ZSL LET'S WORK FOR WILDLIFE

ORIGINAL RESEARCH

Remotely sensed variables explain microhabitat selection and reveal buffering behaviours against warming in a climate-sensitive bird species

Corrado Alessandrini[1] (iD), Davide Scridel[2,3], Luigi Boitani[1], Paolo Pedrini[2] & Mattia Brambilla[2,4,5]

[1]Department of Biology and Biotechnologies, Sapienza University of Rome, 00185, Rome, Italy
[2]MUSE – Museo delle Scienze, Sezione Zoologia dei Vertebrati, 38123, Trento, Italy
[3]Area Avifauna Migratrice, Istituto Superiore per la Protezione e la Ricerca Ambientale (ISPRA), 40064, Ozzano dell'Emilia, Italy
[4]Lipu/BirdLife Italia, 43122, Parma, Italy
[5]Department of Environmental Science and Policies, Milan University, 20133, Milan, Italy

Abstract

Fine-scale habitat selection modelling can allow a mechanistic understanding of habitat selection processes, enabling better assessments of the effects of climate and habitat changes on biodiversity. Remotely sensed data provide an ever-increasing amount of environmental and climatic variables at high spatio-temporal resolutions, and a unique opportunity to produce fine-scale habitat models particularly useful in challenging environments, such as high-elevation areas. Working at a 10-m spatial resolution, we assessed the value of remotely sensed data for investigating foraging habitat selection (in relation to topography, microclimate, land cover) in nestling-rearing white-winged snowfinch (*Montifringilla nivalis*), a high-elevation species highly sensitive to climate change. Adult snowfinches foraged at locations with intermediate vegetation cover and higher habitat heterogeneity, also avoiding extremely warm or extremely cold microclimates. Temperature interacted with other environmental drivers in defining habitat selection, highlighting trade-offs between habitat profitability and thermoregulation: snowfinches likely adopted mechanisms of behavioural buffering against physiologically stressful conditions by selecting for cooler, shaded and more snowy foraging grounds at higher temperatures. Our results matched those from previous studies based on accurate field measurements, confirming the species' reliance on climate-sensitive microhabitats (snow patches and low-sward grassland, in heterogeneous patches) and the usefulness of satellite-derived fine-scale modelling. Habitat suitability models built on remotely sensed predictors can provide a cost-effective method for periodic monitoring of species' habitats both at fine grain and over large extents. Fine-scale models also enhance our understanding of the actual drivers of (micro)habitat selection and of possible buffering behaviours against warming, allowing more accurate and robust distribution models, finer predictions of potential future changes and carefully targeted conservation strategies and habitat management.

Introduction

Biodiversity is under anthropogenic pressure worldwide at all levels, from genes to biomes (Brook et al., 2008; Parmesan & Yohe, 2003), and thousands of species are indeed threatened by climate and habitat changes (Spooner et al., 2018). The impacts of past or future changes have been often evaluated by means of large-scale species distribution models (SDMs; Guisan & Zimmermann, 2000), overlooking fine-scale factors that—acting within the species' home range—are more likely to ultimately drive its response to environmental changes (Engler et al., 2017; Lenoir et al., 2013). The importance of microclimate and microhabitat for many species is now increasingly emerging

(Pincebourde et al., 2016; Scherrer & Körner, 2011; Suggitt et al., 2018). Modelling habitat use at ecologically sound (finer) scales allows us to increase the biological realism of the models (Bellard et al., 2012; Randin et al., 2009) by focussing on the environmental conditions that directly affect a species: depending on its ecology, such 'fine-scale' factors could be roughly conceived as those acting in the order of metres (for instance, ornithological studies referring to 'microhabitat' are implemented at spatial resolutions between 1 and 707 m^2; Morales et al., 2008; Patthey et al., 2012). By suggesting more causal species-habitat relationships (Dormann et al., 2012), fine-scale models may provide better predictions of species exposure (and vulnerability) to future impacts, helping to target more effective *in situ* conservation actions: for example, Bennett et al. (2015) and Brambilla, Resano-Mayor, et al. (2018) reported different levels of adaptability and vulnerability, respectively, to climate change among subpopulations of their target species (the Nearctic butterfly *Euphydryas editha* and the white-winged snowfinch *Montifringilla nivalis*) due to different fine-scale habitat selection patterns; indeed, both studies suggested how these site-specific patterns need to be accounted if effective management is to be implemented. Nevertheless, working on such fine scales is highly demanding, especially in remote areas, both physically and economically. In addition, the need to measure environmental predictors by means of dedicated fieldwork largely prevents the generalization and extrapolation of models worked out at high resolution.

The technological progress of remote sensing (RS) is now opening new opportunities (Arenas-Castro & Sillero, 2021; Nagendra et al., 2013), allowing the collection of environmental data over very large spatio-temporal extents, in a uniform, scalable and fast way, and at relatively low costs (He et al., 2015; Rocchini et al., 2010). Progressively finer spatial resolutions are now available free-of-charge, increasing the opportunity to track environmental gradients and to build fine-grained, robust and transferable models (He et al., 2015; Leitão & Santos, 2019; Randin et al., 2020). These advances also involve climate modelling (Potter et al., 2013; Zellweger et al., 2019), allowing a high-precision characterization of abiotic components of the landscapes (e.g. air temperature, radiation, wind speed, humidity, soil moisture and snow depth; Kearney et al., 2020).

Among the terrestrial biomes, alpine ecosystems are suffering from higher rates of climate warming (Brunetti et al., 2009; Pepin et al., 2015) and other habitat modifications, induced by pastoral abandonment (Laiolo et al., 2004) and recreational activities (Rolando et al., 2007), among others. Such factors often impact simultaneously and synergistically (Brambilla et al., 2016; Chamberlain et al., 2013), with highly detrimental effects on alpine avifauna (Scridel et al., 2018; Tayleur et al., 2016). Within these complex

environments, species' reliance on specific, fine-scale, habitat features could lead to context-specific adjustments of habitat use (Moritz & Agudo, 2013; Oswald et al., 2019), or to different levels of vulnerability even between populations of the same species (Brambilla, Capelli, et al., 2018), with potentially strong consequences for population persistence and related management. Fine-scale models of habitat use by alpine birds have recently shed light on the relevance of fine-grained predictors for understanding the ecology of these species; factors such as local vegetation characteristics, soil humidity, snowmelt pattern or the sward height of alpine grassland proved to be good predictors of habitat use (Barras et al., 2020; Brambilla et al., 2017; Jähnig et al., 2018). Largely based on variables directly assessed by researchers on the ground, such models can hardly be transferred to different areas or over different periods without a substantial load of additional fieldwork. However, given the high warming rates of mountains (Brunetti et al., 2009; Pepin et al., 2015), the sensitivity of alpine species to climate and habitat changes (Scridel et al., 2018; Tayleur et al., 2016) and the relevance of fine-grained predictors for their ecology (Barras et al., 2020; Brambilla et al., 2017; Jähnig et al., 2018), large-scale predictions of fine-scale habitat suitability would be particularly important for prioritizing conservation efforts and designing effective management plans (cf. Chamberlain et al., 2012). RS data could, thus, allow the production of spatially explicit, fine-grained suitability maps to understand, predict and timely monitor threatened species' distributions and their habitats, over entire regions. In addition, thanks to the recent availability of microclimate models, it is now possible to evaluate trade-offs affecting—and buffering behaviours adopted by—animal species facing climate warming, at very relevant spatio-temporal scales.

In this study, we focused on the white-winged snowfinch (*M. nivalis*; Aves: Passeridae), a Palaearctic mountain specialist, particularly sensitive to climate change (Brambilla et al., 2016; Maggini et al., 2014). Previous studies have shown that both the large-scale distribution (Brambilla et al., 2017; Brambilla et al., 2020; de Gabriel et al., 2021) and the fine-scale habitat use (Bettega et al., 2020; Brambilla et al., 2017; Brambilla et al., 2019; Brambilla, Capelli, et al., 2018; Brambilla, Resano-Mayor, et al., 2018; Resano-Mayor et al., 2019) are strongly affected by climate or climate-dependent, often ephemeral, resources. We focused on snowfinch habitat use during the critical nestling-rearing phase, when breeding birds are highly dependent on snow patches, their melting margins and short-sward or low-density alpine grasslands, which are all microhabitats highly vulnerable to climate warming (Choler et al., 2021; Klein et al., 2016).

Here, we investigated habitat selection of foraging snowfinches by combining daily estimates of topography, microclimate and land-cover data, all derived from RS

open-source technologies at a 10 m/px-resolution, and further tested the role of microclimate *per se* and in interaction with other habitat components (Fig. 1). Finally, by comparing the output of our RS-derived models with those provided by previous models based on very high-resolution variables recorded in the field, we explored whether the former may be used in lieu of the latter to generate large-extent evaluation of fine-grained habitat suitability, a key step to identify crucial areas for conservation and habitat management or restoration. This study therefore represents a first step towards (1) a modelling framework aimed to increase the robustness, extent and applicability of fine-scale habitat suitability models to monitor vulnerable species remotely, and (2) a first evaluation of buffering behaviour against warming in an alpine species using RS predictors.

## Materials and Methods

Study area and occurrence data

We investigated the habitat use by foraging snowfinches in central-eastern European Alps during the nestling-rearing period (7 June–19 July) in 2017. We considered 15 pairs, breeding above the treeline (between 2100 and 3000 m asl; Table S1 and Fig. S1), in areas dominated by alpine grassland, rocks and snowfields, in varying proportions, with rare shrubs. Breeding adults were observed while foraging, by means of binoculars, and the exact location of successful foraging events (up to 20 per day per pair; mean ± SD: 17.77 ± 4.76) was recorded by means of a portable GPS or mapped on very detailed aerial photographs (scale 1:2000). This kind of data had been previously used to model fine-scale habitat selection by means of environmental variables mainly recorded by researchers in the field in previous studies (Brambilla

et al., 2017; Brambilla et al., 2019; Brambilla, Resano-Mayor, et al., 2018). Seven out of 15 pairs were surveyed twice, with the temporal gap between the two visits never exceeding 10 days (Table S1).

The foraging locations were imported into *QGIS 3.10.1* (QGIS Development Team, 2018) and a 2-m buffer was added around each point to account for possible measuring error at the moment of the on-field collection. For each location, a control point was randomly generated, being within 300 m from the pair's nest (or the most exploited area in the cases when the nest was not found) and at least 25 m far from any foraging location. This procedure led to a total of 782 records, comprising an equal number of foraging (occurrences, n = 391) and control plots (pseudo-absences, n = 391) for each breeding pair (and for each day of survey, in the case of pairs surveyed twice).

Environmental data

Land-cover data were extracted from open-source, high-resolution multispectral images collected by the Sentinel-2 satellite of the ESA Copernicus mission (Drusch et al., 2012), widely used for ecological mapping, but seldom applied to animal distributions (e.g. Cisneros-Araujo et al., 2021; Stokes et al., 2021; Valerio et al., 2020; Wang et al., 2020). Sentinel-2 images were searched and downloaded from the EarthExplorer website (https://earthexplorer.usgs.gov/) in the format Level-1C (ortho-rectified images); only images with no cloud cover were selected to allow a correct estimation of land-cover features. The study sites fall into two tiles, namely T32TPS (Passo Stelvio and Passo Gavia) and T32TQS (Passo Sella and Passo Pordoi); for the former, three images were selected (capture dates: 13 and 26 June, 16 July 2017), whereas for the latter only one cloud-free image was
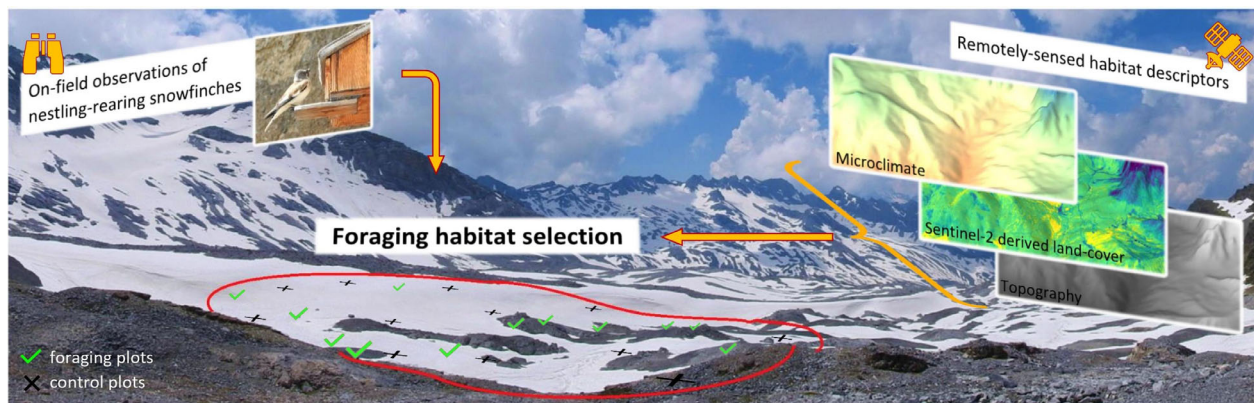
Figure 1. A visual representation of the approach adopted in this study to investigate foraging habitat selection by nestling-rearing snowfinches.

available (13 June 2017). All images were captured by the Sentinel-2A satellite. In QGIS, the images were atmospherically and topographically corrected by means of the Dark Object Subtraction (in Semi-Automatic Classification Plugin; Congedo, 2021) and the Cosine-Correction (Civco, 1989; in SAGA plugin) respectively. For each multispectral image, four spectral indices were derived (see Table S2 for calculation and references):

• Normalized difference vegetation index (NDVI) and secondary modified soil-adjusted vegetation index (MSAVI2) to quantitatively assess the vegetation green-up;
• Soil composition index (SCI) to capture the presence of bare ground and anthropized areas;
• Normalized difference snow index (NDSI) for the snow component of the landscape.

These indices are band operations that highlight specific land-cover features thanks to their unique spectral signature: their values range from −1 to 1, with higher ones associated with the specific feature they are meant to represent. A Tasseled Cap Transformation (Kauth & Thomas, 1976) was implemented starting from bands 2, 3, 4, 8, 11 and 12, using the Sentinel-2-specific coefficients suggested by Shi & Xu (2019); see also Text S1. This PCA-like (but scene-independent) procedure returns a fixed number of uncorrelated axes, that is images, to be used as covariates: brightness, greenness and wetness associated with the soil/albedo, vegetation and water response respectively; the latter proved to be a good proxy of snow cover too (Zhang et al., 2002), also within our data (details not shown). The Tasseled Cap images were also used to derive the multidimensional Rao's Q index (Rocchini et al., 2017), by means of the *paRao* function in the R package *rasterdiv* (Marcantonio et al., 2021), in order to capture the overall spectral (and environmental) heterogeneity of the landscape at the finest spatial scale (i.e. within a 3 × 3 pixel window; Text S1). A 10-m raster of the elevation was obtained from the TINITALY (http://tinitaly.pi.ingv.it/Download_Area2.html; tiles W51560 and W5157; Tarquini et al., 2012) and used to derive the variable aspect (later transformed in aspect_lin; Text S1), roughness and slope (R package *raster*; Hijmans, 2022). Solar radiation was calculated in GRASS 7.2 (Neteler et al., 2012; function *r.sun*) as the global radiation taking into account any shadowing effects of the surrounding reliefs, for 3 days (10 June, 21 June and 19 July), and interpolated to the exact day of the surveys (as for the land-cover variables, see below).

Following Maclean et al. (2019), the microclimatic variables were derived from the R packages *NicheMapR* (Kearney & Porter, 2017) and *microclima* (Maclean et al., 2019), which operate a downscaling of macroclimatic data, based on a high-resolution DEM (here, TINITALY) and a few other inputs (see Text S1). We derived the minimum, median and maximum air temperatures estimated for eight temporal windows covering the survey period (each observation was then associated with the closest window; Table S3). Temperatures were estimated at 1 m height because we had at least one on-field measure per day of air temperature at a 1 m height (recorded according to Brambilla et al., 2017), which we used to validate microclimatic models and to select the most reliable temperature estimate provided by modelling.

For each variable (hereafter, the 'pixel' variable), we derived a measure of its fine-scale spatial variation (the 'stdev' variable, representing heterogeneity within the surrounding area) by calculating its standard deviation in a 3 × 3 pixel window around each pixel of the raster (see Text S1). Roughness was used as the 'heterogeneity counterpart' of elevation and Rao's Q index was considered as a measure of heterogeneity with no 'pixel counterpart' (Table 1).

For each of the 782 records we calculated the value of all variables: if the point circle (i.e. the record with its 2-m buffer) fell into two or more pixels, the value extracted was the mean of the pixel values, weighted according to the overlap between each single pixel and the circle.

For Stelvio and Gavia passes, three values were extracted for each land-cover variable (one for each date of the Sentinel-2 images) and then linearly interpolated to obtain measures at the exact day of the survey (see Text S1). In Passo Sella and Passo Pordoi, we took the value measured for a single Sentinel-2 image since there was no another image available for interpolation; anyway, the short temporal gap between surveys (7, 9, 12 and 14 June) and Sentinel-2 capture (13 June) should prevent any potentially consistent bias (Table S3).

Statistical analysis

The analyses were performed using the software R 4.0.3 (R Development Core Team, 2020).

All the environmental variables derived from RS data were checked for linearity and for the presence of outliers: all the 'stdev' variables and slope were log-transformed, whereas solrad was elevated to the power of 10; two records were removed as outliers.

Before modelling, we checked for consistency between environmental data collected during the fieldwork and RS data (results in Text S3.1).

The perfectly balanced, matched design of 'cases' (observed foraging events) and 'controls' (control points) led us to use conditional logistic regression (Hosmer et al., 2013) to investigate habitat selection by foraging snowfinches. Conditional logistic regressions were implemented by means of the *clogit* function in the *survival* R package (Therneau, 2021). By comparing observations

Table 1. The 29 environmental variables derived from remotely sensed data.

'Pixel' variable	Name or description	Value range (Unit)	Associated 'stdev' variable
Land cover (from Sentinel-2A multispectral images)			
NDVI	Normalized difference vegetation index	$-0.17 \div 0.77$ (−)	stdev_NDVI
MSAVI2	Secondary modified soil-adjusted vegetation index	$-0.05 \div 0.58$ (−)	stdev_MSAVI2
SCI	Soil composition index	$-0.77 \div 0.33$ (−)	stdev_SCI
NDSI	Normalized difference snow index	$-0.69 \div 0.77$ (−)	stdev_NDSI
Brightness	Soil, vegetation and water axes of the Tasseled Cap transformation	$0.08 \div 0.91$ (−)	stdev_Brightness
Greenness		$-0.28 \div 0.18$ (−)	stdev_Greenness
Wetness		$-0.38 \div 0.23$ (−)	stdev_Wetness
-	Multidimensional Rao's Q index, calculated on the three Tasseled Cap axes	$0.05 \div 4.03$ (−)	Rao_TC
Topoclimate (from TINITALY DEM and *NicheMapR/microclima* R packages)			
Elevation	Elevation	$2144 \div 3023$ (m)	roughness
Slope	Slope	$0.22 \div 53.5$ (°)	stdev_slope
aspect_lin	(Transformed) orientation of the slope	$-1.0 \div 1.0$ (−)	stdev_asplin
solrad	Daily solar radiation	$7327 \div 9650$ (Wh/m^{2}d)	stdev_solrad
Tmin_1m	Minimum, medium and maximum air daily temperature 1 m above the ground	$-11.0 \div 4.4$ (°C)	stdev_Tmin_1m
Tmed_1m		$-1.6 \div 9.6$ (°C)	stdev_Tmed_1m
Tmax_1m		$3.6 \div 15.9$ (°C)	stdev_Tmax_1m

The name or a brief description, the value range in the dataset and the measurement unit ('−' stands for adimensional) are provided for the 'pixel' variables (the ones extracted as absolute values of the variable). From every 'pixel' variable, a measure of its fine-scale variation was derived: the 'stdev' variable, calculated as the standard deviation across a 3 × 3 pixel window. All the variables have a 10-m spatial resolution.

and control points within the same 'stratum', this modelling framework allowed us to derive population-averaged estimates of the coefficient effects, accounting for the stratified intrinsic nature of the data: we used the combination 'pair × survey date' as 'stratum', distinguishing two visits to the same breeding pair into two different strata (Table S3). We adopted an Information Theoretic Approach (Burnham & Anderson, 2002), and ranked models by BIC (Bayesian information criterion, which gave more parsimonious results than AIC and AICc in a preliminary analysis). To develop and test models on independent datasets, we split the data into a training and a testing dataset by a ratio of 68:32 observations. Hence, 13 and 5 independent strata (i.e. 10 and 5 pairs respectively) were included in the training and testing dataset respectively (Table S3).

We built univariate and multivariate models, scaling the variables prior to each model fitting in order to make their coefficients more interpretable and their effect size comparable. The inclusion of squared terms and interactions was tested if ecologically relevant and retained only if statistically supported (i.e. when it led to a model with a lower BIC). For multivariate modelling, we first built within-group models (i.e. having only 'pixel' or 'stdev' variables), to test the utility of heterogeneity measures, and then a synthetic model including them all (further details in Text S2). Prior to each model estimation, we retained only variables with variance inflation factor <5 to reduce multicollinearity problems (Chatterjee &

Hadi, 2006). We estimated and ranked the models by means of the *dredge* function in the *MuMIn* R package (Bartoń, 2020). When more competing models had similar BIC values (ΔBIC <2 from the most supported one; after excluding those having uninformative parameters, *sensu* Arnold, 2010), they were averaged by means of the 'full average' method (Bartoń, 2020).

Adjusted R^2 (function *MuMIn::r.squaredLR*) was calculated on the training dataset for each most supported model. The latter were validated on the testing dataset visually and by means of the AUC (area under the curve) estimate from the ROC plot (Fielding & Bell, 1997): values closer to 1 indicate a better discriminatory power of the model, while a value of 0.5 indicates a completely random behaviour of the model. As suggested by Therneau et al. (1990), the model residuals were plotted against each predictor to check for their random behaviour.

Results

In the univariate analysis, the heterogeneity variables ('stdev') were distinctly better predictors than 'pixel' variables (particularly those related to snow and land cover; Table S4 and Text S3.2). In the multivariate analysis, the 'stdev' models were outperformed by the 'pixel' ones, while the BIC values of both were markedly higher than the BICs of synthetic models (Table 2). The adjusted R^2 of the most supported models were invariably high,

ranging from 0.589 for the 'stdev' model, to 0.655 for the 'pixel' one, up to 0.746 for the synthetic model (Table 2).

The most supported synthetic models were averaged, leading to a model with 13 terms, including all types of predictors (both land cover and topoclimatic, both pixel and of heterogeneity), four quadratic effects and three interactions (Table 3; see also Fig. S2). According to this averaged synthetic model, fine-scale foraging habitat suitability for breeding snowfinches was highest in patches with higher snow cover heterogeneity (stdev_Wetness_LOG); intermediate levels of NDVI, temperature and solar radiation; and lower values of the ground index (SCI) and roughness (Fig. 2A). The interaction effects suggested that, when temperature was higher, snowfinches tended to forage in sites with higher levels of snow cover heterogeneity, with lower solar radiation and on more rugged terrains (Fig. 2B).

The validation procedure suggested that the averaged synthetic model had a very good discriminatory power when tested on the training data (AUC$_{train}$ = 0.881 ± 0.029), and still good when transferred to the testing dataset (AUC$_{test}$ = 0.802 ± 0.055). The residuals showed a random behaviour, aligning roughly along a horizontal line (Fig. S3).

Discussion

Local environmental characteristics directly affect habitat use and modulate the species' response to current climatic alterations (Massimino et al., 2020; Pateman et al., 2016). Effective methods to investigate such fine-scale patterns are hence needed to derive sound management recommendations for conservation. With this work, we explored the potential value of RS variables for describing the fine-scale foraging habitat selection in white-winged snowfinches, taking advantage of the possibility to compare the outcomes with already available fine-scale models developed on predictors measured in the field. RS predictors led to statistically high-performing models, which depicted ecologically sound species-habitat relationships, fully consistent with results based on field-measured predictors (see Table 4 for a quantitative comparison). Land

cover, topography and climate, all contributed to patterns of habitat selection.

In the alpine context, the seasonal phenological development of grass vegetation provides the main contribution to the NDVI values derived by satellite, hence the intermediate values (preferred by the species) in 10-m pixels may represent a uniform grassy patch at intermediate stages of phenological development or describe a scattered distribution of developed but sparse grassy microhabitats. In both cases, such a pattern of selection mirrored the preference for low-sward, or partial cover of, grassland, observed in the field (Brambilla et al., 2017; Brambilla, Resano-Mayor, et al., 2018; Resano-Mayor et al., 2019). NDVI hence was confirmed as a good proxy for the phenology and also for the structure of vegetation (Fontana et al., 2008). This selection operated by foraging snowfinches likely represents the trade-off between abundance and detectability/accessibility of prey items (arthropods): their availability is higher in dense high-sward alpine grassland (Antor, 1995), but their detectability for birds increases in more open (micro)habitats, as low-sward grassland interrupted by bare ground (Butler & Gillings, 2004; Stillman & Simmons, 2006). The strong effects of stdev_Wetness_LOG (representing fine-scale variation in snow cover) on the foraging suitability distinguished the two most important foraging (micro)habitats for the species: the grassland (at low levels of snow cover heterogeneity) and the snow (at higher ones; Fig. S4). For the latter, the 10-m resolution prevented the distinction between the foraging on snow patches from the use of snow margins (Brambilla et al., 2017; Brambilla et al., 2019; Brambilla, Capelli, et al., 2018; Brambilla, Resano-Mayor, et al., 2018; Resano-Mayor et al., 2019). Snowfields provide highly detectable and easily collectable invertebrates, blown by the wind (Antor, 1995), whereas the margins host tipulid larvae which frequently represent the most abundant prey items during the nestling-rearing phase of the species (Heiniger, 1991). The effect of NDVI and stdev_Wetness_LOG, as well as the results of the univariate analysis, clearly suggest the importance of habitat heterogeneity (especially for snow cover) at this scale, confirming the positive association between foraging

Table 2. Most supported multivariate models fitted on training dataset with 'pixel' variables only, 'stdev' variables only and with both ('synthetic').

Model	Predictors included	df	BIC	Adjusted R^2	AUC$_{test}$ (±SD)
Pixel	Landcover_pix + Topoclimatic_pix	10	532.53	0.655	0.774 ± 0.059
Stdev	Landcover_stdev + Topoclimatic_stdev	9	555.25	0.589	0.751 ± 0.063
Synthetic	All	13	477.72	0.746	0.802 ± 0.055

All the variables were scaled before model fitting. Degrees of freedom (df), BIC, adjusted R^2 and the AUC scores (mean ± SD) on the test dataset are reported. For the 'stdev' and 'synthetic' models, BIC and adjusted R^2 refer to the most supported model among those used for averaging.

Table 3. Beta coefficients (mean ± SE) of the most supported synthetic models and averaged model (AVG) describing foraging habitat selection by breeding snowfinches (for all the other models ΔBIC >4).

Selected predictors	Effect	M1	M2	M3	AVG
NDVI	Linear	−0.014 ± 0.235	−0.042 ± 0.230	0.177 ± 0.227	0.032 ± 0.249
	Quadratic	−0.904 ± 0.168	−0.854 ± 0.165	−0.707 ± 0.148	−0.829 ± 0.180
solrad10	Linear	−0.323 ± 0.182	−0.276 ± 0.168	−0.271 ± 0.168	−0.291 ± 0.175
	Quadratic	−0.478 ± 0.122	−0.500 ± 0.121	−0.525 ± 0.122	−0.499 ± 0.123
Tmax_1m	Linear	−3.55 ± 1.61	−2.54 ± 1.59	−2.09 ± 1.60	−2.77 ± 1.71
	Quadratic	−3.28 ± 0.965	−4.49 ± 0.916	−4.18 ± 0.895	−3.97 ± 1.07
stdev_Wetness_LOG	Linear	0.861 ± 0.215	0.857 ± 0.206	1.27 ± 0.223	0.978 ± 0.283
	Quadratic			0.445 ± 0.148	0.130 ± 0.218
SCI	Linear	−0.698 ± 0.202	−0.601 ± 0.196		−0.460 ± 0.342
roughness_LOG	Linear	−0.163 ± 0.147			−0.058 ± 0.118
solrad10:Tmax_1m	–	−0.527 ± 0.173	−0.600 ± 0.162	−0.586 ± 0.159	−0.570 ± 0.168
stdev_Wetness_LOG:Tmax_1m	–	1.30 ± 0.231	1.35 ± 0.219	1.15 ± 0.234	1.28 ± 0.242
roughness_LOG:Tmax_1m	–	0.564 ± 0.195			0.201 ± 0.294
Model statistics					
df		12	10	10	13
LogLik		−205.36	−210.96	−211.14	–
BIC		477.72	477.75	478.11	–
ΔBIC		0	0.033	0.394	–

All models also included stratum-specific intercepts (not displayed). Model statistics are reported for each model, below the beta coefficients.
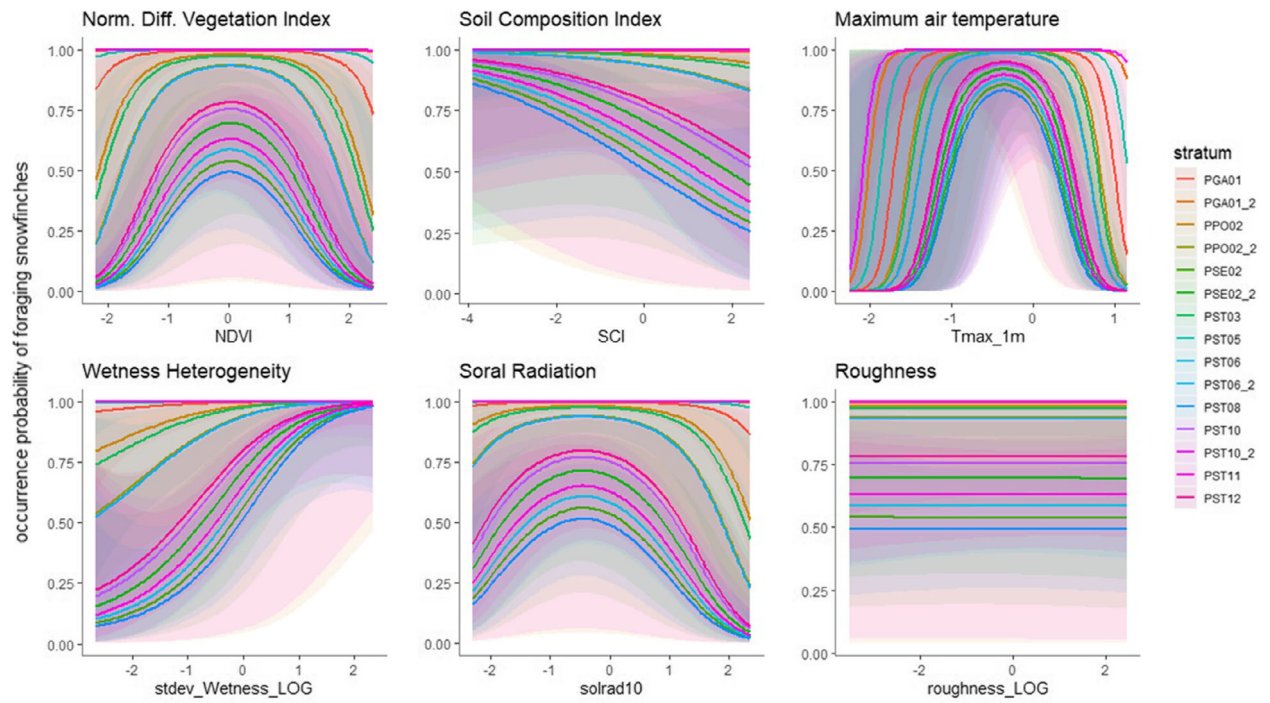
suitability and the number of different habitat patches found in Brambilla et al. (2017); Table 4. The negative selection for the SCI, which reached lowest values at or around snow patches (Fig. S4), provides further support for the preference for foraging habitats closer to snow and for the avoidance for anthropized areas (as revealed by Brambilla, Resano-Mayor, et al., 2018). The avoidance for higher and lower values of solar radiation is also consistent with previous results (Brambilla et al., 2017), especially for what concerns the avoidance of highly radiated patches.

Remotely derived, spatially explicit estimates of air temperature were never used before for habitat modelling in this species and gave crucial, interesting results, highlighting how thermal conditions may shape the foraging behaviour of a cold-adapted species. Such a kind of evidence has been rarely integrated into fine-scale habitat selection studies and collected only for a few other mountain species (Oswald et al., 2019; partially by Visinoni et al., 2015). Extreme temperatures were deemed by the models to reduce the foraging suitability: on the one hand, very cold conditions may reduce the gain-cost foraging trade-off by reduced rates of invertebrate activity (Somme, 1989), hence hampering prey availability (i.e. abundance modified by accessibility; Schaub et al., 2010); on the other hand, hot conditions may increase the costs for thermoregulation, reducing foraging gains. This second aspect clearly emerged analysing the temperature interactions: as the air 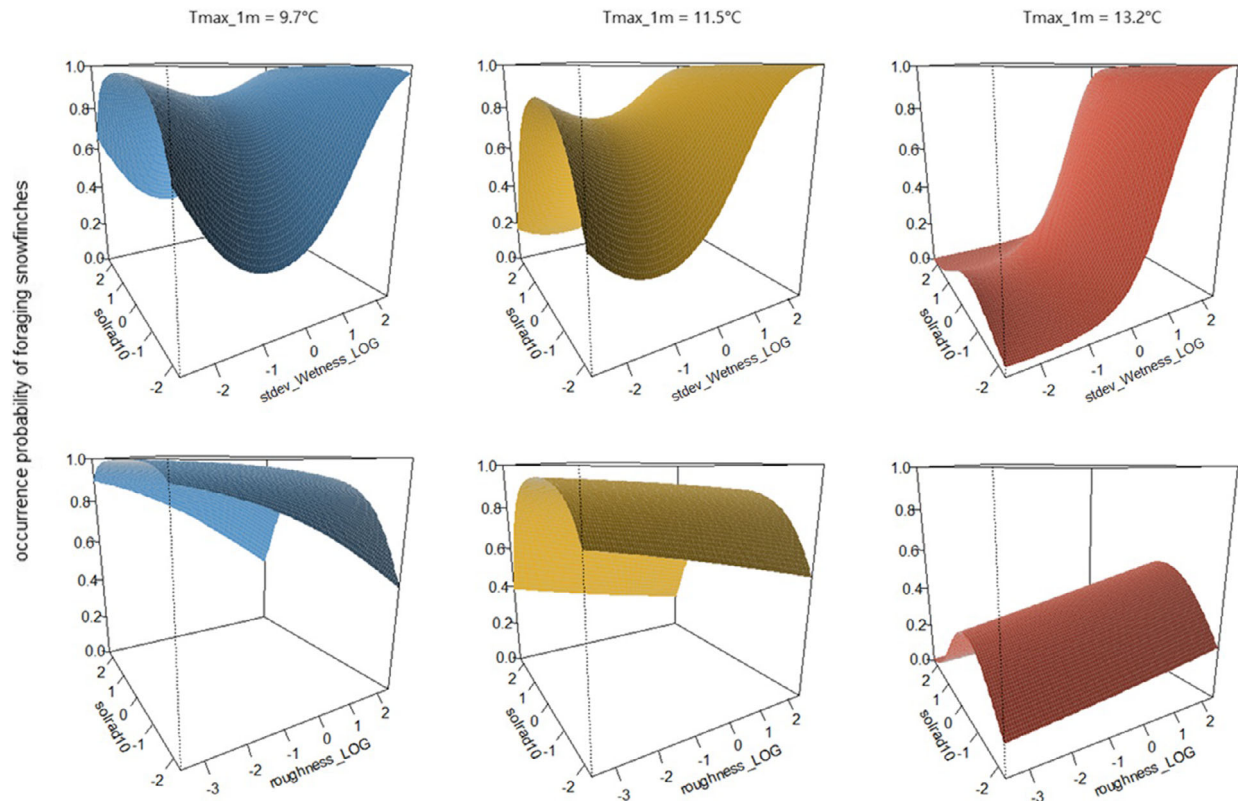temperature increased, snowfinches tended to forage closer to the snow and in cooler sites (i.e. more rugged and less radiated). This may represent a mechanism of behavioural buffering (Huey et al., 2012) to avoid the most physiologically stressful conditions during the foraging activity. Unlike what has been observed in the Cape rock-jumper (*Chaetops frenatus*), a South African endemic alpine passerine, that reduces its foraging activity not to expose to stressful hot conditions (Oswald et al., 2019), here warmer temperatures (within the range covered by our study) may shape, rather than prevent, foraging activity (as in Hayford et al., 2015; Wachob, 1996). Moreover, the increased selection for the snow patches might suggest the double function of this habitat in warmer conditions, both as foraging ground and as relief habitat (Ion & Kershaw, 1989). Other cold-adapted avian species had been observed using the snow as a relief habitat (e.g. *Lagopus* spp.; Rosvold, 2016), although not while foraging. By balancing temperature and solar radiation, foraging snowfinches could select the microhabitats that maximize energy gains according to the trade-off between profitability and thermoregulatory costs. Considering that nestling rearing is energy- and time-consuming and that it takes place during the warmest season, thermoregulatory costs may be particularly limiting in this phase for an elevation-specialist and cold-adapted species such as the snowfinch.

All these insights would have been very hard (and expensive) to get without the use of RS predictors: microclimatic models (Kearney et al., 2020) provided affordable

(A) Main effects (linear + quadratic)

(B) Interactions with Maximum air temperature

2065485, 2022, 5, Downloaded from https://zslpublications.onlinelibrary.wiley.com/doi/10.1002/rse2.265 by Universita Degli Studi Di Mila, Wiley Online Library on [21/10/2022]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Figure 2. Effects of variables included in the averaged synthetic model describing fine-scale habitat selection by foraging snowfinches. (A) Main effects (and 95% CI) drawn for each stratum of the training dataset (colour legend on the right). Conditional logistic regression provides population-averaged estimates of predictors' effects and a stratum-specific intercept. The effects of NDVI, solrad10, Tmax_1m and stdev_Wetness_LOG include the quadratic term. (B) 3D plots representing how foraging occurrence probability varies according to the concomitant effects of variables interacting with temperature, that is solar radiation, roughness and wetness heterogeneity (stratum 'PST10' taken as reference; confidence intervals not shown). The columns represent colder, mean and warmer conditions in blue, yellow and red respectively; lower and upper temperature intervals were selected as (mean ± 0.5 × SD). All the variables were scaled before modelling; to know their original values, see 'Value Range' in Table 1.

Table 4. A summary of the quantitative comparison between previous habitat selection (synthetic) models derived from the in-the-field environmental data collection (Brambilla et al., 2017; Brambilla, Resano-Mayor, et al., 2018) and the present study, where environmental data were totally derived from remote sensing.

	'In the field'				Remotely sensed	
	Brambilla et al. (2017)		Brambilla, Resano-Mayor, et al. (2018)		Present study	
Year of data collection	2015		2016		2017	
No. pairs/Foraging events	18/134		22/235		15/391	
Model type	c-logit		c-logit		c-logit	
Spatial resolution	314 m^2		78.5 m^2		100 m^2	
Predictor measure	% cover in a 10-m radius		% cover in a 5-m radius		10-m pixel value and St. dev. among 3 × 3 px window	
Predictor type	**Predictors included estimate (SE)**					
Vegetation	*Grassland cover*	*0.313 (0.010)*	*Grassland cover*	*0.57 (0.14)*	*NDVI*	*0.032 (0.249)*
	Sward height	−0.156 (0.059)	Sward height	−0.85 (0.16)	$NDVI^2$	−0.829 (0.180)
	SD Sward height	0.032 (0.087)				
Snow	Snow cover[1]	−0.033 (0.028)	*Snow cover*	*2.00 (0.32)*	*stdev_Wetness*	*0.978 (0.283)*
			Snow cover[2]	−0.72 (0.13)	$stdev\_Wetness^2$	0.130 (0.218)
					stdev_Wet × Tmax	1.28 (0.242)
Rock/anthrop.	*Rocks*	−0.021 (0.018)	*Anthropized*	−1.21 (0.45)	*SCI*	−0.460 (0.342)
	Boulders	0.023 (0.012)				
	Bare ground	0.018 (0.031)				
Other abiotic factors	*Solar radiation*	−0.0012 (0.0006)			*solrad*	−0.291 (0.175)
	Slope	−0.017 (0.002)			solrad × Tmax	−0.570 (0.168)
	Water	−0.049 (0.039)			roughness	−0.058 (0.118)
					roughness × Tmax	0.201 (0.294)
					Tmax	−2.77 (1.71)
					$Tmax^2$	−3.97 (1.07)
Others cover factors	No. of patches	0.075 (0.031)				
	Snow × Grassland	0.0063 (0.002)				
Model performance statistics	R^{22}	0.30	R^2	0.35	Adjusted R^2	0.75
	AUC^2	0.75 ± 0.06			AUC	0.80 ± 0.06

The concordance among effects' estimates is marked in italics. A more comprehensive qualitative comparison is presented in the Discussion section and includes other previous studies as well. Note the novelty of using microclimatic estimates and the higher model performance statistics related to the RS-derived model.
[1]Quadratic effect according to univariate model, and positive/quadratic according to the MARS model; interaction effect fundamental to evaluate its true impact.
[2]Refers to a MARS model run with the same dataset (see Brambilla et al., 2017).

but reliable estimates of local temperature at highly relevant spatio-temporal scales, allowing us to disclose how (1) maximum temperature was a direct driver of habitat selection, and (2) its interaction with other factors

revealed fundamental mechanisms affecting the microhabitat selection patterns.

In terms of RS data retrieval and their contribution to model performance, Sentinel-2 images were subject to

cloud limitations that halved our initial dataset (data from other years and/or other sites, also because the satellite Sentinel-2B was not yet fully operating at that time) but gave crucial land-cover information. On the other hand, topoclimatic data had less explanatory power—though ecologically paramount—but did not suffer from any temporal or atmospheric shortcoming, and could be implemented at even finer scales (hourly temperature estimates and 1-m DEMs are already available). In our case, well-developed snow models might provide complementary and important information in addition to satellite multispectral images (also resolving some of their main shortcomings). Such models could be very relevant in high-elevation alpine landscapes, where the snow melting and the subsequent grass development represent the main drivers of key habitat characteristics. However, such models are still poorly implemented (Braunisch et al., 2021; but see Zanotti et al., 2004).

The high consistency with previous studies based on predictors manually measured in the field demonstrates that RS environmental data provided relevant information, at an acceptable spatio-temporal resolution, accurate enough to investigate habitat selection (and infer potential behavioural mechanisms) at the very local scale. Our results (1) confirmed snowfinch vulnerability to climate change, highlighting how it relies on climate-sensitive microhabitats, increasingly jeopardized by ongoing warming, and (2) provided quantitative evidence to preserve suitable microhabitats (e.g. by targeted habitat management) for this (and likely other) species during the critical period of nestling rearing.

The use of RS open-source data should be tested over other environments and species, and undoubtedly promoted. Since land-cover heterogeneity stands out as particularly important, RS data are particularly suited for multiscale analyses allowing to find the right scale at which such heterogeneity mostly affects a target species (Seavy et al., 2009; Tapia et al., 2017). These insights would be much harder to gain with variables recorded 'by hand' in the field. Equally relevant, microclimatic models enable a continuous, spatially explicit estimate of temperatures that would be prohibitive to obtain by means of field equipment.

Finally, the potential extrapolation of RS-derived models opens the door to remote assessments of habitat suitability at unprecedented spatial and temporal details. A weekly assessment of the habitat suitability could allow us to track habitat changes in occurrence sites, and to timely address conservation actions towards those sites (or even single pairs) most affected by unsuitable alterations. The procedure chosen to extract information from the multispectral images (i.e. by means of spectral indices and the Tasseled Cap Transformation, rather than by an image classification) was exactly meant to provide the most rigorous and replicable workflow, totally independent from on-field measures. Moreover, these essential features, coupled with the global extent of Sentinel-2 data, make possible to model the potential fine-scale habitat suitability for foraging snowfinches over much broader areas, allowing an upscale of the fine-grained habitat use to a macroecological level and an explicit test of model transferability across different portions of the species' range.

Conclusions

In the current study, the foraging habitat selection by adult white-winged snowfinches, during the critical phase of nestling rearing, has been modelled by the means of RS environmental variables at a 10-m spatial resolution. Despite the relative scarcity of available images, land-cover variables derived from the satellite Sentinel-2 proved to be good proxies of the foraging patterns by snowfinches. Even better performance arose when such variables were integrated with other RS topoclimatic variables. Models outlined foraging patterns extremely consistent with previous studies based on environmental predictors collected directly in the field. This confirms: (1) the already supposed drivers of foraging habitat selection in breeding snowfinches, (2) the importance of temperature in modulating fine-scale species' responses and (3) the strict relationship that links the snowfinch to climate-sensitive habitat features, resulting in a high vulnerability to the impacts of climatic and environmental alterations. Even more relevant, this approach disclosed the key interaction between temperature and other drivers of habitat use that determines trade-offs between foraging opportunities and thermoregulation in a cold-adapted species. The information derived can be a solid base for further ecological modelling at larger extents, made possible using RS data, demonstrating the potentiality of the high-resolution RS tools in the 'fine-grained revolution' (Hannah et al., 2014) occurring in the field of ecology and conservation biology.

Acknowledgements

REFERENCES

Antor, R.J. (1995) The importance of arthropod fallout on snow patches for the foraging of high-alpine birds. *Journal of Avian Biology*, **26**(1), 81.

Arenas-Castro, S. & Sillero, N. (2021) Cross-scale monitoring of habitat suitability changes using satellite time series and ecological niche models. *Science of the Total Environment*, **784**, 147172.

Arnold, T.W. (2010) Uninformative parameters and model selection using Akaike's information criterion. *Journal of Wildlife Management*, **74**(6), 1175–1178.

Barras, A.G., Marti, S., Ettlin, S., Vignali, S., Resano-Mayor, J., Braunisch, V. et al. (2020) The importance of seasonal environmental factors in the foraging habitat selection of alpine ring ouzels *Turdus torquatus alpestris*. *Ibis*, **162**(2), 505–519.

Bartoń, K. (2020) MuMIn: multi-model inference. R package version 1.43.17.

Bellard, C., Bertelsmeier, C., Leadley, P., Thuiller, W. & Courchamp, F. (2012) Impacts of climate change on the future of biodiversity. *Ecology Letters*, **15**(4), 365–377.

Bennett, N.L., Severns, P.M., Parmesan, C. & Singer, M.C. (2015) Geographic mosaics of phenology, host preference, adult size and microhabitat choice predict butterfly resilience to climate warming. *Oikos*, **124**(1), 41–53.

Bettega, C., Fernández-González, Á., Ramón Obeso, J. & Delgado, M.D.M. (2020) Circannual variation in habitat use of the white-winged snowfinch *Montifringilla nivalis nivalis*. *Ibis*, **162**(4), 1251–1261.

Brambilla, M., Capelli, F., Anderle, M., Forti, A., Bazzanella, M., Masiero, G. et al. (2018) Landscape-associated differences in fine-scale habitat selection modulate the potential impact of climate change on white-winged snowfinch *Montifringilla nivalis*. *Bird Study*, **65**, 525–532.

Brambilla, M., Cortesi, M., Capelli, F., Chamberlain, D., Pedrini, P. & Rubolini, D. (2017) Foraging habitat selection by alpine white-winged snowfinches *Montifringilla nivalis* during the nestling rearing period. *Journal für Ornithologie*, **158**(1), 277–286.

Brambilla, M., Pedrini, P., Rolando, A. & Chamberlain, D.E. (2016) Climate change will increase the potential conflict between skiing and high-elevation bird species in the Alps. *Journal of Biogeography*, **43**(11), 2299–2309.

Brambilla, M., Resano-Mayor, J., Arlettaz, R., Bettega, C., Binggeli, A., Bogliani, G. et al. (2020) Potential distribution of a climate sensitive species, the white-winged snowfinch *Montifringilla nivalis* in Europe. *Bird Conservation International*, **30**(4), 522–532.

Brambilla, M., Resano-Mayor, J., Scridel, D., Anderle, M., Bogliani, G., Braunisch, V. et al. (2018) Past and future impact of climate change on foraging habitat suitability in a high-alpine bird species: management options to buffer against global warming effects. *Biological Conservation*, **221**, 209–218.

Brambilla, M., Scridel, D., Sangalli, B., Capelli, F., Pedrini, P., Bogliani, G. et al. (2019) Ecological factors affecting foraging behaviour during nestling rearing in a high-elevation species, the white-winged snowfinch (*Montifringilla nivalis*). *Ornis Fennica*, **96**(3), 142–151.

Braunisch, V., Vignali, S., Oggier, P.-A. & Arlettaz, R. (2021) Present in the western European Alps but absent in the eastern part: can habitat availability explain the differences in red-billed chough occurrence? *Journal of Avian Biology*, **52**(4). https://doi.org/10.1111/jav.02682

Brook, B.W., Sodhi, N.S. & Bradshaw, C.J.A. (2008) Synergies among extinction drivers under global change. *Trends in Ecology & Evolution*, **23**(8), 453–460.

Brunetti, M., Lentini, G., Maugeri, M., Nanni, T., Auer, I., Böhm, R. et al. (2009) Climate variability and change in the greater alpine region over the last two centuries based on multi-variable analysis. *International Journal of Climatology*, **29**(15), 2197–2225.

Burnham, K.P. & Anderson, D.R. (2002) *Model selection and multimodel inference.* New York, NY: Springer, p. 515.

Butler, S.J. & Gillings, S. (2004) Quantifying the effects of habitat structure on prey detectability and accessibility to farmland birds. *Ibis*, **146**, 123–130.

Chamberlain, D.E., Arlettaz, R., Caprio, E., Maggini, R., Pedrini, P., Rolando, A. et al. (2012) The altitudinal frontier in avian climate impact research. *Ibis*, **154**, 205–209.

Chamberlain, D.E., Negro, M., Caprio, E. & Rolando, A. (2013) Assessing the sensitivity of alpine birds to potential future changes in habitat and climate to inform management strategies. *Biological Conservation*, **167**, 127–135. https://doi.org/10.1016/j.biocon.2013.07.036

Chatterjee, S. & Hadi, A.S. (2006) *Regression analysis by example*, 4th edition. Hoboken, New Jersey: John Wiley & Sons, Inc. pp. 1–385.

Choler, P., Bayle, A., Carlson, B.Z., Randin, C., Filippa, G. & Cremonese, E. (2021) The tempo of greening in the European Alps: spatial variations on a common theme. *Global Change Biology*, **27**(21), 5614–5628.

Cisneros-Araujo, P., Goicolea, T., Mateo-Sánchez, M.C., García-Viñás, J.I., Marchamalo, M., Mercier, A. et al. (2021) The role of remote sensing data in habitat suitability and connectivity modeling: insights from the cantabrian brown bear. *Remote Sensing*, **13**(6), 1138.

Civco, D.L. (1989) Topographic normalization of Landsat thematic mapper digital imagery. *Photogrammetric Engineering and Remote Sensing*, **55**(9), 1303–1309.

Congedo, L. (2021) Semi-automatic classification plugin: a python tool for the download and processing of remote sensing images in QGIS. *Journal of Open Source Software*, **6**(64), 3172.

de Gabriel, H.M., Fernández-Gil, J., Roa, I., Juan, J., Ortega, F., de la Calzada, F. et al. (2021) Warming threatens habitat suitability and breeding occupancy of rear-edge alpine bird specialists. *Ecography*, **44**(8), 1191–1204.

Dormann, C.F., Schymanski, S.J., Cabral, J., Chuine, I., Graham, C., Hartig, F. et al. (2012) Correlation and process in species distribution models: bridging a dichotomy. *Journal of Biogeography*, **39**(12), 2119–2131.

Drusch, M., Del Bello, U., Carlier, S., Colin, O., Fernandez, V., Gascon, F. et al. (2012) Sentinel-2: ESA's optical high-resolution mission for GMES operational services. *Remote Sensing of Environment*, **120**, 25–36.

Engler, J.O., Stiels, D., Schidelko, K., Strubbe, D., Quillfeldt, P. & Brambilla, M. (2017) Avian SDMs: current state, challenges, and opportunities. *Journal of Avian Biology*, **48**, 1483–1504.

Fielding, A.H. & Bell, J.F. (1997) A review of methods for the assessment of prediction errors in conservation presence/absence models. *Environmental Conservation*, **24**(1), 38–49.

Fontana, F., Rixen, C., Jonas, T., Aberegg, G. & Wunderle, S. (2008) Alpine grassland phenology as seen in AVHRR, VEGETATION, and MODIS NDVI time series - a comparison with in situ measurements. *Sensors*, **8**(4), 2833–2853.

Guisan, A. & Zimmermann, N.E. (2000) Predictive habitat distribution models in ecology. *Ecological Modelling*, **135**(2–3), 147–186.

Hannah, L., Flint, L., Syphard, A.D., Moritz, M.A., Buckley, L.B. & McCullough, I.M. (2014) Fine-grain modeling of species' response to climate change: holdouts, stepping-stones, and microrefugia. *Trends in Ecology & Evolution*, **29**(7), 390–397.

Hayford, H.A., Gilman, S.E. & Carrington, E. (2015) Foraging behavior minimizes heat exposure in a complex thermal landscape. *Marine Ecology Progress Series*, **518**, 165–175.

He, K.S., Bradley, B.A., Cord, A.F., Rocchini, D., Tuanmu, M.N., Schmidtlein, S. et al. (2015) Will remote sensing shape the next generation of species distribution models? *Remote Sensing in Ecology and Conservation*, **1**(1), 4–18.

Heiniger, P.H. (1991) Anpassungsstrategien des Schneefinken (*Montifringilla nivalis*) an die extremen Umweltbedingungen des Hochgebirges. *Der Ornithologische Beobachter*, **88**(3), 193–207.

Hijmans, R.J., Van Etten, J., Cheng, J., Mattiuzzi, M., Sumner, M., Greenberg, J.A. . . . & Hijmans, M.R.J. (2020) raster: geographic data analysis and modeling. R package version 3.5-15. https://CRAN.R-project.org/package=raster

Hosmer, D.W., Lemeshow, S. & Sturdivant, R.X. (2013) *Applied logistic regression*, 3rd edition. Hoboken, New Jersey: John Wiley & Sons, Inc.

Huey, R.B., Kearney, M.R., Krockenberger, A., Holtum, J.A.M., Jess, M. & Williams, S.E. (2012) Predicting organismal vulnerability to climate warming: roles of behaviour, physiology and adaptation. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **367**(1596), 1665–1679.

Ion, P.G. & Kershaw, G.P. (1989) The selection of snowpatches as relief habitat by woodland caribou (*Rangifer tarandus caribou*), Macmillan Pass, Selwyn/Mackenzie Mountains, NWT, Canada. *Arctic and Alpine Research*, **21**(2), 203–211.

Jähnig, S., Alba, R., Vallino, C., Rosselli, D., Pittarello, M., Rolando, A. et al. (2018) The contribution of broadscale and finescale habitat structure to the distribution and diversity of birds in an alpine forest-shrub ecotone. *Journal of Ornithology*, **159**, 747–759.

Kauth, R.J. & Thomas, G. S. (1976) Purdue e-pubs the Tasselled cap-a graphic description of the spectral-temporal development of agricultural crops as seen by LANDSAT.

Kearney, M.R., Gillingham, P.K., Bramer, I., Duffy, J.P. & Maclean, I.M.D. (2020) A method for computing hourly, historical, terrain-corrected microclimate anywhere on earth. *Methods in Ecology and Evolution*, **11**(1), 38–43.

Kearney, M.R. & Porter, W.P. (2017) NicheMapR – an R package for biophysical modelling: the microclimate model. *Ecography*, **40**(5), 664–674.

Klein, G., Vitasse, Y., Rixen, C., Marty, C. & Rebetez, M. (2016) Shorter snow cover duration since 1970 in the Swiss Alps due to earlier snowmelt more than to later snow onset. *Climatic Change*, **139**(3–4), 637–649.

Laiolo, P., Dondero, F., Ciliento, E. & Rolando, A. (2004) Consequences of pastoral abandonment for the structure and diversity of the alpine avifauna. *Journal of Applied Ecology*, **41**(2), 294–304.

Leitão, P.J. & Santos, M.J. (2019) Improving models of species ecological niches: a remote sensing overview. *Frontiers in Ecology and Evolution*, **7**(JAN), 1–7.

Lenoir, J., Graae, B.J., Aarrestad, P.A., Alsos, I.G., Armbruster, W.S., Austrheim, G. et al. (2013) Local temperatures inferred from plant communities suggest strong spatial buffering of climate warming across northern Europe. *Global Change Biology*, **19**(5), 1470–1481.

Maclean, I.M.D., Mosedale, J.R. & Bennie, J.J. (2019) Microclima: an R package for modelling meso- and microclimate. *Methods in Ecology and Evolution*, **10**(2), 280–290.

Maggini, R., Lehmann, A., Zbinden, N., Zimmermann, N.E., Bolliger, J., Schröder, B. et al. (2014) Assessing species vulnerability to climate and land use change: the case of the Swiss breeding birds. *Diversity and Distributions*, **20**(6), 708–719.

Marcantonio, M., Iannacito, M., Marchetto, M., Thouverai, E., Da Re, D., Tattoni, C. et al. (2021) rasterdiv: diversity indices for numerical matrices.

Massimino, D., Beale, C.M., Suggitt, A.J., Crick, H.Q.P., Macgregor, N.A., Carroll, M.J. et al. (2020) Can microclimate offer refuge to an upland bird species under climate change? *Landscape Ecology*, **35**(9), 1907–1922.

Morales, M.B., Traba, J., Carriles, E., Delgado, M.P. & de la Morena, E.L.G. (2008) Sexual differences in microhabitat selection of breeding little bustards *Tetrax tetrax*: ecological segregation based on vegetation structure. *Acta Oecologica*, **34**(3), 345–353.

Moritz, C. & Agudo, R. (2013) The future of species under climate change: resilience or decline? *Science*, 341(6145), 504–508.

Nagendra, H., Lucas, R., Honrado, J.P., Jongman, R.H.G., Tarantino, C., Adamo, M. et al. (2013) Remote sensing for conservation monitoring: assessing protected areas, habitat extent, habitat condition, species diversity, and threats. *Ecological Indicators*, 33, 45–59.

Neteler, M., Bowman, M.H., Landa, M. & Metz, M. (2012) GRASS GIS: a multi-purpose open source GIS. *Environmental Modelling & Software*, 31, 124–130.

Oswald, K.N., Smit, B., Lee, A.T.K. & Cunningham, S.J. (2019) Behaviour of an alpine range-restricted species is described by interactions between microsite use and temperature. *Animal Behaviour*, 157, 177–187. https://doi.org/10.1016/j.anbehav.2019.09.006

Parmesan, C. & Yohe, G. (2003) A globally coherent fingerprint of climate change impacts across natural systems. *Nature*, 421(6918), 37–42.

Pateman, R.M., Thomas, C.D., Hayward, S.A.L. & Hill, J.K. (2016) Macro- and microclimatic interactions can drive variation in species' habitat associations. *Global Change Biology*, 22(2), 556–566.

Patthey, P., Signorell, N., Rotelli, L. & Arlettaz, R. (2012) Vegetation structural and compositional heterogeneity as a key feature in alpine black grouse microhabitat selection: conservation management implications. *European Journal of Wildlife Research*, 58(1), 59–70.

Pepin, N., Bradley, R.S., Diaz, H.F., Baraer, M., Caceres, E.B., Forsythe, N. et al. (2015) Elevation-dependent warming in mountain regions of the world. *Nature Climate Change*, 5, 424–430.

Pincebourde, S., Murdock, C.C., Vickers, M. & Sears, M.W. (2016) Fine-scale microclimatic variation can shape the responses of organisms to global change in both natural and urban environments. *Integrative and Comparative Biology*, 56(1), 45–61.

Potter, K.A., Arthur Woods, H. & Pincebourde, S. (2013) Microclimatic challenges in global change biology. *Global Change Biology*, 19(10), 2932–2939.

QGIS Development Team. (2018) QGIS Geographic Information System. QGIS geographic information system. Open Source Geospatial Foundation Project.

R Development Core Team. (2020) *A language and environment for statistical computing*. Vienna: R Foundation for Statistical Computing.

Randin, C.F., Ashcroft, M.B., Bolliger, J., Cavender-Bares, J., Coops, N.C., Dullinger, S. et al. (2020) Monitoring biodiversity in the Anthropocene using remote sensing in species distribution models. *Remote Sensing of Environment*, 239(December 2019), 111626. https://doi.org/10.1016/j.rse.2019.111626

Randin, C.F., Engler, R., Normand, S., Zappa, M., Zimmermann, N.E., Pearman, P.B. et al. (2009) Climate change and plant distribution: local models predict high-elevation persistence. *Global Change Biology*, 15(6), 1557–1569.

Resano-Mayor, J., Korner-Nievergelt, F., Vignali, S., Horrenberger, N., Barras, A.G., Braunisch, V. et al. (2019) Snow cover phenology is the main driver of foraging habitat selection for a high-alpine passerine during breeding: implications for species persistence in the face of climate change. *Biodiversity and Conservation*, 28(10), 2669–2685.

Rocchini, D., Balkenhol, N., Carter, G.A., Foody, G.M., Gillespie, T.W., He, K.S. et al. (2010) Remotely sensed spectral heterogeneity as a proxy of species diversity: recent advances and open challenges. *Ecological Informatics*, 5(5), 318–329. https://doi.org/10.1016/j.ecoinf.2010.06.001

Rocchini, D., Marcantonio, M. & Ricotta, C. (2017) Measuring Rao's Q diversity index from remote sensing: an open source solution. *Ecological Indicators*, 72, 234–238.

Rolando, A., Caprio, E., Rinaldi, E. & Ellena, I. (2007) The impact of high-altitude ski-runs on alpine grassland bird communities. *Journal of Applied Ecology*, 44(1), 210–219.

Rosvold, J. (2016) Perennial ice and snow-covered land as important ecosystems for birds and mammals. *Journal of Biogeography*, 43(1), 3–12.

Schaub, M., Martinez, N., Tagmann-Ioset, A., Weisshaupt, N., Maurer, M.L., Reichlin, T.S. et al. (2010) Patches of bare ground as a staple commodity for declining ground-foraging insectivorous farmland birds. *PLoS One*, 5(10), e13115.

Scherrer, D. & Körner, C. (2011) Topographically controlled thermal-habitat differentiation buffers alpine plant diversity against climate warming. *Journal of Biogeography*, 38(2), 406–416.

Scridel, D., Brambilla, M., Martin, K., Lehikoinen, A., Iemma, A., Matteo, A. et al. (2018) A review and meta-analysis of the effects of climate change on Holarctic mountain and upland bird populations. *Ibis*, 160(3), 489–515.

Seavy, N.E., Viers, J.H. & Wood, J.K. (2009) Riparian bird response to vegetation structure: a multiscale analysis using LiDAR measurements of canopy height. *Ecological Applications*, 19(7), 1848–1857.

Shi, T. & Xu, H. (2019) Derivation of tasseled cap transformation coefficients for Sentinel-2 MSI at-sensor reflectance data. *IEEE Journal of Selected Topics in Applied Earth Observations and Remote Sensing*, 12(10), 4038–4048.

Somme, L. (1989) Adaptations of terrestrial arthropods to the alpine environment. *Biological Reviews*, 64(4), 367–407.

Spooner, F.E.B., Pearson, R.G. & Freeman, R. (2018) Rapid warming is associated with population decline among terrestrial birds and mammals globally. *Global Change Biology*, 24(10), 4521–4531.

Stillman, R.A. & Simmons, V.L. (2006) Predicting the functional response of a farmland bird. *Functional Ecology*, 20(4), 723–730.

Stokes, A.W., Catry, P., Matthiopoulos, J., Boldenow, M., Clark, T.J., Guest, A. et al. (2021) Combining survey and

remotely sensed environmental data to estimate the habitat associations, abundance and distribution of breeding thin-billed prions *Pachyptila belcheri* and Wilson's storm-petrels *Oceanites oceanicus* on a South Atlantic tussac Island. *Polar Biology*, **44**(4), 809–821.

Suggitt, A.J., Wilson, R.J., Isaac, N.J.B.B., Beale, C.M., Auffret, A.G., August, T. et al. (2018) Extinction risk from climate change is reduced by microclimatic buffering. *Nature Climate Change*, **8**(8), 713–717.

Tapia, L., Regos, A., Gil-Carrera, A. & Domínguez, J. (2017) Unravelling the response of diurnal raptors to land use change in a highly dynamic landscape in northwestern Spain: an approach based on satellite earth observation data. *European Journal of Wildlife Research*, **63**(2), 40.

Tarquini, S., Vinci, S., Favalli, M., Doumaz, F., Fornaciai, A. & Nannipieri, L. (2012) Release of a 10-m-resolution DEM for the Italian territory: comparison with global-coverage DEMs and anaglyph-mode exploration via the web. *Computers & Geosciences*, **38**(1), 168–170. https://doi.org/10.1016/j.cageo.2011.04.018

Tayleur, C.M., Devictor, V., Gaüzère, P., Jonzén, N., Smith, H.G. & Lindström, Å. (2016) Regional variation in climate change winners and losers highlights the rapid loss of cold-dwelling species. *Diversity and Distributions*, **22**(4), 468–480.

Therneau, T.M. (2021) A package for survival analysis in R. Available from: https://cran.r-project.org/package=survival [Accessed 23rd September 2021].

Therneau, T.M., Grambsch, P.M. & Fleming, T.R. (1990) Martingale-based residuals for survival models. *Biometrika*, **77**(1), 147–160.

Valerio, F., Ferreira, E., Godinho, S., Pita, R., Mira, A., Fernandes, N. et al. (2020) Predicting microhabitat suitability for an endangered small mammal using Sentinel-2 data. *Remote Sensing*, **12**(3), 1–18.

Visinoni, L., Pernollet, C.A., Desmet, J.-F., Korner-Nievergelt, F. & Jenni, L. (2015) Microclimate and microhabitat selection by the alpine rock ptarmigan (*Lagopus muta helvetica*) during summer. *Journal für Ornithologie*, **156**(2), 407–417.

Wachob, D.G. (1996) The effect of thermal microclimate on foraging site selection by wintering mountain chickadees. *Condor*, **98**(1), 114–122.

Wang, G., Wang, C., Guo, Z., Dai, L., Wu, Y., Liu, H. et al. (2020) A multiscale approach to identifying spatiotemporal pattern of habitat selection for red-crowned cranes. *Science of the Total Environment*, **739**, 139980.

Zanotti, F., Endrizzi, S., Bertoldi, G. & Rigon, R. (2004) The GEOTOP snow module. *Hydrological Processes*, **18**(18), 3667–3679.

Zellweger, F., De Frenne, P., Lenoir, J., Rocchini, D. & Coomes, D. (2019) Advances in microclimate ecology arising from remote sensing. *Trends in Ecology & Evolution*, **34**, 327–341.

Zhang, X., Schaaf, C.B., Friedl, M.A., Strahler, A.H., Gao, F. & Hodges, J.C.F. (2002) MODIS tasseled cap transformation and its utility. *IEEE International Geoscience and Remote Sensing Symposium*, **2**, 1063–1065.

Supporting Information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Figure S1. The study area.
Figure S2. Graphical representation of the coefficients estimated for the variables included into the three most supported synthetic models.
Figure S3. The deviance residuals of the averaged synthetic model plotted against each variable included into it.
Figure S4. Boxplots of the remotely sensed values of NDVI, NDSI and SCI among the distance classes recorded on the field in 2017.
Figure S5. Boxplot of the variable Rao_TC (a remotely sensed measure of fine-scale landscape heterogeneity) over different distance classes recorded in the field in 2017.
Figure S6. Visual checking of consistency between on-field temperatures (recorded in 2017) and remotely sensed ones (maximum, mean, and minimum daily temperature, respectively in red, orange, and blue).
Table S1. Number of pairs and foraging locations recorded in the four study sites.
Table S2. Formulas used to derive the land-cover spectral indices from Sentinel-2 multispectral images.
Table S3. Overview of the occurrence data used in this study, splitted according to site, pairs' identity, and date of the survey (dates refers to the year 2017).
Table S4. Univariate models of all the variables analysed in this study, ranked by increasing values of BIC (the most supported models come first).
Text S1. Notes on the analytical workflow.
Text S2. Notes on modelling procedure.
Text S3. Notes on the results.