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RESEARCH ARTICLE

Cost-effective biodiversity protection through multiuse-conservation landscapes

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Abstract
Context Intensive land use and exploitation of natural resources are the main direct drivers of biodiversity loss. Transformative changes in land management are called for as conservation and management actions have not been sufficient to support the viability of species populations. It has been proposed that to solve the sufficiency problem one could segregate the landscape into an intensively managed part, and into so-called multiuse-conservation landscapes that aggregate set asides with managed areas for multiple uses.
Objectives We describe a scenario analysis where we evaluate the effects and cost-efficiency of transforming the boreal forest from intensively managed production landscapes progressively towards multiuse-conservation landscapes.
Methods We simulated Finnish boreal forests under various managements and optimized management to produce six scenarios to reveal the ecological, economic, climate and management regime implications of multiuse-conservation landscapes. Ecological effects explored included habitat availability and metacommunity capacity of dead wood dependent species.

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Results Increasing the area of set aside and multiuse management increased the habitat availability and metacommunity capacity as well as climate benefits but caused economic losses in terms of timber revenues. Pooling the set asides and multiuse management areas together into the same landscapes reduced the economic losses, had negligible added climate benefits and produced mixed biodiversity effects: pooling decreased habitat availability but increased metacommunity capacity across all landscapes.

Conclusions Changing land management and aggregating conservation efforts can be a cost-efficient way to protect biodiversity. Our results suggest biodiversity benefits in landscapes where the set aside and multiuse is aggregated. Careful spatial planning can also alleviate the conflicts between ecological and economic values of land.

Keywords Biodiversity loss · Connectivity · Forestry · Land sharing · Land sparing · Population ecology · Spatial planning

Introduction

Land-use and the exploitation of natural resources have had globally large negative impacts on nature (Foley 2005; IPBES 2019). Species are facing increased risk of extinction while the functioning of ecosystems is being compromised (The Millennium Ecosystem Assessment 2005; Butchart et al. 2010). Although changes in land management can help safeguard biodiversity and ecosystem services, there is also a need to increase area under protection (CBD 2010; IPBES 2019). The target of UN Convention of Biological Diversity (CBD) has been raised from protecting 17% of the total terrestrial area (CBD 2010) to conservation of 30% of the terrestrial areas through protected areas and other effective area-based conservation measures (i.e., OECMs; CBD 2022). In alignment with the global CBD target, the EU Biodiversity Strategy aims for protecting 30% of the EU land area by 2030, stating that one third of that protection should be strict protection (European Commission 2020).

One of the reasons why current protected areas fail to retain viable species populations in the long term is habitat loss and fragmentation in the surrounding landscapes (Hanski 2011; Geldmann et al. 2013; Rybicki and Hanski 2013). While the negative impacts of habitat loss on populations are well established, the independent effects of habitat fragmentation are debated and likely context-dependent (Fahrig 2017; Haddad et al. 2017; Fletcher et al. 2018; Fahrig et al. 2019; Miller-Rushing et al. 2019; Chase et al. 2020; Riva and Fahrig 2023). From the perspective of species richness, the effects of fragmentation may be positive, but from the perspective of species' populations, the effects are typically negative. When the habitat cover is low, it is likely that fragmentation does reduce the viability of species' populations (Andrén 1994; Lienert 2004; Honnay et al. 2005).

The probability that a habitat is fragmented increases with decreasing habitat cover (Andrén 1994; Hanski 2011). As a consequence, individuals of species with limited dispersal ability may not be able to access and use all suitable habitat patches. Moreover, the quality and size of suitable habitat can decrease with increasing fragmentation due to increased edge effect (Pfeifer et al. 2017). However, there is evidence that the effects of fragmentation become apparent after a certain degree of habitat loss, set around 30% of the original habitat cover remaining; above this rough threshold, the effect of fragmentation on populations is likely to be small (Andrén 1994; Pardini et al. 2010; Hanski 2011; Rybicki & Hanski 2013).

To increase population viability within fragmented landscapes, Hanski (2011) and Kotiaho (2017) proposed to partition the overall landscape into intensively managed production landscapes, where resource extraction is the primary land-use objective, and less intensive multiuse-conservation landscapes within which a third of the area is set aside for biodiversity protection, aligned with the 30% habitat coverage threshold. This can be achieved when both production landscapes and multiuse-conservation landscapes cover 50% of the overall landscape, and 17% of the total area is set aside for biodiversity protection as part of the multiuse-conservation landscapes, thus covering 33% of the multiuse-conservation landscapes (Kotiaho 2017). Less intensive multiuse management in the remaining 67% of the multiuse-conservation landscapes may further support biodiversity protection and provision of ecosystem services (Ranius and Roberge 2011; Kotiaho 2017; Grass et al. 2019; Vauhkonen and Packalen 2019; Himes et al. 2022a, b). Such management includes various actions not aiming for maximizing economic value of forests, e.g., leaving more retention trees than required or postponing harvesting, to produce biodiversity and/or climate benefits. However, studies about the multi-sectorial impacts of these kinds of multiuse-conservation landscapes are rare.

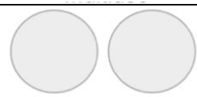
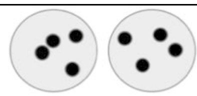
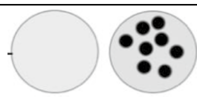
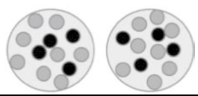
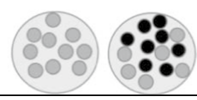
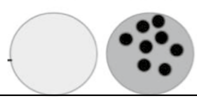
Our research focuses on boreal forests in Finland, which provide an ideal case to test the impacts of multiuse-conservation landscapes. Generally, Fennoscandian boreal forests are intensively managed for timber production, which has negatively affected forest biodiversity and the provision of key ecosystem services, such as climate regulation (Triviño et al. 2015; Pohjanmies et al. 2017a; Hyvärinen et al. 2019; Mönkkönen et al. 2022). The efforts to reduce negative environmental impacts of forestry include, e.g., retaining retention trees and applying less-intensive forest management regimes (Koivula and Vanha-Majamaa 2020). In addition, there have been forest conservation programs to increase the amount of set asides. However, to date there is no evidence that these current efforts can stop the loss of forest biodiversity or ensure continued provision of ecosystem services (Eyvindson et al. 2018; Hyvärinen et al. 2019). Therefore, more efficient approaches to forest management planning are called for.

Here we analyze the ecological, economic, climate and management regime implications of transforming the boreal forests under six scenarios from intensively managed production landscapes progressively towards multiuse-conservation landscapes (from S1 to S6 in Table 1). Comparisons between different scenarios enable us to distinguish the individual effects of traditional forest conservation (i.e., set aside, Box 1) and multiuse management (i.e., forest managed to produce biodiversity, climate and timber benefits simultaneously, Box 1) as well as the effects of aggregating them to specific landscapes. The results of our study offer new insights to the discussion of land sparing and sharing approaches (e.g., Grass et al. 2019).

Box 1 Definition of different terms in the text

Term	Meaning
Aggregation	Spatial clustering of a certain management to some landscapes
Connectivity	Reachability of suitable habitat patches from the perspective of the members of the species populations
Conservation landscape	A landscape where set asides are aggregated, covering 33% of the stands within the landscape
Habitat availability	An index of the amount of suitable habitat, including both area and quality of the habitat
Landscape	A spatially unified larger area; in this study, a watershed
Multiuse-conservation landscape	A landscape where both set asides and multiuse stands are aggregated
Multiuse stand	Stands where forest management is optimized to maximize biodiversity and climate benefits of forests with timber NPV as a constraint (set aside is not an option and stands providetimber benefits as well)
Metacommunity capacity	An index of the habitat availability that takes into account the amount of fragmentation (i.e., connectivity of habitats) using specified dispersal distances. In this study, dispersal abilities of 0.5 km, 1 km, 3 km, and 6 km were used in the calculations
Production landscape	A landscape where all the stands are under timber production
Production stand	Stands where forest management is optimized to maximize timber net present value (NPV)
Set aside stand	Stands where biodiversity through dead wood resources is maximized and forest management is not allowed, i.e., protected stands
Third-of-half approach	Conservation landscapes cover 50% of the overall region. In conservation landscapes, one third of the area is set aside. Setting aside one third of half returns roughly 17% set asides in the overall region

Table 1 (a) Different scenarios and their management objectives, share of area allocated to each management objective, and aggregation of set aside or multiuse

a)	Scenario	Management objective of stands	Share (%) of allocation	Aggregation
S1		Production Set aside Multiuse	100 0 0	 NO NO
S2		Production Set aside Multiuse	83 17 0	 NO NO
S3		Production Set aside Multiuse	83 17 0	 YES NO
S4		Production Set aside Multiuse	50 17 33	 NO NO
S5		Production Set aside Multiuse	50 17 33	 YES NO
S6		Production Set aside Multiuse	50 17 33	 YES YES

b) Scenario comparisons	Effect over all landscapes
S1 vs S6	Effect of 50% multiuse- conservation landscapes.
S1 vs S2	Effect of 17% set aside.
S2 vs S3	Effect of aggregation of set asides.
S2 vs S4	Additional effect of 33% multiuse on top of the effect of 17% set asides.
S4 vs S5	Effect of aggregation of 17% set asides when 33% multiuse located anywhere.
S5 vs S6	Additional effect of aggregation of 33% multiuse on top of 17% aggregated set asides.

In figures under scenarios, large circles represent the watersheds (in this example only two) and the small circles the stands. Light gray indicates production, black indicates set aside and dark grey indicates multiuse as the management objective of the stands. Note that the production objective is also targeted to stands, but for illustration here we color the background of the watershed with light gray and do not illustrate them as separate stands. Moreover, in S6, the background of the other watershed has dark-gray shading to represent that multiuse is the management objective for all other stands besides set aside stands. YES/NO in the aggregation column indicates that the management in question is or is not aggregated to half of the landscapes. b) Comparisons between scenarios which reveal the effects of management objectives and their aggregations

Methods

General overview of the methods

In this study, we used forest simulations, modelling, and optimization tools in boreal forests in Finland. We first simulated forest growth in each of the 31,489 production forest stands located in 17 different watersheds (i.e., landscapes) in Finland over 100 years under 22 different forest management regimes. We then applied a systematic optimization approach to construct six management scenarios. These scenarios had variations in how landscapes varying in their share of allocation to set aside, multiuse and production as well as whether set aside, multiuse or both were aggregated (Box 1, Table 1). Set aside stands were selected to maximize dead wood resources as dead wood is a crucial resource for most of the forest dwelling species in Nordic boreal forests (de Jong and Dahlberg 2017; Kotiranta et al. 2019). In stands allocated to multiuse, management regime optimization maximized climate and biodiversity benefits, while ensuring a predefined timber net present value (NPV) as a constraint, and in stands allocated to production, management regime optimization maximized timber NPV. As response variables for economic, climate or biodiversity benefits, we used timber NPV, carbon storage, or habitat availability and metacommunity capacity of the landscapes for the dead wood dependent species, respectively.

Study area

The study area consists of 31,489 production forest stands (i.e., planning units) located in 17 different watersheds (i.e., landscapes) in Southern-, Eastern-, and Central-Finland (Fig. 1). The total size of the study area is 47,561 ha and the mean size of forest stands is 1.5 ha (standard deviation 1.9). There is variation in size and productivity among watersheds (Supplementary Table S1). The initial forest data, based on a combination of field data collection, aerial photogrammetry and laser scanning data, originates from the local forest authority (Finnish Forest Centre). The forest data contain stand-level characteristics, such as forest soil and site type, tree species composition, and size distribution of trees. Mineral soils cover 77% and peatlands 23% of the total area. Forest stands are mainly Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*) dominated with varying amounts of deciduous mixture, and they vary in terms of initial development stage and age. A more detailed description of the study area is found in a previous study (Pohjanmies et al. 2017b). The initial data did not contain dead wood and therefore initial values for dead wood were set to be consistent with the Finnish National Forest inventory data, which provided for different site fertility classes an average volume per hectare of dead wood for tree species for southern Finland (Peltola 2014).

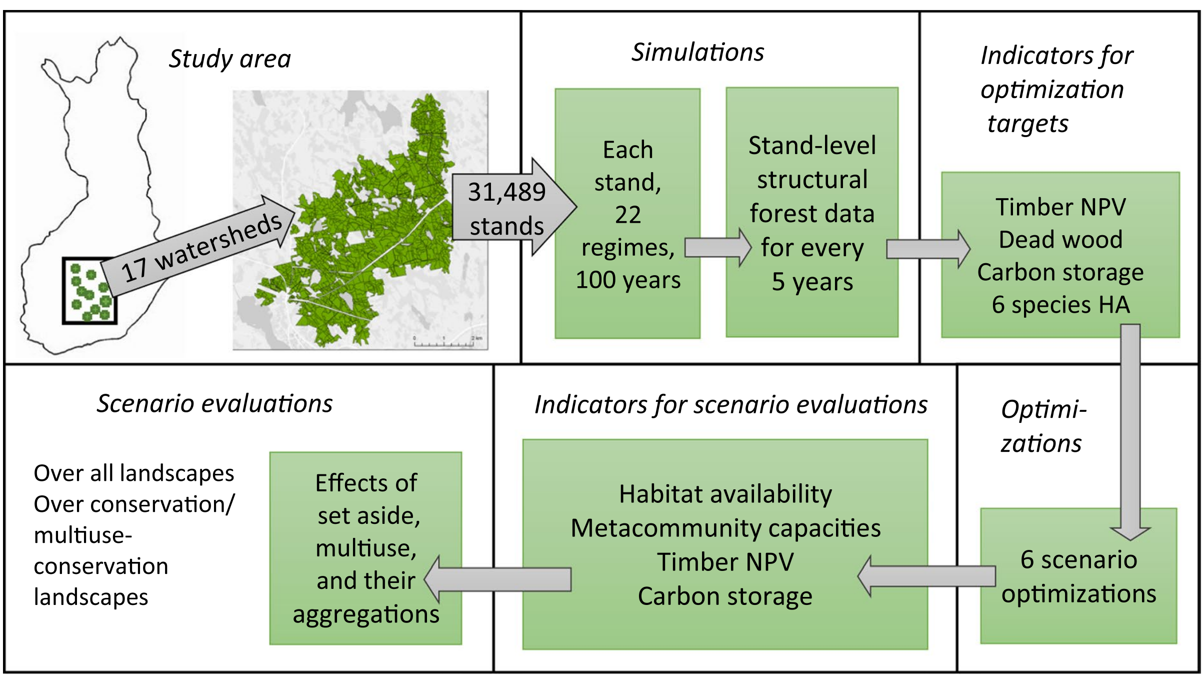


Fig. 1 Illustration of different steps in methods. HA stands for habitat availability, and NPV for net present value

Simulations

We simulated each stand over 100 years using the open-source forest simulator SIMO (Rasinmäki et al. 2009) in 5-year intervals under 22 different forest management regimes. The simulator creates structural forest data for each stand at each time step and under each regime. A total of 17 regimes were modifications of rotation forestry where rotation lengths, thinning frequencies, and green tree retention levels were varied (in all regimes at least 10 retention trees per ha) (Eyvindson et al. 2018). Four regimes were modifications of continuous cover forestry where harvesting intervals were varied (Pukkala et al. 2013). In set aside, forests were allowed to grow without any forest management practices. The development under rotation forestry and set asides were modelled using the statistical model set of Hynynen et al. (2002), which consists of species-specific individual-tree models for ingrowth, growth, and mortality. The development under continuous cover forestry was predicted using the statistical model set of Pukkala et al. (2013), which consists of species-specific individual-tree diameter increment and survival models, and a stand-level model for ingrowth. Natural disturbances, such as wind or insect outbreaks, were not taken into account. Neither was the potential impact of climate change on forest growth considered.

Indicators for optimization targets

Structural forest data from simulations and other stand-level information was used to estimate indicators for the optimization targets (Fig. 1). Indicators were calculated for each stand, time step and management regime. Dead wood is one of the most limited resources for biodiversity in commercial boreal forests (Hyvärinen et al. 2019). Dead wood resources were estimated as the total volume of dead wood (m^3) multiplied by the diversity of dead wood tree species (Scots pine *Pinus sylvestris*, Norway spruce *Picea abies*, and birch species *Betula pendula* and *Betula pubescens*) and decay stages (five categories (Mäkinen et al. 2006)). Habitat availabilities for six different species were estimated using the models from a previous study (Mönkkönen et al. 2014). These species were Capercaillie (*Tetrao urogallus),* Hazel grouse (*Bonasa bonasia*), Lesser-spotted woodpecker (*Dryobates minor*), Long-tailed tit (*Aegithalos caudatus*), Siberian flying squirrel (*Pteromys volans*) and Three-toed woodpecker (*Picoides tridactylus*).

The role of boreal forests in climate change mitigation is crucial and boreal forests contain a large share of global carbon storages in above and below-ground biomass (Bradshaw and Warkentin 2015). Carbon in living biomass was evaluated by multiplying the tree biomass by 0.5 (IPCC 2003, European Commission 2021) and carbon in dead wood and soil was modelled using Yasso07 (Tuomi et al. 2009, 2011) for mineral soils and carbon flux models for peatlands (Ojanen et al. 2014). The net present value was evaluated by aggregating the income of harvested timber, the costs of silvicultural actions (such as scarification, planting, pre-commercial thinning; Table S3), the value of forest land and the value of standing timber at the end of the simulation period all discounted to the present value using a discount rate of 1%. The discount rate was selected only 1%, as high interest rates are often not realistic and they can lead to very intense cuttings at the beginning of the planning period (Hepburn and Koundouri 2007). To calculate the value of the standing timber at the end of the simulation period, we applied models from Pukkala (2005). These models apply a typical management of the stand, depending on site characteristics such as site fertility, standing trees and geography. The average stumpage prices for clear-cuts and thinnings from the study region were used (Supplementary Table S2, Peltola 2014). In continuous cover forestry, the prices of second thinning were used. For readers interested in the impacts of higher discount rate, the main results are also provided with 3% interest rate in the Supplementary Data and Table S7.

Optimizations and scenarios

The construction of the scenarios was accomplished through mathematical optimization, with modifications to vary the conservation and multiuse prioritizations. We used the commercial optimization software (CPLEX version 12.8) to find solutions for the optimization models. The input data for all scenarios was the stand level management regimes, each of the 22 potential management regimes simulated at the stand scale.

We ran optimizations separately for all six scenarios (Table 1a). In scenario S1, all stands were optimized for production [timber NPV maximized (Box 1)]. Scenarios S2 and S3 were optimized in two steps. In the first steps, 17% of area was set aside to maximize the dead wood resources. In S2, set aside stands were allowed to locate anywhere whereas in S3, set asides stands were forced to locate within half of the watersheds (i.e., half of the watersheds with the largest dead wood potential). These landscapes where set asides are aggregated are called conservation landscapes. In the second steps of S2 and S3, stands which were not set aside in the first step (83% of total area) were optimized for production.

Scenarios S4, S5 and S6 were optimized in three steps (Table 1a). The first steps of S4 and S5 are identical with the first steps of S2 and S3, respectively. In the second steps of S4 and S5, stands which were not set aside in the first step were optimized for multiuse (33% of total area, climate and biodiversity benefits maximized but set aside not an option meaning that stands provided timber benefits as well (Box 1)). In the third steps of S4 and S5, stands which were not set aside or multiuse stands were optimized for production (50% of total area). In the scenario S6, both set aside and multiuse stands were aggregated within same half of landscapes (Table 1a). The first step of S6 was identical to the first step of S3. In the second step, stands which were located in conservation landscapes, but were not set aside stands, were optimized for multiuse (33% of the total area and 67% of the area in conservation landscapes). In scenario S6, these landscapes were both set asides and multiuse stands are aggregated are called multiuse-conservation landscapes. In the third step, stands which were located in landscapes which were not multiuse-conservation landscapes, were optimized for production (50% of total area). The full optimization problems are given in the Supplementary Equations.

Indicators for scenario evaluations

Biodiversity, climate and economic benefits of forests were evaluated over all landscapes for each scenario (Table 1). Carbon storage (average over 100 years) was used as an index for climate benefits and timber NPV as an index for economic benefits. For ecological evaluation we constructed two different indices, a habitat availability (HA) of dead wood dependent species, which takes into account the area and quality of habitats, and a metacommunity capacity (MC) of dead wood dependent species, which in addition to area and quality, takes into account the spatial connectivity of habitats. Note that here we no longer consider the six species mentioned in the last paragraph that were only used as targets for optimizations.

First, we created a habitat suitability index for dead wood dependent species scaling the stand-level resources of dead wood between 0 and 1 (Supplementary Fig. S1). The diversity weighted dead wood volume correlates strongly with the volume of dead wood. Thus, we set the lower threshold of dead wood to 5 m^3 ha^{-1} as this is slightly more than the average amount of dead wood in production forests in our study area (NFI 2018) and approximately 10% of the minimum average amount of dead wood in natural boreal forests (Siitonen 2001). We set the upper threshold to 20 m^3 ha^{-1} as this is the required minimum amount of dead wood for many demanding dead wood dependent species to persist (Junninen and Komonen 2011). The stand-level habitat availability was the habitat suitability index multiplied by the area of the stand. Then basically a large stand with a smaller volume of dead wood per ha can be as good as a small stand with higher volume per ha.

Second, we took into account the fragmentation of habitats and calculated a metacommunity capacity (Hanski and Ovaskainen 2000) of habitats separately for each watershed since they were not connected. In this case, metacommunity capacity is a relative estimation of the watershed ability to support a metacommunity of a dead wood dependent species. It was calculated as the dominant eigenvalue of a watershed matrix that takes into account the areas, qualities and distances between suitable stands in the watershed, as well as the dispersal ability of the species. We used the function metacapa from the R-package *vegan* (Oksanen et al. 2017) and distances between stands were calculated using the function dist. Dispersal ability of dead wood dependent species and taxa varies (Komonen and Müller 2018) and, therefore, we calculated metacommunity capacities for dead wood dependent species with dispersal abilities 0.5 km, 1 km, 3 km and 6 km. We calculated metacommunity capacities separately for each time step so the temporal connectivity of habitats was not taken into account.

Scenario evaluations

The comparison between scenarios S1 and S6 reveal the total effects of multiuse-conservation landscapes on different benefits (described in a previous chapter). To better understand the role of each of the management objectives and aggregation on the biodiversity and climate benefits as well as the economic costs, we analyse the individual effects of each of the management objectives and aggregation in turn. First, we calculated the share of set asides per landscapes in scenarios without aggregation (S2 and S4 in Table 1) and with aggregation (S3, S5 and S6 in Table 1) to explore whether there was any natural aggregation and if our aggregation rule remarkably changed it. We also calculated the share of relocated set asides in aggregation scenarios. Then, we compared the levels of indicators over all landscapes among scenarios. Comparing specific scenarios (Table 1b) revealed the relative overall effects of set aside, multiuse and their aggregations on different benefits. The area of set asides and multiuse is same in scenarios with and without aggregations, which makes possible to study the individual effects of aggregations.

In the case of biodiversity measures where spatiality matters, we also evaluated the effects of aggregation separately in conservation and multiuse-conservation landscapes, and in landscapes without conservation. For example, comparing the average biodiversity indices over all landscapes from the scenario S2 with average indices over conservation landscapes from the scenario S3 reveal the effect of aggregation of set asides on indices in conservation landscapes. More detailed descriptions of these comparisons are given in the Supplementary Table S4. We also explored the amount of dead wood dependent species' habitat availability and metacommunity capacity over time to see their development. Moreover, we explored the optimal allocation of management regimes in different management options and scenarios. The results of these analyses are given in Supplementary Data and Figure S3. All calculations were done using R-software version 3.6.1 (R Development Core Team 2014).

Results

Effect of the 50% multiuse-conservation landscapes

Transforming half of the production landscapes into multiuse-conservation landscapes (S1 vs. S6 in Table 1; for definitions of landscapes see Box 1), increased total habitat availability (i.e., habitat availability over all landscapes) by nearly 700% and total metacommunity capacities, depending on the dispersal abilities, by 2000–3000% (Fig. 1a, Table 2). Total carbon storage was increased by 10% (Fig. 1c, Table 2), while the total timber NPV was decreased by 31% (Fig. 1b, Table 2).

Effect of 17% set aside without and with aggregation

Relative to 100% production landscapes, setting aside 17% of the best stands in terms of their potential for dead wood resources without targeting aggregation (S1 vs S2 in Table 1) increased the total habitat availability by 500%, total metacommunity capacities by 1600–2000%, total carbon storage by 7%, and decreased the total timber NPV by 23% (Fig. 2, Table 2). Habitat availability and metacommunity capacity of the overall production landscape was low initially, but transforming 17% of the area into set aside resulted in very large relative biodiversity benefits (Fig. 3a).

When the 17% of the overall area is set aside but aggregated into half of the landscapes, a third-of-half becomes set aside. Relative to setting aside 17% anywhere (S2 in Table 1), aggregating set asides (S3 in Table 1) decreased the total habitat availability by 5%, decreased the total metacommunity capacity of short-distance dispersers by 4–10%, increased the total metacommunity capacity of mid-distance dispersers by 4%, did not affect the total carbon storage and increased the total timber NPV by 2% (Fig. 2, Table 2). Over all landscapes, aggregating set asides within half of the landscapes changed the location of 23% of the set aside area (i.e., distribution of set aside changed among watersheds (Supplementary Table S1)). Decreased habitat availability in the overall region due to relocation of 23% set asides means that the quality of relocated set asides was lower in the scenario where set asides were aggregated (S3 in Table 1) than in the scenario where set asides were not aggregated (S2 in Table 1). Aggregation caused

Table 2 The relative and absolute (in brackets) effects of multiuse-conservation landscapes, set asides, multiuse, and their aggregation on total habitat availability, metacommunity capacities, carbon storages and timber NPV over all landscapes

The effects over all landscapes	Dead wood dependent species: Habitat availability	Dead wood dependent species: Metacommunity capacity 500 m	1 km	3 km	6 km	Carbon storage (kTC)	Timber NPV (M€)
State in S1 (all production landscapes)	***987***	***49***	***111***	***278***	***406***	***8090***	***1067***
50% multiuse-conservation landscapes S1 → S6	697% (6876)	2255% (1080)	2430% (2698)	2927% (8138)	3106% (12635)	10% (827)	-31% (-327)
17% set aside S1 →S2	515% (5086)	1660% (795)	1577% (1750)	1874% (5209)	2039% (8296)	7% (527)	-23% (-243)
Aggregation of set aside S2 → S3	-5% (-314)	-10% (-86)	-4% (-73)	4% (209)	4% (357)	0% (5)	2% (20)
Additional 33% multiuse on top of 17% set aside S2 → S4	40% (2451)	24% (199)	30% (562)	36% (1995)	38% (3271)	5% (412)	-16% (-132)
Aggregation of set aside with 33% multiuse located anywhere S4 → S5	-3% (-213)	3% (28)	6% (143)	5% (372)	3% (417)	0% (21)	0% (2)
Additional effect of aggregation of 33% multiuse along with the 17% aggregated set asides S5 → S6	-5% (-448)	5% (58)	9% (242)	7% (562)	5% (650)	-1% (-133)	7% (50)

The absolute state of each indicator in scenario S1 where all landscapes contain exclusively production stands are given in the first row. All indicators except timber NPV have been averaged over the 100-year simulation period. Orange and blue colors indicate a negative or positive effect respectively and the intensity of the color the strength of the effect

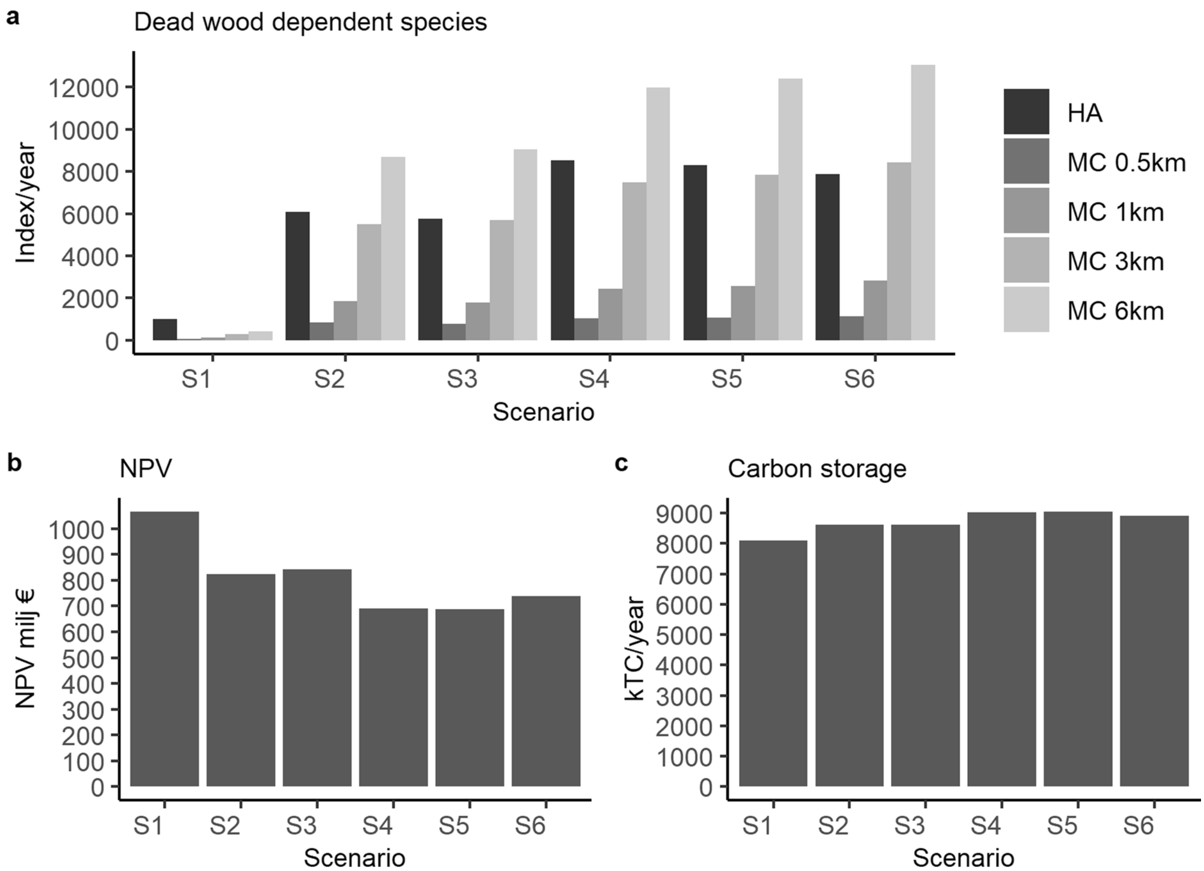


Fig. 2 The total **a** biodiversity, **b** economic and **c** climate benefits of forests over all landscapes in different scenarios. HA indicates average annual habitat availability over 100-year simulation period and MC indicates average annual metacommunity capacity with different dispersal abilities. NPV indicates timber net present value in million euros over 100-year simulation period. Carbon storage indicates average annual storage over 100-year simulation period in thousands of tons of carbon

a different effect on the metacommunity capacity of short and mid-distance dispersers and caused further decrease in habitat connectivity of short-distance dispersers (0.5 km, 1 km) as their metacommunity capacity decreased in the overall region (Fig. 2, Table 2). However, positive responses on aggregation were also found, as the metacommunity capacities of mid-distance dispersers (3 km, 6 km) increased.

For biodiversity, it is important to focus on the effects of set aside and aggregation within each type of landscape in addition to the above-reported overall landscape effects. This is because we assume that each of the landscapes is large enough to be able to support most of the biodiversity if the habitat availability within the landscape is high enough. In landscapes where set asides were aggregated (i.e., conservation landscapes, scenario S3 in Supplementary Fig. S2), the aggregation of set asides increased the habitat availability by 84% and metacommunity capacities by 75–113% (Fig. 3, Supplementary Table S5). In contrast, the habitat availability decreased by 86% and metacommunity capacities decreased by 96% in the landscapes which were not conservation landscapes and from which the set asides were removed (Fig. 3, Supplementary Table S5). Thus, in the case of habitat availability and metacommunity capacities of short-distance dispersers (0.5 km, 1 km), the relative benefit of aggregation in conservation landscapes was smaller than the relative cost of aggregation in landscapes with production stands only. However, in the case of mid-distance dispersers (3 km, 6 km), the benefit of aggregation in conservation landscapes was larger than the cost of aggregation in non-conservation landscapes. Nevertheless, aggregation increased the habitat availability and thus metacommunity capacities in conservation landscapes remarkably, and the likelihood that these conservation landscapes could support viable populations is high.

The additional effect of 33% multiuse management without and with aggregation

Compared to setting aside 17% anywhere without multiuse management, additionally allocating multiuse on 33% of the area anywhere (S2 vs S4 in Table 1b), increased the total habitat availability by an additional 40%, increased total metacommunity capacities by an additional 24–38%, increased the total carbon storage by an additional 5% and decreased the total timber NPV by an additional 16% (Fig. 2, Table 2).

Compared to a situation where the 17% and 33% of the overall area is allocated for set aside and multiuse stands anywhere, respectively, aggregating set asides into half of the landscapes (S4 vs S5 in Table 1b) decreased the total habitat availability by 3% but increased total metacommunity capacity by 3–6% (Fig. 2a, Table 2). Aggregation had no effect on the total carbon storage and the total timber NPV (Fig. 2b-c, Table 2). The comparison suggests that aggregating set asides was more efficient from the metacommunity capacity perspective when multiuse was applied on 33% of the area located anywhere than when no multiuse was applied. With multiuse anywhere, also total metacommunity capacities of species with short-distance dispersal ability increased due to the aggregation of set asides. Stands under multiuse, even when located anywhere, seemed to increase the connectivity of set asides importantly for species with short-distance dispersal ability (scenario S5 in Supplementary Fig. S2).

However, compared to a situation where 17% of the overall area is set aside and aggregated and 33% of multiuse is located anywhere, aggregating multiuse (the area of multiuse is constant) into the same landscapes with aggregated set asides (S5 vs S6 in Table 1b) decreased the total habitat availability by an additional 5%, increased total metacommunity

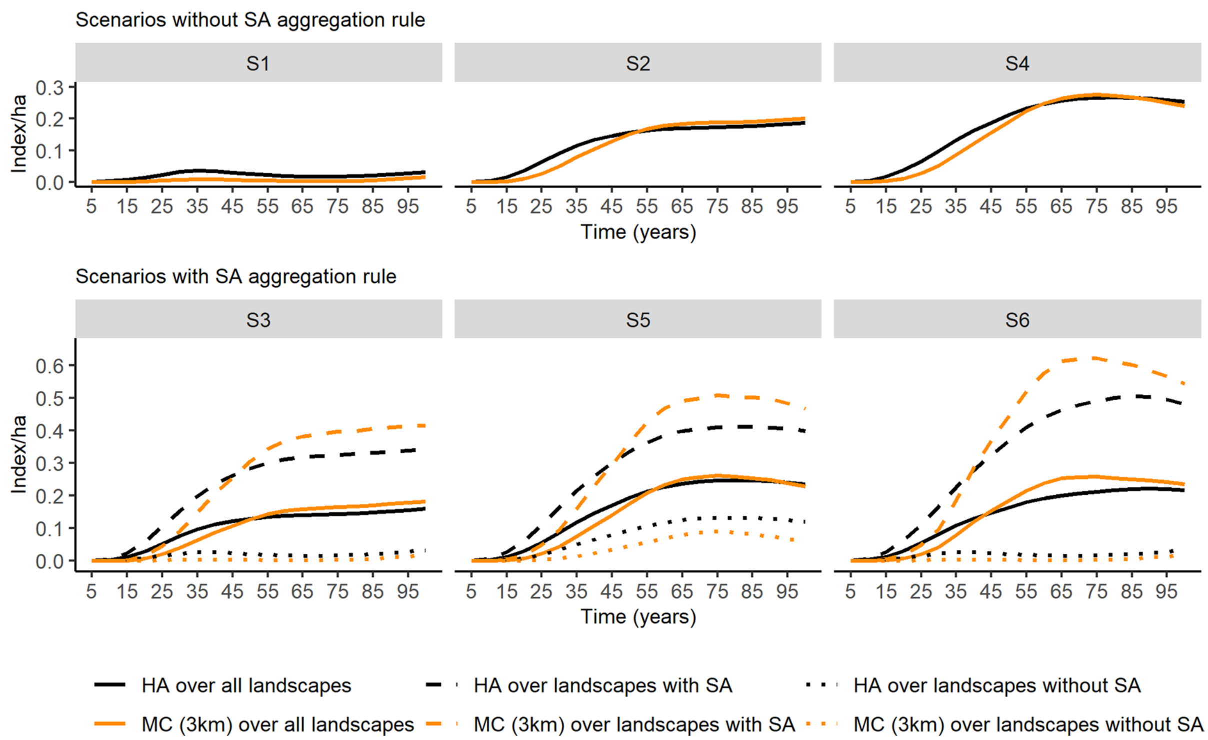


Fig. 3 The average development of habitat availability (HA, black lines) and metacommunity capacity with 3 km dispersal ability (MC, orange lines). Solid lines indicate average values over all landscapes. Dashed and dotted lines indicate average values over landscapes with and without set asides (SA) respectively in scenarios with aggregation (i.e., conservation landscapes in S3 and S5, and multiuse-conservation landscapes in S6)

capacity by an additional 5–9%, decreased the total carbon storage by an additional 1% and increased the total timber NPV by an additional 7% (Fig. 2, Table 2). The relative increases in metacommunity capacities were as large as or larger than the relative decrease in habitat availability over all landscapes. Moreover, increased timber NPV on the other hand means that the economic cost of multiuse was decreased due to the aggregation of multiuse. Thus, this comparison suggests that set asides and multiuse stands as conservation efforts were the most cost-efficient in multiuse-conservation landscapes.

Focusing on the landscapes where set asides and multiuse were aggregated (i.e., multiuse-conservation landscapes, S6 in Supplementary Fig. S2), the aggregation of set asides and multiuse increased the habitat availability by 83% and metacommunity capacities by 109–128% (Fig. 3, Supplementary Table S5). In contrasts, in production landscapes the aggregation of both set asides and multiuse stands decreased the habitat availability by 90% and metacommunity capacities by 96–97%. Thus, as in the case of conservation landscapes, the increase in habitat availability of multiuse-conservation landscapes was not as large as the decrease in habitat availability of production landscapes, whereas the increases in metacommunity capacities of multiuse-conservation landscapes were larger than their decreases in production landscapes. In multiuse-conservation landscapes, most of the stands seemed to provide resources for dead wood-dependent species and the amount of habitat fragmentation was small (scenario S6 in Supplementary Fig. S2).

Discussion

Here we showed that partitioning the overall region to intensively managed landscapes and to landscapes that are managed as multiuse-conservation landscapes, can be a cost-efficient way to protect biodiversity. From the biodiversity benefit perspective increasing the area of set aside and multiuse management invariably increases the habitat availability and metacommunity capacity with some economic losses in terms of timber NPV. The cost was expected as strong conflicts between economic and other benefits are prevalent (de Groot et al. 2010; Seppelt et al. 2013; Isbell et al. 2015) and also exist in boreal forests (Siitonen 2001; Gauthier et al. 2015; Felton et al. 2016; Pohjanmies et al. 2017a, 2019). However, our results suggest that aggregating the set asides and multiuse management reduce the economic losses in terms of timber NPV but produce mixed biodiversity effects: aggregation decreases the habitat availability but increases metacommunity capacity across all landscapes. Nevertheless, the biodiversity benefits in landscapes where the set aside and multiuse is aggregated are great. If indeed the overall habitat area of 17% is not sufficient to retain viable populations of species in the long term when it is evenly distributed across the landscapes, then aggregating the same area still overall serves the biodiversity better.

The largest impacts to individual outcomes came from allocating 17% of the area for biodiversity protection. The relative decrease in timber NPV was larger than the relative share of the set aside area (23% decrease in NPV with a 17% increase in SA). This difference indicates that forests that have the highest dead wood potential are simultaneously most valuable in terms of timber production, which supports earlier findings of strong conflicts between timber production and dead wood resources (Pohjanmies et al. 2019). The relative increase of carbon storage due to set asides was smaller than that of the dead wood resources, because while managed boreal forests do not often accumulate dead wood enough to support the persistence of dead wood dependent species they nevertheless do store carbon (Triviño et al. 2015). However, it is well known that unmanaged and old-growth forests are large carbon storages (Luyssaert et al. 2008; Pukkala 2018) and also in our study, set aside stands had larger carbon storages than production stands.

Relative to setting aside 17% anywhere, aggregating set asides decreased the total habitat availability and the total metacommunity capacity of short-distance dispersers slightly but in contrast, increased the total metacommunity capacity of mid-distance dispersers slightly. A similar result was found in an earlier study from Fennoscandia, which concluded that dead wood dependent species having medium dispersal ability can benefit from spatial planning and habitat aggregation (Ranius and Roberge 2011). The economic benefit of aggregating set asides is explained by the release of economically valuable stands for timber production in landscapes without set asides. Thus, the main conclusion is that the aggregation of set asides can slightly alleviate the challenging conflict between biodiversity and economic benefits in forests (Pohjanmies et al. 2017a; Eyvindson et al. 2018).

The opposite response of habitat availability and metacommunity capacity on aggregation (Table 2) means that in land use planning we are faced with an unavoidable trade-off between habitat quality and connectivity (Hodgson et al. 2009). The relative importance of the three fundamental spatio-ecological variables (habitat area, quality and connectivity) affecting the viability of population is debated (Hodgson et al. 2009; Doerr et al. 2011) and in particular the independent influence of spatial connectedness of habitats has been questioned as connectivity of habitats predominantly increases with habitat area and quality (Hodgson et al. 2009; Fahrig 2017). In our simulations, the area of set aside and multiuse stands was the same in scenarios with and without aggregation. This means that habitat availability decreased exclusively due to decreased quality of habitats in scenarios with aggregation. However, metacommunity capacities increased in scenarios with aggregation meaning that the effect of increased habitat connectivity on metacommunity capacity was larger than the effect of decreased habitat quality on metacommunity capacity.

Although they are almost prohibitively difficult to conduct in the landscape scales needed, empirical studies are called for to substantiate our intriguing findings, as the modelled numeric responses may differ from the true biological responses (see also Tollefson 2021; Himes et al. 2023). In particular, it has been suggested that species may not be as dispersal limited as we assume through the modelled dispersal abilities in this study (Komonen & Müller 2018). However, even if dispersal was not a limiting factor, small and isolated habitat patches are exposed to edge effect, which can decrease the area and quality of suitable habitat (Murcia 1995; Haddad et al. 2015; Pfeifer et al. 2017). It should be noted that this was not directly included into the modelling in this study. Nevertheless, in addition to connectivity between habitats, aggregation can affect the quality of habitat patches and so impact the viability of populations at the patch scale (Hodgson et al. 2011; Haddad et al. 2015; Jaquiéry et al. 2016).

Spatial allocation of land-use for different management targets relates to the ongoing discussion about land sharing and sparing (Kremen 2015; Grass et al. 2019). Land sparing strategies (i.e., set asides) are particularly important for the protection of vulnerable and specialized species whereas land sharing strategies (i.e., multiuse) are often applied to retain ecosystem services and the habitats of generalist species. Previous research suggests that the combination of strategies is the most effective way to reduce the loss of biodiversity and ecosystem services (Grass et al. 2019). Our results support this idea and particularly show that aggregating both land sparing and sharing strategies in multiuse-conservation landscapes can increase the effectiveness. Especially species with short-distance dispersal ability may benefit from the improved quality of landscape around set asides due to multiuse stands. Even if multiuse stands do not provide high-quality habitat, they could improve the movement of individuals between suitable habitat patches (Eycott et al. 2012). However, in terms of climate benefits, our results suggest that the spatial location of set aside and multiuse stands is insignificant. This is a positive outcome, as it means that spatial planning can be done from biodiversity perspective without compromising climate benefits.

While the aggregation of set aside and multiuse stands improve biodiversity prospects through increased metacommunity capacities, it simultaneously reduces the economic losses in timber NPV from set asides and multiuse stands. This win–win situation indicates, that when resources for conservation are limited, planning land-use management with a moderate emphasis on habitat connectivity through landscape partitioning to multiuse-conservation and production landscapes can decrease the conservation costs (Foley 2005; Seppelt et al. 2013). This finding is rare as in balanced solutions economic costs of conservation are typically decreased with the expense of biodiversity values (Naidoo et al. 2006). Thus, our results suggest that while transformative changes in land management are needed to reduce the loss of biodiversity and ecosystem services, careful spatial planning can alleviate the conflicts between ecological and economic values of land.

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Author contributions All authors contributed the designing of the study and the planning of the scenarios and the optimizations. KE and MP prepared the data, KE performed the initial simulations and optimizations, and MP analyzed the output data and calculated the final results. MP wrote the first draft of the manuscript, JK did the main revision and all authors contributed substantially to other revisions. All authors have approved the final manuscript.

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Data availability The datasets generated during and/or analysed during the current study are available from the corresponding author upon reasonable request.

Declarations

Competing interests The authors have no relevant financial or non-financial interests to disclose.

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