Predicting habitat availability for the Red-billed chough in the western and eastern Swiss Alps: why is the species occurring in the West but not in the East?

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SUMMARY

The distribution of the Red-billed chough (*Pyrrhocorax pyrrhocorax*) in the Alpine arch is currently restricted to its western side, in France, Italy and SW Switzerland. The Alps East of the Gotthard massif seem to have only been occupied sporadically during the 19th and 20th century: a few scattered historical records exist from S Austria, while a few pairs were still breeding in Lower Engadin until the 1960s but have vanished since (Denkinger 2011). Moreover, contrary to what is encountered in the western Alps, the last Engadin pairs were not occurring in upper subalpine and alpine habitats, but at middle elevation, breeding in derelict historical buildings instead of cliff walls. The reason for this apparent difference in ecology between the western and eastern Alps is not known. This raises the question whether the use of middle elevation breeding (and probably foraging) sites in Grisons was dictated by a lack of habitat suitability in the uplands. We therefore modelled habitat preferences and suitability of Red-billed choughs across Valais – the region which harbours the only Swiss population – in different seasons (winter, breeding, post-breeding and dispersal) using long-term observation data of foraging birds and nesting sites as well as a wide palette of environmental predictors. The information accrued from the Valais Red-billed chough spatial model was then extrapolated to E Switzerland (Canton of Grisons) to see whether potential suitable habitat occurs there, and if so where and to what extent. Foraging habitat as well as potential nesting sites could be predicted with a high level of accuracy (foraging habitat during post-breeding: AUC >0.8; all other models: AUC > 0.9). The environmental predictors determining suitable foraging habitat in Valais varied between seasons, but south-exposed grasslands (notably dry meadows and extensively grazed pastures) were preferred, while forested and snow-covered areas were avoided. Availability of, and distance to suitable foraging habitats were the main determinants of nest-site selection in Valais, probably reflecting strong energetic constraints during reproduction. The spatially-explicit extrapolation of the models to E Switzerland shows that the overall amount and relative percentage of both potential foraging and nesting habitat appears even greater in Grisons than in Valais. It remains therefore to explain why the species doesn't occur in Grisons naturally and why the last breeding pairs were occurring at middle instead of high elevation. One explanation could be that the environmental predictors we relied upon in this analysis are too coarse to encapsulate fairly subtle regional qualitative differences in the structure and composition of grasslands. This may concern in particular very xeric grasslands such as climacic steppe, an important habitat for winter foraging which is only widespread in Valais. Finer analyses are needed until we can conclude about the reasons beyond the absence of the Red-billed chough from Grisons.

ZUSAMMENFASSUNG

Die Verbreitung der Alpenkrähe (*Pyrrhocorax pyrrhocorax*) im Alpenbogen beschränkt sich heute vorwiegend auf dessen westlichen Gebiete, in Frankreich, Italien und der Schweiz (Maumary et al. 2007). Die Alpen östlich des Gotthardmassivs waren während des 19. Und 20. Jahrhundert nur sporadisch besiedelt: Einige historische Einzelbeobachtungen sind aus Südösterreich bekannt, und einige wenige Paare brüteten bis in die 1960er Jahre im Unterengadin, sind jedoch inzwischen verschwunden. Im Gegensatz zu den Westalpen brüteten diese letzten Engadiner Paare nicht in Felswänden in den höheren subalpinen und alpinen Gebiete sondern in verfallenen Gebäuden in den mittleren Höhenlagen. Der Grund für diese Unterschiede zwischen West- und Ostalpen ist unbekannt. Insbesondere stellte sich dabei die Frage, ob die Nutzung der mittleren Höhenlagen (zur Brut, aber vermutlich auch zur Nahrungssuche) und das Verschwinden der Art in den Ostalpen mit einer unzureichenden Habitatqualität in den Hochlagen zu erklären ist. Um diese Frage zu klären, modellierten wir die Habitatpräferenzen und die daraus abgeleitete Habitateignung für die Alpenkrähe im Wallis - der Region in der die einzige Population der Schweiz beheimatet ist - auf Grundlage langjähriger Beobachtungsdaten und unterschiedlicher Habitatvariablen. Der Fokus lag auf Nahrungshabitaten in drei verschiedenen Jahreszeiten (Winter, Brutsaison und Herbst) sowie potentielle Neststandorten. Die Modelle wurden auf die Ostalpen zu übertragen, um dort potentielle Lebensräume zu identifizieren und ihre Qualität zu quantifizieren. Alle Modelle wiesen einen hohen Grad der Vorhersagequalität auf (Modell zur Vorhersage von Nahrungshabitaten im Herbst: AUC>0.8; alle anderen Modelle: AUC > 0.9). Die Hauptprädiktoren für geeignetes Nahrungshabitat variierten zwar zwischen den Jahreszeiten, in allen Jahreszeiten wurden jedoch Trockenwiesen und/oder extensive Weideflächen in südlichen Expositionen bevorzugt, während bewaldete und schneereiche Gebiete gemieden wurden. Die Verfügbarkeit von und die Distanz zu geeignetem Nahrungshabitat in der Brutsaison stellte sich als wichtiger Faktor für die Nistplatzwahl heraus, was auf ein limitiertes Energiebudget während der Reproduktionszeit hinweist. owohl die absolute Fläche als auch der prozentuale Anteil an potentiellem Nahrungs- und Nesthabitat auf der Landschaftsebene im Kanton Graubünden höher ist als im Wallis. Auf der Grundlage der vorliegenden Modelle lässt sich das Verschwinden der Alpenkrähe in den Schweizer Ostalpen und vor Allem das frühere Vorkommen in den Mittleren Lagen demanch nicht erklären. Eine Möglichkeit dafür könnte sein, dass die kleinräumigen Unterschiede die im Hinblick auf der Struktur und Qualität der Wiesen und Weideflächen in den beiden Regionen bestehen, mit den relativ groben, verfügbaren Geodaten nicht erfasst werden werden. Dies betrifft insbesondere die Bereiche der Trockensteppe in den tieferen Lagen, die in schneereichen Wintern zur Nahrunsgaufnahme genutzt werden und im Wallis häufiger wesentlich häufiger als in Graubünden. Eine abschließende Klärung der Frage nach dem Fehlen der Alpenkräh in den Ostapen erfordert daher Untersuchungen auf einer kleinräumigeren Massstabsebene.

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INTRODUCTION AND BACKGROUND

The strongholds of the distribution of the Red-billed chough (*Pyrrhocorax pyrrhocorax*) in the Alpine arch have always been restricted to its western side, in France, Italy and Switzerland (Glutz et al. 1993). There were only a few sporadical historical observations in S Austria. In Switzerland, the species occurs exclusively in the West, in the Alps of Valais, with an estimated fairly stable breeding population of 60-70 pairs (Oggier, unpublished data). The slight population increase reported in the past 25 years by the Swiss Ornithological Institute (http://www.vogelwarte.ch) may result from more intensive prospection. The Red-billed chough is listed as endangered by the Swiss National Red list. In the Eastern Swiss Alps, in particular in the Grisons, Red-billed choughs are today extinct as breeders and only observed extremely sporadically. Yet, breeding was documented in the Grisons until the 1960s (Glutz von Blotzheim 1993), where it occurred at middle elevation in partly derelict historical buildings in Lower Engadin, which contrasts with the situation in Valais (and most of the rest of the W Alps) where breeding sites have to the best of our knowledge always occurred in upper subalpine and alpine cliff walls. On behalf of the *Monticola* assocation and three zoos from Switzerland and Austria that foresee a reintroduction programme in the eastern Alps, the research group WILMA of the ZHAW Wädenswil, under the supervision of Dr Roland Graf, investigated the population development of the Red-billed chough in the eastern Alps (Graf & Bitterlin 2015). These authors concluded that it remains unclear whether insufficient habitat availability and/or quality could explain the historical restricted occurrence and current absence of the Red-billed chough in the eastern Alps. Until this question is properly resolved, reintroduction cannot be envisioned.
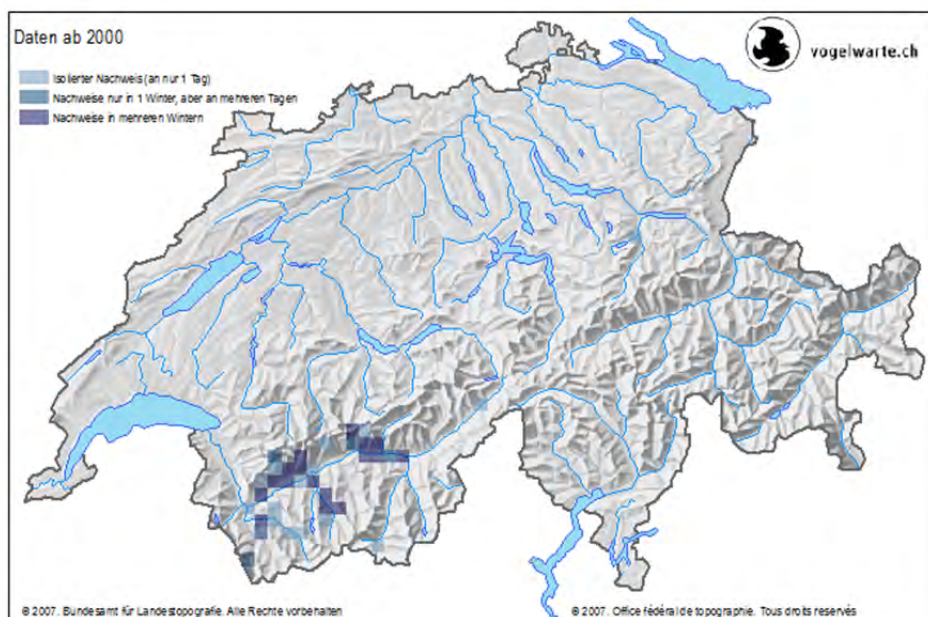

Figure 1: Winter-distribution of *Pyrrhocorax pyrrhocorax* in Switzerland since 2000, showing the current distribution restricted to Valais. Excerpt from the Swiss Ornithological Institute website.

In this study we used long-term observation data of foraging birds and nesting sites collected in Valais, together with spatially explicit habitat modelling to identify seasonal habitat selection and suitable habitat distribution for the Red-billed chough in the SW Swiss Alps. We focused on foraging habitat in three seasons (winter, breeding, and post-breeding dispersal) as well as on nest site selection. More specifically, we predicted that: 1) the selection of foraging grounds during the breeding season correlates with the retreating snow-front (because food availability is greater in grassy patches recently freed by snow) and/or the presence of short grass; 2) nest site selection results from a trade-off between the availability of suitable cliff walls offering crevices and niches, and the presence of optimal foraging patches not too far; 3) winter foraging concentrates in areas that remain largely freed of snow such as wind-blown ridges and south-exposed grasslands at relatively low elevation. The outcomes of our spatially-explicit model constructed for the Valais Red-billed choughs were then extrapolated to Grisons to see whether suitable habitat occurs there, and if so where and to which extent.

METHODS

STUDY AREA

Species-habitat associations were first investigated in the western Swiss Alps (Valais) and then extrapolated to the eastern Alps (Grisons). Both regions belong to the inner Alps (Gonseth *et al.* 2001) which are characterised by subcontinental to continental climate conditions with relatively warm and dry summers, and cold, wet winters. Precipitation is typically 600-900 mm/year at 1000 m a.s.l. (Ott et al. 1997). The geological substrate consists mostly of limestone and silicates, depending on the area. The valley bottoms in both regions are populated, but much more so in Valais than in the Grisons. Two major differences between Valais and Grisons, however, are 1) that the valley bottoms are on average at higher elevation in Grisons than in Valais, notably in Engadin where Red-billed choughs once occurred, while 2) Valais has much higher mountains in general. Land use on the mountain slopes not covered by forest and rocks is mostly devoted to extensive farming (grazing) in summer, and winter recreation in winter, with several major ski resorts existing in both regions.

SPECIES DATA

Red-billed chough foraging locations were extracted from the database of the Swiss Ornithological Institute (in particular www.ornitho.ch) for the years 2000–2014, which contains observations from amateur bird watchers and professional ornithologists. This data was complemented with the (partly unpublished) observations collected by two of our co-authors (P.-A.O. and R.A.). Only locations where foraging was ascertained where retained, providing that location accuracy was ± 100 m. The dataset was split into three seasons: winter (November-April, N = 139), breeding (May-July, N = 193) and post-breeding dispersal (August-October, N = 78). Nest site locations (N = 76) were obtained from long-term field surveys (1974-2016) by one of our co-authors (P.-A.O.; unpublished

data). Given the high stability of the Red-billed population in Valais, this conveys information on contemporaneous nest site selection in that area.

ENVIRONMENTAL PREDICTORS

As environmental predictors we used information on topography, climate, snow condition and land cover, including human infrastructure (Table 1).

Topography was described by elevation, slope, exposition (i.e. northness and eastness, defined as cosine and sine of aspect) as derived from the digital elevation model of Switzerland.

Climate information included the average temperature and precipitation in summer and winter, as obtained from the worldclim-dataset (Hijmans *et al.* 2005) (www.worldclim.org), downscaled to a 100 m resolution based on the SRTM-V4 digital elevation model (DEM) and the method described in (Zimmermann & Roberts 2001).

Snow cover for the years 2006-2011 was modelled according to (Bavay, Gruenewald & Lehning 2013) at 200 m resolution. To obtain a measure of snow cover heterogeneity among years, we calculated the average number of days with snow cover (snow depth >5 cm) per year, and the variance thereof, for each of the pre-defined seasons within this time period. In addition, we calculated the average percentage of area covered by snow within 1 km^2 (radius = 564 m) for each of the study months separately. Monthly values of snow cover were calculated by averaging the values of four days randomly selected from each of the four weeks per study month, to account for within-month snow cover heterogeneity.

Information on land cover, i.e. the percentage of forest, shrubland, grassland, permanent cultures (orchards and vineyards), waterbodies, glaciers, scree and rock was obtained from the Vector 25 map (SWISSTOPO 2009). In addition, we calculated the distance to steep rock (>45°). Dry meadows and pastures were adopted from the mapping of the Swiss Federal Adminstration of the Environment. In addition, we calculated the mean number of sheep and goat per community in the years 2004-2014 and related them to the amount of pastureland per community in order to obtain a rough estimate of the density of livestock per hectare of pastureland. Human infrastructure was included as the distance to transportation infrastructure (roads and railways), trails, ski-lift and cableways.

All predictor variables were prepared as raster maps (cell size: 25 x 25 m) with the exception of snow-layer, which was only available at a 200 x 200 m resolution. In order to both capture the environmental conditions prevailing around the foraging locations and to account for sampling accuracy, we calculated means (continuous variables), percentages (boolean and categorical variables) or densities (for point and linear features) within a circular moving window with a radius 100 m. Snow cover heterogeneity was considered within a 1km^2 area (radius = 564m). For the nest site model, for which we had accurate nest locations, we used the data of rocks and slope at the original 25 m resolution.

In addition, to test whether the amount of, and distance to suitable foraging habitat affected nest site selection, we generated three additional *ad hoc* variables, directly drawn from the breeding-foraging habitat model. First, we calculated the average suitability of foraging habitat (i.e. Maxent logistic output) within a 3-km radius around the nest site, which roughly corresponds, we estimated, to the distance most birds usually fly in their foraging trips (P.-A. Oggier, unpublished data). Second, we converted this continuous variable into a binary map of nest site presence and absence (as specified below) and calculated the distance of the nest to the next foraging patch. Finally, we calculated the percentage of suitable foraging habitat within a 3-km radius overall.

Table 1: Variables used for predicting Red-billed chough foraging and breeding occurrence with their respective codes, metrics, units, window size and data sources.

VARIABLE CODE	DESCRIPTION	UNIT	WINDOW SIZE	SOURCE
TOPOGRAPHY				
ELEVATION	Elevation	m a.s.l.	100 m	DEM[1]
SLOPE	Slope	degree	100 m	DEM
SLOPE_1	Slope		-	
NORTH	Northness (cosine of aspect)	-1 to 1	100 m	DEM
EAST	Eastness (sine of aspect)	-1 to 1	100 m	DEM
CLIMATE				
TAVE57	Average summer ambient temperature (May-July)	°C	100 m	Worldclim[2]
TAVE122	Average winter temperature (Dec-Feb)	°C	100 m	Worldclim
PREC57	Mean summer precipitation (May-July)	mm	100 m	Worldclim
PREC122	Mean winter precipitation (Dec-Feb)	mm	100 m	Worldclim
SNOW COVER				
DWS_M	Average number of days with snow (>5 cm)	days	100 m	Bavay et al. 2013
DWS_V	Between-year variance in number of snow days (>5 cm)	days	100 m	Bavay et al. 2013
SNOW(1-12)_FR	Average snow cover within 1 km^2 per month (1-12: January-December)	%	564 m	Bavay et al. 2013
LAND COVER AND LAND USE				
FOREST	Percentage of forest	%	100 m	Vector 25
BUSH	Percentage of bushes	%	100 m	Vector 25
GRASS	Percentage of grassland	%	100 m	Vector 25
TWW	Percentage dry meadows and pastures	%	100 m	BAFU[3]
PERM	Percentage of permanent cultures (orchards, vineyards)	%	100 m	Vector 25[4]
GLACIER	Percentage of glacier	%	100 m	Vector 25
SCREE	Percentage of scree	%	100 m	Vector 25
ROCK	Percentage of rock	%	100 m	Vector 25
ROCK_1	Presence of rock	1/0	-	
ROCK45D	Distance to steep rocks >45°	m	100 m	Vector 25
WATER	Percentage of waterbodies	%	100 m	Vector 25

SHEEPGOAT	Average number of sheep or goat per ha pastureland (2004-2014)	N	100 m	BfS[5]
ROADRAIL	Distance to roads and railways	m	100 m	Vector 25
TRAILDIS	Distance to trails	m	100 m	Vector 25
SKICW_D	Distance to skilifts and cableways	m	100 m	Vector 25
INFORMATION ON FORAGING HABITAT IN THE BREEDING SEASON USED FOR THE NEST SITE MODEL ONLY				
F2_VS_MEAN3K	Average foraging habitat suitability within 3 km radius	0-1	3000 m	Foraging model
F2_VS_PERC3K	Percentage of suitable foraging habitat within 3 km radius	%	3000 m	Foraging model
FOR_VS_DIST	Distance to the next suitable foraging patch	m	-	Foraging model

[1]DEM: Digital elevation model (SWISSTOPO):
http://www.swisstopo.admin.ch/internet/swisstopo/en/home/products/height.html
[2]Worldclim: www.worldclim.org, downscaled.
[3] Federal Administration for the Environment Switzerland (BAFU):
https://www.bafu.admin.ch/bafu/de/home/themen/biodiversitaet/fachinformationen/massnahmen-zur-erhaltung-und-foerderung-der-biodiversitaet/oekologische-infrastruktur/biotope-von-nationaler-bedeutung/trockenwiesen-und--weiden.html
[4]Vector25: Digital landscape model of Switzerland (SWISSTOPO):
http://www.swisstopo.admin.ch/internet/swisstopo/de/home/products/landscape/vector25.html
[5]Federal Administration for Statistic Switzerland (BfS):
https://www.bfs.admin.ch/bfs/de/home/statistiken/land-forstwirtschaft/landwirtschaft.html

STATISTICAL APPROACH

As only data on species presence were available, but no data on ascertained absence, we used Maxent (version 3.3.3k), a machine-learning technique based on the principle of maximum entropy (Jaynes 1957), in its adapted form for predictive species distribution modelling (Phillips, Dudik & Schapire 2004; Phillips, Anderson & Schapire 2006) implemented in the *dismo* package in R (R Core Team 2016) (Hijmans & Elith 2016).

Maxent compares the environmental conditions at the observed species locations with 10'000 locations randomly sampled across the study area. Maxent allows to fit complex models by using the environmental variables as well as different functions thereof (in the following termed "feature classes" FCs) as predictors, which includes linear, quadratic and two-way interaction terms as well as threshold and hinge features (for detailed information see Phillips, Dudik & Schapire 2004; Elith *et al.* 2006; Phillips, Anderson & Schapire 2006; Phillips & Dudik 2008). To avoid overfitting and limit model complexity, a regularization procedure is commonly applied (Phillips, Anderson & Schapire 2006), which constrains the average predicted value for a given feature to be close (i.e. within the confidence intervals) but not exactly similar to the empirical value measured at the presence locations.

Since the default value of the regularization multiplier (RM; default = 1.0) (Phillips & Dudík 2008), is not necessarily optimal for any specific dataset (Warren & Seifert 2011; Radosavljevic & Anderson 2014; Warren *et al.* 2014) and can result in poorly performing

models (Shcheglovitova & Anderson 2013; Radosavljevic & Anderson 2014), we adopted a stepwise procedure to tune model complexity (i.e. trade it off against performance) in order to choose an optimal set of predictors: for each predefined season we selected an initial set of ecologically meaningful predictors from which we generated a set of models using six different FC combinations (L, LQ, H, LQH, LQHP, LQHPT; where L = linear, Q = quadratic, H = hinge, P = product and T = threshold). For the nest-site model, where we had only 76 locations (which still represent most nest sites in the area), we tested only three variants (L, LQ, LQH), following the recommendations by Philips & Dudik (2008). Each combination was tested using different regularization multiplier (RM) values, ranging from 0.5 to 10.0, with increments of 0.5, which resulted in 120 different models (Warren *et al.* 2014; Wright *et al.* 2015; Jueterbock *et al.* 2016). We then selected the settings that provided the most parsimonious model based on the sample-size-adjusted AICc (Akaike information criterion) (Akaike 1974).

From this initial model we then performed a selection of variables. First, from pairs or groups of highly correlated variables (Pearson correlation coefficient $|r| > 0.75$) we retained only those that achieved the highest gain (i.e. increase in regularized log-likelihood) in univariate models using the starting FC-RM settings. With the remaining variables, we generated another set of models, again testing the six FC combinations described above, within the predefined range of RMs, retaining the model with the lowest AICc value. From this model we discarded all variables with a contribution of less than 2%. We finally ran another set of models using the resulting variable subset (again varying FCs and RMs) and selected our final model based on the AICc value. That final model was then evaluated using 5-fold cross validation, with predictive accuracy assessed using the area under the receiver operating characteristics curve (AUC). Models were calibrated for Valais and then projected to Grisons. Finally, to estimate the absolute and relative amount of potential foraging and nesting habitat, continuous predictions were converted into binary maps of species presence-absence, applying the threshold values at which sensitivity and specificity were maximised with the training data (Appendix 1).

RESULTS

Result presentation refers to the amount and distribution of foraging and nesting habitat (presented in the figures and tables included in the main text) and the species' responses to the variables included in the models (Appendices 3-6). Foraging and nesting habitat was predicted with a high accuracy in all three seasons (given are mean AUC and standard deviation across 5 cross-validation replicates; winter foraging: 0.938, 0.008; breeding season foraging: 0.920, 0.002; post-breeding and dispersal season foraging: 0.881, 0.035; nesting habitat: AUC: 0.977, 0.016). Model extrapolation to the eastern Swiss Alps indicated that both the absolute amount and relative proportion of predicted suitable foraging and nesting habitat at the landscape scale was higher in Grisons than in Valais, and these for all three seasons (Appendix 2).

Foraging habitat in winter

Winter foraging habitat was mainly characterized by a high proportion of grassland, especially dry meadows and pastures, and an intermediate cover of rocks (30-40%, with some preference for steep rocky areas) on south-exposed slopes under very xeric circumstances (low precipitation). Optimal winter foraging habitat is furthermore characterized by a very low snow cover, with a peak at 20%, in the wider surroundings. Red-billed choughs also foraged closer to roads than expected from a random selection pattern. As in the other two seasons, forested areas were clearly avoided.

Table 2: Variables explaining the selection of foraging habitat of *Pyrrhocorax pyrrhocorax* in winter in Valais. The percent contribution to the final model and the response type are given with +, – and ∩ indicating a positive, negative or unimodal response, respectively.

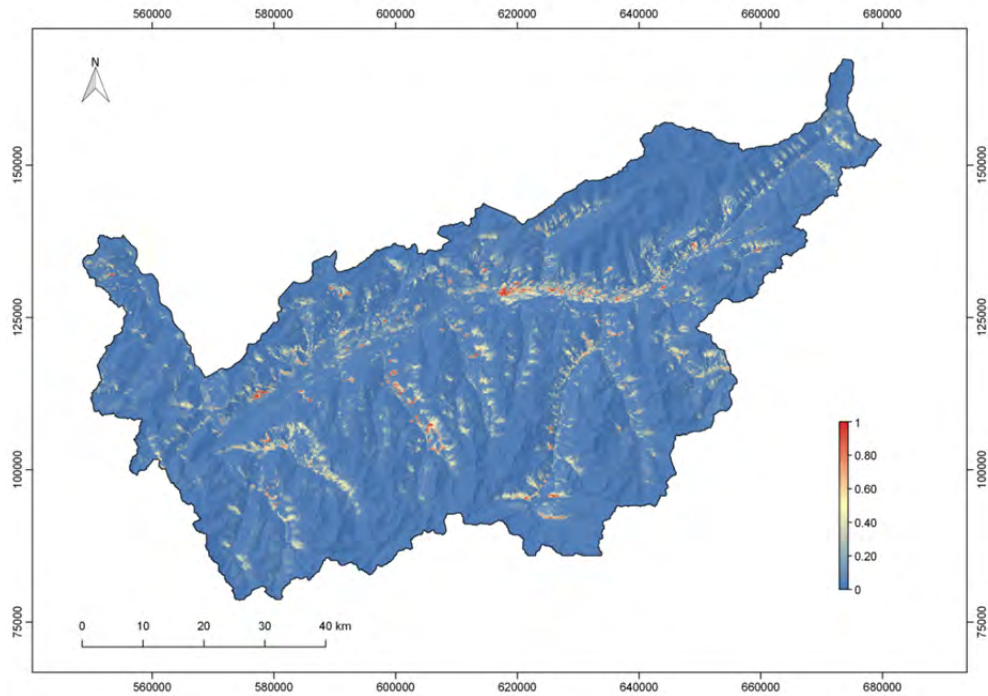| VARIABLE	PERCENT CONTRIBUTION	RESPONSE TYPE
GRASS	25.7	+
TWW	23.6	+
NORTH	16.4	–
ROADRAIL	7.3	–
SNOW11_FR	6.7	∩
EAST	5.4	∩
ROCK	4.7	∩
FOREST	4.6	–
ROCK45D	3	–
PREC122	2.5	–

Figure 2: Foraging habitat suitability for *Pyrrhocorax pyrrhocorax* in Valais during the winter season. Habitat suitability gradient drops from red (highly suitable) to blue (unsuitable). According to this model, 16.1 % of the area (723 km^2) are potentially suitable for the species in Valais (binary transformation).
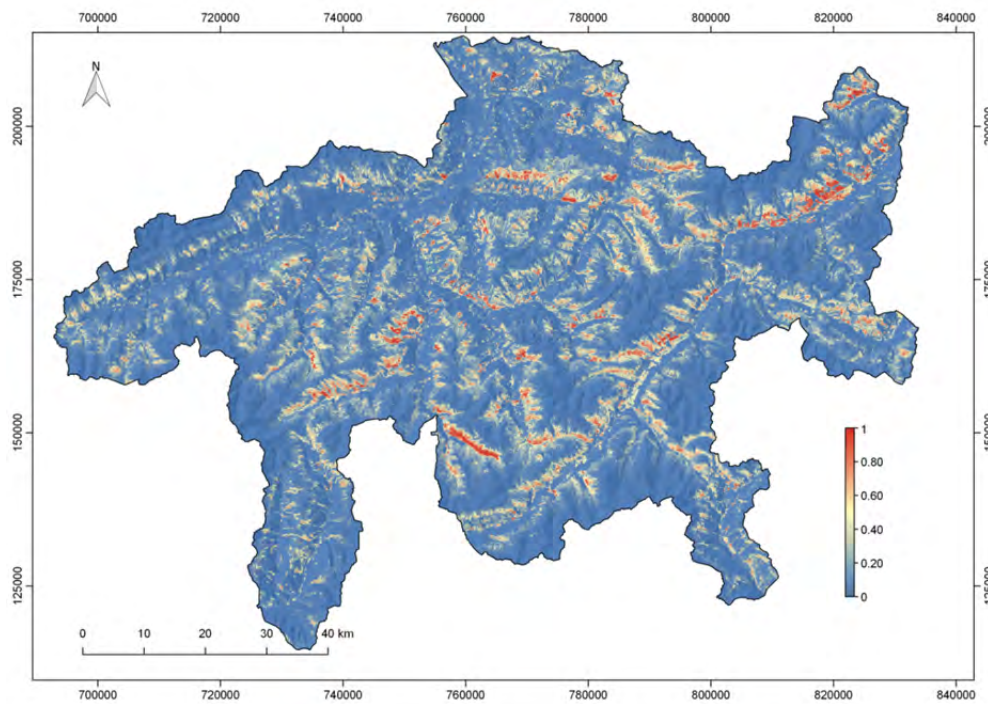

Figure 3: Winter foraging habitat suitability for *Pyrrhocorax pyrrhocorax* in Grisons as extrapolated from the Valais model. Habitat suitability gradient drops from red (highly suitable) to blue (unsuitable). According to this projection, 57.8 % of the area (2601 km^2) are potentially suitable for the species in Grisons (binary transformation).

Foraging habitat during the breeding season

Breeding-season foraging habitat is characterized by a very low proportion of forest and, again, a high proportion of grassland close to rocky sites, located in areas with fairly moderate precipitation and a low to moderate snow cover within 1 km^2. Compared to the winter season, the birds forage on steeper slopes. Southern expositions are still strongly preferred, as in winter, but the birds also extend their activity to southwestern expositions. Glaciers and areas close to skilifts and cableways are avoided. Moreover the birds show a preference for areas subjected to low to middle intensity grazing by sheep and goats, heavy grazing appearing detrimental.

Table 3: Variables explaining the selection of foraging habitat of *Pyrrhocorax pyrrhocorax* in the breeding season in Valais. The percent contribution to the final model and the response type are given with +, – and ∩ indicating a positive, negative or unimodal response, respectively.

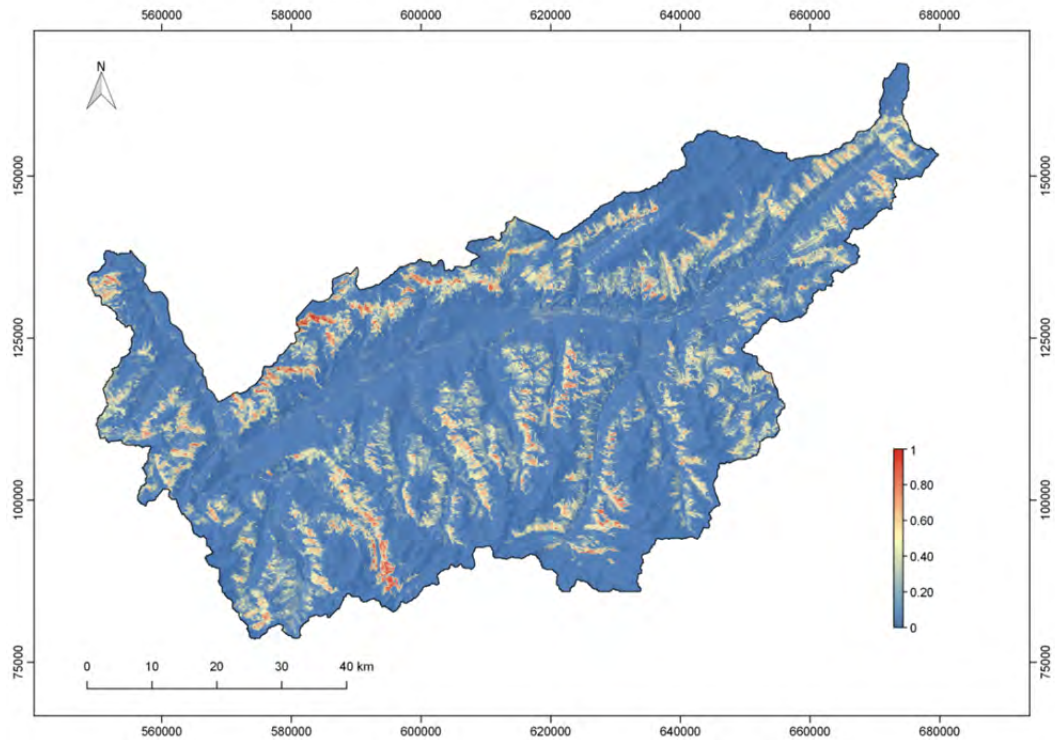| VARIABLE	PERCENT CONTRIBUTION	RESPONSE TYPE
FOREST	17.4	–
NORTH	15.7	–
GRASS	12.4	+
SNOW7_FR	11.4	–
GLACIER	11.3	–
SHEEPGOAT	10.4	∩
EAST	4.4	∩
SKICW_D	3.8	+
ROCK45D	3.6	–
SCREE	3.5	∩
PREC57	3	∩
SLOPE	3	+

Figure 4: Foraging habitat suitability for *Pyrrhocorax pyrrhocorax* in Valais during the breeding season. Habitat suitability gradient drops from red (highly suitable) to blue (unsuitable). According to this model, 20.1 % of the area (869 km^2) are potentially suitable for the species in Valais (binary transformation).
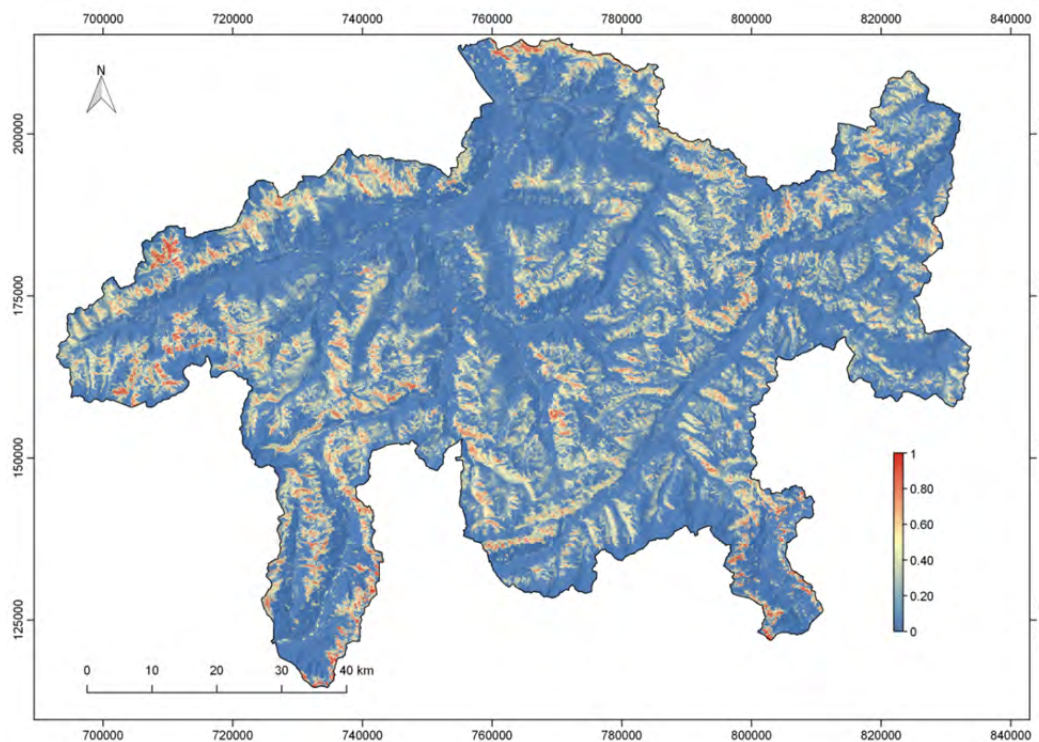

Figure 5: Breeding-season foraging habitat suitability for *Pyrrhocorax pyrrhocorax* in Grisons as extrapolated from the Valais model. Habitat suitability gradient drops from red (highly suitable) to blue (unsuitable). According to this model, 33.0 % of the area (1762 km^2) are potentially suitable for the species (binary transformation).

Foraging habitat during the post-breeding and dispersal season

Foraging habitat during the post-breeding and dispersal season is characterized firstly by the absence of forest and glaciers. Grasslands, especially dry meadows and pastures on south-exposed slopes and near rocky areas are preferred, waterbodies and areas dominated by screes avoided. Compared to the other seasons, the birds forage on average in closer vicinity to skilifts and cableways, but still clearly avoid them up to a distance of 1000 m.

Table 4: Variables explaining the selection of foraging habitat of *Pyrrhocorax pyrrhocorax* in the post-breeding and dispersal season in Valais. The percent contribution to the final model and the response type are given with +, – and ∩ indicating a positive, negative or unimodal response, respectively.

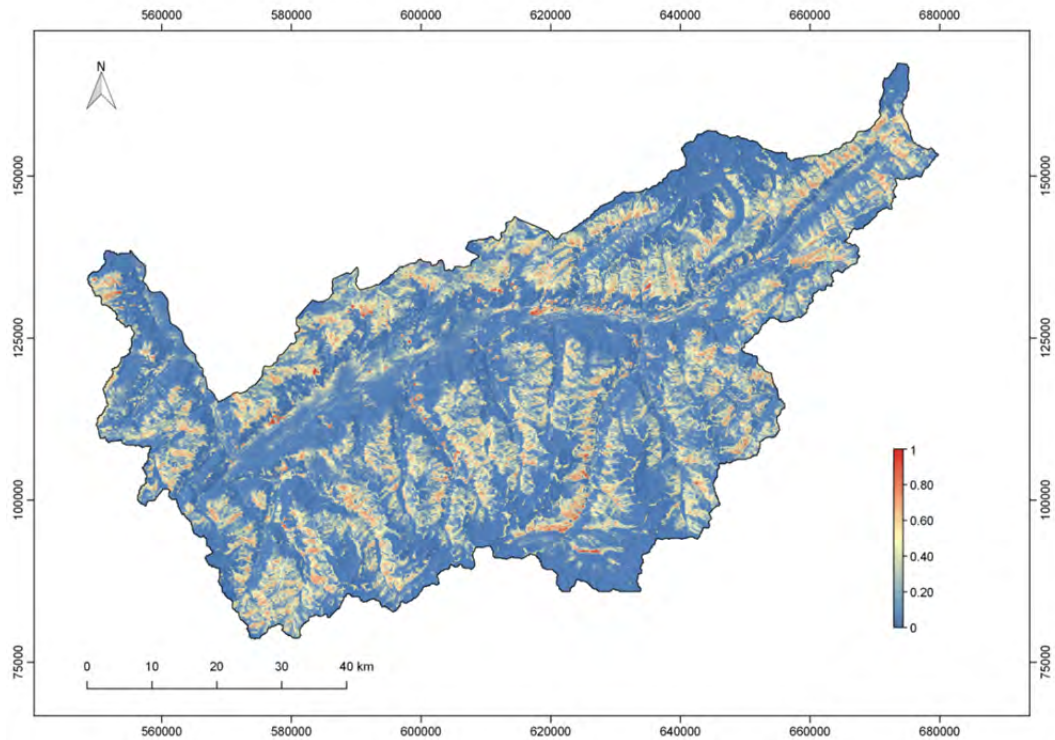| VARIABLE	PERCENT CONTRIBUTION	RESPONSE TYPE
FOREST	25.9	–
GLACIER	17.6	–
NORTH	15	–
TWW	10.7	+
GRASS	10.2	+
ROCK45D	7.8	–
WATER	5.3	–
SCREE	3.9	–
SKICW	3.9	∩

Figure 6: Foraging habitat suitability for *Pyrrhocorax pyrrhocorax* in Valais during the post-breeding and dispersal season. Habitat suitability gradient drops from red (highly suitable) to blue (unsuitable). According to this model, 40.6 % of the area (1505 km^2) are potentially suitable for the species (binary transformation).
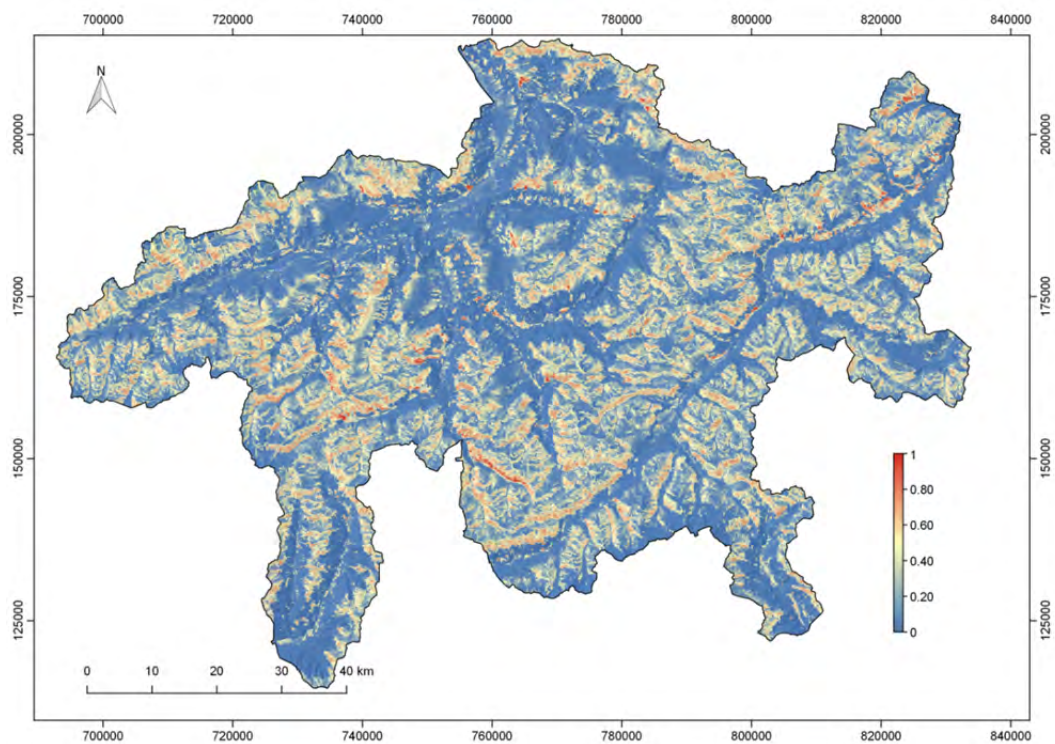

Figure 7: Foraging habitat suitability for *Pyrrhocorax pyrrhocorax* in Grisons during the post-breeding and dispersal season as extrapolated from the Valais model. Habitat suitability gradient drops from red (highly suitable) to blue (unsuitable). According to this model, 57.0 % of the area (2578 km^2) are potentially suitable for the species (binary transformation).

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NEST SITES

Next to the presence of and vicinity to steep rock, i.e. potentially cliff walls, the average foraging habitat suitability within a 3 km radius and a fairly low to an intermediate cover of snow were the main predictors. Also the distance to the next foraging patch played a role in nest site selection. Southern exposed sites (from SE to SW) were preferred over northern expositions.

Table 4: Variables explaining the nest site selection of *Pyrrhocorax pyrrhocorax* in Valais. The percent contribution to the final model and the response type are given with +, – and ∩ indicating a positive, negative or unimodal response, respectively.

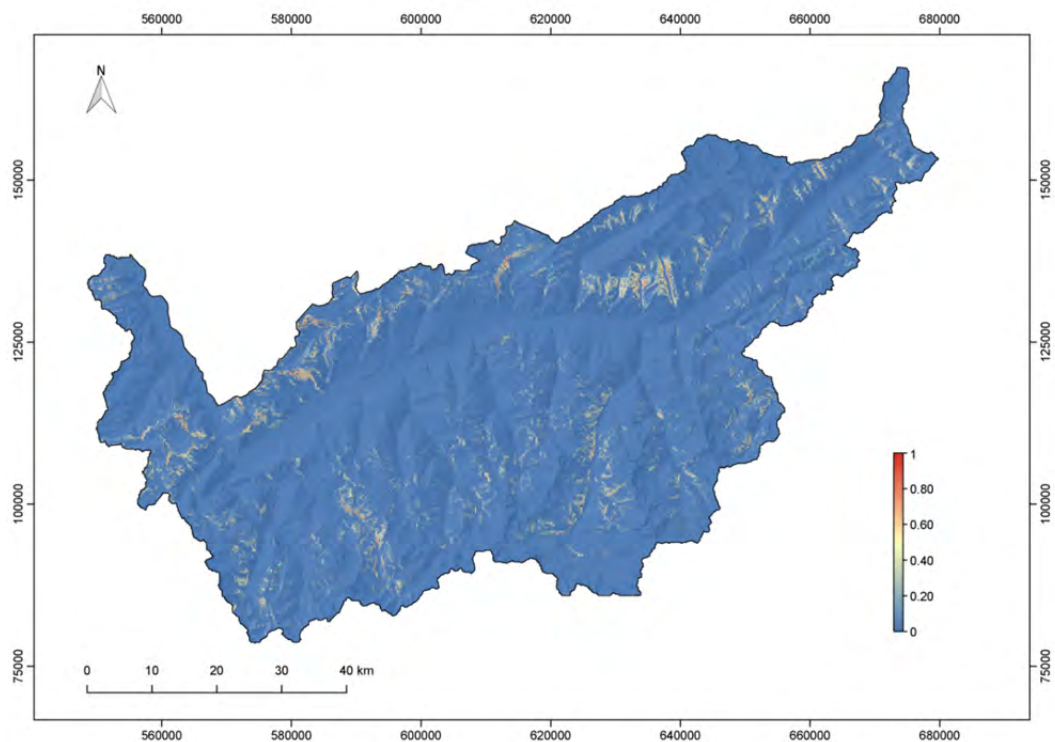| VARIABLE	PERCENT CONTRIBUTION	RESPONSE TYPE
ROCK_1	47.0	+
SLOPE_1	29.0	+
F2_VS_MEAN3K	7.6	+
SNOW7_FR	7.3	∩
NORTH	4.9	∩
FORS2_VS_DIST	2.3	–
ROCK45_D	2.0	–

Figure 8: Availability of potentially suitable nesting areas for *Pyrrhocorax pyrrhocorax* in Valais. Suitability gradient drops from red (highly suitable) to blue (unsuitable). According to this model, 10.7 % of the area (504 km^2) offers potentially suitable sites for breeding (binary transformation).
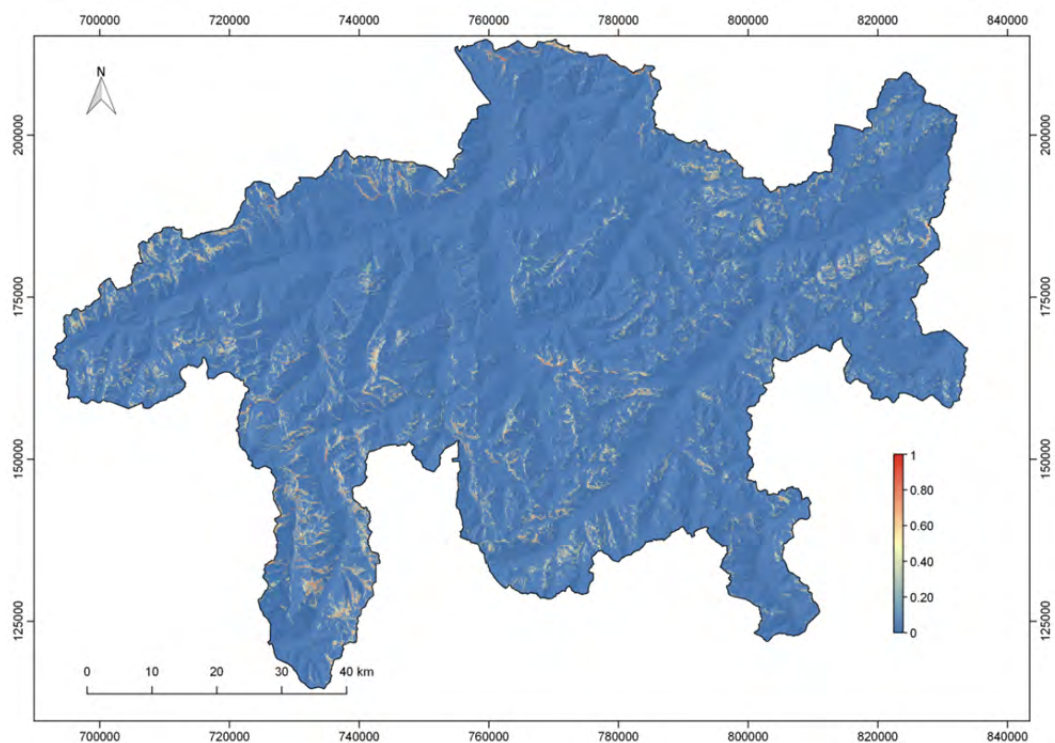

Figure 9: Availability of potentially suitable nesting areas for *Pyrrhocorax pyrrhocorax* in Grisons as extrapolated from the Valais model. Red areas indicate highly suitable sites whereas areas in blue are unsuitable as nesting site. Suitability gradient drops from red (highly suitable) to blue (unsuitable). According to this model, 13.0 % of the area (818 km^2) offers potentially suitable sites for breeding (binary transformation).

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DISCUSSION

The Alpine distribution of the Red-billed chough is restricted to the western Alps. Situated in the centre of the Alps, Switzerland harbours flourishing populations in the West (Valais) while the species has always been rare in the rest of the country. Since the 1960s it is even extinct as breeder in the East (Grisons). By modelling habitat requirements of the Valais population and projecting them onto the Grisons territory, we hypothesised that Valais should offer a much greater relative extension of potential habitat, notably foraging habitat in winter, than Grisons, which may explain the contrasted spatial distribution pattern that is observed since ever. This information was furthermore sought to provide the necessary evidence-based guidance about the appropriateness of a reintroduction scheme to reconstitute a Red-billed chough population in the eastern Alps.

Contrary to our expectations, our models suggest that the availability of potentially suitable foraging and nesting habitat is not greater in Valais, where the red-billed chough commonly breeds, compared to Grisons, where the species is now extinct. In particular, the finding that winter foraging habitat – which had been assumed to be a key factor for the persistence of the species – doesn't appear to be a limiting factor in the Grisons is puzzling.

There is one main limitation to our models, though, which might explain this finding: while the spatial scale and the variables considered for the analysis allowed us to capture suitable broad-scale landscape-ecological framework conditions (i.e. habitat potential sensu Braunisch & Suchant 2007) of the species, they might not have enabled us to embrace the sheer complexity of species's fine-grained ecological requirements. For instance, the quite coarsely defined and mostly abiotic environmental predictors at a radius of 100 m may have failed to account for subtle spatial variation in micro-habitat structure and, of course, food supply. In particular the grassland variables used in the model are too unspecific to capture the fine-grained structural differences that exist between different types of grasslands. For instance, Central Valais is characterised by climacic steppe-like vegetation on some south-exposed slopes, especially at low elevation, which are frequently visited by foraging Red-bill choughs in winter, but such a habitat doesn't occur in Grisons to the same extent. Here, a finer approach that allows discriminating between various types and structural characteristics of the prevailing grassland would be necessary but such detailed variables don't exist currently in the freely available geo-databases.

The Red-billed chough is a highly specialized predator of below-ground arthropods (Rolando & Laiolo 1997) as indicated by its long curved beak. (Rolando & Laiolo 1997) its soil digging-probing feeding tactic is energetically costly (notably in comparison with that of its sibling species the Alpine chough *Pyrrhocorax graculus* that takes prey from ground surface and can feed on human scraps), requiring sufficient prey availability for being profitable. This must be especially crucial during the winter season when snow is likely to block access to soil-dwelling arthropods. Food availability typically results from

prey abundance modified by its accessibility. Red-billed choughs forage exclusively in open grassy habitats, where short swards provide the necessary micro-habitat structure for accessing below-ground prey. Short swards persist under variegated circumstances. First, where environmental, notably extreme edaphic conditions naturally hamper vegetation growth. In Valais, such conditions are typically encountered, first, on meadows and alpine pastures, in particular where moderate grazing activity takes place, as denoted by the relationship evidenced to the presence of sheep and goats. Grazing ungulates, either domestic or wild, thus guarantee good feeding opportunities for Red-billed choughs (McCracken *et al.* 1992). Second, the patches recently freed by the melting snow pack provide ideal foraging conditions. Not only is vegetation cover absent or short, but soil moisture enhances soil penetrability for beaks in search of prey, while it in the same time boosts the populations of some ground-dwelling insects such as leatherjackets (tipulid larvae, J. Savioz, unpublished). Third, similar favourable micro-habitat structures are typically present in the climacic steppes that cover some steep sun-exposed slopes on superficial soils in Central Valais (between Martigny and Mörel) at low elevation (below ca 1200 m). As said above the latter habitat seems particularly important in winter because such areas are very rapidly void of snow, usually within a few days after and heavy snow fall, because of slope steepness and intense solar radiation. Our model could not account for these specific circumstances that probably make Valais special from a Red-bill chough point of view. We thus conclude that a more refined approach is necessary to get the final picture and to be able to explain why the Red-billed chough is currently thriving in Valais while it has abandoned the Eastern Swiss Alps since decades.

The availability of, and distance to suitable grassy foraging patches also played a major role in nest site selection, as earlier suggested by Rolando & Laiolo (1997). Our results show a strong preference for cliffs that offer suitable foraging habitat within 1 km radius. Although we have observed breeding pairs in Valais that were collecting food as far as 4-6 km from their nest (Oggier, unpublished), it is likely that optimal foraging energetics constrains such long-distance, costly provisioning trips, with probable implications for reproductive success. As a matter of fact, some long-distance commuting pairs have been observed during the course of time to eventually opt for alternative breeding cliffs closer to their main foraging grounds (Oggier, unpublished). Our models suggest that nest sites in close vicinity of suitable foraging habitat are not a limiting factor for the species in Grisons: actually, suitable breeding cliffs are widespread in Eastern Switzerland as well. This is another indicator for not having captured the subtle differences in foraging conditions that actually occur between the two areas. If the grasslands in Grisons classified as foraging habitat by our model would actually be as attractive as those in Valais, it remains to explain why the last Red-billed choughs in Grisons were breeding at just a few sites at middle elevation in Lower Engadin whereas the high elevation zones were apparently never occupied by the species in recent historical times, contrary to what is observed in Valais. This again indirectly points to foraging conditions during over-wintering that differ between the two regions, but could not be evidenced by our model.

Environmental change, which is particularly acute in Alpine ecosystems (with double the global warming rate that is observed at lower elevation), will probably affect the ecology and distribution of the Red-billed chough into the future. Climate change will first lead to earlier snow-melt (Körner 2000) which might result in the long run in an average altitudinal shift of the snow front (and associated suitable foraging conditions for the Red-billed chough), i.e. in changing the spatial distribution of the suitable foraging patches in the landscape during the reproduction period. Red-billed choughs are likely to be able to track these conditions in space and time, possibly by electing better situated cliffs for efficient breeding. Second, climate change change will mean less snow precipitation in winter, especially at low and middle elevations. This may be an advantage in the long term for Red-billed choughs which have to find short grassy foraging grounds in winter, i.e. steepy steppic slopes, meadows and pastures that are rapidly freed by snow melting after heavy snow falls. Valais Red-billed choughs are known to commute long distances every day in winter to reach such suitable foraging patches, which probably bear high energetic costs. Such daily transhumances can benefit from less snow cover on the ground in the future. Difficult to achieve in the present context in Grisons due to a lack of extensive steppe-covered slopes, these daily transhumances might be eased in the future with a predicted decrease in snow cover, especially at low and middle elevation. Third, land abandonment, especially the cessation of traditional grazing practices, leads to progressive vegetation encroachment by bushes and trees (Dullinger, Dirnböck & Grabherr 2003), i.e. a loss of grassy habitats for the Red-billed chough. Fourth, the intensification of grassland management in areas that are accessible to agricultural machinery promotes meadows with tall and dense sward that are incompatible with the ground-foraging strategy of the Red-billed chough. Unfortunately, this change in farming practice hardly occurs currently at high elevation in the subalpine and alpine zone, with thus limited consequences for the Red-billed choughs. On wintering grounds, however, this may lead to a decrease in food supply as meadow intensification is usually accompanied by reductions in arthropod abundance (Andrey, Humbert & Arlettaz 2016).

Focusing on spatial habitat configuration and topo-climatic conditions, our modelling approach appears to be too coarse to elucidate why the Red-billed chough is so rare in the Eastern Alps but thrives along its western margin. Fine-grained comparisons of the structural and qualitative characteristics of the different types of grasslands in both regions are a next necessary step in that direction. Our models can be used to define the areas in which these investigations should take place, as they show the potential foraging sites that are suitable from a topo-climatic and land-use related point of view. For now, however, it remains impossible to explain the current distribution of the species in the Alps. First naturalistic considerations about its winter ecology suggest that the availability of accessible foraging grounds in winter, i.e. grassy patches that are void of snow or where snow melts rapidly, appears to be a key factor. Further analyses will show whether such conditions exist currently in Grisons, in comparison to the Valais context.

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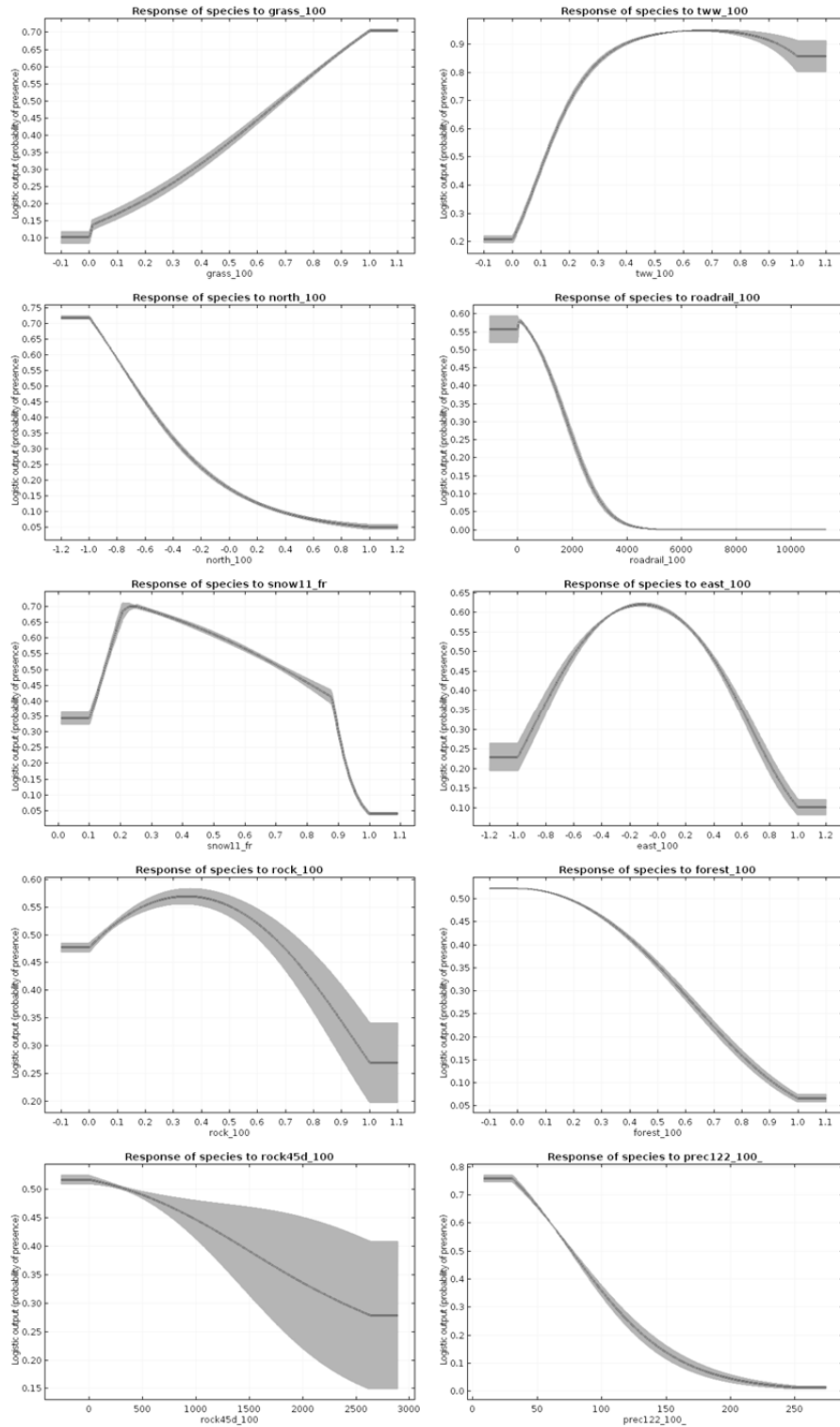
APPENDIX

Appendix 1: Cut-off values (threshold for maximizing sensitivity plus specificity on the training data) used for converting the continuous predictions into presence-absence maps.

MODEL	CUT-OFF VALUE
FORAGING HABITAT WINTER	0.079
FORAGING HABITAT BREEDING SEASON	0.232
FORAGING HABITAT AUTUMN	0.255
NESTING SITES	0.039

Appendix 2: Predicted amount and percentage of potential foraging (during winter, breeding and post-breeding) and nesting habitat in the cantons of Valais and Grisons.
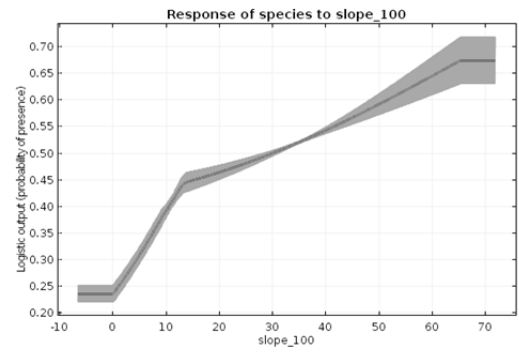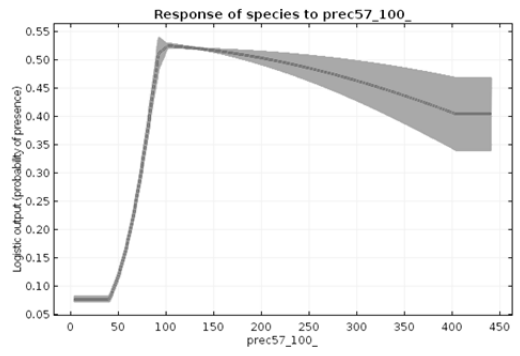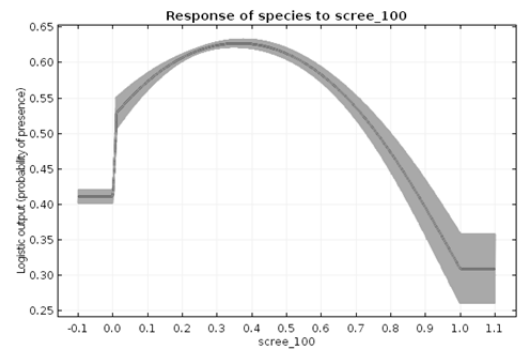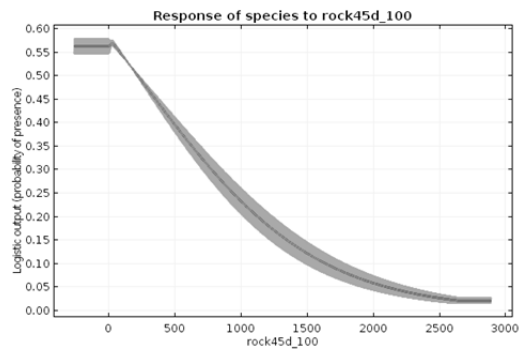
SEASON	HABITAT	VALAIS (KM^2)	%	GRISONS (KM^2)	%
WINTER	absence	4484.85		4502.73	
	presence	722.61	16.1	2601.49	57.8
BREEDING-	absence	4337.45		5342.06	
SEASON	presence	869.99	20.1	1762.17	33.0
AUTUMN	absence	3702.58		4525.96	
	presence	1504.86	40.6	2578.3	57.0
NESTSITES	absence	4702.8		6285.27	
	presence	503.97	10.7	818.42	13.0

Appendix 3: Response curves of *Pyrrhocorax pyrrhocorax* to the different variables explaining foraging habitat selection in winter (mean and SD based on 5 cross-validation replicates). The order of the variables corresponds to their relative importance as indicated in Table 2 (variable codes as in Table 1). In order to facilitate interpretation, univariate response curves (i.e. without considering interactions with other variables included in the model) are shown.
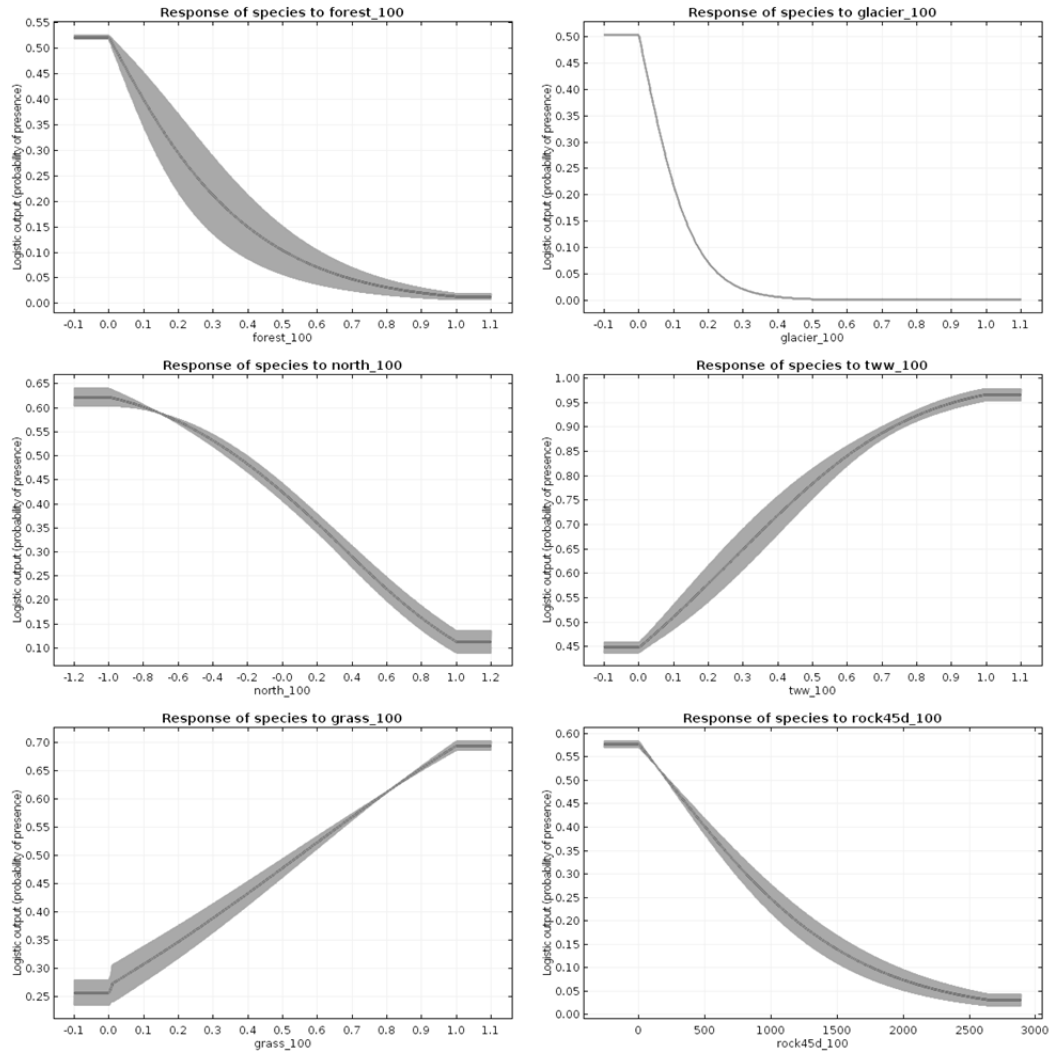
Appendix 4: Response curves of *Pyrrhocorax pyrrhocorax* to the different variables explaining foraging habitat selection in the breeding season (mean and SD based on 5 cross-validation replicates). The order of the variables corresponds to their relative importance as indicated in Table 2 (variable codes as in Table 1). In order to facilitate interpretation, univariate response curves (i.e. without considering interactions with other variables included in the model) are shown

Response of species to rock45d_100

Response of species to scree_100

Response of species to prec57_100_

Response of species to slope_100
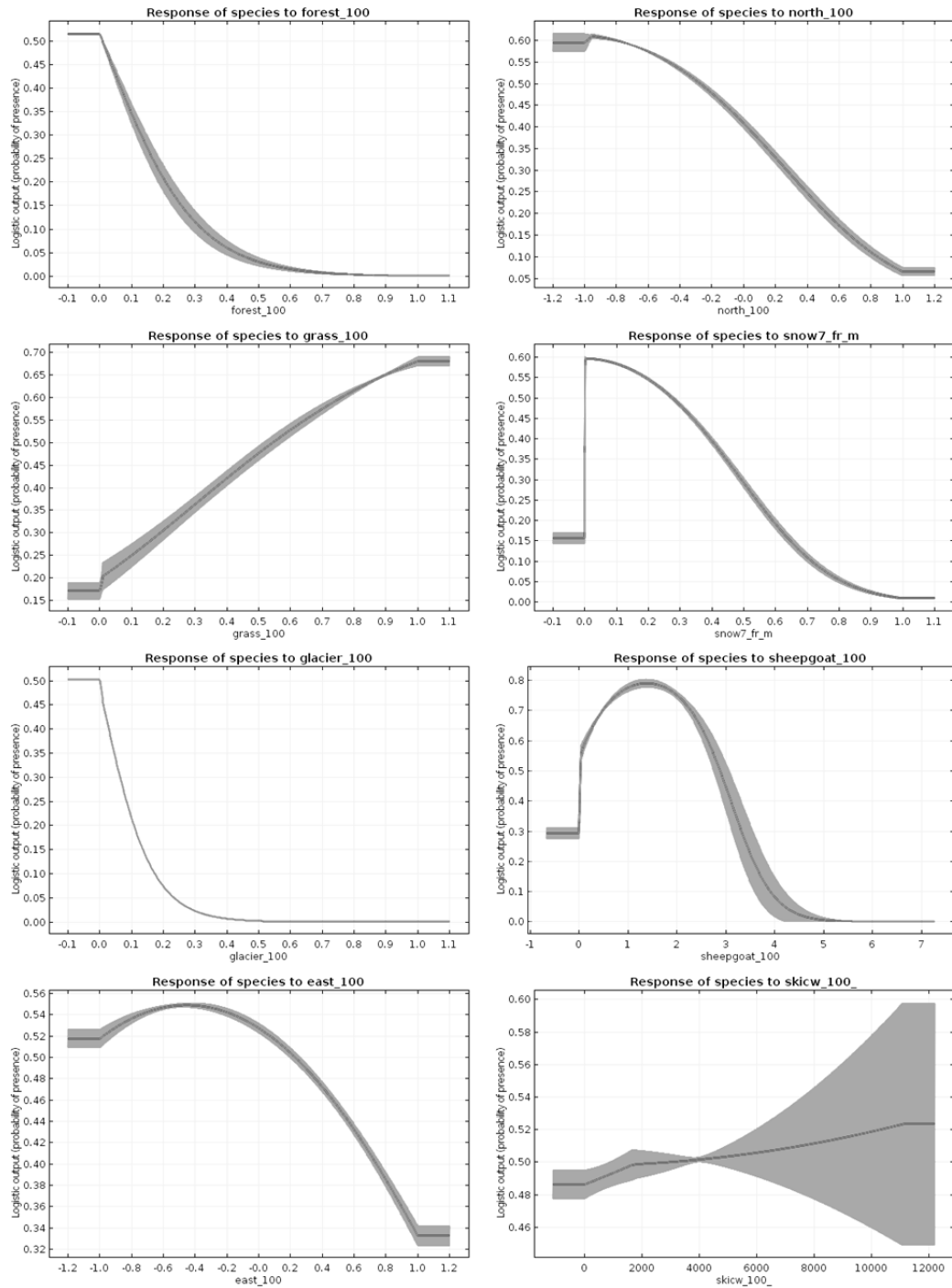
Appendix 5: Response curves of *Pyrrhocorax pyrrhocorax* to the different variables explaining foraging habitat selection in the post-breeding and dispersal period (mean and SD based on 5 cross-validation replicates). The order of the variables corresponds to their relative importance as indicated in Table 2 (variable codes as in Table 1). In order to facilitate interpretation, univariate response curves (i.e. without considering interactions with other variables included in the model) are shown.
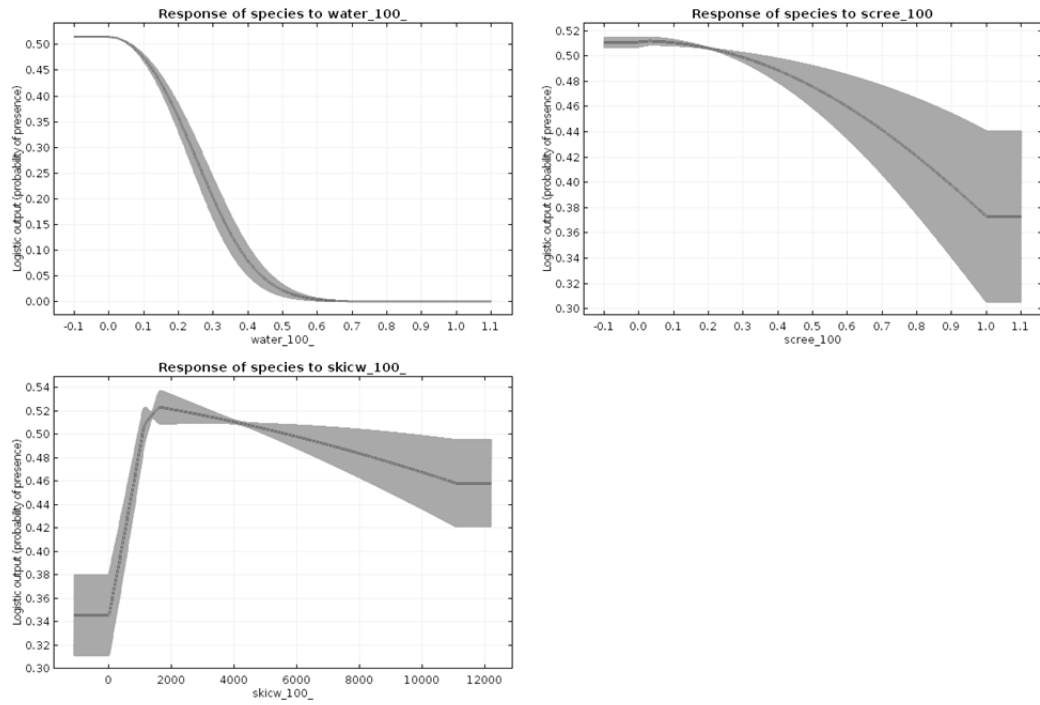
Appendix 6: Response curves of *Pyrrhocorax pyrrhocorax* to the different variables explaining nest site selection (mean and SD based on 5 cross-validation replicates). The order of the variables corresponds to their relative importance as indicated in Table 2 (variable codes as in Table 1). In order to facilitate interpretation, univariate response curves (i.e. without considering interactions with other variables included in the model) are shown.

Response of species to north_100

Response of species to fors2_vs_dist

Response of species to rock45d_100