



Research article

Different stakeholder-based forest management scenarios facilitate balancing conservation and production in the bioeconomy

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ABSTRACT

Land-use policies founded on the expertise and interests of key stakeholders are likely the most implementable and politically long-lasting, assuming stakeholders share a broader, similar perception of the future. We investigated whether there is a difference in how eleven indicator species of conservation concern may be affected given policy and forestry scenarios of four key forest stakeholders for a 100 000 ha Swedish landscape over the coming 100 years. We used colonization-extinction models and species distribution models. Most species had stable or increasing metapopulation sizes or occurrence probabilities after 100 years under all except the most production-oriented scenario by private landowners. For six wood-decaying fungi, forests protected or managed with continuous cover forestry (CCF) drove the positive developments. By contrast, these species essentially disappeared from stands with even-aged clearcutting forestry. Regarding the 14.5% strict protection applied by the state-owned forest company increased the area occupied by these species. Protecting an even larger area and application of CCF in the scenarios of the (non-)governmental conservation organizations increased fungal metapopulation sizes even more. Four bird species showed stable or positive developments in all scenarios. The same held true for the epiphytic lichen *Lobaria pulmonaria*, because the management applied projected increasing host tree numbers and densities. Thus, protecting up to 20% of the productive forest, applying more alternative management regimes and less even-aged clearcutting rotation forestry has the potential to greatly increase the (meta)population size and improve the red-list status of all the focal species, and presumably also of other species of conservation concern.

1. Introduction

The long history of intensive management in Europe's boreal forest has resulted in conflicts between society's goals for wood-biomass production and biodiversity conservation (EU, 2021; Naumov et al., 2018). As a means of decreasing greenhouse gas emissions, there are strong incentives for countries to move towards bio-based economies, where carbon will originate from non-fossil sources, preferably from forests (Birch et al., 2010). This development will inevitably increase the pressure on forest biodiversity, even though several forest habitats and

species do already have an unfavorable conservation status (SEPA, 2007). There is thus increasing need for rigorous processes to identify management and policy instruments that can reconcile societies' different aims (Nordström et al., 2016; Söderberg and Eckerberg, 2013). One such process is the involvement of key stakeholders in land-use planning and policy-making.

Land-use policies that are founded on the expertise and particular interests of key stakeholders are known to be more implementable and politically long-lasting compared to policies lacking stakeholder involvement (Altman and Petkus, 1994). However, one obstacle in this

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process is the difficulty of anticipating the long-term consequences of the stakeholders' management suggestions. While stakeholders are experts in their fields, it can also be assumed that they anticipate a future in favor of their own agenda (Sandström et al., 2016). This is particularly problematic in an inert system like forests, where the consequences of a decision today may take a long time to be fully visible, of course varying depending on what the decision concerns. Simulation studies, where the development of an ecosystem is projected into the future based on different management and policy scenarios, can be used to expose the most likely ecosystem trajectories (Lämås et al., 2023). If the trajectories diverge from stakeholders' expectations, re-contemplation is possible and land-use conflicts might be more easily resolved (Merideth and Yaseen, 2000; Zachrisson and Beland Lindahl, 2013).

Currently, the scientific literature does not provide sufficient information for stakeholders to anticipate the long-term consequences of their policies for species of conservation concern in European boreal forests. Reasons include that the stakeholders lack the tools for simulating effects of the policies that they advocate, that scientists have not simulated the effects of the policies stakeholders advocate, and that there is a lack of long-term follow up studies on effects of conservation actions. Instead, our knowledge is limited to the short-term consequences of conservation actions (e.g. Klein et al., 2022; Koivula and Vanha-Majamaa, 2020) or scenario analyses addressing general questions on strategies or management (e.g. Mönkkönen et al., 2014; Moor et al., 2022). A few studies have addressed this shortcoming by assessing stakeholder scenarios based on the prevalence of different forest structures generally important for biodiversity (Eggers et al., 2020; Haatanen et al., 2014). To understand the response of rare or threatened species within the forest ecosystem, it is essential to simulate the response of several species representing different organism groups and utilizing different habitats. The reason is that although an increase in beneficial forest structures or habitats, such as dead wood or old forest, generally results in a higher number or density of species (Burner et al., 2021; Lassaue et al., 2011), different species have different spatial dynamics that depend on the spatiotemporal quantity of their required structures or habitats in the landscape (Belinchón et al., 2017; Moor et al., 2021).

In boreal Europe, the conflict among the different stakeholders on the balance between wood-biomass production and biodiversity conservation generally boils down to advocating for different proportions of protected forest versus forest used for wood production, and further using even-aged clearcutting rotation forestry (with retention) versus uneven-aged continuous cover forestry (CCF). Even-aged clearcutting forestry has been predominant since the Second World War in boreal Europe (Gustafsson et al., 2012). In Sweden, it has been applied to more than 90% of all productive forest land, accompanied by a drastic reduction of dead wood volumes, and of the area of forests with continuous crown cover or with a high share of deciduous trees (Östlund and Zackrisson, 1997). This transformation of the landscape has on the one hand led to a strongly reduced prevalence of many forest species, but on the other hand to an extremely efficient wood production (SLU Artdatabanken, 2020; Tikkanen et al., 2006). Sweden has ~1% of global forest land but provides 10% of the wood to the global wood market (Kumar et al., 2021).

In the Nordic forestry, a stand is clear-felled and replanted with either Norway spruce (*Picea abies*) or Scot's pine (*Pinus silvestris*). After 10-20 years, it is cleared of undesired tree species, and after two to three commercial thinnings from below (i.e. the smaller trees), the forest is clear-felled again (Kuuluvainen et al., 2012). The rotation length is 60-120 years. Even-aged clearcutting forestry typically also involves soil scarification to enhance regeneration. Due to concerns about the impact of clearcutting forestry on biodiversity, retention practices, where forest patches and structures particularly important for biodiversity are retained or created during clear-felling, has become the standard since the 1990s (Simonsson et al., 2015). This practice aims at maintaining or enhancing biodiversity and ecosystem services by ensuring temporal and spatial continuity of key habitat elements and processes (Gustafsson

et al., 2012). Also, as a result of decreasing forest diversity, as well as due to concerns about higher carbon emissions from clearcut rotations (Vestin et al., 2020), alternative management methods such as CCF (Joelsson et al., 2017) have been advocated. In fact, the New EU Forest Strategy for 2030 specifies CCF as a potential management method to reach a low-intensive forest management share of 20% to complement the 10% strictly protected (Lier et al., 2021). CCF is a silvicultural system without a clearcut phase (Pommerening, 2004), which aims at mimicking late-successional forest characteristics. In CCF, individual trees are harvested or small gaps created to enable natural regeneration (Kuuluvainen et al., 2012). CCF can benefit biodiversity, ecosystem services (Peura et al., 2018), as well as increase forest resilience against storms (Pukkala et al., 2016), insect damage (Klapwijk et al., 2016), and the changing climate (Keskitalo, 2011). CCF also outperforms even-aged methods in overall societal benefits (Pukkala, 2021). From the perspective of biodiversity conservation an increased area of forest protected from management has also been regarded necessary to meet environmental goals (Angelstam et al., 2020). Decreasing forestry intensity or setting aside more forest land likely comes with a loss in wood-biomass production and monetary income, accompanied by increasingly severe land-use conflicts (Jakobsson et al., 2021).

The overall aim of the current study is to contribute to resolving the conflict between conservation and wood production in European boreal forest. This is conducted based on our study Eggers et al. (2020) with stakeholder dialogues forming the basis for scenarios of future forest management and conservation aimed for learning about long-term consequences of forestry they could advocate. Specifically, we answer the four questions: 1) Is there a stakeholder scenario that allows reconciling wood production and the recovery of focal species of conservation concern in the long term? 2) How do the different management regimes impact the future species occurrences across scenarios? 3) Which are the forest conditions driving the focal species occurrences in the simulated scenarios and management regimes? 4) To what extent do the different stakeholder scenarios focus on wood production and biodiversity?

2. Material and methods

We first, in Eggers et al. (2020), established a dialogue with the private forest owners Federation of Swedish Farmers (LRF), the governmental Swedish Environmental Protection Agency (SEPA), the environmental advocacy group Swedish Society of Nature Conservation (SSNC), and the forestry company Sveaskog (SVEA, Fig. 1). Specifically, they formulated their preferred forest management and protection policy, that we then simulated 100 years into the future for a representative study landscape. For the current study, we conducted projections of occupancies of metapopulation dynamics or distributions of eleven species of conservation concern, including six wood-decaying fungi, one lichen, and four birds. All species are emblematic of old-growth or natural-like forests and indicative of a healthy forest ecosystem (Nitare, 2019; Pakkala et al., 2014).

2.1. Study landscape

The study landscape (103,313 ha productive forest) is located in middle boreal Sweden (Fig. 2). As detailed in Appendix 1 and Eggers et al. (2020), we used the segmented country-wide forest map to define the boundaries (Reese et al., 2003) of the 10,782 productive forest stands (mean growth $>1 \text{ m}^3 \text{ ha}^{-1} \text{ yr}^{-1}$). Specifically, we used land cover information to associate the stands with biomass productivity and to determine whether they were nature reserves or woodland-key habitats (areas with a high significance for biodiversity but not legally protected; together 7.8% of the area). Forest stand data for the simulation start year were extracted from National Forest Inventory data for middle boreal Sweden. The tree species composition was 40% Scots pine, 42% Norway spruce, 16% birch (*Betula* spp.), 0.4% aspen (*Populus tremula*), and 1.3%

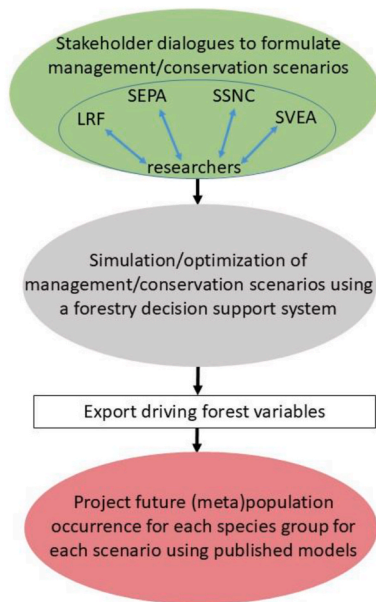


Fig. 1. Schematic illustration of the work process. It started with dialogues with stakeholders representing landowner, governmental, conservation, and wood industry organizations (LRF, SEPA, SSNC and SVEA) about which forest management and conservation scenario they wanted to be simulated (Table 1) for a case landscape (Fig. 2). The scenarios were simulated using the forestry decision support system Heureka. Finally, we projected future occurrence of the focal wood-decaying fungi, birds and a lichen under the scenarios (Fig. 3) using published models. For a technical description, see App. 3.

other broadleaves. The mean forest age was 72 years with 55% of the stands younger than 60 years. For the computationally intensive single-tree simulations of the epiphytic lichen *Lobaria pulmonaria* (see

Species models and simulations procedure below), we reduced the landscape area to a smaller representative area of 12,042 ha, split into 1600 stands, and with 6.6% of the area protected (Fig. 2).

2.2. Participating stakeholders and their forest management scenarios

The stakeholders who formulated forest management and policy requests were 1) the Federation of Swedish Farmers (LRF), representing ~140,000 private landowners that together own more than 25% of the Swedish forest, 2) the Swedish Environmental Protection Agency (SEPA), which is the governmental branch responsible for the Swedish Environmental Quality Objectives (SEPA, 2007), 3) the Swedish Society of Nature Conservation (SSNC), which is Sweden's largest NGO working for nature conservation with ~230,000 members, and 4) the state-owned company Sveaskog (SVEA), which is Sweden's largest forest owner (15% of the forest area).

The background study of Eggers et al. (2020) started with a series of group dialogues that included the authors of the current study (except JK) and one representative from each stakeholder (Fig. 1). There were also discussions within each stakeholder. Specifically, the stakeholders were asked to describe how they would manage the forest in the study landscape and which specific goals they would like to see accomplished during the simulation period of 100 years. For Swedish forest management practice and historical background, see Swedish Forest Agency (2020). During scenario formulation, the stakeholders could 1) choose whether a stand should be managed or protected (never less area protected than the initial 7.8%), 2) if managed, choose which proportion of the stands should be subjected to either even-aged forestry or uneven-aged continuous cover forestry (CCF), 3) choose if trees should be regenerated naturally or by planting, 4) choose which tree species to prioritize during pre-commercial and commercial thinnings and how many thinnings should usually be done, 5) define which proportion of a stand should be retained during felling, 6) choose the number of retained trees and high stumps on the non-retained parts during felling,

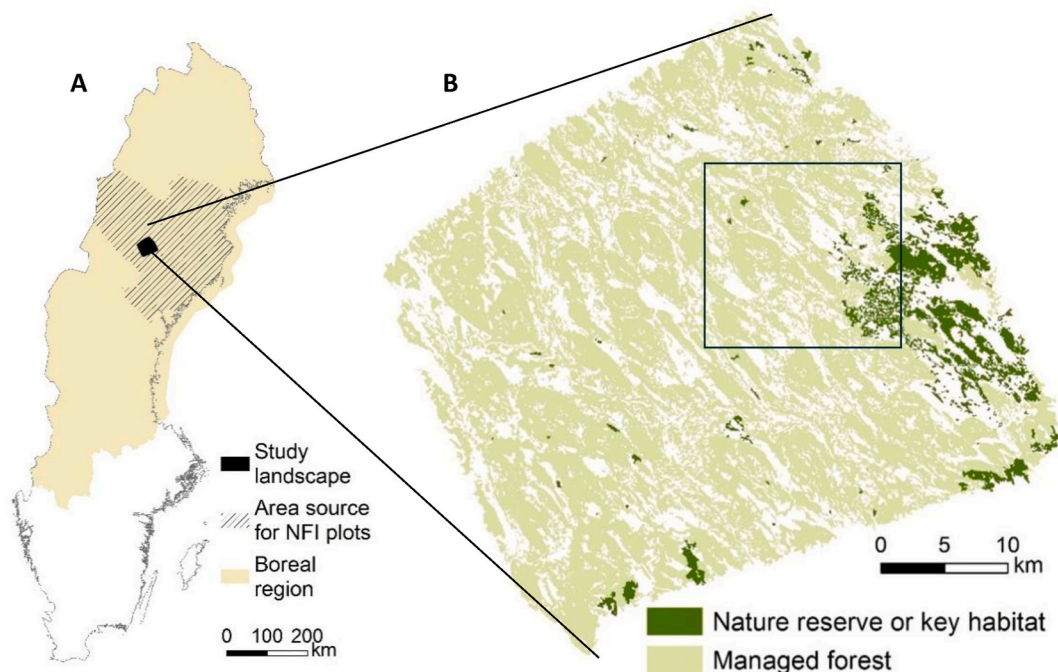


Fig. 2. A) The study landscape is located in Vilhelmina county in the middle of the boreal region in Sweden. Forest data for the simulation start year were extracted from the National Forest Inventory plots in the region shaded surrounding the study landscape. B) Most of the study landscape is covered by productive forest, of which 7.8% is permanently protected in our simulations (nature reserves and woodland key habitats). However, some stakeholders allocated more land for protection (Table 1). The square shows the 12,042 ha area for which we simulated the metapopulation dynamics of *Lobaria pulmonaria*. For further details on how the study landscape was set up, see Eggers et al. (2020).

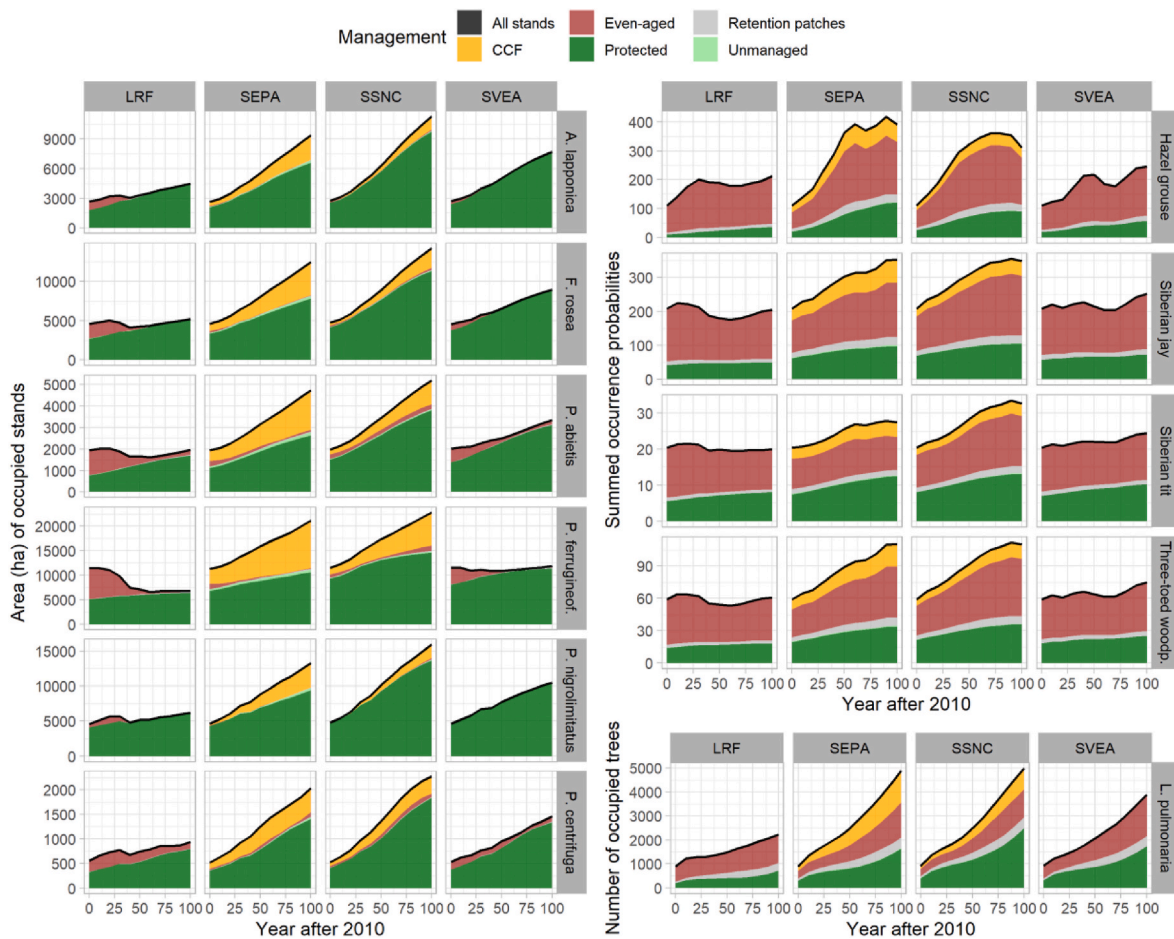


Fig. 3. Projections of metapopulation dynamics or occurrence probability of wood decaying fungi (left panels), the lichen *Lobaria pulmonaria* (bottom right panels) and bird species (top right panels) given four stakeholder scenarios (LRF, SEPA, SSNC and SVEA, Table 1) with different management and conservation regimes 100 years into the future for a study landscape (Fig. 1). Results are presented by management regime and summed for all stands (black) with either of the five regimes. Contributions by unmanaged and retention patches are marginal and detailed in Fig. S1. See *Focal species of conservation concern* for full species names.

and 7) define targets for the tree species composition, rotation length, deadwood volume, monetary output as well as for harvest related variables. The group discussions focused on management practices (Table 1, Table S1) that can be simulated in the forest decision support system Heureka, which is widely used in Sweden to investigate impacts of forest management on wood harvest but also some other ecosystem services and biodiversity indicators (Lämås et al., 2023). After a first round of scenario definition, preliminary results were presented to the stakeholders with the opportunity to modify their scenario. At the end of this second round of discussion, we used four definitive scenarios, hereafter called LRF, SEPA, SSNC and SVEA (see above, Fig. 1, Table 1).

2.2.1. Forest scenario simulation and optimization

The forest management scenarios were simulated and optimized using the PlanWise application of the Heureka forest decision support system, which includes a built-in optimization tool (Lämås et al., 2023). For scenario descriptions, see Table 1 and for management regimes described, see Table S1. The Heureka simulation tool contains a suite of empirical regression models describing tree growth, ingrowth and mortality, including management effects such as thinning response. The models are based on data from the National Forest Inventory (Fridman et al., 2014), long-term experiments and yield plots. Heureka also includes models for deadwood decomposition, soil carbon dynamics and other ecosystem processes. The windows-based, freely available Heureka system is widely used in Sweden: in practical forestry to determine long-term harvest levels and in research to study the effects of different

forest management strategies on future forest development and how to balance various goals related to forests and forestry (Lämås et al., 2023). We thus chose Heureka to simulate the forest management scenarios because it is the best available tool for simulating forest management of Swedish forests. PlanWise simulates a set of potential management alternatives for each forest stand across a certain period (in this study 100 years) in 5-year time steps and selects the optimal combination of management regimes given targets and constraints defined by the user (here the stakeholders). Scenarios are thus generated by adjusting the parameters that define how forests are managed. At every time step and for every forest stand, a large number of variables describing forest condition can be extracted, e.g. harvested volume, volume of living or dead spruce, net present value and variables driving the (meta)population dynamics and distribution patterns of the focal species (Fig. 1). A detailed description of the Heureka simulations and optimizations used for the current study is presented in Eggers et al. (2020). For every stakeholder scenario and every 5-year period for 100 years, we extracted all forest variables that constituted explanatory variables in the models of the forest species studied. This then allowed making projections of species metapopulation sizes or occurrence probabilities into the future given each scenario (Fig. 1, App. 3). To further detail the contrasts between the scenarios in terms of wood production and biodiversity, we also calculated the mean annual harvest and growth, growing stock, net present value (3% discounting rate), old forest area (≥ 140 years), mature broadleaf-rich forest area (≥ 80 years & $\geq 25\%$ of basal area are broadleaves), and dead wood volume.

Table 1

Characteristics of the four stakeholder scenarios projected. The objective function was to maximize net present value (NPV), and additionally there were constraints on the management, economy or environment (A-C). See Eggers et al. (2020) where the scenarios were simulated for a full description of the protocol. CCF is Continuous Cover Forestry.

	Federation of Swedish Farmers (LRF)	Swedish Environmental Protection Agency (SEPA)	Swedish Society of Nature Conservation (SSNC)	Sveaskog (SVEA)
Protected (%)	7.8	17	20.1	14.5
Management regimes on non-protected land	Even-aged	Even-aged, CCF	Even-aged, CCF	Even-aged
Retention patches (% of stand)	6%	10%	10%	9%
Retention trees (per ha)	8	30	20	10
High stumps (per ha)	4	6	5	3
<i>Optimization constraints</i>				
A. management		Proportion of forest managed with CCF: 65% of total forest area	Proportion of forest managed with CCF: 30% of total forest area	
B. economic indicators	Even net revenues (maximum deviation between consecutive periods: $\pm 20\%$); $\geq 50\%$ of final fellings occur ≥ 20 years after minimum legal final felling age has been reached	Even harvest flow (maximum deviation between consecutive time steps: $\pm 20\%$)	Non-decreasing harvest flow	Even harvest flow (maximum deviation between consecutive periods: $\pm 10\%$)
C. environmental indicators		Deadwood target 25 m ³ /ha in production forest Proportion of mixed forest $\geq 35\%$ ^a Proportion of broadleaf forest does not decrease over time	Deadwood target in production forest: 20 m ³ /ha ³ Broadleaf volume at least 20% of total volume ^a At least 20% of production forest ≥ 140 years old ¹	

^a At the end of the simulation, i.e. after 100 years.

2.3. Focal species of conservation concern

We chose species, which combined are indicative of the state of a broad range of the boreal forest's biodiversity, and that differ in their sensitivity to the intensity of forestry practices.

All six wood-decaying fungi particularly occur in forests with high amounts of Norway spruce deadwood. They are to a diverging degree limited by spore dispersal, and by the quality, humidity, and decay stage of the deadwood (Nordén et al., 2013; Runnel and Löhmus, 2017). The presence of all six fungi indicates the entire breadth of wood decay stages and thereby the availability of habitat for a large number of deadwood-dependent species of many organism groups. While *Phellinus abietis* (red-list category Near Threatened NT, SLU Artdatabanken, 2020) can grow on fresh dead trees that are still standing, *P. nigrolimitatus* (NT) fruitbodies are found on already strongly decayed wood. Fruitbodies of *P. ferrugineofuscus* (NT), *Phlebia centrifugia* (Vulnerable VU), *Fomitopsis rosea* (NT) and *Amylocystis lapponica* (VU) are found on logs of intermediate decay stages. *Phlebia centrifugia* and *A. lapponica* are indicators of forests with a long history of undisturbed development and a constant humidity (Nitare, 2019; von Bonsdorff et al., 2014). *Amylocystis lapponica* is almost entirely limited to pristine old-growth forests (Runnel et al., 2020).

Lobaria pulmonaria (NT) is a foliose lichen that uses aspen and goat willow as host trees in boreal Europe (Gu et al., 2001). The species is a good indicator of forest with a long substrate continuity and a stable microclimate. It is an umbrella species for many rare and threatened macrolichens.

Among birds, the Siberian jay (*Perisoreus infaustus*, Least Concern LC in Sweden) and the Siberian tit (*Poecile cinctus*, NT) are indicative of coniferous forests with a high variation in vegetation density both vertically at the stand level, but also horizontally at the landscape scale (Klein et al., 2020; Virkkala, 1990). The three-toed woodpecker (*Picoides tridactylus*, NT) indicates high abundance of fresh and decaying coniferous dead wood (Angelstam et al., 2004) and through its presence, high abundance of cavities for hole-nesters (Pakkala et al., 2018). The hazel grouse (*Tetrastes bonasia*, NT), indicates mixed-leaf forests with an intact understorey (Swenson, 1993).

2.4. Species models and simulations procedure

For each species and stakeholder scenario, we used published models for metapopulation dynamics and species distribution. These were used to project the species developments 100 years into the future. For wood-decaying fungi, we used models for spatially implicit colonization-extinction dynamics developed in Moor et al. (2021), for *L. pulmonaria* we used the model for spatially explicit colonization-extinction dynamics developed in Moor et al. (2022), and for birds we used models for species occurrence developed in Henckel et al. (2020). For model details, see Appendix 2, Tables S2–S3. Data on the driving explanatory variables in the species models were provided from the Heureka simulations described in *Forest scenario simulation and optimization* above. For birds, we also used the average temperature and precipitation in spring and winter with an approximate 6.5 km² grid resolution across the period 1989–2010 (EURO4 Mesan; Landelius et al., 2016). The species models were originally built using field data collected in Sweden and Finland, in areas with similar climatic conditions as in our study landscape. In the studies where the models were built, we also explored basic spatiotemporal properties of the (meta) 2population dynamics and distributions (see also² Belinchón et al. (2017); Bradter et al. (2021, 2018); Fabritius et al. (2019) answering further such questions). Whether the model concerned (meta) population dynamics or species occurrence depended on the species data available for model building. For the

² The Swedish NFI uses a systematic, sample-based survey design that covers the whole of Sweden and forms the basis for official forest statistics. It started in 1923, has been expanded since then and is now conducted annually by the Swedish University of Agricultural Sciences (SLU). The design consists of circular sample plots arranged in a systematic grid with a random start, ensuring spatial coverage across the country. These plots are grouped into clusters (tracts) of square or rectangular shape, with the number of plots per cluster varying by region. Around 12,000 plots are measured in the field annually. Permanent tracts are revisited every five years to track change over time, while temporary tracts are visited only once. Plot radius is 10 m for permanent plots, and 7 m for temporary plots. Field data from the plots provide measurements for tree characteristics and other forest attributes, which are expanded to national estimates.

wood-decaying fungi, we simulated the metapopulation colonization-extinction dynamics among the 10,782 stands in the landscape. For *L. pulmonaria*, we simulated the spatially explicit colonization-extinction dynamics among all aspens/goat willows in the reduced study area. For birds, we predicted occurrence probability for every 1 km³ of the study landscape. The grain size of 1 km² was chosen by Henckel et al. (2020) as a suitable compromise of territory/home range size of the species considered. These spatial characteristics are summarized in Table S4.

To aggregate the simulation results, we first calculated the mean predicted occupancy per species, policy scenario, management regime, and five-year period. To calculate the metapopulation size for wood-decaying fungi and *L. pulmonaria* we then multiplied the mean occupancy with the total stand area (103,313 ha) or total number of trees (starting with 31,900 trees, then varying through time), respectively, assigned to a certain management regime. For the birds, we summed the 1 km square occurrence probabilities. The number of squares was 1416, which is thus the maximum achievable summed occurrence probability for the whole study area. Squares could include stands with different management regimes. To calculate bird occupancy per management regime, the occurrence probability was weighted by the proportion of the square area to which the regime was applied. In Moor et al. (2022), we used the same models and methods as herein, but unrelated scenarios. All analyses were performed in R 4.0.4 (R Core Team, 2021).

3. Results

3.1. Response of the species to the stakeholder scenarios

The area of occupied stands of wood-decaying fungi, the number of trees occupied by *Lobaria pulmonaria* (i.e. their metapopulation sizes) and the summed occurrence probabilities of birds increased strongly during the 100 years simulation for all species in the SEPA and SSNC scenarios (Fig. 3). In the SVEA scenario, all species either remained stable or increased. In the LRF scenario, *P. ferrugineofuscus* decreased, but *A. lapponica*, *P. centrifuga*, the hazel grouse and *L. pulmonaria* increased, while other species remained stable. Considering a maximum achievable summed occurrence probability of 1416 for each bird species, the summed occurrence probabilities were still low after 100 years, irrespective of the scenario, especially for the three-toed woodpecker and the Siberian tit. The same holds true for the fungi maximally occupying 22 809 ha in the SSNC scenario, out of 103 313 ha possible. Finally, the lichen occupied maximally 4986 trees out of maximally of 88,052 (Fig. 3).

The metapopulation size of wood-decaying fungi increased in all stands not managed by even-aged clearcutting forestry, irrespective of the scenario (Fig. 3). This is also the case for unmanaged and retention patches, although their contributions are marginal (Fig. S1). The area protected in all scenarios and the area managed with CCF in the SEPA and SSNC scenarios were the main contributors to the increasing metapopulation size in the coming 100 years. All wood-decaying fungi decreased, in most cases strongly, in all scenarios on land managed with even-aged forestry and were almost absent from this management regime after 100 years. The only species, which did not decrease in stands managed with even-aged forestry, was *P. ferrugineofuscus* in the SSNC scenario. The final consequence of this is shown by comparing maps of management regimes (Fig. S2) and species distributions at the

³ The NFI data is regularly transformed into a database that contains all information needed by Heureka. This includes site-specific information such as location, soil moisture class, vegetation type and site index, as well as a description of the tree layer with information on mean age, mean height, mean diameter, tree species proportions, basal area and number of stems. We used a database containing information on NFI plots collected during 2008-2012 to extract the information needed by Heureka and construct the study landscape.

start and end (year 100) of the simulations (Figs. S3–S8). In the SEPA and SSNC with considerable CCF (Fig. S2), all fungal species are retained in the production landscape. The SVEA scenario is intermediate in that the higher area protected throughout the landscape here also retains the species, albeit at lower occupancy. In the LRF scenario, the species are generally retained in only the eastern part where protection dominates.

The metapopulation size of *L. pulmonaria* increased on all management regimes, but most dramatically in protected areas, in all scenarios (Fig. 3, Fig. S1). The increase was strongest in the SSNC and SEPA scenarios protecting up to 20%. In these, even-aged forestry also made up the smallest share and also CCF partly explained the increase. Comparing maps of species distributions at the start of the simulation with simulation year 100 (Fig. S9) clarify the only somewhat lower future metapopulation size in the SVEA scenario compared to the conservation-oriented SEPA and SSNC scenarios – the retention trees and retention patches (Table 1) in the stands managed with even-aged forestry partly compensates for the lack of CCF. The *L. pulmonaria* occupancy pattern in simulation year 100 is similar among these three scenarios.

The summed occurrence probabilities of all birds increased in the SEPA and SSNC scenarios, irrespective of the management regime in the 1 km² cell (Fig. 3, Fig. S1). The same was true for the hazel grouse in the LRF and SVEA scenarios. The occurrence probability of the Siberian jay and the three-toed woodpecker was stable in the LRF and SVEA scenarios, although they had somewhat different management regimes. The Siberian tit increased in protected areas in the LRF and SVEA scenarios, but decreased in LRF and was stable in SVEA in all other management regimes.

The spatio-temporal dynamics over the 100 year projection period (Figs. S10–S13) show that across all scenarios, the eastern part of the study area where protection dominated, contained the highest density of squares with higher occurrence probabilities for all four bird species in simulation year 100. In the conservation-oriented SEPA and SSNC scenarios, single squares or small clusters with similarly high occurrence probabilities were scattered at lower densities throughout the rest of the landscape for Siberian jay, three-toed woodpecker, hazel grouse and to a lesser extent Siberian tit. In the LRF scenario, there were few squares with higher occurrence probabilities outside of the eastern area for any species while the SVEA scenario was intermediate. Nonetheless, with maximum occurrence probabilities per square of only 0.1 and 0.2 for Siberian tit and three-toed woodpecker, respectively, these two species remained rare in all scenarios.

3.2. Response of forest conditions driving the species responses

The volume of downed spruce deadwood driving the fungal metapopulation dynamics increased in all scenarios and particularly on protected and unmanaged land (Fig. 4). In stands managed with even-aged clearcutting forestry spruce deadwood decreased in LRF and SVEA and was stable in the SEPA and SSNC scenarios. The other driving environmental variable in the models for these species, stand age, increased strongly in all management regimes except with the regime even-aged forestry. Across all management regimes, the area-weighted average stand age substantially increased only in the SSNC and SEPA scenarios (Fig. 4).

The area-weighted stand age driving the *Lobaria pulmonaria* metapopulation dynamics decreased in all but the SSNC scenarios (Fig. 4). This decrease takes place in stands with even-aged management, which was the only management with a decreasing weighted age across all scenarios. Weighted age particularly increased in protected and unmanaged stands. The total number of suitable host trees, and hence tree density affecting the connectivity-dependent colonization rate, increased the most and was highest in the SEPA and SVEA scenarios. This positive development mainly took place in even-aged forestry across all scenarios.

All environmental variables driving the bird species distribution

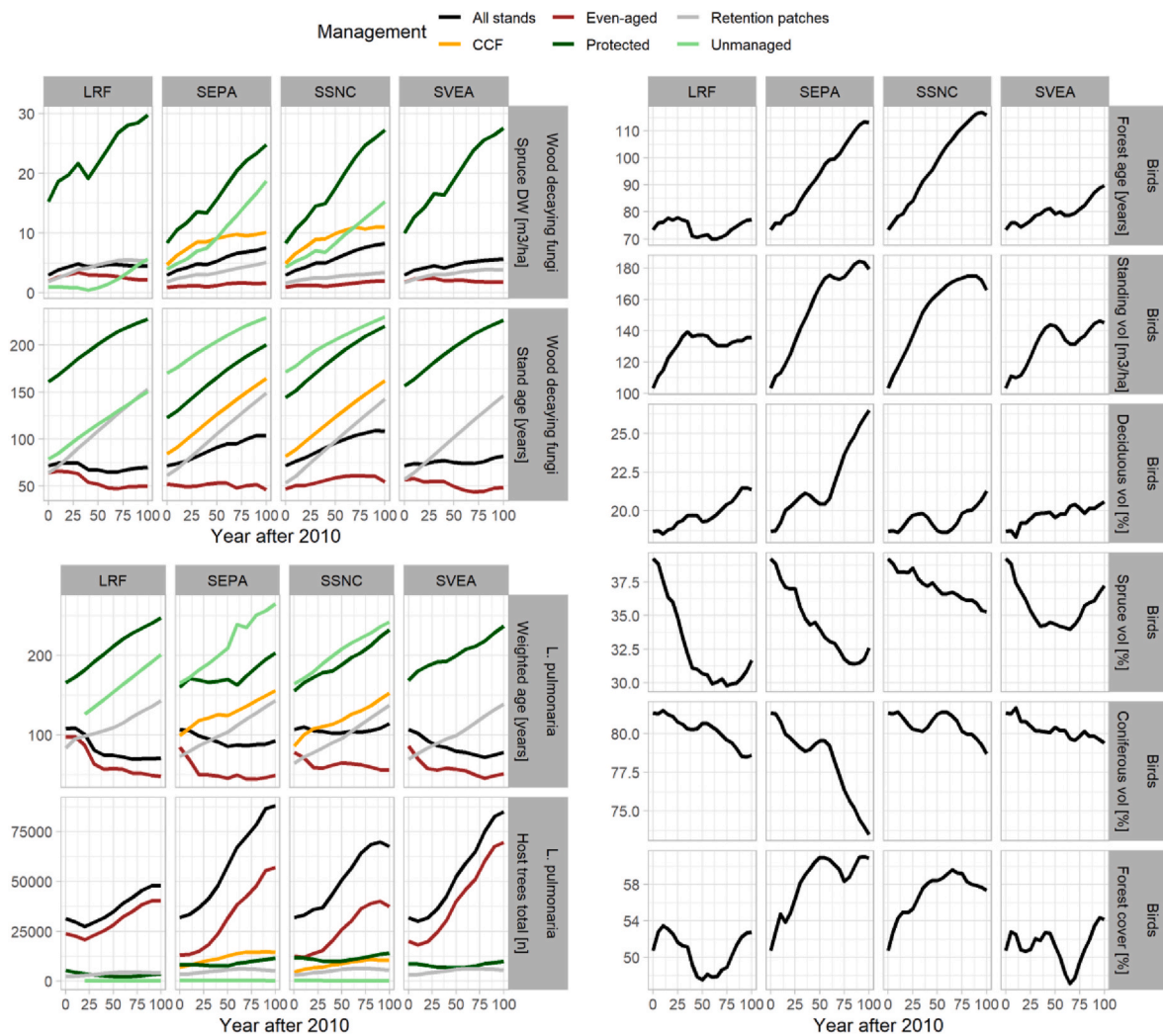


Fig. 4. Projections of the driving environmental variables used to project metapopulation dynamics or occurrence probability (Fig. 3) of wood decaying fungi (upper left panels), the lichen *Lobaria pulmonaria* (lower left panels) and bird species (right panels) given four stakeholder scenarios (LRF, SEPA, SSNC and SVEA, Table 1) with different management and conservation 100 years into the future for a study landscape (Fig. 1). Spruce DW = Spruce dead wood. Results are presented by management regime and summarized for all stands (black) with either of the five regimes.

models except the standing volume of spruce and coniferous species increased in all scenarios. The increases were strongest in the SEPA and SSNC scenarios. The increase of the standing volume of deciduous trees and the corresponding decrease of coniferous trees were particularly strong in the SEPA scenario (Fig. 4).

3.3. Multi-criterion comparison between scenarios

The comparison of stakeholder scenarios with regard to their prioritization of monetary income, growing stock, harvest, and biodiversity showed that LRF clearly prioritized net present value, growing stock, and harvest over biodiversity indicators (mature broadleaved forest, deadwood, and old forest; Fig. 5). SVEA prioritized similar to LRF, except for growing stock, which was not in focus in the SVEA scenario. The SEPA and SSNC scenarios were almost identical, with a clear focus on biodiversity indicators and growing stock (Fig. 5).

4. Discussion

Land-use conflicts, here between wood production and biodiversity conservation in the boreal forest, have repeatedly been shown to be most successfully resolved by stakeholder involvement (Altman and Petkus, 1994; Lees et al., 2021). Here we present effects of different key

stakeholders' advocated management and conservation policies on developments of eleven species of conservation concern the coming 100 years, also revealing the contrasting species responses to different management regimes. We show that stakeholders who advocate decreasing the area managed with even-aged forestry will contribute to a positive development of all species groups and that, more specifically, a higher proportion of continuous cover forestry (CCF) than today will benefit many species on the production land. By contrast, in the two most production-oriented scenarios, species increased almost only in protected areas. Among these two scenarios, the SVEA scenario was more successful in increasing the areas occupied than the LRF scenario due to the larger area protected scattered through the landscape. Finally, some species of conservation concern will continue being rare after 100 years, even in the scenario advocated by the non-governmental conservation organization SSNC. This means that there was no scenario reconciling wood production and revenue with a recovery of all the focal red-listed species of conservation concern in the long term. However, the knowledge gained can form the basis for boreal European stakeholders to re-evaluate their management and conservation strategies to become more cost-efficient, for guiding policy to find compromises among stakeholders, as well as to facilitate decision making by lawmakers. Unfortunately, there is limited legal support for collective planning among landowners or stakeholders in the Nordic countries. However,

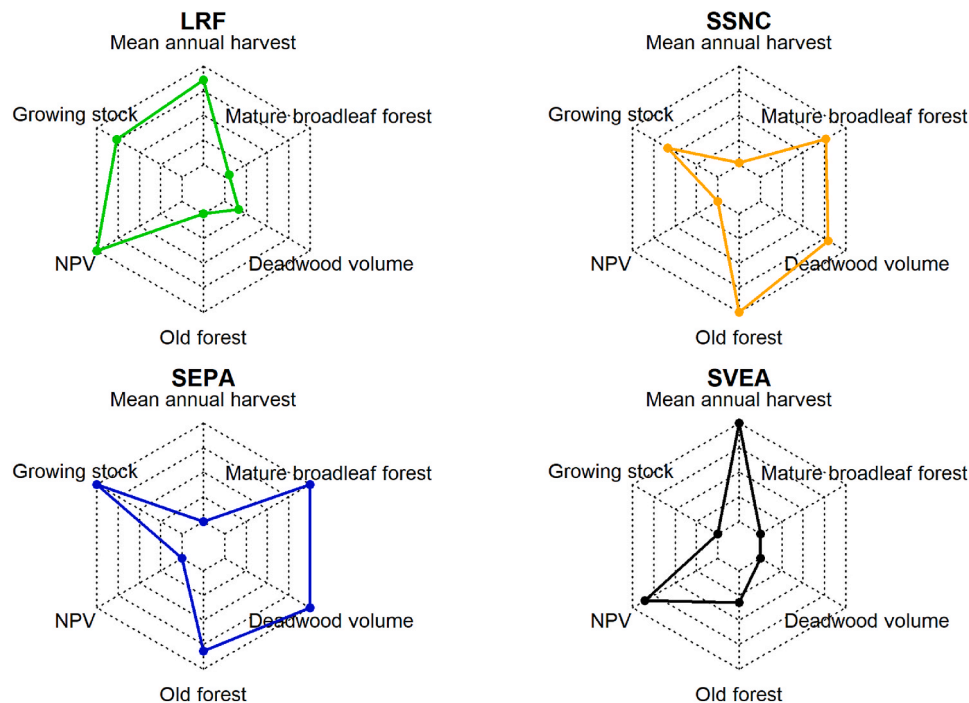


Fig. 5. Priorities of stakeholders in terms of production (growing stock, net present value (NPV), mean annual harvest) and the biodiversity indicators old forest area (≥ 140 years), mature broadleaf-rich forest area (≥ 80 years & $\geq 25\%$ of basal area are broadleaves), and dead wood volume. The quantity of each indicator is the proportion of maximum obtained for the indicator among the results of the scenarios. Hence, each indicator reach maximum quantity in one of the scenarios.

alternatives have been proposed. One example is a tax-fund system, building on the concept of common but differentiated responsibility among forest landowners (Zabel et al., 2018). The landowners in the landscape periodically make a monetary contribution collected in a fund. The proceeds are then used to compensate forest owners that must comply with restrictions that considerably restrict their ongoing land use. At least Croatia has piloted such a system related to forests (Lovric and Lovric, 2013). Yet another approach is auction, where land-owners offer their land for conservation at a cost they specify, and the authority then chooses among offers depending on also the conservation value of the land offered (Latacz-Lohmann and Van der Hamsvoort, 1998). However, experiences are mixed and can be surprising (Primmer, 2017).

The SVEA scenario projected more positive species developments than the other production-oriented scenario LRF. One reason is the larger area protected without forest management leading to greatly increasing volumes of living and dead wood and (mean) stand age driving the positive development of a wide range of organism groups, here especially the fungi (Moor et al., 2021; Nördén et al., 2013). Forest protection also benefits the four bird species: hazel grouse prefers richly structured stands with a high proportion of deciduous trees; Siberian jay prefers older forests and has higher reproductive success in patches of structurally rich forest which offer better visual protection from predators; Siberian tit depends on dead trees as it nests in cavities and its invertebrate food has a higher availability in older, more structurally diverse forests, while the cavity-nesting three-toed woodpecker depends on dying and dead trees for both nesting and foraging (Åberg et al., 2003; Eggers et al., 2008; Griesser and Lagerberg, 2012; Henckel et al., 2020; Klein et al., 2020; Mathys et al., 2006; Pakkala et al., 2002, 2018; Versluijs et al., 2020; Virkkala, 1990; Virkkala and Liehu, 1990). Yet another mechanism is the increasing density of host trees of *L. pulmonaria* also in the managed landscape increasing its colonization rate (Belinchón et al., 2017; Fabritius et al., 2019), occupancy and distribution throughout the landscape. The fact that the proportion of protected forestland is essential for many red-listed forest species has been stressed repeatedly, e.g. Berglund and Jonsson (2008), Gu et al. (2001), Layton-Matthews et al. (2018), including several of the current

focal species. The number usually proposed for the boreal forest is 20-30% of the forest area, which is indeed also a target of the Kunming-Montreal Global Biodiversity Framework. However, the species developments also depend on the intactness of the green infrastructure on production land (Angelstam et al., 2020; Moor et al., 2022). The management regime has a strong influence on the extent to which the studied species can exist in the production forest. Thus, recovery and conservation of species, in particular threatened species, to significantly reduce extinction risk (target 4 of the Kunming-Montreal Global Biodiversity Framework) also requires applying management regimes that allow developing habitat suitable for the species negatively affected by forestry. For example, wood-decaying fungi increased on land managed with CCF and on retention patches, but retention patches, which are part of the modern even-aged forestry, still had very small total occupied areas of the focal species after 100 years. Uneven-aged management also benefits birds such as the Siberian jay through more continuous provision of important resources and maintenance of a more structurally rich forest (Pukkala et al., 2012). The strong increase on CCF confirms findings of earlier studies that landscapes with a higher proportion of CCF are more multifunctional (Eyvindson et al., 2021). They may also be the most cost-efficient management regime for reconciling production and biodiversity (Pukkala, 2021), and are indeed also required for re-building the green infrastructure (Moor et al., 2022). CCF in combination with a lower proportion of protected forests (than without CCF) may sustain the (meta)populations of species in these organism groups, at least for some species of conservation concern. If we had also included species known to be highly dependent on tree continuity, such as certain mycorrhizal fungi (Kim et al., 2021), the importance of CCF for forest biodiversity would probably have been even more evident.

Some species, especially *P. centrifuga*, the Siberian tit, and the three-toed woodpecker had a low total area occupied or low occurrence probability at the start of the simulation. Even though these metrics increased, in some cases drastically, the species or their habitat nevertheless remained rare and the species will likely be susceptible to stochastic local extinction in all scenarios (Hanski and Ovaskainen, 2000). This risk may be particularly high for species like the three-toed

woodpecker that commonly depend on resources from outside their core breeding territory and for regions of low habitat quality where sites with high quality habitat are too sparse to be continuously occupied (Pakkala et al., 2002).

The reason for this strong potential to improve the state of biodiversity within 100 years is the fact that the managed forests in the study region have been used very intensively since the Second World War (Gauthier et al., 2015; Östlund and Zackrisson, 1997). Consequently, at the start of the simulation, the forests are very young and deprived of structures generally important for biodiversity, such as dead wood as well as old and deciduous trees (see Fig. 4). In addition, even many unmanaged forests in the region have been affected by forestry historically (Linder et al., 1997), such that for example dead wood levels are much lower than in old-growth forests (Nilsson et al., 2002). Thus, because of the currently unfavorable state of the EU boreal forest from the perspective of biodiversity (e.g. SEPA, 2007), any action by a stakeholder to enhance biodiversity will likely have a clear positive future impact. This can be seen for the four bird species with increases in occurrence probabilities also in even-aged forestry in the conservation-oriented scenarios, and in some instances even in the production-oriented scenarios. Increases in forest age and volume, more structurally-rich forests from less severe clearings and thinnings, structural diversity among patches, and specifically for the hazel grouse a higher proportion of deciduous trees, will improve the suitability of habitats (Åberg et al., 2003; Griesser and Lagerberg, 2012; Henckel et al., 2020; Mathys et al., 2006; Virkkala, 1990). This is also clear in the case of *L. pulmonaria*, with metapopulation increases in all scenarios because its boreal host trees *S. caprea* and *P. tremula* are not cut during early prunings, clearings and thinnings in any of the scenarios. Especially in combination with sparsely occurring protected areas spread out through the landscape (presumably constituting dispersal sources) in the SVEA scenario, this led to almost equally positive projections and distribution patterns in year 100 as with the SEPA and SSNC scenarios. This policy seems not realized in Swedish forests though, evidenced by a lack of increase in at least *P. tremula* ever since the new Forestry Act was adopted in 1993 (Kyaschenko et al., 2022). We are not aware of national trends in other Nordic countries, but it is clear that this tree species is currently decreasing in Nordic forest reserves (Hardenbol et al., 2020). However, a higher volume of deciduous trees could even increase gross societal benefits of forestry (Pukkala, 2021). We show that also minor changes in forest management can improve conditions for species that depend on higher deciduous volumes. Also *L. pulmonaria* recolonization after disturbance in Switzerland has been shown to be effective (Wagner et al., 2006), although the study concerned a more local scale.

Another important aspect, when discussing results of simulations as long as 100 years into the future, is different uncertainties. All quantitative scenario simulations based on field-based models conducted in science are associated with three uncertainties, model formulation, sampling and natural variation in space and time. However, these scenario simulations are the only way that science can do quantitative projections of future developments of species. They are thus the available tool to anticipate effects of future, alternative management on future developments, and they build on the current understanding of population dynamics, trends and their drivers. While uncertainty goes both ways, it is the uncertainty in decreases of (meta)population size or occurrence probability that is most relevant in conservation. For the sake of very rare species, a higher proportion of area protected than the 14.5% in the SVEA scenario might be necessary to counteract the possibility that we projected a too high (meta)population size or occurrence probability. For example, *P. centrifuga* occupied only 1500 ha (ca. 1.5% of the area) after 100 years even though 14.5% (14,935 ha) were protected in the SVEA scenario. Indeed, the exact projected numbers are uncertain, but they make it clear that landscape-level occupancies can be minimal also in landscape with 14.5% protection (although occupancies can be increased in old, protected forest with large amount of spruce deadwood, Moor et al., 2021). These low occupancies lead to

significant landscape extinction risks (Hanski and Ovaskainen, 2000), as indeed also projected for *L. pulmonaria* in landscapes with low host tree density and short rotation length (Belinchón et al., 2017). A higher proportion of protected area in the SSNC and SEPA scenarios had a positive effect on the species, with metapopulation sizes and occurrence probabilities drastically increased. In fact, several species would no longer be red-listed in the coming decades under these two scenarios. Despite the above limitations, the results of the scenario projections for Siberian jay from this study were in good agreement with projections of the number of individuals of Siberian jays given the LRF, SEPA and SSNC scenarios with a detailed individual-based model based on long-term observational data of population processes (Bradter et al., 2021), thus increasing confidence in our conclusions.

As discussed already in Eggers et al. (2020) where these scenarios were developed, the stakeholder discussions did not include potential effects of climate change. Global warming is expected to increase growth in northern Europe, but it also involves increased risks through extreme weather events and changed disturbance regimes (Lindner et al., 2014). These may particularly benefit deciduous trees, both as a natural response and because of adaptation of the management (Kellomäki et al., 2018). This in turn will affect the focal species (e.g. Mair et al., 2017). The focus here, however, is on relative differences between stakeholder-defined forest management scenarios, and we believe that these will be valid also under a future changing climate.

In summary, stakeholder scenarios allowing the currently young forest landscapes to become older, practicing significant retention and protecting up to 20% should lead to future occupancy increases of several species of conservation concern. Additionally switching some of the even-aged forestry to CCF may even increase the occupancies of the more specialized species on the production land. Forthcoming studies should also investigate impacts of alternative future climates, and conversely, how different forest use may affect climate change mitigation (e.g. Niemi et al., 2025).

CRedit authorship contribution statement

Laura Henckel: Writing – review & editing, Writing – original draft, Visualization, Investigation, Formal analysis, Conceptualization. **Julian Klein:** Writing – review & editing, Writing – original draft, Investigation, Formal analysis, Conceptualization. **Jeannette Eggers:** Writing – review & editing, Methodology, Conceptualization. **Ute Bradter:** Writing – review & editing, Conceptualization. **Henna Fabritius:** Writing – review & editing, Methodology, Formal analysis, Conceptualization. **Helen Moor:** Writing – review & editing, Methodology, Conceptualization. **Tord Snäll:** Writing – review & editing, Writing – original draft, Supervision, Project administration, Methodology, Conceptualization.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Tord Snäll reports financial support was provided by Swedish Research Council Formas. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.jenvman.2026.129234>.

Data availability

No data was used for the research described in the article.

References

- Åberg, J., Swenson, J.E., Angelstam, P., 2003. The habitat requirements of hazel grouse (*Bonasa bonasia*) in managed boreal forest and applicability of forest stand descriptions as a tool to identify suitable patches. *For. Ecol. Manag.* 175, 437–444. [https://doi.org/10.1016/S0378-1127\(02\)00144-5](https://doi.org/10.1016/S0378-1127(02)00144-5).
- Altman, J.A., Petkus, E., 1994. Toward a stakeholder-based policy process: an application of the social marketing perspective to environmental policy development. *Policy Sci.* 27, 37–51. <https://doi.org/10.1007/BF00999598>.
- Angelstam, P., Ekelund, P., Schlaepfer, R., 2004. Dead wood threshold values for the three-toed woodpecker presence in boreal and sub-Alpine forest. *Biol. Conserv.* 119, 305–318. <https://doi.org/10.1016/j.biocon.2003.11.014>.
- Angelstam, P., Manton, M., Green, M., Jonsson, B.-G., Mikusiński, G., Svensson, J., Maria Sabatini, F., 2020. Sweden does not meet agreed national and international forest biodiversity targets: a call for adaptive landscape planning. *Landscape Urban Plan.* 202, 103838. <https://doi.org/10.1016/j.landurbplan.2020.103838>.
- Belinchón, R., Harrison, P.J., Mair, L., Várkonyi, G., Snäll, T., 2017. Local epiphyte establishment and future metapopulation dynamics in landscapes with different spatiotemporal properties. *Ecology* 98, 741–750. <https://doi.org/10.1002/ecy.1686>.
- Berglund, H., Jonsson, B.G., 2008. Assessing the extinction vulnerability of wood-inhabiting fungal species in fragmented northern Swedish boreal forests. *Biol. Conserv.* 141, 3029–3039. <https://doi.org/10.1016/j.biocon.2008.09.007>.
- Birch, K., Levidow, L., Papaioannou, T., 2010. Sustainable capital? The Neoliberalization of nature and knowledge in the European “Knowledge-based bio-economy.”. *Sustainability* 2, 2898–2918. <https://doi.org/10.3390/su2092898>.
- Bradter, U., Mair, L., Jönsson, M., Knappe, J., Singer, A., Snäll, T., 2018. Can opportunistically collected Citizen Science data fill a data gap for habitat suitability models of less common species? *Methods Ecol. Evol.* 9, 1667–1678. <https://doi.org/10.1111/2041-210X.13012>.
- Bradter, U., Özgül, A., Griesser, M., Layton-Matthews, K., Eggers, J., Singer, A., Sandercock, B.K., Haverkamp, P.J., Snäll, T., 2021. Habitat suitability models based on opportunistic citizen science data: Evaluating forecasts from alternative methods versus an individual-based model. *Divers. Distrib.* 27, 2397–2411. <https://doi.org/10.1111/ddi.13409>.
- Burner, R.C., Birkemoe, T., Stephan, J.G., Drag, L., Muller, J., Ovaskainen, O., Potterf, M., Skarpaas, O., Snäll, T., Sverdrup-Thygeson, A., 2021. Choosy beetles: how host trees and southern boreal forest naturalness may determine dead wood beetle communities. *For. Ecol. Manag.* 487, 119023. <https://doi.org/10.1016/j.foreco.2021.119023>.
- Eggers, S., Griesser, M., Ekman, J., 2008. Predator-induced reductions in nest visitation rates are modified by forest cover and food availability. *Behav. Ecol.* 19, 1056–1062. <https://doi.org/10.1093/beheco/arn063>.
- Eggers, J., Rätty, M., Öhman, K., Snäll, T., 2020. How well do stakeholder-defined forest management scenarios balance economic and ecological forest values? *Forests* 11, 86. <https://doi.org/10.3390/f11010086>.
- Eu, C., 2021. Regulation - 2021/1119 - EN - EUR-Lex [WWW Document]. URL. <http://eur-lex.europa.eu/eli/reg/2021/1119/oj/eng>.
- Eyvindson, K., Dufrot, R., Triviño, M., Blattert, C., Potterf, M., Mönkkönen, M., 2021. High boreal forest multifunctionality requires continuous cover forestry as a dominant management. *Land Use Policy* 100, 104918. <https://doi.org/10.1016/j.landusepol.2020.104918>.
- Fabritius, H., Singer, A., Pennanen, J., Snäll, T., 2019. Estimation of metapopulation colonization rates from disturbance history and occurrence-pattern data. *Ecology* 100. <https://doi.org/10.1002/ecy.2814>.
- Fridman, J., Holm, S., Nilsson, M., Nilsson, P., Ringvall, A.H., Ståhl, G., 2014. Adapting national forest inventories to changing requirements – the case of the Swedish national forest inventory at the turn of the 20th century. *Silva Fenn.* 48. <https://doi.org/10.14214/sf.1095>. Article 1095.
- Gauthier, S., Bernier, P., Kuuluvainen, T., Shvidenko, A.Z., Schepaschenko, D.G., 2015. Boreal forest health and global change. *Science* 349, 819–822. <https://doi.org/10.1126/science.aaa9092>.
- Griesser, M., Lagerberg, S., 2012. Long-term effects of forest management on territory occupancy and breeding success of an open-nesting boreal bird species, the Siberian jay. *For. Ecol. Manag.* 271, 58–64. <https://doi.org/10.1016/j.foreco.2012.01.037>.
- Gu, W.-D., Kuusinen, M., Kontinen, T., Hanski, I., 2001. Spatial pattern in the occurrence of the lichen *Loberia pulmonaria* in managed and virgin boreal forests. *Ecography* 24, 139–150. <https://doi.org/10.1034/j.1600-0587.2001.240204.x>.
- Gustafsson, L., Baker, S.C., Bauhus, J., Beese, W.J., Brodie, A., Kouki, J., Lindenmayer, D. B., Löhms, A., Pastur, G.M., Messier, C., Neyland, M., Palik, B., Sverdrup-Thygeson, A., Volney, W.J.A., Wayne, A., Franklin, J.F., 2012. Retention forestry to maintain multifunctional forests: a World perspective. *Bioscience* 62, 633–645. <https://doi.org/10.1525/bio.2012.62.7.6>.
- Haatanen, A., den Herder, M., Leskinen, P., Lindner, M., Kurtila, M., Salminen, O., 2014. Stakeholder engagement in scenario development process – bioenergy production and biodiversity conservation in eastern Finland. *J. Environ. Manage.* 135, 45–53. <https://doi.org/10.1016/j.jenvman.2014.01.009>.
- Hanski, I., Ovaskainen, O., 2000. The metapopulation capacity of a fragmented landscape. *Nature* 404, 755–758. <https://doi.org/10.1038/35008063>.
- Hardenbol, A.A., Junninen, K., Kouki, J., 2020. A key tree species for forest biodiversity, European aspen (*Populus tremula*), is rapidly declining in boreal old-growth forest reserves. *For. Ecol. Manag.* 462, 118009. <https://doi.org/10.1016/j.foreco.2020.118009>.
- Henckel, L., Bradter, U., Jönsson, M., Isaac, N.J.B., Snäll, T., 2020. Assessing the usefulness of citizen science data for habitat suitability modelling: opportunistic reporting versus sampling based on a systematic protocol. *Divers. Distrib.* 26, 1276–1290. <https://doi.org/10.1111/ddi.13128>.
- Jakobsson, R., Olofsson, E., Ambrose-Oji, B., 2021. Stakeholder perceptions, management and impacts of forestry conflicts in southern Sweden. *Scand. J. For. Res.* 36, 68–82. <https://doi.org/10.1080/02827581.2020.1854341>.
- Joelsson, K., Hjältén, J., Work, T., Gibb, H., Roberge, J.-M., Löfroth, T., 2017. Uneven-aged silviculture can reduce negative effects of forest management on beetles. *For. Ecol. Manag.* 391, 436–445. <https://doi.org/10.1016/j.foreco.2017.02.006>.
- Kellomäki, S., Strandman, H., Heinonen, T., Asikainen, A., Venäläinen, A., Peltola, H., 2018. Temporal and spatial change in diameter growth of boreal Scots pine, Norway spruce, and birch under Recent-Generation (CMP5) global climate model projections for the 21st century. *Forests* 9, 118. <https://doi.org/10.3390/f9030118>.
- Keskitalo, E.C.H., 2011. How can forest management Adapt to climate change? Possibilities in different forestry systems. *Forests* 2, 415–430. <https://doi.org/10.3390/f2010415>.
- Kim, S., Axelsson, E.P., Girona, M.M., Senior, J.K., 2021. Continuous-cover forestry maintains soil fungal communities in Norway spruce dominated boreal forests. *For. Ecol. Manag.* 480, 118659. <https://doi.org/10.1016/j.foreco.2020.118659>.
- Klapwijk, M.J., Bylund, H., Schroeder, M., Björkman, C., 2016. Forest management and natural biocontrol of insect pests. *Forestry* 89, 253–262. <https://doi.org/10.1093/forestry/cpw019>.
- Klein, J., Haverkamp, P.J., Lindberg, E., Griesser, M., Eggers, S., 2020. Remotely sensed forest understory density and nest predator occurrence interact to predict suitable breeding habitat and the occurrence of a resident boreal bird species. *Ecol. Evol.* 10, 2238–2252. <https://doi.org/10.1002/ece3.6062>.
- Klein, J., Low, M., Sjögren, J., Eggers, S., 2022. Short-term experimental support for bird diversity retention measures during thinning in European boreal forests. *For. Ecol. Manag.* 509, 120084. <https://doi.org/10.1016/j.foreco.2022.120084>.
- Koivula, M., Vanha-Majamaa, I., 2020. Experimental evidence on biodiversity impacts of variable retention forestry, prescribed burning, and deadwood manipulation in Fennoscandia. *Ecol. Process.* 9, 11. <https://doi.org/10.1186/s13717-019-0209-1>.
- Kumar, A., Adamopoulos, S., Jones, D., Amiamandhen, S.O., 2021. Forest biomass availability and Utilization potential in Sweden: a review. *Waste Biomass Valorization* 12, 65–80. <https://doi.org/10.1007/s12649-020-00947-0>.
- Kuuluvainen, T., Tahvonen, O., Aakala, T., 2012. Even-aged and uneven-aged forest management in boreal Fennoscandia: a review. *Ambio* 41, 720–737. <https://doi.org/10.1007/s13280-012-0289-y>.
- Kyaschenko, J., Strengbom, J., Felton, A., Aakala, T., Staland, H., Ranius, T., 2022. Increase in dead wood, large living trees and tree diversity, yet decrease in understory vegetation cover: the effect of three decades of biodiversity-oriented forest policy in Swedish forests. *J. Environ. Manage.* 313, 114993. <https://doi.org/10.1016/j.jenvman.2022.114993>.
- Lämås, T., Sängstuvall, L., Öhman, K., Lundström, J., Årevall, J., Holmström, H., Nilsson, L., Nordström, E.-M., Wikberg, P.-E., Wikström, P., Eggers, J., 2023. The multi-faceted Swedish Heureka forest decision support system: context, functionality, design, and 10 years experiences of its use. *Front. For. Glob. Change* 6. <https://doi.org/10.3389/ffgc.2023.10947>.
- Landelius, T., Dahlgren, P., Gollvik, S., Jansson, A., Olsson, E., 2016. A high-resolution regional reanalysis for Europe. Part 2: 2D analysis of surface temperature, precipitation and wind. *Q. J. R. Meteorol. Soc.* 142, 2132–2142. <https://doi.org/10.1002/qj.2813>.
- Lassauce, A., Paillet, Y., Jactel, H., Bouget, C., 2011. Deadwood as a surrogate for forest biodiversity: meta-analysis of correlations between deadwood volume and species richness of saproxylic organisms. *Ecol. Indic.* 11, 1027–1039. <https://doi.org/10.1016/j.ecolind.2011.02.004>.
- Latacz-Lohmann, U., Van der Hamsvoort, C.P.C.M., 1998. Auctions as a means of creating a market for public goods from Agriculture. *J. Agric. Econ.* 49, 334–345. <https://doi.org/10.1111/j.1477-9552.1998.tb01276.x>.
- Layton-Matthews, K., Özgül, A., Griesser, M., 2018. The interacting effects of forestry and climate change on the demography of a group-living bird population. *Oecologia* 186, 907–918. <https://doi.org/10.1007/s00442-018-4100-z>.
- Lees, C.M., Rutschmann, A., Santure, A.W., Beggs, J.R., 2021. Science-based, stakeholder-inclusive and participatory conservation planning helps reverse the decline of threatened species. *Biol. Conserv.* 260, 109194. <https://doi.org/10.1016/j.biocon.2021.109194>.
- Lier, M., Köhl, M., Korhonen, K.T., Linsler, S., Prins, K., 2021. Forest relevant targets in EU policy instruments - can progress be measured by the pan-European criteria and indicators for sustainable forest management? *For. Policy Econ.* 128, 102481. <https://doi.org/10.1016/j.forpol.2021.102481>.
- Linder, P., Elfving, B., Zackrisson, O., 1997. Stand structure and successional trends in virgin boreal forest reserves in Sweden. *For. Ecol. Manag.* 98, 17–33. [https://doi.org/10.1016/S0378-1127\(97\)00076-5](https://doi.org/10.1016/S0378-1127(97)00076-5).
- Lindner, M., Fitzgerald, J.B., Zimmermann, N.E., Reyher, C., Delzon, S., van der Maaten, E., Schelhaas, M.-J., Lasch, P., Eggers, J., van der Maaten-Theunissen, M., Suckow, F., Psomas, A., Poulter, B., Hanewinkel, M., 2014. Climate change and European forests: what do we know, what are the uncertainties, and what are the

- implications for forest management? *J. Environ. Manage.* 146, 69–83. <https://doi.org/10.1016/j.jenvman.2014.07.030>.
- Lovric, M., Lovric, N., 2013. Integration of Nature Protection in Forest Policy in Croatia, INTEGRATE Country Report for Croatia. European Forest Institute. EFICEEC – EFISEE Regional Office.
- Mair, L., Harrison, P.J., Rätty, M., Bärning, L., Strandberg, G., Snäll, T., 2017. Forest management could counteract distribution retractions forced by climate change. *Ecol. Appl.* 27, 1485–1497. <https://doi.org/10.1002/eap.1541>.
- Mathys, L., Zimmermann, N.E., Zbinden, N., Suter, W., 2006. Identifying habitat suitability for hazel grouse *Bonasa bonasia* at the landscape scale. *Wildl. Biol.* 12, 357–366. [https://doi.org/10.2981/0909-6396\(2006\)12\[357:IHSFHJ\]2.0.CO;2](https://doi.org/10.2981/0909-6396(2006)12[357:IHSFHJ]2.0.CO;2).
- Merideth, R., Yaseen, R., 2000. Using Role-Play simulations to Teach environmental decision making and conflict resolution Techniques. *Environ. Pract.* 2, 139–145. <https://doi.org/10.1017/S1466046600001356>.
- Mönkkönen, M., Juutinen, A., Mazziotta, A., Miettinen, K., Podkopaev, D., Reunanen, P., Salminen, H., Tikkanen, O.-P., 2014. Spatially dynamic forest management to sustain biodiversity and economic returns. *J. Environ. Manage.* 134, 80–89. <https://doi.org/10.1016/j.jenvman.2013.12.021>.
- Moor, H., Eggers, J., Fabritius, H., Forsell, N., Henckel, L., Bradter, U., Mazziotta, A., Nordén, J., Snäll, T., 2022. Rebuilding green infrastructure in boreal production forest given future global wood demand. *J. Appl. Ecol.* n/a. <https://doi.org/10.1111/1365-2664.14175>.
- Moor, H., Nordén, J., Penttilä, R., Siitonen, J., Snäll, T., 2021. Long-term effects of colonization–extinction dynamics of generalist versus specialist wood-decaying fungi. *J. Ecol.* 109, 491–503. <https://doi.org/10.1111/1365-2745.13526>.
- Naumov, V., Manton, M., Elbakidze, M., Rendenieks, Z., Priednieks, J., Uhljanets, S., Yamelynets, T., Zhivotov, A., Angelstam, P., 2018. How to reconcile wood production and biodiversity conservation? The Pan-European boreal forest history gradient as an “experiment.”. *J. Environ. Manage.* 218, 1–13. <https://doi.org/10.1016/j.jenvman.2018.03.095>.
- Niemi, J., Soimakallio, S., Hurmekoski, E., Myllyviita, T., Kunttu, J., Lingua, F., Snäll, T., 2025. Carbon Credits through wood Use: Revisiting the maximum potential and sensitivity to key Assumptions. *GCB Bioenergy* 17, e70017. <https://doi.org/10.1111/gcbb.70017>.
- Nilsson, S., Niklasson, M., Hedin, J., Aronsson, G., Gutowski, J.M., Linder, P., Ljungberg, H., Mikusinski, G., Ranius, T., 2002. Densities of large living and dead trees in old-growth temperate and boreal forests. *For. Ecol. Manage.* 161, 189–204. [https://doi.org/10.1016/S0378-1127\(01\)00480-7](https://doi.org/10.1016/S0378-1127(01)00480-7).
- Nitare, J., 2019. Skyddsvärd skog-Naturvärdsarter och andra kriterier för naturvärdesbedömning. Skogsstyrelsen, Jönköping. 2.
- Nordén, J., Penttilä, R., Siitonen, J., Tomppo, E., Ovaskainen, O., 2013. Specialist species of wood-inhabiting fungi struggle while generalists thrive in fragmented boreal forests. *J. Ecol.* 101, 701–712. <https://doi.org/10.1111/1365-2745.12085>.
- Nordström, E.-M., Forsell, N., Lundström, A., Korosuo, A., Bergh, J., Havlík, P., Kraxner, F., Frank, S., Fricko, O., Lundmark, T., Nordin, A., 2016. Impacts of global climate change mitigation scenarios on forests and harvesting in Sweden. *Can. J. For. Res.* 46, 1427–1438. <https://doi.org/10.1139/cjfr-2016-0122>.
- Östlund, L., Zackrisson, O., 1997. The History and Transformation of a Scandinavian Boreal Forest Landscape since the 19th Century, vol. 27, p. 14.
- Pakkala, T., Hanski, I., Tomppo, E., 2002. Spatial ecology of the three-toed woodpecker in managed forest landscapes. *Silva Fenn.* 36.
- Pakkala, T., Lindén, A., Tiainen, J., Tomppo, E., Kouki, J., 2014. Indicators of forest biodiversity: which bird species predict high breeding bird Assemblage diversity in boreal forests at Multiple spatial scales? *Ann. Zool. Fenn.* 51, 457–476. <https://doi.org/10.5735/086.051.0501>.
- Pakkala, T., Tiainen, J., Piha, M., Kouki, J., 2018. How important are nest cavities made by the three-toed woodpecker *Picoides tridactylus* for cavity-nesting forest bird species? *Acta Ornithol* 53, 69–79. <https://doi.org/10.3161/00016454AO2018.53.1.007>.
- Peura, M., Burgas, D., Eyvindson, K., Repo, A., Mönkkönen, M., 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>.
- Pommerening, A., 2004. A review of the history, definitions and methods of continuous cover forestry with special attention to afforestation and restocking. *Forestry* 77, 27–44. <https://doi.org/10.1093/forestry/77.1.27>.
- Primmer, E., 2017. Institutional constraints on conservation auction: Organizational mandate, competencies and practices. *Land Use Policy* 63, 621–631. <https://doi.org/10.1016/j.landusepol.2015.05.011>.
- Pukkala, T., 2021. Measuring the social performance of forest management. *J. For. Res.* 32, 1803–1818. <https://doi.org/10.1007/s11676-021-01321-z>.
- Pukkala, T., Lähde, E., Laiho, O., 2012. Continuous cover forestry in Finland – Recent research results. In: Pukkala, T., von Gadow, K. (Eds.), *Continuous Cover Forestry*. Springer, Netherlands, Dordrecht, pp. 85–128. https://doi.org/10.1007/978-94-007-2202-6_3.
- Pukkala, T., Laiho, O., Lähde, E., 2016. Continuous cover management reduces wind damage. *For. Ecol. Manage.* 372, 120–127. <https://doi.org/10.1016/j.foreco.2016.04.014>.
- R Core Team, 2021. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. R version 4.0. 4.
- Reese, H., Nilsson, M., Pahlén, T.G., Hagner, O., Joyce, S., Tingelöf, U., Egberth, M., Olsson, H., 2003. Countrywide estimates of forest variables using satellite data and field data from the National Forest Inventory. *AMBIO A J. Hum. Environ.* 32, 542. [https://doi.org/10.1639/0044-7447\(2003\)032\[0542:CEOFVU\]2.0.CO](https://doi.org/10.1639/0044-7447(2003)032[0542:CEOFVU]2.0.CO).
- Runnel, K., Löhmus, A., 2017. Deadwood-rich managed forests provide insights into the old-forest association of wood-inhabiting fungi. *Fungal Ecol.* 27, 155–167. <https://doi.org/10.1016/j.funeco.2016.09.006>.
- Runnel, K., Sell, I., Löhmus, A., 2020. Recovery of the Critically Endangered bracket fungus *Amylocystis lapponica* in the Estonian network of strictly protected forests. *Oryx* 54, 478–482. <https://doi.org/10.1017/S0030605319000334>.
- Sandström, C., Carlsson-Kanyama, A., Lindahl, K.B., Sonnek, K.M., Mossing, A., Nordin, A., Nordström, E.-M., Rätty, R., 2016. Understanding consistencies and gaps between desired forest futures: an analysis of visions from stakeholder groups in Sweden. *Ambio* 45, 100–108. <https://doi.org/10.1007/s13280-015-0746-5>.
- SEPA, 2007. Sweden's environmental objectives. www.miljomal.se/SwedishParliament. <https://doi.org/10.1037/e517682009-009>.
- Simonsson, P., Gustafsson, L., Östlund, L., 2015. Retention forestry in Sweden: driving forces, debate and implementation 1968–2003. *Scand. J. For. Res.* 30, 154–173. <https://doi.org/10.1080/02827581.2014.968201>.
- SLU Artdatabanken, 2020. Red-listed Species in Sweden 2020. Swedish University of Agricultural Sciences, Uppsala.
- Söderberg, C., Eckerberg, K., 2013. Rising policy conflicts in Europe over bioenergy and forestry. *For. Policy Econ., Forest Land Use and Conflict Management: Global Issues and Lessons Learned* 33, 112–119. <https://doi.org/10.1016/j.forpol.2012.09.015>.
- Swedish Forest Agency, 2020. Forest Management in Sweden Current Practice and Historical Background.
- Swenson, J.E., 1993. The importance of Alder to hazel grouse in Fennoscandian boreal forest: evidence from four levels of scale. *Ecography* 16, 37–46.
- Tikkanen, O.-P., Martikainen, P., Hyvärinen, E., Junninen, K., Kouki, J., 2006. Red-listed boreal forest species of Finland: associations with forest structure, tree species, and decaying wood. *Ann. Zool. Fenn.* 43, 373–383.
- Versluijs, M., Hekkala, A.-M., Lindberg, E., Lämäs, T., Hjältén, J., 2020. Comparing the effects of even-aged thinning and selective felling on boreal forest birds. *For. Ecol. Manage.* 475, 118404. <https://doi.org/10.1016/j.foreco.2020.118404>.
- Vestin, P., Mölder, M., Kljun, N., Cai, Z., Hasan, A., Holst, J., Klemetsson, L., Lindroth, A., 2020. Impacts of clear-Cutting of a boreal forest on carbon Dioxide, Methane and Nitrous Oxide Fluxes. *Forests* 11, 961. <https://doi.org/10.3390/f11090961>.
- Virkkala, R., 1990. Ecology of the Siberian tit *Parus cinctus* in relation to habitat quality: effects of forest management. *Ornis Scand. Scand. J. Ornithol.* 21, 139–146. <https://doi.org/10.2307/3676810>.
- Virkkala, R., Liehu, H., 1990. Habitat selection by the Siberian Tit *Parus cinctus* in virgin and managed forests in northern Finland. *Ornis Fenn.* 671–12, 1–12.
- von Bonsdorff, T., Kytövuori, I., Vauras, J., Huhtinen, S., Halme, P., Rämä, T., Kosonen, L., Jakobsson, S., 2014. *Sienet ja metsien luontoarvot [Identification book on fungi that can be used as indicators in recognizing valuable forest habitats]*. Norrlinna. Luonnontieteellinen keskusmuseo. kasvitieteen, yksikkö 1–272.
- Wagner, H.H., Werth, S., Kalwij, J.M., Bolli, J.C., Scheidegger, C., 2006. Modelling forest recolonization by an epiphytic lichen using a landscape genetic approach. *Landsc. Ecol.* 21, 849–865. <https://doi.org/10.1007/s10980-005-5567-7>.
- Zabel, A., Bostedt, G., Ekvall, H., 2018. Policies for forest landscape management – a conceptual approach with an empirical application for Swedish conditions. *For. Policy Econ.* 86, 13–21. <https://doi.org/10.1016/j.forpol.2017.10.008>.
- Zachrisson, A., Beland Lindahl, K., 2013. Conflict resolution through collaboration: Preconditions and limitations in forest and nature conservation controversies. *For. Policy Econ. Forest Land Use and Conflict Management: Global Issues and Lessons Learned* 33, 39–46. <https://doi.org/10.1016/j.forpol.2013.04.008>.