



Unraveling the characteristic spatial scale of habitat selection for forest grouse species in the boreal landscape

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ABSTRACT

The characteristic spatial scale at which species respond strongest to forest structure is unclear and species-specific and depends on the degree of landscape heterogeneity. Research often analyzes a pre-defined spatial scale when constructing species distribution models relating forest variables with occupancy patterns. This is a limitation, as forest characteristics shape the species use of habitat at multiple spatial scales. To explore the drivers of this relationship, we conducted an in-depth investigation into how scaling forest variables at biologically relevant spatial scales affects occupancy of grouse species in boreal forest. We used 4,790 grouse observations (broods and adults) collected over 39,303 stands for 15 years of four forest grouse species (capercaillie, black grouse, hazel grouse, and willow grouse) obtained from comprehensive Finnish wildlife triangle census data and forest variables obtained from Airborne Laser Scanning and satellite data originally sampled at 16 m resolution. We fitted Generalized Additive Mixed Models linking grouse presence/absence in the Finnish boreal forest with forest stand structure and composition. We estimated the effects of predictor variables aggregated at three spatial scales reflecting the species use of the landscape: local level at stand scale, home range level at 1 km radius, and regional level at 5 km radius. Multi-grain models considering forest-species relationships at multiple scales were used to evaluate whether there is a specific scale at which forest characteristics best predict local grouse occupancy. We found that the spatial scale affected the predictive capacity of the grouse occupancy models and the characteristic scale of habitat selection was the same (i.e., stand scale) among species. Different grouse species exhibited varying optimal spatial scales for occupancy prediction. Forest structure was more important than compositional diversity in predicting grouse occupancy irrespective of the scale. A limited number of forest predictors related to availability of multi-layered vegetation and of suitable thickets explained the occupancy patterns for all the grouse species at different scales. In conclusion, modeling grouse occupancy using forest predictors at different spatial scales can inform forest managers about the scale at which the species perceive the landscape. This evidence calls for an integrated multiscale approach to habitat modelling for forest species.

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1. Introduction

The characteristic spatial scale at which species best respond to the environment is unclear. Often, species distribution studies assume the existence of a single species characteristic selection scale (Holland et al., 2004). However, we know that different environmental attributes can shape the species resource needs at multiple spatial scales (Stuber and Fontaine, 2019). One factor determining the scale dependency is the degree of environmental variation (heterogeneity) in the landscape (Lu and Jetz, 2023). The extent to which spatial scale affects how species respond to the environment is determined by the influence of habitat structure and composition on the resource needs of individuals (Wiens, 1989; Jokimäki and Huhta, 1996). Knowledge of the scale at which these two dimensions influence individual site selection is crucial for optimal occupancy modeling to inform species management (Jackson and Fahrig, 2015; Bradter et al., 2013).

In the boreal biome, forest grouse species are birds for which habitat selection is known to be a multi-scale process (Miettinen et al., 2008; Lande et al., 2014). Regional grouse density is likely to best account for variation in grouse nesting success at local scale (c.f., Kurki et al., 2000 for black grouse and capercaillie). Therefore, forest variables correlated with grouse density at regional scale can improve the capacity of local-scale forest variables of predicting local grouse occupancy (Graf et al., 2005). Most of the studies assume that the spatial scale of the habitat preferences of phylogenetically related species is similar, likely because of the common life-history traits (Thornton and Fletcher, 2014), like body size and dispersal ability (Lu and Jetz, 2023), and consequently the most important spatial scales of multiple environmental attributes are averaged within species. On the basis of LiDAR data, Melin et al. (2016) concluded that broods of hazel grouse, black grouse and capercaillie had similar responses to forest structure, with the occupancy of all three species being positively related to high shrub cover, high canopy cover or both. On the other hand, Swenson and Angelstam (1993) in Sweden concluded that habitat preferences of different forest grouse species differ as a function of forest age and successional stages: black grouse selects forest stands 0–20 years old, hazel grouse stands 20–50 years, and capercaillie stands ≥ 90 years.

Grouse habitat quality is strongly affected both by the forest structure, which affects the species trophic and reproductive niche at local level, and by forest composition, which determines the regional grouse patterns of occurrence in the landscape (Melin et al., 2016). Forest characteristics related to its structure include tree age, stem density, tree diameter, volume, stand fertility class (directly positively related with forest types with high bilberry ground cover, see Cajander, 1949) and canopy cover. Forest composition is related to the diversity in the attributes of forest structure measured by tree species. However, the effect of the spatial scale on the process of selection of forest structure and composition for grouse species has been poorly explored.

We fitted multi-grain (i.e., multi-scale) models to consider whether there is a specific scale at which forest characteristics best predict local grouse occupancy (cf., Gray et al., 2010). The expectation is that multi-grain models will improve model accuracy with respect to the accuracy achieved by single-scale models retaining forest predictors affecting grouse occupancy at the best spatial scale (cf., Graf et al., 2005; Mertes et al., 2020). We evaluated whether different phylogenetically related grouse species share a similar scale-dependent response to environmental characteristics. Specifically, we tested whether local occupancy patterns of different forest grouse species were better explained either by common or exclusive forest predictors at different spatial scales. Finally, we evaluated the effects of habitat structure (i.e., local forest characteristics) and habitat composition (i.e., diversity in forest structure) to test the hypothesis that species will respond to different types of environmental variables at different spatial scales (Stuber and Fontaine, 2019). The expectation is that forest variables related to habitat structure would be more important than habitat composition in predicting local grouse occupancy. This is likely because, at the local

scale, the stand structure directly affects the suitability of the forest as habitat, while the diversity of tree species is limited due to the intrinsic limited tree diversity in the boreal biome, which is further restricted by the selection of one or two tree species for timber harvesting in production forest (cf., Ludwig and Klaus, 2017). This process is likely to create more homogenous forests both in terms of composition and structure in the study region.

We specifically asked the following questions: (1) Does the spatial scale affect the accuracy of the grouse habitat models? (2) Is there an optimal spatial scale for modelling grouse occupancy? (3) Are there common forest predictors explaining the occupancy patterns for all the grouse species at different scales? (4) Do forest variables related to habitat structure and composition affect grouse occupancy differently at different scales?

2. Materials and methods

2.1. Study area

Our study area comprises a rectangle (width: 225 km, length: 750 km) encompassing inland boreal areas in Northern, Central and Southern Finland (Fig. 1). The rectangle shaped study area was placed inland to avoid the impact of extensive agricultural landscape in the coastal areas of Finland that may confound the patterns of grouse habitat preferences. The study area is represented by typical Finnish boreal forest with Scots pine (*Pinus sylvestris* L.), Norway spruce (*Picea abies* (L.) H. Karst.), and birch (*Betula* spp. L.) dominating the landscape. 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.).

2.2. Wildlife census data

The grouse data were compiled from the Finnish wildlife triangle monitoring scheme (www.riistakolmiot.fi/), which is coordinated by the Natural Resources Institute Finland, with the goal to provide information on changes in wildlife populations (Lindén et al., 1996; Pellikka et al., 2005). The wildlife triangles are 12 km long transect routes, which are shaped like equilateral triangles with 4 km sides and surveyed twice annually: during the winter and the summer. We retrieved data from the summer census (mid-July to August), designed primarily for surveying grouse, where the route is surveyed by a three-person team of volunteers (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 (*Tetrao 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). The data for the locations of every observed bird is spatially accurate and available in a GIS format.

We included data from years 2005–2019 from Northern, Central and Southern Finland, fitting the defined study area (Fig. 1). 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, for instance. 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 (mean stand area = 2.6 ha, ranging between 0 and 226 ha), 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. Also, for each forest stand, we have a measure of the spatial and temporal

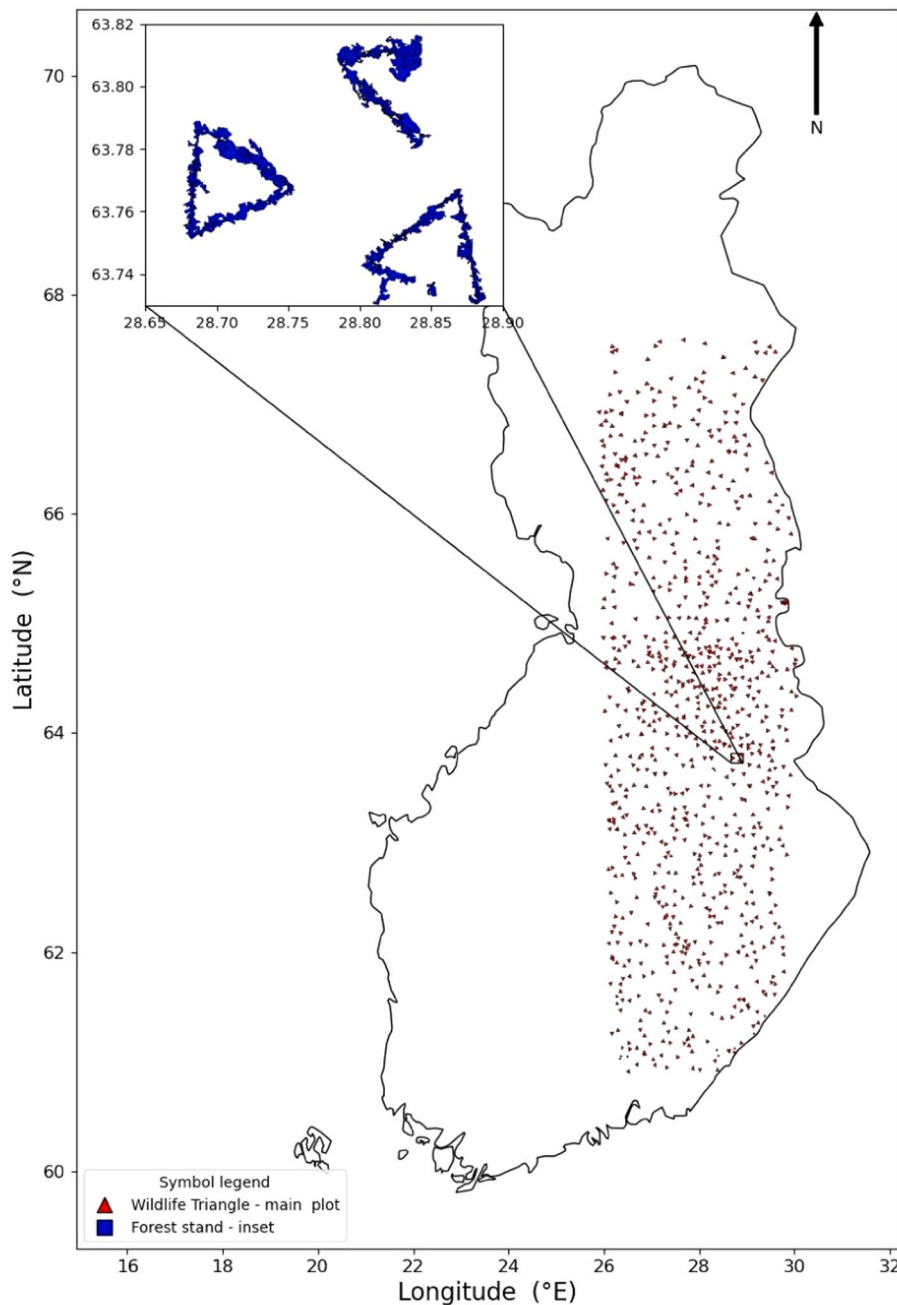


Fig. 1. Map of the locations of the wildlife triangles for grouse species for 2005–2019 within the regions of Finland. The inset map reports a detail of the stands that were crossed by inventory routes within each triangle.

dimensions of the sampling effort, which were respectively quantified as (1) the length of a surveyed transect segment that intersects with a forest stand (survey area = segment length in meters times the 60-m segment width), and (2) how many years the survey was done.

The final data consisted of 4,790 grouse observations (broods and adults) over 39,303 stands. Observations for each of the four grouse species are reported in [Table 1](#).

2.3. Forest variables

Forest characteristics considered relevant for predicting grouse occupancy were extracted for each stand from the database produced, owned, and archived by the Finnish Forest Centre (www.metsään.fi) (specifically, stand total area, basal area, mean tree age, area of peatland by drainage level, and stand geometry) and [supplemental information](#)

Table 1

Number of presences and absences and relative percentages for grouse species based on the locations of the wildlife triangles for 2005–2019 within the sampled regions of Finland.

Species	N. Presences (%)	N. Absences (%)
All grouse species	4,790 (12.2)	34,513 (87.8)
Black grouse	2,162 (5.5)	37,141 (94.5)
Capercaillie	1,233 (3.1)	38,070 (96.9)
Hazel grouse	1,969 (5.0)	37,334 (95.0)
Willow grouse	92 (0.2)	39,211 (99.8)

aggregated to the stand level from the Luke data download service (<https://kartta.luke.fi/opendata/valinta-en.html>) (specifically, canopy cover (%) and stand fertility class (with categorical values from 1, corresponding to maximum soil fertility, to 10, minimum soil fertility)). A

complete list of the variables included in the grouse models is reported in Table 2. All the variables obtained from the maps of the Finnish Forest Centre were remotely sensed via Airborne Laser Scanning (ALS), but with field inventory as a background reference. The assessment of vegetation structure via ALS has proven promising to assess species distribution patterns (Moudrý et al., 2023a). The variables from the Luke maps were based on multi-source National Forest Inventory, which utilizes satellite data (Landsat imagery) and the NFI data to produce wall-to-wall estimates of the forest variables (Mäkisara et al., 2019). The interpretation unit of all variables was a 16 × 16 m grid square, which corresponds to the area of the reference plot for tree stand interpretation, that is the smallest inventory unit. In the boreal Fennoscandia, canopy cover and soil fertility are assumed to have a negligible variation (Kulha et al., 2020) across the 15 years grouse inventorying period and along a large area, therefore were sampled only for the Multi-source National Forest Inventory raster maps of 2013.

The canopy cover of trees is the vertical projection area on the horizontal plane of the canopies of the individual trees on a field plot (without double counting the overlapping canopies). In the Finnish system, the “site” classes are used for grouping the forest by vegetation zones into uniform classes according to their fertility and wood production capacity. Site fertility is also positively related with the forest capacity to produce bilberry (*Vaccinium myrtillus* L.). In national land-use classification, all stands on mineral soil with site fertility class in 1–6 were classified as forest land (1 is herb rich sites, 2 is herb rich heath forests, 3 is mesic forests, 4 is sub-xeric forests, 5 is xeric forests, 6 is barren forests). Class 7 (rocky and sandy soils and alluvial lands) can be forest land, poorly productive forest land, or unproductive land, and class 8 (summit and field land with single coniferous trees) either poorly productive forest land or unproductive land. Classes 9 (mountain birch dominated fields) and 10 (Open fields) are poorly productive forest land or unproductive land.

Stem density, basal area, diameter, and volume were calculated both

in a cumulative way for each stand and separately for tree species, i.e., for Scots pine, Norway spruce and deciduous trees (cumulated values for the set of all the species). Variables related to forest composition were calculated from the respective variables of forest structure and included Shannon diversity indexes for tree stem density and mean diameter. Diversity indexes were obtained by separating the forest variables from the Finnish Forest Centre for each of the 28 tree species potentially occurring in each forest stand.

2.4. Models of grouse occupancy

To evaluate the impact of forest characteristics on the species probability of occurrence in Finnish forests, we fitted (1) Generalized Additive Mixed Models (GAMM) linking (2) the forest stand-specific presence/absence of each grouse species with (3) a representation of the geographic location of the stands, (4) the species sampling effort, (5) regional density of grouse, (6) variables related with forest structure and composition, and (7) a random effect underlying the hierarchical spatial structure of the data, as detailed here:

(1) GAMMs were fitted with the function “gamm” in the “mgcv” package (Wood and Wood, 2015) within R Statistical Software (R Core Team, 2023). In our study, GAMMs allowed the spatial component to be non-linear (see point 3) while the effects of other variables were assumed to be linear (see points 4, 5 and 6). The “gamm” function makes use of a Penalized Maximum Likelihood Estimation. This estimation technique incorporates a penalty term into the likelihood function, which helps control the complexity of the model. The penalty term discourages extreme or non-smooth parameter estimates, effectively imposing a smoothness constraint on the estimated relationships. By penalizing complexity, Penalized Maximum Likelihood Estimation aims to strike a balance between goodness of fit and model complexity.

(2) The species occupancy was modelled as the local probability of occurrence reported for each stand intersecting a wildlife triangle

Table 2

Legend of the codes of the variables (in alphabetic order) included as effect in the Generalized Additive Mixed Models (GAMMs) and their mean and range at different spatial scale.

Variable code	Description	Units	X=stand mean (min-max)	X=1 km mean (min-max)	X=5 km mean (min-max)	5–100 km
LAT_UP_stand	Stand Latitude	degrees N (°)	63.5 (61–68)	-	-	-
LONG_UP_stand	Stand Longitude	degrees E (°)	27.9 (26–30)	-	-	-
effort_yrs_km2	Sampling effort	km ²	0.05 (0.0–1.5)	-	-	-
Meanage_X	Mean age	years	48.6(0–229)	48.6(0–186)	48.6(0–140)	-
Area_herb-rich_heath_(1)_X	Area with drainage state 1	ha	1.6 (0–213)	1.6 (0–213)	1.6 (0–22)	-
Area_natural_peatland_(6)_X	Area with drainage state 6	ha	0.4 (0–226)	0.4 (0–226)	0.4 (0–27)	-
Area_drained_peatland_(7)_X	Area with drainage state 7	ha	0.1 (0–26)	0.1 (0–22)	0.1 (0–3)	-
Fertility_Class_X	Fertility class	-	3.2 (1–10)	3.2 (1–7)	3.2 (2–6)	-
basalarea_X	Basal area	m ²	15.9 (0–47)	15.9 (0–39)	15.9 (0–29)	-
Canopy_Cover_X	Canopy cover	%	50.1 (0–95)	50.1 (1–85)	50.1 (1–69)	-
Mean_diameter_deciduous_X	Mean Diameter deciduous trees	cm	9.5(0–44)	9.5(0–35)	9.6(0–26)	-
Mean_diameter_pine_X	Mean Diameter Scots pine	cm	15.3(0–96)	15.3(0–40)	15.3(0–31)	-
Mean_diameter_spruce_X	Mean Diameter Norway spruce	cm	13.3(0–112)	13.3(0–42)	13.3(0–31)	-
Vol_deciduous_X	Volume deciduous trees	m ³	20.3(0–299)	20.2(0–146)	20.3(0–127)	-
Vol_pine_X	Volume Scots pine	m ³	54.8(0–419)	54.9(0–250)	54.7(0–148)	-
Vol_spruce_X	Volume Spruce	m ³	41.6(0–578)	41.5(0–337)	41.7(0–161)	-
Stem_count_deciduous_X	Stem density deciduous trees	N. stems	587(0–23261)	588(0–7134)	585(0–4569)	-
Stem_count_pine_X	Stem density Scots pine	N. stems	489(0–10000)	489(0–4710)	489(0–1891)	-
Stem_count_spruce_X	Stem density Norway spruce	N. stems	386(0–5777)	386(0–2164)	385(0–1200)	-
Shannon_Mean_diameter_X	Mean diameter diversity index	-	0.08(0.0–2.6)	0.28(0.0–2.8)	0.42(0.0–2.1)	-
Shannon_Stem_X	Density diversity index	-	0.07(0.0–2.4)	0.32(0.0–2.4)	0.62(0.0–2.2)	-
Grouse_density_5_100_km	Estimated density of all grouse species in an area between 5 and 100 km from each stand	N. individuals / km ²	-	-	-	19.4 (3.1–32.2)
Black_grouse_density_5_100_km	Estimated density of black grouse in an area between 5 and 100 km from each stand	N. individuals / km ²	-	-	-	7.9 (0.5–15.5)
Capercaillie_density_5_100_km	Estimated density of capercaillie in an area between 5 and 100 km from each stand	N. individuals / km ²	-	-	-	4.1 (2.1–7.2)
Hazel_grouse_density_5_100_km	Estimated density of hazel grouse in an area between 5 and 100 km from each stand	N. individuals / km ²	-	-	-	6.9 (0.0–12.0)
Willow_grouse_density_5_100_km	Estimated density of willow grouse in an area between 5 and 100 km from each stand	N. individuals / km ²	-	-	-	0.6 (0.0–3.6)

(ranging between 0 and 1): for all grouse species combined, and separately for hazel grouse, black grouse, capercaillie and willow grouse. 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.

(3) The effect of the geographic location of the stand on the patterns of species occupancy was accounted for by a tensor explicitly representing the continuous spatial surface, i.e., $te()$, summarized by three main components, i.e., latitude (Fx1) and longitude (Fx2) and their interaction (Fx3). Adding this term improved the capacity of the models to account for anisotropic patterns of species distribution over the study area. Including the tensor term in all the models is a way to partially account for the variance explained by the possible non-linear effects of the habitat predictors and their interactions (Pedersen et al., 2019).

(4) Imperfect detection can substantially reduce the inferential and predictive accuracy of presence-absence models that do not account for detectability (Lahoz-Monfort et al., 2014). Therefore, we added in all the models the sampling effort (log-transformed), which was related both with extent of sampled area and years of species sighting. It was measured as the effective area covered by the part of the surveyed transect (segment) going through a unique forest stand. Specifically, the sampling effort is the area measured in km^2 ($0.06 \text{ km} \times \text{“segment length inside stand” km}$) times the number of years during which a certain triangle (and its segments) was surveyed within the period 2005–2019.

(5) Total density of grouse (incl. young) at radius 5–100 km (unit: individuals / km^2) from each wildlife triangle while excluding the focal triangle. Total density of grouse was averaged over the included years and thus relates the observed pattern in each triangle to average grouse density in the region. The densities of grouse species tend to fluctuate (e.g., Ludwig et al., 2006), which is predicted to affect the order of preference of the habitat types (Fretwell and Lucas, 1969).

(6) Ecologically relevant forest variables (centered and standardized) sampled for planning purposes and available from the Finnish Forest Centre and from Luke raster databases and related to forest structure and composition (see paragraph 2.3).

The forest variables were estimated at three spatial scales: i) at local level (at the forest stand scale, where the mean value was calculated from the pixels within stand polygon), ii) at the home range level (at the scale of 1 km from the segment centroid) and iii) at the regional level (at the wildlife triangle scale of 5 km from the segment centroid). Home range sizes inevitably varies among the study species due to, for example, body size differences (average body mass on hazel grouse and capercaillie are 250–450 g and 1,900–4,000 g, respectively). However, for the sake of consistency we used 1 km radius reflecting the average home range size for all species. For example, capercaillie broods can move >1 km from capture sites in a few days (Wegge et al., 2007), and in this case their dependence from forest characteristics at larger (5 km) scale would be detected by our models. Within a circular buffer located within 1 km and 5 km from the segment centroid, all predictor variables were averaged. The procedure of summarizing environmental data from neighborhood windows of various sizes around each occurrence is in line with recent recommendations suggesting that improved model predictions can be obtained by focal analyses (Miguet et al., 2017; Hu and Tong, 2022; Lu and Jetz, 2023).

(7) The hierarchical spatial structure of the data was accounted for, as stands were clustered in wildlife triangles, by including the triangle as a random effect within which stands were aggregated (i.e., random ‘site’ effect).

Models for grouse probability of occurrence were fitted separately for each species at each scale. Furthermore, the results from single-scale models were used to build multi-grain models, including every forest variable at its best-explaining scale (i.e., the scale with the strongest effect) (cf., Graf et al., 2004).

When fitting GAMMs, mean estimated effects of the predictors were

reported along with standard errors, t , to address the magnitude of the effect of each predictor and its significance under the null hypothesis of no effect.

2.5. Model selection procedure

The predictor variables to include in the final models were selected in three steps: *first*, highly collinear variables (Variance Inflation Factor (VIF)>0.7) were excluded with the collinearity-filtering algorithm “vifstep” of the “usdm” R package (Naimi, 2015); *second*, a backward selection procedure based on the Akaike Information Criterion (AIC; Akaike, 1973), balancing model fit and number of predictors, was applied to the glm version (i.e., without spatial tensor and random effect) of the model fitted with the variables retained after the first step with the “stepAIC” function of the “MASS” R package (Venables and Ripley, 2002), which finally retained only forest predictors significant at $P < 0.10$. The logarithm of the sampling effort and the total grouse density were forced to be retained in all models; *third*, a gamm with only the selected variables was fitted including the terms of the spatial tensor and the random effect.

2.6. Measures of model accuracy and spatial autocorrelation of residuals (Moran’s I)

A confusion matrix transformed the predicted probability values into observed absences (0) and presences (1) through a discrimination metrics based on the optimal threshold for binary classification estimated with the algorithm “optCutoff” of the “MKclass” R package (Kohl, 2020).

The predictive accuracy of each model was measured calculating the Percentages of Correctly Classified Cases, the Percentages of True Presences (sensitivity) and True Absences (specificity), the Area Under the Curve of a ROC plot (AUC, Swets, 1988) with the function “auc” of the “PresenceAbsence” R package (Freeman and Moisen, 2008), and the True Skill Statistics (TSS), a threshold-dependent measure of accuracy insensitive to prevalence ($TSS = \text{Sensitivity} + \text{Specificity} - 1$, Allouche et al., 2006). Models with $AUC < 0.60$ or $TSS < 0.10$ were considered no better than random (Scridel et al., 2021). In general, an AUC of 0.5 suggests no discrimination, 0.7–0.8 is considered acceptable, 0.8–0.9 is considered excellent, and more than 0.9 is considered outstanding (Hosmer et al., 2013).

The cross-validation accuracy was estimated with the function “Cvgam” of the “gamclass” R package (<https://maths-people.anu.edu.au/~johnm/nzsr/taws.html>). The function provides a check on the extent of downward bias in the estimated standard error of residuals for each GAMM. The function provides a Cross-Validation Mean Squared Error, which is a measure of the predictive model performance when evaluated using cross-validation across 10 folds. MSE measures the average squared difference between the predicted values and the actual (observed) values. Smaller values of MSE are better because they indicate that model’s predictions are closer to the actual values.

We evaluated the degree of spatial autocorrelation of the GAMMs’ residuals at multiple spatial scales estimating the Moran’s I and its associated significance test (“moran.test” algorithm in “spdep” R package, Bivand and Wong, 2018).

3. Results

3.1. Effect of scale on model accuracy, goodness-of-fit, number and effect of predictors

The accuracy values (i.e., AUC and TSS) of the gamm models were different among species but similar across spatial scales: accuracy was similarly acceptable (average AUC across scales ≈ 0.7 –0.8, average TSS across scales ≈ 0.3 –0.4) for the models for all grouse species, for hazel grouse, black grouse and capercaillie and outstanding (average AUC ≈ 0.9 , average TSS ≈ 0.7) for the willow grouse models (Table 3; Fig. A.1

Table 3

Metrics of accuracy for grouse Generalized Additive Mixed Models (GAMMs) including forest predictors at different spatial scales compared with GAMMs including only spatial tensor surfaces (te), log (sampling effort) and total grouse density (D). Acronyms: AUC = Area Under the ROC (Receiver Operating Characteristic) Curve, TSS = True Skill Statistics.

Species	AUC - te (lat, long)	AUC - te(lat, long)+ log (effort)+ D	AUC - Stand	AUC - 1 km	AUC - 5 km	AUC - Multi-grain	TSS - te (lat, long)	TSS - te(lat, long)+ log (effort)+ D	TSS - Stand	TSS - 1 km	TSS - 5 km	TSS - Multi-grain
Total grouse	0.636	0.729	0.729	0.732	0.733	0.734	0.228	0.333	0.331	0.335	0.340	0.341
Black grouse	0.633	0.738	0.738	0.743	0.742	0.744	0.226	0.358	0.359	0.362	0.363	0.363
Capercaillie	0.667	0.752	0.753	0.759	0.759	0.759	0.275	0.372	0.373	0.387	0.383	0.387
Hazel grouse	0.663	0.747	0.747	0.754	0.752	0.758	0.254	0.370	0.369	0.383	0.374	0.382
Willow grouse	0.898	0.907	0.906	0.906	0.913	0.912	0.711	0.701	0.700	0.695	0.695	0.707

in Appendix A). In general, the inclusion of significant forest predictors in the models did not appreciably improve the level of accuracy with respect to the level of accuracy already achieved incorporating in the models only the spatial tensor, the sampling effort and the species regional density (Table 3; Fig. A.1).

The models for all grouse species pooled together showed on average a lower estimate of accuracy across scales (i.e., average Cross-Validation Mean Squared Error=0.0997) than the models for single species (average CV-mse = 0.0321) (Table A.1). Among all the species, the models for hazel grouse (average CV-mse = 0.0460) and black grouse (average CV-mse = 0.0502) showed the lowest accuracy across scales, the model for capercaillie an intermediate accuracy (average CV-mse = 0.0298) and the models for willow grouse the highest accuracy (average CV-mse = 0.0023) (Table A.1).

The number of significant forest predictors decreased from the stand (on average among species, 5.2 predictors) to the 1-km (2.8 predictors) and 5-km (2.6 predictors) scale models (Fig. 2). The number of significant forest structure predictors of occupancy was higher for the stand

scale models (on average among species, 5.2 predictors) than for the higher scale models (2.0 predictors at 1-km scale, 2.2 predictors at 5-km scale) (Fig. 2). Instead, the number of significant forest composition predictors was the highest at intermediate scale (at 1-km scale, average number of forest composition predictors among species = 0.8 predictors) intermediate at 5-km scale (0.4 predictors) and the lowest at stand scale (0 predictors) (Fig. 2).

In the multi-grain models the number of significant forest predictors (structure and composition) was the highest (on average, 6.2 predictors), as this model incorporated predictors from all the spatial scales (Fig. 2). The multi-grain models included mostly predictors at stand scale (on average among species, 62% of the predictors), and similarly less predictors at 1-km (22%) and 5-km (17%) scale (Fig. 2). However, the effect of forest variables on grouse occupancy varied with scale and species.

We tested the differences in the absolute (i.e., modulus) effects (Fig. 3) of all the forest predictors across spatial scales for each grouse species with the Pairwise Test for Multiple Comparisons of Mean Rank

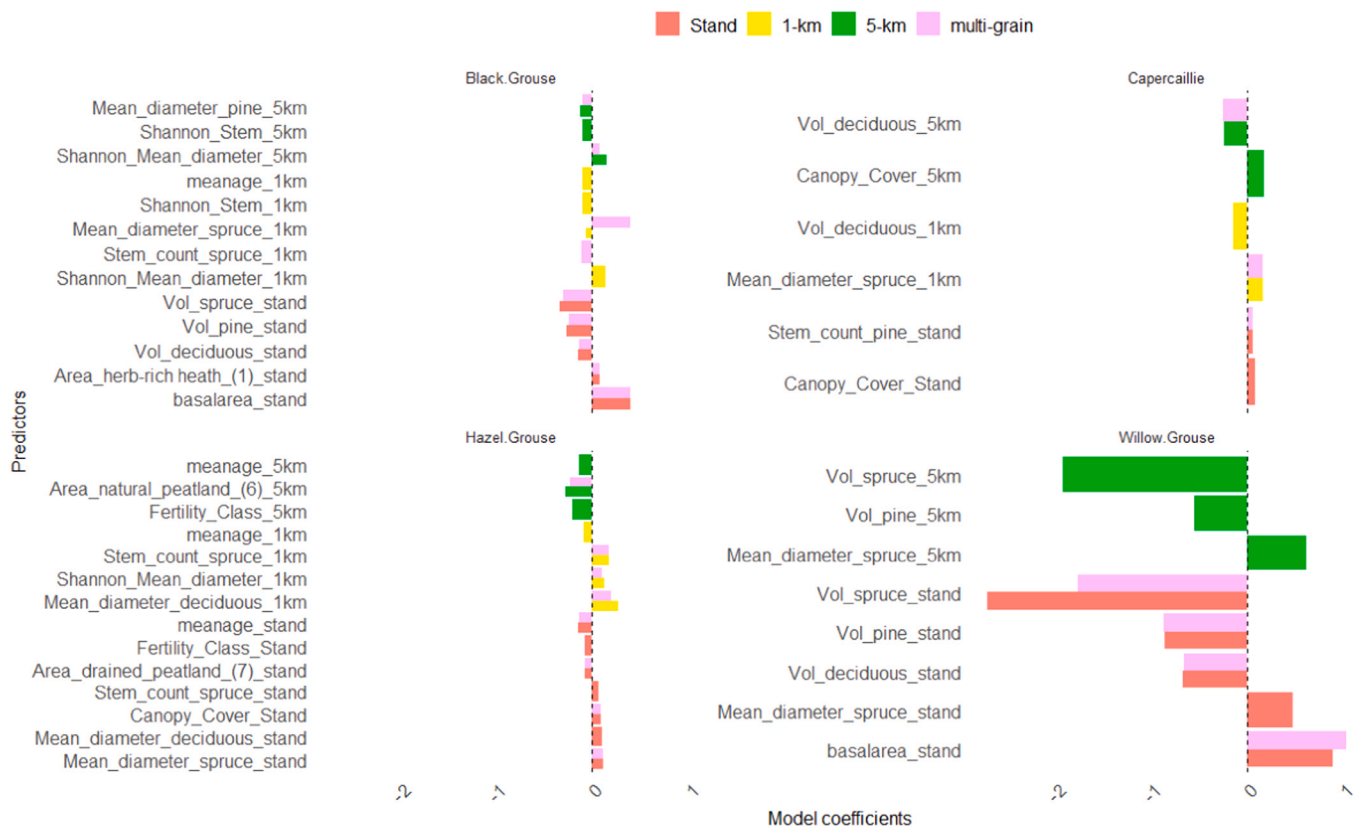


Fig. 2. Estimates of the effects of significant forest predictors (at $P < 0.1$) included in the Generalized Additive Mixed Models (GAMMs) for occupancy of grouse species at different spatial scales.

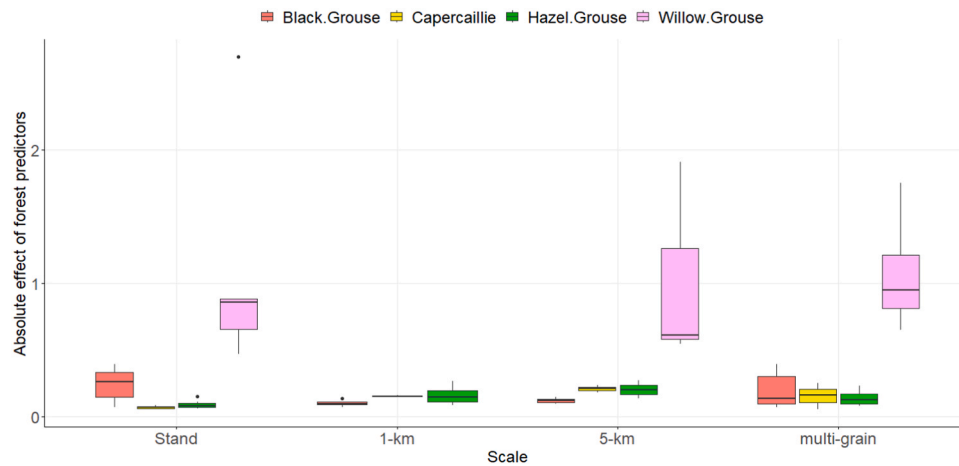


Fig. 3. Boxplots for the range of the absolute effects of the forest predictors for the models for each species at different spatial scales and multi-grain scale. The box represents the interquartile range and the whiskers the reasonable extremes of the data, that is the minimum and maximum values that do not exceed 1.5 times the interquartile range from the middle of the data.

Sums (Dunn’s-Test) (Dunn, 1964). The mean rank score showed a decreasing trend from stand, to 1-km to 5-km scale for black grouse (in stand model = 3.0, in 1-km model = 2.5, in 5-km model= 2.0), hazel grouse (in stand model = 4.0, in 1-km model = 2.5, in 5-km model= 2.0) and willow grouse (in stand model = 3.0, in 1-km model = no forest predictor, in 5-km model= 2.0) (Fig. 3). Instead, for capercaillie the mean rank score was the same at all spatial scales (mean rank score in all models = 1.5) (Fig. 3). All the multi-grain models were characterized by high mean rank score respect to the single scale models, as they embedded more predictors at stand scale than at higher spatial scales (mean rank score for black grouse = 4.9, for capercaillie = 2.0, for hazel grouse = 4.5, for willow grouse = 2.5) (Fig. 3).

3.2. Effect of scale on the selection of forest predictors of grouse occupancy

A high sampling effort and high regional grouse density were generally positively correlated with high grouse occupancy (details for all the models are reported in Tables B.1-B.20 in Appendix B). The predictors of forest structure differently affected grouse occupancy at different scales, as follows (see Fig. 2):

High mean tree age decreased occupancy of black grouse (at 1-km scale) and hazel grouse (at all spatial scales) (Fig. 2). High basal area increased occupancy of black grouse and willow grouse at stand scale (Fig. 2). High canopy cover increased occupancy of capercaillie (in stand and 5-km scale models) and hazel grouse (in stand scale model) (Fig. 2). High values of the soil fertility class, corresponding to less fertile soil types (which are also the soil types with lower bilberry vegetation cover) decreased occupancy of hazel grouse (in stand and 5-km scale models) (Fig. 2). On the other hand, high area of drained peatland and natural peatland decreased its occupancy (respectively, at stand and 5-km scales) (Fig. 2). Instead, high area of herb-rich heath on mineral soil increased occupancy of black grouse (at stand scale) (Fig. 2).

Structural variables (i.e., tree diameter, tree volume and stem density) related either with coniferous or deciduous trees differently affected grouse occupancy:

High diameter of Scots pine decreased occupancy of black grouse (at stand scale) (Fig. 2). High diameter of Norway spruce decreased occupancy of black grouse (at 1-km scale), but on the contrary increased occupancy of capercaillie (at 1-km scale), hazel grouse (at stand scale) and willow grouse (at stand and 5-km scales) (Fig. 2). High diameter of deciduous trees increased occupancy only for hazel grouse (at stand and 1-km scale) (Fig. 2). High diversity in diameters increased occupancy of black grouse (at 1-km and 5-km scales) and hazel grouse (at 1-km scale)

(Fig. 2).

High volume of Scots pine and Norway spruce decreased occupancy of black grouse (at stand scale) and willow grouse (at stand and 5-km scale) (Fig. 2). High volume of deciduous trees decreased occupancy for black grouse (at stand scale), capercaillie (at 1-km and 5-km scales) and willow grouse (at stand scale) (Fig. 2).

High density of Scots pine increased occupancy of capercaillie (at stand scale) and hazel grouse (at stand and 1-km scale) (Fig. 2). High diversity in stem density decreased occupancy of black grouse (at 1-km and 5-km scales) (Fig. 2).

3.3. Effect of scale on the selection of variables of forest structure and composition

Variables related with forest structure, like basal area, canopy cover, mean age, mean diameter, stem density, volume, fertility class and drainage status were most often included in the occupancy models at stand scale (Fig. 2). Structural variables were still most often represented at 1-km and 5-km scale in comparison to Shannon diversity variables, which were significant only in the models for black grouse and hazel grouse at 1-km and 5-km scales (Fig. 2). Diameter diversity variables was incorporated in the multi-grain models for black grouse (at 5-km scale) and for hazel grouse (at 5-km scale) (Fig. 2).

3.4. Spatial autocorrelation of the residuals

Only similarly weak spatial autocorrelation values were found in the residuals of all the GAMM models at each spatial scale. Spatial autocorrelation was low ($0.103 \leq \text{Moran's } I \leq 0.203$) even if significantly different from zero in all the residuals ($P \leq 2.2 * 10^{-16}$) (Table 4). Given

Table 4

Values for the Moran’s index (I) defining the level of clustering of the residuals of the GAMMs for each grouse species at different spatial scales.

Species	te(lat, long)	te(lat, long)+log (Effort)+D	Stand scale	1-km scale	5-km scale	Multi-grain scale
Grouse	0.202	0.201	0.200	0.203	0.202	0.199
Black grouse	0.137	0.135	0.134	0.133	0.135	0.134
Capercaillie	0.137	0.126	0.125	0.126	0.127	0.125
Hazel grouse	0.152	0.154	0.153	0.156	0.159	0.151
Willow grouse	0.103	0.104	0.111	0.103	0.107	0.107

the weak spatial dependence of the residuals at the level of the first neighbor, we did not evaluate spatial autocorrelation via correlograms.

4. Discussion

Our findings highlight how the spatial dimension of habitat selection affects predictions of occupancy patterns. Different grouse species exhibited similar optimal spatial scales for occupancy prediction. Forest structure was consistently more influential than compositional diversity in predicting occupancy patterns. Our finding that different forest predictors are important at different spatial scales for defining grouse habitat has demonstrated the importance of an integrated multiscale approach to species habitat modelling.

4.1 Does the spatial scale affect the accuracy of the grouse habitat models? (Q1) Is there an optimal spatial scale for modelling grouse occupancy? (Q2)

The likely reason why forest predictors increased only marginally the grouse model accuracy irrespective of the scale is that the spatial patterns of occupancy described by the geographic terms and the sampling effort (and in few cases by the regional density) reflect already well the spatial variability in the forest characteristics associated with the species presence/absence. However, the marginal improvement in the grouse model accuracy can also be due to the limited capacity of ALS and satellite forest variables to characterize grouse habitat. 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).

We found that the spatial scale does not substantially affect the accuracy of the grouse habitat models, as confirmed by the substantially invariant values of AUC and cross-validation across scales. In general, the capacity of environmental conditions in predicting species distribution is grain size-invariant only when measured environmental variables are homogeneous, like in our case (Lu and Jetz, 2023). However, the stand-level models included a higher number of significant forest predictors than home range and regional models. This was also confirmed by the higher representation of predictors and their effect at the stand scale in the multi-grain models with respect to the predictors at the higher scale. These are indications that the local scale is the most informative single scale for modelling grouse occupancy from forest characteristics. Another reason is that there is less variation in the forest predictors at larger scales (see the decrease of significant forest ranges at 5-km scale in Table 2), likely because the Finnish boreal forest landscape is quite homogeneous in terms of tree age, diameters, volumes and density profile (Korhonen et al., 2021).

The occupancy of different grouse species was preferentially affected by forest characteristics at stand scale and less affected at higher spatial scales, with the exception of capercaillie which did not show any clear preference for a particular scale. These results do not support the hypothesis postulating the existence of a species-specific characteristics' selection scale (*sensu* Holland et al., 2004). While we acknowledge that four species is not enough to make strong conclusions about phylogenetic effects, our results imply that the preferred scale for habitat preferences may be similar among phylogenetically close species (cf. Thornton and Fletcher, 2014). Indeed, Kurki et al. (2000) found that the probability of an observed grouse hen of capercaillie and black grouse being with brood was more related with land cover types resampled at large scale (5 and 10 km) than at small scale (0.5 and 1 km). This difference with our analysis is likely due to our availability of higher resolution forest variables (16 m pixel) respect to the study from Kurki et al. (2000) (with predictors at 100 m resolution), which were likely more effective in describing the local and home-range use of the habitat.

Auto-covariates like sampling effort and total grouse density between 5 and 100 km from each stand significantly increased the variance explained by the models at all scales. This finding confirms that a higher detection rate can substantially increase the inferential and predictive accuracy of presence-absence models by accounting for imperfect species detectability (Lahoz-Monfort et al., 2014). The general

importance of regional density for all grouse species and for black grouse and hazel grouse, but not for capercaillie and willow grouse, reflects the evidence that the extent of landscape accounting best for variation in grouse nesting success is of an order of magnitude larger ($\sim 100 \text{ km}^2$) than the grouse home range area (at least $\sim 1 \text{ km}^2$) (c.f., Kurki et al., 2000). However, Miettinen et al. (2008) noticed that species density is not necessarily the best indicator of habitat quality because during a short time high densities may occur even in poor habitats, but the large temporal (14 years) and spatial (over a latitudinal strip covering the whole of Finland) scales used in our study make this source of error negligible. In our study, grouse long-term scale occupancy is related directly with population processes (birth, death, immigration, and emigration) rather than with habitat selection, a process important at smaller scales.

In agreement with the findings from Mertes et al. (2020), we confirmed the usefulness of the multi-grain models because they allow the selection of the best scale separately for each predictor variable significantly affecting species occupancy (cf., Meyer, 2007). However, we also confirmed the findings from Graf et al. (2005) and from a review by Moudry et al. (2023b) who noticed that the improvements in model accuracy (i.e., AUC and TSS) reported for multi-grain models are generally low with respect to what is already achieved by single-scale models, as most of the predictors embedded in multi-grain models still belong to the finest stand spatial scale. This agrees with what was found by Ferrier and Watson (1997) that coarsening the analysis grain deteriorates model performance.

4.2 Are there common forest predictors explaining the occupancy patterns for all the grouse species at different scales? (Q3)

We found that, in general, few common forest predictors explained the occupancy patterns for all the grouse species irrespective of the spatial scales.

Specifically, the negative relationship we found between mean tree age and the occupancy of black grouse and hazel grouse confirmed their habitat preference for young stands found in Sweden by Swenson and Angelstam (1993). In Finland, the forest suitability for hazel grouse is the highest when the stand age is between 20 and 60 years (Mönkkönen et al., 2014). In Norway, black grouse is a species favoring more open landscapes where the structure of the forest does not resemble "old growth forests" (Elvesveen et al., 2023). Instead, for capercaillie and black grouse, Lande et al. (2014) found that chick production is negatively related to the proportion of old forest, while Miettinen (2009) concluded that the capercaillie does not need old forest as such, but the right forest structure (which can be found from younger forests as well). For capercaillie, previous evidence from Finnish and Norwegian studies showed, respectively, that the number of males in the lekking site is correlated with the proportion of young-middle-aged forests (Miettinen et al., 2005) and that capercaillie lek formation takes place in this type of forests (Rolstad et al., 2007).

For black grouse and willow grouse occupancy increased with an increase of basal area, a cumulative measure of the tree area, increasing the proportion of available habitat. These highly dense forests, generally occur on rich soil dominated by bilberry (Myrtillus and herb-rich forest types, *sensu* Cajander, 1949), which is the main trophic resource for grouse birds (Wegge and Kastdalen, 2008) and was found to directly increase population size (cf., Jansson and Andrén, 2003 for capercaillie). As a matter of fact, rich forest soil and mineral soil (i.e., non-peat soil) was associated with high occupancy for black grouse and hazel grouse. As a proof of evidence, we confirmed the findings from Melin et al. (2016) that grouse broods of forest dwellers like hazel grouse and capercaillie are positively related with canopy cover. This is an indirect evidence that hazel grouse and capercaillie do not prefer open clear-cut areas, which can be explained in three ways: clear-cuts narrow the grouse living space (Helle et al., 2003); clear-cuts reduce locally the abundance of bilberry by reducing the surface of old forests, one of the grouse main trophic resources abundant in this habitat (Wegge and Kastdalen, 2008); open habitats left after clear-cutting sustain local

populations of potential grouse predators (cf., Kurki et al., 1997; Wegge and Rolstad, 2011; Haakana et al., 2020).

For what concerns the structural diversity of the forest, we confirmed the preference of black grouse and willow grouse for low diameter/volume of Scots pine and Norway spruce in the forest, likely associated with low productivity bogs which represent the preferential trophic habitats for their broods (Ludwig et al., 2008; Wegge and Kastdalen, 2008). Indeed, for willow grouse most of the species' sightings in Finland are in fact from treeless (northern populations) or open forested habitats (northern populations) (Melin et al., 2020). The practically total absence of willow grouse in southern Finland is instead related with the process of habitat fragmentation (induced by peatland drainage and intensive forestry) occurring up to the 90 s and the negative effects of climate change (diminishing snow covers, cf., Melin et al., 2020). On the other hand, hazel grouse and capercaillie were positively associated with large diameter spruce forests and with highly dense Scots pine forests. For capercaillie this finding reflects its habit as typical forest-dweller mostly related with highly dense pine forest (cf., Miettinen, 2009; Löhmus et al., 2023). Finally, we confirmed the preference of hazel grouse for mixed forested areas with high deciduous volumes while black grouse, capercaillie and willow grouse were negatively associated.

The preference of black grouse and hazel grouse for forest with high diversity in diameters reflects the species' association with a thick shrub and field layer, which is likely to increase the availability of food resources and protection from predation for chicks (Huhta et al., 2017). These forest characteristics guarantee a homogeneous thicket of small trees for shelter (cf., Lindén et al., 2019; Haara et al., 2021). The availability of multi-layered vegetation and of highly dense thickets has been considered as an important requirement not only for grouse but for most game species in Finland (Lindén et al., 2019).

The specific -late summer field season for our triangle survey certainly had an importance on the characterization of grouse habitat. This choice was done to maximize the probability of detection for single adults and broods, hence, to supply an accurate description of grouse ecology. If the survey would have been conducted in the winter season it is likely that the habitat needs of each species would be partially different and subsequently also the relationships between forest characteristics and grouse occupancy patterns would differ.

4.3 Do forest variables related to habitat structure and composition affect grouse occupancy differently at different scales? (Q4)

Our results confirmed that, irrespective of the scale, forest variables related to habitat structure were more represented than compositional/diversity variables in models predicting local grouse occupancy. This low importance of compositional variables at all scale is likely related with their low landscape-level variation (at 5-km scale), explained by the fact that the Finnish forest landscape included in our study area is represented by even-aged, homogeneous stands, in terms of tree age, diameters, and density profile (Korhonen et al., 2021). At regional scale, heterogeneity in forest characteristics is constantly low (Ludwig and Klaus, 2017).

4.1. Implications for forest management

Our findings suggest that modeling grouse occupancy by testing forest predictors at different spatial scales can better inform forest managers about the scale at which the species perceive the landscape (Kurki et al., 2000; Graf et al., 2005; Miettinen et al., 2008; Lande et al., 2014) and where game-friendly management is most effective. This evidence calls for an integrated multiscale approach to species habitat management (Ludwig and Klaus, 2017). In Fennoscandia, game management is almost always implemented in managed forests, which in the light of our results creates a need to modify forest management so that it would enhance the existence of game birds (Lindén et al., 2019). This will be facilitated if multi-scale habitat models are implemented in Decision Support Systems capable to project forest characteristics under

alternative management scenarios. Our result on the importance of the forest structure at the stand scale suggests that management decisions of single forest owner have direct impact for grouse presence.

All grouse species are highly valued game species in Finland, and they are hunted recreationally. Grouse populations in Finland have suffered substantial declines in the past few decades, especially in southern parts of the country (Helle et al., 2003). Suspected causes of this have been linked to over-hunting and predation, but also forestry and climate change (Miettinen, 2009; Melin et al., 2020; Huhta et al., 2017). Our results suggest that when managing grouse brood habitats, attention should be given to maintaining a multi-layered forest embedding both protective canopy cover and a good understory cover (c.f., the findings by Miettinen et al., 2008 for capercaillie). However, our results also specify that grouse species have their specific habitat preferences which should be considered when managing forests for different uses.

To enable the benefits of multi-layered landscapes, forestry in private lands would need to be planned in agreement with multiple forest owners, also in relationship with the allocation of the protected area network (Lindén et al., 2019). In general, a diversification of forest management has proven important in increasing forest multi-functionality (Mönkkönen et al., 2014; Duflo et al., 2022). Our findings suggest that to be relevant, management planning should be integrated at the appropriate spatial scale to improve the habitat dimensions enhancing local grouse occupancy. In general, an integrated multiscale approach is likely to improve grouse habitat management.

5. Conclusions

This research has confirmed that the spatial scale affects the predictive capacity of the grouse habitat models and that there is a specific selection scale for modelling grouse occupancy: in our case, stand-scale forest variables were more important than variables at coarser resolution in explaining patterns of local grouse occurrence. A multi-scale approach to habitat modelling is necessary to reveal this habitat selection scale. It is also important from an applied perspective to implement meaningful models that match the scale of forest planning units in decision support systems. Variables related to forest structure were more important than compositional diversity variables in predicting grouse occupancy patterns irrespective of the scale. We found that, in general, few common forest predictors related to the availability of multi-layered vegetation and of suitable thickets explained the occupancy patterns for all the grouse species at different scales. However, all four grouse species showed their own distinct habitat preferences.

CRedit authorship contribution statement

Jukka Forsman: Writing – review & editing, Investigation, Conceptualization. **Kyle Eyvindson:** Writing – review & editing, Methodology, Investigation, Data curation. **Simone Bianchi:** Writing – review & editing, Methodology. **Adriano Mazziotta:** Writing – original draft, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Andreas Lindén:** Writing – review & editing, Methodology, Investigation. **Annika Kangas:** Writing – review & editing, Methodology. **Markus Melin:** Writing – review & editing. **Leena Ruha:** Writing – review & editing, Methodology, Formal analysis.

Declaration of Competing Interest

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

Data availability

Data will be made available on request.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2024.122008.

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