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RESEARCH ARTICLE

Rebuilding green infrastructure in boreal production forest given future global wood demand

Helen Moor[1,2] | Jeannette Eggers[1,3] | Henna Fabritius[1,4] | Nicklas Forsell[5] | Laura Henckel[1,6] | Ute Bradter[1,7] | Adriano Mazziotta[1,8] | Jenni Nordén[9] | Tord Snäll[1]

[1]SLU Swedish Species Information Centre, Swedish University of Agricultural Sciences, Uppsala, Sweden

[2]Swiss Federal Research Institute WSL, Birmensdorf, Switzerland

[3]Department of Forest Resource Management, Swedish University of Agricultural Sciences, Umeå, Sweden

[4]Smart City Centre of Excellence, Tallinn University of Technology, Tallinn, Estonia

[5]International Institute for Applied Systems Analysis (IIASA), Laxenburg, Austria

[6]INRAE (French National Institute for Agriculture, Food, and Environment), UMR1347, Dijon, France

[7]Norwegian Institute for Nature Research (NINA), Trondheim, Norway

[8]Natural Resources Institute Finland (Luke), Bioeconomy and Environment, Helsinki, Finland and [9]Norwegian Institute for Nature Research (NINA), Oslo, Norway

Correspondence
Helen Moor
Email: helen.moor@wsl.ch

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Abstract

1. Global policy for future biodiversity conservation is ultimately implemented at landscape and local scales. In parallel, green infrastructure planning needs to account for socioeconomic dynamics at national and global scales. Progress towards policy goals must, in turn, be evaluated at the landscape scale. Evaluation tools are often environmental quality indicators. How developments of different organism groups will relate to developments of these indicators is unclear.
2. We evaluated three management scenarios for a 100,000 hectare boreal forest landscape in the coming 100 years in terms of their effects on the future habitat suitability/occupancy of four bird species, six wood-decaying fungi and one lichen, most of them red-listed. The scenarios optimize financial returns and account for downscaled projected global demand of wood given a middle-of-the road Shared Socioeconomic Pathway (SSP2). We contrast a *reference* scenario meeting the wood demand against an *economy* scenario with no upper harvest limit, and a *green infrastructure* scenario optimizing the levels of environmental indicators.
3. Environmental indicators generally reached the highest and lowest levels in the *green infrastructure* and *economy* scenarios, respectively. Most indicators increased further in set-asides. The profit was 14% lower in the *green infrastructure* and 2% higher in the *economy* than in the reference scenario.
4. In the *green infrastructure* scenario, the species increased on average by 135%, followed by the *reference* scenario (+65%), and the *economy* scenario (+47%). All bird species increased in the *green infrastructure* scenario, while in the other scenarios, only hazel grouse increased and Siberian tit instead decreased. Most fungi increased in the production forest of the *green infrastructure* scenario but decreased in the *economy* scenario. All increased in set-asides. In all scenarios, the lichen *Lobaria pulmonaria* increased, owing to host tree retention.
5. *Synthesis and applications*. Effects of global socioeconomic developments can be downscaled and accounted for in planning landscape-scale forest and

conservation management. Accounting for indicators of environmental quality identified forest management scenarios for reaching targets on both revenue and conservation. Rebuilding green infrastructure in the production forest was possible at a relatively minor economic cost and to the benefit of species of conservation concern.

KEYWORDS
conservation, downscaling, environmental indicators, forestry, GLOBIOM, green infrastructure, land-use scenario, socioeconomic pathways

1 | INTRODUCTION

International concern around the global degradation of forest and its impact on the loss of biodiversity and ecosystem services has increased over the last decade. Global policies are in place to address this challenge with broad international support. The Convention on Biological Diversity (CBD), with the Aichi targets of the Strategic Plan for Biodiversity 2011–2020, and the UN Sustainable Development Goals (SDGs) have formulated ambitious goals to halt forest degradation and biodiversity loss. A recent assessment, however, found that none of the 20 Aichi targets were fully achieved (CBD, 2020). Similarly, the latest Global Biodiversity Outlook report on the SDGs found that only a third of 113 countries were on track to achieve their target to integrate biodiversity into national planning and that the conservation of terrestrial ecosystems is not trending towards sustainability (UN, 2020). Both reports emphasize the need for global policy to be operationalized at regional and national levels. Correspondingly, the European Union (EU) has adopted the EU Biodiversity Strategy for 2030, requesting members states to 'increase the quantity, quality and resilience of its forests' (EC, 2020). In parallel, the EU's Green Infrastructure strategy emphasizes the importance of landscape connectivity and multifunctionality in spatial planning (EC et al., 2019). The responsibility to achieve these goals lies with the member states and in practice depends on actions taken at the landscape scale. In Sweden for example, a subset of the environmental quality objectives are the national manifestation of EU and global policies. Progress towards these objectives is monitored via measurable environmental indicators. The evaluation of the efficacy of management and conservation ultimately takes place at the landscape and local level (Figure 1).

Policy at global and national scales needs to be translated to management strategies at landscape and local scales. Scenarios and models are invaluable tools to ensure that landscape management actually achieves stated policy goals (Nicholson et al., 2019). Global and regional constraints are however rarely accounted for when assessing national policies or landscape level planning (Nordström et al., 2016). Parallel to the policy chain from global to local levels, political and socioeconomic developments need to be considered when designing and evaluating environmental management strategies (Figure 1). Demands on local land use should be framed in the context of global developments (Popp et al., 2017).

The global shared socioeconomic pathways (SSPs) provide plausible future scenarios of human demographics, economy, institutions, technology and natural resources (O'Neill et al., 2017). The SSPs can be augmented with forest sector pathway narratives (Daigneault et al., 2019) to improve their representativeness of the forest sector and its future developments. The combination of SSPs and forest sector pathways thus offers alternative pathways with varying degrees of macroeconomic and socioeconomic change (Daigneault et al., 2019). In addition, the SSPs can be combined with the representative concentration pathways (RCP) to simulate how forest sector adjustments can help achieve global climate targets, and what effects the achievement of global climate targets will have on the forest sector. For each SSP-RCP combination, global land use models such as GLOBIOM (Havlík et al., 2015) can simulate the corresponding implication for the forest sector and project the future wood demand for countries and regions (Lauri et al., 2017). Furthermore, we can now downscale future global demand for forest products to landscape-scale demand for wood assortments (Eriksson et al., 2020), forming the quantitative objectives of optimization of forestry and conservation planning given the demand resulting from global socioeconomic developments.

Boreal forests carry the legacy of decades of intensive forestry. Nearly two-thirds of the boreal forest is managed, mostly for industrial wood production; in Fennoscandia, the proportion of managed forest is as high as 90% with one of the highest wood extraction intensities in Europe (Gauthier et al., 2015; Levers et al., 2014). Protected areas are an important component of forest biodiversity conservation, but may not be sufficient to ensure species persistence in heavily managed, fragmented landscapes (Driscoll et al., 2013). Green infrastructure, i.e., a functioning network of high-quality habitat, must be restored in the matrix of production forest, in order to maintain functional connectivity for many species and the landscape's capacity to support viable metapopulations (Hanski & Ovaskainen, 2000; Lindenmayer et al., 2006). While the EU defines green infrastructure more broadly (including forest multifunctionality), we here focus on biodiversity of conservation concern.

Production forest differs profoundly from natural forest in Fennoscandia. Since the onset of large-scale industrial forestry in Sweden in the 1950s, even-aged stand management and clear-cut

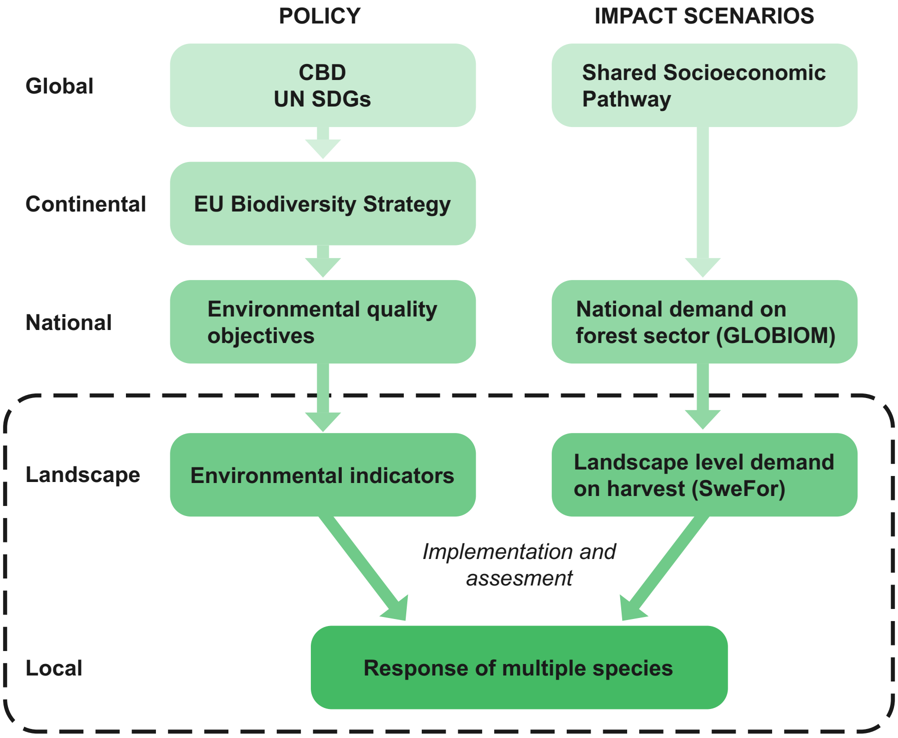

FIGURE 1 Overview of the chain of policies for biodiversity conservation and parallel impact scenarios for socioeconomic constraints from global to national to landscape scale, for the example of Sweden. Implementation of policy in the form of management decisions and evaluation of their success takes place at landscape and local levels. Global constraints, given by shared socioeconomic pathways, are rarely accounted for when designing landscape level management strategies; models such as GLOBIOM and SweFor can simulate and downscale global developments to national and landscape levels, respectively. The final assessment of the efficacy of global policy requires studying the responses of multiple species at the local level

harvesting have been the predominant management form with broad-scale, long-term negative impacts on forest structure and function (Svensson et al., 2019). Even-aged management with a clear-cutting cycle of *c*. 100 years has led to a drastic decrease of old forest and of the densities of large, old trees (Kuuluvainen, 2009). The amount and diversity of deadwood have been reduced to a fraction of conditions in natural forests (Jonsson et al., 2016; Siitonen, 2001). The preference for conifers and mono-specific stands has reduced the proportion of deciduous trees in the landscape (Kuuluvainen, 2002; Mikusiński et al., 2003).

The recognition of the negative impacts of these developments on biodiversity has led to the adoption of national environmental quality objectives in several EU member states (Jakobsson et al., 2021). A basis for evaluating progress on forest quality objectives in Sweden are four quantifiable environmental indicators. Absolute targets have not been defined, but they reflect landscape and habitat structures that are reduced in intensively managed landscapes: the area of old forest, the area of mature broadleaf-rich forest, the amount of deadwood and the density of large trees (Andersson et al., 2019; Table 1).

Effects of forest management scenarios or of changes in environmental indicators on biodiversity are often studied using a small number of species (e.g., Belinchón et al., 2017; Mönkkönen et al., 2014). In order to assess the full spectrum of forest biodiversity, multiple taxa should be used since different taxa may have different habitat requirements at different spatial scales. We here use 11 model species from three different species groups with widely differing habitat requirements. The studied species either are of conservation concern or considered indicator species for forest of high conservation value. They are responsive to forest management effects on different aspects of green infrastructure, and we expect them to show different responses to management strategies and environmental indicators (Table 1). We used a suite of models to project species responses to future forest management scenarios: species distribution models, dynamic occupancy models and a spatially explicit metapopulation model.

The main aim was to investigate the impact of landscape-scale forest management accounting for demand from global socio-economic developments on forest species. We asked two sets of questions: First, given future global demand on wood, can green infrastructure be restored in boreal production landscapes that are currently intensively managed? What is the financial cost of maximizing green infrastructure? Second, does forestry planning focusing on environmental indicators lead to an improvement of green infrastructure, as assessed by the responses of species of conservation concern? How do these species' responses differ between production forest and forest permanently set-aside for conservation?

We present three management scenarios that optimize financial and environmental quality objectives to different degrees,

TABLE 1 Overview and definition of the evaluated environmental indicators for assessing progress towards the Swedish environmental quality objectives, and expectations on species responses to each of them

Environmental indicator	Definition	Expectation on species response
Old forest	Area of forest aged ≥140 years (ha)	Positive response by all species
Mature, broadleaf-rich forest	Area of mature (≥80 years) forest with a proportion of basal area of broadleaves ≥25% (ha)	Especially positive response by the lichen *Lobaria pulmonaria* requiring deciduous host trees and hazel grouse *Tetrastes bonasia* utilizing mixed forest
Deadwood volume	Total standing and lying deadwood of all decay stages (m^3/ha)	Especially positive response by wood-decaying fungi and for some birds, especially the Eurasian three-toed woodpecker (*Picoides tridactylus*) using dead trees for foraging and nesting (for birds assessed indirectly via forest age)
Large trees	Density of trees with diameter at breast height ≥ 40 cm (trees/ha)	Especially positive response by the lichen *Lobaria pulmonaria* and some wood-decaying fungi with higher occupancy on large diameter deadwood (*Amylocystis lapponica*, *Phlebia centrifuga*)

while meeting the projected demand on wood assortments. The success of these scenarios in restoring green infrastructure was assessed with measures of model species population performance. To this end, we first translated societal, economic and technological trajectories of global SSPs to national scale demand on wood products. Second, the national demand for Sweden was downscaled to the landscape scale. This demand was specified as a constraint in the three optimized scenarios for the large, representative boreal Swedish landscape in the coming 100 years. In addition to meeting the global demand for wood, the *green infrastructure* (*GI*) scenario maximized the levels of environmental indicators (Table 1). We contrasted this *GI* scenario with an *economy* scenario with no upper limit on harvest volumes, and a baseline *reference* scenario only constrained not to harvest more than the landscape scale demand.

2 | MATERIALS AND METHODS

2.1 | Downscaling from global to landscape scale

We applied GLOBIOM with 59 economic regions (27 in the EU) and for each SSP, we projected the future wood demand for Sweden at the national level (see Figure S1). National demand was next downscaled to projected harvest at landscape level using a national partial-equilibrium forest sector model (SweFor, Eriksson et al., 2020, details in Appendix S2).

We first investigated the effect of different SSPs on landscape scale wood demand, but they did not markedly differ (Appendix S2). For our landscape-level scenarios, we therefore chose SSP2, which represents a middle-of-the-road development in the mitigation and adaptation challenges space, and global socioeconomic trends that broadly follow their historical patterns (Fricko et al., 2017). In terms of climate forcing, we assumed the RCP2.6 scenario, which agrees with the Paris Agreement (van Vuuren et al., 2011).

2.2 | Scenarios

Given the landscape scale demand for wood, we simulated three scenarios of forest management for 100 years, starting from 2010, using PlanWise/Heureka (Wikström et al., 2011). PlanWise/Heureka makes detailed projections of stand conditions into the future based on empirical tree growth functions, ingrowth of new trees, mortality and management decisions. Available management strategies (Table S3) represent the full spectrum of currently employed management, from high-intensive wood extraction to leaving stands unmanaged. We further assumed actions taken for FSC certification (FSC, 2020) and Swedish Forest Agency guidelines for forest owners, such as leaving retention trees and high stumps in final fellings. In addition, aspen *Populus tremula* and goat willows *Salix caprea* were retained in pre-commercial and commercial thinnings. Optimal combinations of management were selected across all stands given constraints and targets using mathematical optimization.

All three scenarios optimized financial returns, measured by the Net Present Value (NPV), subject to the minimum harvest constraint derived from regional downscaling of the national wood demand for SSP2-RCP2.6 and additional scenario-specific constraints. NPV was calculated as the sum of discounted revenues minus costs, for an infinite time horizon, assuming a discount rate of 2.5%. The *green infrastructure* (*GI*) scenario additionally maximized the mean values of four key environmental indicators throughout the simulation (Table 1). Due to expected trade-offs between these indicators (Eggers et al., in review), we first optimized the value of each indicator alone in separate simulations to estimate their maximum possible values. Then, we identified the maximum value that can be attained for all four indicators simultaneously, which resulted in ~82% of each of their potential maximum values. We then constrained the NPV optimization to simultaneously reach the aggregated highest possible level of environmental indicators. The other two scenarios did not consider environmental indicator values. The baseline *reference* scenario optimized NPV and was constrained not to harvest more than the landscape scale demand. The *economy* scenario optimized NPV without an upper limit on harvest volumes.

2.3 | Study landscape

We studied a case landscape of 103,313 ha of productive boreal forest divided into 10,782 stands. The landscape was constructed to be representative of Swedish middle-boreal forest in 2010 (detailed in Eggers et al., 2020; Appendix S4). It is dominated by conifers, mean forest age is 72 years, with 55% younger than 60 years, owing to intensive harvesting since the 1950s (Svensson et al., 2019). 7.8% of the forest area was permanently set-aside in reserves. Because of the high-resolution single tree data needed for projections of the metapopulation dynamics of the lichen *Lobaria pulmonaria*, these simulations were conducted on a smaller, but representative, subarea (Appendix S4).

2.4 | Study species and models

The bird species included are hazel grouse *Tetrastes bonasia*, Siberian jay *Perisoreus infaustus*, Siberian tit *Poecile cinctus* and three-toed woodpecker *Picoides tridactylus*. Hazel grouse prefers mixed forests with a varied habitat structure and is an indicator species of adequate levels of deciduous trees in boreal landscapes (Åberg et al., 2003). The remaining species are coniferous forest specialists and indicate older forests (Lindbladh et al., 2020); the three-toed woodpecker is considered a good indicator for habitat quality of conifer-dominated forests and a potential umbrella species (Roberge & Angelstam, 2006). Bird species' habitat suitability was projected into the future with logistic regression models developed by Henckel et al. (2020), fitted to national data from the Swedish Bird Survey (Appendix S5).

The wood-decaying fungi included are five polypores, *Amylocystis lapponica*, *Fomitopsis rosea*, *Phellinus ferrugineofuscus*, *Phellinus nigrolimitatus* and *Phellinus viticola*, and one corticioid species, *Phlebia centrifuga*. *P. viticola* is considered an indicator species for forest of high conservation value, and all other species are red-listed (SLU Artdatabanken, 2020). All species mainly occur on *Picea abies* deadwood in old-growth forest, and for all but *P. viticola* occupancy further increases with increasing deadwood diameter (Berglund et al., 2011). The occupancy probability of wood-decaying fungi at the stand level was projected using dynamic occupancy models, modelling colonization and extinction rates as a function of environmental covariates, while accounting for imperfect detection (Appendix S5; Moor et al., 2021).

Finally, we included the well-studied epiphytic lichen *Lobaria pulmonaria*. It indicates high conservation value of boreal forest, where it occurs on old aspen *Populus tremula* and goat willow *Salix caprea* (Belinchón et al., 2017). The occupancy probability of *L. pulmonaria* at the level of mature aspens (≥15 cm diameter at breast height; DBH) and goat willows (≥10 cm DBH) was projected using dynamic occupancy models, modelling colonization and extinction rates as a function of environmental covariates, while accounting for imperfect detection. Explanatory variables retained in the final model were a negative exponential dispersal function of the distance to trees occupied by *L. pulmonaria* during the preceding decade (assumed dispersal sources) and a linear effect of stand age weighted by the number of mature host trees in the stand as a random effect (Appendix S5). The model and model fitting procedure for *L. pulmonaria* are described in Appendix S6; Appendix S7 describes how we created a realistic pattern of host trees within forest stands.

No ethical approval was required for this study.

3 | RESULTS

3.1 | Landscape scale demand on wood products and effect on total standing volumes

The initially low total standing volumes in the production forest increased (Figure 2) in spite of increasing harvest volumes over time (Appendix S2). Increases in total standing volume were greatest in the *reference* scenario (final value +57% relative to 2010), followed by the *GI* (+35%) and the *economy* scenario (+28%). The low increase in the *economy* scenario was a direct result of the higher harvest volumes. Total standing volume and mean stand age increased more in the set-asides than in the production forest.

3.2 | Environmental quality indicators

The environmental indicators reached the highest levels in the *GI* scenario, with the exception of deadwood volume, which reached the highest final level in the *reference* scenario (Figure 3). All environmental indicators had the lowest levels in the *economy* scenario.

In the permanently set-aside stands (7.8% of total productive forest area), the area of mature, broadleaf-rich forest decreased with 80%, owing to increased competition from coniferous trees during forest succession in maturing stands. The levels of the other indicators increased over time (Figure 3). The density of large trees increased with a factor 20; the area of old forest increased to cover 98% of the total set-aside area; and the total deadwood volume increased with 42%.

In the production forest (including unmanaged production stands and retention patches), the environmental indicators achieved the highest levels in the *GI* scenario, except deadwood volume. The final area of old forest reached 24%; the final area of mature broadleaf-rich forest 21%; and the final density of large trees was 13.8 ha^{-1}. Deadwood volume reached the highest final level in the *reference* scenario (18.8 m^3/ha), but was comparable throughout the simulation to the *GI* scenario (final level 17.1 m^3/ha), reflecting the trajectories of the standing volumes (Figure 2). In the production forest, the area of mature broadleaf-rich forest and of old forest increased only

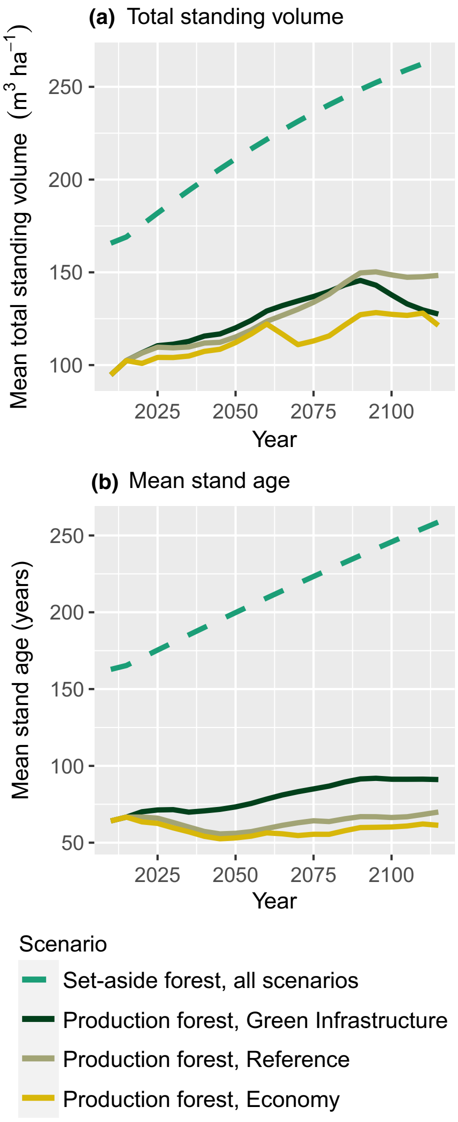

FIGURE 2 Future trajectories of total standing volume (a) and the mean age of forest stands (b), shown separately for permanently set-aside forest (dashed; the same in all scenarios) and the production forest (solid) for the three scenarios

in the *GI* scenario, while they decreased in the *reference* and *economy* scenarios (Figure 3).

The *economy* scenario generated the highest net present value (1,865 €/ha), followed by the *reference* scenario (1,837 €/ha) and the *GI* scenario (1,583 €/ha). Unlimited harvest volumes in the *economy* scenario thus resulted in a 2% increase in economic returns compared to the *reference*, while optimization of environmental indicators resulted in a 14% decrease.

3.3 | Species trajectories

Species performed on average best in the *GI* scenario (mean percent change in habitat suitability or the amount of habitat occupied across all species by the end of the simulation +135%, range +45% to +260%), followed by the *reference* scenario (mean +65%, range −6% to +216%), and finally the *economy* scenario (mean +47%, range −12% to +162%). When considering the production forest only (excluding birds, for which we could not differentiate between set-aside and production forest), differences between scenarios were accentuated. In production stands, the mean percent change across the fungi and lichen species was +228% in the *GI* scenario, +11% in the *reference* scenario, and −28% in the *economy* scenario.

Total habitat suitability increased for all bird species in the *GI* scenario (Figure 4); in the other scenarios, only hazel grouse increased. Hazel grouse had the highest habitat suitability in the *reference* scenario, as well as strong increases in the *GI* and the *economy* scenario, driven by large increases in the total standing volume from low levels in all three scenarios (Figure 2, Appendix S5). Three-toed woodpecker increased slightly and Siberian jay had relatively stable habitat suitability in the *reference* and *economy* scenarios, both largely reflecting the development of mean forest age. The habitat suitability of Siberian tit decreased in these two scenarios, reflecting its sensitivity to decreases in forest age and the proportion of coniferous forest (Figure 4, Appendix S5).

The metapopulation size of fungi (area occupied) increased in set-asides, and in the *GI* scenario also in the production forest (except for *P. centrifuga*, −10%; Figure 4). In production forest, *P. viticola* increased slightly in the *reference* (+8%) scenario, while the metapopulation size of all other fungi decreased. In the *economy* scenario, the metapopulation size of all fungi decreased in the production forest. These dynamics were driven by increasing volumes of downed dead spruce and stand age in the *GI* production forest, which did not change in the other scenarios (Appendix S5).

The metapopulation size of the lichen *L. pulmonaria* (number of trees occupied) also showed different trajectories between the scenarios, and in the set-asides (Figure 4). In the production forest, it partly tracked the strong increase in host tree densities (Appendix S5) resulting from not cutting them in thinnings. It particularly increased in the *GI* scenario, more than expected given the only somewhat higher tree density increase here than in the *reference* and *economy* scenarios (Appendix S5). Moreover, the built up metapopulation size was resilient (Figure 4) to the decreasing host tree density around 2100 in particularly the *GI* scenario (Appendix S5). In the set-asides, the metapopulation size further kept increasing although the host tree density decreased, because trees were colonized at a rate higher than the rate of tree mortality. The high lichen colonization rate resulted from high stand age and high connectivity to surrounding occupied trees constituting dispersal sources.

4 | DISCUSSION

Global policy for biodiversity conservation is ultimately implemented and evaluated at the landscape and local scale. In parallel,

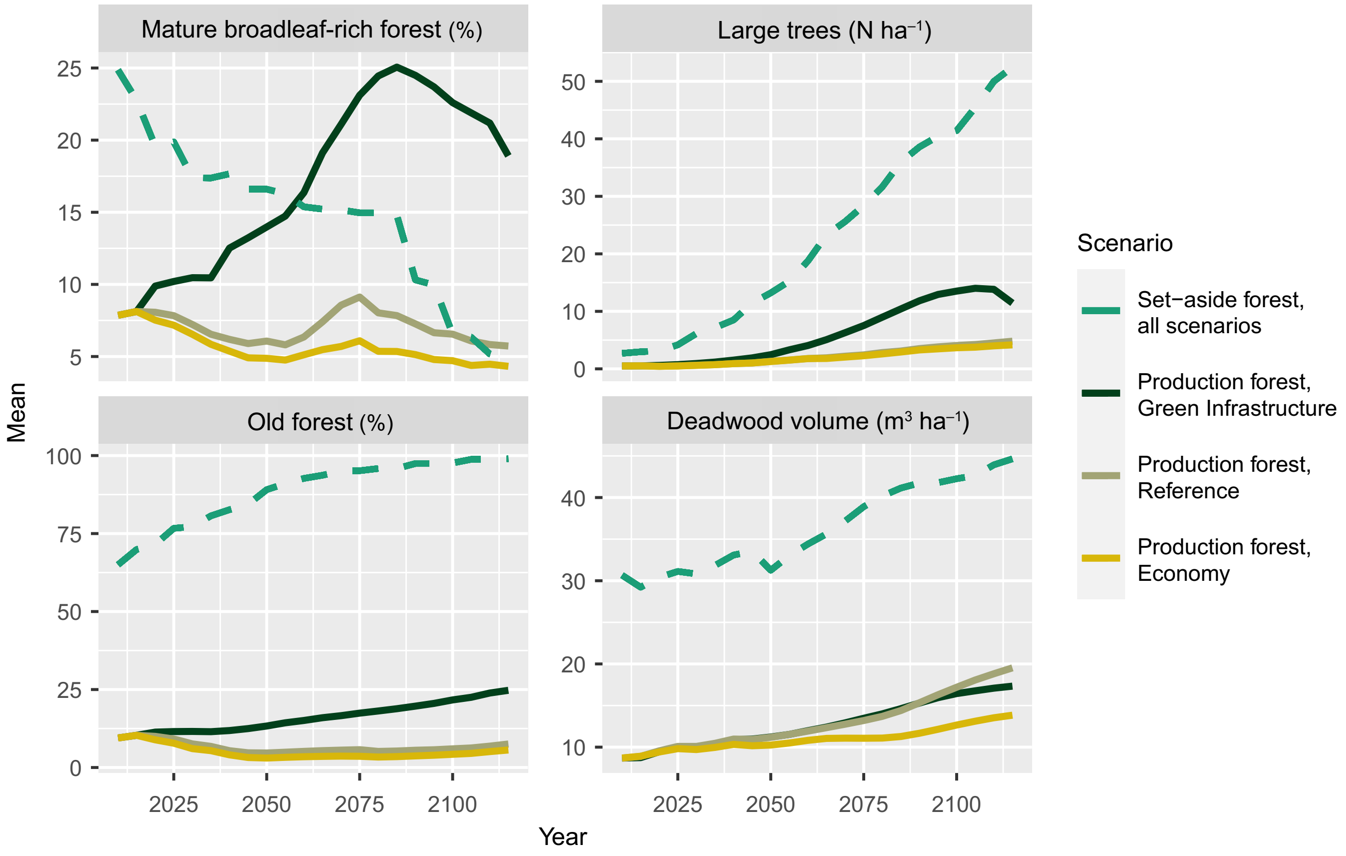

FIGURE 3 Mean among stands of the environmental indicators in the three scenarios, shown separately for permanently set-aside areas (dashed line, the same in all scenarios) and the production forest. The area-based indicators mature broadleaf-rich forest and old forest are shown as percent of the total area of set-asides and production forest

landscape scale management is constrained by economic dynamics at national and global scales. Accounting for the consequences of a global shared socioeconomic pathway (SSP2), we here show that green infrastructure can be restored in a representative boreal production forest landscape, while meeting the projected demand for wood products. The levels of indicators for national environmental quality objectives could be substantially increased, at a relatively minor economic cost and to the benefit of multiple species of conservation concern. In scenarios where forest management targeted only financial returns, many species remained confined to areas permanently set-aside from wood production and declined further in the production forest.

4.1 | Accounting for global developments in landscape scale scenarios

The SSPs are a broadly accepted basis for integrated scenarios of future land use and climate change mitigation (O'Neill et al., 2017). These scenarios provide insights into potential global impacts on regional markets and land use. Our approach links the demand on forest products projected by global scale scenarios of socioeconomic development to a landscape scale demand, thus ensuring the relevance and adequacy of the landscape management scenarios. This adequate downscaling is necessary since landscape scale harvest activity can deviate from the national average (Eriksson et al., 2020) projected by global scenarios.

The landscape scale wood demand under SSP2-RCP2.6 increased by 45% over the coming one hundred years (Appendix S2), but could be satisfied in all scenarios, demonstrating that green infrastructure can be restored without compromising wood production in heavily managed landscapes. Even after harvesting wood satisfying the demand, total standing volumes increased over time in all scenarios. The explanation is the currently young stand age distribution (Eggers et al., 2020), resulting from intensive harvesting since the 1950s, and nowadays higher net increment of forest due to more refined silvicultural practices. This surplus standing volume constitutes the forest resource that can be utilized to restore green infrastructure and promote biodiversity.

Our conclusions could have been different in landscapes with other management histories and initial age distributions. Moreover, future climate change will add to uncertainties in the conclusions, e.g., through changing frequencies and strengths of storms and pest outbreaks, and likely adaptations of forest management might have different impacts (Hahn et al., 2021).

Harvesting more wood than the projected demand increased financial returns only marginally (2% higher NPV in the *economy* scenario). This was because harvest volumes for high-value timber of

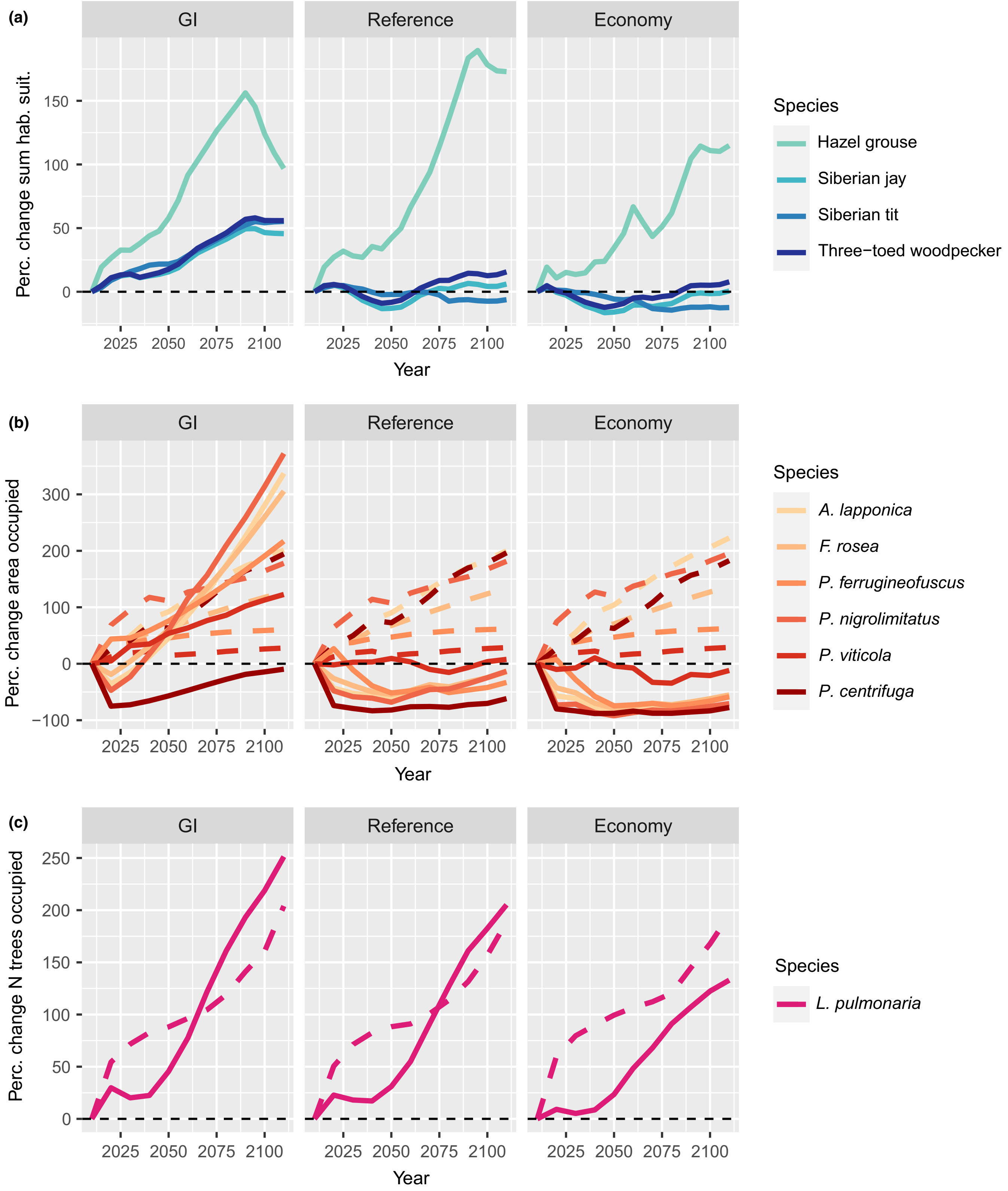

FIGURE 4 Species responses to forest management scenarios (panels) shown as percent change relative to 2010, of (a) total habitat suitability of birds, (b) metapopulation size of fungi (area occupied), and (c) metapopulation size of the lichen (number of trees occupied). For fungi and the lichen, trajectories are split into production forest (solid) and permanent set-asides (7.8% of the total area; dashed)

today's young forests were not much higher in the *economy* scenario (on average 5% higher) and occurred mainly towards 2110. At the same time, the environmental indicators were lowest in this scenario, and the majority of the studied species declined. This small increase in financial returns should be weighed against the resulting negative effects on forest biodiversity in forestry policy and planning.

4.2 | Management diversification improved environmental indicator status of production forest

We have shown how green infrastructure can be rebuilt from a legacy of half a century of intensive forestry. While set-aside areas remain important refuges for threatened species, sustainable management of the production forest is necessary for the long-term maintenance of forest biodiversity (Felton et al., 2020). Conditions and dynamics of the production matrix influence movement and dispersal, resources, and the abiotic environment within remaining protected patches (Driscoll et al., 2013). In line with this, Kremen (2015) argued that the polarized dichotomy of land sparing versus land sharing should be abandoned in favour of a synthetic view, where both protected areas and a biodiversity-friendly matrix synergistically promote long-term species persistence. Our work supports this synergistic approach, increasing environmental indicators and future viability of species of conservation concern.

All environmental indicators increased in the *GI* scenario, at 14% lower NPV than in the *reference*. The increasing levels of environmental indicators do not necessarily mean improved conditions for red-listed species. The environmental indicator deadwood volume did not reach highest levels in the *GI* scenario, but instead increased the most in the *reference* scenario, mainly due to higher proportions of stands managed without commercial thinning (Appendix S8). Owing to the low increases in the density of large trees, and hence coarse deadwood suitable for the study species, and decreasing area of old forests in the *reference* and *economy* scenarios, the focal red-listed fungi were projected to decline in the production forest. Although on average increasing more in the *reference* scenario, the deadwood may thus be located in forests that are cut before the fungi succeed in colonizing, a mechanism captured with our dynamic colonization-extinction models. Mönkkönen et al. (2014) recommended the omission of commercial thinning as a cost-effective way to increase the availability of deadwood. However, if deadwood increases in stands that are later clear-cut, then this deadwood increase will not have an effect. The different conclusions are probably explained by Mönkkönen et al. (2014) not applying dynamic models that adequately represent the underlying processes, e.g., low colonization rate and high extinction rate of stands with unsuitable habitat conditions (Moor et al., 2021). Indeed, the fungal metapopulations benefitted from the combined increasing deadwood volumes and area of old stands in the *GI* scenario. The utility of using only total deadwood volume as an environmental indicator, without regard to other deadwood or stand characteristics may thus be questioned.

4.3 | Environmental quality and species of conservation concern could increase in the production forest

The projected increases in habitat suitability and metapopulation sizes of most species in the *GI* scenario suggest that improving environmental indicator status in the production forest will benefit species of conservation concern. Management diversification can remediate current deteriorated forest conditions, and even threatened species have the potential to increase their population sizes also in the production forest.

All fungi except the most common species (*P. viticola*) decreased in the production forest in the *reference* and *economy* scenarios. Here, the driving variable spruce deadwood volume changed only marginally (Appendix S5), although the environmental indicator total deadwood volume starts to increase towards 2100 (Figure 3). However, in the *GI* scenario where also stand age increased (Figure 2), all species increased. This shows that improving the environmental indicator total deadwood volume alone, and to less than the threshold 20 m^3/ha^{-1} proposed by Junninen and Komonen (2011), is not sufficient to make certain species increase. Also, mean stand age in the production forest must increase. Otherwise these species' abundance in forest landscapes will be determined by the area of forest set-aside from production. *Phlebia centrifuga* initially decreased in both the *GI* scenario and on set-aside land. This results from high initial occupancy predicted by the occupancy model used for simulation initialization. However, the subsequent increase in the production forest of also this species is highest in the *GI* scenario.

The only species that did not benefit the most from the *GI* scenario was the hazel grouse, increasing in all, and the most in the *reference* scenario. This near threatened species has recently declined (SLU Artdatabanken, 2020). Its increase was driven by greatly increasing the total standing volume. The environmental indicator mature broadleaf-rich forests was not closely related to the habitat suitability of hazel grouse. Likely reasons are small changes in tree composition relative to the large increase in standing volume in all scenarios, and that hazel grouse also utilizes younger broadleaf-rich forests not included in the indicator mature broadleaf-rich forests (Åberg et al., 2003).

In scenarios that did not aim to improve environmental indicator status but optimized management for financial gains alone, some species maintained stable populations. Among birds, habitat suitability across the whole landscape remained stable, or increased slightly for Siberian jay and three-toed woodpecker. This was likely caused by the continuously increasing standing volumes, while interdecadal variation is further explained by the variation in forest age. The stable metapopulation size of the least specialized fungus *P. viticola* (Nordén et al., 2013) is explained by its fairly high colonization rate also at low deadwood volume and an almost linearly increasing colonization rate with forest age (Moor et al., 2021). The lichen *L. pulmonaria* increased in all scenarios also in the production forest. However, it only partly tracked the host trees densities, as also the connectivity to surrounding occupied trees and the rate of host tree increase and decrease (determined by cuttings) explain metapopulation dynamics (Belinchón et al., 2017). The environmental indicator mature broadleaf-rich forest did not strongly determine this outcome. Instead, retaining aspen and goat willow trees during all thinnings drove this increase. These ambitious simulation settings lead to densities higher than the FSC regulations (at least 5 trees/ha), but may be overly optimistic given actual land-owner actions and wildlife browsing.

In summary, we have shown that the increasing landscape-scale demand on wood from boreal forests, as predicted by a middle-of-the road global socioeconomic development while reaching the Paris agreement on climate change mitigation, can be met in the future. The low current standing volumes in these intensively managed landscapes were projected to increase and this surplus constitutes a resource that can be used for progress towards environmental quality objectives if management is not exclusively focused on economic outcomes. While species not always responded directly to higher levels of environmental quality indicators, the overall improvements benefitted this wide range of species.

CONFLICT OF INTEREST

The authors have no conflict of interest to declare.

AUTHORS' CONTRIBUTIONS

T.S., H.M. and J.E. conceived the ideas and designed methodology; N.F. simulated SSPs; J.E. simulated forest management scenarios; H.M., H.F. and L.H. contributed species models and simulated species responses; U.B., J.N. and A.M. contributed to data interpretation; H.M. and T.S. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository https://doi.org/10.5061/dryad.c866t1g8k (Moor et al., 2022).

ORCID

Helen Moor https://orcid.org/0000-0002-1340-2039
Jeannette Eggers https://orcid.org/0000-0003-1530-2581
Henna Fabritius https://orcid.org/0000-0002-3886-3149
Nicklas Forsell https://orcid.org/0000-0002-4984-3231
Laura Henckel https://orcid.org/0000-0002-1944-319X
Ute Bradter https://orcid.org/0000-0001-5687-1233
Adriano Mazziotta https://orcid.org/0000-0003-2088-3798
Jenni Nordén https://orcid.org/0000-0001-8894-5815
Tord Snäll https://orcid.org/0000-0001-5856-5539

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