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Selecting from correlated climate variables: a major source of uncertainty for predicting species distributions under climate change

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Correlative species distribution models are frequently used to predict species' range shifts under climate change. However, climate variables often show high collinearity and most statistical approaches require the selection of one among strongly correlated variables. When causal relationships between species presence and climate parameters are unknown, variable selection is often arbitrary, or based on predictive performance under current conditions. While this should only marginally affect current range predictions, future distributions may vary considerably when climate parameters do not change in concert. We investigated this source of uncertainty using four highly correlated climate variables together with a constant set of landscape variables in order to predict current (2010) and future (2050) distributions of four mountain bird species in central Europe. Simulating different parameterization decisions, we generated a) four models including each of the climate variables singly, b) a model taking advantage of all variables simultaneously and c) an un-weighted average of the predictions of a). We compared model accuracy under current conditions, predicted distributions under four scenarios of climate change, and – for one species – evaluated back-projections using historical occurrence data. Although current and future variable-correlations remained constant, and the models' accuracy under contemporary conditions did not differ, future range predictions varied considerably in all climate change scenarios. Averaged models and models containing all climate variables simultaneously produced intermediate predictions; the latter, however, performed best in back-projections. This pattern, consistent across different modelling methods, indicates a benefit from including multiple climate predictors in ambiguous situations. Variable selection proved to be an important source of uncertainty for future range predictions, difficult to control using contemporary information. Small, but diverging changes of climate variables, masked by constant overall correlation patterns, can cause substantial differences between future range predictions which need to be accounted for, particularly when outcomes are intended for conservation decisions.

Species' range-shifts due to recent climate change have been observed across all continents and taxonomic groups (Parmesan and Yohe 2003, Chen et al. 2011) and are expected to accelerate in the future (Houghton et al. 2001), which will further exacerbate the risks of species and population extinction (Thomas et al. 2004). Since this raises questions concerning currently prevailing conservation goals and strategies (Araújo et al. 2004, 2011), the prediction of climate-change effects on species distribution has become a research field of prime scientific and political relevance (Wiens et al. 2009).

Species distribution models (SDMs) are the most common tools for forecasting species range shifts under climate change. These models use a variety of statistical approaches (Guisan and Zimmermann 2000) to describe

species occurrence (or abundance, Renwick et al. 2011) as a function of climate and other environmental predictors, often in a spatially explicit way. The models are usually fitted based on current conditions and extrapolated to future scenarios, on the assumption of niche conservatism (Pearson and Dawson 2003, Dormann 2007, Wiens et al. 2010). SDMs have frequently been criticised for their reliance on that assumption, as well as for neglecting ecological processes such as changes in biotic interactions (but see: Guisan et al. 2006, Araújo and Luoto 2007, Heikkinen et al. 2007), dispersal (but see: Schloss et al. 2012), genetic adaptation (Williams and Jackson 2007, Pearman et al. 2008) or species behavioural plasticity in the face of climate change (Root et al. 2003). Moreover, from a statistical viewpoint, SDMs are considered problematic since they are

not only affected by the various sources of uncertainty inherently associated with correlative modelling (Guisan and Zimmermann 2000, Dormann 2007, Dormann et al. 2008), but they additionally suffer from problems linked with extrapolating to unknown (and un-evaluable) future conditions, which may strongly deviate from the conditions used for calibration (Elith et al. 2010).

Not surprisingly, the steady increase in predictive models is paralleled by a growing number of critical appraisals of their caveats, and by attempts to quantify their various sources of uncertainty in order to refine future projections (Pearson and Dawson 2003, Dormann 2007, Wiens et al. 2009). The focus has been on evaluating the effects of using different statistical modelling approaches (Thuiller 2004, Lawler et al. 2006), data quality in terms of precision (Dormann et al. 2008) and extent (Thuiller et al. 2004, Barbet-Massin et al. 2010), model parameterization (Beaumont et al. 2005, Sydes and Osborne 2011), threshold-selection methods (Thuiller 2004), different greenhouse gas emission scenarios (Thuiller 2004), global atmospheric circulation models or downscaling approaches (Beaumont et al. 2007). One aspect, to our knowledge rarely assessed, is the uncertainty introduced by the selection of climate variables, given the high degree of collinearity between them (Madden and Williams 1978).

SDMs draw on correlations between species occurrence and environmental predictors. However, driven by the same underlying atmospheric circulation processes, climate variables often are strongly correlated (Madden and Williams 1978, Trenberth and Shea 2005, Zhou et al. 2009). Hence, when causal mechanisms of species–climate relationships are unknown, the ‘true’ predictor from a set of collinear variables cannot be identified. As long as the models are only used for interpolation, i.e. for predicting species occurrence under currently prevailing conditions, the selection of a strong correlate instead of the causal driver is of little concern, since similar outcomes can be expected. Extrapolations, however, can be problematic when correlation patterns change over space or time (Dormann et al. 2012). In climate-change forecasts this may be the case, when different climate variables change non-concomitantly, leading to diverging projective outcomes. This problem can be further amplified when one variable out of a ‘correlation-cluster’ needs to be selected, since many modelling approaches are not amenable to high levels of collinearity between predictors (Dormann et al. 2012). In the absence of ecological knowledge about the influence of the descriptors on the process at stake, selection of variables is commonly based on their statistical explanatory performance, under currently prevailing conditions. However, with a set of highly correlated, statistically indistinguishable predictors, the risk of dropping the relevant variable is high, which – in the case of diverging climate change patterns – may even result in predicting opposed trends in future range-developments. In ambiguous situations, particularly when the intention is to predict rather than infer, the inclusion of several correlated, potentially relevant variables in the same model may thus be preferable, as it may lead to a ‘less wrong’ result than when operating with only one single irrelevant predictor arbitrarily selected. Moreover, there are cases in which several

climate parameters are hypothesized, if not recognized, to affect species’ ecology and thus need to be considered. Several approaches specifically designed for – or less sensitive to – collinearity problems may conducive to this purpose, the most common among which have been reviewed by Dormann et al. (2012). Although not free from the above discussed caveats when it comes to extrapolation, machine learning techniques may be among the most suitable, since they enable correlated variables to be considered separately and in interaction, in non-linear relationships (Segurado and Araújo 2004, Araújo et al. 2005).

Even so, evaluating the effect of climate variable selection on species’ range forecasts under unknown future climatic conditions is a challenging task. While variance in range predictions can readily be assessed, their accuracy will remain unknown. Accuracy measurements obtained with present-time data, e.g. using re-substitution or data partitioning methods, may not reflect the models’ performance under altered conditions (Araújo et al. 2005, Elith et al. 2010). Preferably, a temporally independent evaluation should be carried out, which tests the capacity to predict species ranges under former climate conditions. This however requires historical species data of adequate accuracy, from areas undergoing sufficient climatic variation and change (Araújo et al. 2005).

Characterized, as they are, by high spatial variation in both climatic conditions and predicted changes, mountain environments are considered to be ideal regions for exploring the response-ranges of SDMs under scenarios of climate change (Maggini et al. 2011). Moreover, mountain species adapted to cold climatic conditions and with little tolerance to climatic variation (Hulme 2005) are expected to face a particularly high risk of range reduction, if not local extinction (Hughes 2000, Parmesan 2006) and forecasts of this process are a focus of conservation management and policy.

In this study we investigated effects of climate variable selection (in terms of model parameterization) on species range predictions under different climate change scenarios and explored the potential benefit of using several correlated climate variables in combination, using four mountain bird species of conservation concern as a case example. Thereby our objective was not to obtain an optimal prediction for the modelled species’ ranges or to explore the full range of uncertainty thereof, but to evaluate the variation in outcomes introduced by diverging parameterization-decisions at this stage of the model building process while holding all other potential sources of uncertainty constant. Using a small set of ‘standard climate variables’ as an example and comparing the resulting predictions under current, future and – for one of the four species – past historical climatic conditions, we demonstrate the importance of thoroughly appraising change and correlation-patterns of climate variables before parameterizing and interpreting range-forecast models for conservation management.

Material and methods

Model species

We chose four mountain birds, targeted for conservation as model species: the capercaillie *Tetrao urogallus*, the hazel

grouse *Bonasa bonasia*, the pygmy owl *Glaucidium passerinum* and the three-toed woodpecker *Picoides tridactylus*. All four species are listed in Annex 1 of the European Birds Directive (Directive 2009/147/EC) and have been included in regional conservation plans (for the study area see: Mollet et al. 2008, Suchant and Braunisch 2008, Keller et al. 2010). The species were chosen for several reasons. Firstly, their distribution ranges show a high variability with respect to climatic conditions and predicted patterns of climate change, which may be reflected in highly diverging range-forecasts. Secondly, the available species data are precise enough to capture small-scale spatial divergence. Thirdly, due to their ability to fly, range shifts are less likely to be constrained by dispersal limitations that were therefore disregarded in the models. Climatic conditions are considered to affect these species both directly, particularly in the breeding season (Moss et al. 2001, Summers et al. 2004, Fayt 2006, Lehtikoinen et al. 2011), and indirectly by influencing the required vegetation conditions (Braunisch and Suchant 2007, 2008). Nevertheless, causal relationships quantifying how particular climate parameters affect the species' distribution patterns remain largely unknown.

Study area

The study area encompassed Switzerland and the federal state of Baden-Württemberg in Germany, comprising a total area of 77 025 km² (Fig. 1). It was selected so as to cover a broad climatic gradient (Supplementary material Appendix 1, Table A1), representative of the four model species' distributions in central Europe, and included three mountain ranges with different altitudinal profiles and sympatric species occurrence: the Black Forest in southwestern Germany, a mainly forested lower mountain range of about 7200 km² in size with an elevation ranging from 120 to 1493 m a.s.l. (mean: 663); the Swiss Jura extending over 4200 km² in western Switzerland and covering an altitudinal range between 500 and 1718 m a.s.l. (mean: 817), and the Swiss Alps with altitudes from 370 up to 4634 m a.s.l. (mean: 1754) covering 17 300 km².

Species data

Current species data

Species data were extracted from two databases, one at the Swiss Ornithological Inst., Sempach, Switzerland (<www.vogelwarte.ch/id>) and the other at the Forest Research Inst. of Baden-Württemberg (FVA), Germany (<www.wildtiermonitoring.de>). Both databases contain long-term observation data from ornithologists, foresters, hunters, birdwatchers as well as research personnel at a minimum resolution of 1 km². For the analyses we selected all observations from 2000 to 2010. Since data were not systematically sampled, we reduced the potential bias arising from spatially variable observation intensities by retaining only one record 1 km⁻², resulting in 542 locations for capercaillie (C), 1473 for hazel grouse (H), 614 for pygmy owl (P) and 577 for the three-toed woodpecker (T), mainly but not



Figure 1. The study area (light gray), encompassing Switzerland and Baden-Württemberg (Germany), with the three major mountain ranges (gray), the Black Forest, Swiss Jura and the Swiss Alps. The dotted polygon indicates the test-area for the independent evaluation of the species distribution model for capercaillie, using back-projection and historical distribution data of 1920.

exclusively distributed across the three mountain ranges of the study area (Supplementary material Appendix 1, Table A2).

Historical capercaillie data

To evaluate the predictive performance of back-projected models, we used historical occurrence data of capercaillie. Exact locations of displaying grounds ('lekking sites', $n = 359$), mapped during the mating season between 1900 and 1920 were available from yearly, area-wide surveys of baronial hunting grounds that covered a large part of the Black Forest (Fig. 1). In order to calculate evaluation indices based on a confusion-matrix, we additionally generated twice the number of (pseudo-) absence locations ($n = 718$), which were randomly drawn from the forest areas within the minimum convex polygon encompassing the lekking sites, but outside a 1 km buffer around these lek locations (Fig. 1). A 1 km-buffer was chosen because it has been shown that capercaillie activity and reproduction typically concentrates within 1 km around the lek (Wegge and Rolstad 1986, Wegge and Larsen 1987).

Environmental variables

Our predictor set included variables of climate, topography and land cover (Table 1). Since the aim of our study was to

Table 1. Environmental variables included in the models, with indication of the sources for Switzerland (CH) and Baden-Württemberg (BW). Vector25/ATKIS: vector formats of landscape objects from topographic maps at a scale of 1:25 000; GEOSTAT/Landsat 5: raster representation of land cover types, resolution of 100×100 m and 30×30 m, respectively; DEM: digital elevation model; BAFU: Federal Office of the Environment; FVA: Forest Research Inst. of Baden-Württemberg; WSL: Swiss Federal Inst. of Forest, Snow and Landscape Research.

Category	Variable	Description	Unit	Source CH	Source BW
Climate	T57	Average temperature May–July	°C	Wordclim/WSL	Wordclim/WSL
	T122	Average temperature Dec.–Feb.	°C	Wordclim/WSL	Wordclim/WSL
	P57	Precipitation sum May–July	mm	Wordclim/WSL	Wordclim/WSL
	P122	Precipitation sum Dec.–Feb.	mm	Wordclim/WSL	Wordclim/WSL
Topography	SLOPE	Slope	degree	DEM	DEM
	TOPEX	Topographic position index	index	DEM	DEM
	EAST	Eastness (sine of aspect)	(–1)–1	DEM	DEM
	NORTH	Northness (cosine of aspect)	(–1)–1	DEM	DEM
	SOLAR57	Pot. solar radiation May–July	Wh m ^{–2}	DEM	DEM
	FOREST	Forest	%	Vektor25 ¹	ATKIS ²
	FOEDGE	Outer forest edge density	m km ^{–2}	Vektor25	ATKIS
Land cover	INTENSIVE	Intensive grassland and arable land	%	GEOSTAT ³ /Vector25	Landsat5 ⁴ /ATKIS
	EXTENSIVE	Extensive grassland	%	GEOSTAT/Vector25	Landsat5/ATKIS
	WETSOIL	Proportion of mires and wet soils	%	Mire inventory BAFU, Vektor25	Mire inventory FVA, ATKIS
	ROADDENS	Density of roads	m km ^{–2}	Vektor25	ATKIS
	SETTLEDIST	Distance to settlements	m	Vektor25	ATKIS

¹<www.swisstopo.admin.ch/internet/swisstopo/de/home/products/landscape/vector25.html>

²<www.lgl-bw.de/lgl-internet/opencms/de/05_Geoinformation/AAA/ATKIS.de>

³<http://brsweb.lubw.baden-wuerttemberg.de>

⁴<www.bfs.admin.ch/bfs/portal/de/index/dienstleistungen/geostat.html>

single out the effects of climate variable selection on range forecasts, we varied only the climate data when projecting to different time-periods, while holding all other variables constant over time.

Climate

We used a simple set of four highly correlated (Spearman's rank correlation coefficient $r_s > 0.7$) climate variables, each of which could reasonably be assumed to affect species ecology: the average temperature (TAVE) in the breeding season (May–July) and in winter (December–February) [°C], and the sum of precipitation (PRCP) in both periods [mm]. Current 'baseline-data' (long-term averages from 1971 to 2000) were derived from the worldclim-dataset (Hijmans et al. 2005) (<www.worldclim.org>), which were downscaled from a resolution of 1 km to 100 m based on the SRTM-V4 digital elevation model and the method described in (Zimmermann and Roberts 2001).

Climate change scenarios for the year 2050 represented long-term averages compiled from data relating to 2031–2050. Since changes of climate variables, and consequential correlation patterns between climate variables, may strongly

differ between climate models, we used four different scenarios (S1–S4, Table 2) based on four regional circulation models (RCM) with four underlying general circulation models (GCM), stemming from different sources and chosen so as to capture the widest range of diverging predictions with respect to the used variables (Table 2). All projections referred to the moderate IPCC (International Panel for Climate Change) emission scenario A1B, with the underlying storyline assuming very rapid economic growth, a global population that will peak in mid-century and decline thereafter, a rapid introduction of new and more efficient technologies, and a balanced use of fossil and non-fossil energy (Nakicenovic et al. 2000). Data were provided at a 100 m resolution that was obtained by adding the anomalies between current and future climate conditions, which were downscaled to 1 km using the change factor methodology (Diaz-Nieto and Wilby 2005) to the current baseline data.

Historical climate data (long-term averages from 1901 to 1920) were obtained from the CRU TS 1.2 Europe (original resolution: 10 arc-minutes (Mitchell et al. 2004)), downscaled to 30 arc-seconds (~1 km) using the worldclim dataset with the change factor methodology (Diaz-Nieto and

Table 2. Climate scenarios used here rely on regional atmospheric circulation models (RCM) developed by different institutes for downscaling general circulation models (GCM). Predicted changes by 2050 (mean and standard deviation) within the study area are provided for the climate variables included in the models. (For variable codes see Table 2.)

Scenario	GCM	RCM	Institute ¹	Δ T57 (°C)	Δ T122 (°C)	Δ P57 (mm)	Δ P122 (mm)
S1	ECHAM5	CLM	MPI ¹	+1.26 (0.36)	+1.77 (0.11)	–3.90 (5.11)	–1.52 (4.89)
S2	HadCM3	HADRN3	HC ²	+2.89 (0.41)	+3.20 (0.19)	–19.06 (5.63)	+1.00 (2.87)
S3	Arpège	HIRHAM3	DMI ³	+1.04 (0.35)	+2.22 (0.16)	+2.48 (5.79)	–8.20 (7.92)
S4	CCSM3	RCA30	SMHI ⁴	+2.32 (0.37)	+2.11 (0.22)	–21.06 (8.44)	+1.44 (3.25)

¹HC: Hadley Center (<www.metoffice.gov.uk>); ²MPI: Max Planck Inst. (<http://cera-www.dkrz.de>); ³DMI: Danmark Meteorological Inst. (<www.dmi.dk/dmi/en/index/klima.htm>); ⁴SMHI: Swedish Meteorological and Hydrological Inst. (<www.smhi.se/en>).

Wilby 2005). All climate data were processed and provided by the Research Unit Landscape Dynamics of the Swiss Federal Research Inst. WSL.

Topography

Five topographical variables (slope, topographic position, eastness, northness and potential solar radiation) were derived from the digital elevation model (DEM) of both countries (Table 1). The topographic position index, calculated with the extension TPI 1.3a for ArcView 3.3 (Jenness 2006), qualifies a point's position relative to the surrounding terrain, with positive values indicating exposed sites such as hilltops or ridges, and negative values representing depressions. The potential solar radiation [Wh m^{-2}] in the breeding season (May–July) was calculated according to (Fu and Rich 2002) using the function 'area solar radiation' in ArcGIS 9.3 (ESRI 2008).

Land cover

Land cover variables encompassed forest cover, outer forest edges, intensively and extensively used agricultural land, wetland (mires and other habitat types on wet soils), as well as roads and settlements. Since different data sources were available for the different variables in the two countries (Table 1), definition of the land use categories was partly constrained by the need to extract similar information from different sources; for this reason intensively used grasslands and arable fields were subsumed to 'intensive farmland', because these categories are not distinguished in the Swiss dataset. With one exception (ROADDENS and SETTLEDIST, Table 1), bivariate correlations for topography and land-cover variables did not exceed $r_s = 0.7$ (Supplementary material Appendix 1, Table A3).

All variables were prepared as ASCII raster maps with a resolution of 50×50 m in the Gauss–Krueger Coordinate system (DHDN 3, Gauss–Krueger Zone 3). To adjust variable resolution to that of the species data, the environmental variables were analysed and summarized within a moving window of 1 km^2 , calculating the mean in the case of continuous variables (e.g. climate and topography variables, distance to settlements), the proportion in the case of binary land cover variables (e.g. forest, wetland) and the density of linear elements (e.g. roads, forest edges) (Table 1). The window size also approximates the home-range size of three of the study species (capercaillie, pygmy owl and three-toed woodpecker) and double the home-range size of the fourth (hazel grouse).

Statistical analysis

Modelling approach

As a method both robust regarding collinearity problems and able to deal with missing absence data (Phillips et al. 2006), we chose a Maximum entropy modelling approach implemented in the software Maxent (Phillips et al. 2004, 2006). Maxent is a machine-learning technique that contrasts the conditions at the species' locations with those prevailing throughout the study area. Thereby an iterative algorithm is used to approach the probability distribution of species presence over all cells of the study area that fits best the environmental conditions at the presence locations,

but at the same time remains as close as possible to uniform (principle of maximum entropy). Environmental variables and functions thereof are used as predictors, including linear, quadratic and product terms, as well as hinge, or threshold, functions (Phillips et al. 2006). Each predictor is weighted by a coefficient, which – starting with a uniform distribution – is iteratively changed until the resulting distribution converges to maximise the likelihood of the occurrence data. In order to avoid over-fitting, the average value for a given predictor is constrained to be close (i.e. within the confidence intervals), but not similar to the empirical average measured over the species locations (for detailed information see Phillips et al. 2004, 2006, Elith et al. 2006, Phillips and Dudík 2008). To best capture the complexity of species–habitat interactions we fitted the models with all predictor functions included ('auto-features'), with a random background sample of 10 000 cells (Barbet-Massin et al. 2012), a maximum of 500 iterations and a convergence threshold of 10^{-5} . The models were evaluated using 10-fold cross-validation, measuring the accuracy by means of area under the receiver operating characteristics curve (AUC, Fielding and Bell 1997). With no absence data available, AUC-statistics were calculated on the random background cells instead (Wiley et al. 2003, Phillips et al. 2006), thus assessing the models' ability to discriminate between 'presence' and 'random' rather than between 'presence' and 'absence'. In this case the maximum achievable AUC is not 1 but $1 - a/2$, where a is the true, but unknown distribution (Phillips et al. 2006, Raes and ter Steege 2007) and AUC values do not reflect absolute, but the relative model performance. The resulting maps, showing the predicted probability of species presence for each raster cell of the study area, were converted into binary 'presence–absence' maps, using the threshold at which the sum of sensitivity and specificity calculated on the test data was maximised (average over the 10 cross-validation replicates).

Model comparison

For each species we generated five models. Four of them (M1–M4) used the environmental variables (Table 1), together with only one of the four climate variables, while the fifth (M5) took advantage of all four climate variables simultaneously. In addition, a sixth map (AV) was generated by producing the un-weighted average of the predictions of M1–M4 (committee averaging, see Araújo and New 2007). We tested for overall differences between the models' predictive accuracy under current conditions by applying a Kruskal–Wallis test to the cross-validation replicates, using a post-hoc Mann–Whitney U-test with Bonferroni-corrected p-values to detect pairwise differences between models.

All models were projected to the climate scenarios of 2050 and the results converted to binary maps of predicted presence and absence. From these, we calculated for each species, and each model-type and scenario: a) the total area of predicted presence under present and future conditions [km^2], b) the proportional change in distribution area compared to the predictions of 2010 (%), and c) the changes in terms of gained, lost and retained area within the selected time horizon. We compared the variation due to climate variable selection within the same scenario ('within scenario

variation') to the variation of the same model in different scenarios ('between scenario variation') by calculating the maximum difference (i.e. the difference between the largest and smallest predicted distribution area, Δ) and the variance (i.e. the standard deviation, σ) between predictions obtained with models using different climate variables (M1 to M4) in the same scenario S_i ($\Delta M_{(Si)}$, $\sigma M_{(Si)}$) and those between models using the same variable M_i in different scenarios (S1–S4) ($\Delta S_{(Mi)}$, $\sigma S_{(Mi)}$). The relation between the two sources of variation were then quantified for each species by calculating the ratio between $\Delta M_{(Si)}$ and $\Delta S_{(Mi)}$ ($\sigma M_{(Si)}/\sigma S_{(Mi)}$, respectively) for the 4×4 possible combinations. As models based on different climate variables may already predict different distribution areas under current climate conditions – which then may add to the differences between future distribution ranges, i.e. bias the results – we used the proportional deviance from the predicted current distribution (b), which corresponds to the species range change index (Buisson et al. 2010), to determine the range of between-model variation.

Back-projections

To compare the predictive performance of differently parameterized models, the models for capercaillie were back-projected to past climate conditions of 1920 and evaluated using historical occurrence data. We calculated different measures of accuracy, the AUC, the maximum Kappa (κ_{\max}) and the percentage of correctly classified evaluation points (PCC) at κ_{\max} (Cohen 1960, Fielding and Bell 1997). Since the same test-data were used, the AUC values of the different models were compared using the method for correlated ROC-curves (DeLong et al. 1988), with Bonferroni-corrected p-values to account for multiple testing. Pairwise differences between Kappa-values were assessed by first estimating the supposed 'common Kappa', as described by Fleiss (1981), which was then used to test for equal Kappa values on the Chi-square distribution. Accuracy measures were calculated and compared in R (R Development Core Team) using the packages PresenceAbsence (Freeman and Moisen 2008) and pROC (Robin et al. 2011) as well as the ArcView 3.3 extension KAPPA_STATS (Jenness and Wynne 2006).

Consistency across SDM-approaches

Since the selection of the modelling technique can considerably affect model outcomes (Thuiller 2004, Lawler et al. 2006), we compared the predictions for current, future and historical distribution of capercaillie obtained with Maxent with the outcomes of three other SDM-approaches that deal differently with collinearity (Dormann et al. 2012): generalized linear models (GLM), generalized additive models (GAM) and boosted regression trees (BRT) were calibrated using the same set of presence and pseudo-(absence) points. GLMs included linear, quadratic and 3rd order polynomials of the predictors, which were retained in the final model based on a stepwise selection function based on Akaike's information criterion (AIC, Burnham and Anderson 2002) (AICstep, R-library MASS). GAMs were fitted using a cubic spline smoother with 3 degrees of freedom (Hastie and Tibshirani 1990), also employing stepwise variable selection for defining the final predictor

set. With BRT, another machine learning technique was employed. This method uses a recursive partitioning algorithm to fit a large number of classification and regression trees, each splitting the response data into groups that are most homogeneous with regard to the predictors, finally combining the trees to provide robust predictions (Friedman 2001). BRT-models were calibrated with a maximum of 2000 trees and a cross-validation procedure to sequentially remove the least important predictors to define the most parsimonious final model (Elith et al. 2008). The models were evaluated and compared as described above.

Results

Climate variables and their changes

Strong collinearity ($r_s > 0.7$) between temperature and precipitation variables was recorded across the study area, and overall correlation patterns did not, or only marginally, differ between current and future conditions and between different scenarios (Table 3, Supplementary material Appendix 1, Table A4). However, the predicted changes of the climate variables (both within and between scenarios) were not correlated in a similar way (Table 3), indicating non-linear changes with regionally diverging developments

Table 3. Correlations (Spearman's rank correlation) between climate variables (current conditions and change scenarios, upper right), and between their changes since 1920 or predicted for 2050, respectively (lower left), measured at 10000 points randomly selected across the study area. For variable and scenario codes see Table 2.

	T57	T122	P57	P122
Current (2010)				
T57	–	0.97	–0.80	–0.81
T122	–	–	–0.75	–0.73
P57	–	–	–	0.78
P122	–	–	–	–
Historical (1920)				
T57	–	0.96	–0.84	–0.87
T122	0.92	–	–0.81	–0.79
P57	–0.16	–0.28	–	0.78
P122	–0.08	–0.22	0.44	–
S1 (E/CLM)				
T57	–	0.98	–0.79	–0.78
T122	–0.16	–	–0.76	–0.73
P57	–0.50	–0.15	–	0.78
P122	–0.55	0.14	0.05	–
S2 (H/HAD)				
T57	–	0.97	–0.77	–0.78
T122	0.32	–	–0.75	–0.74
P57	–0.63	–0.23	–	0.73
P122	–0.38	–0.13	0.38	–
S3 (A/HIR)				
T57	–	0.97	–0.72	–0.78
T122	0.25	–	–0.66	–0.70
P57	0.19	0.42	–	0.76
P122	–0.38	–0.57	–0.42	–
S4 (C/RCA)				
T57	–	0.97	–0.80	–0.78
T122	0.87	–	–0.75	–0.70
P57	–0.59	–0.73	–	0.77
P122	–0.46	–0.36	0.11	–

(Supplementary material Appendix 1, Fig. A1). Differences were recorded for both the strength of the correlations, as well as for their directions, with even opposite changes predicted for the same climate variable in different seasons (e.g. summer temperature was predicted to rise locally in places where winter temperature was predicted to decrease).

Range predictions

All species showed a similar distribution pattern, and climate variables always ranked among the most important predictors (Supplementary material Appendix 1, Table A5). Temperature during the breeding season explained most, winter precipitation the least of the variance in all species, except for the pygmy owl for which precipitation in the breeding season was the least important climate parameter. In the following the results are described for the Maxent-models, unless stated otherwise.

All models performed well in predicting current species distributions (Table 4). Accuracy was highest for the models of capercaillie (mean AUC: 0.937–0.945) and lowest for those of hazel grouse (mean AUC: 0.868–0.882). No significant differences in accuracy were found between models including the different climate variables singly or simultaneously, although the latter models tended to perform best in all species, which was significant in some GLMs, GAMs and BRTs (Supplementary material Appendix 1, Table A6).

Whereas predicted current distribution areas differed only marginally between the models, with regard to both area size and location, great differences were recorded for future forecasts (Fig. 2, 4; Supplementary material Appendix 1, Fig. A2). This finding was consistent over modelling approaches (Fig. 3) and applied to all climate scenarios (Fig. 2), being most pronounced under scenario S2. The variance in future distributions predicted by models using alternative climate variables from the same scenario ($\sigma M_{(Si)}$) was 3.40 (pygmy owl) to 4.53 (capercaillie) times greater than when using different climate change scenarios with the same model ($\sigma S_{(Mi)}$) (3.68 for hazel grouse and 3.55 for three-toed woodpecker); a similar pattern was found for the maximum differences between area-predictions ($\Delta M_{(Si)}$), which were 2.71 (hazel grouse) up to 4.03 times (capercaillie) greater, (3.41 for pygmy owl and 3.58 for three-toed woodpecker). In addition, in the case of capercaillie, the uncertainty in range-forecasts attributable to variable selection was substantially larger than the uncertainty introduced by selecting different modelling methods,

with a 14.82 times greater variance and a 15.69 greater maximum difference between range-changes.

Most models predicted a reduction of the study species' distribution ranges, which was particularly pronounced when including only winter temperature (M3, Fig. 2). On the other hand, range-expansions were also predicted, mainly by models focusing only on precipitation. The area expected to be lost by 2050 was mainly situated at lower altitudes in the lower mountain ranges, Black Forest and Jura, and was generally greater than the area predicted to be gained in higher altitudes in the Alps (Fig. 3, Supplementary material Appendix 1, Table A7, Fig. A2). The averaged models naturally predicted intermediate situations, while the areas obtained with the models including all variables (M5) were always smaller than the average.

Back-projections

Projected back to 1920, the models predicted the historical distribution of capercaillie lekking sites with moderate accuracy ($0.7 < AUC < 0.8$) (Table 5), (Hosmer and Lemeshow 2000), and showed a fair agreement ($0.2 < \kappa_{max} < 0.4$) in terms of Kappa values (Landis and Koch 1977) (Supplementary material Appendix 1, Table A8). As regards the AUC, the models taking into account all variables outperformed the single-variable models, whereas the averaged predictions of these models did not perform better than the best of the single-variable models. This finding was significant for Maxent, GLM, GAM, but remained only a trend for BRT's after applying Bonferroni-correction. A similar pattern was evident for the other evaluation measures (Supplementary material Appendix 1, Table A8).

Discussion

Previous studies have comprehensively discussed and quantified the various sources of uncertainty in SDM-based climate change impact assessments (Araújo et al. 2005, Dormann 2007, Elith et al. 2010). Next to method-inherent aspects (e.g. disregarding biotic interactions, dispersal limitations, and the adaptive potential of the species considered), decisions taken during the model-building process, such as the choice of the statistical approach, the climate change scenarios, or the data used for calibration are among the most frequently mentioned issues. Our study, in line with Synes and Osborne (2011), adds another important aspect, showing that models of similar fit, but

Table 4. Model accuracy (AUC and standard deviation of Maxent-models) based on 10-fold cross-validation. No significant differences exist between the models (Kruskal–Wallis test with post-hoc Mann–Whitney U-tests for pairwise differences, Bonferroni corrected p-values > 0.05 in all cases).

Model	Climate variable	Capercaillie		Hazel grouse		Pygmy owl		Threetoed wp	
		AUC	(SD)	AUC	(SD)	AUC	(SD)	AUC	(SD)
M1	P122	0.939	(0.013)	0.868	(0.015)	0.902	(0.012)	0.903	(0.013)
M2	P57	0.937	(0.013)	0.871	(0.012)	0.895	(0.015)	0.909	(0.013)
M3	T122	0.942	(0.010)	0.876	(0.013)	0.905	(0.011)	0.915	(0.010)
M4	T57	0.942	(0.010)	0.876	(0.013)	0.907	(0.011)	0.916	(0.010)
M5	All	0.945	(0.009)	0.882	(0.011)	0.909	(0.010)	0.919	(0.009)

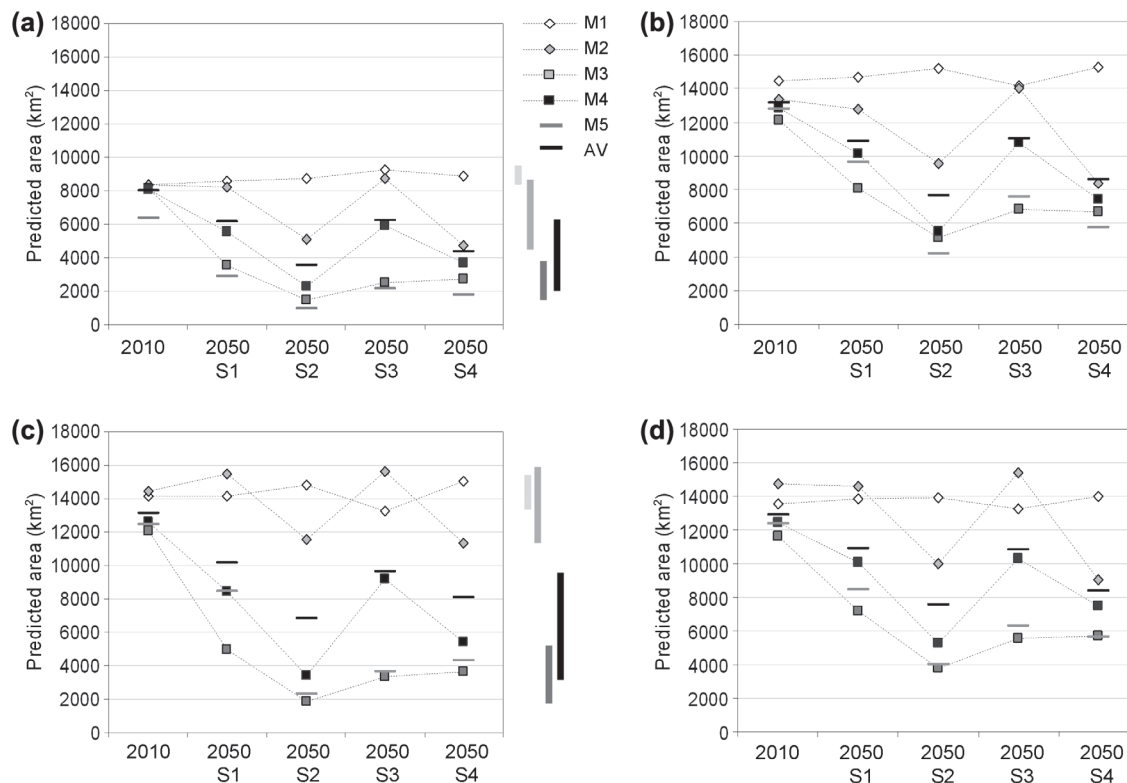


Figure 2. Distribution area of (a) capercaillie, (b) hazel grouse, (c) pygmy owl and (d) three-toed woodpecker, predicted by models based on different correlated climate variables (M1–M4) under current (2010) and future (2050) climate conditions, as predicted by four scenarios of climate change (S1–S4). The lines show the averaged predictions of M1–M4 (black) and a model (M5) including all four climate variables together (grey). The bars on the right indicate the differences between the scenarios for each model (M1: light grey, M2: grey, M3: dark grey, M4: black). The climate change scenarios (S1–S4) are described in Table 2; the models (M1–M5) are defined in Table 3.

parameterized with different but correlated climate variables, may not only predict divergent, unidirectional range changes, but even contradictory range developments, both within and between climate change scenarios. While being aware of the further sources of uncertainty, including possible interactions thereof, we intentionally avoid any comparison or ranking, because we expect the results to be largely dependent on the particular characteristics of the species data and study area. In the following, we focus only on the problem of model parameterization with correlated

climate variables and the consequences for species range predictions.

Correlation patterns and variation in predictions

Climate parameters generally show a high collinearity in space and time, which can cause several problems in species distribution modelling. Effects on the predictive accuracy of SDM's under changing collinearity structures were

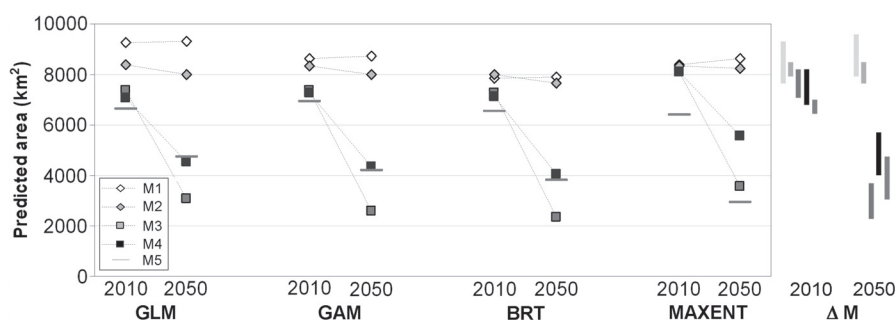


Figure 3. Distribution area of capercaillie predicted by models based on different climate variables used singly (M1–M4) and in combination (M5) under current (2010) and future (2050) climate conditions, comparing 4 different modelling approaches: generalized linear models (GLM); generalized additive models (GAM); boosted regression trees (BRT); and maximum entropy models (Maxent). The bars on the right (ΔM) indicate the differences between the modelling approaches for each model (from left to right: M1: light grey, M2: grey, M3: dark grey, M4: black, M5: medium grey). The models (M1–M5) are specified in Table 3.

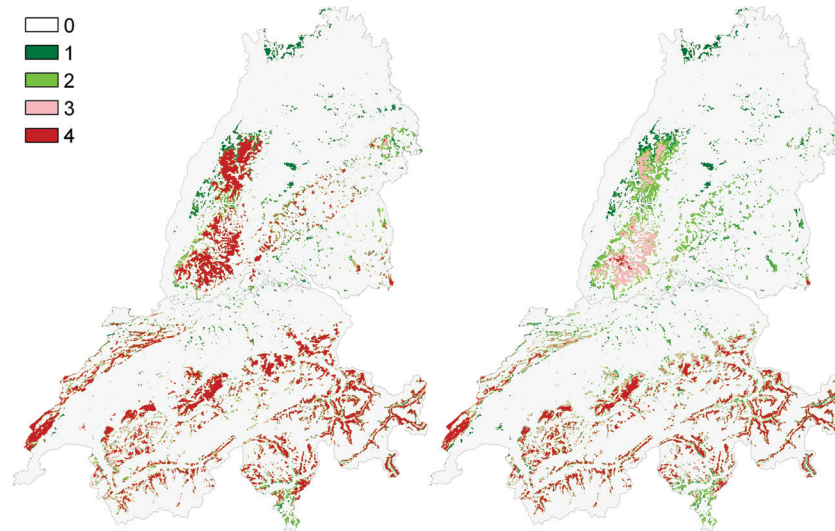


Figure 4. Predicted distribution of capercaillie under current (2010, left) and future (2050, right) climate conditions (scenario S1: ECHAM5/CLM) as predicted by the models M1–M4 (Table 3) including different climate variables (SDM-approach: Maxent). Different colours indicate the consensus between the models, defined as the number of models predicting presence in a pixel.

recently demonstrated by Dormann et al. (2012), who recommended an a priori assessment of collinearity in both the training and the prediction dataset, preferably by means of pairwise diagnostic tools such as correlation matrices. Our study shows that this diagnosis may not suffice: while overall correlation patterns between current and future climate variables were similar (Table 3), great differences were found as regards their changes. As these changes are minor in magnitude compared to the total variable range, they are typically masked by the overall correlation patterns. Yet, they remain crucial because it is ultimately through them that climate-related divergences between current and future predictions occurred, since all other factors were kept constant. In the study area, changes in temperature and precipitation showed great regional and seasonal divergence within and between climate scenarios (Supplementary material Appendix 1, Fig. A1), and their correlations differed not only in magnitude but also in direction. As a result, variable selection generated a high variation in modelling outcomes and even led to contradictory future predictions between ‘single-variable’ models (M1–M4) (Fig. 2, 3, Supplementary material Appendix 1, A2). The predictions of models that included all potentially relevant variables (M5) were mostly within this range of

variation (i.e. between the extremes predicted by the single variable models, Fig. 2, 3) and the projected distribution areas coincided spatially with areas characterized by a high-consensus between M1–M4 (Supplementary material Appendix 1, Fig. A2).

Including multiple correlated climate variables

The pros and cons of model complexity has given rise to controversial discussion as regards projective models under changing environmental conditions (Araújo et al. 2005, Elith et al. 2010). Our results point towards an advantage of complexity, showing that higher parameterized models, including multiple climate predictors, not only deliver a better fit (see also Synes and Osborne 2011) but also a better predictive performance in back-projections. This finding was consistent across four SDM approaches that cope differently with collinearity, suggesting that the benefit from including multiple climate variables in ambiguous situations may even outweigh possible collinearity issues. However, the fact that the predicted future distribution ranges obtained with ‘multiple climate models’ were always smaller in size than in the averaged predictions may also

Table 5. Accuracy of differently parameterized models for capercaillie, projected to 1920 and evaluated with historical occurrence data. Differences between the AUC values were tested using the test for correlated ROC-curves (DeLong et al. 1988). Small letters indicate similarities between models, i.e. AUC values not labelled with the same letter differ significantly (Bonferroni-corrected p-values < 0.05). Different SDM-approaches were applied: Maxent: maximum entropy models, GLM: generalized linear models, GAM: generalized additive models, BRT: boosted regression trees.

Method Model	Variable	Maxent		GLM		GAM		BRT	
		AUC	(SD)	AUC	(SD)	AUC	(SD)	AUC	(SD)
M1	P122	0.716 ^{a,b}	(0.016)	0.678	(0.016)	0.690	(0.016)	0.702 ^a	(0.016)
M2	P57	0.713 ^a	(0.016)	0.700	(0.016)	0.705	(0.016)	0.700 ^a	(0.016)
M3	T122	0.729 ^b	(0.015)	0.721 ^a	(0.016)	0.723 ^a	(0.016)	0.715 ^a	(0.016)
M4	T57	0.727 ^b	(0.016)	0.726 ^a	(0.016)	0.728 ^a	(0.016)	0.718 ^a	(0.016)
Av (M1–4)		0.723 ^b	(0.016)	0.711	(0.016)	0.714	(0.016)	0.711 ^a	(0.016)
M5	All	0.745	(0.015)	0.731	(0.016)	0.739	(0.016)	0.722 ^a	(0.016)

indicate a possible problem of over-fitting (Beaumont et al. 2005).

The inclusion of multiple collinear predictors requires a statistical approach that can deal with collinearity. Several methodological approaches have been developed for this purpose (Dormann et al. 2012). They either involve the use of so-called 'latent variables', constructed from a cluster of correlated ones (e.g. using the orthogonal components of a principal component analysis (PCA) instead of the raw variables), or they belong to a group of methods that use model selection techniques in order to balance model complexity and fit, on the expectation that they will be less sensitive to the caveats inherent in collinearity (Dormann et al. 2012). The former methods are problematic in the context of climate-change because the latent variables, extracted from currently prevailing correlation patterns, cannot be used with diverging future patterns. In contrast, the latter methods, such as machine learning techniques, may be advantageous as they consider climate variables separately (Phillips et al. 2006). Furthermore, they allow for non-linear relationships and interactions between variables and may thus capture species response patterns more realistically (Araújo et al. 2005, Phillips and Dudík 2008). Nevertheless, whenever several correlated predictors share a substantial amount of information, their relative importance remains difficult to assess (Meloun et al. 2002). In our case, ranking of the variables in the multi-climate models was constant over all cross validation replicates of the same model (results not shown), and corresponded to both the relative impact of the variable in the single-variable models (Supplementary material Appendix 1, Table A4) and to the ranking of univariate models regarding their predictive accuracy (results not shown). This suggests that Maxent, through its iterative model fitting approach (Phillips et al. 2006), provides a stable ranking of variables, and may even approximate their relative importance – but this requires further investigation.

Model evaluation and back-projection

In line with previous studies showing that measures of accuracy based on contemporary, non-independent evaluation data are unreliable (because generally over-optimistic) in assessing predictive performance under altered climate conditions (Araújo et al. 2005, Elith et al. 2010), our results show that with models of similar accuracy, not only diverging but even contrasting range developments (i.e. range contractions as well as expansions) may be predicted (Fig. 2, Supplementary material Appendix 1, Table A7). This further demonstrates the inadequacy of re-substitution or cross-validation methods in justifying the preference of one range-forecast over another. Testing back-projections with historical species distribution data are believed to represent the best available option in terms of evaluating species range-forecasts in space and time. Even so, there is no guarantee that the accuracy of a model in predicting past range shifts automatically translates into reliable forecasts (Araújo et al. 2005). Future climatic changes may differ in terms of magnitude, celerity and direction compared to what has been recorded historically. This may

result in totally novel, so far unobserved combinations of environmental conditions. Land-use changes occurring in parallel to climate change can further confound the evaluation results. Moreover, when historical species data from the calibration area are used, temporal autocorrelation effects, for example due to habitat tradition in long-lived species, cannot be excluded, particularly when the lag between time slices is short. Our models for capercaillie were projected 90 yr into the past, with the area used for evaluation representing only a limited part of the calibration area, actually the edge of the distribution range for which the greatest changes were to be expected (Braunisch et al. 2008). In fact, the capercaillie population in this region has dropped dramatically during the past century (Roth 1974), accompanied by a substantial range contraction (Braunisch and Suchant 2006), but this change can only partly be attributed to climate change effects. Land use changes, particularly changes in forest structure, which were not accounted for in this model, are considered to be the main drivers (Suchant and Braunisch 2004). However, we assume that these confounding effects may have similarly affected the evaluation results in all models. Hence they are likely to influence model ranking persistently in the same manner, which means that the significantly 'least wrong' model will still be the best under any given circumstances.

Conclusions and applications

Considering the various sources and high levels of inaccuracy in SDM-forecasts under climate change, the usefulness of these models for species conservation planning has frequently been questioned (Pearson and Dawson 2003, Araújo et al. 2005, Dormann 2007, Wiens et al. 2009). Indisputably, SDMs have their value in exploring a range of possible developments and identifying general common trends among a variety of predictions constructed with different underlying sources of uncertainty. However, the present study also points to a serious potential danger of misinterpretation if not misuse. Climate change impacts on endangered species, either observed or predicted, have led not only to calls for adapting and extending existing conservation strategies or areas (Araújo et al. 2011), but also to questioning the investment of limited resources on endangered populations that are 'anyway doomed to extinction'. Although the uncertainty of forecasts is undisputed in the scientific community, and multi-model approaches such as ensemble-forecasting, consensus maps and other methods quantifying inter-model variance (Araújo and New 2007, Wiens et al. 2009) are common standard, politics and management request clear, one-dimensional messages. It emerges from our series of simple case studies, which focus on only one aspect of uncertainty, that there could be a model available to support almost any desired statement or political decision – and each scenario could be equally justified if one merely relies on the outcome of cross-validation.

We thus unite with other authors (Araújo et al. 2005, Araújo and New 2007, Dormann 2007, Wiens et al. 2009, Elith et al. 2010) to re-emphasize the need 1) to better communicate causes and consequences of uncertainty to the

public and policy sectors; 2) to develop new quantitative and spatially explicit methods for determining causes and levels of uncertainty in climate-change SDMs; 3) to balance the risks and costs of using model outcomes for decision making; 4) to prefer mechanistic, causality-based approaches in order to determine species responses to climate change, wherever possible. In addition to these general suggestions, the present study enables us to formulate the following remarks and recommendations that are more specific to climate variable selection.

Firstly, comparing current and future variable correlations is an essential task to be operated before projecting, but with the caveat that mere bivariate correlation measures between variables may fail to provide sufficient information about potential deviations. In order to capture essential divergences between variables, correlations between the predicted changes of variables must be analysed as well. Secondly, when causal mechanisms of species-climate interactions are unknown, the variability of predictions obtained with different model parameterizations should be explored instead of relying on one single parameterization. If time constraints do not allow a thorough assessment of the variation in outcomes introduced by this source of uncertainty, we recommend using methods that enable all potentially relevant climate variables to be included. Finally, accuracy measures based on non-independent, present-time evaluation data are unreliable indicators for estimating the accuracy of predictions under future conditions. Preferably, independent evaluation (e.g. using data of historical distributions or long-term population trends) should be employed, which emphasizes the need for long-term species monitoring programmes.

Using correlative SDMs for range predictions requires a careful selection of climate variables, ideally based on sound ecological causality, such as well documented, strict physiological tolerance thresholds to climatic conditions (Arlettaz et al. 2000). Since this information is rarely available, and might be difficult to quantify at a distribution-relevant scale, a sceptical attitude will be the best guide when balancing the risks and benefits of using SDM forecasts for conservation management.

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References

- 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. 2004. Would climate change drive species out of reserves? An assessment of existing reserve selection methods. – *Global Change Biol.* 10: 1618–1626.
- Araújo, M. B. et al. 2005. Validation of species–climate impact models under climate change. – *Global Change Biol.* 11: 1504–1513.
- Araújo, M. B. et al. 2011. Climate change threatens European conservation areas. – *Ecol. Lett.* 14: 484–492.
- Arlettaz, R. et al. 2000. Physiological traits affecting the distribution and wintering strategy of the bat *Tadarida teniotis*. – *Ecology* 81: 1004–1014.
- Barbet-Massin, M. et al. 2010. How much do we overestimate future local extinction rates when restricting the range of occurrence data in climate suitability models? – *Ecography* 33: 378–386.
- Barbet-Massin, M. et al. 2012. Selecting pseudo-absences for species distribution models: how, where and how many? – *Methods Ecol. Evol.* 3: 327–338.
- Beaumont, L. J. et al. 2005. Predicting species distributions: use of climatic parameters in BIOCLIM and its impact on predictions of species' current and future distributions. – *Ecol. Model.* 186: 250–269.
- Beaumont, L. J. et al. 2007. Where will species go? Incorporating new advances in climate modelling into projections of species distributions. – *Global Change Biol.* 13: 1368–1385.
- Braunisch, V. and Suchant, R. 2006. Das Raufußhühner – Bestandesmonitoring der FVA. – *Berichte Freiburger Forstliche Forschung* 64: 55–67.
- Braunisch, V. and Suchant, R. 2007. A model for evaluating the 'habitat potential' of a landscape for capercaillie *Tetrao urogallus*: a tool for conservation planning. – *Wildl. Biol.* 13: 21–33.
- Braunisch, V. and Suchant, R. 2008. Using ecological forest site mapping for long-term habitat suitability assessments in wildlife conservation – demonstrated for capercaillie (*Tetrao urogallus*). – *For. Ecol. Manage.* 256: 1209–1221.
- Braunisch, V. et al. 2008. Living on the edge – modelling habitat suitability for species at the edge of their fundamental niche. – *Ecol. Model.* 214: 153–167.
- Buisson, L. et al. 2010. Uncertainty in ensemble forecasting of species distribution. – *Global Change Biol.* 16: 1145–1157.
- Burnham, K. P. and Anderson, D. R. 2002. Model selection and multimodel inference, 2nd ed. – Springer.
- Chen, I. C. et al. 2011. Rapid range shifts of species associated with high levels of climate warming. – *Science* 333: 1024–1026.
- Cohen, J. 1960. A coefficient of agreement for nominal scales. – *Educ. Psychol. Meas.* 20: 37–46.
- DeLong, E. R. et al. 1988. Comparing the areas under two or more correlated receiver operating characteristic curves: a nonparametric approach. – *Biometrics* 44: 837–845.
- Diaz-Nieto, J. and Wilby, R. L. 2005. A comparison of statistical downscaling and climate change factor methods: impacts on low flows in the River Thames, United Kingdom. – *Clim. Change* 69: 245–268.
- 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 on the great grey shrike. – *Ecology* 87: 3371–3386.
- Dormann, C. F. et al. 2012. Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. – *Ecography* doi: 10.1111/j.1600-0587.2012.07348.x
- Elith, J. et al. 2006. Novel methods improve prediction of species' distributions 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.
- Elith, J. et al. 2010. The art of modelling range-shifting species. – *Methods Ecol. Evol.* 1: 330–342.

- ESRI 2008. ArcGIS Desktop: release 9.3. – Environmental Systems Research Inst.
- Fayt, P. 2006. Reproductive decisions of boreal three-toed woodpeckers (*Picoides tridactylus*) in a warming world: from local responses to global population dynamics. – *Ann. Zool. Fenn.* 43: 118–130.
- 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.
- Fleiss, J. L. 1981. Statistical methods for rates and proportions, 2nd ed. – Wiley.
- Freeman, E. and Moisen, G. 2008. Presence Absence: a R package for presence absence analysis. – *J. Stat. Softw.* 23: 1–31.
- Friedman, J. H. 2001. Greedy function approximation: a gradient boosting machine. – *Ann. Stat.* 29: 1189–1232.
- Fu, P. and Rich, P. M. 2002. A geometric solar radiation model with applications in agriculture and forestry. – *Comput. Electron. Agric.* 37: 25–35.
- Guisan, A. and Zimmermann, N. E. 2000. Predictive habitat distribution models in ecology. – *Ecol. Model.* 135: 147–186.
- Guisan, A. et al. 2006. Making better biogeographical predictions of species distributions. – *J. Appl. Ecol.* 43: 386–392.
- Hastie, T. J. and Tibshirani, R. 1990. Generalized additive models. – Chapman and Hall.
- Heikkinen, R. K. et al. 2007. Biotic interactions improve prediction of boreal bird distributions at macro-scales. – *Global Ecol. Biogeogr.* 16: 754–763.
- Hijmans, R. J. et al. 2005. Very high resolution interpolated climate surfaces for global land areas. – *Int. J. Climatol.* 25: 1965–1978.
- Hosmer, D. W. J. and Lemeshow, S. 2000. Applied logistic regression, 2nd ed. – Wiley.
- Houghton, J. T. et al. 2001. Climate change 2001: the scientific basis. – Cambridge Univ. Press.
- Hughes, L. 2000. Biological consequences of global warming: is the signal already apparent? – *Trends Ecol. Evol.* 15: 56–61.
- Hulme, P. E. 2005. Adapting to climate change: is there scope for ecological management in the face of a global threat? – *J. Appl. Ecol.* 42: 784–794.
- Jenness, J. 2006. Topographic Position Index (tpi_jen.avx) extension for ArcView 3.x, ver. 1.2. – Jenness Enterprises.
- Jenness, J. and Wynne, J. J. 2006. Kappa analysis (kappa_stats.avx) extension for ArcView 3.x. – Jenness Enterprises.
- Keller, V. et al. 2010. Die prioritären Vogelarten der Schweiz: Revision 2010. – *Der Ornithol. Beobachter* 107: 265–285.
- Landis, J. R. and Koch, G. G. 1977. The measurement of observer agreement for categorical data. – *Biometrics* 33: 159–174.
- Lawler, J. J. et al. 2006. Predicting climate-induced range shifts: model differences and model reliability. – *Global Change Biol.* 12: 1568–1584.
- Lehikoinen, A. et al. 2011. The impact of climate and cyclic food abundance on the timing of breeding and brood size in four boreal owl species. – *Oecologia* 165: 349–355.
- Madden, R. A. and Williams, J. 1978. The correlation between temperature and precipitation in the United States and Europe. – *Monthly Weather Rev.* 106: 142–147.
- Maggini, R. et al. 2011. Are Swiss birds tracking climate change? Detecting elevational shifts using response curve shapes. – *Ecol. Model.* 222: 21–32.
- Meloun, M. et al. 2002. Crucial problems in regression modelling and their solutions. – *Analyst* 127: 433–450.
- Mitchell, T. D. et al. 2004. A comprehensive set of high-resolution grids of monthly climate for Europe and the globe: the observed record (1901–2000) and 16 scenarios (2001–2100). – Tyndall Centre for Climate Change research.
- Mollet, P. et al. 2008. Aktionsplan Auerhuhn Schweiz. – Bundesamt für Umwelt BAFU, Schweizerische Vogelwarte Sempach, Schweizer Vogelschutz SVS/BirdLife Schweiz, Bern, 2008.
- Moss, R. et al. 2001. Climate change and breeding success: decline of the capercaillie in Scotland. – *J. Anim. Ecol.* 70: 47–61.
- Nakicenovic, N. et al. 2000. Special report on emissions scenarios (SRES). – Cambridge Univ. Press.
- Parmesan, C. 2006. Ecological and evolutionary responses to recent climate change. – *Annu. Rev. Ecol. Evol. Syst.* 37: 637–669.
- Parmesan, C. and Yohe, G. 2003. A globally coherent fingerprint of climate change impacts across natural systems. – *Nature* 421: 37–42.
- Pearman, P. B. et al. 2008. Niche dynamics in space and time. – *Trends Ecol. Evol.* 23: 149–158.
- Pearson, R. G. and Dawson, T. P. 2003. Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? – *Global Ecol. Biogeogr.* 12: 361–371.
- Phillips, S. J. and Dudík, M. 2008. Modeling of species distributions with Maxent: new extensions and a comprehensive evaluation. – *Ecography* 31: 161–175.
- Phillips, S. J. et al. 2004. A maximum entropy approach to species distribution modeling. – In: 21st International Conference on Machine Learning. ACM Press, pp. 655–662.
- Phillips, S. J. et al. 2006. Maximum entropy modeling of species geographic distributions. – *Ecol. Model.* 190: 231–259.
- Raes, N. and ter Steege, H. 2007. A null-model for significance testing of presence-only species distribution models. – *Ecography* 30: 727–736.
- Renwick, A. R. et al. 2011. Modelling changes in species' abundance in response to projected climate change. – *Divers. Distrib.* 18: 121–132.
- Robin, X. et al. 2011. pROC: an open-source package for R and S+ to analyze and compare ROC curves. – *BMC Bioinform.* 7: 77.
- Root, T. L. et al. 2003. Fingerprints of global warming on wild animals and plants. – *Nature* 421: 57–60.
- Roth, K. 1974. Die frühere und die heutige Verbreitung des Auerwilds in Baden-Württemberg und die Entwicklung der Bestände. – *Schriftenreihe der Landesforstverwaltung Baden-Württemberg* 42: 8–14.
- Schloss, C. A. et al. 2012. Dispersal will limit ability of mammals to track climate change in the Western Hemisphere. – *Proc. Natl Acad. Sci. USA* doi: 10.1073/pnas.1116791109
- Segurado, P. and Araújo, M. B. 2004. An evaluation of methods for modelling species distributions. – *J. Biogeogr.* 31: 1555–1568.
- Suchant, R. and Braunisch, V. 2004. Multidimensional habitat modelling in forest management – a case study using capercaillie in the Black Forest, Germany. – *Ecol. Bull.* 51: 455–649.
- Suchant, R. and Braunisch, V. 2008. Rahmenbedingungen und Handlungsfelder für den Aktionsplan Auerhuhn: Grundlagen für ein integratives Konzept zum Erhalt einer überlebensfähigen Auerhuhnpopulation im Schwarzwald. – Forstliche Versuchs- und Forschungsanstalt Baden-Württemberg.
- Summers, R. W. et al. 2004. An experimental study of the effects of predation on the breeding productivity of capercaillie and black grouse. – *J. Appl. Ecol.* 41: 513–525.
- Synes, N. W. and Osborne, P. E. 2011. Choice of predictor variables as a source of uncertainty in continental-scale species distribution modelling under climate change. – *Global Ecol. Biogeogr.* 20: 904–914.
- 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. 2004. Effects of restricting environmental range of data to project current and future species distributions. – *Ecography* 27: 165–172.
- Trenberth, K. E. and Shea, D. J. 2005. Relationships between precipitation and surface temperature. – *Geophys. Res. Lett.* doi: 10.1029/2005GL022760

- Wegge, P. and Rolstad, J. 1986. Size and spacing of capercaillie leks in relation to social behavior and habitat. – *Behav. Ecol. Sociobiol.* 19: 401–408.
- Wegge, P. and Larsen, B. B. 1987. Spacing of adult and subadult male common capercaillie during the breeding season. – *Auk* 104: 481–490.
- Wiens, J. A. et al. 2009. Niches, models and climate change: assessing the assumptions and uncertainties. – *Proc. Natl Acad. Sci. USA* 106: 19729–19736.
- Wiens, J. J. et al. 2010. Niche conservatism as an emerging principle in ecology and conservation biology. – *Ecol. Lett.* 13: 1310–1324.
- Wiley, E. O. et al. 2003. Niche modelling and geographic range predictions in the marine environment using a machine-learning algorithm. – *Oceanography* 16: 120–127.
- Williams, J. W. and Jackson, S. T. 2007. Novel climates, no-analog communities, and ecological surprises. – *Front. Ecol. Environ.* 5: 475–482.
- Zhou, L. et al. 2009. Spatial dependence of diurnal temperature range trends on precipitation from 1950 to 2004. – *Clim. Dyn.* 32: 429–440.
- Zimmermann, N. E. and Roberts, D. W. 2001. Final Report of the MLP climate and biophysical mapping project. – Scientific project report, WSL, Birmensdorf, Switzerland.

Supplementary material (Appendix ECOG-00138 at < www.oikosoffice.lu.se/appendix >). Appendix 1.