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Research article

Integrating spatial aspects in forest planning: Optimizing boreal forest landscapes reveals trade-offs between timber and grouse habitats at multiple scales

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ABSTRACT

Integrating spatial aspects in forest planning is essential to account for management effects across scales. Forest management impacts wildlife habitat quality by reducing key reproductive resources, posing challenges for balancing timber production with habitat conservation. Because forest species respond to habitat features at multiple spatial scales, the impact of management on habitat quality also varies across scales but remains poorly understood. In this study we evaluate how trade-offs between timber yield and habitat availability vary across species with different habitat needs and spatial scales.

We simulated and optimized three boreal Finnish production landscapes spanning a gradient of management intensities using the MELA2.0 forest simulation package. Production possibility frontiers revealed trade-off between economic value (Net Present Value (NPV) of timber) and ecological value (grouse occupancy). Occupancy was modelled for four forest grouse species (hazel grouse, black grouse, capercaillie and willow grouse) using nationwide wildlife triangle census data and predictors related to forest structure and composition at biologically relevant scales: local (stand, ~0.05 km), home-range (1 km) and landscape (5 km).

A 1 % reduction in NPV increased occupancy on average by 7 % at the stand, 9 % at the home-range, and 26 % at the landscape scale. While patterns at smaller scales often mirrored broader trends, discrepancies in certain species-scale combinations highlighted the risk of mismanagement. Habitat quality peaked under conservation-oriented management, NPV under intensive forestry, while compromise solutions emerged from balanced management. The variation in trade-offs at different scales underscores the need for tailored, multi-scale planning to align economic and ecological objectives.

1. Introduction

Forest management can play a crucial role to maintain biodiversity, yet it can also pose challenges by altering habitat quality (Mönkkönen et al., 2014). Diversifying management across forest stands can create different habitats (Duflot et al., 2022), with intensive timber harvesting reducing habitat availability in the form of deadwood for forest dwelling species (Lassauce et al., 2011). Sustainable forest management seeks to balance economic objectives with biodiversity conservation, ensuring a continuous supply of timber while mitigating negative impacts on habitat quality (Naumov et al., 2018). Different forest-dwelling species have unique habitat needs, making it difficult to manage landscapes in a way that improves all habitats. The forest-dwelling species respond differently to management practices at various spatial scales, depending on their needs for resources and habitats across different scales during their annual life cycle. Many resident boreal birds have different requirements for territory habitat type and size between breeding and non-breeding seasons (Vatka et al., 2014). For instance, the willow tit's declining adult annual survival rate has been associated to the quality deterioration of large winter territories, which is suggested to be the

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main reason for population decline than the quality of the smaller breeding season territories (Lehikoinen et al., 2024). Therefore, it is important to evaluate how species respond to effects of management practices on forest structure and habitat availability at different scales. In Fennoscandia clear cutting decreases canopy cover which ultimately reduces habitat availability for forest grouse species at stand scale (Helle et al., 2003). This induces the deterioration of the lekking site at home range scale, which ultimately degrades the quality of the whole landscape for the species at the regional scale. A change in harvest intensity will likely modify the conflicts between timber production and species habitat availability (Holland et al., 2004).

More generally, De Pellegrin Llorente et al. (2017) have indicated a need to integrate multiple spatial aspects in forest planning to account for multi-scale interdependencies among planning goals. Various approaches have been suggested to approach this problem, for example the prioritization of a goal (i.e., maximizing deadwood volume) in spatially adjacent stands via the clique approach (Mazziotta et al., 2023) or constraining cuttings in adjacent stands using heuristic optimization such as simulated annealing (Borges et al., 2014). In general, the use of meta-heuristic or combinatorial optimization techniques has proven convenient within the domain of spatial forest planning (Baskent et al., 2024). However, the use of spatial optimization to integrate multiple objectives over large landscapes requires extremely careful planning and is computationally demanding for large-scale spatial harvest scheduling problems (Baskent et al., 2024). Improvements to the solutions are dependent on the degree of landscape heterogeneity and must be evaluated case-by-case.

Grouse species are specialized in boreal forest habitats but their association with forest structure vary (cf.; Ruottinen et al., 2024). For example, hazel grouse especially prefers young mixed forests with a dense layer of bushes and trees of different ages (Huhta et al., 2017). The presence of black grouse and especially willow grouse is also explained by the low volume of trees, which is typical in areas favored by these species: where mires scatter the forest landscapes (Ludwig et al., 2008; Wegge and Kastdalen, 2008). Capercaillie, on the other hand, prefers high canopy coverage, large spruces and dense pine-dominated forests – not necessarily old-growth forests, but structurally resembling old-growth forests (Miettinen, 2009; Lõhmus et al., 2023). The characterization of the habitat for grouse species is mostly related to the local forest stand characteristics. This can can be improved by accounting for the home range and landscape characteristics, which better reflect the different habitat requirements of these species throughout the year (Mazziotta et al., 2024). Home range size requirements are associated with body size (Thornton and Fletcher, 2014), which varies considerably among grouse species from about 0.4 kg (hazel grouse) up to 4 kg (male capercaillie). To manage forests with an aim to enhance the presence of all grouse species will likely require different practices at different scales to create enough habitat and structural diversity. The challenge is that the relationship between multi-scale grouse use of the forest and management is only partially known.

The aim of this study is to evaluate whether the trade-offs between timber production and species probability of occurrence (occupancy) vary across grouse species with different habitat requirements and across spatial scales. We simulate and optimize three boreal production landscapes in Finland. Our study presents novel methods for evaluating trade-offs between conservation and harvest intensity at multiple spatial scales. Specifically, we evaluate the risk induced by not applying spatial optimization on the trade-off (Pareto) curves at different spatial scales by calculating two indices of curve distortion, the Kullback-Leibler Divergence (Kullback and Leibler, 1951) and the Gini coefficient (Gini, 1912). We answer the following questions: 1) How do changes in the economic value of timber production (i.e., the Net Present Value, or NPV) affect the probability of occurrence (or occupancy) for different grouse species at stand, home range and landscape level? 2) How do the trade-offs between timber production and grouse occupancy at stand level reflect the trade-offs at larger spatial scale? 3) How does forest management vary when maximizing NPV, occupancy or both for different grouse species and landscapes?

2. Materials and methods

2.1. Model summary

To explore how changes in the economic value of timber production affect the probability of occurrence (or occupancy) for different grouse species at multiple spatial scales, we use a simulation optimization framework where a landscape is divided into forest stands (Fig. 1). We simulate the development of all forest stands in the landscape, using a range of management alternatives that reflect both intensive and extensive timber extraction across time. These forest simulations provide the input data for use in the optimization. We optimize for the entire landscape by applying specific management alternatives for each forest stand. The forest landscape is represented as an aggregation of individual forest stands, where individual management decisions are made. From the optimization results, we can evaluate and visualize the development of economic and ecological patterns. We can also explore alternative optimal combination of management regimes to achieve specific NPV and occupancy values for different grouse species at different spatial scales and across a latitudinal gradient.

2.2. Study areas

We selected three landscapes belonging to three separate municipalities of similar extent in Northern (Kemijärvi, N. stands = 88,427, Area = 208,826 ha), Central (Sotkamo, N. stands = 121,189, Area = 178,838 ha) and Southern Finland (Mikkeli, N. stands = 191,337, Area = 213,664 ha) (Fig. 2). To limit the computational requirements of the study, only 1 % of the area (i.e., about 884, 1212 and-1913 contiguous stands, respectively) for each municipality were simulated and optimized. This proportion of the municipality area was chosen after ascertaining no appreciable differences in the Pareto curves respect to the optimization solutions obtained by simulating and optimizing 10 % of the area. These three municipalities are part of the inland boreal area that have been previously used to model and predict the occupancy (P), i.e. the probability of occurrence of grouse species at multiple spatial scales (Mazziotta et al., 2024). Grouse occupancy was modelled using nationwide wildlife triangle census data, with variables related to forest structure and composition analyzed at local (stand, with a radius of ~0.05-km for an average circular stand of 1 ha), home-range (1-km), and landscape (5-km) scales.

The three study areas represent typical Finnish boreal forest with decreasing stand size but generally increasing DBH, height, tree volume and diversity in stand attributes (Shannon indices) from North to South (Table 1). Scots pine (*Pinus sylvestris* L.), Norway spruce (*Picea abies* (L.) H. Karst.), and birch (*Betula* spp. L.) dominate the landscape in variable proportions across the three study areas. Additional deciduous species that may be present are European aspen (*Populus tremula* L.), grey alder (*Alnus incana* (L.) Moench), rowan (*Sorbus aucuparia* L.) and various willow species (*Salix* spp. L.). In Table 1 statistics are presented for the deciduous species pooled. The forest stand data was downloaded from the open access databases of the Finnish Forest Centre (www.metsakeskus.fi/) and aggregated to the stand level from the Luke data download service (https://kartta.luke.fi/opendata/valinta-en.html).

2.3. Wildlife census data

The grouse data employed for the grouse models developed in Mazziotta et al. (2024) were compiled from the Finnish wildlife triangle monitoring scheme (www.riistakolmiot.fi/), which is coordinated by the Natural Resources institute Finland (Luke), providing information on changes in wildlife populations (Lindén et al., 1996; Pellikka et al., 2005; Helle et al., 2016) (Fig. 3). The wildlife triangles are 12 km long

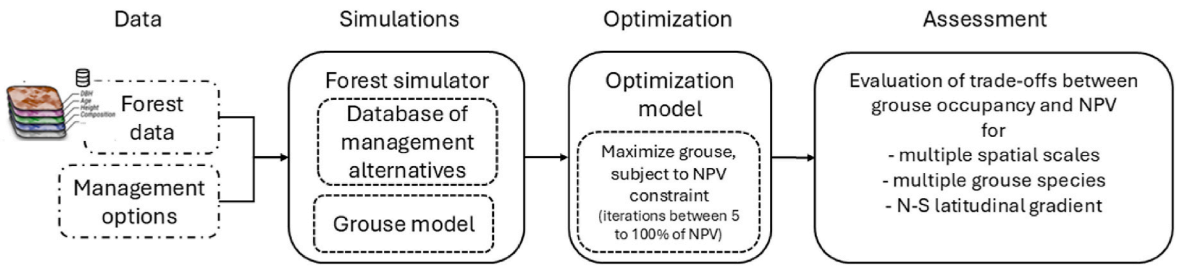

Fig. 1. Flow chart showing the input data, simulations, optimization approach and outputs in this study.

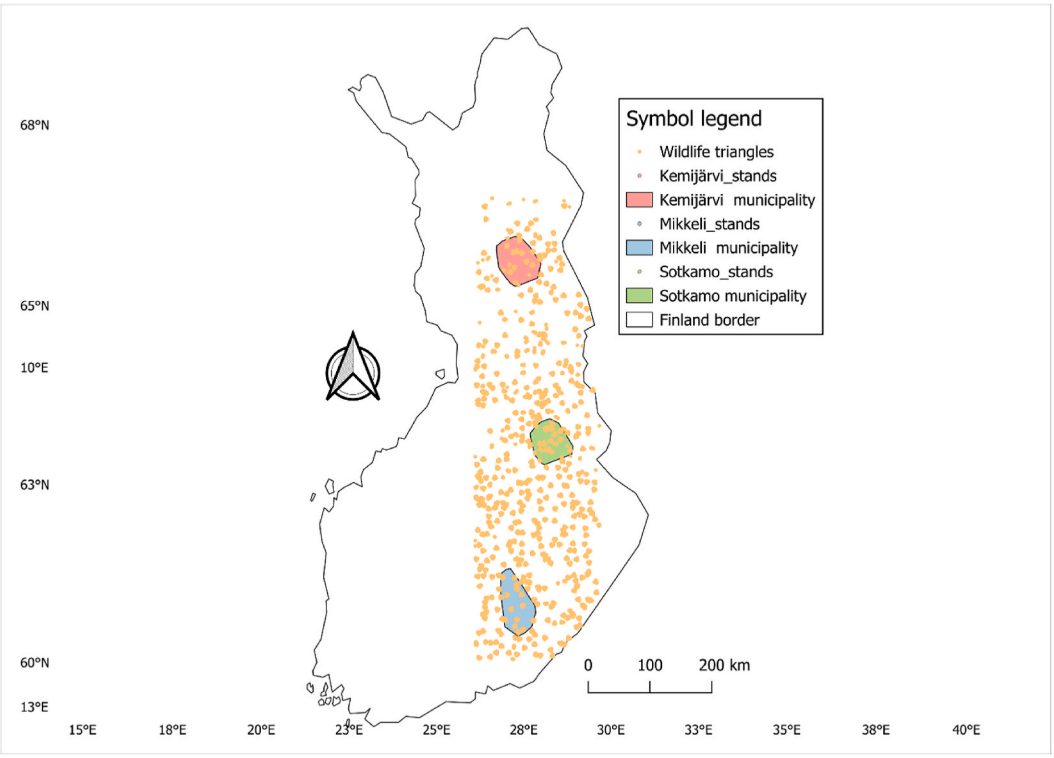

Fig. 2. Map of the locations of the wildlife triangles (source: www.riistakolmiot.fi/) used to model grouse species sampled in the years 2005–2019 (cf., Mazziotta et al., 2024) and the perimeters of the three municipalities utilized to simulate and optimize forests. Coordinate ranges of the sample stands simulated for each municipality are reported in Table 1. The map was drawn with the QGIS software (QGIS Development Team, 2025).

transect routes, which are shaped like equilateral triangles with 4 km sides. Volunteers survey the triangles twice annually during the winter and the summer. We retrieved data from the summer census (late July to early August), designed primarily for surveying grouse. In the summer census, the route is surveyed by a three-person team of volunteers (usually local hunters), who walk the route side-by-side and mark the locations of every grouse observed along the way inside a 60 m wide main belt (see Helle et al., 2016). The data consists of grouse observations of adults (males or females) and broods (with or without adults associated) of four species: capercaillie (*Tetrao urogallus* L.), black grouse (*Lyrurus tetrix* L.), hazel grouse (*Tetrastes bonasia* L.) and willow grouse (*Lagopus lagopus* L.). In the summer triangle survey, the probability of detection is about 60 % for single adults but close to 100 % for broods (Brittas and Karlbom, 1990).

We included data from years 2005–2019 from Northern, Central and Southern Finland, fitting the defined municipalities. Further, the data for each triangle was restricted to the five years preceding the year when the forest inventory in that region was done by laser scanning. This was to ensure that grouse data represent well the surveyed habitat, to avoid a situation where a stand was harvested without our knowledge. All grouse observations were assigned to forest stands, forestry units with relatively homogenous forest structure and site conditions, which in our case are the smallest forest management and reporting unit, resulting in presence-absence data for each species. That is, we knew the stands where grouse broods were observed as well as the stands where they were never observed during the study period.

2.4. Grouse models

We made use of a simplified version of the grouse models developed in Mazziotta et al. (2024) to evaluate the impact of forest characteristics on the species probability of occurrence in Finnish forests. This simplified version of the models (effects of forest predictors on grouse occupancy are summarized in Appendix A in Table S1) was developed by refitting the original grouse models as Generalized Linear Mixed Models (GLMM), including only stand-level forest variables that could be simulated directly by MELA2.0. The other non-forest variables were removed from the models either because they could not be considered as constant along the simulation horizon or because they reduced the explanatory power of the forest variables output from the forest simulator. The removed non-forest variables were a representation of the geographic location of the stands, the species sampling effort and the

Table 1
Forest statistics of the three study areas at the beginning of the simulation period, data extracted from municipal forest information obtained from metsään.fi.

Variables (by municipality)	Mikkeli (S Finland), 2013 stands	Sotkamo (C Finland), 2016 stands	Kemijärvi (N Finland), 2070 stands
Latitude range (°)	61.62–61.68	64.21–64.28	66.74–66.82
Longitude range (°)	27.34–27.43	28.34–28.43	27.47–27.62
Total Area, ha	49791	33235	63635
Mean Stand size, ha	1.0	1.3	1.9
Mean Basal area, m2/ha	8.2	7.6	9.0
Mean stand age, years	55.2	55.0	64.1
Mean of Total N. stems/ha	1537.8	2323.0	1483.5
Mean N. stems/ha Pine	222.2	442.0	572.5
Mean N. stems/ha Spruce	495.6	596.1	218.9
Mean N. stems/ha Deciduous	910.5	1348.0	732.0
Mean height, m	17.5	13.4	11.9
Mean height Pine, m	18.7	14.6	12.7
Mean height Spruce, m	16.4	13.1	11.6
Mean height Deciduous, m	17.9	13.2	11.7
Mean DBH, cm	20.6	16.6	15.5
Mean DBH Pine, cm	23.2	18.1	17.0
Mean DBH Spruce, cm	21.3	17.5	16.2
Mean DBH Deciduous, cm	18.4	14.7	13.8
Mean of Total Volume, m3/ha	233.0	165.1	130.7
Mean Volume Pine, m3/ha	63.9	56.5	59.9
Mean Volume Spruce, m3/ha	98.5	62.2	22.9
Mean Volume Deciduous, m3/ha	93.8	54.1	52.1
Mean Shannon Stem Index	0.76	0.81	0.66
Mean Shannon DBH Index	0.94	0.95	0.86
Mean Shannon Volume Index	0.73	0.81	0.70

regional density of grouse. All the original variables related with forest structure and composition and a random effect underlying the hierarchical spatial structure of the data (stands clustered in wildlife triangles) were retained. The species occupancy was modelled as the local probability of occurrence reported for each stand intersecting a wildlife triangle (ranging between 0 and 1): for all grouse species combined, and separately for each grouse species. The presence-absence of the grouse species (adults and brood) was modelled with a binomial distribution, with a mean (μ) and a logit link function. We removed all the fortuitous observations before analysis, i.e., all the data from triangle segments intersecting the stand for distances shorter than 50 m. Ecologically relevant forest variables were centered and standardized. We selected variables sampled for planning purposes and available from the Finnish Forest Centre and related to forest structure and composition. A model selection procedure was applied to select the predictors, first removing highly collinear variables (Variance Inflation Factor (VIF) > 0.7) and second, performing a backward selection procedure based on the Akaike Information Criterion (AIC; Akaike, 1973) (details in Mazziotta et al., 2024).

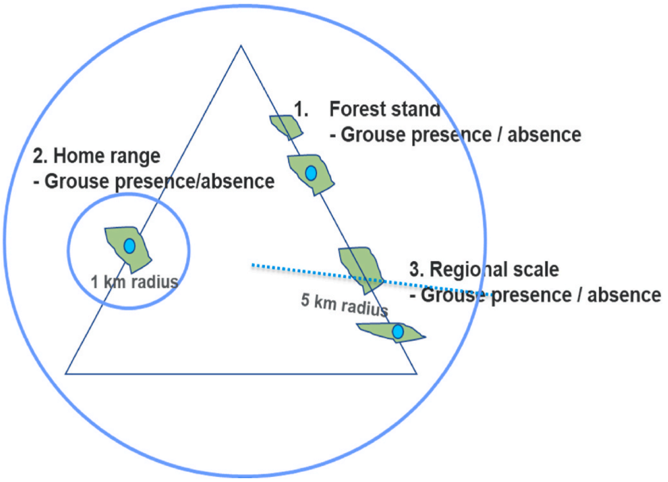

Fig. 3. Scheme of a modelling approach for the different spatial scales within the Finnish wildlife triangle monitoring scheme. Green polygons describe forest stands with (blue dot) and without (no blue dots) grouse observations.

2.5. Simulations

The forests in the three study areas were simulated and optimized over a typical strategic planning horizon of 30 years (2024–2054) with 5-year time steps. A branching approach was applied to construct a large number of management alternatives (Siitonen, 1993). To simplify the presentation of the management applied we summarized the alternatives into 10 general management groups: no management (i.e., set-aside), four thinning alternatives followed by rotation cut (thinning from above, mixed thinning, thinning from below, no thinning), non-commercial first thinning to support growth, four alternatives for commercial thinning (thinning from above, thinning from below, thinning mixed, thinning even). Each treatment schedule describes all silvicultural and harvesting activities carried out in this one branch during the 30-year planning horizon. Forest development was modelled using MELA2.0 forest simulation package, a forest dynamics simulator being developed by the Natural Resources Institute Finland to be a modernized open-source version of the earlier MELA system (Siitonen, 1994; Hirvelä et al., 2017). A version of the forest simulator, Metsi, which is currently still in development, can be accessed at the following GitHub link: https://github.com/lukefi/metsi/.

MELA2.0 can use as input data either NFI plot data (in the form of measured trees) or stand-level inventory data (in the form of stand-level basal area, mean diameter and mean height information predicted with laser scanning features). When using stand-level data, diameter distributions are used to formulate tree-level data (the number of stems by diameter class). Then, the tree height, volume and timber assortments for each measured tree or tree class are predicted. The future growth for 5-year periods is predicted using growth models for the trees representing each diameter class (for details of the growth and yield models used in MELA see Hynynen et al., 2014). In each period, the growth of the stand under all formed treatments options is predicted. The outcomes of these treatment schedules form the basis for the calculation of the NPV needed for the trade-off analyses.

2.6. Optimization problem

We optimized the management in the forest landscape to develop production possibility frontiers (Pareto curves) to illustrate the trade-offs between the forest's economic value, measured as Net Present Value (NPV) of timber at 4 % discount rate (a typical discount rate used in Finnish forestry), and ecological value, represented by the occupancy of forest grouse species. The optimization was conducted only at stand scale for the cumulative grouse occupancy and for each grouse species. To reveal the relationships among these two objectives we used multi-objective optimization (Miettinen, 1999). We formulated the bi-objective optimization problem as maximizing the two objectives (objective functions) on the set of all management plans that can be implemented in the landscape. We used a bi-objective optimization to analyze the severity of the trade-offs between pairs of objectives. Extreme solutions prioritize one objective over all other objectives, while compromise solutions, i.e., single Pareto optimal balanced solutions (sensu Miettinen, 1999), identify management plans that provide efficient combinations of the selected objectives.

At the landscape level achieving the maximal values for all the objectives simultaneously is only possible when there is no conflict between the objectives. Objectives will often incur a trade-off with other objectives, so that when one objective improves another objective deteriorates. Thus, one option is to present a range of solutions to the decision maker, and in this case, we focus on the set of Pareto optimal plans, where the outcome cannot be improved for any objective without deteriorating at least one of the other objectives. We used the ε-constraint method (Miettinen, 1999) to identify the Pareto optimal solutions. In our study we have set NPV greater than epsilon, with ε varying from 1.25 % of max NPV to 100 % (or 99 %) of max NPV, with the objective function then maximizing the probability of grouse occupancy. The detailed mathematical formulation of the bi-objective optimization problem is reported here:

$$maximize(f_1(x), \dots, f_n(x)) \tag{1}$$

subject to:

$$f_i(x) \le \varepsilon_i, i = 1, \dots, n, \tag{2}$$

$$x \in X, \tag{3}$$

Where $(f_1(x), \dots, f_n(x))$ are objective functions and X is the set of alternative management regimes. Here, the objective functions are for timber harvest revenues (NPV) and grouse probability of occurrence (P). The value of each objective function depends on x, i.e., the management regime applied.

Let $s = 1, 2, \dots, m$ be the index of forest stands and $r = 1, 2, \dots, n$ be the index of management regimes. The decision variables x_{sr} are binary variables belonging to {0,1}.

The set of feasible solutions is defined by:

$$X = \left\{ x = (x_{s,r})_{m^*n} \in \{0,1\}^{m^*n}; \sum_{r=1}^{n} x_{sr} = 1 \; for\ each\ s = 1, \dots, m \right\}. \tag{4}$$

Thus, each feasible solution is a management plan where, for each forest stand, one of the management regimes is selected.

Each of the two objective functions is defined by the formula:

$$f_i(x) = \sum_{s=1}^{m} \sum_{r=1}^{n} c_{sr}^{(i)} x_{sr}, \tag{5}$$

Where coefficient $c_{sr}^{(i)}$ is the contribution of the s-th stand to the value of i-th objective in the case where the r-th management regime is selected. In other words, for each forest stand s and each management regime r, the coefficients describe the following outcomes of managing stand s with regime r:

- $c_{sr}^{(1)}$ = – timber harvest revenue (NPV) from the stand; calculated as:

$$c_{sr}^{(1)} = \sum_{t=1}^{T} \sum_{s=1}^{S} \sum_{r=1}^{R_s} \frac{i_{srt} x_{sr} - o_{srt} x_{sr}}{(1+d)^{(t^*5-2.5)}} + \sum_{s=1}^{S} \sum_{r=1}^{R_s} \frac{PV_{sr} x_{sr}}{(1+d)^{(\#T^*5)}} \tag{6}$$

where i_{srt} and o_{srt} is respectively the income and costs from stand s, management regime r for time t, PV_{sr} is the productive value of the forest outside of the planning horizon, with d being the discount rate used.

- $c_{sr}^{(2)}$ – grouse probability of occurrence (P) from the stand, calculated using the specific grouse model at the stand level (All grouse, Hazel grouse, Black grouse, Capercaillie and Willow grouse) from Table S1 in Appendix A.

Optimizations were conducted using CPLEX version 22.1.0, made available through the academic initiative program. Calculations were conducted on a AMD 48-core processor, operating at 2.196 Ghz and 1 TB of physical memory.

2.7. Scale effects in the Pareto curves

Finding Pareto solutions at larger spatial scales would require spatial optimization. This is challenging due to increased computational complexity (Baskent et al., 2024), limited availability of continuous spatial data, and the risk of overfitting to specific spatial patterns. To circumvent these limitations, we calculated the probability of grouse occurrence (occupancy or P) for scales larger than the stand scales using the stand-scale optimized solution. The occupancy at larger scales, hereafter called "predicted" (Fig. 4), was estimated directly from the coefficients of the GLMMs estimated with 1-km and 5-km predictors (Fig. 4, Mazziotta et al., 2024). These occupancy values (P) at larger spatial scale (1-km, 5-km) contained both Pareto optimal and suboptimal values.

To correct the "predicted" occupancy values for non-optimality, we replaced the sub-optimal occupancy with corresponding Pareto optimal occupancy values. To do so, we retained only occupancies for which an increase in NPV, respect to the minimum NPV, decreases or maintain stable occupancy and interpolated them with a linear trend. In this way we estimated the Pareto-optimal solutions that should correspond to the sub-optimal solutions. The final sequence of corrected occupancy values, hereafter called "ideal" (Fig. S1 in Appendix A), contained only Pareto optimal solutions i.e., those solutions where an improvement in one objective requires a degradation of at least another objective.

To evaluate the inefficiency induced on the occupancy curves by estimating grouse occupancy directly with models at larger scales, rather than with spatial optimization, we calculated two indices of distortion, the Kullback-Leibler Divergence (Kullback and Leibler, 1951) and the Gini coefficient (Gini, 1912), both evaluating the difference between the solutions "predicted" directly with the models at larger scale and the corresponding "ideal" Pareto curves, trimmed from the suboptimal solutions, at 1-km, 5-km and multi-grain scale.

The Kullback-Leibler Divergence (D_{KL}) measures the information difference between the "predicted" and the "ideal" Pareto curve distributions, with lower values indicating that the "predicted" solutions closely follow the "ideal" distribution, while higher values indicating divergence. It is expressed by the formula:

$$D_{KL}(Predicted \parallel Ideal) = \sum_{q \in Q} P_{predicted}(q) \cdot log\left(\frac{P_{predicted}(q)}{P_{ideal}(q)}\right) \tag{7}$$

where: $P_{predicted}(q)$ is the grouse occupancy at the q-th NPV value for the "predicted" curve, and $P_{ideal}(q)$ is the grouse occupancy at the same NPV position for the "ideal" curve, where Q is the set of solutions used in the analysis.

The Gini coefficient indicates inequality in the distribution of the occupancy values (P), with respect to the distribution of total species occupancy (or habitat suitability) across stands, and it is computed separately for the "predicted" and "ideal" solutions, for which it is expressed by the formula:

$$G = 1 - 2\sum_{q \in Q} \left(\frac{C(q) + C(q-1)}{2}\right) \cdot \frac{1}{\#Q} \tag{8}$$

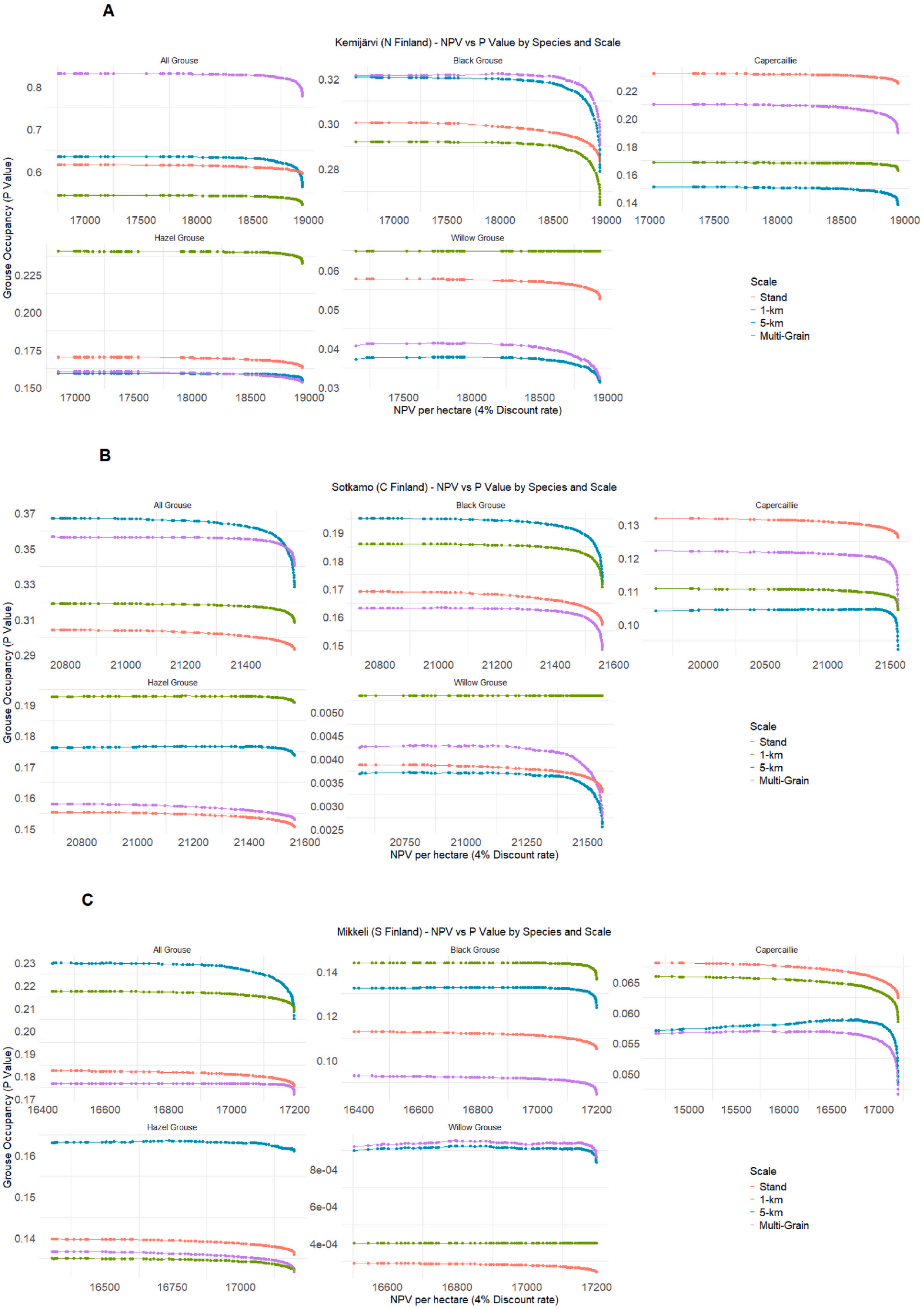

Fig. 4. Trade-off curves between Net Present Value (in x-axes) and bird occupancy (y-axes) across grouse species and spatial scales for the three study areas in the Finnish municipalities (A–C). The optimization produces Pareto efficient solutions for the stand level, and solutions for other scales are assessed from those solutions –this is why the curves may not be efficient.

where: $C(q)$ is the cumulative proportion up to the q-th NPV value in the cumulative array sorted in ascending order. #Q is the cardinality of Q, which is the number of elements in the set Q. This formula approximates the area between the cumulative distribution and the line of equality (the 45-degree line) using a trapezoidal sum.

The “predicted” and “ideal” solutions can be compared calculating the absolute difference in Gini coefficients between the two distributions, as follows:

$$\Delta G = \left| G_{predicted} - G_{ideal} \right| \tag{9}$$

At different spatial scales the relationship between NPV and P grouse occupancy is expected to vary because different forest variables estimated at the relevant spatial scale can affect grouse occupancy, and these variables are differently associated with NPV.

2.8. *Elasticity of Pareto curves*

We compared the curvature of the “ideal” Pareto curves (see previous paragraph for the definition) among species and scales calculating a measure of curve elasticity. Elasticity was calculated along the trade-off curves for each of the 100 solutions (u = intervals), as follows:

$$Elasticity_u = \frac{\Delta P_u / P_u}{\Delta NPV_u / NPV_u} \tag{10}$$

a proportional change in the probability of grouse occurrence (P) respect to the initial occupancy divided by a proportional change in the Net Present Value (NPV) respect to the initial NPV value. Then we computed an average elasticity value across all the intervals, as follows:

$$Average\ Elasticity = \frac{\sum Elasticity_u}{n} \tag{11}$$

This is an indicator of the overall responsiveness of the changes in probability of grouse occurrence (P) to changes in NPV over the entire curve. Larger magnitude elasticity indicates combinations of species and scale for which relative increments in probability of occurrence are more costly in terms of NPV reduction.

2.9. *Management plans for different species*

We compared the variability in the allocation of management strategies to the forest areas to maximize economic value (NPV), ecological value (grouse occupancy) and both the objectives in the three municipalities and among grouse species.

All data elaborations and plots were developed either with R (R Core Team, 2023) or Python (Python Software Foundation, 2023) programming languages.

3. Results

3.1. *Differences in trade-off curves across species, scales and municipalities*

At all scales and for each municipality (Fig. 4A–C), the cumulative initial level of occupancy of all grouse species, at the lowest NPV values, was obviously higher with respect to single species occupancies. The occupancy for single species showed similar initial moderate values for black grouse, capercaillie and hazel grouse, with variability in the prevailing species for each municipality, while willow grouse in general showed the lowest probability of occurrence in all municipalities (Fig. 4). The initial cumulative occupancy of all the grouse species at stand level, and consequently the occupancy of each grouse species, was the highest in Northern Finland (Fig. 4A, P ≈ 0.6), intermediate in Central Finland (Fig. 4B, P ≈ 0.3) and the lowest in Southern Finland (Fig. 4C, P ≈ 0.2).

The comparison of the Pareto possibility frontiers revealed species- and scale-specific trade-offs between timber production and forest grouse occupancy (Fig. 4). The steepness, measured via average elasticity, of the Pareto curves was similarly mild but varied across the three study areas in the three municipalities (Fig. 5C, Fig. S2) and differed across scales (Fig. 5A, Fig. S2) and species (Fig. 5B, Fig. S2).

We evaluated the differences in average elasticity across scales, species and municipalities with Kruskall-Wallis non-parametric ANOVA and pairwise differences with the Dunn test (see Table S2 in Appendix A). Concerning the trade-offs among spatial scales (Fig. 5A), the curves for small spatial scales (stand and 1-km) tended to show lower elasticity, declining less sharply (on average by 7 % and 9 %, respectively) with a NPV 1 % increase. On the other hand, at larger scales (5-km and multi-grain), the occupancy curves showed higher elasticity, declining faster (on average by 26 % and 22 %, respectively) with a NPV 1 % increase.

The trade-offs curves (Fig. 5B) for black grouse, capercaillie and willow grouse displayed a similarly abrupt drop-off, that is a higher average elasticity, showing a steeper decline in occupancy with rising NPVs respect to hazel grouse, which showed comparatively lower average elasticity, that is a lower decline in occupancy with increasing NPV.

Along the N-S latitudinal gradient (Fig. 5C), we observed that the trade-offs were similarly harsher at intermediate and southern latitudes than at northern latitude.

3.2. *Distortion of the trade-off curves across spatial scales*

The analysis of the divergences between “predicted” (Fig. 4) and “ideal” (Fig. S1) Pareto curves allowed an evaluation of the capacity of the trade-off curves at the stand scale to represent trade-offs between economic and ecological values at larger spatial scale. In general, the two indices that we used to compare Pareto solutions across scales showed a strong agreement, with a strong correlation between the Kullback-Leibler Divergence (D_{KL}) and the Gini differences (Kendall correlation ≈ 0.8) (Fig. 6, Fig. S3). However, in some cases in correspondence of high D_{KL}, indicating a deviance in the shapes of the “predicted” Pareto curves respect to the “ideal” solutions, we found a low Gini difference, indicating a similar level of spread or concentration of the solutions between the “predicted” and “ideal” curves, and in other cases there was an opposite correspondence between the two indices. Compared to D_{KL}, Gini differences were relatively low for most species and scales (Fig. 6), which suggests that the inequality or concentration differences between the “predicted” and “ideal” distributions were minimal.

We evaluated the differences in distorsion indices across scales, species and municipalities with Kruskall-Wallis non-parametric ANOVA and pairwise differences with the Dunn test (see Table S3 in Appendix A). In general, trade-off curves at increasingly larger spatial scales (i.e., 1-km and 5-km) had increasingly larger deviations from the “ideal” distribution patterns respect to the stand scale (Fig. 6A,D), likely because of differences between local and large-scale predictors involved in predicting grouse occupancy at different spatial scales (Table S1).

All species, except for the willow grouse, showed limited average deviations between the “predicted” Pareto curves respect to the “ideal” solutions (Fig. 6B,E), likely meaning that the solutions at stand scale for most of the species were already a good approximation of the solutions that could be found at large scale. The larger distortion across scale for willow grouse instead could be explained by the difference in the forest predictors affecting its occupancy at stand and larger spatial scales (see Table S1).

For what concerns municipalities, the results were different for the D_{KL} (Fig. 6C), for which in Northern Finland were observed the largest average deviations between the “predicted” and “ideal” solutions, and for the Gini difference (Fig. 6F), for which instead in Southern Finland were observed the highest average deviations.

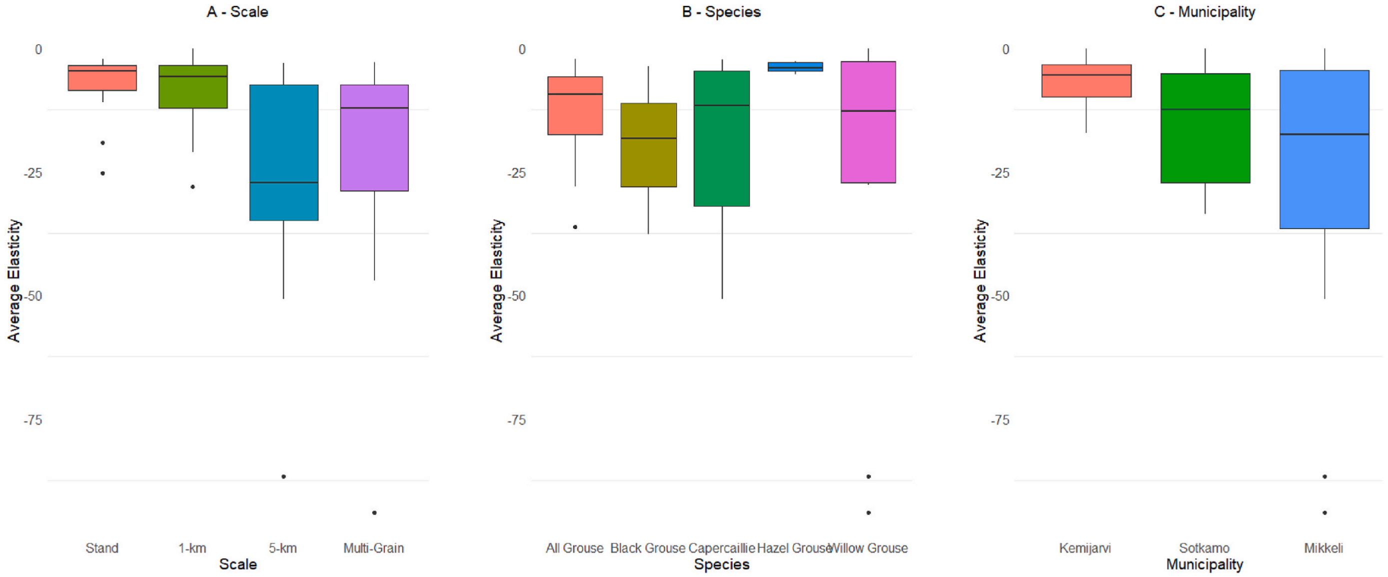

Fig. 5. Differences in average elasticity among trade-off curves between grouse occupancy and NPV for "ideal" optimal solutions summarized by (A) spatial scales, (B) grouse species and (C) study areas in the Finnish municipalities. See the methods for the specifications of the "ideal" distributions of the Pareto solutions.

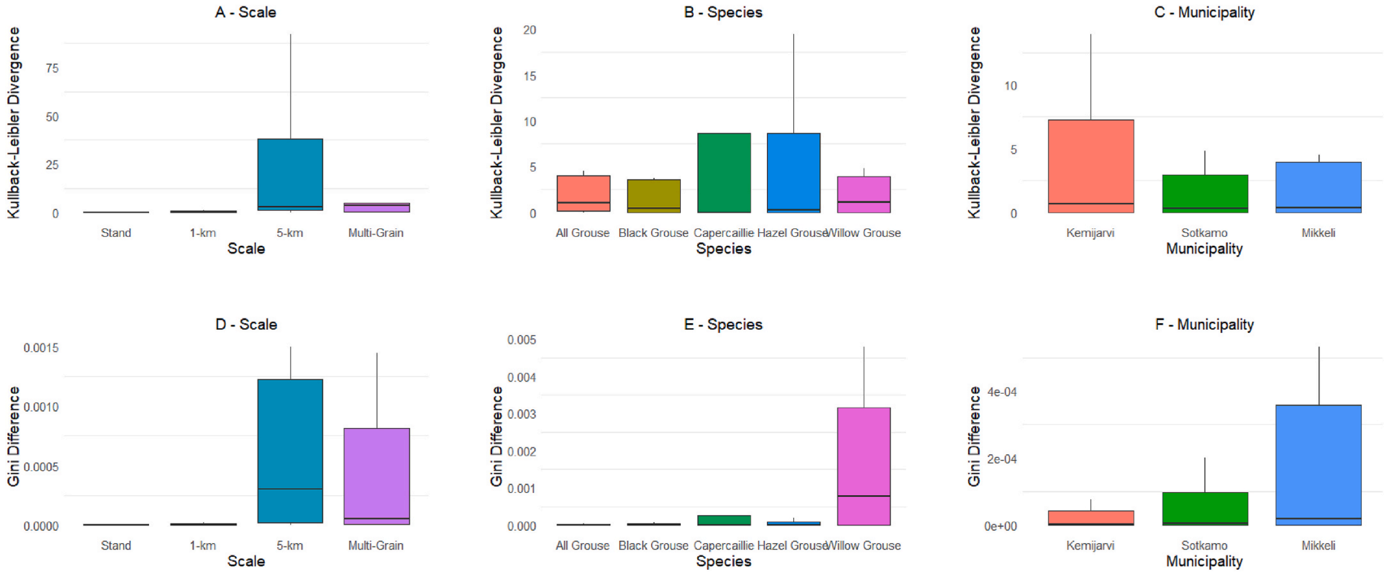

Fig. 6. Distortion of the trade-off curves. Differences between Pareto solutions "predicted" with models at all scales and the corresponding "ideal" optimal solutions for grouse occupancy (P) estimated with the Kullback-Leibler Divergence index (A, B, C) and with differences in the Gini index (D, E, F) summarized by grouse species, spatial scales and study areas in the Finnish municipalities. See the methods for the specifications of the two "predicted" and "ideal" distributions. Y-axis scales vary across different grouping factors.

3.3. Effect of forest management on trade-offs between timber production and grouse occupancy

We evaluated the allocation of the total managed area under different management regime groupings aimed at maximizing the economic value from timber harvesting (Max NPV), grouse occupancy (Max Grouse), and a compromise solution between these two objectives, across species and municipalities (Fig. 7, S4). We did not test differences in management allocation to the forest area across scales, as optimizations were performed only at the stand level. We evaluated the differences in management for the three optimization solutions per se and interaction with species and municipalities with parametric ANOVA and pairwise differences with the Kendall test (see Tables S4–S5 in Appendix A).

Even though there was no significant statistical difference in the area allocated across the three solutions, there were differences in the area allocated to specific management regimes for selected solutions (Table S4). Specifically, there was no difference in the allocation of no management/set-aside to maximize either grouse occupancy or economic value. However, conservation-focused management regimes, including first thinning and thinning from above, were more frequently applied when maximizing grouse occupancy (Fig. 7A). Conversely, when maximizing economic value, the primary management regimes applied were thinning from below, both alone and in association with rotation cutting, and rotation cutting without thinning. The compromise solution used a wide range of varied management regimes. This solution involved greater use of thinning from above but less use of thinning from below, both alone and in association with rotation cutting, compared to

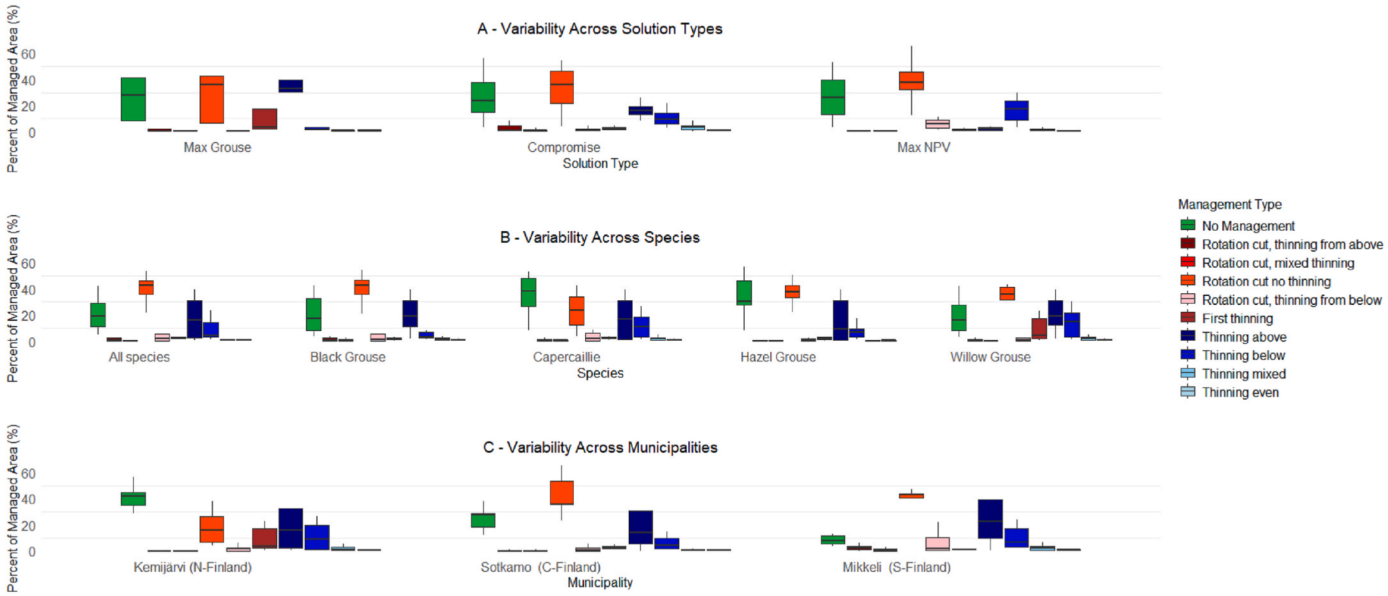

Fig. 7. Variability in the percent allocation of management strategies to the managed area maximizing economic value (Max NPV), ecological value (Max Grouse) and both the objectives (Compromise) by (A) optimization type, (B) grouse species and (C) municipalities.

max NPV. On the other hand, compromise solutions required less thinning from above than max Grouse but more use of thinning from below and mixed thinning (Fig. 7A).

Management practices showed limited variability across species (Tables S5–S6), with no clear differences observed (Fig. 7B). Nonetheless, some species-specific differences were noted, with capercaillie and willow grouse occupancy maximized through greater use of thinning from below compared to black grouse and hazel grouse.

From North to South, there was a progressive diversification of management strategies, characterized by a decrease in set-aside and an increasing integration of both conservation-focused and intensive management alternatives (Fig. 7C; Tables S7–S8). While the application of first thinning and thinning from above remained consistent across municipalities, there was a higher allocation of no management (set-aside) and rotation cutting with no thinning in the North. In the South, there was greater use of rotation cutting with thinning from above, with mixed thinning and with thinning from below. Additionally, different types of thinning not followed by clear-cutting to improve tree growth and increase forest economic value were more commonly applied in the South (Fig. 7C).

4. Discussion

4.1. *Differences in trade-off curves across species, scales and municipalities*

As observed before in previous simulation studies (e.g., Mönkkönen et al., 2014), irrespective of the study area, in our study grouse occupancy tends to decline as timber harvesting increases, indicating a negative relationship between economic returns and bird occupancy. This trade-off pattern aligns with broader findings that grouse broods of forest dwellers, especially hazel grouse and capercaillie, are positively related with canopy cover which decreases with management intensification. These grouse species do not prefer open clear-cut areas, as clear-cuts narrow their living space (Helle et al., 2003), reduce locally the abundance of bilberry, one of their main trophic resources and brood rearing habitat, by reducing the availability of commercially mature stands (Wegge and Kastdalen, 2008), and increases the proportion of open habitats sustaining populations of potential predators (cf., Kurki et al., 1997; Wegge and Rolstad, 2011; Haakana et al., 2020). However, it is possible that increasing the detail in the characterization of the grouse habitat, for example evaluating the consequences of management on the suitability of multi-layered vegetation and thickets, could increase the steepness of the trade-off curves (cf., Lindén et al., 2019).

Overall, the differences in the elasticity of trade-off curves across grouse species were relatively limited. This agrees with the conclusions from Melin et al. (2016) that broods of different grouse species (especially hazel grouse, black grouse and capercaillie) have similar responses to forest structure, with the occupancy of all three species being positively related to high shrub cover, high canopy cover or both. However, different grouse species and spatial scales exhibit unique sensitivities to increasing NPVs, seen in the distinct shapes and ranges of the curves for each combination of species and scale.

The highest decline of grouse occupancy at landscape scale (5-km) compared to more local scales (stand and 1-km) suggests that management intensification deteriorates critical habitat features important for determining habitat quality at larger scale, while at smaller scale the habitat characteristics are less affected by an increase in timber harvesting. This finding is consistent with studies emphasizing that larger scales often encompass broader landscape features that are more vulnerable to fragmentation and degradation (Wiens, 1989; Lindenmayer and Franklin, 2002), which may then negatively affect the most important demographic mechanism, such as breeding success, offspring survival and adult survival, that is triggering population decline (cf. Lehikoinen et al., 2024). Also, successful mating is crucial for viable populations. Grouse species, in particular male capercaillie and black grouse, gather in leks in large numbers to compete for the dominance to mate (Höglund and Alatalo, 1995). Local-level management, protecting the characteristics of the lekking sites, may act as a buffer against the degradation of the forest landscape at the regional scale. However, species-specific differences must be considered here as the black grouse, for instance, is known to flexibly use open mires, fields, frozen lakes and even old clear-cuts as lekking sites whereas the capercaillie has more strict requirements as to what is accepted as a lekking site (Sirkiä et al., 2011). Similarly, the willow grouse is known to benefit from restoration of former drainage sites: an act which has no direct relationship with forest management actions per se, but which results in availability of new breeding grounds (Metsähallitus, 2013).

Among the studied species, black grouse, capercaillie and willow grouse showed the greatest sensitivity to deterioration in habitat quality due to increased economic intensification, while hazel grouse was more resilient. This result aligns with findings that black grouse and capercaillie are being associated with middle-aged or more mature forests (Miettinen et al., 2005) and willow grouse with low-productivity bogs (Ludwig et al., 2008), which are more vulnerable to short-term harvesting impacts. Conversely, hazel grouse, which thrives in mixed-forest layers that develop post-clear-cutting, likely benefits from these conditions in the short term (Huhta et al., 2017).

The trade-offs increase with a decreasing latitude, and this aligns with an intensification of forest management practices, which are more feasible under favorable forest growth conditions in southern regions (Helle et al., 2003). Northern boreal regions, characterized by higher grouse occupancy levels and lower sensitivity to management intensification, retain greater ecological integrity. In contrast, central boreal regions exhibit moderate trade-offs, balancing occupancy and economic objectives. Southern boreal regions are the most affected by management intensification, with lower occupancy levels and stronger trade-offs, particularly for species like willow grouse, which is virtually absent due to historical habitat fragmentation (peatland drainage and intensive forestry) and climate change impacts (Melin et al., 2020). These findings highlight the importance of regionally tailored conservation strategies to mitigate the combined effects of land use and climate change.

4.2. Distortion of the trade-off curves across spatial scales

D_{KL} proved to be more sensitive than Gini difference for detecting deviations from the general shape of Pareto curves at large spatial scales. This sensitivity is consistent with its capacity to detect structural differences between distributions (Kullback and Leibler, 1951). Both indices, however, captured the increasing distortions in Pareto curves introduced when shifting from stand-scale to larger spatial scales, highlighting the inefficiencies of applying non-optimized solutions across scales (De Pellegrin Llorente et al., 2017). This supports the evidence that the predictors influencing ecological patterns may vary at different spatial scales, as larger scales often encompass different uses of the habitats during different seasons while the local (stand and home range) scales refer mainly to habitat characteristics needed for reproduction (Wiens, 1989; Jokimäki and Huhta, 1996).

The relatively low species-specific distortions between “predicted” and “ideal” Pareto solutions reaffirm the importance of stand-scale predictors in determining the occupancy for most grouse species (cf., Mazziotta et al., 2024). This is consistent with studies suggesting that fine-scale predictors often play a dominant role in species distribution modeling, even when extrapolated to larger spatial extents (Guisan and Thuiller, 2005). The limited differences in the performance of the modelling of the grouse at varied scales across the set of solutions can be seen as an indication that the Finnish forest landscapes included in our study areas are generally represented by low heterogeneity in forest characteristics (Ludwig and Klaus, 2017; Lu and Jetz, 2023), being mostly represented by homogeneous stands, in terms of tree age, diameters, and density profile (Korhonen et al., 2021). Furthermore, the short simulation horizon explored here limits the possibility of forest development and likely contributes to the limited grouse niche differentiation across scales. However, the notable deviations for willow grouse indicate that the environmental variables determining occupancy at stand scale differ significantly from those influencing occupancy at larger scales (Miettinen et al., 2008; Lande et al., 2014). This finding aligns with research emphasizing species-specific responses to scale-dependent predictors, likely reflecting differences in habitat selection or resource use across spatial scales (Wiens, 1989; Jansson and Andrén, 2003). For the willow grouse, this is especially true since the occupancy of the species is significantly affected by the availability of open mires, a feature largely lost due to the large-scale drainage campaigns of the past. Therefore, other, non-forest variables would also be needed for willow grouse, but in the case of peatlands and their drainage status this data is often not attainable (Ruottinen et al., 2024).

Interestingly, the divergence between the two distortion indices along the N-S latitudinal gradient may be attributed to variation in species-scale combinations. For instance, the high Gini differences in Southern Finland may reflect stronger spatial clustering of grouse occupancy at these scales, due to higher concentration of resources (Gaston, 2000). The high Gini difference in the south is likely explained by greater heterogeneity in environmental conditions at these latitudes, as in the South there is more variation in site fertility, smaller forest holdings, and smaller stands. Instead, the high D_{KL} observed in Northern Finland can be explained by the fact that willow grouse, the sole grouse species which has very different requirements at different spatial scales, is present practically only in northern Finland (Melin et al., 2020). These differences highlight the utility of employing multiple metrics, as each index captures distinct aspects of distributional distortions, with D_{KL} emphasizing shape differences and Gini focusing on inequality or spread (Sen, 1997).

Finally, the results suggest that the “ideal” solutions derived from stand-scale optimizations may underestimate the outcomes achievable through larger-scale optimizations. This confirms the importance of accounting for space in forest planning problems (Baskent et al., 2024), incorporating multiscale approaches into forest management planning (e.g., for grouse: Kurki et al., 2000; Graf et al., 2005; for saproxylic beetles: Winiger et al., 2023), as different scales may yield unique insights into trade-offs between economic and ecological objectives (Groves et al., 2002; Moilanen et al., 2009). The ability of both indices to capture these distortions reinforces their value in assessing scale-dependent trade-offs in conservation and land-use planning. On the other hand, the choice of not using spatial optimization at larger scale, but instead deriving large scale solutions from optimal stand-level solutions, can bring to inefficiencies that must be carefully evaluated with respect to the “ideal” solutions obtainable with spatially-constrained optimization methods, for example using the clique approach (Weintraub and Murray, 2006).

The main limitation of the present study concerns the fact that we were not able to compare our upscaled optimization solutions with solutions obtained with spatial optimization. A future study could compare these two types of solutions allowing the quantification of the inefficiencies introduced non-optimizing at large spatial scales.

4.3. Effect of forest management on trade-offs between timber production and grouse occupancy

The observed patterns in the allocation of forest management regimes across species, objectives, and municipalities reflect the trade-offs inherent in balancing economic and ecological objectives. The greater use of conservation-focused management regimes (e.g., first thinning and thinning from above) to maximize grouse occupancy aligns with previous findings that less intensive forestry practices maintain structural diversity and habitat features critical for biodiversity. Paillet et al. (2010) emphasized that less intensive forestry practices can sustain critical habitat components like ground vegetation and shrub layers, which are vital not only for grouse but for many game and forest-dwelling species in Finland (cf., Lindén et al., 2019; Haara et al., 2021). Similarly, Gustafsson et al. (2020) noted that low-intensity management fosters conditions conducive to biodiversity, supporting the notion that such practices can coexist with economic objectives.

Conversely, the reliance on intensive practices (e.g., rotation cutting without thinning or thinning from below) to maximize economic value is consistent with the emphasis on optimizing timber production and minimizing stand rotation times. In general, Lindenmayer and Franklin (2002) discussed how intensive forestry often prioritizes short-term economic gains at the expense of long-term ecological health, and specifically, Miettinen et al. (2005) and Haakana et al. (2020) have already highlighted that traditional timber harvesting practices can generate substantial trade-offs with grouse habitat.

The compromise solutions integrating a balanced management regime made with conservation-focused and intensive management strategies suggest that trade-offs can be mitigated, though not eliminated, by employing a balanced approach that supports both timber production and grouse occupancy. This finding aligns with research indicating that multifunctional forest management can simultaneously maintain biodiversity and provide economic benefits, but such approaches require careful spatial planning to optimize outcomes for multiple objectives (Eyvindson et al., 2021; Peura et al., 2024).

The limited variability in management regimes across grouse species underscores partly overlapping habitat requirements of the species in terms of forest structure. This may be attributable to the partial availability of forest indicators directly related to the needs of forest dwelling species. In the future, the use of forest variables obtained by high-resolution airborne LiDAR technology could represent a further step in defining the factors determining species occupancy (see e.g., Garabedian et al., 2014). In addition, data on landscape features such as presence of undrained or non-forested peatlands would be needed for species that mostly or partly dwell in these habitats (e.g. willow grouse and black grouse). The overlap of habitat requirements may be partly due to the short simulation time that likely did not allow a complete development of the forest succession and consequently a diversification of the species habitat niches. However, some differences still were noticeable, such as the greater use of thinning from below to maximize occupancy for capercaillie and willow grouse respect to black grouse and willow grouse.

The regional trends, particularly the increasing diversification of management strategies from North to South, reflect the influence of both ecological and economic gradients. Northern boreal forests, characterized by harsher climates and slower tree growth, tend to prioritize set-aside or low-intensity management due to the more limited economic revenues from intensive forestry. In contrast, southern boreal regions, with their higher productivity and more intensive forestry history (cf., Haakana et al., 2020), exhibit a greater reliance on rotation cutting and other intensive management practices, which may lead to habitat fragmentation and biodiversity loss (Lindenmayer and Franklin, 2002; Melin et al., 2020). Additionally, the greater application of thinning not followed by clear-cutting in the South likely reflects efforts to balance timber production with habitat retention in these highly managed landscapes.

5. Conclusions

Our study highlights the complex interplay between timber production and grouse species occupancy across spatial scales and management strategies, emphasizing the importance of context-specific approaches in forest management. We found that changes in the economic value of timber production consistently reduce grouse occupancy, though the magnitude of these trade-offs varied among species and spatial scales. Larger scales, particularly the landscape level, exhibited the most pronounced habitat degradation under intensive management, inducing the loss of critical habitat features affecting most of the critical grouse demographic processes. The trade-offs observed at the stand level generally reflected those at larger scales, although the differences between "ideal" and "predicted" Pareto solutions suggest that scaling up local management strategies can lead to mismanagement. Species-specific responses revealed that while black grouse, capercaillie and willow grouse are highly sensitive to increased timber harvesting, hazel grouse showed greater resilience, though their conservation remains precarious under intensive forestry practices. Finally, forest management strategies varied in their ability to balance economic and ecological objectives. Conservation-focused practices were more effective in sustaining grouse occupancy, whereas intensive forestry maximized economic value at the cost of deterioration in habitat quality. Compromise solutions integrating both approaches mitigated trade-offs but could not fully eliminate them. Regional variations in the trade-offs further underscored the need for tailored strategies, with northern boreal regions favoring conservation-oriented practices and southern regions showing a stronger reliance on economically driven, high-intensity forestry. These findings emphasize the need for more studies including multiscale, multifunctional forest management to balance ecological conservation and economic objectives.

CRediT authorship contribution statement

Adriano Mazziotta: Writing – review & editing, Writing – original draft, Visualization, Methodology, Formal analysis, Data curation, Conceptualization. **Reijo Mykkänen:** Writing – review & editing, Writing – original draft, Data curation. **Jukka T. Forsman:** Writing – review & editing, Writing – original draft, Supervision, Conceptualization. **Annika Kangas:** Writing – review & editing, Writing – original draft. **Andreas Lindén:** Writing – review & editing, Writing – original draft, Data curation. **Markus Melin:** Writing – review & editing, Writing – original draft, Data curation. **Kyle Eyvindson:** Writing – review & editing, Writing – original draft, Methodology, Formal analysis, Conceptualization.

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Declaration of competing interest

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

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jenvman.2025.126409.

Data availability

Data will be made available on request.

References

Akaike, H., 1973. Information theory as an extension of the maximum likelihood principle. In: Petrov, B.N., Csaki, F. (Eds.), Second International Symposium on Information Theory. Akademiai Kiado, Budapest, pp. 267–281. https://link.springer.com/chapter/10.1007/978-1-4612-1694-0_15.

Baskent, E.Z., Borges, J.G., Kašpar, J., 2024. An updated review of spatial forest planning: approaches, techniques, challenges, and future directions. Curr. For. Rep. 10 (5), 299–321. https://link.springer.com/article/10.1007/s40725-024-00222-8.

Borges, P., Eid, T., Bergseng, E., 2014. Applying simulated annealing using different methods for the neighborhood search in forest planning problems. Eur. J. Oper. Res. 233 (3), 700–710. https://doi.org/10.1016/j.ejor.2013.08.039.

Brittas, R., Karlbom, M., 1990. A field evaluation of the Finnish 3-man chain: a method for estimating forest grouse numbers and habitat use. Ornis Fenn. 67, 18–23. https://ornisfennica.journal.fi/article/view/133296.

De Pellegrin Llorente, I., Hoganson, H.M., Carson, M.T., Windmuller-Campione, M., 2017. Recognizing spatial considerations in forest management planning. Curr. For. Rep. 3, 308–316. https://doi.org/10.1007/s40725-017-0068-x.

Duflot, R., Eyvindson, K., Mönkkönen, M., 2022. Management diversification increases habitat availability for multiple biodiversity indicator species in production forests. Landscape Ecol 37, 443–459. https://link.springer.com/article/10.1007/s10980-021-01375-8.

Eyvindson, K., Duflot, 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.

Garabedian, J.E., McGaughey, R.J., Reutebuch, S.E., Parresol, B.R., Kilgo, J.C., Moorman, C.E., Peterson, M.N., 2014. Quantitative analysis of woodpecker habitat using high-resolution airborne LiDAR estimates of forest structure and composition. Remote Sens. Environ. 145, 68–80. https://doi.org/10.1016/j.rse.2014.01.022.

Gaston, K.J., 2000. Global patterns in biodiversity. Nature 405 (6783), 220–227. https://www.nature.com/articles/35012228.

Gini, C.W., 1912. Variabilità e mutabilità, contributo allo studio delle distribuzioni e delle relazioni statistiche. Stud. Econ.-Giur. R. Univ. Cagl. 3, 3–159.

Graf, R.F., Bollmann, K., Suter, W., Bugmann, H., 2005. The importance of spatial scale in habitat models: capercaillie in the Swiss Alps. Landscape Ecol 20, 703–717. https://link.springer.com/article/10.1007/s10980-005-0063-7.

Groves, C.R., Jensen, D.B., Valutis, L.L., et al., 2002. Planning for biodiversity conservation: putting conservation science into practice. Bioscience 52 (6), 499–512. https://doi.org/10.1641/0006-3568(2002)052[0499:PFBCPC]2.0.CO;2.

Guisan, A., Thuiller, W., 2005. Predicting species distribution: offering more than simple habitat models. Ecol. Lett. 8 (9), 993–1009. https://doi.org/10.1111/j.1461-0248.2005.00792.x.

Gustafsson, L., Kouki, J., Sverdrup-Thygeson, A., 2020. Tree retention as a conservation measure in clear-cut forests of northern Europe: a review of ecological consequences. Scand. J. For. Res. 35 (3–4), 200–219. https://doi.org/10.1080/02827581.2010.497495.

Haakana, H., Huhta, E., Hirvelä, H., Packalen, T., 2020. Trade-offs between wood production and forest grouse habitats in two regions with distinctive landscapes. For. Ecosyst. 7, 1–16. https://forestecosyst.springeropen.com/articles/10.1186/s40663-020-00227-2.

Haara, A., Matala, J., Melin, M., Miettinen, J., Korhonen, K.T., Packalen, T., Varjo, J., 2021. Economic effects of grouse-friendly forest management. Silva Fenn. 55 (3), 10468. https://silvafennica.fi/article/10468.

Helle, P., Belkin, V., Bljudnik, L., Danilov, P.I., Jakimov, A., 2003. Changes in grouse populations in Finland and Russian Karelia during recent decades. Suom. Riista 49, 32–43. https://www.riistasaatio.fi/en/suomen-riista-49/.

Helle, P., Ikonen, K., Kantola, A., 2016. Wildlife monitoring in Finland: online information for game administration, hunters, and the wider public. Can. J. For. Res. 46 (12), 1491–1496. https://cdnsciencepub.com/doi/full/10.1139/cjfr-2015-0454.

Holland, J.D., Bert, D.G., Fahrig, L., 2004. Determining the spatial scale of species' response to habitat. Bioscience 54 (3), 227–233. https://academic.oup.com/bioscience/article/54/3/227/223100.

Huhta, E., Helle, P., Nivala, V., Nikula, A., 2017. The effect of human-modified landscape structure on forest grouse broods in two landscape types. Ecosphere 8 (9), e01950. https://esajournals.onlinelibrary.wiley.com/doi/full/10.1002/ecs2.1950.

Hynynen, J., Salminen, H., Ahtikoski, A., Huuskonen, S., Ojansuu, R., Siipilehto, J., Lehtonen, M., Rummukainen, A., Kojola, S., Eerikäinen, K., 2014. Scenario Analysis for the Biomass Supply Potential and the Future Development of Finnish Forest Resources. Working Papers of the Finnish Forest Research Institute, 302. http://www.metla.fi/julkaisut/workingpapers/2014/mwp302.htm.

Hirvelä, H., Härkönen, K., Lempinen, R., Salminen, O., 2017. MELA2016 the Reference Manual. http://urn.fi/URN. ISBN:978-952-326-358-1.

Höglund, J., Alatalo, R.V., 1995. Leks. Princeton University Press, Princeton, New Jersey.

Jansson, G., Andrén, H., 2003. Habitat composition and bird diversity in managed boreal forests. Scand. J. For. Res. 18 (3), 225–236. https://www.tandfonline.com/doi/abs/10.1080/02827581.2003.9728293.

Jokimäki, J., Huhta, E., 1996. Effects of landscape matrix and habitat structure on a bird community in northern Finland: a multi-scale approach. Ornis Fenn. 73 (3), 97–113. https://ornisfennica.journal.fi/article/view/133442.

Korhonen, K.T., Ahola, A., Heikkinen, J., Henttonen, H.M., Hotanen, J.-P., Ihalainen, A., Melin, M., Pitkänen, J., Räty, M., Sirviö, M., Strandström, M., 2021. Forests of Finland 2014–2018 and their development 1921–2018. Silva Fenn. 55 (5), 10662. https://www.silvafennica.fi/article/10662.

Kullback, S., Leibler, R.A., 1951. On information and sufficiency. Ann. Math. Stat. 22 (1), 79–86. https://www.jstor.org/stable/2236703.

Kurki, S., Helle, P., Lindén, H., Nikula, A., 1997. Breeding success of black grouse and capercaillie in relation to mammalian predator densities on two spatial scales. Oikos 79 (2), 301–310. https://doi.org/10.2307/3546014.

Kurki, S., Nikula, A., Helle, P., Lindén, H., 2000. Landscape fragmentation and forest composition effects on grouse breeding success in boreal forests. Ecologist 81 (7), 1985–1997. https://doi.org/10.1890/0012-9658(2000)081[1985:LFAFCE]2.0.CO;2.

Lande, U.S., Herfindal, I., Willebrand, T., Moa, P.F., Storaas, T., 2014. Landscape characteristics explain large-scale variation in demographic traits in forest grouse. Landscape Ecol 29, 127–139. https://link.springer.com/article/10.1007/s10980-013-9960-3.

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 (5), 1027–1039. https://doi.org/10.1016/j.ecolind.2011.02.004.

Lehikoinen, A., Pakanen, V.-M., Kivinen, S., Kumpula, S., Lehto, V., Rytkönen, S., Vatka, E., Virkkala, R., Orell, M., 2024. Population collapse of a common forest passerine in northern Europe as a consequence of habitat loss and decreased adult survival. For. Ecol. Manage. 572, 122283. https://doi.org/10.1016/j.foreco.2024.122283.

Lindén, H., Helle, E., Helle, P., Wikman, M., 1996. Wildlife triangle scheme in Finland: methods and aims for monitoring wildlife populations. Finn. Game Res. 49, 4–11. https://eurekamag.com/research/009/736/009736125.php#:~:text=The%20wildlife%20triangle%20scheme%20was,detailed%20studies%20of%20predator%2Dprey.

Lindén, M., Lilja-Rothsten, S., Saaristo, L., Keto-Tokoi, P., 2019. (toim.) Metsänhoidon suositukset riistametsänhoitoon, työopas. [Forest management recommendations for game forest management, work guide]. Tapion julkaisuja. https://tapio.fi/wp-content/uploads/2020/09/Metsanhoidon_suositukset_riistanhoitoon_Tapio-2019.pdf.

Lindenmayer, D.B., Franklin, J.F., 2002. Conserving Forest Biodiversity: a Comprehensive Multiscaled Approach. Island Press.

Lõhmus, A., Pass, E., Pensa, M., 2023. Distribution of grouse and their predators in peatland forest landscapes: a case for ecological integrity. For. Ecol. Manage. 546, 121332. https://www.sciencedirect.com/science/article/pii/S0378112723005662.

Lu, M., Jetz, W., 2023. Scale-sensitivity in the measurement and interpretation of environmental niches. Trends Ecol. Evol. 38 (6), 554–567. https://www.sciencedirect.com/science/article/pii/S0169534723000071.

Ludwig, G.X., Alatalo, R.V., Helle, P., Nissinen, K., Siitari, H., 2008. Large-scale drainage and breeding success in boreal forest grouse. J. Appl. Ecol. 45 (1), 325–333. https://besjournals.onlinelibrary.wiley.com/doi/10.1111/j.1365-2664.2007.01396.x.

Ludwig, T., Klaus, S., 2017. Habitat selection in the post-breeding period by hazel grouse Tetrastes bonasia in the bohemian forest. J. Ornithol. 158, 101–112. https://link.springer.com/article/10.1007/s10336-016-1365-z.

Mazziotta, A., Borges, P., Kangas, A., Halme, P., Eyvindson, K., 2023. Spatial trade-offs between ecological and economical sustainability in the boreal production forest. J Environ Manage 330, 117144. https://doi.org/10.1016/j.jenvman.2022.117144.

Mazziotta, A., Lindén, A., Eyvindson, K., Bianchi, S., Kangas, A., Melin, M., et al., 2024. Unraveling the characteristic spatial scale of habitat selection for forest grouse species in the boreal landscape. For. Ecol. Manage. 563, 122008. https://doi.org/10.1016/j.foreco.2024.122008.

Melin, M., Mehtätalo, L., Helle, P., Ikonen, K., Packalen, T., 2020. Decline of the boreal willow grouse (Lagopus lagopus) has been accelerated by more frequent snow-free springs. Sci. Rep. 10 (1), 6987. https://www.nature.com/articles/s41598-020-63993-7.

Melin, M., Mehtätalo, L., Miettinen, J., Tossavainen, S., Packalen, P., 2016. Forest structure as a determinant of grouse brood occurrence–An analysis linking LiDAR data with presence/absence field data. For. Ecol. Manage. 380, 202–211. https://www.sciencedirect.com/science/article/pii/S0378112716305333.

Metsähallitus, 2013. Ojitettujen soiden ennalistamisopas [State forest service - a handbook for restoration of drained peatlands]. In: Finnish with an English Abstract. Available at: https://julkaisut.metsa.fi/wp-content/uploads/sites/2/2023/11/b188.pdf.

Miettinen, K., 1999. Nonlinear Multiobjective Optimization. Kluwer Academic Publishers, Boston.

Miettinen, J., 2009. Capercaillie (Tetrao urogallus L.) habitats in managed Finnish forests – the current status. threats and possibilities. Diss. For. 90, 32. http://www.metla.fi/dissertationes/df90.htmK.

Miettinen, J., Helle, P., Nikula, A., 2005. Lek area characteristics of capercaillie (Tetrao urogallus) in eastern Finland as analysed from satellite-based forest inventory data. Scand. J. For. Res. 20 (4), 358–369. https://www.tandfonline.com/doi/full/10.1080/02827580500201619.

Miettinen, J., Helle, P., Nikula, A., Niemelä, P., 2008. Large-scale landscape composition and capercaillie (Tetrao urogallus) density in Finland. Ann. Zool. Fenn. 45 (3), 161–173. https://doi.org/10.5735/086.045.0301.

Moilanen, A., Wilson, K.A., Possingham, H.P., 2009. Spatial Conservation Prioritization: Quantitative Methods and Computational Tools. Oxford University Press.

Mönkkönen, M., Juutinen, A., Mazziotta, A., Miettinen, K., Podkopaev, D., Reunanen, P., Tikkanen, O.P., 2014. Spatially dynamic forest management to sustain biodiversity and economic returns. J. Environ. Manage. 134, 80–89. https://www.sciencedirect.com/science/article/pii/S030147971300769X.

Naumov, V., Manton, M., Elbakidze, M., Rendenieks, Z., Priednieks, J., Uhlianets, S., et al., 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.

Paillet, Y., Bergès, L., Hjältén, J., et al., 2010. Biodiversity differences between managed and unmanaged forests: Meta-analysis of species richness in Europe. Conserv. Biol. 24 (1), 101–112. https://doi.org/10.1111/j.1523-1739.2009.01399.x.

Pellikka, J., Rita, H., Lindén, H., 2005. Monitoring wildlife richness—Finnish applications based on wildlife triangle censuses. Ann. Zool. Fenn. 123–134. https://www.jstor.org/stable/23736154.

Peura, M., Eyvindson, K., Burgas, D., Mönkkönen, M., Raatikainen, K.J., Kotiaho, J.S., 2024. Cost-effective biodiversity protection through multiuse-conservation landscapes. Landscape Ecol 39 (3), 48. https://link.springer.com/article/10.1007/s10980-024-01803-5.

Python Software Foundation, 2023. Python Language Reference. Retrieved from, version 3.9. http://www.python.org.

QGIS Development Team, 2025. QGIS Geographic Information System (Version 3.0). Open Source Geospatial Foundation Project. http://qgis.org.

R Core Team, 2023. R: a Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/.

Ruottinen, K.M., Melin, M., Miettinen, J., Kervinen, M., Pakanen, V.M., Forsman, J.T., Rytkönen, S., 2024. Assessing the effects of drainage and forest structure on presence and absence of fledglings of boreal grouse. Global Ecology and Conservation 54, e03150. https://doi.org/10.1016/j.gecco.2024.e03150.

Sen, A., 1997. On Economic Inequality. Oxford University Press.

Siitonen, M., 1993. Experiences in the use of forest management planning models. Silva Fenn. 27 (2), 167–178. https://doi.org/10.14214/sf.a15670.

Siitonen, M., 1994. The MELA system as a forestry modelling framework. Lestnictvi-Forestry 41 (4), 173–178. https://www.cabidigitallibrary.org/doi/full/10.5555/19960602549.

Sirkiä, S., Helle, P., Lindén, H., Nikula, A., Norrdahl, K., Suorsa, P., Valkeajärvi, P., 2011. Persistence of Capercaillie (Tetrao urogallus) lekking areas depends on forest cover and fine-grain fragmentation of boreal forest landscapes. Ornis Fenn. 88 (1), 14–29. https://doi.org/10.51812/of.133759.

Thornton, D.H., Fletcher, R.J., 2014. Body size and spatial scales in avian response to landscapes: a meta-analysis. Ecography 37 (5), 454–463. https://doi.org/10.1111/j.1600-0587.2013.00540.x.

Vatka, E., Kangas, K., Orell, M., Lampila, S., Nikula, A., Nivala, V., 2014. Nest site selection of a primary hole-nesting passerine reveals means to developing sustainable forestry. J. Avian Biol. 45, 187–196. https://doi.org/10.1111/j.1600-048X.2013.00250.x.

Wegge, P., Kastdalen, L., 2008. Habitat and diet of young grouse broods: resource partitioning between Capercaillie (Tetrao urogallus) and Black Grouse (tetrao tetrix) in boreal forests. J. Ornithol. 149, 237–244. https://link.springer.com/article/10.1007/s10336-007-0265-7.

Wegge, P., Rolstad, J., 2011. Clearcutting forestry and Eurasian boreal forest grouse: long-term monitoring of sympatric capercaillie Tetrao urogallus and black grouse T. tetrix reveals unexpected effects on their population performances. For. Ecol. Manag. 261 (9), 1520–1529. https://www.sciencedirect.com/science/article/pii/S0378112711000739.

Weintraub, A., Murray, A.T., 2006. Review of combinatorial problems induced by spatial forest harvesting planning. Discr. Appl. Mathem. 154 (5), 867–879. https://doi.org/10.1016/j.dam.2005.05.025.

Wiens, J.A., 1989. Spatial scaling in ecology. Funct. Ecol. 3 (4), 385–397. https://www.jstor.org/stable/2389612.

Winiger, N., Hendel, A.L., Ganz, S., Zielewska-Büttner, K., Segelbacher, G., Braunisch, V., 2023. Saproxylic beetles respond to habitat variables at different spatial scales depending on variable type and species' mobility: the need for multi-scale forest structure management. Biodivers. Conserv. 32 (10), 3355–3377. https://link.springer.com/article/10.1007/s10531-023-02663-2.