

Uncertainty in predictions of range dynamics: black grouse climbing the Swiss Alps

Damaris Zurell, Volker Grimm, Eva Rossmannith, Niklaus Zbinden, Niklaus E. Zimmermann and Boris Schröder

D. Zurell (damaris.zurell@uni-potsdam.de) and B. Schröder, Univ. of Potsdam, Inst. of Earth and Environmental Sciences, Karl-Liebknecht-Str. 24/25, DE-14476 Potsdam, Germany. Present address of DZ: Univ. of Potsdam, Inst. for Biochemistry and Biology, Maulbeerallee 2, DE-14469 Potsdam, Germany. BS also at: ZALF e.V., Leibniz-Centre for Agricultural Landscape Research, Soil Landscape Modelling, Eberswalder Str. 84, DE-15374 Müncheberg, Germany. – V. Grimm, UFZ, Helmholtz Centre of Environmental Research – UFZ, Dept of Ecological Modelling, Permoserstr. 15, DE-04318 Leipzig, Germany. – E. Rossmannith, Univ. of Potsdam, Inst. for Biochemistry and Biology, Maulbeerallee 2, DE-14469 Potsdam, Germany. – N. Zbinden, Swiss Ornithological Inst., Seerose 1, CH-6204 Sempach, Switzerland. – N. E. Zimmermann, Swiss Federal Research Inst. WSL, Landscape Dynamics, Zürcherstr. 111, CH-8903 Birmensdorf, Switzerland.

Empirical species distribution models (SDMs) constitute often the tool of choice for the assessment of rapid climate change effects on species' vulnerability. Conclusions regarding extinction risks might be misleading, however, because SDMs do not explicitly incorporate dispersal or other demographic processes. Here, we supplement SDMs with a dynamic population model 1) to predict climate-induced range dynamics for black grouse in Switzerland, 2) to compare direct and indirect measures of extinction risks, and 3) to quantify uncertainty in predictions as well as the sources of that uncertainty. To this end, we linked models of habitat suitability to a spatially explicit, individual-based model. In an extensive sensitivity analysis, we quantified uncertainty in various model outputs introduced by different SDM algorithms, by different climate scenarios and by demographic model parameters. Potentially suitable habitats were predicted to shift uphill and eastwards. By the end of the 21st century, abrupt habitat losses were predicted in the western Prealps for some climate scenarios. In contrast, population size and occupied area were primarily controlled by currently negative population growth and gradually declined from the beginning of the century across all climate scenarios and SDM algorithms. However, predictions of population dynamic features were highly variable across simulations. Results indicate that inferring extinction probabilities simply from the quantity of suitable habitat may underestimate extinction risks because this may ignore important interactions between life history traits and available habitat. Also, in dynamic range predictions uncertainty in SDM algorithms and climate scenarios can become secondary to uncertainty in dynamic model components. Our study emphasises the need for principal evaluation tools like sensitivity analysis in order to assess uncertainty and robustness in dynamic range predictions. A more direct benefit of such robustness analysis is an improved mechanistic understanding of dynamic species' responses to climate change.

Recent studies in biogeography and macroecology resulted in growing concerns about species' range shifts driven by ongoing climate and land use change. Species dynamically adjust their ranges in response to the complex interplay of environmental forces, changing biotic interactions, and their interactions with key demographic traits (Walther et al. 2002, Araújo and Luoto 2007, Thuiller et al. 2008). To date, a substantial body of literature has amassed on predicting potential range dynamics as well as extinction risks in order to derive mitigation strategies for global change impacts (Midgley et al. 2002, Thomas et al. 2004, Thuiller 2004).

Many, if not most, recent climate impact studies rely on correlative, phenomenological species distribution models (SDMs). These derive statistical relationships between the species' occurrence (or abundance) and prevailing environmental (biotic and abiotic) factors to characterise the environmental niche (Guisan and Zimmermann 2000). Potential future ranges of species are projected by transferring this

relationship to future environmental conditions, thus allowing for rapid assessment of potential threats. SDMs require comparably simple species location data such as presence-absence and do not rely on profound prior knowledge on the species' biology. Therefore, they constitute one of few practical approaches to study environmental change impacts on a wide range of species quickly (Huntley et al. 2004, Elith and Leathwick 2009) and have spurred hundreds of applications and publications on these issues (Zimmermann et al. 2010).

However, SDMs are not intended for making transient predictions under environmental change. Many recent publications have tried to raise awareness to the inherent fundamental as well as methodological limitations accompanying SDMs (Buckley and Roughgarden 2004, Hampe 2004, Guisan and Thuiller 2005, Dormann 2007). Some principal limits for SDMs arise from their conceptual underpinning. Foremost, they assume that species are in equilibrium

with their environment, which may not even be the case for many post-glacial distributional ranges (Svenning and Skov 2004). Correspondingly, when extrapolating to new times and places, SDMs implicitly assume an instantaneous realisation of a new equilibrium situation. Thereby, transient population dynamics and important life history traits such as dispersal capacity and local persistence ability that shape a species' response to environmental change are essentially ignored (Thuiller et al. 2008, Zurell et al. 2009). This may lead to biased estimates of extinction risks. In addition, discussions about methodological issues prevail. Different SDM algorithms, for instance, have led to divergent predictions of habitat suitability for scenarios of climate change (Thuiller 2004, Pearson et al. 2006, Buisson et al. 2010). Among others, model predictions can be expected to be sensitive to model building steps and data characteristics including uncertainty in future climate scenarios (Araújo and Guisan 2006, Heikkinen et al. 2006, Dormann et al. 2008).

Challenges for SDM predictions under environmental change are manifold and, therefore, several steps have been proposed to improve SDMs and to yield more robust predictions. One solution is to make use of multiple models within an ensemble framework which allows analysing the range of uncertainty introduced, for example, by different SDM algorithms and different climate scenarios (Araújo and New 2007, Thuiller et al. 2009). To overcome fundamental limitations of SDMs that are related to their static nature, several authors have urged to supplement SDMs by more mechanistic, stochastic population models that incorporate key demographic processes determining range dynamics (Guisan and Thuiller 2005, Araújo and Guisan 2006, Schröder 2008, Thuiller et al. 2008, Zurell et al. 2009). Stochastic population models explicitly describe demographic processes such as mortality, reproduction and dispersal while taking into account environmental and demographic stochasticity. They allow the assessment of species vulnerability or extinction risks via population viability analyses (PVA, Burgman et al. 1993, Brook et al. 2000) and may help to uncover 'tipping points' that lead to rapid and potentially irreversible species' responses to environmental change (Pereira et al. 2010). However, these models are also highly data demanding, usually involve more complex model structures, and rely on extensive knowledge on species' biology and population processes which often constrains the spatial scale of the studies, the number of species or the generality of results (Jeltsch et al. 2008).

Attempts have been made to make use of both phenomenological and population dynamic approaches when predicting climate change-induced range shifts (Keith et al. 2008, Anderson et al. 2009, Cheung et al. 2009). Thereby, SDMs and comparably simple, spatially explicit population models are integrated by constraining basic demographic parameters of the dynamic model (e.g. carrying capacity) by SDM output (e.g. habitat suitability). As such, the predictive accuracy of SDMs at large spatial scales is retained while being able to capture transient population dynamics in response to climate change (Keith et al. 2008, Gallien et al. 2010). Another simple way is to run a dynamic, multi-species population model under a range of environmental and landscape contextual conditions, and then to fit the major outcome of these simulations, namely migration rate, against climate and competition as predictors, and to combine this

information in a simple GIS time-step model to predict transient responses of the target species to changing land use and climates (Meier et al. 2011).

The goal of all these considerations and efforts is to increase robustness of model predictions under environmental change. Quantitative predictions of models typically carry substantial error margins due to structural (model specification) uncertainty and parameter (data) uncertainty as well as inherent (natural) stochasticity of ecological dynamics (Barry and Elith 2006, Jeltsch et al. 2008). Conclusions regarding the robustness of predictions can only be made conditional on explicit simulation runs. When integrating SDMs and dynamic population models in order to predict range dynamics for scenarios of environmental change final predictions essentially carry errors of three different models (SDM, population model and climate model; Beaumont et al. 2008, Wiens et al. 2009). These uncertainties need to be quantified in order to draw inferences about the robustness of model results.

In this context, the objectives of our study were threefold: 1) to predict climate-induced range dynamics for black grouse in Switzerland, 2) to compare direct and indirect measures of extinction risks, and 3) to quantify uncertainty and robustness of predictions and assess relative contribution of different modelling components to overall uncertainty. To achieve this, habitat suitability maps obtained from spatio-temporal SDM predictions were linked to a spatially explicit individual-based model that described key demographic processes of black grouse. Predictions were derived and compared for multiple key model outputs (population and occupied area size, probability of extinction, mean elevation and mean population centre). Uncertainty in predictions was quantified by extensive sensitivity analysis. Thereby, we focused on three different uncertainty components: climate scenarios, SDM algorithms, and demographic model parameters. Furthermore, sensitivity was evaluated for each key model output to delineate more or less robust features of dynamic range predictions.

Methods

Species data

In the Swiss Alps, black grouse *Tetrao tetrix* mainly occurs in treeline habitats, in dwarf-shrub-rich transition zones between forests and alpine meadows at an altitude of up to 2500 m a.s.l. (Zbinden and Salvioni 2003). Swiss black grouse populations were judged as stable by comparisons between the two observation periods of the Swiss Breeding Bird Atlases 1972–1976 and 1993–1996 (Schifferli et al. 1980, Schmid et al. 1998). However, population sizes are known to fluctuate strongly and, thus, estimates on population status derived from such short time periods may be imprecise. For example, local declines were reported for the northern as well as southern Prealps caused by habitat loss and fragmentation (Schmid et al. 1998, Zbinden and Salvioni 2003).

Species distribution data at 1 km resolution were obtained from the Swiss Breeding Bird Atlas (Schmid et al. 1998). Count data for assessing reproductive success were obtained from a time series observed between 1981 and 2007 in Ticino, Switzerland, where the numbers of chick-rearing

hens and juveniles were recorded annually in the second half of August (Zbinden and Salvioni 2003).

Environmental predictors

Environmental predictors included climatic variables as well as land use and vegetation data at 1 km resolution. Climate data were derived from the BIOCLIM database (Swiss Federal Research Institute WSL) including long-term averages from the period 1961–1990 on summer (June–August), winter (December–February) and annual values for the variables: precipitation sum; mean temperature; potential solar radiation; mean summer moisture index (precipitation – potential evapotranspiration); and growing degree days above 0°C. Details for the derivation of these climate layers are given in Zimmermann and Kienast (1999) and in Guisan et al. (2007). Land use and vegetation data were compiled from the land use and land cover database GEOSTAT (Swiss Federal Statistical Office). From these, we chose five land use categories that we deemed sensible to explain black grouse presences and absences, based on the ecology of the species: scattered forest, bushy forest, grassland and arable land, unproductive vegetation, and residential and infrastructural areas.

Climate change scenarios

Climate change scenarios were obtained from the ENSEMBLES Project (www.ensembles-eu.org). Five scenarios were obtained from three regional circulation models with three different underlying general circulation models and three different emission scenarios (A1B, B1, B2, Table 1). These scenarios were chosen to reflect a range of predictions for the central European Alps that were both realistic and reached from pessimistic to optimistic. Scenarios were downscaled to a 1 km spatial resolution according to the procedure described in Engler et al. (2011). Climate scenarios were available as 10 yr time slices which we interpolated to obtain annual changes in climate. The general climate trend over the 21st century is illustrated in Supplementary material Appendix 1, Fig. A1.

Species distribution model

Black grouse potential distribution was predicted using three different statistical algorithms that take presence-absence input data, are widely used in species distribution modelling and that present different levels of flexibility (Elith

et al. 2006, Heikkinen et al. 2006), namely: generalised linear models (GLM), generalised additive models (GAM) and boosted regression trees (BRT).

In order to minimise multicollinearity problems, we pre-selected the final predictors prior to modelling so that bivariate Spearman correlations were below $|r| = 0.7$ (Fielding and Hawthorn 1995). Thereby, we gave preference to land use variables as we regard these as more proximal predictors for black grouse occurrence and, hence, retained only those climate variables that we expected to have a direct effect on black grouse occurrence. Our final predictor set included five land use variables (see above), two climate variables (mean annual temperature, winter precipitation), and potential solar radiation describing topographic effects.

We allowed second-order polynomials in GLM, and non-parametric cubic smoothing splines with up to four degrees of freedom in GAM. BRT was estimated with a tree complexity of 2, a bag fraction of 0.75 and a learning rate of 0.01 which ensured that the model was fitted with at least 1000 trees (cf. Elith et al. 2008).

A split-sample approach was used to validate SDM performance (Araújo et al. 2005). Models were calibrated on a randomly selected sample of 70% of the data and validated against the remaining 30%. Data splitting was repeated 100 times and evaluation statistics were averaged to yield a final evaluation that is quasi-independent of initial conditions (Thuiller et al. 2009). Several measures of accuracy were calculated: explained deviance R^2 (Menard 2000), the area under ROC curve (AUC; Fielding and Bell 1997), the true skill statistic (TSS) (Allouche et al. 2006), sensitivity (true presences) and specificity (true absences) as well as slope and intercept of the calibration curve which describe spread and bias in the predictions (Reineking and Schröder 2006, Zurell et al. 2009). We derived the deviance by applying Eq. 1.10 in Hosmer and Lemeshow (2000). As TSS, sensitivity and specificity require binary predictions we converted the predicted occurrence probabilities into presence-absence maps by applying the prevalence threshold (Liu et al. 2005). All SDMs with accompanying analysis of their performance were built in R ver. 2.12.1.

The resulting SDMs estimated black grouse occurrence probabilities for entire Switzerland. High occurrence probabilities were interpreted as indicating environmental conditions that define highly suitable habitat for black grouse (Araújo et al. 2002, Söndgerath and Schröder 2002).

Individual-based model

We simulated population dynamics of black grouse by a stochastic, spatially-explicit individual-based model (IBM)

Table 1. Regional circulation models (RCM) used in the ensemble simulations of this study. Each RCM was based on the boundary inputs from a general circulation model (GCM). We used three different SRES scenarios, which translate for the Swiss case study to tabulated climate anomalies by the end of the 21st century (ΔT , ΔP).

Short	RCM	GCM	Institute	SRES	ΔT	ΔP
H-a1	HadRM3qO	HadCM3	HC	A1B	+5.26°C	+4.67 mm
M-a1	CLM	ECHAM5	MPI	A1B	+4.51°C	+5.96 mm
M-b1	CLM	ECHAM5	MPI	B1	+3.07°C	+10.51 mm
S-a1	RCA30	CCSM3	SMHI	A1B	+2.71°C	+0.70 mm
S-b2	RCA30	CCSM3	SMHI	B2	+2.89°C	+1.55 mm

HC: Hadley Center; MPI: Max Plank Inst.; SMHI: Swedish Meteorological and Hydrological Inst.

that followed the fate of individual birds from birth to death. The subsequent model description follows the ODD (overview, design concepts, details) protocol for describing individual-/agent-based models (Grimm et al. 2006, 2010).

Purpose: the main purpose of the model is population viability analysis.

Entities, state variables and scale: female birds constituted the biological entity in our model. In black grouse, females are the limiting sex regarding not only reproduction but also dispersal as the latter is restricted predominantly to first-year hens while first-year cocks affiliate to the nearest lek (mating arena for competitive courtship display), and adults are rather sedentary (movements within the home ranges were ignored, Caizergues and Ellison 2002). Individuals were characterised by the state variables location and age. The model landscape represented entire Switzerland and consisted of a grid of 42 181 cells of 1 km resolution. Each grid cell was characterised by its carrying capacity K . Boundary conditions were reflecting so that emigration from the study area equalled immigration. The model proceeded in annual time steps (from spring to spring).

Process overview and scheduling: at the beginning of each time step, carrying capacity K of all cells was determined from habitat suitability as estimated by SDMs. In summer, hens reproduce and raise juveniles that survive until first autumn with the probability pleadYoung (see Table 2 for IBM parameters). Thus, pleadYoung subsumes the processes of clutch survival, hatching rate and early chick survival. The probability of a hen to lead a certain number of juveniles is $p(x)\text{Fledglings}$. The probability for a fledgling to be female is $p\text{Female}$, otherwise it is a male and is subsequently ignored. In autumn, first-year hens disperse from their natal patch with a probability $p\text{Dispersal}$. Individual birds perceive the environment as heterogeneous and avoid to settle in or to traverse wide stretches of unsuitable habitat (Graf et al. 2007). All sources of mortality are subsumed under an

annual survival probability $p\text{Surv}$, the probability of an individual hen to survive until early spring. Mortality and emigration may increase with density due to increased predation risk or simply due to shortage of resources. At the end of the simulation year (early spring), the age of all individuals is incremented by one year. Individuals growing older than MaxAge are removed.

Design concepts: the model follows a bottom-up approach, and population dynamics and spatial distribution of black grouse emerge from individual behaviour. Life cycle, reproduction, and survival rates are imposed by empirical rules and parameters. Dispersal includes the basic adaptive decision to avoid unsuitable and over-crowded habitat. Demographic stochasticity is included to mimic individual-level variability by interpreting all demographic parameters as probabilities (Burgman et al. 1993). Environmental stochasticity is considered by drawing pleadYoung (probability of hen to reproduce and raise juveniles that survive until first autumn) from a normal distribution. This parameter subsumes the processes of nest predation, hatch rate and early chick survival that are most strongly influenced by environmental fluctuations between years. The normal distribution was defined by the mean and SD derived from empirical data, cut at minimum and maximum of empirically observed values (Table 2). Key outputs monitored from the model are population size, probability of extinction by time t (proportion of replicate runs that went extinct), area size, mean elevation, and mean population centre (long/lat).

Initialisation: initially, 8000 individuals were randomly distributed in suitable habitat, and were assigned a random age (between 1 and 3 yr), which is in accordance with data from the Swiss Breeding Bird Atlas (Schmid et al. 1998). The initial habitat suitability map is obtained from the species distribution model run with current climate. The model ‘spinned-up’ for 25 yr to exclude initialisation effects (Rossmanith et al. 2007). After this ‘spin-up’ climate change was initiated with annual timesteps.

Input data: for each time step, a habitat suitability map is derived from the species distribution model described above given the environmental input layers (climate and land cover).

Submodels: detailed descriptions of submodels implementing the modelled processes are provided in Supplementary material Appendix 1. The entire IBM was implemented in C++.

Sensitivity analysis

We evaluated three major sources of uncertainty in range predictions: underlying species distribution models (SDM), climate scenarios (RCM), and demographic parameters of the individual-based model. In a preliminary local sensitivity analysis we found that IBM parameters affecting survival and reproduction, namely survival probability ($p\text{Surv}$), the probability to be female at birth ($p\text{Female}$) and the probability of a hen to lead young (pleadYoung), were the most sensitive parameters for range predictions while others such as dispersal parameters had little effect on population fate. This is not unexpected because as black grouse range contracts and retrieves to higher elevations of the Swiss Alps in response to warmer regional temperatures the species’ fate

Table 2. IBM parameters.

Parameter	Value	Description
pleadYoung (min, max)	0.6 ± 0.09 (0.39, 0.77)	probability of a hen to lead young during simulation year
$p(x)\text{Fledglings}$	0.103/1, 0.198/2, 0.270/3, 0.249/4, 0.124/5, 0.037/6, 0.013/7, 0.004/8, 0.002/9	probability to produce x fledglings (given as probability/clutch size)
$p\text{Female}$	0.5	probability to be female at birth
$p\text{Dispersal}$	0.81	probability of juveniles to emigrate
meanDist	8	mean dispersal distance [km]
rangeDist	1.0–29.0	range dispersal distance [km]
$p\text{Surv}$	0.5	probability to survive the simulation year
K_{max}	10	maximum carrying capacity [km ⁻²]
MaxAge	10	maximum age

is more restricted by local persistence ability and successful establishment at higher elevations than by dispersal. Thus, in subsequent sensitivity analysis we concentrated on the three above-mentioned survival and reproduction parameters and varied them in a 3^k factorial design (low, intermediate, and high values given by default parameters in Table 2 \pm 5%). As *pleadYoung* is drawn from a normal distribution we manipulated both position and shape of this distribution by shifting the entire distribution by \pm 5% and by varying the standard deviation of this distribution by \pm 5% (resulting in a more peaked or more flattened distribution). Our sensitivity analysis thus crossed three different SDM techniques, five different climate scenarios, and four different demographic parameters (note that *pleadYoung* counts twice) with three levels each resulting in a total of 1215 different model configurations. For each of these we performed 35 replicates (McCarthy et al. 1995). We quantified the sensitivity in the years 2001, 2050 and 2100 for five different model outputs (population size, probability of extinction by year *t*, area size, mean elevation, and mean population centre). First, for each parameter combination we calculated the mean values of the five key model outputs from the 35 replicate simulations. Then, for each model output and for each uncertainty component we performed univariate linear regressions with the respective model output as dependent variable and the respective uncertainty component as independent variable (cf. Dormann et al. 2008). The relative contribution of each uncertainty component to variability in predictions was then given by the explained variance *R*² of the linear regression models. Additionally, we ran ‘control’ simulations with default IBM parameterisation across the different SDM algorithms and climate scenarios with 100 replicates each to obtain an estimate of variation in model outputs due to stochasticity. All analyses of IBM output were carried out in R ver. 2.12.1.

Results

Statistical modelling and range predictions

All three SDM techniques fitted consistent relationships between black grouse occurrence and environmental predictors (Fig. 1) although differences were also apparent, mainly in areas of the environmental space with lower data coverage. Mean annual temperature was by far the most important variable (Supplementary material Appendix 1, Fig. A2), followed by grassland cover type which mainly described species absences, and followed by bushy and scattered forest and unproductive vegetation which were more important for describing species presence. In the split-sample validation (*n* = 100) we found only slight differences in model performance between methods. All three SDMs showed excellent discrimination in terms of AUC (approx. 0.95), very good accuracy in terms of TSS (approx. 0.78), high rates of correctly predicted presences (sensitivity: 0.93–0.95) and absences (specificity: 0.84–0.86), and excellent calibration (calibration slope and intercept near one and zero; Supplementary material Appendix 1, Table A1). BRT showed highest scores for all measures except for sensitivity, which was highest for GLM (although differences were not pronounced). Overall,

SDMs explained between 57.2 and 59% of the deviance in black grouse occurrence (Supplementary material Appendix 1, Table A1).

GLM predicted greatest total area size of potentially suitable habitat for black grouse under current environmental conditions, BRT smallest (year 2001; GLM 11 690 km², GAM 11 240 km², BRT 10 590 km²). Predictions of habitat suitability changes under climate change were very similar across all three SDMs. Differences did not emerge until the end of the 21st century when predictions varied considerably across climate change scenarios with great and abrupt habitat losses under the more extreme scenarios H-a1 and M-a1 (Supplementary material Appendix 1, Fig. A3). For these extreme cases, also differences between SDMs became more apparent with greatest losses predicted by GAM, lowest by GLM. Altitudinal ranges were predicted to shift uphill from mean elevations of approx. 1800 m a.s.l. in 2001 to mean elevations of approx. 2200 m a.s.l. by 2100 (Fig. 2, Table 3). BRT predicted accompanying range contractions while GLM and GAM predicted an eastward shift in suitable habitat. Range contractions were predicted in the western Prealps primarily due to elevational limits (Fig. 3). Consensus on black grouse presence was high for the central and eastern Swiss Alps (Supplementary material Appendix 1, Fig. A4).

Population dynamics

The IBM predicted mean population sizes of ca 5500 female black grouse for current environmental conditions and for default IBM parameterisation (Fig. 4, Table 3). Population size was predicted to gradually decline over the century (Fig. 4). By the end of the century, black grouse population sizes were predicted to drop to 12–22% of their initial size. The strong population decline mainly resulted from a negative population growth rate given the demographic rates (Table 2). For comparison, we manipulated the parameter survival probability so that current population trend was stable (*pSurv* = 0.51). This resulted in higher predicted population sizes and moderate declines which were similar in trend yet not identical in shape to habitat trajectory (Supplementary material Appendix 1, Fig. A5).

Sensitivity analysis

The relative contribution of each uncertainty component to variation in predictions differed for the different time slices considered and for the different model outputs. Great variations across simulations were found in predictions of population dynamic features such as population and occupied area sizes as well as for probabilities of extinction. Variation in predicted population size due to uncertainty in demographic parameters was approximately one order of magnitude greater than variation due to environmental and demographic stochasticity and due to uncertainty in SDMs and climate scenarios (Table 3, 4). On the other hand, geographic features like mean population centre, range extent, and mean elevation showed comparably low variation across simulations. Different climate scenarios had no considerable effect on population dynamic features, yet they were

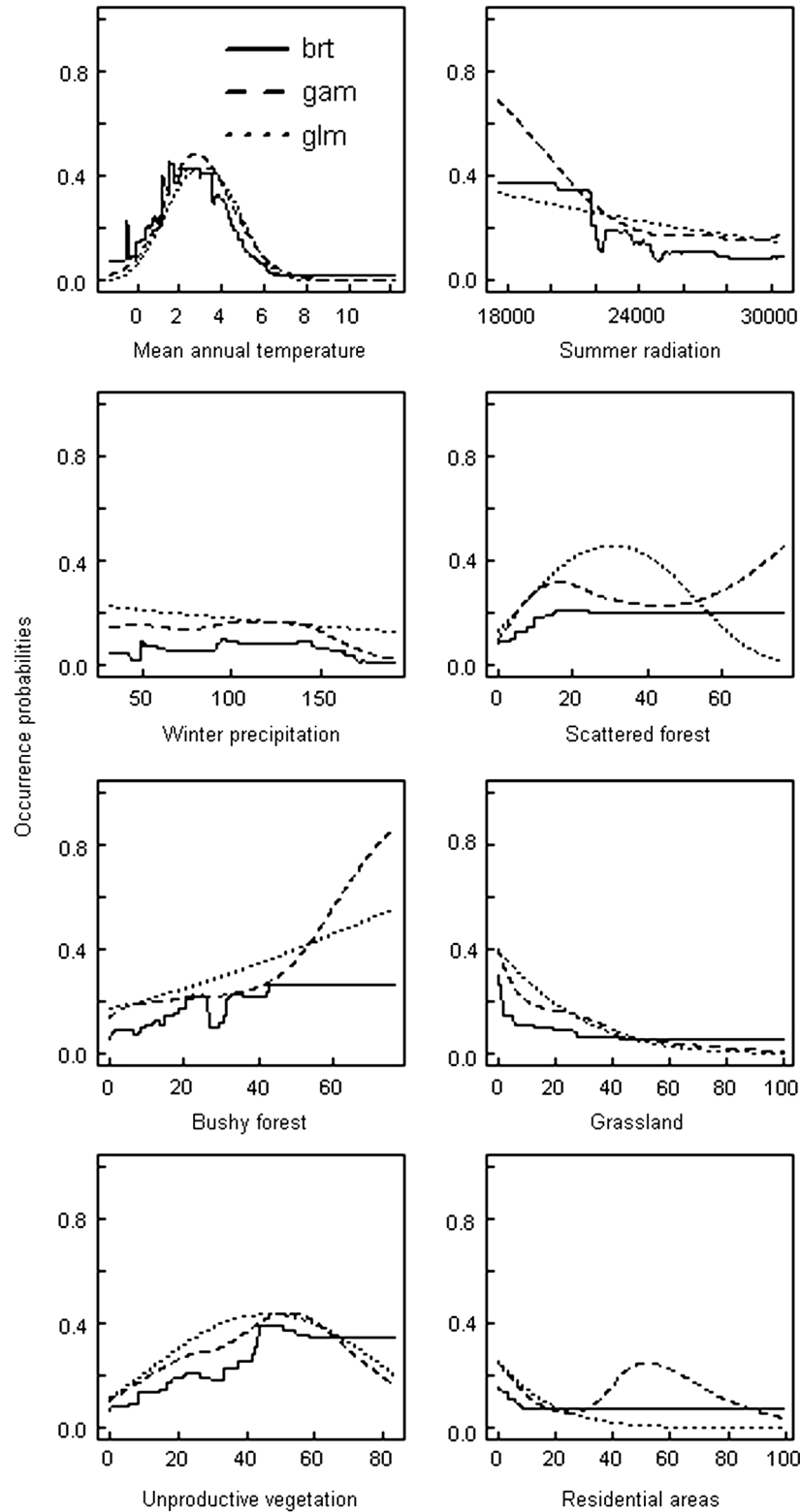


Figure 1. Partial dependence plots for all eight environmental predictors and for the three different SDM algorithms (BRT, GAM, GLM).

the most important uncertainty component for geographic features. Specifically, the variation in mean elevation was best explained by climate scenarios (Table 4, Fig. 2). Also, the choice of SDM algorithms had no effect on population dynamic features, but explained a considerable amount of

variance in mean population centres and in mean elevation. Probability of survival proved to be the most crucial demographic parameter (Table 4). For example, the linear models fitted to the results of the sensitivity analysis estimated that an increase in survival probability of 0.01 would

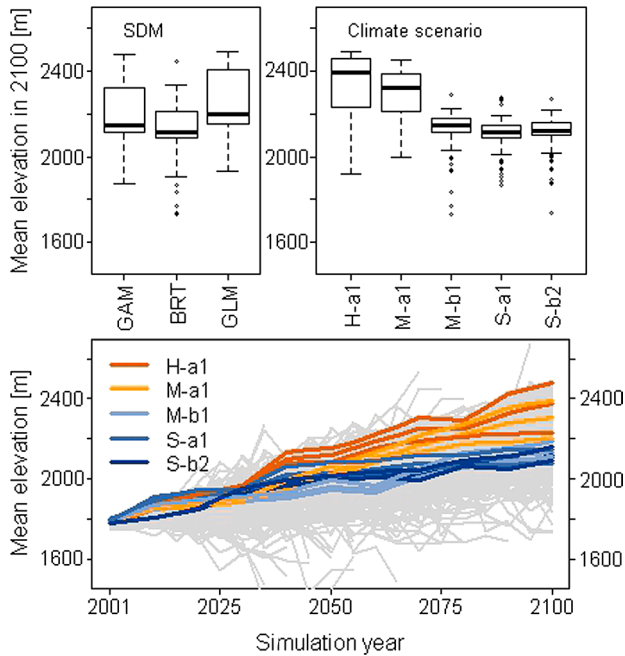


Figure 2. Mean elevation occupied by black grouse for scenarios of climate change. Bottom: grey lines show mean elevations across all simulations, coloured lines those for default IBM parameterisation (cf. Table 2) across different SDMs and climate scenarios. Top: boxplots depict variation of mean elevations predicted for the end of 21st century (2100) and for different SDMs and climate scenarios.

cause an increase in population size of 3000 to 4000 individuals (compare Supplementary material Appendix 1, Fig. A5). Under current climate, survival probability alone represented 55% of variation in population size and even 68% of variation in occupied area size. While probability of extinction by 2100 was zero for the default IBM parameterisation, decreases in the demographic parameters especially survival probability led to black grouse extinction in up to 90% of the simulations on average (Fig. 5). Conversely, increases in the demographic parameters reversed climate-induced population declines and even led to temporarily increasing population sizes (Fig. 4). The shape of the probability distribution of *pleadYoung* (more flattened or more peaked; determined by standard deviation of the Gaussian distribution, Table 2) and, thus, the magnitude of environmental stochasticity, had no effect on the mean predictions but only resulted in slightly increased variability between replicates of simulations. We

Table 3. Model output for default IBM parameterisation, averaged across different SDM algorithms and climate scenarios. For each combination of SDM algorithm and climate scenario the IBM was run with 100 replicate simulations.

Output	Year	Mean	SE	Median
Population size	2001	5508	56	5144
	2050	2318	36	1998
	2100	974	21	703
Area size [km ²]	2001	3221	27	3090
	2050	1478	20	1323
	2100	662	14	504
Mean elevation [m]	2001	1791	1	1791
	2050	2039	15	2026
	2100	2217	32	2171

calculated a consensus map across all simulations as the fraction of simulations ($n = 1215$) that predicted black grouse to be present at a site (Fig. 6). Under current climate, consensus about black grouse presence was very high ($> 80\%$) in the Swiss Alps and intermediate (20–60%) for most parts of the Jura mountains where black grouse are in fact absent (Schmid et al. 1998). With ongoing climate change, consensus on presence sites decreased considerably as extinction probability increased for many model configurations.

Discussion

In this study, we integrated correlative species distribution models and a simple, spatially explicit individual-based model to predict climate-induced range dynamics of black grouse in the Swiss Alps and evaluated variability introduced by different uncertainty components. By this, we were able to better understand important features of range predictions and current as well as transient population dynamics. Our results clearly show that extinction risks cannot simply be approximated by expected changes in suitable habitat (Akçakaya et al. 2006, Keith et al. 2008, Brook et al. 2009). Rather, the expected population trajectory seems to result from a complex interplay between available habitat and demographic processes. Our study also underscores the necessity of sensitivity analyses in dynamic range predictions. Predicted population response to environmental change may be highly variable, both quantitatively as well as qualitatively. Thus, robustness of modelling results can only be assessed if the inherent uncertainty is explicitly considered.

Black grouse population and range dynamics

We were very careful in choosing SDM algorithms and climate scenarios that were both realistic and reflected a range of predictions reaching from pessimistic to optimistic. Overall, all three SDMs produced congruent predictions of habitat change (Supplementary material Appendix 1, Fig. A3). Absolute area size of suitable habitat, however, differed slightly and differences became more pronounced with ongoing climate change. This both corroborates and contradicts findings of previous studies. On the one hand, differences between predictions become more pronounced the further we project into the future which is in line with earlier findings (Thuiller 2004, Pearson et al. 2006, Buisson et al. 2010). Consensus between SDM predictions was still remarkably high though (Supplementary material Appendix 1, Fig. A4) while earlier studies partially reported highly contrasting predictions (Buisson et al. 2010). Nevertheless, further research is needed regarding why method performance and predictions differ (Elith and Graham 2009) and to provide general guidelines on appropriate model choice.

By the end of the 21st century, differences in suitable area were larger between climate scenarios than between SDMs. Considerable loss in suitable habitat was predicted for two out of five climate scenarios, namely for the more extreme climate scenarios with mean temperature increases between 4°C and 5°C. Current trends in CO₂ emissions and global air temperature indicate that expected increases in

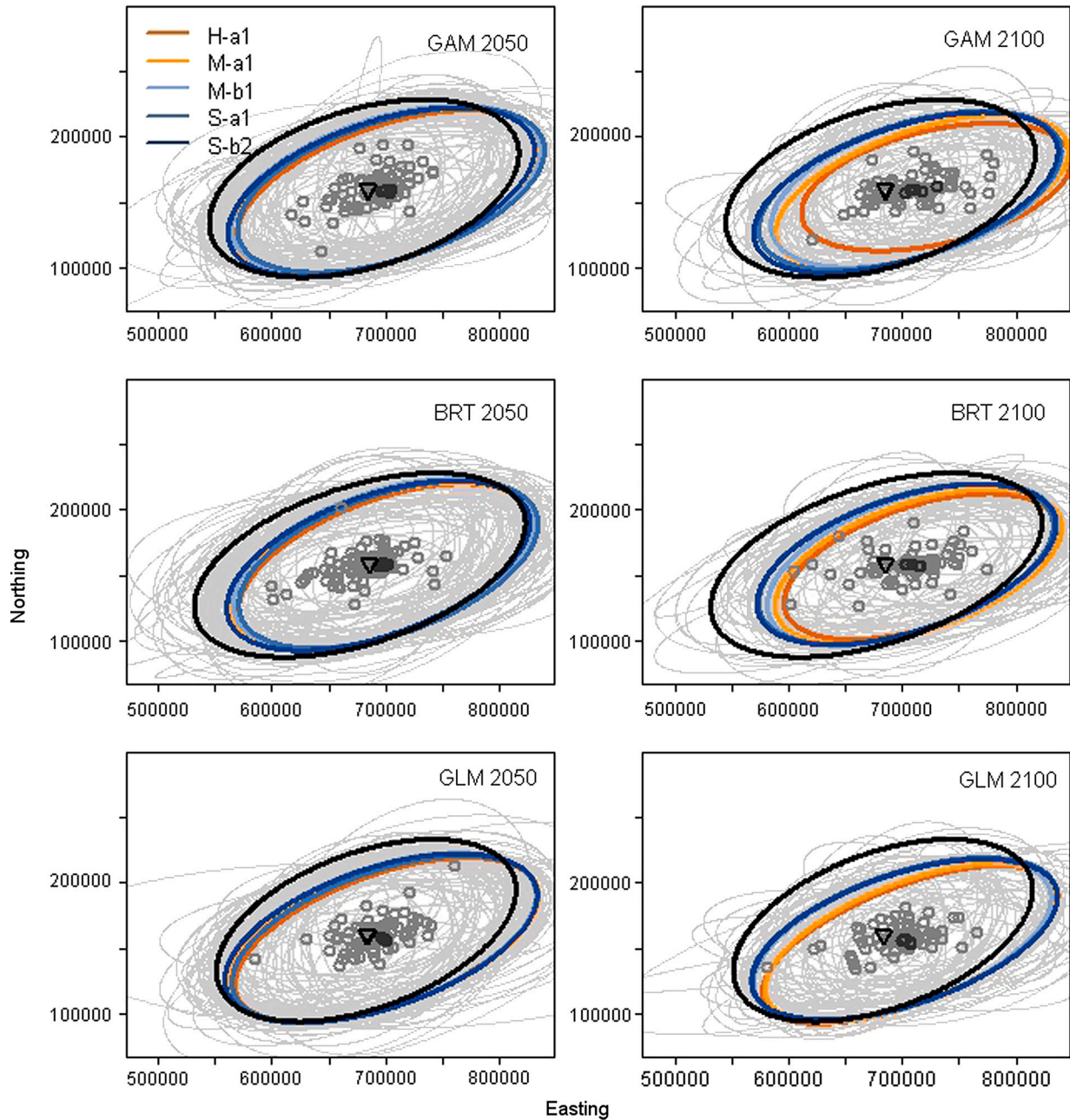


Figure 3. Mean population centres of black grouse for scenarios of climate change. Small symbols show mean population centres predicted for different SDMs (from top to bottom) and for the years 2050 (left) and 2100 (right) across different climate scenarios and model parameterisations. Thereby, dark triangles depict current population centre, dark circles depict default IBM parameterisation (cf. Table 2), light circles depict all simulated population centres for the respective time slice. Ellipses depict 1.5 directional standard deviation. Black ellipses depict current black grouse range, coloured ellipses depict default IBM parameterisation, grey ellipses depict all simulated ranges for the respective time slice.

temperature may be at the upper end of current climate projections or even above (Rahmstorf et al. 2007). Thus, while absolute area size of suitable habitat is predicted to remain more or less unchanged until the middle of the century, in the second half of the century abrupt losses in suitable area of 40% are not unlikely to expect. However, our results also clearly demonstrate that suitable and actual habitat are not directly related and, thus, population trajectory may take a different course than suitable habitat (Supplementary material Appendix 1, Fig. A5).

In the dynamic model runs, the area of suitable habitat was not completely occupied by black grouse. Under current environmental conditions, the high sensitivity of occupied area size to survival probability indicated high site turnover where suitable habitat frequently became unoccupied. Higher survival probabilities and, thus, higher local persistence ability led to lower site turnover, more complete range filling, and consequently to greater area occupied and less fragmented ranges. Although the model predicted only small declines and shifts in suitable habitat early in the 21st

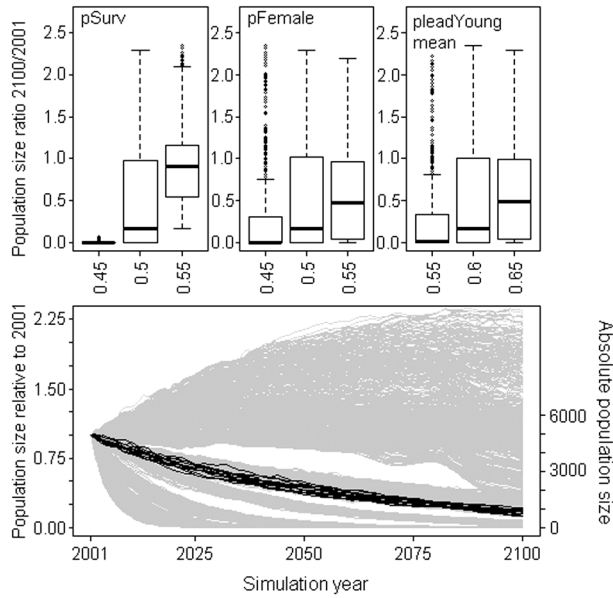


Figure 4. Population size relative to 2001 (current climate). Bottom: grey lines show relative population trajectories across all simulations, black lines those for default IBM parameterisation (cf. Table 2) across different SDMs and climate scenarios. Top: boxplots depict population size ratio of year 2100 relative to 2001 for different demographic parameters.

century, gradual declines in black grouse population and occupied area sizes were predicted across all climate scenarios and underlying SDMs. This primarily resulted from a negative trend in population growth given the observed demographic rates (Fig. 4). On the other hand, Schmid et al. (1998) judged the population to be stable but these estimates rely only on rather short time periods. The strong fluctuation and high site turnover predicted by our model suggest that longer observation periods are needed to accurately assess

black grouse population status. Reassuringly, however, even with the negative trend in current population growth rate, population size is predicted to not fall below 1000 hens by 2100 which is a decent population size especially as that population is predicted to thrive in continuous areas (Fig. 6).

Our results underscore that inferring extinction risks simply from quantity of suitable habitat might be misleading (Supplementary material Appendix 1, Fig. A5; Akçakaya et al. 2006, Keith et al. 2008, Brook et al. 2009). A non-dynamic approach might considerably underestimate extinction risks because important interactions between life history traits and habitat suitability would be ignored. Expected mean abundance is only indirectly related to habitat suitability through demographic functions which determine site turnover and, thus, how much of available habitat is maximally occupied at the time (Table 4). Considering the differences between habitat suitability predictions by different SDM algorithms and the associated population dynamics (Supplementary material Appendix 1, Fig. A5), expected mean abundance also depends on spatial distribution of available habitat and on the degree of fragmentation.

Robustness of range predictions

Our study not only highlights the benefits of a dynamic approach to range predictions but also underlines that we have to deal with immense additional prediction uncertainty when modelling population dynamics and that robustness of model results needs to be explicitly assessed. Here, quantitative predictions of absolute population and occupied area size as well as probability of extinction showed great variations across simulations (Table 4). This is in accordance with previous criticism on spatially explicit simulation models (SEPM, Dunning et al. 1995) and related population viability analysis (PVA) expressing concerns about taking predictions, for example probabilities of extinction, at face value

Table 4. Sensitivity analysis of model outputs based on $n = 1215$ model configurations.

Output	Year	Mean	SE	Median	N	SDM	RCM	Explained variance R^2 by uncertainty components and direction of influence (in parentheses)		
								pSurv	pFemale	plead Young mean
Population size	2001	15 430	558	5127	1215	0	0	0.55 (+)	0.14 (+)	0.10 (+)
	2050	17 330	618	2207	1215	0	0	0.60 (+)	0.11 (+)	0.08 (+)
	2100	13 770	521	856	1215	0	0.04	0.52 (+)	0.09 (+)	0.07 (+)
Probability of extinction	2001	0	0	0	1215					
	2050	0.23	0.01	0	1215	0	0	0.44 (–)	0.10 (–)	0.08 (–)
	2100	0.38	0.01	0	1215	0	0	0.59 (–)	0.08 (–)	0.07 (–)
Area size [km ²]	2001	4462	120	3022	1215	0	0	0.68 (+)	0.12 (+)	0.09 (+)
	2050	4339	138	1389	1215	0	0	0.63 (+)	0.09 (+)	0.07 (+)
	2100	3685	126	585	1215	0	0.02	0.56 (+)	0.08 (+)	0.07 (+)
Mean elevation [m]	2001	1788	0.19	1790	1215	0.18	0.13	0.14 (+)	0.05 (+)	0.03 (+)
	2050	2014	2.33	2013	1102	0.08	0.40	0.11 (+)	0.01 (+)	0.01 (+)
	2100	2199	4.39	2159	900	0.14	0.63	0.03 (+)	0	0
Mean population centre	2001 Easting	683 600	57	684 000	1215	0.18	0	0.21 (+)	0.05 (+)	0.03 (+)
	2001 Northing	160 000	20	159 800	1215	0.50	0	0	0	0
	2050 Easting	694 800	422	697 000	1102	0.01	0.01	0.10 (+)	0	0
	2050 Northing	158 400	176	158 200	1102	0.01	0.01	0.01 (–)	0	0
	2100 Easting	707 200	581	706 700	900	0.05	0.13	0.01 (+)	0	0
	2100 Northing	157 400	187	157 200	900	0.06	0	0.02 (–)	0	0

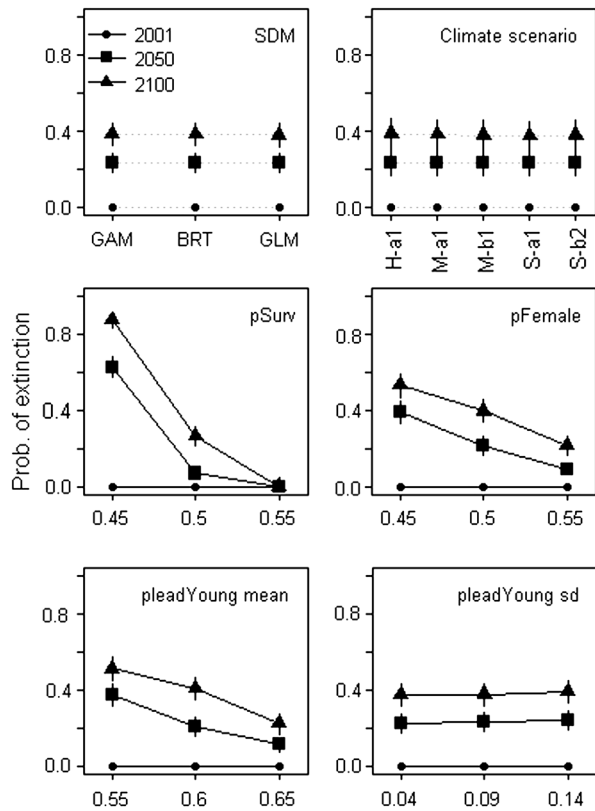


Figure 5. Effects of different uncertainty components on probability of extinction for the years 2001 (current climate), 2050 and 2100. Symbols indicate mean values, errors bars show 99 percent confidence interval.

(Beissinger and Westphal 1998, McCarthy et al. 2003). Alternatively, we could have made qualitative predictions by evaluating relative differences among model outputs. However, previous SEPM and PVA discussions focused on equilibrium population dynamics opposed to transient dynamics as expected under environmental change. In our black grouse system, also predictions of relative population size were fragile across parameter space and rather sensitive to demographic parameters and available habitat (Fig. 4). We believe this is a symptom of two general problems when using such simple SEPMs in combination with SDMs in environmental change context. First, it is difficult to determine reasonable error margins for the highly aggregated demographic parameters to be used in robustness analysis of model predictions. Second, if the structure of the demographic model is very simple this may lead to high parameter sensitivity and thus large prediction uncertainty.

For the sensitivity analysis of the demographic parameters, we chose a heuristic rather than applied view by perturbing the parameters in fixed intervals of $\pm 5\%$ instead of choosing error margins that could be expected in the field. One reason for this was simply because such error margins were difficult to evaluate for Swiss black grouse, which probably holds for the majority of populations/species. On the other hand, longer-term predictions are inherently risky for example due to unforeseeable fluctuations induced by the environment and that way current error margins for demographic parameters might not be very meaningful under climate change. In this respect, we find it reasonable to heuristically choose

the parameter space as it allows theoretically circumscribing possible population outcomes given these boundary conditions. Although, we believe that the fixed interval of $\pm 5\%$ of the respective demographic rate is greater than the error range that could reasonably be expected in Switzerland for these highly aggregated parameters, for example survival probability.

It is known from PVA that very simple population models generally exhibit high parameter sensitivity and thus large prediction uncertainty (Beissinger and Westphal 1998, Grimm and Storch 2000). Arguably, combined population – SDM models should be as simple as possible because they have to cover a wide range of habitat types and environmental conditions. Due to its simplicity the model presented here is also highly general and – especially in conjunction with extensive sensitivity analysis – it provides valuable insights into possible population outcomes for Swiss black grouse. However, the large parameter sensitivity in the demographic model may in part arise because important mechanisms shaping population response are missing or inadequately represented in the model structure. For example, Grimm et al. (2005b) suggested that simple population models may overestimate extinction risk because they lack certain buffer mechanisms that reduce environmental stochasticity. Thereby, the most simple and general buffer mechanism that could be considered is individual variability such that individuals differing in fitness are not equally affected by environmental fluctuations (Rossmanith et al. 2006). Also, the exact form of density dependence and carrying capacity may strongly affect predicted extinction risks (Beissinger and Westphal 1998). Although assuming a linear link between demographic parameters (here, carrying capacity) and predicted habitat suitability is the only practicable approach given general data limitations, this is not fully supported by empirical findings and further research is required in this field (Gallien et al. 2010).

Challenges in species distribution modelling

By integrating predictions of habitat suitability made by correlative species distribution models with spatially explicit, dynamic population models we are able to overcome some limitations associated with SDMs. For example, by relaxing the equilibrium assumption such combined models allow the prediction of transient population response to environmental change. However, spatially explicit population models do not solve all problems associated with correlative SDMs in global change context. Most importantly, we still assume constant species-environment relationships (niche conservatism, Pearman et al. 2008). This assumption underlies both the correlative model producing habitat suitability maps and it also underlies the constant demographic rates in the population model. Thus, spatially explicit population models like our black grouse IBM are only valid as long as environmental change only shifts the environmental conditions in space. Changes in biotic interactions as well as ecological and behavioural adaptations will violate this assumption of niche conservatism. Also, demographic rates might change in response to changing environmental conditions, for example if environmental stress regimes change. As

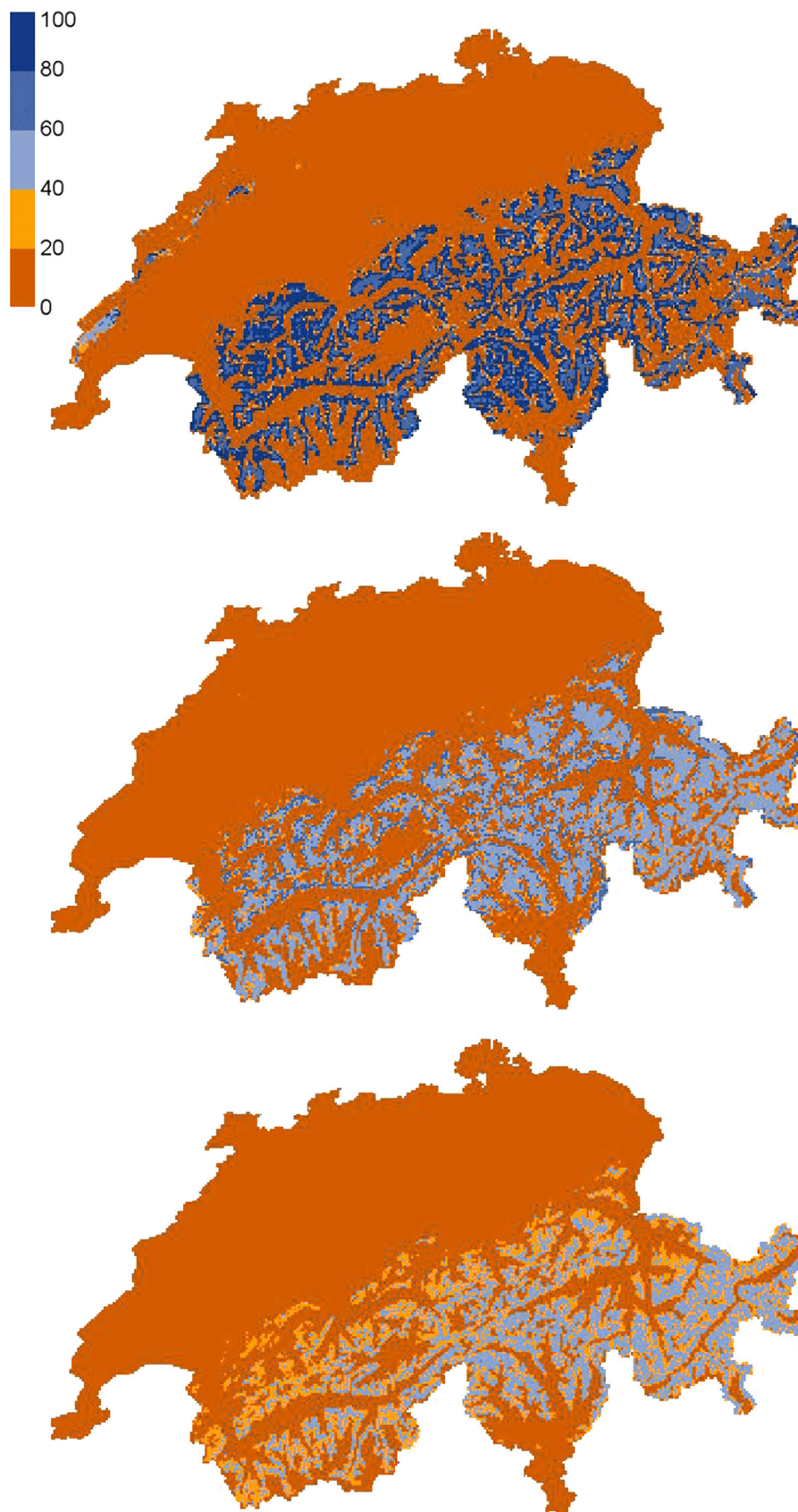


Figure 6. Consensus on black grouse presence for years 2001 (top), 2050 (centre) and 2100 (bottom); calculated as the fraction of all simulations ($n = 1215$) predicting black grouse to be present. (Note that zero percent consensus on presence equal 100 percent consensus on black grouse absence.)

we have shown, possible population outcomes for changing boundary conditions (e.g. demographic rates) can be assessed via sensitivity analyses.

More realistic model assumptions can be achieved by including demographic rates and behavioural adaptations that are ecophysiologicaly informed and based on first principles. For example, biophysical or mechanistic SDMs could provide biophysical calculations as key input data for dynamic population models and include e.g. climate-dependent vital rates, movement potential and sex ratios (Kearney and Porter 2009). Moreover, the individual-based perspective taken here allows easy implementation of diverse behavioural responses such as feeding location or prey selection (Railback and Harvey 2002, Stillman and Goss-Custard 2010), consideration of spatial characteristics such as resource heterogeneity and direct interactions between these two, for example through resource depletion (Grimm and Railsback 2005). Also, selective pressures and genetic adaptation can easily be incorporated (Burton et al. 2010). Thus, various processes could be included in our model framework potentially increasing realism in the model. Dynamic models that are based on first principles can be designed to predict the response of demographic parameters to the full range of environmental conditions of concern, even including conditions for which no demographic data exist (Goss-Custard et al. 2006). Such models require considerable resources for development and testing, and certainly cannot be developed for all species. However, once such a model exists, it can be relatively straightforward to adopt its design to similar species (Stillman 2008). Both simple and more complex population models can be valuable for predicting species distributions. The right choice depends on how important model predictions are for supporting decision making, and on how much resources one is able, or willing, to invest.

A crucial issue for mechanistic range predictions is the availability of data for model parameterisation as well as validation. For making sensitivity analyses of range predictions, a standard tool has the benefit that also indirect sources can be utilised for model parameterisation without sacrificing robustness or reliability of model results. Indirect sources may include life history data obtained from different subpopulations or from related species (Keith et al. 2008) or demographic parameters derived from allometric relationships (Cheung et al. 2009). Pattern-oriented modelling is a general strategy for systematically exploiting the information contained in such multiple, often qualitative, patterns observed at different scales and levels of organization (Wiegand et al. 2003, Grimm et al. 2005a). One important element of this approach, parameterisation by Monte-Carlo filtering of parameter combinations, can be complemented by Bayesian parameterisation methods (Hartig et al. 2011, Martinez et al. 2011).

One source of uncertainty that we did not include in our case study is land use and land cover change. Further investigations are needed to understand the role land use change may play for the persistence of black grouse in the Swiss Alps. For example, black grouse are known to respond sensitively to abandonment of alpine summer pastures with accompanying shrub encroachment and reforestation. Here, we included land use variables as static predictors only. In future studies, the interactions of land use and climate change should be evaluated.

Conclusions

Integrating correlative species distribution models into spatially explicit population models for predictions of large-scale range dynamics allows for a more direct, multifaceted view of complex, spatiotemporal species' response to environmental change and related extinction risks. However, without explicit assessment of robustness of predictions, for example by means of sensitivity analysis, the task remains of more theoretical nature. The merit of developing dynamic population models for climate impact studies only becomes apparent and the effort justified when this undertaking is accompanied by explicit investigation of sensitivity and robustness of the results. This substantially increases the confidence in range predictions and, as a more direct benefit, increases our mechanistic understanding of the studied ecological system and the expected population response. Further research is needed to provide general guidelines for models predicting climate-induced range dynamics. Thereby, challenges remain for both static and dynamic modelling components and include, for example, the choice of appropriate SDM algorithms, the role of land use and climate change, model structure and complexity, or the design of robustness analysis. Addressing these challenges will help to establish this comparably new avenue of climate impact assessment as a feasible and reliable tool.

Acknowledgements – DZ received partial financial support by the Univ. of Potsdam Graduate Initiative on Ecological Modelling UPGradE. We acknowledge the European Commission's 6th Framework Programmes ENSEMBLES (contract GOCE-CT-2003-505539) for climate data provisioning and ECOCHANGE (contract GOCE-CT-2007-036866) for downscaling.

References

- Akçakaya, H. R. et al. 2006. Use and misuse of the IUCN Red List Criteria in projecting climate change impacts on biodiversity. – *Global Change Biol.* 12: 2037–2043.
- Allouche, O. et al. 2006. Assessing the accuracy of species distribution models: prevalence, kappa and the true skill statistic (TSS). – *J. Appl. Ecol.* 43: 1223–1232.
- Anderson, B. J. et al. 2009. Dynamics of range margins for metapopulations under climate change. – *Proc. R. Soc. B* 276: 1415–1420.
- Araújo, M. B. and Guisan, A. 2006. Five (or so) challenges for species distribution modelling. – *J. Biogeogr.* 33: 1677–1688.
- Araújo, M. B. and Luoto, M. 2007. The importance of biotic interactions for modelling species distributions under climate change. – *Global Ecol. Biogeogr.* 16: 743–753.
- Araújo, M. B. and New, M. 2007. Ensemble forecasting of species distributions. – *Trends Ecol. Evol.* 22: 42–47.
- Araújo, M. B. et al. 2002. Dynamics of extinction and the selection of nature reserves. – *Proc. R. Soc. B* 269: 1971–1980.
- Araújo, M. B. et al. 2005. Validation of species-climate impact models under climate change. – *Global Change Biol.* 11: 1504–1513.
- Barry, S. and Elith, J. 2006. Error and uncertainty in habitat models. – *J. Appl. Ecol.* 43: 413–423.
- Beaumont, L. et al. 2008. Why is the choice of future climate scenarios for species distribution modelling important. – *Ecol. Lett.* 11: 1135–1146.

- Beissinger, S. R. and Westphal, M. I. 1998. On the use of demographic models of population viability in endangered species management. – *J. Wildl. Manage.* 62: 821–841.
- Brook, B. W. et al. 2000. Predictive accuracy of population viability analysis in conservation biology. – *Nature* 404: 385–387.
- Brook, B. W. et al. 2009. Integrating bioclimate with population models to improve forecasts of species extinctions under climate change. – *Biol. Lett.* 5: 723–725.
- Buckley, L. B. and Roughgarden, J. 2004. Biodiversity conservation: effects of changes in climate and land use. – *Nature* 430: 34.
- Buisson, L. et al. 2010. Uncertainty in ensemble forecasting of species distribution. – *Global Change Biol.* 16: 1145–1157.
- Burgman, M. A. et al. 1993. Risk assessment in conservation biology. – Chapman and Hall.
- Burton, O. J. et al. 2010. Trade-offs and the evolution of life-histories during range expansion. – *Ecol. Lett.* 13: 1210–1220.
- Caizergues, A. and Ellison, L. N. 2002. Natal dispersal and its consequences in black grouse *Tetrao tetrix*. – *Ibis* 144: 478–487.
- Cheung, W. W. L. et al. 2009. Projecting global marine biodiversity impacts under climate change scenarios. – *Fish Fish. Ser.* 10: 235–251.
- Dormann, C. F. 2007. Promising the future? Global change projections of species distributions. – *Basic Appl. Ecol.* 8: 387–397.
- Dormann, C. F. et al. 2008. Components of uncertainty in species distribution analysis: a case study of the great grey shrike. – *Ecology* 89: 3371–3386.
- Dunning, J. B. et al. 1995. Spatially explicit population models: current forms and future uses. – *Ecol. Appl.* 5: 3–11.
- Elith, J. and Graham, C. H. 2009. Do they? How do they? WHY do they differ? On finding reasons for differing performances of species distribution models. – *Ecography* 32: 66–77.
- Elith, J. and Leathwick, J. R. 2009. Species distribution models: ecological explanation and prediction across space and time. – *Annu. Rev. Ecol. Evol. Syst.* 40: 677–697.
- Elith, J. et al. 2006. Novel methods improve prediction of species' distribution from occurrence data. – *Ecography* 29: 129–151.
- Elith, J. et al. 2008. A working guide to boosted regression trees. – *J. Anim. Ecol.* 77: 802–813.
- Engler, R. et al. 2011. 21st century climate change threatens mountain flora unequally across Europe. – *Global Change Biol.* 17: 2330–2341.
- Fielding, A. H. and Haworth, P. F. 1995. Testing the generality of bird-habitat models. – *Conserv. Biol.* 9: 1466–1481.
- Fielding, A. H. and Bell, J. F. 1997. A review of methods for the assessment of prediction errors in conservation presence/absence models. – *Environ. Conserv.* 24: 38–49.
- Gallien, L. et al. 2010. Predicting potential distributions of invasive species: where to go from here? – *Divers. Distrib.* 16: 331–342.
- Goss-Custard, J. D. et al. 2006. Test of a behavior-based individual-based model: response of shorebird mortality to habitat loss. – *Ecol. Appl.* 16: 2215–2222.
- Graf, R. F. et al. 2007. What you see is where you go? Modeling dispersal in mountainous landscapes. – *Landscape Ecol.* 22: 853–866.
- Grimm, V. and Storch, I. 2000. Minimum viable population size of capercaillie *Tetrao urogallus*: results from a stochastic model. – *Wildl. Biol.* 6: 219–225.
- Grimm, V. and Railsback, S. F. 2005. Individual-based modeling and ecology. – Princeton Univ. Press.
- Grimm, V. et al. 2005a. Pattern-oriented modeling of agent-based complex systems: lessons from ecology. – *Science* 310: 987–991.
- Grimm, V. et al. 2005b. Importance of buffer mechanisms for population viability analysis. – *Conserv. Biol.* 19: 578–580.
- Grimm, V. et al. 2006. A standard protocol for describing individual-based and agent-based models. – *Ecol. Model.* 198: 115–126.
- Grimm, V. et al. 2010. The ODD protocol: a review and first update. – *Ecol. Model.* 221: 2760–2768.
- Guisan, A. and Zimmermann, N. E. 2000. Predictive habitat distribution models in ecology. – *Ecol. Model.* 135: 147–186.
- Guisan, A. and Thuiller, W. 2005. Predicting species distribution: offering more than simple habitat models. – *Ecol. Lett.* 8: 993–1009.
- Guisan, A. et al. 2007. What matters for predicting the occurrences of trees: techniques, data, or species' characteristics? – *Ecol. Monogr.* 77: 615–630.
- Hampe, A. 2004. Bioclimate envelope models: what they detect and what they hide. – *Global Ecol. Biogeogr.* 13: 469–476.
- Hartig, F. et al. 2011. Statistical inference for stochastic simulation models – theory and application. – *Ecol. Lett.* doi: 10.1111/j.1461-0248.2011.01640.x
- Heikkinen, R. K. et al. 2006. Methods and uncertainties in bioclimatic envelope modelling under climate change. – *Progr. Phys. Geogr.* 30: 1–27.
- Hosmer, D. W. and Lemeshow, S. 2000. Applied logistic regression. – Wiley.
- Huntley, B. et al. 2004. The performance of models relating species geographical distributions to climate is independent of trophic level. – *Ecol. Lett.* 7: 417–426.
- Jeltsch, F. et al. 2008. The state of plant population modelling in light of environmental change. – *Perspect. Plant Ecol. Evol. Syst.* 9: 171–189.
- Kearney, M. and Porter, W. 2009. Mechanistic niche modelling: combining physiological and spatial data to predict species' ranges. – *Ecol. Lett.* 12: 334–350.
- Keith, D. A. et al. 2008. Predicting extinction risks under climate change: coupling stochastic population models with dynamic bioclimatic habitat models. – *Biol. Lett.* 4: 560–563.
- Liu, C. et al. 2005. Selecting thresholds of occurrence in the prediction of species distributions. – *Ecography* 28: 385–393.
- Martinez, I. et al. 2011. Disentangling the formation of contrasting tree line physiognomies combining model selection and Bayesian parameterization for simulation models. – *Am. Nat.* 177: E136–E152.
- McCarthy, M. A. et al. 1995. Sensitivity analysis for models of population viability. – *Biol. Conserv.* 73: 93–100.
- McCarthy, M. A. et al. 2003. Reliability of relative predictions in population viability analysis. – *Conserv. Biol.* 17: 982–989.
- Meier, E. S. et al. 2011. Climate, competition and connectivity affect future migration and ranges of European trees. – *Global Ecol. Biogeogr.* doi: 10.1111/j.1466-8238.2011.00669.x
- Menard, S. 2000. Coefficients of determination for multiple logistic regression analysis. – *Am. Stat.* 54: 17–24.
- Midgley, G. F. et al. 2002. Assessing the vulnerability of species richness to anthropogenic climate change in a biodiversity hotspot. – *Global Ecol. Biogeogr.* 11: 445–451.
- Pearman, P. B. et al. 2008. Niche dynamics in space and time. – *Trends Ecol. Evol.* 23: 149–158.
- Pearson, R. G. et al. 2006. Model-based uncertainty in species range prediction. – *J. Biogeogr.* 33: 1704–1711.
- Pereira, H. M. et al. 2010. Scenarios for global biodiversity in the 21st century. – *Science* 330: 1496–1501.
- Rahmstorf, S. et al. 2007. Recent climate observations compared to projections. – *Science* 316: 709.
- Railsback, S. F. and Harvey, B. C. 2002. Analysis of habitat-selection rules using an individual-based model. – *Ecology* 83: 1817–1830.
- Reineking, B. and Schröder, B. 2006. Constrain to perform: regularization of habitat models. – *Ecol. Model.* 193: 675–690.
- Rossmanith, E. et al. 2006. Behavioural flexibility in the mating system buffers population extinction: lessons from the lesser spotted woodpecker *Picoides minor*. – *J. Anim. Ecol.* 76: 540–548.
- Rossmanith, E. et al. 2007. Pattern-oriented modelling for estimating unknown pre-breeding survival rates: the case of the lesser spotted woodpecker (*Picoides minor*). – *Biol. Conserv.* 135: 571–580.

- Schifferli, A. et al. 1980. Verbreitungsatlas der Brutvögel der Schweiz. – Swiss Ornithological Inst., Sempach, Switzerland.
- Schmid, H. et al. 1998. Schweizer Brutvogelatlas. Verbreitung der Brutvögel in der Schweiz und im Fürstentum Liechtenstein 1993–1996. – Swiss Ornithological Inst., Sempach, Switzerland.
- Schröder, B. 2008. Species in dynamic landscapes: patterns, processes and functions. – Habilitation thesis, Univ. of Potsdam, Potsdam.
- Söndgerath, D. and Schröder, B. 2002. Population dynamics and habitat connectivity affecting spatial spread of populations – a simulation study. – *Landscape. Ecol.* 17: 57–70.
- Stillman, R. A. 2008. MORPH – an individual-based model to predict the effect of environmental change on foraging animal populations. – *Ecol. Model.* 216: 265–276.
- Stillman, R. A. and Goss-Custard, J. D. 2010. Individual-based ecology of coastal birds. – *Biol. Rev.* 85: 413–434.
- Svenning, J.-C. and Skov, F. 2004. Limited filling of the potential range in European tree species. – *Ecol. Lett.* 7: 565–573.
- Thomas, C. D. et al. 2004. Extinction risk from climate change. – *Nature* 427: 145–148.
- Thuiller, W. 2004. Patterns and uncertainties of species' range shifts under climate change. – *Global Change Biol.* 10: 2020–2027.
- Thuiller, W. et al. 2008. Predicting global change impacts on plant species' distributions: future challenges. – *Perspect. Plant Ecol. Evol. Syst.* 9: 137–152.
- Thuiller, W. et al. 2009. BIOMOD – a platform for ensemble forecasting of species distributions. – *Ecography* 32: 369–373.
- Walther, G.-R. et al. 2002. Ecological responses to recent climate change. – *Nature* 416: 389–395.
- Wiegand, T. et al. 2003. Using pattern-oriented modelling for revealing hidden information: a key for reconciling ecological theory and application. – *Oikos* 100: 209–222.
- Wiens, J. A. et al. 2009. Niches, models, and climate change: assessing the assumptions and uncertainties. – *Proc. Natl Acad. Sci. USA* 106: 19279–19736.
- Zbinden, N. and Salvioni, M. 2003. Verbreitung, Siedlungsdichte und Fortpflanzungserfolg des Birkhuhns *Tetrao tetrix* im Tessin 1981–2002. – *Der Ornithologische Beobachter* 100: 211–226.
- Zimmermann, N. E. and Kienast, F. 1999. Predictive mapping of alpine grasslands in Switzerland: species versus community approach. – *J. Veg. Sci.* 10: 469–482.
- Zimmermann, N. E. et al. 2010. New trends in species distribution modelling. – *Ecography* 33: 985–989.
- Zurell, D. et al. 2009. Static species distribution models in dynamically changing systems: how good can predictions really be? – *Ecography* 32: 733–744.

Supplementary material (Appendix E7200 at < www.oikosoffice.lu.se/appendix >). Appendix 1.