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# Range loss of a threatened grouse species is related to the relative abundance of a mesopredator

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**Citation:** Kämmerle, J.-L., J. Coppes, S. Ciuti, R. Suchant, and I. Storch. 2017. Range loss of a threatened grouse species is related to the relative abundance of a mesopredator. Ecosphere 8(9):e01934. 10.1002/ecs2.1934

**Abstract.** Mammalian generalist mesopredators can reach high densities in forest–farmland mosaic landscapes in the absence of top-down control. The abundance of generalist mesopredators is a potentially limiting factor for prey populations, especially ground breeding birds such as grouse. High mesopredator abundance has been associated with reduced reproductive success in grouse. There is little evidence, however, on how variation in mesopredator abundance affects grouse population trends while considering other environmental covariates. We make use of range maps spanning two decades (1993–2013) of a locally threatened capercaillie (*Tetrao urogallus*) population in the Black Forest, Germany, to assess whether range loss of grouse in forest–farmland mosaic landscapes can be explained by a gradient in red fox abundance, while accounting for other potential determinants of grouse range loss. We show that capercaillie range persistence was favored by increasing snow cover, decreasing index of red fox abundance, slightly increasing index for soil quality, and increasing population connectivity. Red fox abundance had the largest relative impact in areas already facing an elevated capercaillie extinction risk due to unsuitable site conditions, dense forests, or lack of connectivity, but the negative effect was compensated under otherwise optimal conditions. This indicates that the relative importance of predator abundance for prey population dynamics is mediated by environmental attributes, emphasizing the threat to remnant populations but also indicating potential for species conservation.

**Key words:** capercaillie; fox; generalized mixed-effect model; predation; predator–prey; prey population development; species distribution model.

**Received** 9 May 2017; revised 25 July 2017; accepted 2 August 2017. Corresponding Editor: Eric M. Gese.

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## INTRODUCTION

Mammalian mesopredators commonly gain ecological importance when larger predators are lacking in human dominated landscapes (Crooks and Soulé 1999, Prugh et al. 2009, Ritchie and Johnson 2009, Ripple et al. 2013), and their abundance may limit populations of prey (Crooks and Soulé 1999, Elmhagen et al. 2010, Salo et al. 2010, Smith et al. 2010). Such effects are often found in birds (Brashares et al. 2010), because predation by mesopredators can have a significant impact when a large extent of eggs and/or fledglings are lost to predation (Newton 1993, Côté and Sutherland 1997). Nonetheless, these effects are sometimes compensatory and some avian populations may counteract the negative effects of predation (Côté and Sutherland 1997, Newton 1998, Cresswell 2011). Predation may, however, severely impact bird populations that are already limited by other factors (Newton 1998, Sovada et al. 2001) such as habitat fragmentation (Robinson et al. 1995, Crooks and Soulé 1999) or habitat quality (Schroeder and Baydack 2001, Evans 2004). At the same time, forest landscapes fragmented by productive land cover types (e.g., farmland) are capable of supporting higher mesopredator abundances (Kurki et al. 1998, Güthlin et al. 2013, Pasanen-Mortensen and Elmhagen 2015). Both increased nest predation and reduced reproductive success in birds have been connected to fragmented forest landscapes (for nest predation, see Andrén and Angelstam 1988, Small and Hunter 1988, Storch et al. 2005, for reproductive success, see Kurki and Lindén 1995, Robinson et al. 1995, Kurki et al. 2000). There is, however, little evidence on how variation in predator abundance affects the persistence of bird populations at the landscape scale, while considering how this relationship is influenced by other factors.

Grouse, in particular black grouse (*Lyrurus tetrix*) and capercaillie (*Tetrao urogallus*), are species of major conservation concern in Europe (Storch 2007, Jahren et al. 2016, and references therein). Populations are currently characterized by low reproductive success (Jahren et al. 2016) and range contractions (Storch 2007). It is well known that reproductive success in grouse is reduced at high predator abundance (Marcström et al. 1988, Kurki et al. 1997, Kauhala et al. 2000, Baines et al. 2004) and that high predator abundance may limit grouse abundance (Marcström et al. 1988, Lindström et al. 1994, Smedshaug et al. 1999, Fletcher et al. 2010). Predators of grouse and their eggs in Europe include red foxes (*Vulpes vulpes*) and mustelids (Marcström et al. 1988, Lindström et al. 1994, Kauhala et al. 2000), raptors (Thirgood et al. 2000*a*), and corvids (Summers et al. 2004).

Red foxes, in particular, occupy a dominant trophic position in forest–farmland mosaic landscapes (i.e., human-modified lands comprising a mosaic of land cover types) of Central and Western Europe and occur at relatively high densities due to landscape configuration, high environmental productivity, the absence of top-down control, and the eradication of rabies from many countries (Chautan et al. 2000, Pasanen-Mortensen et al. 2013, Pasanen-Mortensen and Elmhagen 2015).

In this paper, we hypothesized that changes in range extent (i.e., persistence or contraction) of central European grouse populations may reflect landscape-scale variation in the abundance of a generalist mesopredator, the red fox. However, because grouse populations are also sensitive to habitat fragmentation, deterioration, and loss (Thirgood et al. 2000*b*, Sirkiä et al. 2010, Mikoláš et al. 2015), climatic changes (Selås et al. 2011, Braunisch et al. 2013, Moss 2015), and anthropogenic disturbance (Storch 2013, Coppes et al. 2017), the potential impact of mesopredator abundance should be assessed along with other environmental determinants of range loss. Because grouse may compensate for high predation pressure in otherwise optimal habitat conditions (Baines 1991, Schroeder and Baydack 2001, Storch 2007), we expected the relative impact of red fox abundance on grouse persistence to be mediated by environmental attributes.

A comprehensive analysis of the dynamics of predator–prey relationships at the landscape scale is often hindered by a lack of accurate data on prey population trends, predator abundance, and environmental attributes over large spatial scales. In this paper, we used unique field-based range maps of an isolated threatened population of capercaillie in the Black Forest mountain range in southwestern Germany to identify drivers of changes in capercaillie range extent. The population has experienced a range contraction of approximately 25% over the past two decades, with predation, especially by red foxes, being suggested to contribute to this decline (Coppes et al. 2016). The red fox is believed to play the dominant role as a predator of capercaillie, in particular of eggs and chicks, in the area (Suchant and Braunisch 2008). We quantified variation in mesopredator abundance across the study area using a landscape-scale model of red fox abundance (Güthlin et al. 2013, 2014) and combined it with fine-scale information on forest structure, environmental conditions, population connectivity, and other landscape attributes to assess whether range contraction of capercaillie was related to mesopredator abundance.

## METHODS

In this study, we created a dataset describing changes in species range extent (binary response variable: 1 = range persistence, 0 = range loss) of an isolated central European capercaillie population obtained from field-based distribution maps. We modeled the variation of the response variable using mixed-effect models to explain range contraction as a function of environmental attributes under the key hypothesis that mesopredator abundance may negatively affect population development.

### *Study area and species*

The study area encompasses the distributional range of capercaillie in the Black Forest, a low altitude mountain range (120–1493 m a.s.l.) in southwestern Germany (Fig. 1). The Black Forest ecoregion covers ~7000 km$^2$ of which about two-thirds are forested (ForstBW 2015). The dominant tree species in the study area are Norway spruce (*Picea abies*), silver fir (*Abies alba*), beech (*Fagus sylvatica*), and Scots pine (*Pinus sylvestris*).

Capercaillie are large, ground-nesting forest grouse (see BirdLife International 2017 for a detailed species account). In the Black Forest, as elsewhere, capercaillie prefer extensive areas of old forests with moderate canopy cover (Braunisch and Suchant 2008, Graf et al. 2009) rich in

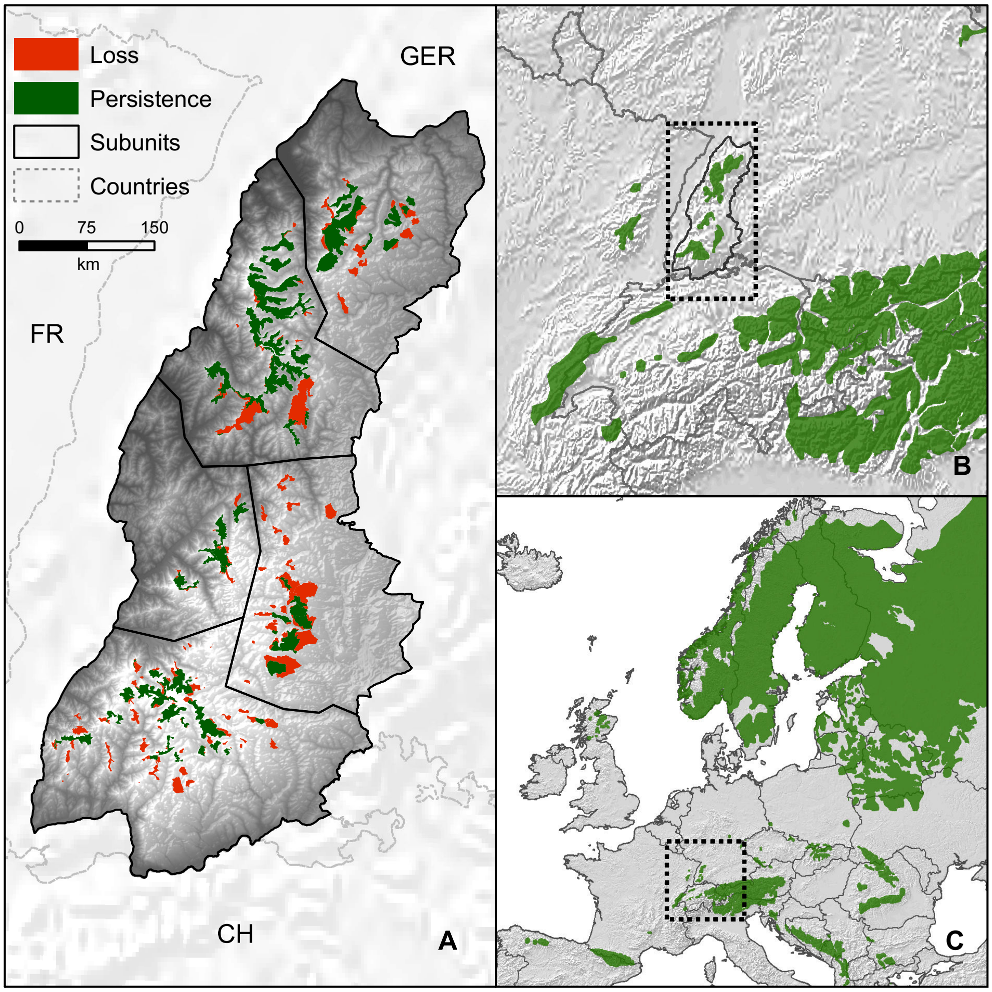

Fig. 1. Overview of the Black Forest study area (A), which is located in southwestern Germany (GER) along the French (FR) and Swiss (CH) borders. The map depicts changes in the range extent of capercaillie in the Black Forest subunits between 1993 and 2013. Range development was obtained through well-established survey methods including field-based range maps combining direct and indirect signs of presence (State Forest Research Institute, official data). Maps B and C show the position of the Black Forest in central Europe with respect to the range of distribution of capercaillie (indicated in green, sensu Coppes et al. 2015, modified).

gaps (Braunisch et al. 2014, Hofstetter et al. 2015) and structurally rich ground vegetation, ideally dominated by bilberry (Storch 1993*a*, 2002, Graf et al. 2009). Due to its large distribution range, the capercaillie is not globally threatened by extinction (Birdlife International 2017), although numbers and distribution are decreasing. At European national and regional levels, however, the capercaillie is red-listed as threatened (Storch 2007, Bauer et al. 2016). The capercaillie population in the Black Forest is isolated (Fig. 1) and estimated to consist of approximately 600 animals (Suchant and Braunisch 2008), based on spring counts of 200–300 displaying males distributed over an area of approximately 457 km$^2$ (Coppes et al. 2016). The distribution range of capercaillie in the study area gradually contracted between 1993 and 2013, although there were strong regional differences in population persistence (Coppes et al. 2016).

### *Species data*

We used range maps of capercaillie in the Black Forest to obtain a binary response variable reflecting range persistence (1) and loss (0) over the past two decades. Range maps resulted from field-based systematic inventories of capercaillie occurrence in the area by the State Forest Research Institute (FVA-BW). The spatial extent of capercaillie occurrence has been monitored using a constant methodology based on direct and indirect signs collected by research personnel and qualified amateurs (e.g., foresters, ornithologists) since 1988. Areas with confirmed capercaillie occurrence are based on a fixed set of quality criteria and delineated along linear landscape features resulting in a detailed digital representation of the capercaillie range in the Black Forest (Braunisch and Suchant 2006, see also Braunisch and Suchant 2007, Coppes et al. 2016). We used the range inventories of 1993 (i.e., first complete digital range map) and 2013 (most recent range map) as a reference for the assessment of range loss and persistence over the study period (Fig. 1).

We sampled locations of range persistence and range loss within the continuous spatial extent depicted by the range inventory (Fig. 1) using a systematic grid of sampling points (Appendix S1: Fig. S1). We preferred a systematic grid over the random sampling previously used by Braunisch and Suchant (2007) to better capture local changes in capercaillie occurrence. To reduce spatial autocorrelation (SAC) while at the same time retaining a high coverage of patches with capercaillie occurrence (i.e., avoid reduced sample size and loss of important data variability), a sensitivity analysis was performed resulting in 660 m as the best distance between sample points. Greater distances would have reduced SAC but also the sample size, whereas smaller distances had no particular gain in terms of patch coverage. At each point, the species was classified to have persisted if areas were occupied in the range maps of both 1993 and 2013, while those points falling into parts of the range in which the species had ceased to occur by 2013 were classified as having been lost. Thus, 1401 sample points were generated of which 886 points (63.25%) were classified as having persisted and 515 points (36.75%) as having been lost from the distribution since 1993 (Appendix S1: Fig. S1).

### *Model predictors*

Our set of predictors included an index of red fox abundance derived from a model, landscape variables, data on forest structure and composition, site variables, and spatial characteristics of the capercaillie population. The model predicting red fox abundance and all the other predictors are described below in individual subsections (see Table 1 for a full overview). We extracted data from circular buffers around sample points, choosing two buffer sizes based on literature. We used values that have previously been used to model capercaillie occurrence (Braunisch and Suchant 2007, Braunisch et al. 2008, Graf et al. 2009). At the "large extent," we considered sample plots with an area of 10 ha (i.e., 180 m radius around sample points). This equals the size of an average forest stand, which provided the best results in Environmental Niche Factor Analysis for capercaillie in the region (Braunisch and Suchant 2007, Braunisch et al. 2008). In addition, following Graf et al. (2009), we sampled environmental variables within 1.6-ha plots around each sample point (i.e., radius of 71.4 m) to serve as a comparison ("small extent"). Distances between the outer edges of 10-ha (large extent) and 1.6-ha (small extent) buffers were 300 m and 517.2 m, respectively.

Table 1. List of predictors considered in the analysis of changes in capercaillie range extent between 1993 and 2013 in the Black Forest, Germany.

| Category | Description | Abbrev. | Unit | Source (Resol.) | Resolution (m) | Decision |
|---|---|---|---|---|---|---|
| Predator | Predicted fox abundance (standardized) | FoxST | Index (0–1) | cf. Güthlin et al. (2013, 2014) | 30 | Retained |
| Landscape | Density of recreation trails | STourDens | km/km$^2$ | ATKIS | 50 | Retained |
| | Density of Forest–open land edges | ForEdge | km/km$^2$ | ATKiS | 50 | Corr. with FoxST |
| | Distance to paved roads | RoadDist | m | ATKIS | 50 | Retained |
| | Distance to farmland | AgriDist | m | ATKIS | 50 | Corr. with FoxST |
| | Variation in slope as SD of cells in sample buffer | SlopeSD | % | DEM | 50 | Retained |
| Forest | Proportion canopy closure | CanopyPer | % | LiDARnDSM† | 1 | Retained |
| | Proportion coniferous forest | ConifRat | % | HRL forest type‡ | 20 | Retained |
| Capercaillie | Density of patches with capercaillie occurrence | CaperDens | Index (0–1) | FVA-BW | 50 | Retained |
| | Size of occupied patch in 1993 before loss | Size1993 | ha | FVA-BW | – | Corr. with CaperDens |
| | Minimum distance to closest occupied patch | DistNear | m | FVA-BW | – | Retained |
| Site | Soil Condition Index | Soil | Index (1–15) | Braunisch and Suchant (2008) | 30 | Retained |
| | Days with snow cover | Snowday | Days | Braunisch and Suchant (2007)§ | 30 | Retained |
| | Type of forest property regime (state vs. other) | ForestMGT | Factor | FVA-BW | 50 | Retained |

*Notes:* The abbreviations given are used throughout the text. Variables dropped due to a pairwise correlation of ≥ |0.5| are marked as "Corr" in the "Decision" column. See the *Methods* section for full details on the temporal resolution of predictors.

† nDSM: a normalized digital surface model was obtained from a digital terrain model and digital surface model interpolated from small footprint pulse ranging LiDAR data recorded between 2002 and 2006.

‡ HRL Forest Layer: forest type layer of the Pan-European High Resolution Layers, copyright EEA (2015).

§ Derived from predictions of Schneider and Schönbein (2003) based on long-term means.

*Predicted relative abundance of red fox.—*Recent research has identified landscape parameters correlated with the relative abundance of red fox in the study area (Güthlin et al. 2013, 2014). We specifically used the results of Güthlin et al. (2014) to predict the relative abundance of red foxes (hereinafter referred to as predicted fox abundance) across the whole study area, which is closely related to the absolute abundance of red foxes (Güthlin et al. 2014). We obtained predictions with a spatial resolution of 30 × 30 m using the original landscape variables described by Güthlin et al. (2013, 2014) and following the protocol described by Güthlin et al. (2014) for data preparation (i.e., for each cell, the mean covariate value within a circle of 1 km radius). The model is spatially but not temporally explicit, meaning that it predicts variation in relative fox abundance across space for the whole study period.

*Landscape variables.—*For mobile species such as the capercaillie, spatial aggregation of predictors using focal neighborhood statistics represents a potential solution to increase their predictive power (Guisan and Thuiller 2005, Graf et al. 2009). To adjust the resolution of landscape variables to the spatial requirements of the species, we calculated the predictor densities as length of feature per spatial unit using a circular moving window of 1 km in diameter to approximate a seasonal home range of capercaillie (≥1 km$^2$, Storch 1993*b*, 1995, Braunisch and Suchant 2007). We used this approach to calculate the density of summer recreation trails (hiking and mountain biking)—as proxy for anthropogenic disturbance from recreational activities—and the density of forest–open land edges as a proxy for forest fragmentation. In addition, we calculated the Euclidean distance to all paved roads in the area as an indicator for human use (as in Braunisch and Suchant 2007) as well as to agricultural land uses (predominantly pastures) as indicator for higher nest-predation rates in forests fragmented by farmland (Andrén and Angelstam 1988, Small and Hunter 1988, Storch et al. 2005; Table 1). We used present-day data on land cover and use as a representation of the whole study period, since in general there was no change in land use between 1993 and 2013 in our study area.

*Forest structure and composition.—*We used small footprint pulse ranging airborne LiDAR data (mean: 1 pulse/1.5–2 $m^2$) to obtain a direct measure of structural density of forest communities, which changed over time between 1993 and 2013. Due to the comparatively long life expectancy of the species (Klaus et al. 1989, Storch 2001), population responses of grouse to environmental change can be characterized by some resilience and slow declines (Zeiler and Grünschachner-Berger 2009). Population responses for grouse have indeed been shown to be characterized by time lags (Walker et al. 2007, Harju et al. 2010, Horvick et al. 2014). Due to the temporal resolution of the response (derived from data collected in 1993 and 2013), we chose a single point in time to represent forest conditions during the study period. We thus used laser data collected on flights between 2002 and 2006 (data from FVA-BW), that is, halfway into the study period. This allowed us to better reflect the conditions experienced by the species during the observed period compared to present-day conditions. Raw laser data were processed and interpolated into a digital terrain model and a digital surface model (DSM) both with a resolution of $1 \times 1$ m, delivering a normalized digital surface model (nDSM) containing the surface height of all objects in the area. Following the classification of Graf et al. (2009) for the analysis of capercaillie habitat, the 1-$m^2$ nDSM cells were classified into either closed stands (1) or open areas (0) using a break value of 3 m height. The resulting binary raster was aggregated into a measure of horizontal stand structure as the proportion of canopy closure in a $50 \times 50$ m cell across the study area.

With regard to forest composition, we obtained information on the dominant forest community in $20 \times 20$ m cells from the forest type layer of the Pan-European High Resolution Layers (HRL, European Environment Agency 2015). Wherever the HRL layer contained missing data within the extent of the study area, we instead extracted values for the missing cells from the forest type data of the CORINE Land Cover Inventory of 2012. We processed the forest type data into the proportion of coniferous forest per sample buffer as an additional predictor of habitat suitability. Both the proportion of canopy closure and the proportion of coniferous forest were only obtained for those parts of a buffer area that were forested, thus preventing misclassification of open areas (i.e., farmland) as open forests.

*Spatial capercaillie population characteristics.—*We prepared three measures of capercaillie population connectivity. To distinguish core areas from marginal sites, we employed a circular moving window of 1 km radius to the range of the species to obtain a measure for the spatial density of capercaillie occurrence. To quantify isolation, we calculated the distance of each occurrence patch to the next closest patch. Finally, we obtained the size of each patch in 1993 (as the size of each distributional polygon object) to distinguish large areas from small population patches.

*Site variables.—*We included a soil condition index with 30 m resolution, which quantifies the capability of the soil to support a forest community suitable for capercaillie (range: 1 = very low, 15 = very high; Braunisch and Suchant 2008). We used the mean number of days with snow cover for the study area in relation to elevation (30 m resolution) as a proxy variable for both increasing elevation (i.e., decreasing productivity) and winter conditions. This variable was derived from predictions of Schneider and Schönbein (2003) that were based on the long-term mean over the period of 1980–2002 and has been previously used to model capercaillie habitat (Braunisch and Suchant 2007, Braunisch et al. 2008). Both attributes are thought to favor the development of an open forest community that is structurally suitable for capercaillie (predictors as used in Braunisch and Suchant 2007; Table 1). Finally, we differentiated between state-managed and private forests due to potential differences in management goals and the intensity of capercaillie habitat management.

### Statistical analysis

All analyses were performed in R (version 3.2.2; R Core Team 2015). We assessed environmental predictors for collinearity by calculating pairwise Pearson correlations and variance inflation factors for each predictor in the set to avoid wrongful identification of relevant predictors in the model (Zuur et al. 2009, Dormann et al. 2013). All variables with a pairwise correlation coefficient of $|r| > 0.5$ were considered potentially collinear and pre-selection was carried out, maintaining those variables of a pair that were thought to contain a higher ecological significance based on our starting set of hypotheses (Table 1).

Changes in capercaillie range extent were modeled as the probability of a location to persist using generalized linear mixed-effect models (GLMMs) with a binary distribution of errors and a logit link. The response was a Bernoulli sample of data points, with "1" representing range persistence and "0" areas that were lost from the distribution. We included the spatial subunit as random intercept to account for grouped sampling and heterogeneity across the five geographical subunits of the population. The definition of the subregions was based on subpopulation clusters linked to topography (Fig. 1).

One global GLMM was estimated for each sampling extent, respectively (i.e., 1.6 and 10 ha). All data were standardized by subtracting the mean and dividing by the standard deviation to allow for comparison of effect sizes and to achieve convergence in mixed models. Higher-order terms were included to account for nonlinearity, as well as interactions of predicted fox abundance with both snow cover and canopy cover to test whether an effect of predator abundance was mediated by environmental attributes.

Initial models were fitted using package lme4 (Bates et al. 2015). Residuals were assessed for SAC with spatial correlograms from package ncf (Bjornstad 2015) using distance between sample points as lag size after ensuring that isotropy was given and by plotting residuals in space. Due to strong SAC in model residuals (SAC present for ≥4–5 lags, i.e., 2.5–3 km) and the very irregular nature of our dataset (i.e., no regular lattice data; Appendix S1: Fig. S1), we proceeded to refit the global model structure in a spatial generalized mixed-effect model with a distance-based spatial correlation term using a wrapper function (i.e., glmmPQL from MASS; Venables and Ripley 2002) for the nlme package (Pinheiro et al. 2016) to allow for incorporation of binary data. Due to concerns about the reliability of Penalized Quasi-Likelihood for clustered binary data (Bolker et al. 2009), before proceeding, we verified the reliability of the model by ensuring that model coefficients and standard errors were identical to those obtained in lme4 (which uses Laplace approximation; Bolker et al. 2009). The incorporation of a Gaussian correlation structure into the model retained the highest predictive accuracy (as area under the receiver-operating characteristic [ROC] curve [AUC]; Fawcett 2006) while exhibiting the best performance in reducing SAC, reducing nugget effects (Beale et al. 2010) from approximately 30% to 70% and strongly decreasing spatial clustering of residuals.

Due to a lack of information criteria in quasi-likelihood estimation, we applied traditional backwards model selection assessing the impact of covariate removal using reduction in both the ROC AUC and the proportion of variance explained by the fixed-effect part of the model measured as the marginal $R^2$ statistic (while the conditional $R^2$ statistic provides an estimate of the variance explained by both random and fixed terms; Nakagawa and Schielzeth 2013). A model was considered as the best model either if the confidence interval of no coefficient estimate overlapped zero or if the removal of an additional covariate caused a notable drop in predictive performance or variance explained.

### *Model validation*

The performance of the best models was validated using fivefold cross-validation (CV) with five randomly assigned bins containing equal proportions of the binary response variable. Model performance was assessed using two complementary metrics, fluctuation in ROC AUC and mean Brier scores (Brier 1950) for each run. We additionally performed block cross-validation (BCV, Roberts et al. 2017) with structural blocking using spatially blocked groups for the large-extent model. We only used the large-extent model, as we were only able to capture an effect of forest structure at this scale (full details in the *Results* section) and consequently proceeded to use this model for assessing the relative impact of fox abundance (see *Model prediction and scenarios*). We grouped the training data using the five population subregions (i.e., fivefold BCV), since this allowed the greatest spatial segregation to an extent greater than the SAC present in the data, thus rendering this scenario the most extreme for coefficient validation. The goal of CV was to assess the stability of coefficient estimates and reveal regional differences.

### *Model prediction and scenarios*

We used the best large-extent model to predict the probability of persistence as a function of predicted fox abundance under eight environmental scenarios to explore whether the relative importance of predator abundance was mediated by environmental characteristics and was reduced under otherwise optimal conditions. We only used the large-extent model to assess this relationship for reasons given above (see full details in the *Results* section). The scenarios illustrate a gradient from an optimal to a completely unsuitable environment (see Appendix S1: Table S2 for detailed specification of all covariate values used), depicted by variation in the environmental potential for suitable habitat to develop (i.e., the combination of snow cover and soil conditions being optimal at high snow cover and soil condition index; snow: very low, 13 d; low, 40 d; high, 80 d; soil: very low, 0.3; high, 8), forest structural density (i.e., from the model optimum of 70% crown closure to a closed canopy [100%] situation for 10-ha stands) and the spatial structure of the population depicting a gradient from a fully connected to a very isolated population patch (i.e., variation in distance to nearest patch: low, 0 km; high, 3 km; and occurrence density: low, ~0; high, ~1). We repeated the predictions under a naive climate change scenario with intermediary impacts on snow cover (~25% reduction in days with snow cover overall for each scenario) based on predictions of Endler and Matzarakis (2011).This serves to carefully explore the potential for changes in the importance of the predator variable in a changing environment and should be understood accordingly. All covariates used for scenario predictions were independent of predicted fox abundance, and we thus used the original predicted fox abundance for all scenarios.

Effect plots were obtained with conditional errors holding all other predictor covariates at their mean. The implementation of a spatial correlation structure prevented bootstrap confidence intervals to be obtained. Thus, we reported conditional Wald confidence intervals over the fixed-effect parameters. We used the final model to predict persistence probabilities across the spatial extent of the distribution of capercaillie in the area in 1993 using focal statistics with a buffer size equal to the large-extent model (i.e., 180 m) to aggregate all environmental data resulting in datasets of 30 × 30 m resolution for prediction.

## RESULTS

### *Model results*

Model selection delivered models containing eight predictors for the large sampling extent and six predictors for the smaller extent (Table 2). On both scales, we found that capercaillie persistence was favored by increasing number of days with snow cover, decreasing predicted red fox abundance, slightly increasing soil quality, and slightly by public forest management regime (Fig. 2 and Appendix S1: Fig. S2).

The effects of trail density and canopy closure as well as the interaction between the predicted fox abundance and the structural density of the forest were only retained in the best large-extent model (Table 2). The density of summer recreation trails exhibited a marginally negative effect on capercaillie persistence (Table 2, Fig. 2). We found a non-linear effect of mean canopy closure on range persistence that interacted with the predicted fox abundance displaying an optimum around 70% canopy cover at very low to intermediate fox abundance (Table 2, Figs. 2, 3). Capercaillie persistence was favored in open forests at low fox abundance, but not if fox abundance was high. The probability to persist decreased in dense forests (>80% crown cover, Fig. 3). Predicted fox abundance in turn had the strongest impact on persistence in forest stands with open to intermediate canopy (Fig. 3).

### *Model validation*

Both the best small- and large-extent models exhibited good predictive performance (sensu Hosmer and Lemeshow 2000) in classifying range loss and persistence of capercaillie in the area (ROC AUC small extent: 0.843, SD = 0.010; large extent: 0.852, SD = 0.010). The fixed effects in both models explained a significant part of the variability in the data, with slightly better performance of the large-extent model (Table 2; marginal $R^2$ small extent: 0.556; large extent: 0.581). The whole model explained a considerably larger

Table 2. Model results of the best spatial GLMMs at both sampling extents. Model coefficients are provided with their standard errors and default $P$-values.

| Predictor | Estimate | Standard error | $P$-value | CI 2.5% | CI 97.5% |
|---|---|---|---|---|---|
| Small-extent model (1.6 ha) | | | | | |
| Intercept | 0.766 | 0.373 | 0.040 | – | – |
| FoxST | −0.379 | 0.089 | 0.000 | −0.554 | −0.204 |
| Soil | 0.249 | 0.140 | 0.076 | −0.026 | 0.525 |
| CaperDens | 0.174 | 0.090 | 0.053 | −0.002 | 0.351 |
| DistNear | −0.381 | 0.143 | 0.008 | −0.662 | −0.100 |
| Snowday | 0.804 | 0.105 | 0.000 | 0.599 | 1.009 |
| Snowday$^2$ | 0.136 | 0.049 | 0.005 | 0.040 | 0.232 |
| ForestMGT (pr.) | −0.329 | 0.152 | 0.030 | −0.626 | −0.032 |
| Large-extent model (10 ha) | | | | | |
| Intercept | 1.075 | 0.394 | 0.006 | – | – |
| FoxST | −0.437 | 0.090 | 0.000 | −0.612 | −0.261 |
| CanopyPer | −0.168 | 0.087 | 0.054 | −0.339 | 0.003 |
| CanopyPer$^2$ | −0.329 | 0.097 | 0.001 | −0.519 | −0.140 |
| CanopyPer$^3$ | −0.056 | 0.027 | 0.039 | −0.110 | −0.003 |
| STourDens | 0.003 | 0.065 | 0.961 | −0.123 | 0.130 |
| STourDens$^2$ | −0.059 | 0.034 | 0.085 | −0.127 | 0.008 |
| Soil | 0.245 | 0.141 | 0.082 | −0.031 | 0.521 |
| CaperDens | 0.187 | 0.090 | 0.039 | 0.009 | 0.364 |
| DistNear | −0.367 | 0.140 | 0.009 | −0.641 | −0.093 |
| Snowday | 0.876 | 0.111 | 0.000 | 0.658 | 1.095 |
| Snowday$^2$ | 0.144 | 0.052 | 0.006 | 0.042 | 0.245 |
| ForestMGT (pr.) | −0.299 | 0.150 | 0.048 | −0.593 | −0.004 |
| FoxST::CanopyPer | 0.192 | 0.074 | 0.010 | 0.047 | 0.337 |

*Notes:* GLMMs, generalized linear mixed-effect models. The upper and lower bounds of the 95% confidence intervals and complementary statistics of model quality (area under the receiver-operating characteristic curve (AUC), marginal $R^2$, and conditional $R^2$) are provided for both models. For the small-extent model, AUC = 0.843, marginal $R^2$ = 0.556, conditional $R^2$ = 0.731; for the large-extent model, AUC = 0.852, marginal $R^2$ = 0.581, and conditional $R^2$ = 0.759.

part (conditional $R^2$ small extent: 0.731; large extent: 0.759), indicating differences between geographical subunits captured by our random effect not fully explained by our covariates.

Both models performed well in fivefold CV, with both mean ROC AUC and mean Brier score across runs being almost identical to the values obtained from the models fit on all data (Appendix S1: Table S1). In spatially blocked CV, the mean coefficient estimates of the large-extent model were equal or close to equal to those estimated using all data (Appendix S1: Fig. S3). None of the coefficients exhibited systematic bias by subregion; however, some degree of regional variation was clearly given indicating some heterogeneity in the effect of the covariates between the subregions. Overall, BCV was less optimistic than random CV in terms of predictive accuracy (ROC AUC), but with the exception of the central Black Forest (subunit 3), loss of predictive accuracy amounted to 5% (ΔAUC = 0.044; Appendix S1: Fig. S4), still delivering a good model (i.e., ROC AUC ≥ 0.8). The results indicate that the dynamics of range persistence in this subunit may differ somewhat from the rest of the population (i.e., influences not well captured here such as extensive local habitat management).

### *Model prediction and scenarios*

Scenario prediction revealed considerable variation in the relative importance of predicted fox abundance for the probability of capercaillie to persist depending on the combination of environmental conditions, forest structure, and connectivity of a given site (Fig. 4). If the environmental situation was optimal, populations retained a high probability to persist regardless of predicted fox abundance. The probability to persist did decrease with increasing predicted fox abundance in scenarios in which at least one of the environmental components was not optimal. The

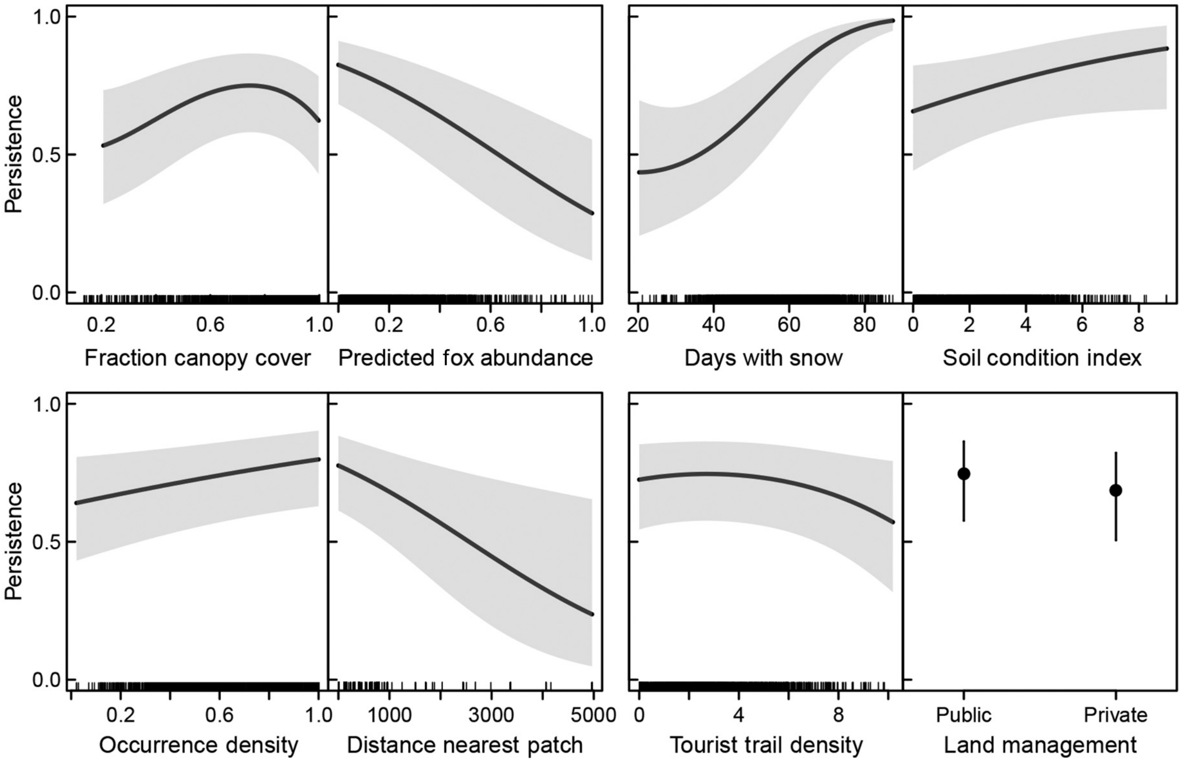

Fig. 2. Effects of model covariates on the probability of range persistence as predicted by the large-extent model (10-ha buffer around each sampling point). Effects are reported with conditional error while keeping the other predictors at their mean value.

effect of predicted fox abundance was found to be highest either in isolated areas that lacked connection to other areas of occurrence or in areas characterized by a low potential for suitable habitat to develop (i.e., low snow cover and unsuitable soil; see Fig. 4). Prediction under the climate change scenario indicated that an overall increase in productivity may lead to an increased relative importance of the predator variable on population development, also under optimal habitat conditions (Fig 4).

The probability of capercaillie to persist across the whole study area as predicted by the large-extent model is shown in Fig. 5.

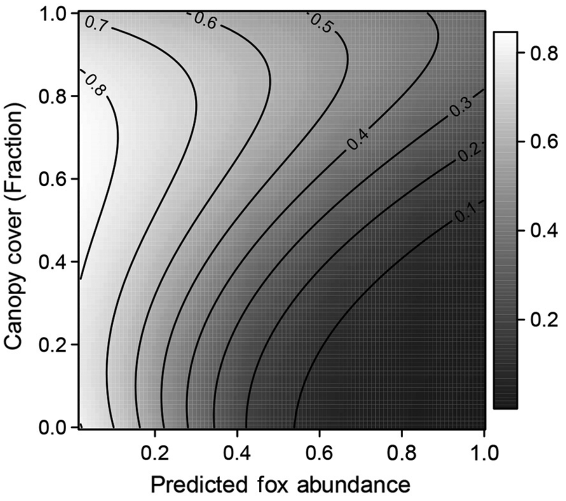

Fig. 3. Interaction between the predicted fox abundance and canopy cover affecting the probability of capercaillie to persist (indicated by isopleths and related probability of persistence) as predicted by the large-extent model (10-ha buffer size around sample locations).

## DISCUSSION

Our results demonstrate that a generalist mesopredator, the red fox, is potentially limiting grouse population persistence in fragmented forest landscapes of Central Europe. We show that recent range loss of a threatened capercaillie

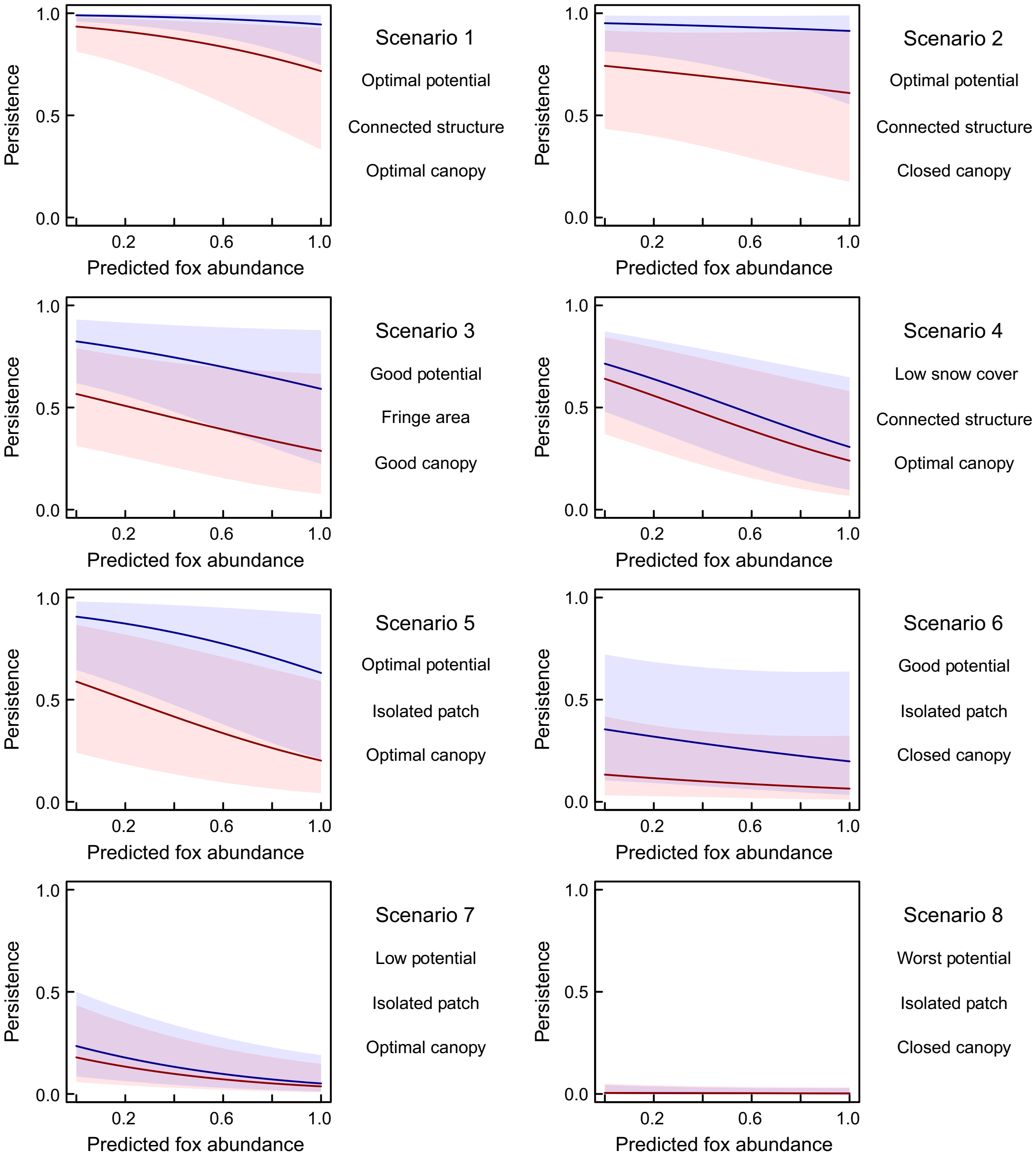

Fig. 4. Effects of predicted fox abundance on the probability of capercaillie to persist under eight environmental scenarios depicting variation in forest structure, environmental conditions (i.e., snow cover, soil quality), and population connectivity as predicted by the large-extent model (for full details, see *Methods* section). Blue lines indicate model predictions for the period 1993–2013. Red lines indicate predictions under a naive climate change scenario with moderate impacts on snow cover (~25% reduction) based on predictions of Endler and Matzarakis (2011). Shaded areas display 95% conditional confidence intervals.

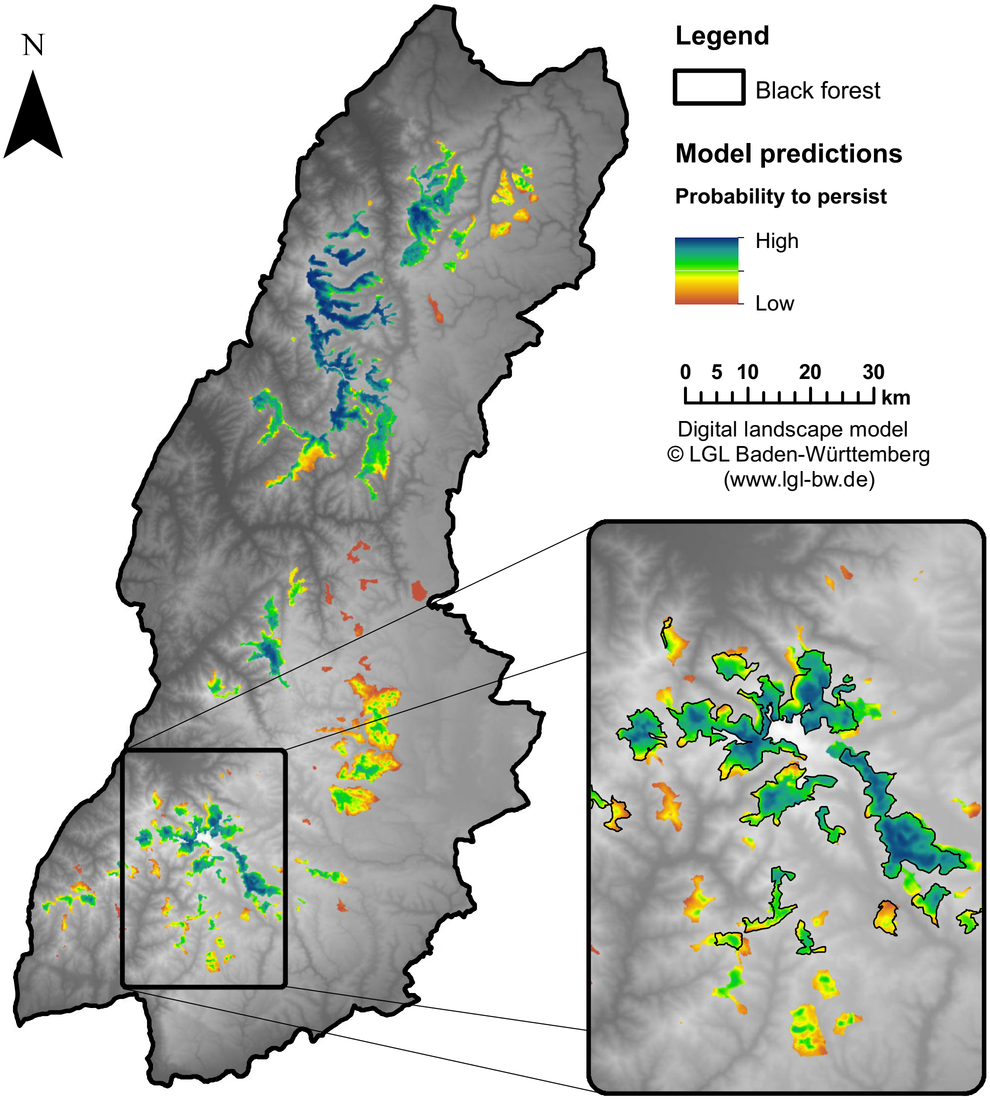

Fig. 5. Probability of capercaillie to persist across the species' area of occurrence in 1993 as predicted by the best large-extent model. The insert map shows predictions for an exemplary part of the range in the southern Black Forest, with black polygons delineating areas in which the species was recorded in 2013.

population was related to the predicted abundance of foxes in the surrounding landscape; however, the effect of fox abundance on grouse population persistence was mediated by other environmental attributes. Our study complements previous work indicating that predation may limit forest grouse abundance (Marcström et al. 1988, Lindström et al. 1994, Smedshaug et al. 1999, Fletcher et al. 2010). Grouse abundance appears to be driven by reproductive success rather than adult survival (Kurki et al. 1997, 2000) and accumulating evidence indicates that grouse reproductive success is negatively related to generalist predator abundance (Marcström et al. 1988, Kurki et al. 1997, Kauhala et al. 2000, Baines et al. 2004, 2016, Moreno-Opo et al. 2015). In the case of red foxes, predation may limit grouse populations in fragmented forest landscapes due to an increase in encounter risk of prey and predator at high predator density (Kurki et al. 2000) and higher search efficiency of foxes in smaller habitat patches (Seymour et al.

2004). Red foxes are believed to be the main predator of capercaillie in our area (Suchant and Braunisch 2008), and our data do not allow conclusions about the role of other predators (e.g., species also associated with human land use such as wild boar and corvids, but also mustelids).

Note that our index of red fox abundance comprises the diversity of land cover types and their composition (i.e., a landscape pattern) as important predictors (Güthlin et al. 2013, 2014). Although the effect of predator abundance in our model might thus be influenced by an effect of landscape composition per se, landscape composition is closely related with the abundance of mammalian mesopredators (Kurki et al. 1998, Kiener and Zaitsev 2010, Güthlin et al. 2013, 2014, Pasanen-Mortensen and Elmhagen 2015). Accordingly, our findings support the assumption that the interspersion of forest by farmland affects grouse populations by favoring a high abundance of predators (Kurki and Lindén 1995, Kurki et al. 2000, Storch et al. 2005). Fragmentation of forest by other land uses has previously been related to range loss of Cantabrian capercaillie (*Tetrao urogallus cantabricus*; Quevedo et al. 2006) and reduced reproductive success of boreal forest grouse, presumably due to higher rates of predation (Kurki and Lindén 1995, Kurki et al. 2000).

Finally, the effect of predicted fox abundance varied with the proportion of canopy cover in our model (Fig. 2). Red foxes, amongst other species, might visit open areas within the forest, because of rodent availability (Henttonen 1989, Hansson 1994, Savola et al. 2013), thus elevating the encounter rate of prey and foxes in forest stands and thus predation risk in open forests (Storch et al. 2005).

Our scenarios highlight that the relative effect of expected red fox abundance on capercaillie persistence was mediated by other environmental attributes. The probability of an occurrence patch to persist was a function of several ecological parameters, with environmental conditions (i.e., climate) and population connectivity as key drivers of capercaillie range loss. There are indications that the relative impact of predation on grouse populations may be co-determined by environmental conditions (Baines 1991, Thirgood et al. 2000*b*, Ludwig et al. 2010). In our study, the predicted predator abundance had the highest relative importance in sites in which extinction risk was already elevated due to lack of connectivity and unsuitable site conditions (Fig. 4). Predation can be an important cause of chick mortality in capercaillie, but especially if suboptimal conditions predispose chicks to predation (Wegge and Kastdalen 2007, Jahren et al. 2016), representing a potential threat for grouse population development in a changing climate (Jahren et al. 2016). By contrast, the negative effect of fox abundance in our models was mitigated by otherwise optimal conditions resulting in high persistence probabilities regardless of fox abundance (Fig. 4). This indicates that management measures which would benefit capercaillie (i.e., habitat improvements) might to some degree mitigate the effects of high fox abundance. It also emphasizes the vulnerability of populations restricted to small and isolated patches or occurring in suboptimal habitats and indicates that fragmented populations are more likely to go extinct (Temple and Cary 1988, Newton 1998). This is also reflected by the spatial pattern of range loss that was most pronounced for fragmented populations at the edge of the range (Fig. 5), a pattern that has also been reported for grouse in the UK (Baines et al. 2016) and sage-grouse persistence in the United States (Aldridge et al. 2008).

Studies on black grouse have indicated that changes in land use may drive range contractions of grouse in Europe (Ludwig et al. 2009*a, b*). This was no issue in our study, because there was no documented change in land cover and use (FVA-BW, *unpublished data*). Accordingly, range loss and persistence in our study area were well explained by the qualitative attributes of a site. In line with other studies (Braunisch and Suchant 2007, Braunisch et al. 2014), our results highlight the role of climate for the development of capercaillie populations and the sensitivity of the species to climate change (Moss et al. 2001, Braunisch et al. 2014). With increasing temperatures and related changes in habitat features resulting from reduced snow cover, earlier snow melt, and higher site productivity, there is a risk of ongoing range loss in capercaillie (Figs. 4, 5). In addition, changes in forest structure resulting from changing paradigms in forestry have been suggested as a central driver of grouse declines (Storch 2007, Jahren et al. 2016). Our study confirmed that dense forests negatively affected population persistence (Fig. 2). However, this was only reflected by a moderate, though significant effect, potentially owing to the resolution of the data and our use of a simple break value in canopy classification (3 m as in Graf et al. 2009). Yet, previous work suggests that differences in capercaillie abundance across sites might be better explained by landscape patterns than habitat structure (Storch 2002), which is in line with our findings. We found no significant effect of recreational infrastructure on long-term capercaillie persistence, although the species has previously been shown to be affected by recreational disturbances (Thiel et al. 2008, Storch 2013, Coppes et al. 2017). We assume that capercaillie are affected by human recreation mainly on a small scale, but that this is not reflected by differences in population trends at the landscape scale (Coppes et al. 2017). In addition, trail density is only an incomplete proxy for recreational trail use, thus providing an explanation for the large associated uncertainty of this effect.

With regard to conservation, we suggest that predictive models of species occurrence as used in this study may be a valuable tool for prioritizing management actions at the landscape scale. Predictions of capercaillie persistence probability may be combined with field observations to select sites with a high conservation value, but also to focus active management on sites where the potential for benefits to be achieved is high. Our scenario predictions indicate that such may apply to sites at the edge of the distribution and well-connected patches currently characterized by suboptimal forest structures. Managers can directly address two drivers of range persistence, which were included in our study—forest density and predator abundance—while the remainder is impractical or impossible to influence (e.g., land ownership or climate). Previous studies have shown that predator removal—if thoroughly conducted—may lead to locally improved grouse reproductive success (Marcström et al. 1988, Kauhala et al. 2000) and sometimes population size (Marcström et al. 1988, Fletcher et al. 2010). However, whether removal practices can achieve an effective reduction of red fox densities at the landscape scale is questionable. We thus advocate a combination of measures to increase the chances of capercaillie survival. This may involve prioritizing sites for capercaillie conservation, which are not favoring high red fox abundance. In such priority areas, high capercaillie habitat suitability should be maintained by capercaillie-friendly forestry. In addition, other factors potentially affecting capercaillie, such as recreational activities (Coppes et al. 2017), should be taken into account. For sites characterized by forest–farmland mosaics (i.e., that favor high red fox abundance), which are considered important for maintaining capercaillie population connectivity (Suchant and Braunisch 2008), targeted predator removal may be considered.

## CONCLUSIONS

This study provides evidence of a link between the disappearance of grouse from forests of central Europe and the environmental attributes of the landscape. Our results indicate that the probability of capercaillie to persist was a function of habitat features, environmental conditions, population connectivity, and the suitability of the landscape for a generalist mesopredator, the red fox. High fox abundance promoted by forest–farmland mosaic landscapes was negatively related to grouse population persistence. The effect of predicted red fox abundance was strongest in those areas that already faced an elevated extinction risk of capercaillie due to unfavorable environmental conditions or lack of connectivity. However, we show that the negative effect of fox abundance was compensated under otherwise optimal habitat conditions, thus indicating a potential for management to aid species conservation through measures such as capercaillie-friendly forestry.

## ACKNOWLEDGMENTS

We are grateful to Veronika Braunisch and Petra Adler of the FVA-BW for granting us access to the environmental datasets used in this study. The article-processing charge was funded by the German Research Foundation (DFG) and the University of Freiburg in the funding program Open Access Publishing.

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