

Habitat at the mountain tops: how long can Rock Ptarmigan (*Lagopus muta helvetica*) survive rapid climate change in the Swiss Alps? A multi-scale approach

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Abstract Ongoing monitoring in the Swiss Alps has shown that Rock Ptarmigan (*Lagopus muta helvetica*) has suffered a significant population decrease over the last decade and climate change has been proposed as a potential cause. In this study, we investigate the response of this high alpine grouse species to rapid climate change. We address a problem often neglected in macro-ecological studies on species distribution: scale-dependency of distribution models. The models are based on empirical field data and on environmental databases for large-scale models. The implementation of several statistical modelling approaches, external validation strategies and the implementation of a recent study on regional climate change in Switzerland ensure robust predictions of future range shifts. Our results demonstrate that, on the territory level, variables depicting vegetation, heterogeneity of local topography and habitat structure have greatest explanatory power. In contrast at the meso-scale and macro-scale (with grain sizes of 1 and 100 km², respectively), bioclimatic and land cover-related

variables play a prominent role. The models predict that, based on increasing temperatures during the breeding season, potential habitat will decrease by up to two-thirds until the year 2070. At the same time, a shift of potential habitat towards the mountain tops is predicted. The multi-scale approach highlights the true extent of potential habitat for this species with its patchy distribution in steep terrain. The small-scale analysis pinpoints the key habitat areas within the extensive areas of suitable habitat predicted by models on large grain sizes and in this way reveals sub-grid variability. Our results can facilitate the adaptation of species conservation strategies to a quickly changing environment.

Keywords Species distribution modelling · Multi-scale · Climate change · Swiss Alps · Sub-grid variability

Zusammenfassung

Habitat auf den Gipfeln der Berge: Wie lange kann das Alpenschneehuhn (*Lagopus muta helvetica*) raschen Klimawandel in den Schweizer Alpen überleben? Ein mehrskaliger Ansatz.

Fortlaufendes Monitoring hat gezeigt, dass innerhalb des letzten Jahrzehnts die Population des Alpenschneehuhns (*Lagopus muta helvetica*) in den Schweizer Alpen stark abgenommen hat. Als mögliche Ursache kommt der Klimawandel in Betracht. In dieser Studie untersuchen wir die Auswirkungen raschen Klimawandels auf dieses hochalpine Raufußhuhn. Dabei setzten wir uns mit einem Aspekt auseinander, der in vielen makroökologischen Studien oft vernachlässigt wird: die Skalenabhängigkeit von Habitatmodellen. Die Modelle basieren auf empirischen Felddaten und auf Umweltdatenbanken für die

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großskaligen Modelle. Die Anwendung mehrerer, statistischer Modelle, externe Validierung und die Daten einer aktuellen Studie zum Klimawandel in der Schweiz legen die Grundlage für robuste Vorhersagen der künftigen Verbreitung des Alpenschneehuhns. Unsere Ergebnisse zeigen, dass auf der Revierskala Variablen, die die Vegetation, die lokale Topographie und Habitatstruktur beschreiben die größte Vorhersagekraft haben. Im Gegensatz dazu spielen auf der Mesoskala (Korngröße 1 km²) und Makroskala (Korngröße 100 km²) bioklimatische und land cover Variablen die herausragende Rolle. Die Modelle sagen vorher, dass sich allein aufgrund einer erhöhten Durchschnittstemperatur während der Brutzeit das potenzielle Habitat bis zum Jahre 2070 um bis zu zwei Drittel verringern wird. Zudem findet eine Verschiebung in Richtung Gebirgsgipfel statt. Insbesondere für Arten, die steiles Terrain bewohnen und lückenhafte Verbreitung aufweisen wie das Alpenschneehuhn, verdeutlicht die Analyse auf mehreren Skalen das wirkliche Ausmaß des potenziellen Habitats. So zeigt die feinskalige Analyse die bevorzugten Gebiete innerhalb der großräumigen Gebiete auf, welche die Modelle auf den großen Skalen vorhergesagen und verdeutlicht auf diese Weise die Variabilität innerhalb der Rasterzellen. Unsere Ergebnisse können einen Beitrag zur Anpassung der Naturschutzstrategien zur Arterhaltung in einer sich schnell verändernden Umwelt leisten.

Introduction

Alpine ecosystems are particularly susceptible to the impacts of climate change, as environmental conditions are predicted to change rapidly within very short horizontal and vertical distances. The species inhabiting these high mountain regions are well adapted to this environment, and thus their distribution is often limited to areas that encompass narrow climatic conditions. Mobile species such as birds are expected to be the first to react, and distributional shift seems to be a common response. For example, Thomas and Lennon (1999) detected a northward shift of British breeding birds by 18.9 km within a 20-year period, and Huntley et al. (2006) predicted a shift in the current spatial distribution of birds of up to 1,000 km within the twenty-first century.

Rock Ptarmigan (*Lagopus muta helvetica*), an arctic grouse species, occurs in an isolated glacial relict population in the Alps. In Switzerland, the breeding territories are located above the timberline and reach up to the glaciers at altitudes ranging from 1,900 to 2,600 m above sea level (Schmid et al. 1998). The bird is highly adapted to the

harsh conditions prevailing at these elevated sites. However, suitable habitat is patchily distributed, and home ranges therefore tend to be large (Favaron et al. 2006). Until recently, the Rock Ptarmigan population in the Swiss Alps has been regarded as stable at 12,000–15,000 breeding pairs (Schmid et al. 1998). Annual surveys on permanent monitoring sites in spring, however, have shown a drastic decrease of 30% during the last decade (unpublished data). As a result, Rock Ptarmigan is listed as near threatened in the Swiss Red List, recently revised (Keller et al. 2010).

Surveys on permanent monitoring sites at the Aletsch glacier, the largest glacier in the Alps situated in southern Switzerland, have shown changes in local distributional ranges following short-term climate variations (Marti, in preparation). We hypothesise that the decline of the Rock Ptarmigan population in Switzerland is primarily caused by increasing temperatures due to climate change.

It has long been shown that habitat selection is a multi-scaled process (Brambilla et al. 2006; Oppel et al. 2004). Therefore, individual habitat variables may vary in their predictive power on different scales (for birds with large home ranges, see Thompson and McGarigal 2002; Graf et al. 2005). Austin and Van Niel (2011) stated that there is a natural scale of resolution for SDMs which is the one maximising the relevant environmental differences between plots. However, thus far, this fact has often been neglected. The empirical studies of Ackerly et al. (2010) and Randin et al. (2009) elucidate why the consideration of spatial and temporal heterogeneity at different scales is of special relevance in climate change studies: The heterogeneity of local topography, for instance, may create critical climatic refugia for the survival of the species. In order to test this hypothesis, macro-ecological studies need to be accompanied by studies with high spatial resolutions. Therefore, this study is based on three different spatial scales ranging from the territory level to two country-wide analyses with grain sizes of 1 km² (meso-scale) and 100 km² (macro-scale). Due to the non-existence of adequate bioclimatic data on the resolution of local territory scale, these results cannot be formally integrated into climate change predictions. However, they pinpoint the sub-grid variability of large-scale modelling and hence elucidate potentially erroneous predictions of the area of suitable habitat. On the other hand, the up-scaling of data to a larger grain size allows comparisons with commonly used scales in macro-ecological studies. Furthermore, the loss or gain of predictive power of environmental predictors with changing resolution illustrates the gradient lengths covered by the predictors and hence their usefulness and applicability on certain spatial scales.

The objectives of this study are:

1. to detect the key factors determining Rock Ptarmigan's distribution and to analyse their varying importance on different spatial scales;
2. to predict suitable habitat in Switzerland under current conditions and to develop scenarios for the potential future distribution of Rock Ptarmigan; and
3. to uncover the effects of spatial scale on the prediction of potential habitat analysing sub-grid variability.

Additionally, the results will contribute to the adaptation of conservation strategies to a quickly changing environment to ensure the persistence of Rock Ptarmigan in the Alps.

Methods

Research area and data

Data on territory level was obtained during a field campaign in the breeding season from May to June 2005. In total, nine study regions were selected in Switzerland covering the core distribution of Rock Ptarmigan in the central Alps and extending to the edges of the distributional range at the southern and northern slopes of the Alps. Data gained during the annual monitoring programme of common breeding birds carried out by the Swiss Ornithological Institute document the use of these sites as breeding habitat over the last decade (see Appendix S1).

At each site, we mapped the presence or absence of Rock Ptarmigan. An occupied territory was identified by recognition of calling cocks in the early morning before sunrise, sightings at daylight or by indirect evidence such as observations of feathers, fresh faeces or footprints. Accordingly, a site was declared unoccupied if none of the signs mentioned above were recorded within 2 days. After mapping the bird's incidence, we randomly selected sample plots sized $25 \times 25 \text{ m}^2$ within occupied and unoccupied areas for the survey of environmental variables. In order to avoid pseudoreplication, we set a minimum distance of 300 m between each plot, corresponding to territories of 10 ha in size (Bossert 1995). For each plot, we mapped explanatory variables representing the presumed autecological requirements of Rock Ptarmigan such as food availability, bioclimatic requirements with respect to the topographic situation and habitat structure (see Table 1 for predictor variables; $n = 84$, prevalence = 0.49).

For the meso-scale and macro-scale analyses, we obtained data from the Swiss breeding bird atlas (Schmid et al. 1998) collected in the years 1993–1996 and mapped with a grid size of 1 km^2 . In addition, we used data recorded during the Monitoring Programme of Common

Breeding Birds carried out annually by the Swiss Ornithological Institute as well as individual observations gathered by the same institution.

We selected suitable predictor variables based on literature (e.g. Glutz von Blotzheim et al. 1973; Fasel and Zbinden 1983) and expert knowledge from various geodatabases at the same resolution as the response variable (1 km^2): bioclimatic data from BIOCLIM (Swiss Federal Research Institute WSL), land use and vegetation data from GEOSTAT (Swiss Federal Statistical Office) and data on vegetation geography from the “Atlas on Vegetation Types” (Hegg et al. 1993). Furthermore, we added data describing the topographic situation and terrain variability by carrying out a digital terrain analysis (Wilson and Gallant 2000). For modelling at the macro-scale with a resolution of 100 km^2 , we used the same database. All variables were aggregated using ESRI ArcGis™ 9.0 (Spatial Analyst Toolbox) applying the median function (and the maximum function for incidence of ptarmigan and vegetation data). For the meso-scale (1 km^2), our sample size was $n = 2,098$ with a prevalence of 0.37, for the macro-scale (100 km^2) $n = 465$ with a prevalence of 0.52. Predictions were made for all of Switzerland, i.e. 40,874 grid cells on the meso-scale and 465 cells on the macro-scale (see Table 1 for predictor variables).

Since multicollinearity of predictor variables can potentially lead to the wrong identification of relevant predictors in a statistical model (Graham 2003; Dormann et al. 2012), we calculated bivariate Spearman rank correlations (ρ_s) for all predictors. In the case of two highly correlated variables ($|\rho_s| > 0.7$), hierarchical partitioning and performance of univariate models served as decision criteria to remove one of the variables from the variable set (cf. Appendix S2; Tanneberger et al. 2010).

Statistical analysis and modelling

We implemented a wide range of advanced statistical species distribution modelling approaches in order to analyse model uncertainty resulting from the statistical model applied (cf. Pearson et al. 2006). We employed three modelling approaches that have successfully been applied in previous studies on species distribution (Guisan and Zimmermann 2000): generalised linear models (GLM, i.e. logistic regression in this case), generalised additive models (GAM), and classification and regression trees (CART). In addition, we used two ensemble forecasting techniques which have recently been introduced to ecological applications (Elith et al. 2006, 2008; Araújo and New 2007): boosted regression trees (BRT; Friedman 2002; Leathwick et al. 2006) and random forest regression (RF; Breiman 2001; Prasad et al. 2006). Both approaches rely on the estimation of a huge ensemble of individual

Table 1 Predictor variables considered in the territory scale (a) and in the meso-scale and macro-scale analysis (b) of Rock Ptarmigan (*Lagopus muta helvetica*)

Predictor variable	Unit	Median ptarmigan = 1	Median ptarmigan = 0
Predictor variables on territory scale			
Topography			
Altitude above sea level	m	2,275.0	2,188.0
Aspect cosine transformed	1	0.4	−0.2
Vertical structure elements	Number	3.0	0.0
Variability of topography	Number	4.0	3.0
Distance to ski fields	m	1,430.0	845.0
Distance to ridge	m	240.0	345.0
Vegetation and resources			
Mean soil thickness	cm	9.8	14.5
Tree cover	%	0.0	0.0
Herbal layer cover	%	0.2	0.3
Vegetation height, maximum	cm	25.0	35.0
Simpson diversity index	metric	0.9	0.8
Vegetation free area	%	0.3	0.1
Cover of <i>Juniperus communis</i> ssp.	%	0.0	0.0
Presence of <i>Vaccinium uliginosum</i>	[0,1]	1.0	1.0
Cover of <i>Vaccinium myrtillus</i>	%	0.0	0.1
Presence of <i>Salix herbacea</i>	[0,1]	0.0	0.0
Cover of <i>Rhododron</i> spp.	%	0.1	0.0
Cover of <i>Salix</i> spp.	%	0.0	0.0
Cover of Ericaceae spp.	%	0.3	0.3
Predictor variables on the macro-scale			
Bioclimate			
Cloud cover July	Cover in ‰	549.5	531
Precipitation year	mm	1,650.1	1,489.15
Insolation July	kWh m ^{−2}	8,300.5	7,032
Mean July temperature	°C	9.01	13.66
Water budget July	mm	84.5	82
Vegetation			
Forest	Cover in %	0	35
Alp pasture	Cover in %	39	8
Uncultivated land	Cover in %	16.5	2
Poor or no vegetation cover	Cover in %	25	0.5
Low growing or sparse vegetation	Cover in %	25	0
Dense, low vegetation	Cover in %	25	25
Sparse, high grass and sedge vegetation	Cover in %	0	0
Dense, higher grass and sedge vegetation	Cover in %	0	25
Perennial plants (50–150 cm)	Cover in %	0.5	0.5
Dwarf and low shrubs	Cover in %	25	0.05
High shrubs	Cover in %	0	0
Deciduous forest with sparse undergrowth	Cover in %	0	0
Deciduous forest with rich shrub layer	Cover in %	0	0
Coniferous forest with sparse undergrowth	Cover in %	0	0
Coniferous forest with rich shrub layer	Cover in %	0	0
Coniferous forest with rich herbal layer, no shrubs	Cover in %	0	25
Vineyards	Cover in %	0	0
Copse	Cover in %	0	0.5

Table 1 continued

Predictor variable	Unit	Median ptarmigan = 1	Median ptarmigan = 0
Snow bed vegetation	Cover in %	0.5	0
Ericaceous dwarf shrubs	Cover in %	0.05	0
Topography			
Range of altitude within grid cell	m	458.5	351.5
Profile curvature	[1]	−0.01	0.01
Slope	Degree	12.46	10.27
Aspect (sine transformed)	[1]	−0.07	0.04
Aspect (cosine transformed)	[1]	0.11	−0.21
Aspect (beers transformed)	[1]	1.05	0.92
Distance to nearest ski lift	m	3,162.28	3,000

For each predictor, estimates of the median are given for absence and presence of ptarmigan separately. On the meso-scale and macro-scale, the following predictor variables had to be eliminated due to high multicollinearity ($|r_{s}| > 0.7$) with mean July temperature: degree days, annual mean temperature, arable crop including vineyards, vegetation free areas, built-up areas, deciduous forest without shrub layer but with rich herbal or dwarf shrub layer, minimal altitude in grid cell, median altitude in grid cell, maximum altitude in grid cell; with yearly precipitation: precipitation January; with water budget July: precipitation July. Moreover, on the macro-scale only, range of altitude within grid cell had to be removed because of multicollinearity with mean July temperature

tree-based models. These models are known not to be sensitive to noise in predictor variables. Moreover, they enable the consideration of complex interactions which often play an important role in ecological relationships.

Unfortunately, every modelling technique offers a unique way to measure variable importance. In GLM, it is measured by hierarchical partitioning calculating the independent and total effect of every variable; in GAM, the so-called drop contribution was used comparing the explained deviance of the model with and without a variable; for CART, the variables serving as decision criteria at the nodes and the rank of the node are given; in BRT, relative influence on model fit is averaged over all trees; and RF makes use of the out-of-bag error and its differences after permuting predictors. Although the calculation differs, the rank of the variables can be compared among the approaches and from scale to scale (for details on model settings, please refer to Appendix S2; for an overview on modelling technique, cf. Virkkala et al. 2010).

Model checking: evaluation and validation

In order to assess the goodness-of-fit of our models from multiple perspectives, we calculated five different measures: the area under the receiver operating characteristic curve (AUC; Fielding and Bell 1997), Cohen’s kappa statistic of similarity (κ ; Cohen 1960), the explained deviance, slope and intercept of the calibration curve (cf. Reineking and Schröder 2006). AUC and κ both assess the discriminatory power of the models. AUC values range from 0.5 (same predictive power as the null model) to 1 (denoting

perfect discrimination). According to Hosmer and Lemeshow (2000), an AUC value exceeding 0.9 reflects an outstanding discrimination. For κ (ranging from 0 to 1), Monserud and Leemans (1992) propose a threshold of $\kappa > 0.85$ for excellent discrimination. The explained deviance measures the lack of fit of the model. It is calculated as the quotient of the residual deviance and the deviance of the null model subtracted from 1. Hence values for models performing better than the null model range from 0 to 1 with 1 depicting the best model. Slope and intercept of the calibration curve investigate the degree of overfitting of the model. Optimally calibrated models exhibit a calibration curve with intercept 0 and slope 1 (Reineking and Schröder 2006; Table 2).

In order to gain reliable estimates of model performance, models were tested on independent data (Araújo et al. 2005). Hence, all models on the country-wide scales were calibrated on training data representing 70% of the original dataset; the remaining 30% served as test data. Subsequently, all five measures (AUC, κ , explained deviance, slope and intercept of calibration curve) were calculated on both datasets. The comparison of results on test and training data reveals any over-confidence of model performance.

A common problem working with spatial data in statistical modelling approaches is spatial autocorrelation. This violates the model assumption of independency of observations and may result in a misleading interpretation of ecological relationships (e.g. Kühn 2007; Lichstein et al. 2002). Therefore, models were checked for residual spatial autocorrelation by calculating a global Moran’s I and correlograms (Dormann et al. 2007).

Table 2 Results of model evaluation and validation on all scales: area under ROC-Curve (*AUC*), Cohen's Kappa (*Kappa*), and explained deviance as well as slope and intercept of the calibration curve

Scale	Method	AUC		Kappa		Explained deviance		Slope of calibration curve		Intercept of calibration curve		Threshold MinROCdist
		Training	Test	Training	Test	Training	Test	Training	Test	Training	Test	
Territory scale	GLM	0.957	0.957	0.831	0.831	0.638	–	1.000	–	0.000	–	0.535
	GAM	0.927	0.927	0.721	0.711	0.484	–	1.133	–	–0.033	–	0.575
	BRT	0.991	0.989	0.928	0.904	0.632	0.679	4.477	3.064	–0.389	–0.307	0.550
	RF	–	0.901	–	0.687	0.391	–	1.507	–	0.125	–	0.490
	CART	0.956	0.856	0.956	0.856	0.698	–	1.000	–	0.000	–	0.355
1 km ²	GLM	0.942	0.920	0.736	0.693	0.564	0.470	1.000	0.812	0.000	–0.159	0.440
	GAM	0.944	0.922	0.727	0.699	0.569	0.478	1.028	0.839	–0.007	–0.175	0.440
	BRT	0.986	0.938	0.864	0.730	0.729	0.530	1.702	0.929	–0.156	–0.210	0.560
	RF	0.947	0.932	0.755	0.727	0.573	0.470	1.224	0.812	–0.035	–0.159	0.470
	CART	0.918	0.892	0.705	0.645	0.511	0.419	1.000	0.866	0.000	–0.091	0.470
100 km ²	GLM	0.999	0.983	0.975	0.913	0.933	0.594	1.000	0.331	0.000	–0.757	0.345
	GAM	1.000	0.956	0.988	0.870	0.961	0.982	2.763	28.757	0.606	12.386	0.530
	BRT	1.000	0.997	1.000	0.942	0.998	0.886	7.218	0.727	–2.236	0.036	0.520
	RF	0.993	0.997	0.939	0.942	0.839	0.857	1.562	2.160	0.287	0.339	0.510
	CART	0.979	0.967	0.926	0.885	0.819	0.423	1.000	0.245	0.000	–0.899	0.430

The results on training and on test data are given, the dimension of the difference depicting the degree of overestimation of model performance. To derive binary predictions, i.e. presence or absence of Rock Ptarmigan, we calculated a threshold according to the approach of the minimal distance to the upper left corner in the ROC-plot

MinROCdist, according to Freeman and Moisen (2008)

Extrapolation in space and time

On the basis of our meso-scale and macro-scale models, we predicted the potential Rock Ptarmigan habitat in Switzerland. For each grid cell, we calculated the probability of the bird's occurrence. To derive binary predictions (e.g. for the calculation of kappa) we applied the approach based on the shortest distance to the top-left corner (0, 1) in the ROC plot, as this method has been shown to be advantageous over the commonly used kappa maximisation approach (Liu et al. 2005). All statistical computing was performed with the statistical package “R 2.9” (R Development Core Team 2009; for packages used, see Appendix S2).

To investigate the effect of climate change on Rock Ptarmigan habitat in Switzerland, we adopted the change of mean July temperature calculated in a probabilistic study carried out by Frei (2004) and Frei et al. (2006). This climate projection is based on four global circulation models and incorporates eight regional climate models, hence considering the local topography—a fact that is important in a mountainous area. The simulations are based on SRES A2 and B2 emission scenarios (Nakicenovic et al. 2000). For the years 2030, 2050 and 2070, three scenarios are calculated: a median scenario representing the best estimation of the temperature rise and minimum and maximum

scenarios representing the lower and the upper limits of a 95% confidence interval for expected temperature rise (see Table 3). Compared to other bird species, Rock Ptarmigan is not a good disperser. However, we still assume that the bird will be able to colonise newly available habitat, and hence the entire area projected by the models is calculated as potential habitat (Pearson et al. 2006). Due to the lack of adequate bioclimatic data on the territory scale, we cannot make any predictions on this scale.

Results

Model evaluation and validation

All models show excellent performance with AUC values exceeding 0.89 on independent test data. The values for Cohen's kappa display less excellent accuracy ranging from 0.65 to 0.95 on test data, but still assert good to very good performance. The best values are reached on the macro-scale (100 km² resolution) where all model approaches reach almost perfect discrimination. The values for explained deviance concur with these results. Again, highest values from 0.819 to 0.998 are reached on the macro-scale whereas meso-scale models range from 0.419

Table 3 Variable importance for the five different model approaches on the three scales (a) territory scale, (b) meso-scale (1 km²) and (c) macro-scale (100 km²)

Predictor variable	Model approach (criterion of predictor importance)				
	BRT Rel. influence	RF Out-of-bag	GLM <i>T</i> -effect (%)	GAM Drop contribution	CART Primary split
(a) Territory scale					
Simpson diversity index (vascular plants)	15.8	14.7	–	–	1st split
Vegetation-free area	11.6	18.6	27.6	32	–
Aspect (cosine transformed)	9.6	–	10.2	–	–
Depth of soil	8.0	12.3	–	–	2nd split
Distance to ski fields	7.3	9.5	–	–	4th split
<i>Vaccinium uliginosum</i>	6.8	9.1	12.8	–	–
Vertical structure elements	6.2	8.2	19.1	–	–
Vegetation height	6.2	8.5	–	–	3rd split
Variability of topography	5.7	9.8	23.1	–	–
Altitude	4.3	–	–	–	2nd split
<i>Salix herbacea</i>	–	9.4	–	–	–
Herbal layer (cover)	–	11.5	–	18.3	–
<i>Juniperus communis</i> (cover)	–	–	7.2	–	–
	Model approach (criterion of predictor importance)				
	BRT Rel. influence	RF %IncMSE	GLM <i>T</i> -effect (%)	GAM Drop contrib.	CART Primary split
(b) Meso-scale (1 km²)					
Snow bed vegetation	29.8	39.5	–	–	1st split
Mean July temperature	26.0	48.7	29.5	101.7	2nd split
Uncultivated land	6.6	39.2	17.3	43.6	3rd split
Forest cover	6.1	42.3	22.9	40.1	2nd split
Profile curvature	4.1	33.2	10.0	56.1	–
Range of altitude within grid cell	3.8	26.6	–	–	–
Alp pasture	2.5	22.3	–	–	–
Low or sparse vegetation	2.3	28.9	–	–	–
Precipitation year	2.0	–	–	–	–
Radiation July	1.9	–	–	–	–
Streams	–	20.0	–	–	–
Poor or no vegetation cover	–	30.2	16.8	26.5	–
Water budget July	–	–	–	–	4th split
Ericaceous dwarf shrubs	–	–	3.5	–	–
(c) Macro-scale (100 km²)					
Mean July temperature	65.19	48.78	34.73	10.22	1st, 2nd and 3rd split
Ericaceous dwarf shrubs	15.30	27.32	12.20	12.40	2nd split
Water budget July	3.36	18.52	5.49	34.66	3rd split
Cloud cover July	3.06	18.28	–	–	–
Low or sparse vegetation	2.66	21.48	–	–	–
Precipitation July	2.10	–	5.74	–	–
Dwarf and low shrubs	1.96	19.87	18.79	–	–
Forest cover	1.71	–	–	–	–
Coniferous forest with rich herbal layer, no shrubs	1.63	14.44	–	10.22	–
Pond weed	0.83	–	–	–	–
Alp pasture	–	13.97	11.64	25.07	–
Perennial plants (50–150 cm)	–	16.01	–	28.83	–

Table 3 continued

	Model approach (criterion of predictor importance)				
	BRT Rel. influence	RF %IncMSE	GLM <i>T</i> -effect (%)	GAM Drop contrib.	CART Primary split
Coniferous forest with rich shrub layer	–	23.27	–	34.35	–
Coniferous forest with sparse undergrowth	–	–	–	34.88	–
Streams	–	–	11.41	–	–
High shrubs	–	–	–	8.90	–

The ten most important variables are displayed for ensemble forecasting techniques (RF and BRT), and for GLM, GAM and CART, the variables composing the final model are shown. Note that different measures of variable importance apply: for BRT, relative influence calculated via permutation test; for RF, difference between the Out-of-bag error of each tree and after permutation (Out-of-bag); for GLM, total contributing effect derived via hierarchical partitioning (*T*-effect); for GAM, increase in deviance for model without variable (drop contribution); and for CART, simply the primary splits are given

to 0.530 and on the territory scale from 0.391 to 0.698. BRT generally exhibits the highest explained deviance. The measures of model calibration, slope and intercept of calibration curve, however, show a significant departure from the ideal curve in BRT, whereas this is not the case within the majority of the other modelling approaches (Table 2). We detected a positive spatial autocorrelation in the raw data, which was greatly reduced in the model residuals. Adding an autocovariate reduced this to a non-significant level (except for BRT, Appendix S3).

Generally, model predictions made by these different approaches show a high correlation with the Spearman rank correlation coefficient (ρ_s) ranging between 0.887 and 0.990 (1 km²) and 0.868 and 0.943 (100 km²). The greatest similarities occur among GLM and GAM; BRT and RF are also closely correlated. Even though ρ_s indicates great coincidence among approaches, a scatter plot matrix and the predicted geographical distribution reveal that for a few individual grid cells the predictions diverge dramatically (see Appendix S4 for scatter plot matrix and Appendix S5 for maps on spatial distribution of predicted potential habitat by the different modelling approaches).

Habitat requirements of Rock Ptarmigan

The modelling approaches applied provide varying quantifications of variable importance (Table 3). However, it is possible to derive a general picture: a few predictor variables show good explanatory power throughout all model approaches and even across scales.

Bioclimate

The most powerful variable on the meso-scale and macro-scale is mean July temperature which is considered in all models—contributing up to two-thirds of the explained deviance in BRT. Response curves are hump-shaped at the

resolution of 1 km² indicating that intermediate ranges of temperature suit best. On the macro-scale, there is a purely negative relationship between mean July temperature and Rock Ptarmigan incidence. Surprisingly, further bioclimatic variables do not seem to have a high impact on the meso-scale. However, on the macro-scale, they gain importance: The predictors annual precipitation, water budget July and cloud cover July contribute clearly to the distribution patterns of Rock Ptarmigan. Generally speaking, regions receiving higher amounts of precipitation represent more suitable habitats.

Vegetation

All modelling approaches single out low-growing vegetation types as adequate for Rock Ptarmigan, as well as areas with sparse vegetation cover. In particular, snow bed vegetation ranks among the variables with the highest influence on the meso-scale, thus reflecting food availability. On the macro-scale, however, this variable had to be discarded due to multicollinearity with mean July temperature and hence is not present in these models. On the territory scale, a diverse composition of dwarf shrubs with vegetation-free patches resembles suitable habitat in contrast to areas covered with a dense herbal layer, the neighbourhood to downhill ski runs or higher vegetation including small trees. Accordingly, large-scale models clearly elucidate a negative relationship between forests and Rock Ptarmigan habitat. However, a certain percentage per grid cell appears to be tolerable, presumably where trees are limited to the lower part of the grid cell.

Topography

On the meso-scale and macro-scale, primary topographic attributes do not serve as good predictors with the exception of profile curvature on the meso-scale indicating ridges

as suitable habitat. In contrast, data on topography acquired during field sampling explain a great part of the bird's preferences on the territory level. Here, the heterogeneity and richness in geomorphologic features as well as vertical structure elements depict suitable habitat as do northwest- to northeast-facing slopes (see Table 3).

Potential habitat in Switzerland today and tomorrow

Figure 1 and Appendix S5 display the predicted geographical distributions of potential Rock Ptarmigan habitat for recent conditions in Switzerland according to the five modelling approaches BRT, GLM, GAM, RF and CART. Furthermore, its potential distribution for the year 2070 is shown based on the scenario assuming an intermediate rise in mean July temperature. Here, the maps indicate that former suitable habitats at the northern and southern flanks of the Alps will become increasingly unsuitable and that suitable habitat is concentrated in the higher mountain regions in the central Alps. Furthermore, highly suitable habitats with occurrence probabilities exceeding 0.9 will fade.

The tendency of this development (i.e. shrinking of potential habitat and forcing it uphill), is consistent throughout all model approaches and at both grain sizes. The intensity, however, varies strongly and ranges from a reduction of 15% (CART) to more than two-thirds (GLM, GAM, and BRT) in the maximum scenario 2070 (see Table 3).

The rise in mean July temperature does not only affect the extent of potential habitat but also the altitudinal range. We predict a maximum upward shift ranging from 68 m (CART) to 480 m (GLM) on the meso-scale and between 108 m (GAM) and 316 m (CART) on the macro-scale by the year 2070. This represents a median upward shift of 21.2–46.5 m/°C on the meso-scale and of 5.2–44.4 m/°C on the macro-scale.

Discussion

Evaluation, validation and uncertainties of the multi-model approach

Our outlined model framework has proven to be successful in modelling the current potential distribution of Rock Ptarmigan and in identifying key habitat requirements controlling the species' distribution patterns. Performance criteria show very good results on independent test data proving a low degree of model overfitting (Table 2).

Generally speaking, the uncertainty in species distribution models can be divided into two parts: first, the algorithmic error arising from data quality, variable selection and applied modelling approach (Dormann et al. 2008);

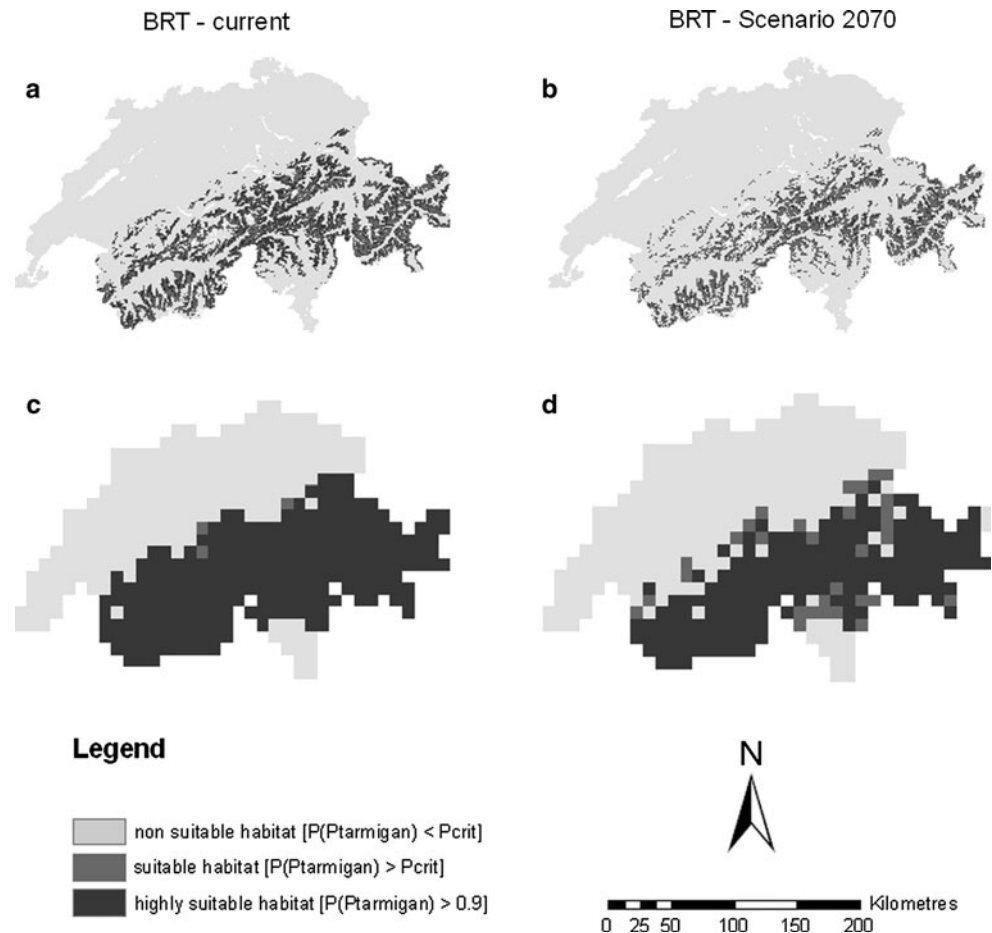
and second, the biotic error that represents failures in capturing all processes governing the species' distribution (of special concern are dispersal abilities, biotic interactions, non-equilibrium situations; cf. Hampe 2004; Pearson and Dawson 2003). It is noted that in our study not all possible sources of biotic errors could be accounted for, even though the study is based on high quality data. The incorporation of many of the above-mentioned processes still poses a great challenge to today's species distribution modelling (Zurell et al. 2009, 2011).

One of the most frequent sources of algorithmic prediction error is the reliance on a single statistical model (Pearson et al. 2006). The implementation of a multiple model approach such as employed in this study leads to a range of possible responses of Rock Ptarmigan to rising temperatures—at a first glance. Although the five modelling techniques differ strongly regarding the modelling procedure—i.e. selecting a single minimum adequate model (GLM, GAM and CART) versus ensemble forecasting (BRT and RF), parametric versus semi-parametric versus non-parametric approaches—the models are overall in broad agreement. This is true in regards to habitat requirements and with respect to the prediction of future potential habitat. While climate change predictions vary in magnitude, all models predict the same tendency: a significant loss of suitable habitat and a shift to higher altitudes (Table 4; Fig. 1; and Appendix S6). Similarly, the characterisation of current Rock Ptarmigan habitat differs slightly among these approaches. However, most predictors with outstanding explanatory power in one model also prove to be decisive in the other approaches (Table 3).

Rock Ptarmigan's habitat requirements: a matter of scale

In the following, we will examine the predicted suitable habitat on the different spatial scales based on the results for variable importance (Table 3). For an herbivorous species such as Rock Ptarmigan one would expect vegetation types to be pivotal habitat determinants. However, many studies state that the major drivers of species ranges are climatic variables. For example, it is argued that land cover plays a minor role as it can be widely explained through climate (cf. Thuiller et al. 2004). This is certainly true for continental-wide scales frequently used in most macro-ecological studies. Our results demonstrate that bioclimatic predictors gain explanatory power at the coarser resolution. However, our results also coincide with the findings of recent studies carried out by Pearson et al. (2004), Luoto et al. (2007), von dem Bussche et al. (2008) and Virkkala et al. (2010) asserting that bioclimatic predictors are large-scale determinants, amended by land cover variables at finer resolutions.

Fig. 1 Potential Rock Ptarmigan (*Lagopus muta helvetica*) habitat in Switzerland at current conditions (a, c) and for the intermediate scenarios 2070 (b, d) according to BRT at the two spatial scales (a, b grain size = 1 km², c, d grain size = 100 km²). If $P(\text{Rock Ptarmigan}) > P_{\text{MinROCdist}}$ grid cells are assumed as suitable (cf. Table 2); grid cells with occurrence probabilities exceeding 0.9 are considered as highly suitable. See Appendix S6 for maps based on the remaining four model approaches



Mean July temperature is the dominant predictor in all countrywide models. However, partial dependence plots show a different correlation with Rock Ptarmigan incidence: a linear, negative correlation on the macro-scale and hump-shaped response curve on the meso-scale. This does not reflect a differing mechanism of habitat selection. It can be explained by the fact that extreme values disappear when grid cells are aggregated to a coarser resolution, thus elucidating the need for analysis on fine scales in order to avoid misleading interpretations of results. The hump-shaped response curve on the meso-scale confirms the observations by Marti and Bossert (1985) indicating the rather narrow climatic niche of Rock Ptarmigan. The countrywide scales indicate that Rock Ptarmigan is confined to regions with mean July temperatures below 10–12°C (slightly higher at the 100 km² resolution). On the territory scale, bioclimatic data as such is not available. However, there are proxies that can explain the climatic constraints of Rock Ptarmigan on this scale. For example, altitude can be regarded as a substitute for temperature to a certain extent (altitude and mean July temperature show a correlation coefficient of $\rho_s < -0.9$ on the meso-scale and

macro-scale data). On the territory scale, altitude has limited predictive power ranking amongst the least influential variables. Here, climatic limitations of Rock Ptarmigan are instead reflected in the preference of a topography offering adequate and diverse micro-climatic conditions. Models single out a preference for locations with northeast- to northwest-facing slopes and habitats with a large variation in topography and geomorphologic features. In these locations, birds can adapt to seasonal and short-term weather fluctuations by taking advantage of differences in micro-site-specific climate. In fact, local variation in climate can be much larger than regional variation (Austin and van Niel 2011). Interpolated climate surfaces commonly used in large-scale modelling are at present not capable to integrate micro-site-specific variations to sufficient detail and therefore the gradient length of bioclimatic predictors is restricted to large grain sizes. Rorison et al. (1986) for instance recorded differences of up 12°C in maximum air temperatures between north- and south-facing slopes during the month of April.

This in turn explains the great explanatory power of topographic variables on the territory scale where adequate

bioclimatic data is not available. On large scales, however, the variables describing the topographic heterogeneity simply lose their justification. Hence, apart from two topographic attributes on the meso-scale, no topographic variables were of importance for the countrywide modelling.

Rock Ptarmigan is a bird species with a patchy distribution and thus the extent of potential habitat is easily overestimated by large-scale models. The true extent however, can be highlighted by results of small-scale analysis. Large-scale models, for instance, suggest Alp pastures as suitable habitats, but the territory level analysis shows that sites covered by a dense herbal layer are not suitable as Rock Ptarmigan habitat. Hence, Alp pastures seem to rather indicate a certain altitudinal range or the neighbourhood of suitable patches within the grid cell. Similarly, macro-scale models suggest grid cells containing a forest cover of up to approx. 30% are still suitable habitat. The territory-scale analysis, however, shows that the occupied habitat lies well above the timberline and trees are hardly tolerated within Rock Ptarmigan habitat. The bird even avoids vegetation exceeding dwarf shrubs in height, which is shown in univariate analysis on the territory scale (data not shown). This is also indicated by vegetation-related predictor variables in large-scale models and supported by observations from a ridge at the Aletsch glacier. There, small *Pinus cembra* trees colonised an area previously used by Rock Ptarmigan. Now, this area is regularly used as a mating territory by Black Grouse (*Tetrao tetrix*) instead (Bossert 1995; Marti et al., in preparation).

The examples discussed above show that predictions made on the territory scale can differ dramatically from those delivered by the meso-scale and macro-scale modelling. Figure 2 illustrates this subgrid variability. It shows that, for the area of a single grid cell of 1 km², the territory model predicts suitable habitat patches as well as unsuitable patches in close vicinity, emphasising the spatial heterogeneity of habitat suitability.

In conclusion, a multi-scale approach is a suitable tool to approach scale-related problems. It contributes several important insights which otherwise would be blurred by scale-dependent effects. First, this approach shows the changing importance of predictor variables across scales, i.e. bioclimatic variables as large-scale determinants and a crucial dependence of Rock Ptarmigan on topographic features on the territory scale (which in turn can be related to temperature tolerance of the bird). Downscaling, therefore, would require consideration of information about topography and vertical structure of habitat patches. Second, it elucidates that observed patterns may be strongly scale-dependent (e.g. a hump-shaped relationship on one scale versus a steadily increasing one on the other).

These patterns do not necessarily depict a different habitat selection process but may be solely explained by the way data were gathered. Third, the assessment on multiple scales allows the identifying of the true extent of suitable habitat. According to performance criteria, all macro-scale models reach nearly perfect results (Table 2). However, this apparent gain of performance is accompanied by a loss of quality of predictions: all macro-scale models largely overestimate the area of suitable habitat (Table 4; Fig. 1). This is especially the case if the species under study relies on patchily distributed habitat and inhabits steep terrain as do Rock Ptarmigan (Rahbek 2005; Popy et al. 2010). It clearly demonstrates how invaluable small-scale atlas data can be to accurately model the species distribution and its range shifts. The territory analysis in turn reveals which habitat features actually form the suitable area within the grid cell predicted as potential habitat on the meso-scale and visualise sub-grid variability.

Response to climate change

Our study indicates that climate—especially summer temperatures—is a main driving factor for Rock Ptarmigan's distribution in Switzerland. It is seen as a striking model result that Rock Ptarmigan appeared to be confined to regions with mean July temperatures below 10–12°C (slightly higher in macro-scale models). The idea of a strongly temperature-constrained dispersal of Rock Ptarmigan is supported by the newly postulated 'heat dissipation theory' (Speakman and Król 2010). This theory suggests that endothermic animals are limited by the ability to dissipate body heat rather than by the competition for a limited energy supply. Hence, Rock Ptarmigan are restricted to areas with rather low temperatures in order to avoid hyperthermia despite the availability of adequate food supply in warmer regions.

The climate change scenarios reflect this matter. Small temperature changes during the breeding season will force the species to higher altitudes. However, the calculated upward shift in average over all models of 39.1 m/°C at the meso-scale and 20.4 m/°C at the macro-scale is much smaller than one would expect presuming a purely temperature-driven distribution (a shift of ca. 160 m/°C; Hughes 2000). Here, our modelling results coincide with the empirical study of Popy et al. (2010) who detected a shift in elevation of bird species in the Italian Alps of 29.4 m/°C. The results are also backed by findings of Randin et al. (2009) as well as Luoto and Heikkinen (2008) who stated that environmental heterogeneity may significantly buffer the impact of climate change on species distribution. In our study, the territory-scale analysis elucidates the crucial dependence of Rock Ptarmigan on a

Table 4 Development of potential Rock Ptarmigan habitat in Switzerland applying scenarios for the rise of mean July temperature in Switzerland according to minimal, median and maximal scenarios represent the lower limit, the best estimation and the upper limit of a

95% confidence interval of temperature predictions for the years 2030, 2050 and 2070; habitat is estimated as suitable if $P(\text{Rock Ptarmigan}) > P_{\text{MinRockdist}}$ (cf. Table 2)

Model	Current	2030			2050			2070		
		Min	Median	Max	Min	Median	Max	Min	Median	Max
Δ July temperature [$^{\circ}\text{C}$]	0	0.6	1.45	2.6	1.4	2.75	4.9	1.9	3.9	7.1
Decrease within scenarios (%)										
Potential habitat (km^2)										
1 km^2 resolution										
BRT	9,450	-7.4	-16.7	-16.7	-7.1	-18.4	-45.4	-10.5	-31.2	-68.5
RF	9,955	-4.8	-8.9	-8.9	-4.6	-9.5	-15.3	-6.3	-12.8	-21.2
GLM	10,355	-1.5	-5.2	-13.5	-4.9	-15	-44	-7.7	-28.4	-81.8
GAM	10,216	-1.7	-5.2	-12.5	-5	-13.7	-39.7	-7.8	-26.3	-76.7
CART	10,699	-6.9	-11	-11	-6.7	-11.5	-14.1	-8.6	-13.5	-15.4
Median	10,216	-4.8	-8.9	-12.5	-5	-13.7	-39.7	-7.8	-26.3	-68.5
100 km^2 resolution										
BRT	241	-1.7	-3.7	-6.6	-3.7	-7.1	-21.2	-4.1	-14.5	-34.9
RF	240	-2.5	-3.8	-6.7	-4.2	-7.5	-15.4	-5.4	-12.1	-20.4
GLM	247	-4	-6.5	-10.5	-6.5	-10.5	-22.7	-8.5	-17.4	-39.3
GAM	234	-0.9	-2.1	-2.1	-1.7	-2.1	-10.3	-3.4	-5.6	-15.4
CART	240	-4.2	-9.6	-17.5	-9.6	-18.3	-31.3	-14.2	-22.9	-48.8
Median	240	-2.5	-3.8	-6.7	-4.2	-7.5	-21.2	-5.4	-14.5	-34.9
Upward shift within scenarios compared to current state (m)										
Median of altitudinal distribution (m)										
1 km^2 resolution										
BRT	2,319	56	100	100	54	108	149	73	145	17
RF	2,315	33	56	56	31	58	73	42	71	55
GLM	2,332	28	66	119	63	128	267	84	195	480
GAM	2,331	30	67	119	65	127	249	87	191	391
CART	2,360	35	55	55	34	57	70	44	68	63
Median	2,331	33	66	100	54	108	149	73	145	63
100 km^2 resolution										
BRT	1,601	12	17	24	17	34	189	18	122	247
RF	1,607	8	13	28	14	42	147	19	99	171
GLM	1,588	25	31	56	31	56	189	37	131	255
GAM	1,615	3	8	8	6	8	57	11	30	108
CART	1,607	14	56	151	56	156	235	116	171	316
Median	1,607	12	17	28	17	42	189	19	122	247

diverse topography offering diverse microclimatic conditions.

The shift of habitat from the current distributional range to higher mountain regions indicates the presence of potentially suitable habitat offering adequate conditions in terms of vegetation and topography. Interestingly, in the strongest scenario in BRT, RF and CART, the shift in elevation is lower than in scenarios with a lesser

temperature rise, thus suggesting that there are no more reserves of suitable habitat beyond a certain altitude. Additionally, in some areas, dispersal to higher altitudes will be simply restricted by the altitude of the mountain ranges. Similarly, Virkkala et al. (2008) predict a drastic reduction of Rock Ptarmigan habitat in northern Scandinavia. Here, the Arctic Ocean forms the northern barrier of dispersal for Rock Ptarmigan.

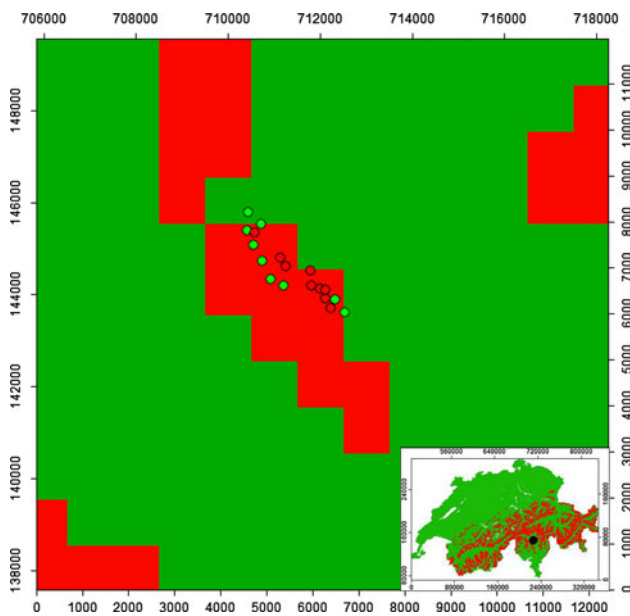


Fig. 2 Example for subgrid variability from Pizo Era ranges in southern Switzerland in the Canton Ticino. Predicted Rock Ptarmigan habitat by the meso-scale model (BRT, $1 \times 1 \text{ km}^2$ grid cells) and the predictions of the territory model (BRT, *dots*). Red denotes suitable habitat whereas green displays unsuitable habitat. Inset shows location of Pizo Era ranges in Switzerland

Thus, the predicted changes in climate will have a severe effect on Rock Ptarmigan distribution. A significant distributional shift will be induced by changes below the internationally agreed target of 2°C to which global warming may be restricted within the twenty-first century (IPCC 2007). If the temperature rise exceeds 4°C , potential Rock Ptarmigan habitat will decrease drastically, between one-quarter and two-thirds in the strongest scenario of 2070. Since we presume static conditions for all other habitat determining factors besides climate, we have to expect a more drastic development. Theurillat and Guisan (2001) forecast a reduction by 63% in area of the alpine layer for a “plus 3.3°C scenario”.

Moreover, changing biotic interactions, shifting vegetation composition and transient dynamics will play important roles (Zurell et al. 2009). For example, studies investigating shifts of vegetational belts predict a certain time lag due to the longevity of alpine shrubs and soil-forming processes (Bolliger et al. 2000; Neilson et al. 2005). Last but not least, the loss of habitat connectivity due to the displacement of the species to mountain tops far apart from each other will also contribute. Therefore, it should be noted that the scenarios presented in this study provide a conservative approach to defining the lower limit of decrease of potential habitat for Rock Ptarmigan. Linking the above-mentioned processes to habitat distribution modelling will provide a helpful tool for conservationists as they will need to adapt their strategies to a dynamic environment.

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