of a common forest type with small volumes of wood and little dead wood. (See panel A as an example of this in Fig. 3.).

When examining the performance curves, the fraction of biodiversity features is the highest in the initial situation where no cells have been removed in the optimization, i.e., the full landscape (Fig. 4). When only a fraction of the landscape is placed under conservation, only a fraction of biodiversity values will be maintained for certain, as the rest of the landscape is under commercial management. Areas are not at all equal

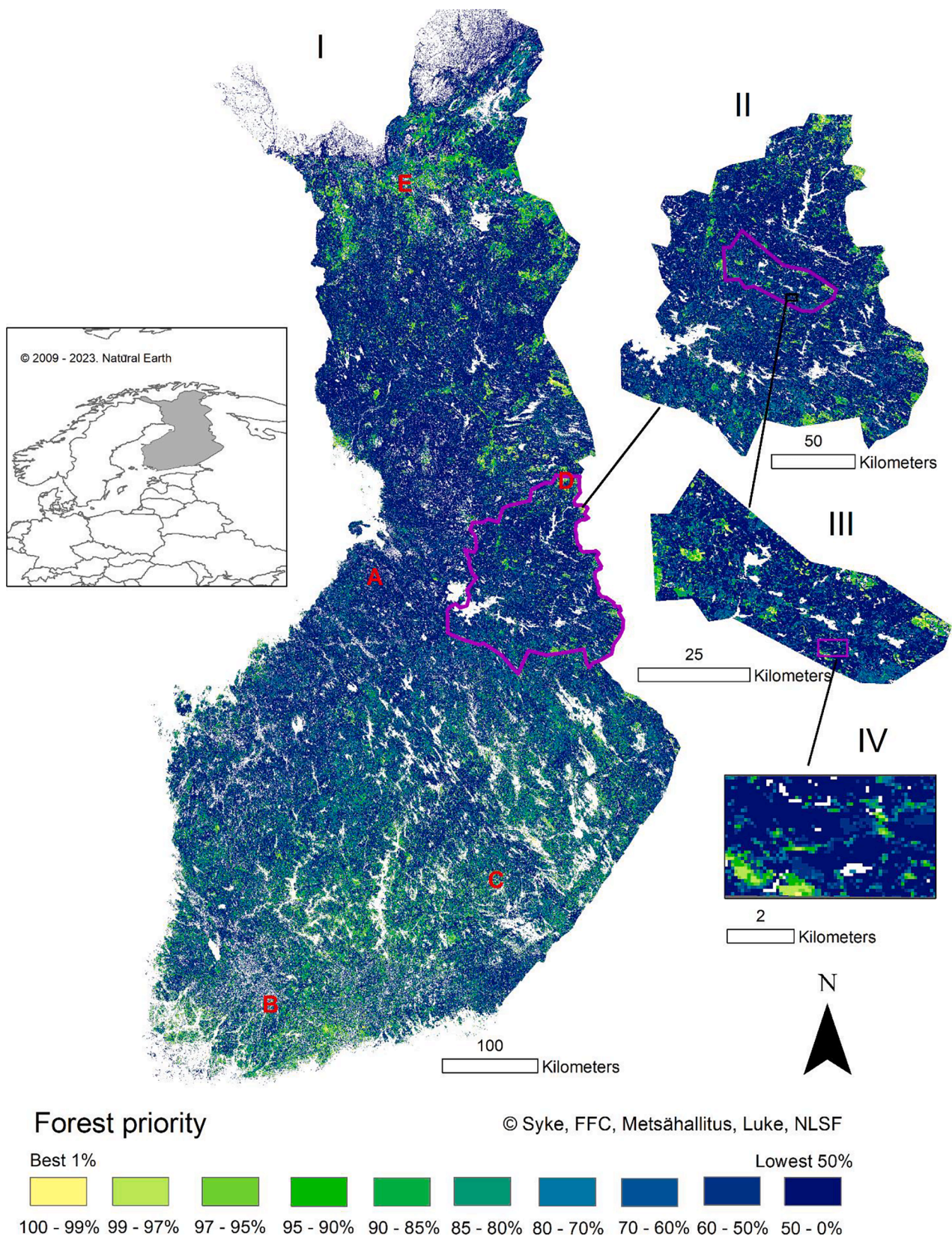


Fig. 2. Maps of forest conservation priority in Finland on different scales: 1) national, 2) regional (the region of Kainuu), 3) municipality (The Municipality of Hyrynsalmi), and 4) local. National-scale prioritisation provides information concerning the distribution of the national forest conservation network. The regional and municipality scales help to understand regional green infrastructure. The local scale provides information relevant for individual landowners. The red letters A–E indicate the locations shown in Fig. 3. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

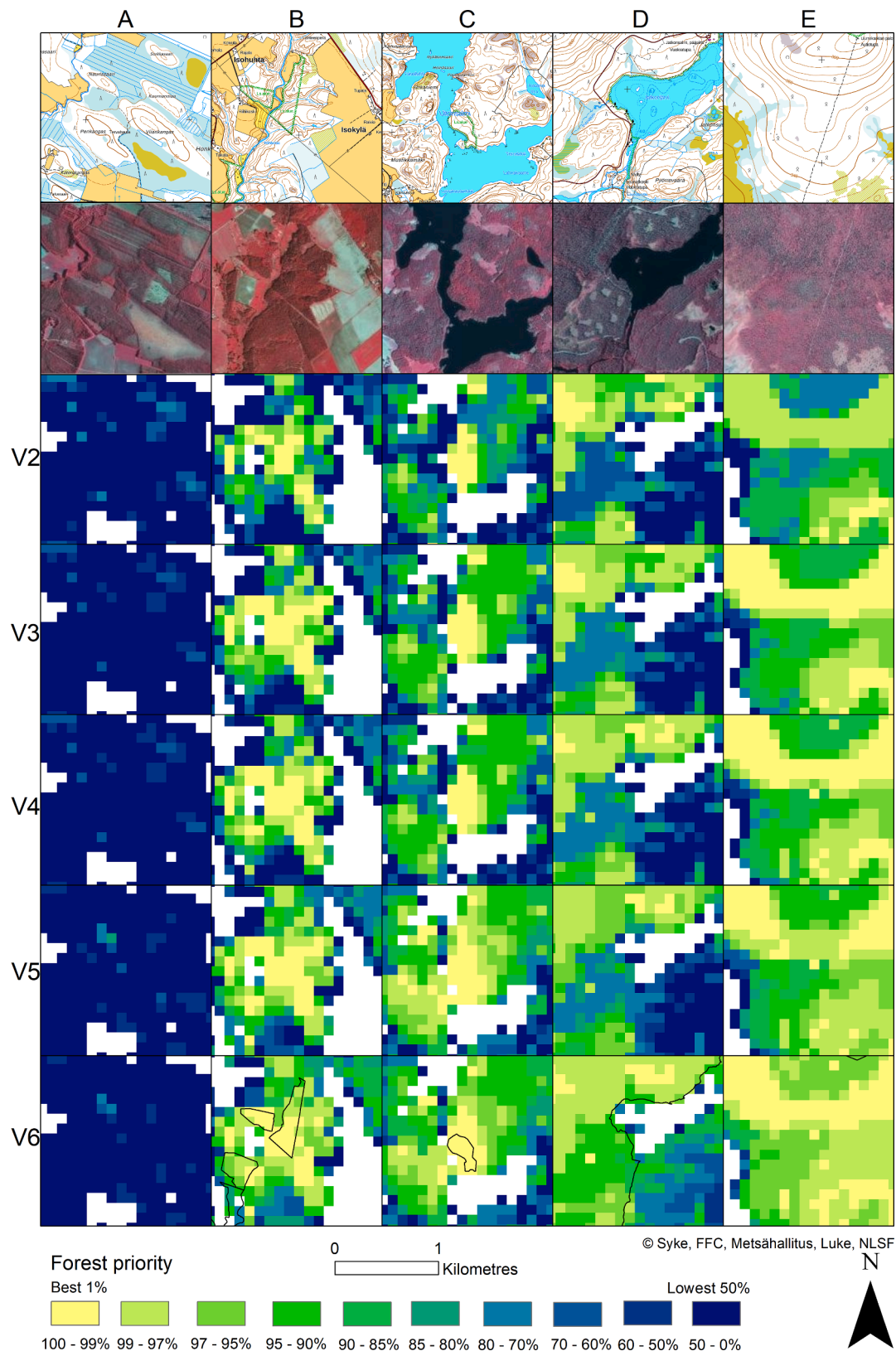


Fig. 3. Differences in forest conservation priority maps between different landscape or land-use situations, and prioritisation versions. The panels A-E present different landscape or land-use situations that are highlighted with red letters in Fig. 2: A) Northern Ostrobothnia with drained peatland forests, no conservation areas, many landowners. B) Southwest Finland with fragmented forests within a largely agricultural environment, small conservation areas (black lines in V6) and many landowners. C) Lakeland forests fragmented by inland waters, small conservation areas, many landowners. D) Extensive Kainuu forest landscape, large conservation area, state-owned forests. E) Lapland, unmanaged landscape with forests and mires next to large conservation area, land mostly state-owned. Rows from top down show the base map, a false colour aerial photo, and prioritization versions 2–6. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

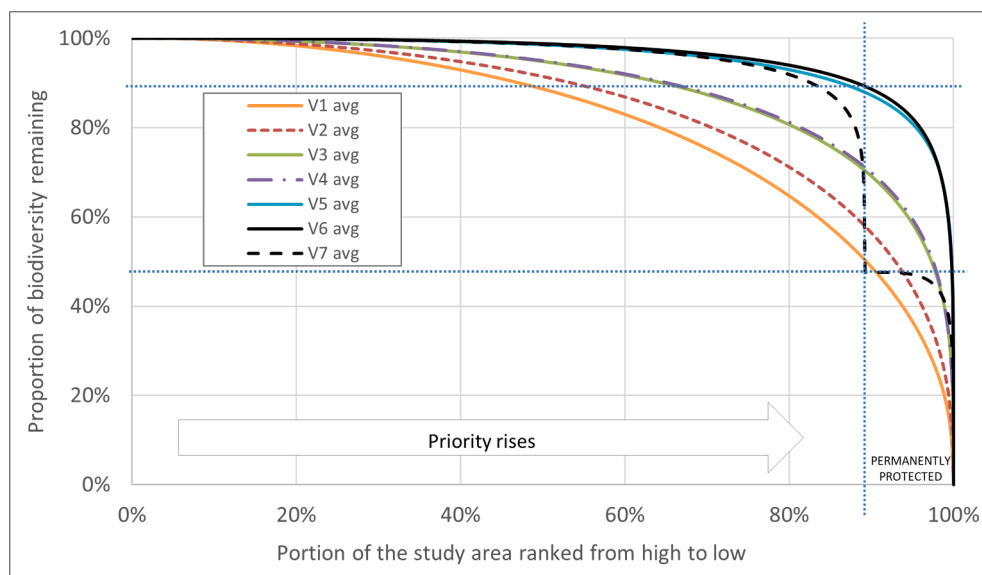


Fig. 4. The average performance curves of all input layers from the seven analysis versions. The x-axis is percentage of study area, and the priority rank rises towards the right. The y-axis shows the mean fraction of feature occurrences remaining in respective top fraction of the landscape. The step in the V7 curve (dotted black) follows from the two-stage ranking that places current permanently protected areas to the highest priorities; the vertical dotted blue line shows the area of the present protected area network, a bit over 10% of the Finnish land area. The lower horizontal dotted blue line shows the fraction of biodiversity values inside the present permanent conservation area network according to present data: a bit below 50%. Analyses 1–6 show how much biodiversity – again according to data used – could be covered with the same area, if forests could be protected without any limitations. The performance curves start from 100% on the left, meaning the full landscape would include all of biodiversity remaining. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

with respect to how much biodiversity they host. Consequently, biodiversity does not scale linearly with area but is more aggregated into the highest priority areas of the landscape. As an example, according to analysis version 2 (red dotted line), the highest 1%, 5%, 10%, 15% and 20% of priority areas (x-axis starting from 100% down) cover on average 24%, 43%, 56%, 64%, and 71% of the distributions of forest biodiversity features (y-axis). Looking at the bottom 20% of the area, it covers only 1% – these areas would mostly be poorly productive areas, clear cuts, or sapling fields. The curves also show that the highest 10% priority of the landscape (2.8 M ha) includes 49% (version 1), 56% (version 2), 69% (version 3), 70% (version 4), 87% (version 5), 88% (version 6), and 48% (version 7) of the biodiversity values entered into analysis.

In **version 2** high priority areas emerge in a scattered pattern (Figs. 2 and 3, row V2). Areas with no known commercial management of forests or drainage are higher in priorities compared to areas where forestry operations or drainage have been notified. The quantitative effect of this condition transform on the priority ranking is visibly obvious in the performance curves (Fig. 4) as the version 1 (orange line) is less convex than the version 2 (red dotted line), meaning that remaining biodiversity is relatively more concentrated in the landscape in analysis 2.

In **version 3** the addition on forest-internal connectivity makes high priority areas show as more aggregated (Fig. 3, row V3, panels B and C). Priorities rise in contiguous or semi-contiguous high DWP-value forest areas. Correspondingly, priorities in fragmented and managed forest areas become slightly lower. The performance curve changes even more than between versions 1 and 2, which indicates that consideration of forest-internal connectivity has significant impact on priorities (V3 in Fig. 4).

Adding the species observations in **version 4** caused modest changes in the analysis (in Fig. 3, row V4, panels D and E). As Zonation operates with fractions of distributions, the smaller the initial distribution area is, the greater its relative effect. Because the red-listed species observations covered only 0.2% of the study area, major localized changes occur in priorities. All grid cells where red-listed species have been observed got priorities inside the top 7% of the landscape. Some areas even rose from the lowest 1% to the top 1% in priorities, with the mean change being 20%. Changes were highest in strongly penalized areas. For the remaining 99.8% of the study area, priorities remained effectively the same, because there were no changes in data there. This is evident also

in performance curves, as the difference between versions 3 and 4 is negligible.

In **versions 5** (Fig. 3, row V5) and **6** (Fig. 3, row V6), the impact of further additional connectivity measures aggregates the high-priority areas around the close neighbourhood of the key forest habitats (i.e., the panel C) and permanently protected areas (i.e., the panel D). This change in feature aggregation clearly shows in the performance curves (Fig. 4), which become more concave than before.

The outcome of the version 6 was compared with the results from the two-stage hierarchical **version 7** (see Appendix E). In this analysis, present conservation areas are forced into top priorities. They are the top 11% of the landscape in Fig. 4, or ranks 89–100%, which cover on average 48% of input feature occurrences. The threshold in performance curve V7 highlights the transition between unprotected and permanently protected forests. The first step of the performance curve shows how part of present conservation areas are good, but some are not, seen from the levelling-off of the performance curve around top 5–10% of the landscape. The less effective protected areas typically are sparse forests, mountainous or mire areas in poorly productive forest land areas with low DWP. When moving to the unprotected part of the landscape (vertical blue line), the V7 performance curve rises very quickly, demonstrating that many areas of highest importance for forest biodiversity are unprotected. These areas would excellently complement the present protected area network. If the protected area network could be established from scratch (analysis 6), the top 11% area of the landscape would contain almost 90% of biodiversity values. To close the gap – and according to present data – the Finnish forest conservation area network should be supplemented with a 6% increase of area (top 11–17% of analysis V7; 1.7 M ha).

The greatest interest is typically on areas with highest priorities and therefore we studied the top 15% fractions of each analysis version (4.3 M ha) with a pairwise comparison (see Figure F.1 in Appendix F). The spatial overlap, i.e., the portion of the same grid cells within the top 15% fractions, varied between 56% (versions 1 and 6) to nearly 100% (versions 3 and 4). The penalization changed the top priority areas by 31.3%, the implementation of connectivity inside forest areas by 8.9%, adding the observations of red-listed forest species by 0.5%, and the connectivity to key forest habitats and permanent conservation areas by 18.3% and 13.6%, respectively. In analyses 1–6 the top priority areas

aggregate around southern boreal forests in all versions. The distribution and the protection status of the top 15% fraction was also investigated across 3 vegetation zones and nationally (Table F.1 in Appendix F). The protection status rose towards north varying between 6% (version 1, southern boreal zone) and 63% (version 6, northern boreal zone). Nationally, the present permanently protected areas only covered from 15% to 30% of the 15% top fraction. In hierarchical analysis 7, all present protected areas must by definition be inside the top 11% of the landscape, making this comparison largely irrelevant.

4. Discussion

Our work provides an evaluation of conservation values of forests in national scale in high resolution. This approach and especially the spatial data serves the needs of a forest-dependent society, which pursues ecological sustainability as one of its cornerstones. Similar approaches have been used before for, e.g., forests, peatlands, traditional rural biotopes, and marine areas (Leathwick et al., 2008; Lehtomäki et al., 2009; Leathwick et al., 2010; Leinonen et al., 2013; Raatikainen et al., 2017; Zwiener et al., 2017; Virtanen et al., 2018; Kareksela et al., 2020). In case of the forests, the previous analyses were done at smaller extent or lower resolution, with less accurate forest data, with less detailed information on forest management history, without forest species observations, or the information has been available only for few. Nevertheless, the research and development of the SCP analyses have paved the way for our research.

The previous studies on forests do not satisfy the present requirements for open, up-to-date, and useful spatial data for land-use planning. In Finland, every year more than one million hectares of forests (3% of all forests) is commercially managed (Kulju et al., 2023). As the old trees are important for both logging (Henttonen et al., 2019, 2020; Kulju et al., 2023) and conservation (Tikkanen et al., 2006), as well as other land uses and values (see, e.g., IPBES, 2019), society at large needs to set its priorities (CBD, 2022). For other needs than forest industry, and not always for industry either, the old and large trees cannot be replaced with fast growing young trees. The tree material itself, the 3D-structure of the tree, and the microenvironments the tree provides for species are very different in managed forests compared to natural forests (Lindenmayer et al., 2012, 2013; Lindenmayer et al., 2014). For example, old and large aspens *Populus termula* L. are a keystone species for biodiversity as they host a significant high species richness with specialised species (Kivinen et al., 2020). Therefore, the development of our spatial conservation prioritisation for forests is well-justified.

Our results provide information for land-use decisions from multiple perspectives. One is preservation of red-listed species in Boreal forests. The results are useful at the local level, when balancing between the value of tree stock and negative impacts of forest management on forest biodiversity. Additionally, they offer information for land-use decision-making at regional and nation scales, supported by the three different connectivity methodologies that were implemented in the analyses. Analysis with multiple connectivity components highlight semi-contiguous forest areas with high conservation value. They suggest buffer zones for the key forest habitats and protected areas. As our results are limited by data and analysis structure, they should not be used as the only source of information when deciding about land-use; additional information should be used when relevant and as available. It is also possible to balance between biodiversity, societal considerations, and economics, assuming data is available (Virtanen et al., 2022).

To be more precise, analysis 6 integrates all features that are needed for identifying high conservation value forests: type, quality, location, species, and aggregation (Brooks et al., 2006; Hodgson et al., 2011; Kukkala and Moilanen, 2013). However, sometime individual decisions may need to be made about individual stands, which leads us to local habitat quality, the main determinant of species distributions (see, e.g., Hodgson et al., 2011). Accordingly, the importance of securing all

irreplaceable forests such as old pristine forests or corridors that cannot be restored (Hodgson et al., 2011; Watson et al., 2018; Wintle et al., 2019) are emphasised by analysis versions 2 and 4. The irreplaceability is related to irreversibility where a cut forest does not reverse back to the forest it used to be due to, e.g., climate change (Kaarlejarvi et al., 2021). Buffer zones, highlighted in analyses 3, 5, 6, and 7, reduce edge effects, increase connectivity, and provide habitat to be colonized from the core forest fragments (Haddad et al., 2015; Häkkinen et al., 2021). They could be treated with nature-oriented management practices, such as retention forestry and restoration (Halme et al., 2013; Koivula and Vanha-Majamaa, 2020; Koivula et al., 2022), continuous cover forestry (Peura et al., 2018; Eyvindson et al., 2021), or natural disturbance-based forest management (Kuuluvainen et al., 2021). Additionally, combining various management approaches in time and place instead of using the prevailing even-aged management will promote landscape diversification including species richness in general (Kuuluvainen et al., 2021; Duflo et al., 2022).

Our results show that the high priority forest areas are not equally distributed across Finland. It is also notable that a significant portion of these lie outside the current permanently protected forest network. Apart from the extensive continuous conservation areas in northern Finland, the high value forests show a very fragmented pattern across much of the Finnish landscape. This is the case especially in southern and central Finland, which are regions that have experienced heavy habitat loss, degradation, and fragmentation due to intensive use of natural resources by people.

It is notable that some areas get high priorities regardless of the analysis version. Many of these are previously known for their forest biodiversity values, including such as the already protected herb-rich and old pristine forests. Nevertheless, many high-priority areas remain unprotected, including patches of natural forests, which should be secured urgently to avoid further fragmentation or degradation that could harm their conservation values (see, e.g., Määttä et al., 2022). Notably, these areas also include key forest habitats and their surroundings. Although key forest habitats are protected to some degree, they can presently be delineated as very small fragments without effective buffer areas. Preferably, they should be managed and developed as a crucial part of the forest conservation network and not just as isolated biodiversity spots in the middle of the managed forest landscape (Wintle et al., 2019). Small habitat patches in a weakly connected landscape are prone to the extinction debt, a phenomenon where specialist species, including many red-listed species, experience decline and later local extinction due to habitat degradation and the dynamics of small populations (Hanski and Ovaskainen, 2002; Fischer and Lindenmayer, 2007; Abrego et al., 2015).

Although environmental aspects have been identified as one of the main motivator for forest ownership (Husa and Kosenius, 2021), the majority of forest owners do not share a concern on the decline in forest biodiversity, at least in Finland (Juutinen et al., 2020; Takala et al., 2022). This can be one of the reasons why areas with the highest conservation potential are not always available for conservation (see, e.g., Niemelä, 2005; Paloniemi, 2018). While there are doubts concerning the effectiveness of voluntary conservation, the recent assessments of METSO programme have pointed out its success in forest conservation in Finland. The programme has also promoted a generally positive attitude towards saving forest biodiversity (Anttila et al., 2019; Hohti et al., 2019). Lack of knowledge has been identified as one of the most important factors that restrict the implementation of the voluntary conservation agreements, which however is among the factors authorities can influence (Doremus, 2003; Miljand et al., 2021). The present analysis responds to the need for useable knowledge (Martinez-Harms et al., 2015; Pynnönen et al., 2018), targeted to both landowners and the advisors contacting them. We have implemented analyses via a participatory SCP approach and our results are openly available as raster-format but also as a pre-treated information via the internet service of the Finnish Forest Centre. There, spatial data have been converted to a

verbal interpretation of the biodiversity potential, which for most promising areas is: “You might have a possibly suitable forest area for the METSO programme” (Suomen metsäkeskus et al., 2019). This note does not oblige anything, and it only informs landowners about other than commercial values in their forests. The potential must be confirmed with field work before making an official conservation contract. While impacts are hard to verify, information now available for decision-making has been gratefully received. Some of the high conservation value forests identified here should be relatively easy additions to the existing protected area network, as their economic use may already be restricted due to the Forest Act (Forest Act, 1996, updated 2013; Siitonen et al., 2021).

Although our results have provided useful information to improve the network of environments from the perspective of red-listed forest species, we have recognized issues that could be improved. The most important one is the quality and availability of ecological data. First, the puzzle of different data sources might become simplified in the near future as more accurate stand level data becomes available, due to global and national development of remote sensing techniques and still continuing national forest inventory data collection. Second, the collected information about commercial management of forests is increasing and diversifying rapidly (see, e.g., Kangas et al., 2018; Hardenbol et al., 2022), which provides material for assessment of forests from varying perspectives, including its ecological state. This also serves the needs of data accuracy as data updates are expected to happen more frequently, and they will be automatized, which will improve the reliability of results. Thirdly, the uncertainties in the DWP modelling will be reduced with further development of the Finnish forest simulators and the data underlying them (see, e.g., Härkönen et al., 2010). There, the estimations on forest growth could be improved especially for other than traditionally managed forests – areas that have been managed atypically, or even left unmanaged – as these have been one of our challenges (See Appendices B.1 and C). Fourthly, one major improvement can be collection of data about biodiversity and ecosystem services in the national forest inventory, the main data source used by forest simulations (Chirici et al., 2012; Kangas et al., 2018), as this would enable the study of these factors together with stand characteristics and in general increase the information on species occurrences.

We suggest continuations to the present research. First, the analysis should be updated at regular intervals, due to ongoing commercial management of forests (Margules and Pressey, 2000; Kulju et al., 2023). Second, the ecological model could be improved with new useful data (Kangas et al., 2018) or enhanced calculation methods for DWP or the forest simulators (e.g., Mäyrä et al., 2021). Improved data on forest structure could allow better separation of the mature managed stands from more natural forests. Distribution models for indicator species (e.g., Virkkala et al., 2022), biodiversity data for boreal streams and riparian forests (e.g., Mykrä, 2023), and data on sun-exposed eskers or other specific biotopes would improve our estimation of biodiversity in forests. Also, information on nature management (e.g., Koivula and Vanha-Majamaa, 2020) or nature restoration (Halme et al., 2013) would benefit the analyses. Additional information about carbon storage and sequestration would widen the perspective to include climate change mitigation and bioeconomy considerations (Forsius et al., 2021). Most of our input features facilitate further analysis as they are openly accessible under the CC BY 4.0 licence.

5. Conclusions

Combining data-driven analysis with a participatory approach can help mitigate the biodiversity crisis. Our results demonstrate the importance of landscape-level planning, connectivity within each forest patch but also to conservation areas, using models to prioritise among potential conservation values, and using potential future conservation values instead of only present values. We produced the best SCP analyses presently possible about the biodiversity potential of Finnish forests. We

highlight significant variation in quality between different forests and identify considerable amounts of unprotected areas that are most valuable for biodiversity. As forestry and nature conservation are typically interested in the same forest areas, our openly available data supports both management planning and voluntary forest conservation efforts in the METSO programme. Our results support biodiversity-friendly forest management, by providing information about forest connectivity around high conservation value forest areas as well as forests local importance on biodiversity. We emphasize the need for up-to-date data on biodiversity and ecosystem services and point out the desirability of updating and developing analyses regularly. Finally, we emphasise broad and open communication with stakeholders, landowners, researchers, experts, and practitioners within the analysis process and when using the results in decision support for on-the-ground decisions.

6. Licence and attribution

Most of the data is licensed under a [Creative Commons Attribution 4.0 International License \(CC BY 4.0\)](https://creativecommons.org/licenses/by/4.0/). Some individual data, such as locations of red-listed species and key forest habitats on state owned forests, are not publicly available. Therefore, input data concerning these have been omitted from the data package. Ask for the data from Finnish Biodiversity Info Facility FINBIF (species) and Metsähallitus Forestry Ltd Finland (key forest habitats on state owned areas). See details of individual data in Appendix A.

CRedit authorship contribution statement

Ninni Mikkonen: Conceptualization, Methodology, Software, Validation, Formal analysis, Resources, Data curation, Writing – original draft, Writing – review & editing, Visualization, Project administration, Funding acquisition. **Niko Leikola:** Conceptualization, Methodology, Validation, Visualization, Writing - original draft, Writing - review & editing. **Joona Lehtomäki:** Conceptualization, Methodology, Writing – original draft, Writing – review & editing. **Panu Halme:** Conceptualization, Methodology, Writing – original draft, Writing – review & editing. **Atte Moilanen:** Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

The data package including input and output data are available in following address DOI 10.5281/zenodo.7919143. It contains the dead wood potential input layers, similarity matrix, layer of permanently protected areas, and output layers from analysis version 1 to 7. The setup files are available for version 7. According to CC BY 4.0 you are free to copy and redistribute the material in any medium or format, and to transform and build upon the material for any purpose, even commercially. You must give appropriate credit, provide a link to the license, and indicate if changes were made.

Acknowledgements

First, the authors would like to thank all the people who worked with us to make this happen: Ari Lahtinen from Metsähallitus Parks & Wildlife Finland for participating in planning and executing the analyses with us; rest of the project group that planned the analysis with us: Tuomas Haapalehto and Marja Hokkanen (Metsähallitus Parks & Wildlife Finland), Kimmo Syrjänen (The Finnish Environment Institute), Saara Lilja-Rothsten (Tapio oy) and Tarja Wallenius (Metsähallitus Forestry Ltd); and the group of forest ecologists for their expert opinion

in determining the penalties for forest management and ecological interactions for connectivity: Pekka Punttila and Kimmo Syrjänen (The Finnish Environment Institute), Lauri Saaristo (Tapio oy), Juha Siitonen (Natural Resources Institute Finland) and Matti Koivula (The University of Eastern Finland). We also thank Torsti Schulz, Topi Tanhuanpää, Raimo Virkkala, and Sonja Virta for their help with preparing the manuscript. We would also like to thank Finnish Forest Centre for the cooperation with forest data and Metsähallitus Forestry Ltd for the cooperation in developing the methodology. Lastly, we thank all the four reviewers for their constructive feedback. N.M., N.L., and A.M were supported by the Finnish Ministry of the Environment (Forest Biodiversity Programme in Southern Finland METSO YM8/221/2010, VN/6587/2018, VN/12123/2019-YM-2, and VN/28601/2020-YM-3). The work of P.H. was supported by VN/12123/2019-YM-2. A.M. was also supported by the Academy of Finland and the Strategic Research Council project IBC-Carbon, grant #312559.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.foreco.2023.121079>.

References

- Aakala, T., 2010. Coarse woody debris in late-successional *Picea abies* forests in northern Europe: Variability in quantities and models of decay class dynamics. *For. Ecol. Manage.* 260, 770–779. <https://doi.org/10.1016/j.foreco.2010.05.035>.
- Abrego, N., et al., 2015. Implications of reserve size and forest connectivity for the conservation of wood-inhabiting fungi in Europe. *Biol. Conserv.* 191, 469–477. <https://doi.org/10.1016/j.biocon.2015.07.005>.
- Anttila, S. (Ed.), 2019. METSO-tilannekatsaus 2018: Etelä-Suomen metsien monimuotoisuuden toimintaohjelma 2008–2025 (in Finnish). Luonnonvarakeskus, Helsinki.
- Arnkil, N., et al., 2020. Uhanalaisten lajien esiintymätiedon hyödyntäminen metsätaloudessa (in Finnish). *Tapion raportteja* 41, 43.
- Arponen, A., et al., 2012. Effects of Connectivity and Spatial Resolution of Analyses on Conservation Prioritization across Large Extents. *Conserv. Biol.* 26, 294–304. <https://doi.org/10.1111/j.1523-1739.2011.01814.x>.
- Blatter, C., et al., 2022. Sectoral policies cause incoherence in forest management and ecosystem service provisioning. *Forest Policy Econ.* 136, 15. <https://doi.org/10.1016/j.forpol.2022.102689>.
- Brooks, T.M., et al., 2006. Global biodiversity conservation priorities. *Science* 313, 58–61. <https://doi.org/10.1126/science.1127609>.
- Butchart, S.H.M., et al., 2010. Global Biodiversity: Indicators of Recent Declines. *Science* 328, 1164–1168. <https://doi.org/10.1126/science.1187512>.
- Cajander, A.K., 1926. The theory of forest types. *Acta Forestalia Fennica* 29, 108. <https://doi.org/10.14214/aff.7193>.
- Cbd, 2022. Kunming-Montreal Global Biodiversity Framework. UN environment programme 14. <https://www.cbd.int/doc/c/e6d3/cd1d/daf663719a03902a9b116c34/cop-15-l-25-en.pdf>.
- Chirici, G., et al., 2012. National Forest Inventory Contributions to Forest Biodiversity Monitoring. *For. Sci.* 58, 257–268. <https://doi.org/10.5849/forsci.12-003>.
- Ćosović, M., et al., 2020. Stand Structural Characteristics Are the Most Practical Biodiversity Indicators for Forest Management Planning in Europe. *Forests* 11, 343. <https://doi.org/10.3390/f11030343>.
- Doremus, H., 2003. A policy portfolio approach to biodiversity protection on private lands. *Environmental Science & Policy* 6, 217–232. [https://doi.org/10.1016/s1462-9011\(03\)00036-4](https://doi.org/10.1016/s1462-9011(03)00036-4).
- Duflot, R., et al., 2022. Management diversity begets biodiversity in production forest landscapes. *Biol. Conserv.* 268, 10. <https://doi.org/10.1016/j.biocon.2022.109514>.
- Esseen, P.-A., et al., 1997. Boreal forests. *Ecological bulletins* 46, 16–47. <https://www.jstor.org/stable/20113207>.
- European Commission, 2020. EU Biodiversity Strategy for 2030 - Bringing nature back into our lives. Communication from The Commission to The European Parliament, The Council, The European Economic and Social Committee and The Committee of The Regions.
- Eyvindson, K., et al., 2021. High boreal forest multifunctionality requires continuous cover forestry as a dominant management. *Land Use Policy* 100, 10. <https://doi.org/10.1016/j.landusepol.2020.104918>.
- Finnish Environment Institute, 2011. [dataset] National peatland drainage data SOJT_09b1 (based on data of National Land Survey of Finland 2008 and Corine 2006). <https://ckan.ymparisto.fi/dataset/soiden-ojitustilanne>.
- Finnish Environment Institute, 2015. [dataset] Finnish environmental database HERTTA.
- Finnish Forest Centre, 2015a. Field and forest stand database AARNI.
- Finnish Forest Centre, 2015b. Forestry operation notifications from 1983 to 8.5.2015.
- Finnish Forest Centre, 2017. Forestry operation notifications from 9th of June 2014 to 12th of October 2017.
- Fischer, J., Lindenmayer, D.B., 2007. Landscape modification and habitat fragmentation: a synthesis. *Global Ecol. Biogeogr.* 16, 265–280. <https://doi.org/10.1111/j.1466-8238.2007.00287.x>.
- Forest Act, 1996, updated 2013. Chapter 3 – Safeguarding the biodiversity of forests (1085/2013). Section 10 - Preserving biodiversity and habitats of special importance.
- Forsius, M., et al., 2021. Developing a spatially explicit modelling and evaluation framework for integrated carbon sequestration and biodiversity conservation: application in southern Finland. *Sci. Total Environ.* 775, 16. <https://doi.org/10.1016/j.scitotenv.2021.145847>.
- Gao, T., et al., 2015. Reviewing the strength of evidence of biodiversity indicators for forest ecosystems in Europe. *Ecol. Indicators* 57, 420–434. <https://doi.org/10.1016/j.ecolind.2015.05.028>.
- Gauthier, S., et al., 2015. Boreal forest health and global change. *Science* 349, 819–822. <https://doi.org/10.1126/science.aaa9092>.
- Haddad, N.M., et al., 2015. Habitat fragmentation and its lasting impact on Earth's ecosystems. *Sci. Adv.* 1, 9. <https://doi.org/10.1126/sciadv.1500052>.
- Häkkinen, M., et al., 2021. Are small protected habitat patches within boreal production forests effective in conserving species richness, abundance and community composition? A systematic review. *Environmental Evidence* 10, 20. <https://doi.org/10.1186/s13750-020-00216-6>.
- Halme, P., et al., 2013. Challenges of ecological restoration: Lessons from forests in northern Europe. *Biol. Conserv.* 167, 248–256. <https://doi.org/10.1016/j.biocon.2013.08.029>.
- Hansen, A.J., et al., 1991. Conserving biodiversity in managed forests. *Bioscience* 41, 382–392. <https://doi.org/10.2307/1311745>.
- Hansen, M.C., et al., 2013. High-resolution global maps of 21st-century forest cover change (Data on forest cover loss 2000–2014). *Science*, 342. DOI10.1126/science.1244693.
- Hanski, I., Ovaskainen, O., 2002. Extinction Debt at Extinction Threshold. *Conserv. Biol.* 16, 666–673. <https://doi.org/10.1046/j.1523-1739.2002.00342.x>.
- Hardenbol, A.A., et al., 2022. Detection of standing retention trees in boreal forests with airborne laser scanning point clouds and multispectral imagery. *Methods Ecol. Evol.* 13. <https://doi.org/10.1111/2041-210x.13995>.
- Härkönen, S., et al., 2010. Evaluation of forest growth simulators with NFI permanent sample plot data from Finland. *For. Ecol. Manage.* 259, 573–582. <https://doi.org/10.1016/j.foreco.2009.11.015>.
- Henntonen, H.M., et al., 2019. Large trees have increased greatly in Finland during 1921–2013, but recent observations on old trees tell a different story. *Ecol. Indicators* 99, 118–129. <https://doi.org/10.1016/j.ecolind.2018.12.015>.
- Henntonen, H.M., et al., 2020. Size-class structure of the forests of Finland during 1921–2013: a recovery from centuries of exploitation, guided by forest policies. *European Journal of Forest Research* 139, 279–293. <https://doi.org/10.1007/s10342-019-01241-y>.
- Hodgson, J.A., et al., 2011. Habitat area, quality and connectivity: striking the balance for efficient conservation. *J. Appl. Ecol.* 48, 148–152. <https://doi.org/10.1111/j.1365-2664.2010.01919.x>.
- Hohti, J., et al., 2019. Kymmenen vuotta METSOa – Väliarviointi Etelä-Suomen metsien monimuotoisuuden toimintaohjelman ensimmäisestä vuosikymmenestä (in Finnish). *Ympäristöministeriön julkaisuja* 4 (2019), 116.
- Husa, M., Kosenius, A.K., 2021. Non-industrial private forest owners' willingness to manage for climate change and biodiversity. *Scand. J. For. Res.* 36, 614–625. DOI10.1080/02827581.2021.1981433.
- Hynynen, J., et al., 2014. Scenario analysis for the biomass supply potential and the future development of Finnish forest resources. *Metlan työraportteja - Working Papers of the Finnish Forest Research Institute* 302, 106. <http://urn.fi/URN:ISB N:978-951-40-2487-0>.
- Hynynen, J., et al., 2015. Long-term impacts of forest management on biomass supply and forest resource development: a scenario analysis for Finland. *European Journal of Forest Research* 134, 415–431. <https://doi.org/10.1007/s10342-014-0860-0>.
- Hyvärinen, E. (Ed.), 2019. *The 2019 Red List of Finnish Species*. Ministry of the Environment & Finnish Environment Institute, Helsinki.
- IPBES (Ed.), 2018. *The IPBES assessment report on land degradation and restoration*. L. Montanarella, R. Scholes, A. I. Brainich (editors). IPBES - Secretariat of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services, Bonn, Germany.
- IPBES (Ed.), 2019. *Global assessment report on biodiversity and ecosystem services of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services*. E. S. Brondizio, J. Settele, S. Díaz, H. T. Ngo. (Eds.). IPBES secretariat, Bonn, Germany.
- Johnson, C.N., et al., 2017. Biodiversity losses and conservation responses in the Anthropocene. *Science* 356, 270–275. <https://doi.org/10.1126/science.aam9317>.
- Jung, M., et al., 2021. Areas of global importance for conserving terrestrial biodiversity, carbon and water. *Nat Ecol Evol* 5, 1499–1509. <https://doi.org/10.1038/s41559-021-01528-7>.
- Junninen, K., Komonen, A., 2011. Conservation ecology of boreal polypores: A review. *Biol. Conserv.* 144, 11–20. <https://doi.org/10.1016/j.biocon.2010.07.010>.
- Juutinen, A., et al., 2020. Forest owners' future intentions for forest management. *Forest Policy Econ.* 118, 10. <https://doi.org/10.1016/j.forpol.2020.102220>.
- Kaarlejarvi, E., et al., 2021. Temporal biodiversity change following disturbance varies along an environmental gradient. *Global Ecol. Biogeogr.* 30, 476–489. <https://doi.org/10.1111/geb.13233>.
- Kangas, A., et al., 2018. Remote sensing and forest inventories in Nordic countries – roadmap for the future. *Scand. J. For. Res.* 33, 397–412. <https://doi.org/10.1080/02827581.2017.1416666>.

- Kareksela, S., et al., 2020. Combining spatial prioritization and expert knowledge facilitates effectiveness of large-scale mire protection process in Finland. *Biol. Conserv.* 241, 8. <https://doi.org/10.1016/j.biocon.2019.108324>.
- Kivinen, S., et al., 2020. A keystone species, European aspen (*Populus tremula* L.), in boreal forests: Ecological role, knowledge needs and mapping using remote sensing. *For. Ecol. Manage.* 462, 118008. <https://doi.org/10.1016/j.foreco.2020.118008>.
- Kohl, M., et al., 2015. Changes in forest production, biomass and carbon: Results from the 2015 UN FAO Global Forest Resource Assessment. *For. Ecol. Manage.* 352, 21–34. <https://doi.org/10.1016/j.foreco.2015.05.036>.
- Koivula, M., et al., 2022. Talousmetsien luonnonhoidon ekologisten vaikutusten synteesi (in Finnish). *Luonnonvara- ja bionalouden tutkimus* 60, 83. <http://urn.fi/URN:ISB N:978-952-380-472-2>.
- Koivula, M., Vanha-Majamaa, I., 2020. Experimental evidence on biodiversity impacts of variable retention forestry, prescribed burning, and deadwood manipulation in Fennoscandia. *Ecological Processes* 9. <https://doi.org/10.1186/s13717-019-0209-1>.
- Kontula, T., Raunio, A., (Eds.), 2019. *Threatened Habitat Types in Finland*, 2018. *Red List of Habitats – Results and Basis for Assessment*. Finnish Environment Institute and Ministry of the Environment, Helsinki.
- Korhonen, K., et al., 2021. Forests of Finland 2014–2018 and their development 1921–2018. *Silva Fenn.* 55, 49. <https://doi.org/10.14214/sf.10662>.
- Kouki, J., et al., 2001. Forest fragmentation in Fennoscandia: Linking habitat requirements of wood-associated threatened species to landscape and habitat changes. *Scand. J. For. Res.*, 27–37. <https://doi.org/10.1080/028275801300090564>.
- Kouki, J., 2018. *Forests*. In: Kontula, T., Raunio, A. (Eds.), *Threatened Habitat Types in Finland*, et al., 2018. *Red List of Habitats – Results and Basis for Assessment*. Finnish Environment Institute and Ministry of the Environment, Helsinki, pp. 475–567.
- Kujala, H., et al., 2018a. Not all data are equal: Influence of data type and amount in spatial conservation prioritisation. *Methods Ecol. Evol.* 9, 2249–2261. <https://doi.org/10.1111/2041-210x.13084>.
- Kujala, H., et al., 2018b. Spatial characteristics of species distributions as drivers in conservation prioritization. *Methods Ecol. Evol.* 9, 1121–1132. <https://doi.org/10.1111/2041-210x.12939>.
- Kukkala, A.S., Moilanen, A., 2013. Core concepts of spatial prioritisation in systematic conservation planning. *Biological Reviews* 88, 443–464. <https://doi.org/10.1111/brv.12008>.
- Kulju, I. (Ed.), 2023. *Metsätilastollinen vuosikirja 2022 - Finnish Statistical Yearbook of Forestry 2022*. Luonnonvarakeskus (Luke), Natural Resources Institute Finland.
- Kuuluvainen, T., et al., 2019. Low-level retention forestry, certification, and biodiversity: case Finland. *Ecological Processes* 8. <https://doi.org/10.1186/s13717-019-0198-0>.
- Kuuluvainen, T., et al., 2021. Natural Disturbance-Based Forest Management: Moving Beyond Retention and Continuous-Cover Forestry. *Frontiers in Forests and Global Change* 4, 17. <https://doi.org/10.3389/ffgc.2021.629020>.
- Kuuluvainen, T., Aakala, T., 2011. Natural Forest Dynamics in Boreal Fennoscandia: a Review and Classification. *Silva Fenn.* 45, 823–841. <https://doi.org/10.14214/sf.73>.
- Kuuluvainen, T., Gauthier, S., 2018. Young and old forest in the boreal: critical stages of ecosystem dynamics and management under global change. *Forest Ecosystems* 5, 15. <https://doi.org/10.1186/s40663-018-0142-2>.
- Lassauce, A., et al., 2011. Deadwood as a surrogate for forest biodiversity: Meta-analysis of correlations between deadwood volume and species richness of saproxylic organisms. *Ecol. Indicators* 11, 1027–1039. <https://doi.org/10.1016/j.ecolind.2011.02.004>.
- Leathwick, J., et al., 2008. Novel methods for the design and evaluation of marine protected areas in offshore waters. *Conserv. Lett.* 1, 91–102. <https://doi.org/10.1111/j.1755-263X.2008.00012.x>.
- Leathwick, J.R., et al., 2010. Complementarity-based conservation prioritization using a community classification, and its application to riverine ecosystems. *Biol. Conserv.* 143, 984–991. <https://doi.org/10.1016/j.biocon.2010.01.012>.
- Lehtomäki, J., et al., 2009. Applying spatial conservation prioritization software and high-resolution GIS data to a national-scale study in forest conservation. *For. Ecol. Manage.* 258, 2439–2449. <https://doi.org/10.1016/j.foreco.2009.08.026>.
- Lehtomäki, J., et al., 2015. What data to use for forest conservation planning? A comparison of coarse open and detailed proprietary forest inventory data in Finland. *PLoS One* 10, 25. <https://doi.org/10.1371/journal.pone.0135926>.
- Lehtomäki, J., Moilanen, A., 2013. Methods and workflow for spatial conservation prioritization using Zonation. *Environ. Model. Software* 47, 128–137. <https://doi.org/10.1016/j.envsoft.2013.05.001>.
- Lehtomäki, J., 2014. Academic dissertation: Spatial conservation prioritization for Finnish forest conservation management. Department of Biosciences, 60. <http://hdl.handle.net/10138/229466>.
- Leinonen, A., et al., 2013. Metsäelinympäristöjen Zonation-analyyysien tulosten käyttöohje (Instructions for using Zonation analysis results on forest environments, in Finnish). 31.
- Lindenmayer, D.B., et al., 2012. Global Decline in Large Old Trees. *Science* 338, 1305–1306. <https://doi.org/10.1126/science.1231070>.
- Lindenmayer, D.B., et al., 2014. Broad Decline of Populations of Large Old Trees. *Conserv. Lett.* 7, 72–73. <https://doi.org/10.1111/conl.12079>.
- Lindenmayer, D.B., et al., 2013. Old Trees: Large and Small Response. *Science* 339, 905–905. <https://doi.org/10.1126/science.339.6122.905-a>.
- Määttä, A.M., et al., 2022. Increasing loss of mature boreal forests around protected areas with red-listed forest species. *Ecological Processes* 11, 13. <https://doi.org/10.1186/s13717-022-00361-5>.
- Mäkinen, H., et al., 2021. Site carrying capacity of Norway spruce and Scots pine stands has increased in Germany and northern Europe. *For. Ecol. Manage.* 492, 8. <https://doi.org/10.1016/j.foreco.2021.119214>.
- Mäkisara, K., et al., 2016. *The multi-source national forest inventory of Finland – methods and results 2013*. Natural Resources Institute Finland, Helsinki.
- Margules, C.R., Pressey, R.L., 2000. Systematic conservation planning. *Nature* 405, 243–253. <https://doi.org/10.1038/35012251>.
- Martinez-Harms, M.J., et al., 2015. Making decisions for managing ecosystem services. *Biol. Conserv.* 184, 229–238. <https://doi.org/10.1016/j.biocon.2015.01.024>.
- Mäyrä, J., et al., 2021. Tree species classification from airborne hyperspectral and LiDAR data using 3D convolutional neural networks. *Remote Sens. Environ.* 256, 16. <https://doi.org/10.1016/j.rse.2021.112322>.
- Metsähallitus Forestry Ltd, 2017. *SILVIA 2017. Forestry resource and planning system*. Metsähallitus Parks & Wildlife Finland, Centres for Economic Development Transport and the Environment, 2015. SutiGIS 2015: Protected area biotope information system, biotope and tree stock data on private conservation areas.
- Metsähallitus Parks & Wildlife Finland, The Ministry of the Environment's Administrative Branch, 2017a. SAKTI 2017: Protected area biotope information system, biotope data.
- Metsähallitus Parks & Wildlife Finland, The Ministry of the Environment's Administrative Branch, 2017b. SAKTI 2017: Protected area biotope information system, biotope data on state-owned conservation areas.
- Metsähallitus, 2015. [dataset] SutiGIS 2015. Forestry resource and planning system for Metsähallitus Forestry Ltd and Protected Area Biotope Information System; biotope, and tree stock data on state-owned conservation areas, for Metsähallitus Parks & Wildlife Finland.
- Metsähallitus Parks and Wildlife Finland, 2018. *The Ministry of the Environment's Administrative Branch, 2018. SATJ Protected area information system*.
- Mikkonen, N., et al., 2018. Monimuotoisuudelle tärkeät metsäalueet Suomessa - Puustoisten elinympäristöjen monimuotoisuusarvojen Zonation-analyyysin loppuraportti (in Finnish). *Suomen ympäristökeskuksen raportteja* 9, 104.
- Mikkonen, N., et al., 2020. Modeling of Dead Wood Potential Based on Tree Stand Data. *Forests* 11, 21. <https://doi.org/10.3390/f11090913>.
- 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>.
- Milijand, M., et al., 2021. Voluntary agreements to protect private forests-A realist review. *Forest Policy Econ.* 128, 14. <https://doi.org/10.1016/j.forpol.2021.102457>.
- Ministry of Agriculture and Forestry of Finland, 2015. *Suunnitelma metsien suojelualue- ja METSO-tilastoinnin kehittämiseksi*. METI-työryhmämuistio 2015 (2), 58.
- Moilanen, A., et al., 2009a. The Zonation framework and software for conservation prioritization. In: Moilanen, A. (Ed.), *Spatial conservation prioritization - Quantitative Methods & Computational tools*. Oxford University Press Inc., New York, pp. 196–210.
- Moilanen, A. (Ed.), 2009b. *Spatial Conservation Prioritization - Quantitative Methods & Computational Tools*. Oxford University Press Inc., New York.
- Moilanen, A., et al., 2011. Spatial prioritization of conservation management. *Conserv. Lett.* 4, 383–393. <https://doi.org/10.1111/j.1755-263X.2011.00190.x>.
- Moilanen, A., et al., 2014. *Zonation - Spatial conservation planning methods and software. Version 4. User Manual*. Informatics Group, Department of Biosciences, University of Helsinki, Finland, Helsinki. C-BIG Conservation Biology.
- Moilanen, A., et al., 2022. Novel methods for spatial prioritization with applications in conservation, land use planning and ecological impact avoidance. *Methods Ecol. Evol.* 13, 1062–1072. <https://doi.org/10.1111/2041-210x.13819>.
- Moilanen, A., et al., 2005. Prioritizing multiple-use landscapes for conservation: methods for large multi-species planning problems. *Proceedings of the Royal Society B - Biological Sciences* 272, 1885–1891. <https://doi.org/10.1098/rspb.2005.3164>.
- Mönkkönen, M., et al., 2022. More wood but less biodiversity in forests in Finland: a historical evaluation. *Memoranda Societatis Pro Fauna Et Flora Fennica* 98, 1–11. <https://journal.fi/msff/article/view/120306/71798>.
- Myers, N., et al., 2000. Biodiversity hotspots for conservation priorities. *Nature* 403, 853–858. <https://doi.org/10.1038/35002501>.
- Mykrä, H., et al., 2023. GIS-based planning of buffer zones for protection of boreal streams and their riparian forests. *For. Ecol. Manage.* 528, 9. <https://doi.org/10.1016/j.foreco.2022.120639>.
- Nathan, R., Muller-Landau, H.C., 2000. Spatial patterns of seed dispersal, their determinants and consequences for recruitment. *Trends Ecol. Evol.* 15, 278–285. [https://doi.org/10.1016/s0169-5347\(00\)01874-7](https://doi.org/10.1016/s0169-5347(00)01874-7).
- Natural Resources Institute Finland, 2015a. *Segmented multi-source national forest inventory data of Finland: estimates of mean diameter at breast height for tree species based on National Forest Inventory 2013*. Unpublished. Date of datacut 19 (8), 2015.
- Natural Resources Institute Finland, 2015b. *The Multi-Source National Forest Inventory of Finland (MS-NFI) 2013*. CC BY 4. <http://kartta.luke.fi/index-en.html>.
- Newbold, T., et al., 2016. Has land use pushed terrestrial biodiversity beyond the planetary boundary? A global assessment. *Science* 353, 288–291. <https://doi.org/10.1126/science.aaf2201>.
- Niemelä, J., et al., 2005. Identifying, managing and monitoring conflicts between forest biodiversity conservation and other human interests in Europe. *Forest Policy Econ.* 7, 877–890. <https://doi.org/10.1016/j.forpol.2004.04.005>.
- Nirhamo, A., et al., 2023. *Habitat associations of red-listed epiphytic lichens in Finland*. *Silva Fenn.* 57. <https://doi.org/10.14214/sf.22019>.
- Norros, V., et al., 2023. Spore production monitoring reveals contrasting seasonal strategies and a trade-off between spore size and number in wood-inhabiting fungi. *Funct. Ecol.* 13. <https://doi.org/10.1111/1365-2435.14254>.
- Olden, A., et al., 2019. The effect of buffer strip width and selective logging on streamside plant communities. *BMC Ecol.* 19, 9. <https://doi.org/10.1186/s12898-019-0225-0>.
- Paillet, Y., et al., 2010. Biodiversity differences between managed and unmanaged forests: meta-analysis of species richness in Europe. *Conserv. Biol.* 24, 101–112. <https://doi.org/10.1111/j.1523-1739.2009.01399.x>.

- Paloniemi, R., et al., 2018. Integrating Social and Ecological Knowledge for Targeting Voluntary Biodiversity Conservation. *Conserv Lett* 11, 10. <https://doi.org/10.1111/conl.12340>.
- Parks, M., Finland, W., 2021. The Ministry of the Environment's Administrative Branch, 2021. SATJ. Protected area information system.
- Pereira, H.M., et al., 2010. Scenarios for Global Biodiversity in the 21st Century. *Science* 330, 1496–1501. <https://doi.org/10.1126/science.1196624>.
- Peura, M., et al., 2018. Continuous cover forestry is a cost-efficient tool to increase multifunctionality of boreal production forests in Fennoscandia. *Biol. Conserv.* 217, 104–112. <https://doi.org/10.1016/j.biocon.2017.10.018>.
- Pouzols, F.M., et al., 2014. Global protected area expansion is compromised by projected land-use and parochialism. *Nature* 516, 383–+.doi:10.1038/nature14032.
- Pressey, R.L., 1994. *Ad Hoc Reservations - Forward or Backward Steps in Developing Representative Reserve Systems?* *Conserv. Biol.* 8, 662-668.<http://www.jstor.org/stable/2386507>.
- Pukkala, T., et al., 2012. Relationships between economic profitability and habitat quality of Siberian jay in uneven-aged Norway spruce forest. *For. Ecol. Manage.* 276, 224–230. <https://doi.org/10.1016/j.foreco.2012.04.006>.
- Punttila, P., 2020. Metsäsertifiointin historia metsäluonnon monimuotoisuuden turvaajana Suomessa – turvan taso lakitasoon verrattuna (Liite 3). In: *Impact Assessment of the Implementation of National Strategy and Action plan for the Conservation and Sustainable use of Biodiversity in Finland (2012–2020)* (in Finnish). Prime Minister's Office, Publications of the Government's analysis, assessment and research activities 263–273.
- Pykälä, J., 2007. Metsälain erityisen tärkeät elinympäristöt ja luonnon monimuotoisuus -esimerkkinä Lohja. *Suomen ympäristö* 32, 60.
- Pykälä, J., 2004. Effects of new forestry practices on rare epiphytic macrolichens. *Conserv. Biol.* 18, 831-838.<https://www.jstor.org/stable/3589093>.
- Pynnönen, S., et al., 2018. Recognizing the Interest of Forest Owners to Combine Nature-Oriented and Economic Uses of Forests. 28.<https://doi.org/10.1007/s1184-2-018-9397-2>.
- Raatikainen, K.J., et al., 2017. Systematic targeting of management actions as a tool to enhance conservation of traditional rural biotopes. *Biol. Conserv.* 207, 90–99. <https://doi.org/10.1016/j.biocon.2017.01.019>.
- Rayfield, B., et al., 2009. Incorporating consumer-resource spatial interactions in reserve design. *Ecol. Model.* 220, 725–733. <https://doi.org/10.1016/j.ecolmodel.2008.11.016>.
- Sala, O.E., et al., 2000. Biodiversity - Global biodiversity scenarios for the year 2100. *Science* 287, 1770–1774. <https://doi.org/10.1126/science.287.5459.1770>.
- Salminen, H., et al., 2005. Reusing legacy FORTRAN in the MOTTI growth and yield simulator. *Comput. Electron. Agric.* 49, 103-113.<https://doi.org/10.1016/j.compag.2005.02.005>.
- Santangeli, A., et al., 2012. Successful voluntary conservation of raptor nests under intensive forestry pressure in a boreal landscape. *Anim. Conserv.* 15, 571–578. <https://doi.org/10.1111/j.1469-1795.2012.00551.x>.
- Santangeli, A., et al., 2016. Voluntary non-monetary approaches for implementing conservation. *Biol. Conserv.* 197, 209-214.<http://dx.doi.org/10.1016/j.biocon.2016.03.013>.
- Sarkar, S., Margules, C., 2002. Operationalizing biodiversity for conservation planning. *J. Biosci. Bangalore* 27, 299–308.<https://doi.org/10.1007/BF02704961>.
- Selonen, V., Hanski, I.K., 2004. Young flying squirrels (*Pteromys volans*) dispersing in fragmented forests. *Behav. Ecol.* 15, 564–571. <https://doi.org/10.1093/beheco/arr049>.
- Sitonen, J., 2001. Forest management, coarse woody debris and saproxylic organisms: Fennoscandian boreal forests as an example. *Ecological bulletins* 11–41.<https://www.jstor.org/stable/20113262>.
- Sitonen, J., et al., 2021. Metsälain arvioinnin jatkoselvitys 10 §:n muutosten vaikutuksista monimuotoisuuden turvaamiseen (in Finnish). Luonnonvarakeskus, Helsinki.
- Similä, M., et al., 2006. Co-variation and indicators of species diversity: Can richness of forest-dwelling species be predicted in northern boreal forests? *Ecol. Indicators* 6, 686–700. <https://doi.org/10.1016/j.ecolind.2005.08.028>.
- Skovsgaard, J.P., Vanclay, J.K., 2008. Forest site productivity: a review of the evolution of dendrometric concepts for even-aged stands. *Forestry* 81, 13–31. <https://doi.org/10.1093/forestry/cpm041>.
- Stokland, J.N., et al., 2012. Biodiversity in dead wood. Cambridge University Press.
- Storch, I., Segelbacher, G., 2000. Genetic correlates of spatial population structure in central European capercaillie Tetrao urogallus and black grouse T-tetrix: a project in progress. *Wildl. Biol.* 6, 305–310. <https://doi.org/10.2981/wlb.2000.014>.
- Suomen metsäkeskus, 2021. Tietotuotekuvaus, Hila-aineisto. 3, <https://www.metsakeskus.fi/sites/default/files/document/tietotuotekuvaus-hila-aineisto.pdf>.
- Suomen metsäkeskus, et al., 2019. Tiedätkö metsäsi suojelumahdollisuudet? Metsään-fi-palvelun mahdollinen METSO-kohde. 1, https://metsonpolku.fi/documents/115183005/124281117/Mahdollinen_METSO-kohde_esite_fi_A4.pdf/19220d2a-a13f-d60-1bd5-4926df6e32e5/Mahdollinen_METSO-kohde_esite_fi_A4.pdf?t=1655465275483.
- Takala, T., et al., 2022. Discursive barriers to voluntary biodiversity conservation: The case of Finnish forest owners. *Forest Policy Econ.* 136, 10. <https://doi.org/10.1016/j.forpol.2021.102681>.
- The Finnish Government, 2008. Decision-in-Principle of The Finnish Government on the Forest Biodiversity Programme for Southern Finland for years 2008-2016. 13.
- The Finnish Government, 2014. Decision-in-Principle of the Finnish Government on extension of the Forest Biodiversity Programme for Southern Finland (METSO) for years 2014-2025. 18.
- Tikkanen, O.P., et al., 2006. Red-listed boreal forest species of Finland: associations with forest structure, tree species, and decaying wood. *Ann. Zool. Fenn.* 43, 373–383. <https://www.jstor.org/stable/23736858>.
- Tuominen, S., et al., 2017. Improving Finnish Multi-Source National Forest Inventory by 3D aerial imaging. *Silva Fenn.* 51, 21.10.14214/sf.7743.
- UN, 1992. 8. Convention on biological diversity. Rio de Janeiro, 5th June 1992, United Nations. 28.
- Vihervaara, P., et al., 2017. How Essential Biodiversity Variables and remote sensing can help national biodiversity monitoring. *Glob. Ecol. Conserv.* 10, 43–59. <https://doi.org/10.1016/j.gecco.2017.01.007>.
- Virkkala, R., et al., 2022. Developing fine-grained nationwide predictions of valuable forests using biodiversity indicator bird species. *Ecol. Appl.* 32, 16. <https://doi.org/10.1002/eap.2505>.
- Virkkala, R., Rajasärkkä, A., 2007. Uneven regional distribution of protected areas in Finland: Consequences for boreal forest bird populations. *Biol. Conserv.* 134, 361–371. <https://doi.org/10.1016/j.biocon.2006.08.006>.
- Virtanen, E.A., et al., 2018. Evaluation, Gap Analysis, and Potential Expansion of the Finnish Marine Protected Area Network. *Frontiers in Marine Science* 5. <https://doi.org/10.3389/fmars.2018.00402>.
- Virtanen, E.A., et al., 2022. How threats inform conservation planning-A systematic review protocol. *PLoS One* 17, 9. <https://doi.org/10.1371/journal.pone.0269107>.
- Wallenius, T., et al., 2010. Loss of habitats, naturalness and species diversity in Eurasian forest landscapes. *Ecol. Indicators* 10, 1093–1101. <https://doi.org/10.1016/j.ecolind.2010.03.006>.
- Ward, M., et al., 2020. Just ten percent of the global terrestrial protected area network is structurally connected via intact land. *Nature communications* 11, 1-10.<https://doi.org/10.1038/s41467-020-18457-x>.
- Watson, J.E.M., et al., 2018. The exceptional value of intact forest ecosystems. *Nat Ecol Evol* 2, 599-610.<https://doi.org/10.1038/s41559-018-0490-x>.
- Wintle, B.A., et al., 2019. Global synthesis of conservation studies reveals the importance of small habitat patches for biodiversity. *Proc. Natl. Acad. Sci. U. S. A.* 116, 909–914. <https://doi.org/10.1073/pnas.1813051115>.
- Zwiener, V.P., et al., 2017. Planning for conservation and restoration under climate and land use change in the Brazilian Atlantic Forest. *Divers. Distrib.* 23, 955–966. <https://doi.org/10.1111/ddi.12588>.