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# Present in the western European Alps but absent in the eastern part: Can habitat availability explain the differences in red-billed chough occurrence?

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The absence of a species in apparently suitable regions is often attributed to habitat deterioration, which, according to the IUCN-guidelines, would preclude reintroduction unless the habitat is sufficiently restored. The crux is therefore to determine species' key habitat requisites and to localize potentially restorable sites based on the habitat selection of thriving populations in similar environments. The distribution of the red-billed chough *Pyrrhocorax pyrrhocorax* in the Alpine arch is currently restricted to its western side. The eastern Alps have only been occupied sporadically during past centuries, which triggered a discussion around reintroduction. The fact that the last confirmed pairs bred at middle elevation, in derelict buildings instead of alpine cliffs, suggested a lack of habitat suitability in the uplands. To test this hypothesis, we modelled seasonal foraging habitat (during winter, breeding and dispersal) and nest site-selection in the western Swiss Alps using long-term observation data together with a wide palette of environmental predictors. The models were extrapolated to eastern Switzerland to estimate the quality and extent of the available habitat. Both foraging and nesting habitats were predicted with a high level of accuracy (AUC > 0.8). Despite variation between seasons, south-exposed dry meadows and extensively-grazed pastures were always preferred as foraging habitat, while forested and snow-covered areas were avoided. Availability of, and distance to suitable foraging habitats were the main determinants of nest-site selection, probably reflecting strong energetic constraints during reproduction. However, the extrapolation to eastern Switzerland revealed an even higher overall amount and relative percentage of all habitat types. One explanation could be that our predictors were too coarse to encapsulate qualitative, structural or compositional differences of the grasslands. However, the results could also point to an alternative hypothesis, namely that post-glacial recolonization patterns, in particular the absence of nearby source populations, precluded the occupation of the eastern Alps.

Keywords: foraging habitat, habitat modelling, nest site selection, post-glacial population separation, *Pyrrhocorax pyrrhocorax*, species distribution

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## Introduction

The human-induced erosion of biodiversity worldwide, especially the decline or disappearance of emblematic species, often raises calls for reintroduction programs with the aim to reinstall extinct populations. However, in line with the IUCN guidelines, the reasons for a species' absence need first to be deciphered and, second, eliminated, as absolute prerequisites for envisioning reintroduction operations. In the absence of direct persecution by humans, habitat deterioration is often presumed as the most likely reason for a species' absence in apparently suitable geographic regions. Even so, the challenge remains to properly identify the requirements of a species in terms of key habitat and food supply so as to locate potentially suitable areas for the restoration of adequate ecological conditions.

The red-billed chough *Pyrrhocorax pyrrhocorax* is a non-migratory corvid with a fairly contiguous geographic distribution across Asia and scattered populations in Europe (BirdLife-International 2021). During the past two centuries, the species has undergone severe population declines throughout its European range and is now listed in Annex of the European Union Directive on the Conservation of Wild Birds (EC 2010). In the Alpine arch, the strongholds of the distribution have always been restricted to the western part in France, Italy and Switzerland, with only a few historical observations reported from Austria (Glutz von Blotzheim 1993). In Switzerland, the nationally red-listed species currently occurs exclusively in the west, in the Alps of Valais and Vaud, with a stable breeding population estimated at ca 80 pairs with a possible slight population increase reported for the past 25 years (<http://www.vogelwarte.ch>). In the eastern Swiss Alps, particularly in the Grisons, red-billed choughs are today extinct as breeders and non-breeding individuals are observed only very sporadically. Yet, breeding was documented in the Grisons until the 1960s (Glutz von Blotzheim 1993), where the species occurred at middle elevation in partly derelict historical buildings (Denkinger 2011), which contrasts with the situation in Valais and most other Alpine populations, where breeding sites are located in upper subalpine and alpine cliffs.

Habitat deterioration, especially agricultural intensification and the abandonment of extensive pasturing, is considered the main cause for the European-wide decline of the red-billed chough (Blanco et al. 1998, Whitehead et al. 2005, Kerbiriou et al. 2006), as the species prefers foraging in grasslands with a short sward which enhances prey accessibility (McCracken et al. 1992). Especially in winter, when snow-cover makes many suitable grasslands in the uplands inaccessible, the availability of this habitat type in lower regions might be critical for the species presence. Furthermore, during the breeding period, a lack of suitable foraging grounds located in the vicinity of the nest sites may impose energetic constraints on breeding pairs, with negative effects on reproductive success (Kerbiriou et al. 2006).

To investigate 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, we used long-term observation data of foraging and nesting birds collected in Valais, together with spatially-explicit modelling to assess seasonal habitat selection and identify suitable habitat in the Swiss Alps. We focused on foraging habitat in three seasons (winter, breeding and post-breeding dispersal) as well as on nest site selection, hypothesizing lower amounts of suitable habitat in Grisons, especially in winter, to be the reason for the species' absence. We predicted that 1) winter foraging concentrates in snow-free areas such as wind-blown ridges and south-exposed grasslands at relatively low elevation, 2) the selection of foraging grounds during the breeding season is linked to grassy sites, in particular along the retreating snow-front and 3) nest site selection is driven by a trade-off between the availability of suitable cliff walls offering crevices and niches, and the nearby presence of optimal foraging patches. Models were calibrated in Valais and extrapolated to Grisons to assess whether seasonal habitat suitability could explain the population situation there, to identify the key factors for the species' absence, and ideally to locate suitable sites for habitat restoration (as far as deemed necessary) prior to possible reintroduction operations.

## Methods

### Study area

Species–habitat associations were investigated in the western Swiss Alps (Canton of Valais, from now on referred to as Valais) and extrapolated to the eastern Alps (Canton of Grisons: Grisons) (Fig. 1). Both regions belong to the Inner Alps biogeographic region (Gonseth et al. 2001) which is characterised by subcontinental to continental climate conditions with relatively warm and dry summers, and cold, wet winters. Precipitation is typically 600–900 mm year$^{-1}$ at 1000 m a.s.l. (Ott et al. 1997). The geological substrate consists mostly of limestone or silicates, with both bedrock types present in both areas. The valley bottoms are populated, but much more so in Valais than in Grisons where they are situated at higher elevation. Another major difference between the two areas is that Valais has much higher mountains in general (up to – 4634 m a.s.l.). Land use on the mountain slopes not covered by forest and rocks is mostly devoted to extensive grazing in summer and winter recreation in winter, with several major ski resorts existing in both regions.

### Species data

Red-billed chough foraging locations for the years 2000–2014 were extracted from the database of the Swiss Ornithological Institute (<www.ornitho.ch>), which contains opportunistically collected observations from amateur bird watchers and professional ornithologists. Only locations with a minimum accuracy of 100 m and ascertained foraging activity were retained (Fig. 1). The dataset was subdivided into three seasons: winter (November–April, n = 140), breeding
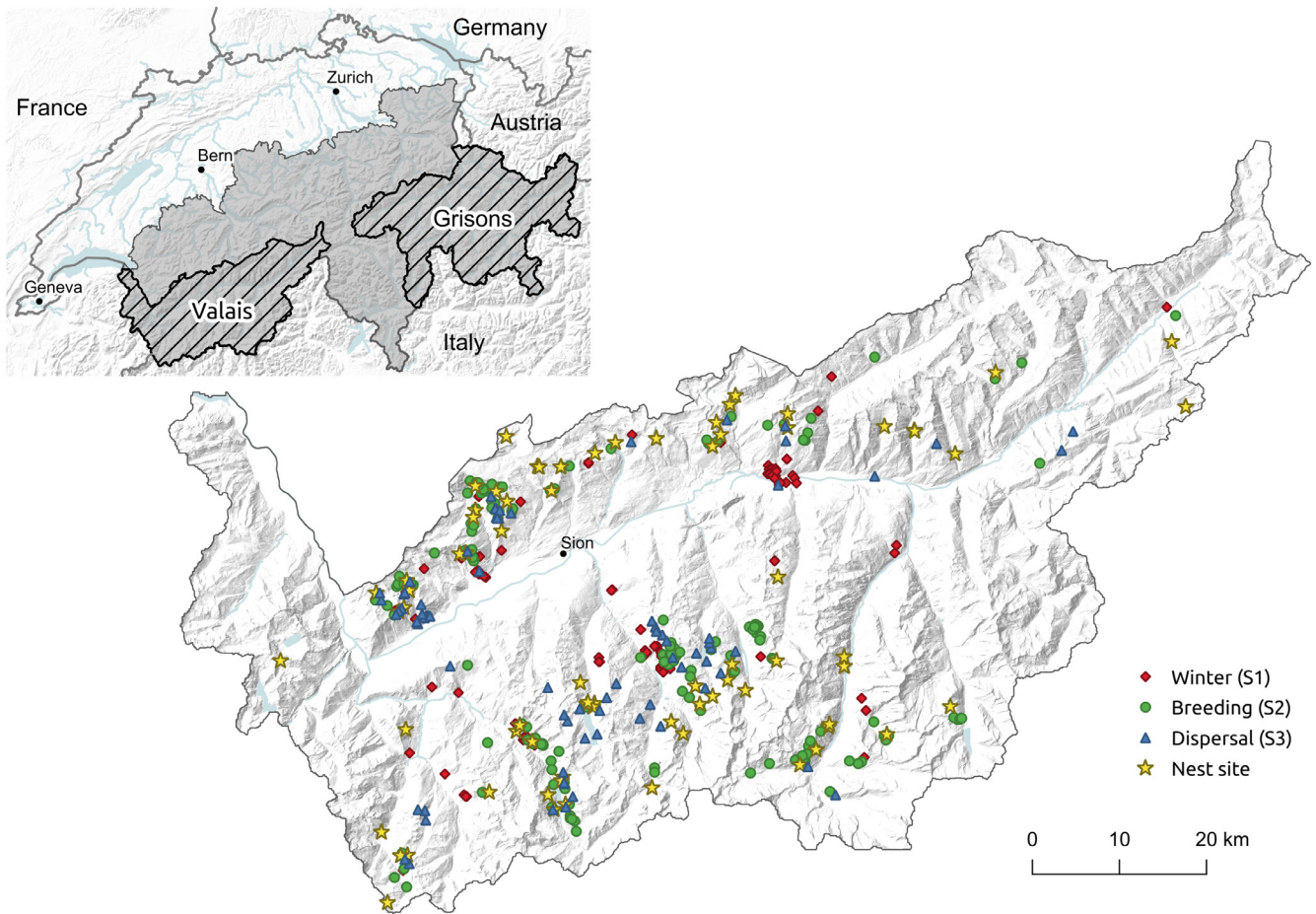
Figure 1. Switzerland (inset) with the study areas (hashed black) Valais (left) and Grisons (right) in the Swiss Alps (grey). In addition, the seasonal foraging locations for winter, breeding season and autumn dispersal as well as the locations of the nest sites used for modelling habitat selection are shown.

(May–July, n = 193) and post-breeding dispersal (August–October, n = 78). Nest site locations (n = 76) were based on long-term, annual field surveys conducted from 1974 to 2016, mostly by one of the co-authors (PAO). All known and potential nesting sites were regularly visited during the breeding period and checked for breeding activity, using normal (10 × 40 mm) and large (25–50 × 80 mm) binoculars on tripods. Given the high nest-site fidelity and apparent stability of the red-billed population in Valais, this conveys information on contemporary nest site selection patterns 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 and 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 and Roberts (2001). Snow cover data for the years 2006–2011 were generated by the WSL Institute for Snow and Avalanche Research SLF according to (Bavay et al. 2013). This model, based on the underlying alpine surface process model Alpine3D (Lehning et al. 2006) and the SNOWPACK model (Fierz and Lehning 2001) provided daily snow cover data at a spatial resolution of 200 × 200 m. 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,

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Table 1. Variables tested for predicting red-billed chough foraging and breeding occurrence with their respective codes, descriptions, units, original resolution, the radius of the moving window and the original data sources. Variables that were originally in vector format were directly transformed to raster maps of 25 × 25 m resolution.

| Variable type No. | Variable code | Description | Unit | Resolution (m) | Window radius (m) | Source |
|---|---|---|---|---|---|---|
| Topography | | | | | | |
| 1 | ELEVATION | Elevation | m a.s.l. | 25 | 100 | DEM[1] |
| 2 | SLOPE | Slope | degree | 25 | 100 | DEM |
| 3 | SLOPE_1 | Slope | | 25 | – | |
| 4 | NORTH | Northness (cosine of aspect) | −1 to 1 | 25 | 100 | DEM |
| 5 | EAST | Eastness (sine of aspect) | −1 to 1 | 25 | 100 | DEM |
| Climate | | | | | | |
| 6 | TAVE57 | Average summer ambient temperature (May–July) | °C | 100 | 100 | Worldclim[2] |
| 7 | TAVE122 | Average winter temperature (Dec–Feb) | °C | 100 | 100 | Worldclim |
| 8 | PREC57 | Mean summer precipitation (May–July) | mm | 100 | 100 | Worldclim |
| 9 | PREC122 | Mean winter precipitation (Dec–Feb) | mm | 100 | 100 | Worldclim |
| Snow cover | | | | | | |
| 10 | DWS_M | Average number of days with snow (> 5 cm) | days | 200 | 100 | Bavay et al. 2013 |
| 11 | DWS_V | Between-year variance in number of snow days (> 5 cm) | days | 200 | 100 | Bavay et al. 2013 |
| 12 | SNOW(1-12)_FR | Average snow cover within 1 km$^2$ per month (1–12: January–December) | % | 200 | 564 | Bavay et al. 2013 |
| Land cover and land use | | | | | | |
| 13 | FOREST | Percentage of forest | % | Vector | 100 | Vector 25 |
| 14 | BUSH | Percentage of bushes | % | Vector | 100 | Vector 25 |
| 15 | GRASS | Percentage of grassland | % | Vector | 100 | Vector 25 |
| 16 | TWW | Percentage dry meadows and pastures | % | Vector | 100 | BAFU[3] |
| 17 | PERM | Percentage of permanent cultures (orchards, vineyards) | % | Vector | 100 | Vector 25[4] |
| 18 | GLACIER | Percentage of glacier | % | Vector | 100 | Vector 25 |
| 19 | SCREE | Percentage of scree | % | Vector | 100 | Vector 25 |
| 20 | ROCK | Percentage of rock | % | Vector | 100 | Vector 25 |
| 21 | ROCK_1 | Presence of rock | 1/0 | Vector | – | |
| 22 | ROCK45D | Distance to steep rocks > 45° | m | Vector | 100 | Vector 25 |
| 23 | WATER | Percentage of waterbodies | % | Vector | 100 | Vector 25 |
| 24 | SHEEPGOAT | Average number of sheep or goat per ha pastureland (2004–2014) | N | Vector | 100 | BfS[5] |
| 25 | ROADRAIL | Distance to roads and railways | m | Vector | 100 | Vector 25 |
| 26 | TRAILDIS | Distance to trails | m | Vector | 100 | Vector 25 |
| 27 | SKICW_D | Distance to ski-lifts and cableways | m | Vector | 100 | Vector 25 |
| Information on foraging habitat in the breeding season (used for the nest site model only) | | | | | | |
| 28 | F2_VS_MEAN3K | Average foraging habitat suitability within 3 km radius | 0–1 | 25 | 3000 | Foraging model |
| 29 | F2_VS_PERC3k | Percentage of suitable foraging habitat within 3 km radius | % | 25 | 3000 | Foraging model |
| 30 | FORS2_VS_DIST | Distance to the next suitable foraging patch | m | 25 | – | 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>.

we calculated the distance to steep rock (> 45°). Dry meadows and pastures were adopted from the mapping of the Swiss Federal Administration of the Environment (<https://www.bafu.admin.ch>). In addition, we calculated the mean number

of sheep and goat per community in the years 2004–2014, as obtained from the Swiss Federal Administration for Statistic Switzerland (BfS) (<https://www.bfs.admin.ch>) 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-lifts and cableways as obtained from the Vector 25 map.

All predictor variables were prepared as raster maps (cell size: $25 \times 25$ m). In order to capture the environmental conditions prevailing around the foraging locations, and at the same time account for both sampling accuracy and avoid pseudo-accuracy given the original resolution of some of the predictor variables (Table 1), 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 1 km$^2$ area (radius = 564 m). 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 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 to the distance birds use for foraging (Kerbiriou et al. 2006). Second, we converted this continuous variable into a binary map of foraging habitat 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.

### Statistical approach

As only data on species presence were available, but no data on ascertained absence, we used Maxent, a machine-learning technique based on the principle of maximum entropy (Jaynes 1957), adapted for predictive species distribution modelling (Phillips et al. 2004, 2006) and implemented in the *dismo* package in R (<www.r-project.org>) (Hijmans et al. 2017). Maxent compares the environmental conditions at the observed species locations with 10 000 locations randomly sampled across the study area, using the environmental variables as predictors as well as different functions thereof (in the following termed 'feature classes' FCs), which includes linear, quadratic and two-way interaction terms as well as threshold and hinge features (for detailed information see Phillips et al. 2004, 2006, Elith et al. 2006, Phillips and Dudik 2008). To avoid overfitting and limit model complexity, a regularization procedure is commonly applied (Phillips et al. 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 values measured at the presence locations.

Since the default value of the regularization multiplier (RM; default = 1.0) (Dudik et al. 2007, Phillips and Dudik 2008) is not necessarily optimal for any specific dataset (Warren and Seifert 2011, Radosavljevic and Anderson 2014, Warren et al. 2014) and can result in poorly performing models (Shcheglovitova and Anderson 2013, Radosavljevic and 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, based on only 76 nest site locations, we tested only three variants (L, LQ, LQH), following the recommendations by (Phillips and Dudik 2008). Each combination was tested using different 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 the variable selection. 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%. With the resulting variable subset we finally ran another set of models (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 calibrated for Valais were then projected to Grisons. To avoid erroneous extrapolations beyond the environmental range of the training area, we applied 'clamping', i.e. keeping the response outside the training range constant (Merow et al. 2013). Moreover, to illustrate differences between the calibration and the projection range we calculated a multivariate environmental similarity surface (MESS) map (Elith et al. 2010) for the variable combinations used in each of the four seasonal models and compared the correlations between these variables in the two regions. 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 plus specificity were maximised for the training data (Supporting information).

### Results

Foraging and nesting habitat selection was predicted with a high level of accuracy in all seasons (foraging winter: AUC: 0.938, SD: 0.008; breeding season: AUC: 0.920, SD: 0.002; dispersal: AUC: 0.881, SD: 0.035; nesting: AUC: 0.977, SD: 0.016).

## Foraging habitat

Winter foraging habitat was mainly characterized by a high proportion of grassland (Fig. 2a), especially dry meadows and pastures (Fig. 2b), and an intermediate cover of rocks (30–40%) on south-exposed slopes (Fig. 2c) under very xeric circumstances (low precipitation). Optimal winter foraging habitat is furthermore characterized by a very low snow cover (Fig. 2d), with an optimum of 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 2a, Supporting information).

During the breeding season foraging habitats also showed a very low proportion of forest and high proportion of grasslands (Fig. 2e) close to rocky sites. They were located in areas with fairly moderate precipitation, and showed a low to moderate snow cover within 1 km² (Fig. 2f). Compared to the winter season, the birds foraged on steeper slopes. Southern expositions were still strongly preferred, but the activity was extended to southwestern expositions. Glaciers and areas close to ski-lifts and cableways were avoided. A preference for areas subjected to low to middle intensity grazing by sheep and goats became obvious, while heavy grazing appeared unfavourable (Table 2b, Supporting information).

During the post-breeding and dispersal season, grasslands, especially dry meadows and pastures on south-exposed slopes and near rocky areas were still preferred, while forests, glaciers, waterbodies and areas dominated by screes were avoided. Compared to the other seasons, the birds foraged on average in closer vicinity to ski-lifts and cableways, but still clearly avoided them up to a distance of 1000 m (Table 2c, Supporting information).

## Nesting habitat

Nest sites were located in steep rock, i.e. cliffs, with the most important factors for nest site selection being high foraging habitat suitability within a 3 km radius (Fig. 2g) and a fairly low to intermediate cover of snow. Also the distance to the next foraging patch played a role (Fig. 2h). South-exposed sites (from southeast to southwest) were preferred over northern expositions (Table 2d, Supporting information).

## Extrapolation to the eastern Alps

Model extrapolation to the eastern Swiss Alps indicated that both the absolute amount and relative proportion of predicted suitable foraging and nesting habitat was higher in Grisons than in Valais for all three seasons (Fig. 3, Supporting information). In Valais 13.8% (723 km²), 16.7% (870 km²) and 28.9% (1505 km²) of the total area were predicted as suitable foraging habitat in the winter, breeding and dispersal season, respectively, while in Grisons the proportions amounted to 36.6% (2601 km²), 24.8% (1762 km²) and 36.3% (2578 km²). Valais had 9.7% (504 km²) of its area offering suitable nesting habitat, while 11.5% (818 km²) were predicted

for Grisons. The environmental conditions in the extrapolation region did not substantially differ from the calibration range (Supporting information). The only discrepancies were found for winter conditions in the densely populated parts of some valley bottoms, which are not predicted relevant to the species.

## Discussion

We analyzed habitat selection of a fairly stable breeding population of the red-billed chough in the southwestern Swiss Alps (Valais) and compared the amount of suitable habitat to that in the eastern Swiss Alps (Grisons) where the species is now extinct. While the habitat selection patterns corresponded well to what is known from other studies (Blanco et al. 1998, Whitehead et al. 2005, Kerbiriou et al. 2009) and the models accurately predicted species distribution in the calibration range, the projection-results did not confirm our hypothesis: potentially suitable foraging grounds, and to a lesser extent nesting sites, are not less abundant in Grisons than in Valais, even on the contrary. Particularly surprising was the finding that winter foraging habitat – which had been assumed to be the key factor for the regional persistence of the species – doesn't appear to be a limiting factor, with wintering opportunities being even more widespread in Grisons.

There are three possible explanations for this last finding: 1) our models may have neglected some key habitat variables responsible for species' presence versus absence in Valais and Grisons, respectively; 2), as a result of 1, the included variables were too unspecific and the considered spatial scale too coarse to capture fine-grained, specific habitat requirements; and 3) habitat availability is actually not the cause for the species' absence in the eastern Swiss Alps.

Our models show that suitable foraging habitat in all three seasons is mainly characterised by grasslands, especially dry meadows and pastures, on south-exposed slopes which are at least partially free of snow year-round. The red-billed chough is a highly specialized predator of below-ground arthropods (Rolando and Laiolo 1997), as indicated by its long curved beak. Its soil digging-probing feeding tactic is energetically costly (notably in comparison with that of its sibling species, the Alpine chough *Pyrrhocorax graculus*, that mostly picks up prey from the ground surface and can also feed on human scraps), and requires sufficient prey supply for being profitable (Rolando and Laiolo 1997). 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 (McCracken et al. 1992, Whitehead et al. 2005). Short swards persist under different circumstances, where either management or environmental (notably extreme edaphic) conditions hamper vegetation growth. In Valais, such conditions are typically encountered in three situations. First, on meadows and
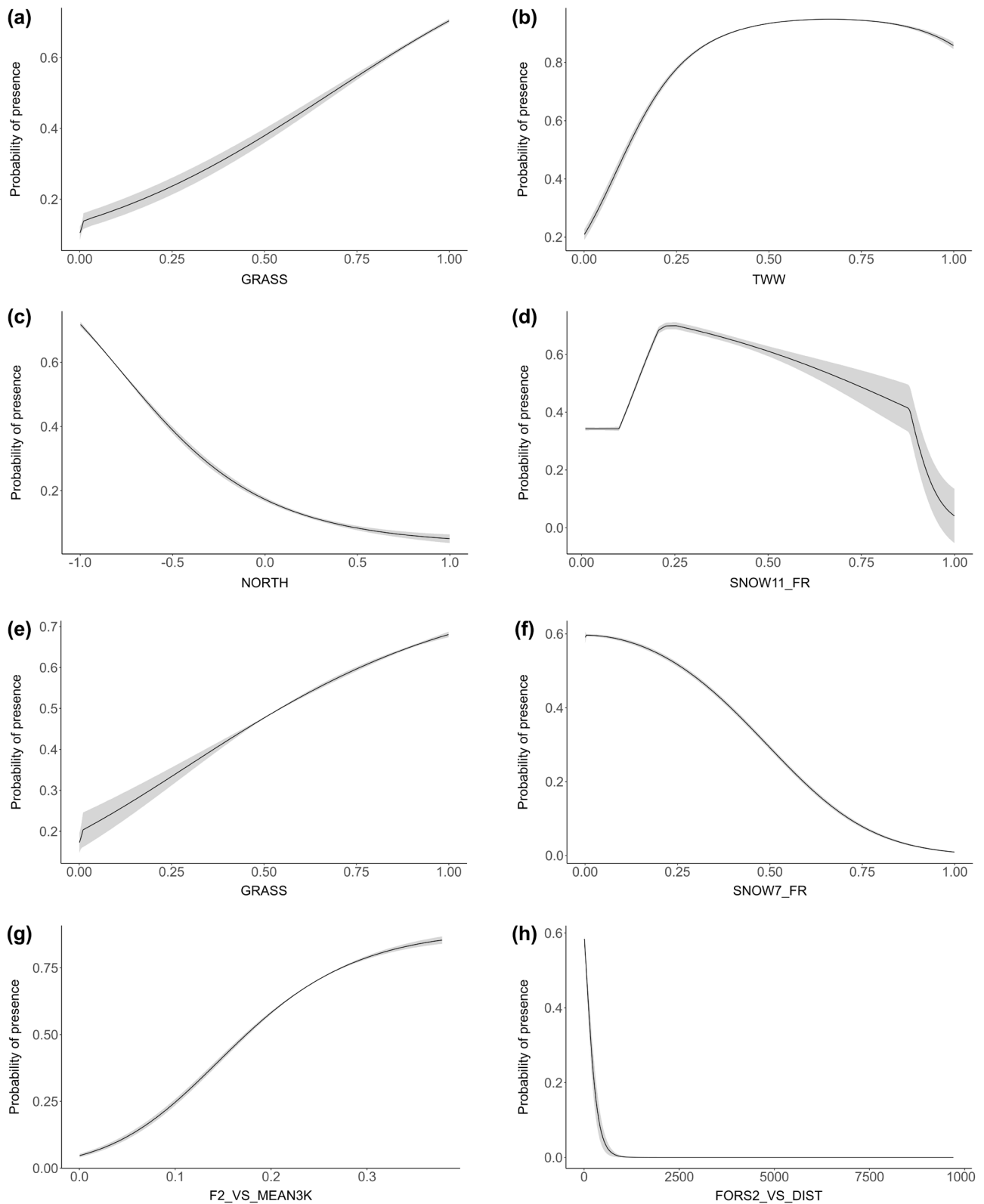
Figure 2. Response curves of *Pyrrhocorax pyrrhocorax* to selected variables (mean and SD based on 5 cross-validation replicates) explaining foraging habitat selection in winter (a–d), foraging habitat in the breeding season (e–f) and nest site selection (g–h). For variable codes see Table 1, the response curves for all variables selected in the models are shown in Supporting information. In order to facilitate interpretation, univariate response curves (i.e. without considering interactions with other variables included in the model) are shown.

Table 2. Variables explaining the seasonal selection of foraging habitat (a–c) and nesting sites (d) of *Pyrrhocorax pyrrhocorax* in Valais. The variables' percent contribution to the final model and the response type are given, with +, – and ∩ indicating a positive, negative or unimodal response, respectively. For variable codes see Table 1.

| Model (season) | Variable | Percent contribution | Response type |
|---|---|---|---|
| a) Winter | GRASS | 25.74 | + |
| | TWW | 23.61 | + |
| | NORTH | 16.43 | – |
| | ROADRAIL | 7.35 | – |
| | SNOW11_FR | 6.73 | ∩ |
| | EAST | 5.36 | ∩ |
| | ROCK | 4.66 | ∩ |
| | FOREST | 4.61 | – |
| | ROCK45D | 2.99 | – |
| | PREC122 | 2.52 | – |
| b) Breeding | FOREST | 17.39 | – |
| | NORTH | 15.67 | – |
| | GRASS | 12.43 | + |
| | SNOW7_FR | 11.38 | – |
| | GLACIER | 11.34 | – |
| | SHEEPGOAT | 10.50 | ∩ |
| | EAST | 4.39 | ∩ |
| | SKICW_D | 3.78 | + |
| | ROCK45D | 3.61 | – |
| | SCREE | 3.55 | ∩ |
| | PREC57 | 3.00 | ∩ |
| | SLOPE | 2.96 | + |
| c) Dispersal | FOREST | 25.86 | – |
| | GLACIER | 17.61 | – |
| | NORTH | 15.02 | – |
| | TWW | 10.72 | + |
| | GRASS | 10.21 | + |
| | ROCK45D | 7.76 | – |
| | WATER | 5.30 | – |
| | SCREE | 3.92 | – |
| | SKICW_D | 3.60 | ∩ |
| d) Nesting sites | ROCK_1 | 46.96 | + |
| | SLOPE_1 | 29.02 | + |
| | F2_VS_MEAN3K | 7.60 | + |
| | SNOW7_FR | 7.32 | ∩ |
| | NORTH | 4.85 | ∩ |
| | FORS2_VS_DIST | 2.26 | – |
| | ROCK45D | 1.99 | – |

alpine pastures, especially 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 support feeding opportunities for red-billed choughs (McCracken et al. 1992, Blanco et al. 1998). Second, on patches recently freed by the melting of the snowpack: in these patches not only the vegetation cover is absent or short, but the high soil moisture enhances soil penetrability, creating favorable conditions for beak drilling while in search of prey (Whitehead et al. 2005). At the same time, soil moisture boosts the populations of some ground-dwelling insects such as tipulid larvae (Resano-Mayor et al. 2019), which make up the staple food of the species during the winter season in coastal Atlantic habitats (Kerbiriou and

Julliard 2007) and probably during the breeding season in the Alps (own unpubl. field obs.). Third, on climactic steppes that cover some steep sun-exposed slopes on superficial soils in Central Valais at low elevation (below ca 1200 m). The latter habitat seems particularly important in winter because such areas are very rapidly void of snow, usually within a few days after a heavy snow fall, because of slope steepness and intense solar radiation. It is also on those south-exposed slopes that the major aggregations of red-billed choughs occur in winter in Valais. Although our models do not account for flock size, they seem to encapsulate most key circumstances linked to foraging by including and showing the importance of grazing, snow presence and topoclimatic conditions for identifying and locating suitable feeding patches. However, we cannot fully exclude that the variables used may still be too coarse to capture the fine-grained structural differences in micro-habitat that may exist between different types of grasslands and might make Valais special from a red-bill chough's perspective. Finally, our model lacks direct information on food supply. Only field-based analyses at finer resolution, comparing composition and structural characteristics of the prevailing grasslands and linking these characteristics to food availability, might elucidate whether qualitative differences can explain why the red-billed chough is thriving in Valais but abandoned the eastern Swiss Alps.

The availability of suitable foraging patches also played a major role for nest site selection, as earlier suggested by Kerbiriou et al. (2006). Our results show a strong preference for cliffs that offer suitable foraging habitat within a 3 km radius. Although we observed breeding pairs collecting food up to 8–10 km in straight line from their nest (PAO pers. obs.), it is likely that optimal foraging energetics constrains such costly long-distance provisioning trips, with probable implications for reproductive success. Although Kerbiriou et al. (2006) found no effect of mean foraging-flight distance on reproductive success, they showed that fledgling success was influenced by the amount of foraging habitat in close vicinity (up to 300 m) to the nest. While red-billed choughs seem to be able to cope with low-quality foraging habitats by commuting, they still optimize this energetic trade-off if possible. Actually, 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 (PAO pers. obs.). Our models suggest that nest sites in close vicinity to suitable foraging habitat, which seems to determine breeding territory quality, is not a limiting factor for the species in Grisons: actually, suitable breeding cliffs seem also widespread in eastern Switzerland. However, this might be another indicator for not having captured possible subtle differences in foraging conditions between the two areas. If the grasslands in Grisons classified as suitable foraging habitat by our model would be of the same quality as in Valais, it remains to explain why the last red-billed choughs in Grisons were breeding in buildings at middle elevation and why – contrary to what is observed in Valais – the high elevation zones had apparently never been occupied by the species in recent historical times. On

**(a)** Winter foraging

**(b)** Foraging during breeding

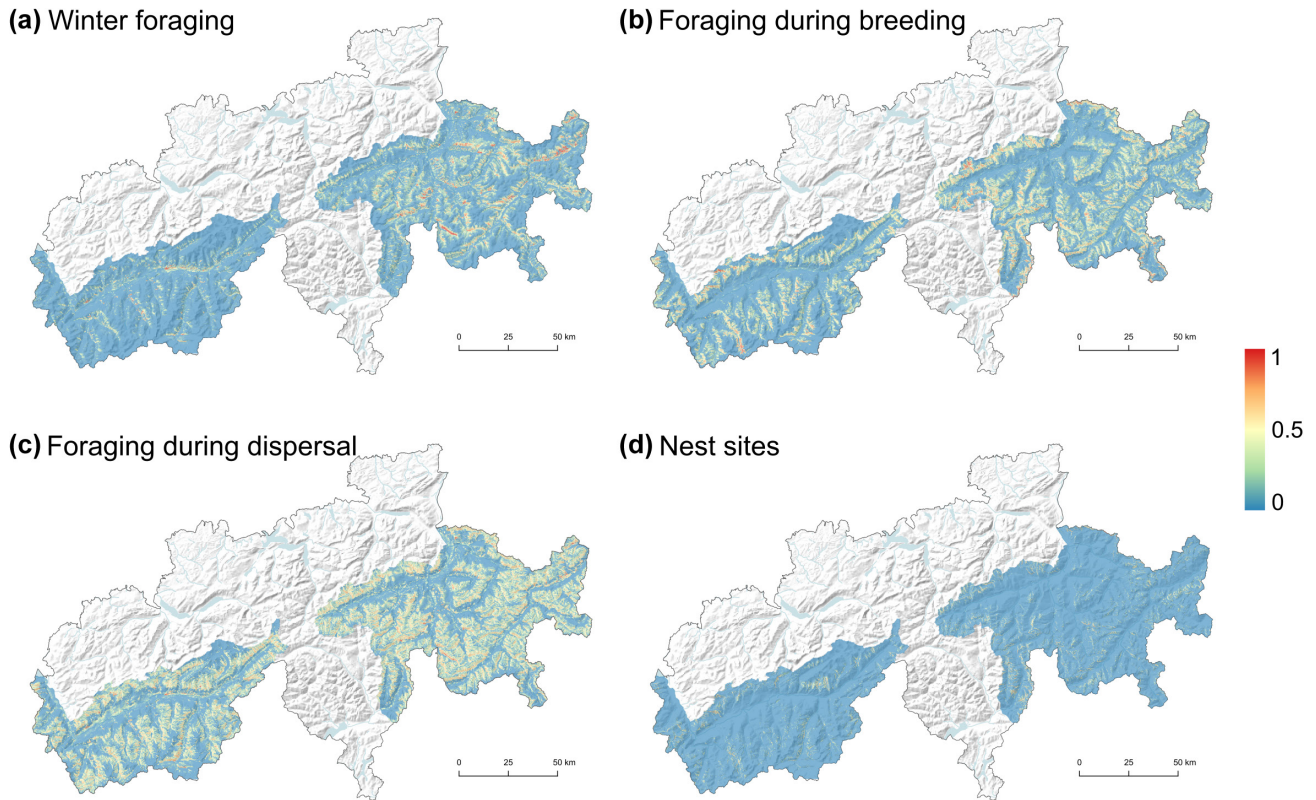**(c)** Foraging during dispersal

**(d)** Nest sites

Figure 3. Predicted seasonal foraging (a–c) and nesting (d) habitat suitability for *Pyrrhocorax pyrrhocorax* in Valais (West, left) and Grisons (East, right), as extrapolated from the Valais model. Foraging habitat was calculated for (a) winter, (b) the breeding season and (c) the dispersal season. Habitat suitability increases from blue (unsuitable) to red (highly suitable).

the other hand, nesting in houses is common in other, non-Alpine populations (Banda and Blanco 2017) and our model predicts suitable foraging grounds in the breeding season to be present also at middle elevations (Supporting information), which might have driven the selection of breeding sites offering the better – as snow-free – spring foraging opportunities in nest surroundings.

Snow cover and snow melt were identified as important drivers of foraging habitat conditions in both winter and reproduction time, as reported for several other Alpine bird species (Brambilla et al. 2019, Resano-Mayor et al. 2019, Barras et al. 2020). Snow conditions, however, have already dramatically changed and are further expected to change significantly within decades (Beniston 2003, CH2018 2018). Climate shifts are particularly acute in Alpine ecosystems, with double the warming-rate compared to lower elevations (Beniston 2000), and may thus affect the ecology and distribution of the red-billed chough. Climate warming leads to earlier snow-melt (Körner 2000), which in the long run results in an average altitudinal upwards-shift of the snow front and a consequential change in the spatial distribution of suitable foraging patches during the reproduction period. However, red-billed choughs are likely to be able to track these conditions in space and time, e.g. by selecting better situated cliffs for breeding so as to maintain provisioning trips as short as possible. Moreover, climate 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 given their preference for short grassy foraging grounds in winter, i.e. steep steppe slopes, meadows and pastures that are rapidly freed from snow, even after heavy snow falls. Concerning their daily commuting trips between territories and suitable feeding grounds in winter, less snow cover may reduce the need for and the distance of transhumance in the future. In this regard, it seems fairly unlikely that adverse climatic changes were the main reasons for the extinction of the small and marginal Grisons population in the second half of the 20th century.

In contrast to the potentially positive effects of climate change, negative effects can be expected from various forms of land use changes taking place in the Alps. First, land abandonment, especially the cessation of traditional alpine grazing practices, leads to progressive vegetation encroachment by bushes and trees (MacDonald et al. 2000, Dullinger et al. 2003, Laiolo et al. 2004), and a consequential loss of short-sward grassland habitats for foraging red-billed choughs (Morinha et al. 2017a). Second, the intensification of vast grassland areas – which have become more and more accessible to agricultural machinery – boosts tall and dense swards (Tasser and Tappeiner 2002), i.e. reduces both prey abundance (Britschgi et al. 2006, Andrey et al. 2016) and availability (which is abundance modified by accessibility).

This contributes to generating conditions that are definitely adverse to the ground-foraging strategy of the red-billed chough. If this change in farming practice fortunately rarely occurs at high elevation in the alpine zone at present, thus not impacting foraging habitats during the breeding or dispersal periods, it may already compromise the provisioning of prey supply on wintering grounds. While shrub encroachment was captured by the variables in our model, and extensively managed dry meadows and pastures were explicitly evaluated, the management type and intensification level in the remaining grassland patches was unknown. It thus cannot be ruled out that a higher level of intensification in Grisons may have led to a lower quality of the grasslands classified as suitable by our model, and may have triggered the extinction of the last pairs breeding at middle elevation in the Grisons.

Despite the fact that we cannot entirely exclude that our models may fail to embrace the complexity of the species' fine-grained ecological requirements, there is another – not habitat related – possibility to explain why the red-billed chough is – and has always been – rare in the eastern Alps while it thrives along its western margin. The post-glacial distribution of the red-billed chough in Europe is characterized by a large, rather contiguous southwestern range and scattered populations in the southeast (BirdLife-International 2021). The Valais population represents the easternmost and northernmost outpost of this 'western complex', i.e. of the Alpine-Arc population, which is a prolongation, without any distribution gaps, to the larger populations occurring in the southern Alps in France and Italy, themselves connected to Spain and Morocco. Hence, these populations may function as source populations for Valais in a metapopulation network, while Grisons, situated in the eastern part of the Alpine arc, has no comparable dense neighbouring populations, neither in the east nor, and in particular, in the south. In effect, the next small and scattered populations are in far distance, in the southern Balkans (Montenegro, Macedonia, Albania) and Greece. Despite the great theoretical dispersal capacity of the species, a high degree of genetic structuring has been found within Spanish (Morinha et al. 2017b) and British (Wenzel et al. 2012) populations, suggesting breeding philopatry. The relatively high degree of isolation and the absence of a source population at more southern latitudes may thus explain why the red-billed chough in the eastern Swiss Alps has always been reported rare in historical times and no dramatic population decline has been documented as it is usually observed when habitat deterioration is the cause of species absence.

## Conclusions

Until the ultimate reasons for the species absence in the eastern Swiss Alps are not conclusively settled, programs aiming at reintroducing the species in that area are to be deemed premature. Despite our attempt to comprehensively capture the environmental conditions that characterize species' habitat, large-scale species–habitat analyses like the one performed here are limited by the lack of fine-grained variables capable of encapsulating decisive species-specific ecological features, such as farming management intensity and availability of food supply. Nevertheless, our model identifies areas with suitable landscape-ecological framework conditions (i.e. the species habitat potential, sensu Braunisch and Suchant 2007), which can help establishing study sites to further investigate possible fine-grained structural or qualitative differences in foraging grounds or nesting sites in the two regions. Finally, population genetic analyses could be used to test the alternative hypothesis that post-glacial isolation is possibly the ultimate cause for the current absence of the red-billed chough in the eastern Alps.

## Author contributions

**Veronika Braunisch**: Conceptualization (lead); Formal analysis (equal); Funding acquisition (equal); Methodology (lead); Validation (equal); Writing – original draft (lead). **Sergio Vignali**: Conceptualization (equal); Formal analysis (equal); Methodology (equal); Validation (equal); Writing – review and editing (equal). **Pierre-Alain Oggier**: Conceptualization (supporting); Data curation (equal); Writing – review and editing (supporting). **Raphaël Arlettaz**: Conceptualization (equal); Data curation (equal); Funding acquisition (lead); Methodology (supporting); Writing – review and editing (equal).

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## Data availability statement

Data available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.0vt4b8gz5> (Braunisch et al. 2021).

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