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Quantifying the effectiveness of habitat management to counter local extinction: A case-study on capercaillie

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ABSTRACT

The degradation of forest habitats in managed forests is a major threat to biodiversity. Accordingly, the conservation of forest-dwelling species has to be integrated with other goals and paradigms of production forestry. As those objectives may differ, it is crucial to quantify the potential effectiveness of habitat management for conservation to demonstrate its actual value. Here, we analysed detailed field-based distribution maps of a declining population of capercaillie (*Tetrao urogallus*), an indicator of open, structurally diverse conifer-dominated forests, in southwestern Germany to quantify the potential effect size of habitat management. We modelled range loss dynamics as a function of habitat structures obtained from high-resolution aerial stereo imagery, in order to estimate the potential increase in the probability of local capercaillie persistence under different management scenarios. Furthermore we identified situations in which habitat management would produce the largest conservation benefits. The probability of local capercaillie persistence during the study period was positively related to population connectivity, winter snow height and the availability of suitable forest structures. The positive effect of habitat management was largest at sites where persistence probability would otherwise be low to intermediate. Potential negative effects of decreasing snow load under climate change on local capercaillie persistence could be compensated more effectively by habitat improvement than a lack of population connectivity, implying that focusing habitat management on the edges of the distribution in addition to core areas would maximize conservation returns. Our results may thus contribute to an effective allocation of conservation investments where their leverage is highest.

1. Introduction

The loss and fragmentation of habitat is a landscape-scale phenomenon (Fahrig, 2003; Mitchell et al., 2015) and a key driver of global biodiversity loss (Fischer & Lindenmayer, 2007). In contrast to the ongoing forest loss in tropical forests (Bradshaw et al., 2009; Norris et al., 2010), the land cover composition in the temperate and boreal zone of Europe is currently relatively constant. However, most forest landscapes have long been modified to accommodate human needs (Bengtsson et al., 2000; Paillet et al., 2010). In these fragmented landscapes, the degradation of remaining forest habitats by production forestry is considered a major threat for biodiversity, since forest management is a pervasive influence on species composition and the availability of structural attributes (Paillet et al., 2010; Halme et al., 2013). Strict reserves alone are insufficient for large-scale biodiversity conservation, because currently < 2% of European forests are strictly protected (Bollmann & Braunisch, 2013; Forest Europe, 2015) and returning recently protected plantation forests to a natural state requires decades or more (Paillet et al., 2010, 2015). Accordingly, the conservation of forest-dwelling species has to be integrated with other goals and paradigms of production forestry (Ausden, 2007; Gustafsson et al., 2020).

A common approach to integrate biodiversity goals into forest management is to retain or create structural attributes considered favourable for a target species or species community (Ausden, 2007; Gustafsson et al., 2012; Halme et al., 2013). For birds, this may include retention of dead wood or tree microhabitats (Bauhus et al., 2009; Gutzat & Dormann, 2018; Basile et al., 2020) or understory composition and quality (Broome et al., 2014; Eckerter et al., 2019). Perhaps surprisingly, the long-term effectiveness of such management actions is seldom studied systematically, at least within continuous-cover forestry regimes, despite the apparent prevalence of habitat management for supporting forest biodiversity (Götmark, 2013; Storch et al., 2020). The focus of research has rather been on the deficiency of structural

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complexity in managed forests (Paillet et al., 2010; Halme et al., 2013) and the potential benefits of management for certain attributes often remains unclear. In part, this may be because the conservation value of management interventions, particularly for birds and mammals can often only be evaluated retrospectively, over long time periods and at substantial cost.

The reduced biological and structural diversity in intensively managed production forests as compared to natural forests (Bauhus et al., 2009; Paillet et al., 2010; Gustafsson et al., 2012) generally challenges the conservation value of forest habitats. This can be critical for those species dependent on the most deficient habitat characteristics. The forest grouse (*Tetraoninae*) are a good example of this. In Europe, the hazel grouse (*Bonasa bonasia*), the black grouse (*Lyrurus tetrix*) and the capercaillie (*Tetrao urogallus*) are associated with different successional stages of boreal and montane forest and the prevailing structural attributes (e.g. Johnsgard, 1983; Bergmann et al., 1996, Storch, 2002). The capercaillie in particular is considered an indicator species for species-rich, open, structurally diverse mature conifer-dominated forests (Suter et al., 2002; Pakkala et al., 2003) and is associated with the forest structures caused by natural disturbance events (i.e. wind throw, bark beetle; Mikoláš et al., 2017, Kortmann et al., 2018). Structural attributes typical of late successional stages and natural disturbance dynamics (i.e. open stands, canopy gaps) are, however, often lacking in the economic cycle of commercial forests (Bauhus et al., 2009; Gustafsson et al., 2012). Currently, most forests in central Europe are subject to continuous-cover forestry, which is often associated with increasing standing tree volume and closed canopies (e.g. Gustafsson et al., 2020).

The capercaillie is not threatened at the global scale, but many local populations are declining or have gone extinct, particularly in southern and central Europe (Storch, 2007a; Jahren et al., 2016). Although high predation risk (Jahren et al., 2016; Kämmerle et al., 2017), increased disturbance by human recreational activities (Coppes et al., 2017), and climate change (Braunisch et al., 2013) are considered to play a role, a reduction in habitat suitability due to fundamental changes in land use practices is considered to be a central driver of the decline (Storch 2000; 2007b). Accordingly, conservation largely relies on habitat management to mimic forest dynamics suitable for the species (e.g. Mollet et al., 2008; Braunisch & Suchant, 2013; Poole & Haysom, 2015), for instance by creating small clear-cuts (< 1 ha) or stand thinning to improve habitat suitability (Moss & Picozzi, 1994; Braunisch & Suchant, 2013; Broome et al., 2014). The capercaillie thus provides a suitable model species on which to evaluate the effectiveness of habitat management to improve population persistence in managed forests.

Here we make use of accurate and spatially explicit field-based distribution maps of a declining population of capercaillie in south-western Germany to a) model range loss dynamics as a function of habitat structures obtained from high-resolution aerial stereo imagery to b) quantify the potential of habitat management to increase the probability of local capercaillie persistence and c) identify conditions and locations in which habitat management would produce the largest conservation benefits.

2. Material and methods

2.1. Study area and species

The study was conducted using data on capercaillie occurrence collected in the Black Forest low-altitude mountain range in south-western Germany (max. elevation 1493 m a.s.l.; Fig. 1 A,B). The Black Forest ecoregion (~7000 km^2) is characterized by mixed montane forests, fragmented by settlements, mountain pastures, and agriculturally used valleys. Forest stands are primarily managed for timber production and are dominated by Norway spruce (*Picea abies*), silver fir (*Abies alba*), beech (*Fagus sylvatica*), and Scots pine (*Pinus sylvestris*; Kändler & Cullmann, 2014). The area supports a remnant population of capercaillie that has experienced significant declines in abundance and range extent over the past decades and is currently threatened with extinction (Kämmerle et al., 2017; Coppes et al., 2019a). Capercaillie are large-bodied forest grouse that prefer semi-open, structurally diverse forests with moderate canopy cover and rich in gaps and stand edges (Klaus et al., 1989; Graf et al., 2009; Braunisch et al., 2014; Hofstetter et al., 2015). Previous studies on the capercaillie distribution in the study area have demonstrated relationships of species occurrence mainly with winter severity (i.e. measured as days with snow), population connectivity, soil type and landscape composition (Braunisch & Suchant, 2007; Kämmerle et al., 2017).

2.2. Sampling design

To model "local capercaillie persistence" over the study period (i.e. the probability of a site within the local capercaillie distribution to remain occupied between 2008 and 2018) as a function of environmental characteristics we relied on accurate field-based distribution maps of capercaillie in the study area. The distribution maps are the result of systematic inventories of capercaillie occurrence in the area. They are based on continuously collected direct and indirect signs and have been compiled using a consistent methodology at five year intervals using clearly defined criteria since 1988 (Braunisch & Suchant, 2006, see also Coppes et al., 2019a). We compared the distribution maps of 2008 (based on signs collected from 2004 to 2008) and of 2018 (2014 to 2018) to depict recent changes in the capercaillie distribution range in the Black Forest.

For this purpose, the extent of the capercaillie distribution in 2008 was represented by a raster map with grid cells of 10 ha size (Fig. 1 B, C). This cell size corresponds to an average forest stand and has repeatedly been identified as a suitable scale to model capercaillie occurrence (Braunisch & Suchant, 2007; Kämmerle et al., 2017). Cells were classified either as "range loss" (0, i.e. capercaillie presence in the inventory of 2008 but not in 2018) or "range persistence" (1, capercaillie presence in both inventories). This process is henceforth called "range development" and represents changes in the capercaillie distribution in the study area over the study period. We generated raster cells after applying an interior buffer of 100 m to the polygons of the distribution maps, and separately for the two classes (range loss or persistence; buffer to the inside of each polygon), to minimize the number of cells overlapping both states or located at the edge of the distribution (Fig. 1 C). Cells containing both classes were assigned according to the majority. In total we classified 3811 grid cells (1 = 2531; 0 = 1280), all located in forests.

2.3. Environmental covariates and suitable forest structure

We modelled capercaillie range development using a set of environmental covariates known to be related to both the occurrence and the decline of the species in the area (Braunisch & Suchant, 2007; Kämmerle et al., 2017; Table 1). Variables were prepared for each 10 ha cell, using data representing the conditions during the study period. We used the multi-annual (2010–2015) average weekly snow height (in cm) during the winter season (1st of November to April 30st), in the following referred to as "snow load". Snow data were available at a resolution of 1 km2 based on an interpolation using the SNOW4 model of Germany's National Meteorological Service (Deutscher Wetterdienst DWD, 2020), and served as a proxy for winter severity and harsh environmental conditions, which in turn favour the development of forest structures suitable for capercaillie (Braunisch & Suchant, 2007). We calculated an index of population connectivity as the density of area with capercaillie occurrence in 2008 within a moving window of 1 km radius (*cf* Kämmerle et al., 2017) to test whether small and isolated patches were more prone to population decline than well-connected patches. This is based on the assumption that exchange is less frequent with increasing distance (Braunisch et al., 2010). In addition, we

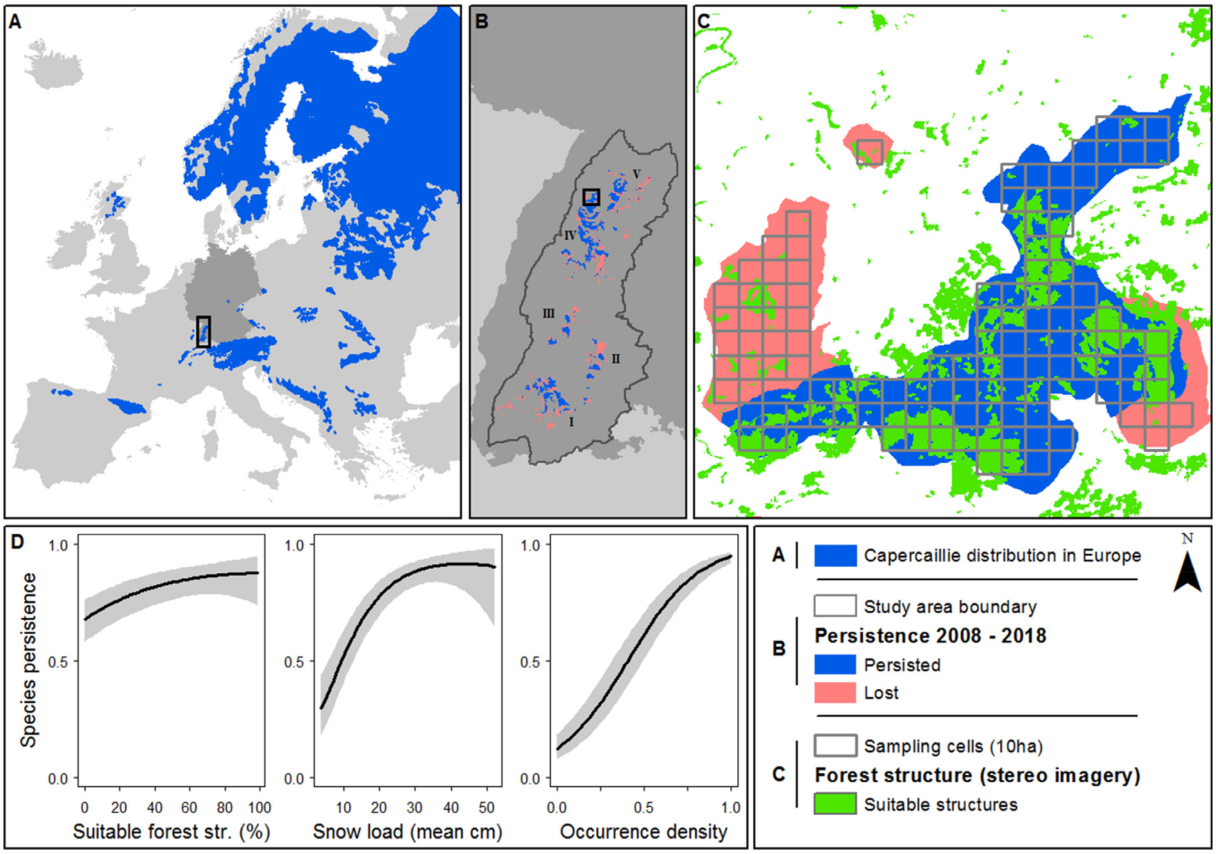

Fig. 1. Location of the study area in the Black Forest mountain range in Germany (A). Range development of the capercaillie population in the study area between 2008 and 2018 (B) was combined with high-resolution data on forest structure obtained from stereo aerial imagery in a grid-based sampling design (C), in order to model the probability of a site to be retained in the capercaillie distribution (i.e. local species persistence during the study period; D) as a function of suitable forest structure (gaps and open forest), climatic conditions (long-term mean of snow height) and population connectivity (i.e. the proportion of area with species occurrence in 2008 within a 1 km-radius).

obtained the edge-density of forest-open land cover edges within a moving window of 1 km radius, as a proxy for forest fragmentation (*cf* Braunisch and Suchant, 2007) and mesopredator abundance (*cf* Güthlin et al., 2013) in the study area. Finally, we calculated Euclidean distances to both summer (hiking and bike trails) and winter recreational infrastructure (hiking and ski trails, ski slopes), averaged within each 10 ha cell, as recreational use is known to negatively influence capercaillie habitat use (*cf* Thiel et al., 2008, Coppes et al., 2017).

We quantified the availability of certain forest structural components favoured by capercaillie (i.e. small gaps and open canopy; henceforth '*forest structure*') during the study period using a normalized digital surface model (nDSM) obtained by stereo aerial imagery between 2010 and 2012 (Zielewska-Büttner et al., 2016; Coppes et al., 2019b). A classification algorithm was employed to quantify canopy cover and identify gaps in the canopy that were subsequently evaluated with regard to their relevance for capercaillie (Zielewska-Büttner et al., 2016; Coppes et al., 2019b). Two types of suitable structural components were classified: "gaps" (i.e. vegetation height $<$ 2 m) with $<$ 20% canopy cover and a diameter $>$ 10 m; as well as "open forest", defined as forest patches of at least 1 ha in size and a minimum diameter of at least 50 m, with a canopy cover between 20 and 70%. We calculated the percent area covered by suitable structure per 10 ha-cell to be used as predictor in the analysis. In addition, we repeated this approach for stereo aerial imagery obtained between 2016 and 2018 to quantify persistence probability of the remaining areas of capercaillie occurrence (i.e. as of 2018) given the current habitat conditions.

2.4. Modelling capercaillie persistence during the study period

All analyses were performed in software R (v. 3.6.1; R Core Team,

Table 1
List of predictors considered in the analysis of capercaillie range persistence between 2008 and 2018 in the Black Forest Germany. The predictor names are used throughout the text. Variables were calculated for 10 ha cells. We provide data source, original resolution and whether the predictor was retained in the final model.

Predictor	Description	Unit	Source	Original resolution	Decision
Snow load	Multi-annual weekly mean of snow height during winter in 1 km^2	cm	DWD; timeframe 2010–2015	1 km	retain
Population connectivity	Proportion of area with species occurrence within a moving window (1 km radius)	0 – 1 (%)	FVA-BW	30 m	retain
Forest structure	Amount of forest structure suitable for capercaillie in 10 ha cell	ha/10 ha	FVA-BW	10 m	retain
Edge density	Density of forest-open land edges within a moving window (1 km radius)	km/km^2	ATKIS / FVA-BW	50 m	omit
Recreation summer	Average distance to summer recreation trails/sites	m	ATKIS / FVA-BW	50 m	omit
Recreation winter	Average distance to winter recreation trails/sites	m	ATKIS / FVA-BW	50 m	omit
Subunit	Geographical subunit of the local population	Integer	FVA-BW	–	retain

2019). The probability of local persistence of capercaillie during the study period was modelled using generalized linear mixed models (GLMM) with a binary response (1 = range persistence; 0 = range loss). Clearly distinguishable geographical subunits of the capercaillie population in the study area (N = 5; roman numerals in Fig. 1 B) were included as a random intercept to account for differences among subunits not accounted for by our covariates and to fit meaningful models for spatial autocorrelation within geographical subunits rather than across the whole study area. All covariates were standardized by subtracting the mean and dividing by the standard deviation to aid model convergence. The initial model included linear terms of all environmental variables and quadratic terms for forest structure and snow cover to identify thresholds at a given level of the predictor (e.g. because the availability of gaps as well as snow load may only increase persistence probability up to a certain amount, above which there is no added, or even a reverse, effect). In addition, we assessed whether there was support for an interaction of forest structure with both snow cover and connectivity. Initial models were fitted using the lme4 package (Bates et al., 2015) and residuals were assessed for spatial autocorrelation using semivariograms using cell width as lag size. There was evidence for residual autocorrelation to be present up to approximately 2 km distance. We thus applied the approach of Kämmerle et al. (2017) and re-fitted the global model with the addition of a spatial correlation term using a wrapper function (i.e. glmmPQL from MASS; Venables & Ripley, 2002) for the nlme package (Pinheiro et al., 2019). We fitted models with Gaussian, exponential (Pinheiro et al., 2019) and Matérn autocorrelation structure (Rousset & Ferdy, 2014), and visually assessed their performance by plotting residual semivariograms. We chose an exponential structure as it most effectively accounted for autocorrelation in the residuals and modelled autocorrelation by distance, grouped within the geographical subunits of the population (Fig. 1 B). We compared the fits obtained using glmmPQL with mesh-based spatial models based on a Matérn structure fitted with the package INLA (Lindgren & Rue, 2015), but chose to maintain the former approach for handling and computational efficiency, because coefficient estimates were nearly identical in both packages for models without spatial terms and the estimated effect patterns were similar after including spatial terms (but not identical as spatial terms differed between the models owing to the specific implementation frameworks). Due to a lack of information criterion in quasi-likelihood models, we employed backwards model selection to obtain the most parsimonious model. We visually assessed effect plots and retained the quadratic terms to depict ecologically meaningful effects (i.e. no unlimited linear increase in persistence probability). Finally, we calculated the marginal and conditional coefficient of determination for the final model (i.e. Pseudo-R^2; Nakagawa et al., 2017).

2.5. Effect of habitat management

We employed two approaches to evaluate the potential of habitat management, i.e. increasing the area covered by gaps and open forest, to increase the probability of capercaillie to persist at a site. Firstly, we used the final model to predict the probability of capercaillie persistence in dependence of the availability of forest structure under a range of environmental scenarios to assess variation in its relative effect strength. We constructed nine scenarios that varied “snow load” and “population connectivity” in a 3x3 design, with each variable represented in an unfavourable situation (set at the 5% percentile), a moderate situation (40% percentile) and a very favourable situation (75% percentile). We then produced conditional effect plots for the availability of suitable forest structure in each scenario to quantify the potential effectiveness of habitat management.

Secondly, we used the final model to predict the probability of capercaillie persistence across the range extent of 2018, but updated the availability of suitable forest structure with recent data (i.e. 2016–2018; see *Environmental covariates and suitable forest structures*) to estimate the variation in the degree of threat across the current, remaining population. We then built two alternative scenarios, in which 1) the area covered by suitable forest structure (gaps and open forests) was set to the optimum (i.e. 80%, Fig. 1 D) or 2) to 30%, which is the currently existing management target specified in the Action Plan for the species (Braunisch & Suchant, 2013). For both scenarios, we then predicted persistence probability across the extent of the capercaillie distribution of 2018, calculated the difference in probability per sampling cell as compared to the current situation and summarized and visualized this difference in relation to the predicted current probability of persistence, subdivided in 10 classes (i.e. binned in steps = 0.1). Finally, to obtain balanced sample sizes across all levels of local persistence probability as a benchmark for the predictions on the real situation (i.e. because the majority of cells within the range extend of 2018 had probability values ≥ 0.5), we repeated the same procedure using a simulated dataset that uniformly covered the gradient of environmental conditions prevailing across the capercaillie range extent of 2018. For this purpose, we divided the value-range of the predictors “snow-load” and “population connectivity” into 100 equal intervals each and assigned all possible combinations, resulting in a dataset of 100 x100 possible values, while the availability of suitable forest structure was uniformly set to the current mean (as of 2018). Initial local persistence probability was then predicted using the final model, set in relation to predictions obtained in both scenarios (i.e. 30% and 80% availability of suitable forest structure), and summarized as above.

3. Results

3.1. Probability of capercaillie persistence during the study period

The probability of capercaillie to persist at a site during the study period was positively related to the degree of population connectivity and the mean snow load at a site, up to an average weekly snow height of ≥ 30 cm (Fig. 1 D). In addition, there was a positive effect of forest structure with increasing availability favouring capercaillie persistence, but its effect size was considerably smaller than those of snow cover (> 3 times) and connectivity (≈1.5 times; Table 2). We found no relationship between the probability of local persistence and the degree of forest fragmentation or distance to recreational infrastructure (summer and winter). The fixed effect part of the final model explained approximately 50% of the variability in the data; the whole model explained only marginally more (i.e. conditional $R^2 = 0.53$), indicating a high level of similarity in the drivers of range loss between the geographical subunits.

3.2. Effect of habitat management

The predictions for the nine environmental scenarios indicated that the relative effect size of increasing suitable forest structure varied, depending on the connectivity and snow load at a site (Δ in Fig. 2). The relative effect size of suitable forest structures was highest in intermediate scenarios, in which either snow cover, connectivity or both were not optimal, while there was hardly any additive effect of forest

Table 2
Results of the final generalized linear mixed model explaining capercaillie range persistence between 2008 and 2018 in the Black Forest, Germany. Coefficient estimates are provided with their standard errors and p-values.

Predictor	Estimate	SE	p-value
Intercept	1.075	0.215	< 0.001
Forest structures	0.429	0.079	< 0.001
Forest structures^2	−0.053	0.042	0.214
Connectivity	1.424	0.055	< 0.001
Snow cover	0.658	0.071	< 0.001
Snow cover^2	−0.083	0.031	0.008

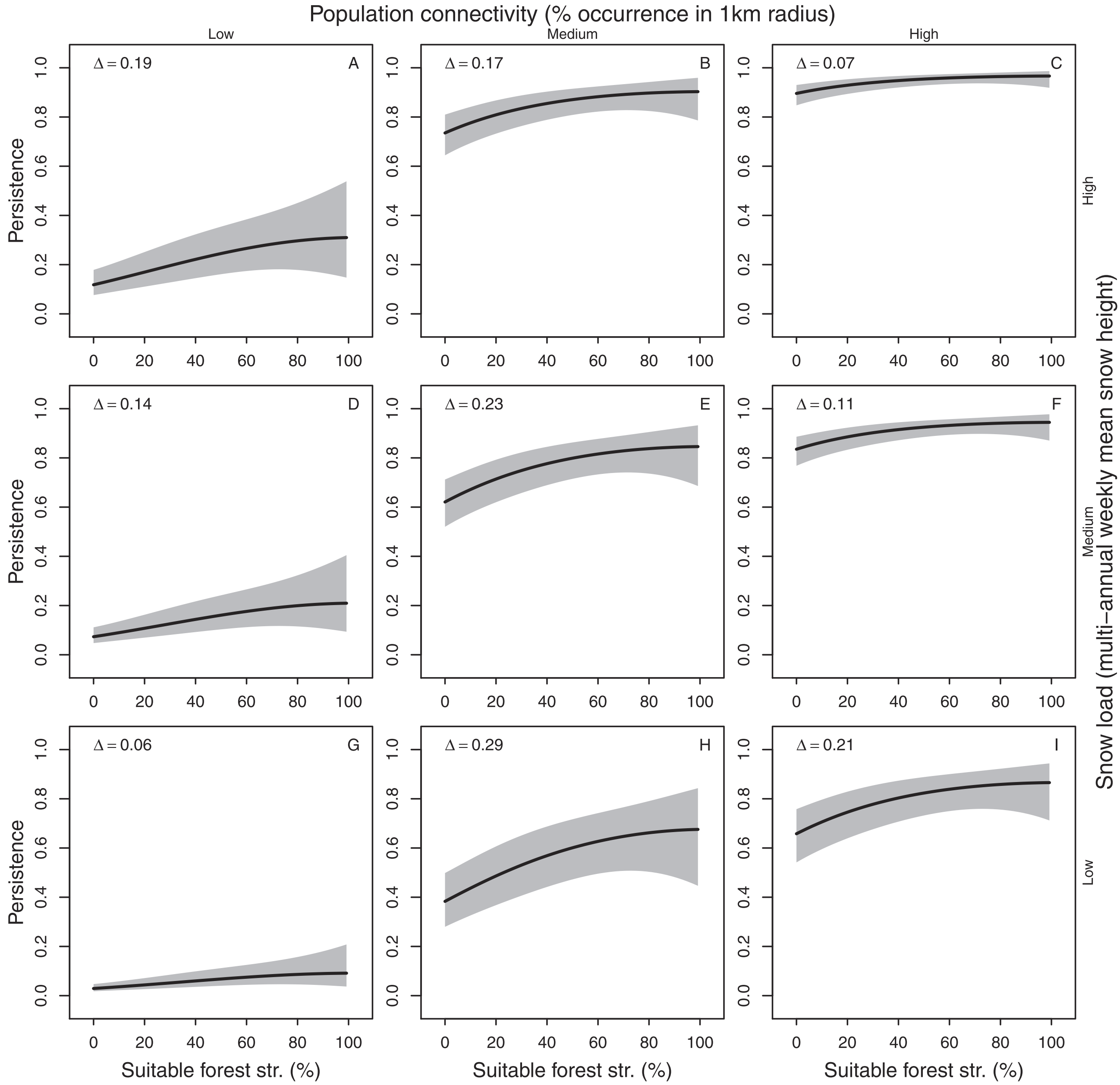

Fig. 2. Relative effect size of increasing the amount of suitable forest structure in a 10 ha sampling cell on the probability of local capercaillie persistence (also indicated as difference (Δ) in probability) under different scenarios of low, medium or high amount of long-term mean snow load and population connectivity (*see method section*). Habitat management has the largest potential benefit under less-than-optimal conditions in at least one covariate (e.g. E, H).

structure when snow cover and connectivity were either optimal or near-optimal (e.g. Scenario C) or completely unsuitable (e.g. Scenario G). The maximum effect was achieved when snow cover was low and connectivity intermediate (Scenario H), corresponding to an increase in the mean probability to persist from 0.38 to 0.68 (i.e. Δ ≈ 0.3 in probability or an increase of 176%; Fig. 2).

Under current conditions, sampling cells occupied by capercaillie in 2018 had a mean of 8% suitable forest structure and 75% of the cells had ≤ 10% suitable structure, falling short of the current management target of ≥ 30%, which was only achieved in 8.7% of the cells. Under the currently prevailing environmental and forest structural conditions, the persistence probability across the whole capercaillie distribution increased on average by 0.10 (median = 0.08; sd = 0.08) when applying the maximum intensity management scenario (i.e. suitable structure on 80% of the plots) and by a mean of 0.053 (median = 0.042; sd = 0.048) when using the existing management targets scenario as comparison (i.e. 30% suitable structure). However, the predicted increase in local persistence probability under actual conditions per grid cell ranged from 0.01 to 0.28 (Figs. 3 and 4).

For the simulated data, in which the complete environmental gradient was uniformly represented and the availability of forest structure was set to the current mean, the mean increase in persistence probability was 0.13 (median = 0.13, sd = 0.08) for the maximum management scenario and 0.06 (median = 0.06, sd = 0.03) for the current management target scenario, respectively (Fig. 3). Under both scenarios, habitat management had the largest relative impact in areas of low to intermediate persistence probability (i.e. in areas with uncertain persistence; Fig. 3). Accordingly, the relative effect size of the benefits obtained by increasing the amount of suitable forest structure was not evenly distributed across the area of interest, but dependent on site-characteristics (Fig. 4).

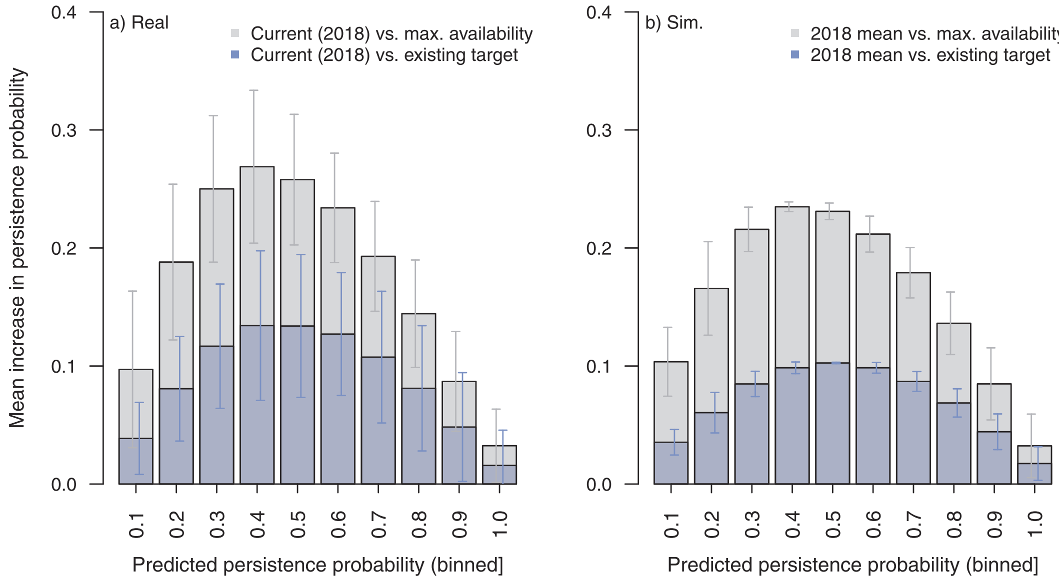

Fig. 3. Predicted mean increase in the probability of local capercaillie persistence in dependence of the initial probability when increasing the availability of suitable forest structures to the optimum values (i.e. 80% per plot; grey) or according to the existing management targets (i.e. 30%; blue) compared to two baselines: a) the current availability of suitable forest structure (i.e. as of 2018) across the real distribution of capercaillie in the area and b) the current (2018) mean availability of suitable forest structure and a simulated dataset uniformly depicting the environmental gradient present across the range of capercaillie occurrence in 2018. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

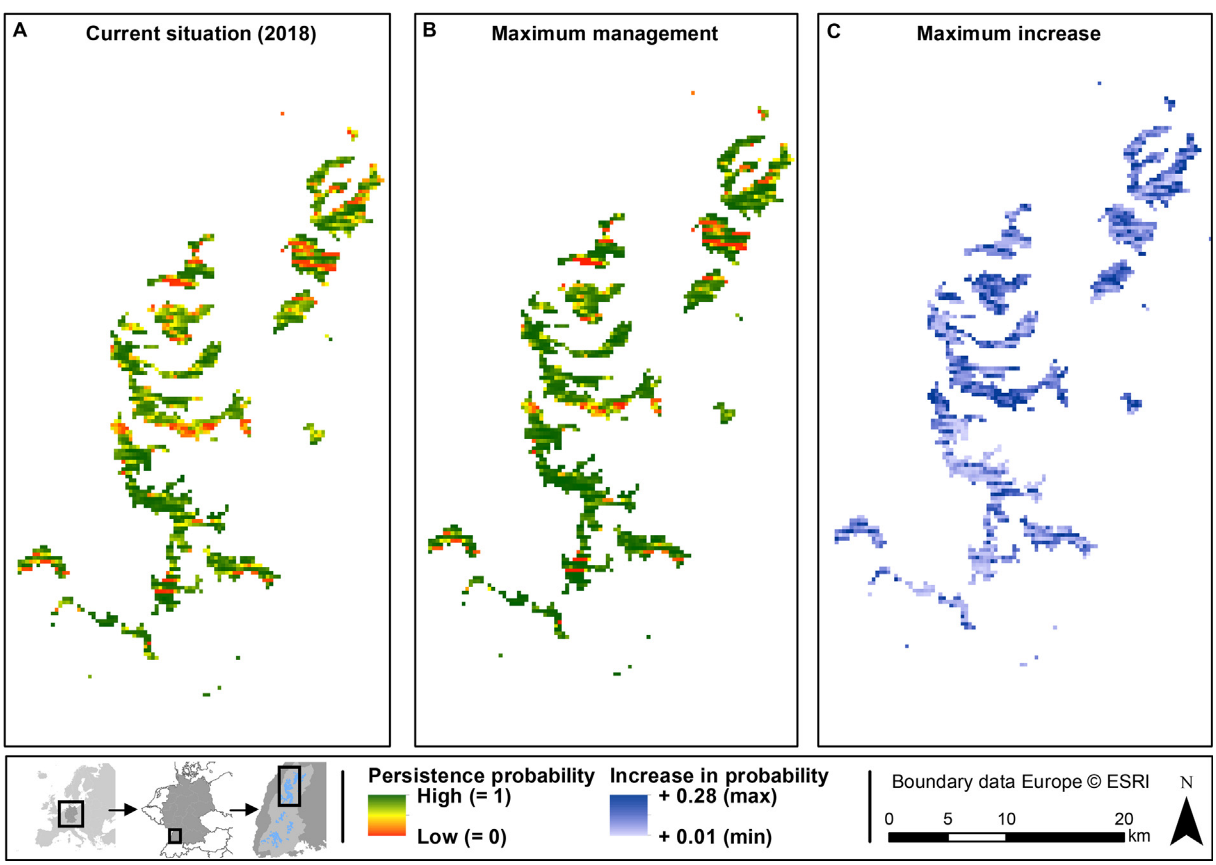

Fig. 4. Predicted probability of local capercaillie persistence (i.e. a raster cell to be retained in the distribution) in an exemplary part of the species distribution in the study area, depending on A) the current availability of suitable forest structure (as of 2018) and B) a maximum intensity management scenario with optimal availability of suitable forest structure throughout, as well as C) the achieved increase in persistence probability when comparing A to B.

4. Discussion

The management of structural attributes within habitat types to benefit threatened species is omnipresent in applied conservation and, for forest species, has to be integrated with commercial forest management (Ausden, 2007; Gustafsson et al., 2020). Clearly, the objectives in conservation and commercial forestry may differ and it is thus crucial to quantify the potential effectiveness of habitat management. In this study, we combined accurate and spatially explicit records of capercaillie range development and high-resolution data on forest structure at the landscape scale and at multiple points in time to evaluate the potential effect of habitat management for promoting local population persistence. We demonstrate that increasing habitat suitability can be associated with considerable improvements in persistence probability, especially at sites where it would otherwise be low to intermediate (i.e. between 0.3 and 0.6; Fig. 3). At these sites, effect sizes were sufficient to enhance, if not ensure, the local persistence of our model species by an increase in probability of up to 0.25. However, values were lower if less ambitious management goals were set (Fig. 3). Notwithstanding, as exemplified in Fig. 4, benefits of habitat management also improved persistence probability in initially less threatened sites.

The suitability of capercaillie habitats is largely determined by the availability of extensive open forest structure and habitat suitability is closely related to population density (Suchant & Braunisch, 2004). The high availability of suitable structure assumed under our maximum intensity management scenario (on 80% of the sampling cell area) does not however imply that the majority of forest stands within the species local range would need to be cut or subjected to other intensive management actions to sustain the capercaillie population. The forest structures used in our analysis included a combination of the availability of small canopy gaps (width ≥ 10 m) and stands with low to medium canopy cover, ideally in a relation of approximately 1:2 (Suchant & Braunisch, 2004). Increasing sunlight availability on the ground by canopy thinning favours bilberry growth and fruit development (Grämiger et al., 2015; Montané et al., 2016; Eckerter et al., 2019), which in turn favour capercaillie (Storch, 1993; Hancock et al., 2011). While a very large number of gaps may be locally beneficial for the target species, this it likely not realistic when forestry is focused solely on timber production and not multiple resource values (Braunisch et al., 2014). Our scenario involving existing management targets (i.e. 30%, which corresponds to the species' minimum requirements, Suchant & Braunisch, 2004) exemplified that substantial benefits at threatened sites can already be achieved when management goals are less ambitious (e.g. an increase in probability by 0.13 ± 0.055 for sites in our study area with an initial probability of between 0.4 and 0.6; see Fig. 3). Accordingly, habitat management in favour of capercaillie - as intended here - implies the integration of small gaps and canopy thinning into current production forestry practices, to various degrees, across the whole range of a population. In our case, stands ≥ 1 ha were classified as open if they had between 20 and 70% canopy cover. Such values can be achieved by increasing harvesting intensity in close-to-nature and continuous-cover forestry, which otherwise are associated with denser canopy cover. However, in spite of existing targets for capercaillie habitat management in production forests in the study area (which are largely state-owned forests), the currently very low availability of suitable structure across the range of the population (i.e. the target of at least 30% was achieved in 8.7% of sampling cells only) illustrates the magnitude of the practical challenges involved.

Moreover, our results imply that the conservation returns of habitat management may differ between sites as a function of the site's current probability of local persistence. This is relevant given the limited resources and competing interests in forest management. While investments in sites with very high or very low chances of local persistence produced little additional conservation benefit, the benefit was largest in areas of intermediate persistence probability (Fig. 3), and under suboptimal, but not entirely unfavourable conditions (i.e. intermediate snow load and population connectivity). The scenario predictions (Fig. 2) indicate that negative effects of decreasing snow load on local capercaillie persistence probability may be compensated more effectively by habitat improvement (i.e. due to its overall smaller effect size) than a lack of population connectivity. Given globally increasing temperatures, snow load in the Northern hemisphere has decreased and is expected to further diminish (Pachauri et al., 2014), also in our study area (Schneider & Schönbein, 2003), and this development is beyond the scope of local management. Our results thus agree with the results of Braunisch et al. (2014), who also reported that increasing habitat suitability can partly compensate the negative effects of climate change. In contrast to climatic conditions, population connectivity can maintained by habitat management. For instance, this could be achieved by improving habitat suitability in connecting elements such as the edges of the distribution and stepping-stone habitats (Braunisch et al., 2014). We found the largest effect sizes in scenarios where connectivity was retained and snow cover moderate or low, indicating a large potential for habitat management to benefit conservation (e.g. scenarios E,H,I; Fig. 2). In our study area, such sites were often found at the edges of the local distribution (see maximum values in Fig. 4 C) and thus in areas of high value for population connectivity. Accordingly, managers may choose to spatially focus management there to maximize conservation returns. It is crucial, however, to emphasize that the small effect sizes of increasing habitat characteristics achieved at sites with high persistence probability certainly do not imply that suitable habitat is less important there. On the contrary, management should strive to preserve high habitat suitability, especially at these sites, in order to ensure local population persistence, especially in the face of future uncertainty with regards to climate change (Braunisch et al., 2013).

In contrast to a previous study (Kämmerle et al., 2017) we could not detect a relationship of local persistence probability with forest-open land edge density (as a proxy for forest fragmentation and mesopredator abundance). This is likely for two reasons: for one, there was insufficient variation in this variable across the area of interest in this study to show a significant association with range development. We suggest that this is related to the decline of capercaillie in the Black Forest, which underwent two subsequent, but distinct phases (i.e. 1993–2003 and 2008–2018; Coppes et al., 2019a). The previous study also referred the earlier phase of heavy decline (i.e. 1993–2003) in which the most unfavourable sites with highest degrees of forest fragmentation and mesopredator abundance were lost, but availability of high-resolution aerial imagery restricted us to a more recent time period in the current analysis. The pattern we find now may suggest that - partly as a result of past developments - population connectivity, habitat suitability and climate conditions are now the central drivers of population persistence. Accordingly, preserving connectivity through improving habitat suitability (i.e. creating canopy gaps and open forests) at a landscape scale and protecting suitable corridor areas for inter-patch dispersal (Braunisch et al., 2010) appears crucial to halt the current decline and prevent the population from extinction.

Using capercaillie as a model species, our study illustrates the importance of quantifying the potential benefits of conservation interventions in forests, especially in relation to other drivers of population decline. By predicting the magnitude of conservation returns in a spatially explicit way our results may contribute to an allocation of conservation investments where their potential leverage is highest.

CRediT authorship contribution statement

Jim-Lino Kämmerle: Conceptualization, Data curation, Formal analysis, Writing - original draft, Writing - review & editing. **Veronika Braunisch:** Supervision, Writing - review & editing. **Rudi Suchant:** Project administration, Writing - review & editing. **Joy Coppes:** Conceptualization, Data curation, Supervision, Writing - review & editing.

Declaration of Competing Interest

The authors declared that there is no conflict of interest.

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