

# **8. Modelling Large-Scale Patterns in Mountain Bird Diversity and Distributions**

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## **8.1 Introduction**

Modelling distributions of species is a key task for modern ecologists. Species distribution models (SDMs), aimed at quantitatively identifying factors driving occurrence and/or characterizing ecological niches (Guisan & Thuiller 2005), have replaced the largely descriptive investigations that dominated the discipline previously. SDMs have also become a key method for making predictions, usually of species distributions, under different future scenarios of environmental change and as such are important in conservation planning (Rodríguez *et al.* 2007). Similarly, spatially explicit modelling of communities has gained importance in ecology and conservation, with a progressive shift from a simple characterization of richness and diversity, to more nuanced investigations assessing the variation of functional, ecological and other life-history traits in relation to environmental drivers or time (Villéger *et al.* 2011; White *et al.* 2018).

Distribution modelling over broad scales poses several challenges to researchers because of potentially altered equilibrium between distribution and environmental characteristics, resulting in non-stationarity in space and time (Guisan & Thuiller 2005), due to, for example, interspecific interactions, dispersal limitation, demographic dynamics, key resources not adequately represented in the available information, and several types of environmental filtering (Zurell 2017). Birds represent a particular challenge for distribution modelling (Engler *et al.* 2017). They are generally highly mobile, often displaying important seasonal changes in distributions and ecological niches (Ponti *et al.* 2020). Long-distance migrant species may be affected by the climate in their wintering and/or breeding areas, complicating the selection of factors influencing niches and therefore covariates used in distribution modelling (Eyres *et al.* 2017). They may also be subject to carry-over effects (conditions in one season that affect resources and/or survival in a subsequent season; Yu *et*

*al.* 2010; Frey *et al.* 2016a; Latimer & Zuckerberg 2020). Furthermore, bird species respond to environmental drivers at different and potentially multiple spatial scales. Large raptors regularly roam over thousands of hectares, often travelling over several kilometres (and different valleys in mountain regions) in a single day, whereas small passerines may spend all their breeding season within one thousand square meters (a difference of several orders of magnitude). In addition, habitat selection in many bird species is a multi-scale process (Jedlikowski *et al.* 2016); this could be particularly true for mountain birds exploiting a habitat encompassing three-dimensions (e.g., Brambilla *et al.* 2010). Many bird species may require different habitats for the acquisition of various resources (Brambilla & Saporetti 2014; D'Elia *et al.* 2015), further complicating the identification of the drivers of distribution. All of these issues result in complex decisions about the best scale(s) to use and lead to multi-scale approaches to modelling species distributions and communities (Mertes & Jetz 2018; Brambilla *et al.* 2019a; Goljani Amirkhiz *et al.* 2021).

The above complications are exacerbated in the case of mountain birds because of the characteristics of mountain ecosystems and the effects they have on such endothermic, mobile organisms (García-Navas *et al.* 2020). Endothermy allows birds to extend the range of temperatures they can tolerate. In particular, if resources are adequate, they can buffer against lower temperatures, which are particularly frequent in mountains. This implies that the limit of mountain bird distributions may be affected by resource availability, especially at the lowest extreme (Engler *et al.* 2017). High mobility enables species to exploit highly seasonal, almost ephemeral, habitats and resources in high elevation sites, and to cope with environments that are subject to marked and abrupt temporal variation (Barras *et al.* 2021a). Multi-scale habitat selection may involve several drivers that are difficult to identify along the steep environmental gradients of mountain ecosystems, determined by the interaction between climate, topography and habitat. Key factors such as temperature, wind, humidity and solar radiation vary over much finer scales than in most other ecosystems. Finally, the harsh conditions found in high-elevation areas have resulted in a mix of adaptations (Barve *et al.* 2021; Chapter 2) and plasticity of organisms inhabiting such 'extreme' habitats. Such difficult conditions, and especially the difficulty in accessing many mountain areas, also impede intensive sampling and data collection. The high mobility of birds, coupled with the complex interactions involving rapid turnover in vegetation, topography and micro-climate, make it difficult to collect data, but also to analyse them

with a high degree of confidence when it comes to modelling distributions, community characteristics and monitoring mountain birds over time.

In this chapter, we deal with crucial issues for modelling bird distribution and diversity in mountains. Given that modelling species distributions is often undertaken at fairly large spatial scales, we consider a broad definition of mountain habitats that can encompass all vegetation zones (see Chapter 1, Table 1.1). We discuss the role of environmental constraints at different scales, the importance of interactions between species and among drivers in impacting bird distributions, and the factors shaping bird communities. We point out the major challenges for modelling distributions and community structure. We keep a prevalent focus on temperate mountains, given that a specific chapter of the book is dedicated to tropical mountains (Chapter 9). We conclude by discussing potential solutions to the main challenges, implications for research and conservation, and future steps that could be envisioned to fill the remaining gaps in our knowledge of avian distribution and communities in mountain ecosystems.

## **8.2 Modelling Distributions of Mountain Birds**

### **8.2.1 Environmental Constraints**

Since the work of Alexander Humboldt (von Humboldt & Bonpland 1807), mountains have been used as model systems to study the geographical distributions of species, specifically with respect to ecological niches. Their steep environmental gradients enable examination of species range limits without the need to cover large geographical distances. These steep environmental gradients have conferred similar potential benefits to bird species under climate change, as the potential exists for birds to disperse to locations that become suitable in terms of environmental niche. Indeed, upward shifts in the distribution of both avian and non-avian species towards mountain summits have been widely observed across mountain ranges of the world (Sheldon *et al.* 2011; Neate-Clegg *et al.* 2021), even if a lack of tangible shifts is also frequent (Chapter 6). Furthermore, bird species distributions have often shifted more slowly than would be expected based on temperature change alone, likely because of other environmental constraints (Scridel *et al.* 2018).

Climate-envelope models relate species distributions to climatic (and often other environmental) variables and then project future distributions based on expected climate change over the coming decades (Thomas *et al.* 2004; Jantz *et al.* 2015; Scridel *et al.* 2021). Many of these models predict that mountain birds will lose habitat rapidly, and become imperilled under future climate warming as 'sky islands' shrink in size (Şekercioğlu *et al.* 2008, 2012). Shifting upslope often comes with the risk of extirpation or extinction, as habitat area shrinks with increasing shifts toward mountain peaks, although such effects vary according to the physical form of a mountain (Elsen & Tingley 2015; Chapter 6). The orientation and topographical complexity of mountains (concave 'bowls', convex 'mounds', gullies etc.) often results in complex thermal properties across elevations, with potential for 'microrefugia' that may buffer species from the effects of climate change, at least temporarily (Dobrowski 2011; Wolf *et al.* 2021). Therefore, species may not necessarily shift upwards under climate change – cooler patches may occur at lower elevations due to cold-air drainage (Pypker *et al.* 2007), or on pole-facing slopes where mountainsides receive less solar radiation due to shading (Feldmeir *et al.* 2020). This may lead to shifts toward 'cold spots' that are not necessarily upslope (Frey *et al.* 2016b). Distribution modelling of mountain birds should thus ideally include rather fine-scaled, temperature-relevant environmental information next to or instead of widely used, broader topographical variables serving as proxies for temperature (elevation, inclination, orientation).

Modelling the fundamental niche of a species, and thus its potential to adapt to changing climatic conditions, may be limited by the difficulty to approximate its 'true' fundamental niche as the current species distribution does not cover its overall climatic range. This may be due to species ranges moving more slowly than temperatures, e.g., due to site fidelity in many species. For long-lived species in particular, this may lead to an extinction debt at the trailing (retreating) edge of a species' niche (Devictor *et al.* 2008; Lehikoinen & Virkkala 2016). Furthermore, current species distribution is often limited by historical habitat loss or by former persecution, both of which lead to an underestimation of climate suitability for the species (Ratcliffe 2010; Brambilla *et al.* 2021).

Even when the fundamental niche is known, the capacity of bird species to follow it as the climate shifts will depend upon a number of important factors, few of which have been included in modelling efforts to date. First, the structural components of the habitat itself (e.g., forest type) must be present in the new area, otherwise nesting substrate or foraging

surfaces will not be available. Second, interspecific interactions may limit the capacity of species to move (Section 8.2.2). If a more dominant competitor already occupies the new niche locations, colonization may not occur. Finally, the species must have the capacity for *finding* new habitat as the climate shifts. Birds use a variety of behaviours to find new habitat during natal or breeding dispersal, with some approaches more effective than others. For instance, using personal experience can be time consuming (Danchin *et al.* 2004), in comparison to social information (i.e., using information about the breeding success of others), which can be a very efficient mechanism for finding habitat under changing conditions (Betts *et al.* 2008).

In species distribution modelling, the broad environmental gradients afforded by mountain landscapes allow sampling across wide ranges of both climatic and vegetation predictor variables. Incorporating the full climatic and vegetation niches of species is likely to make models more transferable to other regions and future time periods (Yates *et al.* 2018).

### **8.2.2 The Importance of Biotic Interactions**

Species distributions and abundances are not only shaped by abiotic (Burner *et al.* 2020), but also by biotic factors, which could significantly contribute to setting bird elevational range limits (e.g., Jankowski *et al.* 2013; Freeman *et al.* 2019). Interspecific interactions, such as competition, facilitation, prey availability or predation influence where species can persist and how abundant they are. Biotic interactions are, however, often neglected in SDMs (Guisan & Thuiller 2005; Zurell 2017). To obtain a better ecological understanding of spatial occurrence, it often makes sense to include the presence or absence (or probability of occurrence) of other species which are either advantageous or disadvantageous for the focal species. Some biotic interactions may involve food availability (e.g., earthworms for ring ouzel *Turdus torquatus*, Barras *et al.* 2021b), and providers of or competitors for a certain resource (e.g., common blackbirds *Turdus merula* as competitors for ring ouzels, von dem Bussche *et al.* 2008; woodpecker holes as nesting resources for different owl species, Heikkinen *et al.* 2007; Brambilla *et al.* 2020a). Interactions with potential predators may also be important. For example, in the boreal region, black grouse *Lyrurus tetrix* were more abundant further from nests of the northern goshawk *Accipiter gentilis*, a main predator

(Tornberg *et al.* 2016). However, the proportion of black grouse hens with broods was higher close to goshawk nests, indicating that they may also have an indirect facilitation effect on black grouse by reducing the number of corvids which prey on their nests.

Therefore, including biotic interactions in distribution models is of great importance for understanding the ecological responses of species and their spatial distribution. In mountain systems, these models may shed light on the factors that promote zonation and species replacement observed along elevational gradients, and allow inferences about the occurrence of interactions that are otherwise difficult to disclose (such as competition and facilitation). This is normally performed by correlative models fitting species distribution and environmental data with patterns of co-occurrence among species (Zurell 2017). These correlative models look for excesses (possibly indicating positive interactions such as facilitation or mutualism) and deficits in co-occurrence (possibly indicating negative interactions, such as competition or predation; Dorman *et al.* 2018). Excesses and deficits are normally established based on null models of species distribution following abiotic and habitat factors alone. Among correlative models, joint species distribution models (jSDMs) infer the role of species associations in the residuals of the model, after controlling for abiotic and habitat factors (Pollock *et al.* 2014).

Bastianelli *et al.* (2017) used jSDMs to study the influence of interspecific competition in determining the spatial turnover between two pipit species (water pipit *Anthus spinoletta* and tree pipit *A. trivialis*) and two bunting species (yellowhammer *Emberiza citrinella* and ortolan bunting *E. hortulana*) in the Cantabrian Mountains, each species pair being made up of one relatively high and one relatively low elevation species along the gradient. The jSDMs for pipits highlighted divergent climate and habitat requirements, but also negative correlations between species not explained by environmental variables. Evidence from modelling was then compared with experimental evidence of interference competition obtained by means of playback experiments, but no evidence of interspecific aggressiveness was found. The significant residual correlation of jSDMs therefore possibly reflected forms of competition other than direct interference, or the influence of unmeasured environmental predictors. The jSDMs for buntings indicated shared habitat preferences, but a possible limitation to dispersal as a cause of the parapatric distribution of these congeneric species.

As an alternative to jSDMs, the sources of variation in species abundance can be modelled by taking into account environmental suitability and the occupancy and detection probabilities of other species (e.g., N-mixture models; Joseph *et al.* 2009). Using this approach, Brambilla *et al.* (2020a) modelled the potential distributions of black woodpecker *Dryocopus martius*, boreal owl *Aegolius funereus*, tawny owl *Strix aluco* and Ural owl *Strix uralensis* in montane and subalpine forests of the entire region of the European Alps, and tested whether the spatial patterns of the more widespread species were shaped by interspecific interactions. Models revealed an effect of interspecific interactions on current species abundance, especially in boreal owl (positive effects of black woodpecker because boreal owls breed in woodpecker holes; negative effects of tawny owl, which can prey on boreal owls and compete with them for nest holes and prey). Climate change is altering the pattern of co-occurrence and hence the potential interspecific relationships. For example, boreal owl is predicted to share a greater proportion of its range with tawny owl in the future, especially due to the latter's expansion along the elevational gradient, mainly promoted by warming temperatures (Brambilla *et al.* 2020a).

All this evidence suggests that ignoring interspecific interactions could hamper the ability of SDMs to predict species distributions. There are limitations on the inferences about interactions that can be drawn from these methods, and fundamental problems remain. Patterns in species distributions and abundances can often be explained by factors that suggest different underlying processes. Without detailed knowledge of the processes occurring, or subsequent experiments to confirm the hypotheses suggested by correlative methods, it is often difficult, or even impossible, to distinguish between the effects of biotic interactions and those of environmental covariates not included in the model (Dormann *et al.* 2012, 2018).

### **8.2.3 Challenges in Quantifying Micro-climate and Microhabitat**

Although some mountain bird species have exhibited range shifts in response to climate change (Tingley *et al.* 2009), many species have not been observed to track their climatic niche by adjusting their spatial distributions (Neate-Clegg *et al.* 2021; Chapter 6). One hypothesis for this mismatch between bird-climate envelope predictions and observed responses is that the climate data used to define suitable envelopes are collected at

resolutions much coarser than those perceived and used by organisms in habitat selection (Plate 6, Storlie *et al.* 2014). Most temperature data are collected at scales  $10^4$ -fold larger than the territory sizes of focal organisms (Potter *et al.* 2013), and there is high potential for hidden micro-climate variation within broader regional patterns. This hidden microclimatic variation and its potential to affect distribution dynamics is often overlooked (Riddell *et al.* 2021), but is considered to be particularly relevant to mountain vertebrates. Additionally, lack of high-resolution climate data, particularly understory temperatures (Scherrer *et al.* 2011), has prohibited effective testing of the role of micro-climate in fine-scale distribution dynamics. In forests, measuring climate below the canopy is particularly important because this is the environment experienced by most bird species (Frey *et al.* 2016a) and likely has implications for their population trends (Betts *et al.* 2019).

Thankfully, micro-climate is increasingly quantified in population and community ecology studies of mountain landscapes (de Frenne *et al.* 2021). However, quantification of micro-climate involves substantial challenges. Because micro-climate is so variable, and can be driven by a host of variables including microtopography and forest structure (Plate 6), data loggers must be deployed in large numbers to enable spatial extrapolation of temperature and humidity variables. Data loggers are often relatively inexpensive, but the logistics of data download, storage and handling can be considerable. Recent advances indicate that micro-climate can be estimated even without extensive on-the-ground devices, by means of highly refined downscaling based on the information of fine-scale variation in solar radiation, albedo, vegetation, topography and coastal effects (Maclean *et al.* 2019; Kearney *et al.* 2020). If effective, such micro-climate modelling approaches could result in an explosion of new micro-climate studies that use existing long-term bird distribution or abundance data along with back-cast micro-climate predictions.

It is important to note that even studies that purportedly quantify micro-climate may not necessarily do so at scales relevant to the species or individuals under study. Frequently, loggers are deployed at a set level above the ground (e.g., 1.5 m; Frey *et al.* 2016b) which is not necessarily relevant to birds nesting or foraging either at ground level or in the canopy. Indeed, there is still substantial climatic variability even *within* the forest canopy if one considers tree cavities, sun spots and shaded areas that are available for highly mobile birds, thereby enabling a behavioural buffering against weather and climate conditions (Shaw & Flick 1999). Micro-loggers are already available to track the body temperatures and ambient



conditions surrounding the animal (air temperatures) for larger bird species (Kerr *et al.* 2004; Chmura *et al.* 2018). When it becomes available, such technology will shed new light on micro-climate habitat use by smaller birds. Other potential advances include use of thermal imaging to determine micro-climate availability in forests (Kim *et al.* 2018) along with radio-telemetry (Hadley & Betts 2009) to quantify habitat selection in relation to very fine-scale micro-climate features.

All these advances will also make it easier to investigate the short-term (i.e., within the same season) adjustments in species' distribution (Betts *et al.* 2008), with those occurring within the breeding season being of particular importance for conservation in hilly and mountain areas (Brambilla & Rubolini 2009). Likely because of the strong gradients and seasonality of mountain environments, within-season changes in local or regional distribution of breeding birds have been observed in forests (Frey *et al.* 2016a), meadows (Brambilla & Pedrini 2011) and along broad habitat gradients, spanning from subalpine forest to high-elevation alpine grassland and rocky habitats (Ceresa *et al.* 2020).

Finally, it will be important to link micro-climate use and bird distributions to key avian demographic stages such as reproduction and survival. To our knowledge, few, if any, studies have linked micro-climate use by mountain birds to overall population dynamics across space, but there are studies that relate it to some key demographic variables, highlighting, for example, that inclement weather may have varying stage-specific impacts on offspring development (and hence on breeding success) among alpine songbirds with diverging traits (de Zwaan *et al.* 2020). Long-term studies on avian population trends will also be hugely beneficial as they integrate these demographic parameters to address the direct and indirect effects of mountain climate change on bird populations (e.g., Strinella *et al.* 2020; Kim *et al.* 2022).

#### **8.2.4 Challenges and Opportunities for Modelling Distribution and Abundance in Mountain Birds**

Advances in the spatial, temporal and thematic resolution of remote sensing data may prove to be particularly useful for modelling mountain bird distributions in the future.

Mountain habitats can be snow covered for long periods, and frequent cloud cover can limit the collection of data with optical sensors from airborne or satellite platforms. High revisit

frequencies of satellite platforms are therefore particularly important to provide full data coverage to enable mapping of mountain habitats or the monitoring of changes in vegetation and phenology. Several recent and planned satellite missions have high revisit frequencies, high spatial resolutions and spectral channels suitable for mapping and monitoring vegetation (Feilhauer *et al.* 2013; Rapinel *et al.* 2019). High revisit frequencies should also result in greater availability of multi-temporal imagery in frequently cloud-covered areas. Furthermore, the reflectance of vegetation varies temporally due to changes in the chemical compositions of plants, the structure of the plant tissue and the structure of the canopy (Lillesand *et al.* 2008; Thenkabail *et al.* 2011). Such temporal variation can be captured by multi-temporal imagery and can improve the accuracy with which habitat classes can be mapped (Wakulinska & Marcinkowska-Ochtyra 2020). Studies using data from airborne or satellite platforms in upland and mountain habitats have already shown the potential for mapping vegetation at the high thematic and spatial resolutions relevant for bird distribution modelling (Bradter *et al.* 2011; Wakulinska & Marcinkowska-Ochtyra 2020).

Another potentially major limitation to species modelling is the lack of knowledge of how species are affected by ecological processes. Species distributions emerge from the underlying demographic processes determining reproduction, survival, immigration and emigration, which in turn are affected by abiotic and biotic conditions and interactions. Due to the often difficult logistics, the ecology of many mountain birds is less well studied compared to some species in more accessible regions (Chamberlain *et al.* 2012; Chapter 1).

Whether a lack of ecological knowledge limits the modelling of mountain bird distributions depends on the aim of the study. If the aim of modelling is to produce a map of the distribution or abundance of a species for the area and time in which sample data were collected (interpolation), incomplete knowledge of ecological processes does not necessarily result in less accurate mapping. Well-performing distribution maps can be produced by using spatial predictors to substitute unknown abiotic or biotic processes (Bahn & McGill 2007), for example using distance-based eigenvectors (Borcard & Legendre 2002; Dray *et al.* 2006). Therefore, mapping applications to facilitate conservation planning or prioritization can often produce the desired results despite some of the limitations highlighted above.

If the aim of the study is to identify ecological processes from observed patterns, a lack of ecological knowledge may hamper progress. As discussed above, selected covariates in

correlative analysis methods express associations, not necessarily causation (Dormann *et al.* 2012; Hawkins 2012). The realism of associations between a species and abiotic or biotic covariates suggested by models needs to be assessed through the filter of ecological knowledge or verified by independent experiments and are otherwise often better seen as suggested hypotheses of potential associations. Moreover, a lack of knowledge of relevant ecological processes can lead to specifying a covariate wrongly, for example at an incorrect spatial scale, which can lead to biased regression coefficients, and consequently biased conclusions, even if spatial models are used to eliminate residual spatial autocorrelation (de Knegt *et al.* 2010).

Lack of ecological knowledge can be a limitation for the increasingly important field of projecting distributions into the future, or to other areas (Wenger & Olden 2012; Urban *et al.* 2016; see below). Some other disciplines make greater use of process-based or mechanistic models avoiding the limitations of correlative approaches. However, they require comprehensive ecological knowledge and population data (Urban *et al.* 2016; Singer *et al.* 2018), often acquired from intensive studies. Usually, such intensive data collection is less feasible in logistically challenging mountain areas.

### **8.3 Modelling Bird Diversity in Mountains**

Many fundamental concepts of ecology, biogeography and evolution, such as species richness-environment relationships, species turnover across life zones and speciation, originate from models of species diversity in montane regions, often with birds as the target system (McCain 2009). Modelling diversity serves two major functions (Scheiner *et al.* 2011). The first is to produce quantitative estimations related to  $\alpha$ -,  $\beta$ - and/or  $\gamma$ -diversity for descriptive comparisons, for instance among different mountain chains, habitats or time periods. The second is to explore the causes of different diversity patterns, i.e., to understand the ecological, stochastic and historical processes underlying diversity relationships. Linking diversity metrics to environmental and climatic parameters is key to understanding changes in avian communities in response to climate and habitat changes, providing further insights into the understanding of biodiversity drivers in mountains, and providing knowledge complementary to that relative to species distributions for

conservation. Modelling diversity in a mountain environment requires disentangling the complex interactions among drivers along the elevational and topographical gradients.

Species richness, a common measure of bird diversity, is estimated as the number of species for a particular spatial or temporal grain. It generally shows a monotonic decline with elevation, reflecting the effect of temperature and productivity on species abundance (Laiolo *et al.* 2018). The grain and the sampling design can have important effects on the observed patterns, and should be formulated *a priori* to respond to different questions. Here, we will focus on the conceptual and methodological aspects of diversity modelling. The methods used for field sampling may also affect results, an issue that is dealt with in Box 8.1. The spatial decomposition of species richness into  $\alpha$ -,  $\beta$ - and  $\gamma$ -diversity has been the subject of a rich literature (Whittaker 1960; Tuomisto 2010). Briefly,  $\alpha$ -diversity refers to the diversity of local communities and  $\gamma$ -diversity to the total species diversity of all local communities.  $\beta$ -diversity encompasses many aspects of compositional heterogeneity, from species turnover to community nestedness (Anderson *et al.* 2011; Tuomisto 2010).

### Box 8.1 *Collecting and analysing observations of birds in mountain regions*

Modelling the distribution and diversity of species requires data on the occurrence or abundance of species, often over large areas. Many countries collect data each year through systematic bird monitoring programmes that follow specific survey designs and protocols to produce representative and comparable data, specifying when, what, where, how, and how often, to survey and to report (Chapter 5).

National bird monitoring protocols may be tailored to the specific requirements and logistical challenges of a country, but mountain ranges are often shared by multiple countries. Differences across national survey protocols can include the recording units (pairs or individuals) or the survey type (point count stations or line transects). A simple way to analyse data collected with different protocols is to degrade the data to a common standard, such as conversion from counts to the detection or non-detection of a species. However, this involves the loss of potentially valuable information. Alternatively, modelling methods can increasingly account for differences in data characteristics (Bowler *et al.* 2019; Isaac *et al.* 2020).

An alternative type of data comprises species observations collected without a survey protocol. Such opportunistic data are often referred to as Citizen Science data, although this term may also refer to systematic data collected by volunteers. Opportunistic data are increasingly available for regions and species for which little or no systematic data exist (Hochachka *et al.* 2012; Amano *et al.* 2016). Common breeding bird monitoring programmes often collect relatively little data for rarer species or those occurring in localized areas. On the other hand, bird watchers are often particularly interested in the rarer species. For example, for the Eurasian dotterel *Charadrius morinellus* in Norway (Fig. B8.1), the number of records from the Norwegian breeding bird monitoring programme Norsk hekkefugloverbvåking (co-ordinated by the Norwegian Institute for Nature Research and BirdLife Norway) is small (309 records) compared to records available from the Norwegian Citizen Science portal Artsobservasjoner during the same time period (c. 1250 records for the period 1<sup>st</sup> June – 10<sup>th</sup> July 2006 – 2020).

Opportunistic data may reflect large variation in recording intensity in time and space, and in observer skills, and often are spatially biased towards areas that are easily accessible or popular (Mair & Ruete 2016; Tye *et al.* 2017). Species records may have

complementary information on species non-detections and recording intensity, or may be unstructured without this information (Sullivan *et al.* 2009). Appropriate data preparation and modelling increasingly account for the challenges of opportunistic data (Jackson *et al.* 2015; Bradter *et al.* 2018; Johnston *et al.* 2018, 2021). Additionally, methods to model jointly systematic and opportunistic data to combine the strengths of both are being developed (Fithian *et al.* 2015; Fletcher *et al.* 2019). Habitat suitability is commonly modelled based on unstructured detection-only records with presence-background methods such as MaxEnt (Phillips *et al.* 2006; Elith *et al.* 2011; Yackulic *et al.* 2013). However, the inclusion of species non-detection data is preferable (Royle *et al.* 2012; Bradter *et al.* 2018, 2021; Johnston *et al.* 2021). Occurrence probability can only be estimated from detection-only data if randomly sampled in space, and from detections paired with the background or non-detections if the data reflect the prevalence of the species (Elith *et al.* 2006; Royle *et al.* 2012). Occupancy models can account for imperfect detection in both systematic and opportunistic data, but require repeat observations and suitable information on the reporting intensity to account for the reporting bias of opportunistic data (MacKenzie *et al.* 2003; Kéry *et al.* 2010a, b; Isaac *et al.* 2014; Bradter *et al.* 2021).



*Figure B8.1* Eurasian dotterel  
*Charadrius morinellus* (Photo: Ute  
Bradter).

The definitions above are suited to species richness data, but may also include variation beyond this component of diversity. Diversity descriptors can be calculated by weighting the contribution of each species to richness by its abundance, biomass or other adaptive phenotypic traits, or by phylogenetic relatedness. These functional and phylogenetic facets of diversity, reflecting, respectively, the diversity of morphological, physiological and ecological traits, and the diversity of biogeographic histories, have been

used to predict biodiversity contributions to ecosystem functions. Models assume, for instance, that functional diversity equates to resource use complementarity, so that differences in how species gain resources is the variation represented by functional diversity (Petchey & Gaston 2002). Foraging birds exert important ecosystem functions (e.g., seed dispersal by frugivorous birds; pest control by insectivorous birds and birds of prey, nutrient recycling by avian scavengers), thus bird functional diversity can represent the diversity of services birds can provide, and be associated with their economic value (Şekercioğlu *et al.* 2016). Quantifying these metrics may serve to track temporal changes in bird functional contributions to the (alpine) ecosystem (García-Navas *et al.* 2020), or the occurrence of spatial or habitat barriers to specific bird functions (Altamirano *et al.* 2020), and geographic patterns of phylogenetic and functional structure of bird communities (Boyce *et al.* 2019). Notably, scale can also affect results when evaluating functional traits (Laiolo *et al.* 2017).

## **8.4 Assessing and Predicting Impacts of Environmental Changes and Implications for Conservation**

### **8.4.1 Working with Relevant Scales and Drivers**

The widespread occurrence of steep gradients in mountains represents a challenge in modelling bird distributions at high elevation. In part, this is due to restrictions on data availability at appropriate spatial and temporal scales (Section 8.2.3), but also due to the high mobility and multi-scale habitat selection of birds. Distribution models integrating multiple scales could help identify the individual spatial scales at which the ecological responses by mountain birds are most likely (Mertes & Jetz 2018; Brambilla *et al.* 2019a). Nevertheless, approaches based on univariate evaluation of the scale-dependency in the effect of single predictors may lead to a partial or an incorrect view of their ecological and spatial relevance (Brambilla *et al.* 2020b). Here, the use of PCA-based methods (Bettega *et al.* 2020) or multi-scale approaches (e.g., Bradter *et al.* 2013) may help. For some species that require different resources for different purposes, the use of approaches based on the partition of the ecological niche into functional habitats may greatly help both modelling and conservation (Brambilla & Saporetti 2014; D'Elia *et al.* 2015). However, detailed data

allowing such an approach are rarely available. When high-resolution data are available, in terms of the accuracy and spatial and temporal precision of bird records, microhabitat and micro-climate modelling may provide more direct 'mechanistic' assessments of habitat use by mountain birds (e.g., Frey *et al.* 2016a; Barras *et al.* 2020), allowing deeper insights into species' ecology. Assessing the effect of distribution drivers at the relevant scale is key to identifying robust relationships (e.g., de Knecht *et al.* 2010), and for obtaining meaningful model extrapolations to other geographical or temporal contexts. The covariation of climate and other, sometimes more direct, environmental traits may lead to an overestimation of the importance of climate, and this risk likely grows as the discrepancy increases between the spatial scale at which a predictor is evaluated (and entered into models) and the scale at which it actually affects a species. Large-scale evaluation of climatic drivers of occurrence or distribution in mountain birds, based on environmental predictors measured over sample units of several square kilometres, is unlikely to capture accurately the true nature of species-climate relationships, with consequences for estimates of potential future impacts of climate change (Trivedi *et al.* 2008; Randin *et al.* 2009; Meineri & Hylander 2017). Assessments over different spatial scales may be needed to pinpoint robust, causal effects, or alternatively to identify (and hence discard) non-causal, indirect impacts of other potential drivers of occurrence.

Scale is an essential feature when assessing species-environment relationships, as these are often relevant only at particular spatial scales, especially in birds (e.g., Jedlikowski *et al.* 2016). Direct effects of climatic features on species should be consistent across all, or most, spatial scales. For indirect associations between a species and climate, the modelled species-variable relationships are much more likely to show scale-dependent variations (Brambilla *et al.* 2019a). Furthermore, species-specific differences in the relevance of spatial scales may also complicate the use of jSDMs, where variables are considered over the same scale(s) for all species. For a species for which a direct effect of a climatic predictor could be expected, the modelled effects should be consistent across scales, and the predictions well outside the study area should be accurate (as for the white-winged snowfinch *Montifringilla nivalis*, Box 8.2).



### Box 8.2 *Modelling the ecology and distribution of the white-winged snowfinch*

For some species particularly adapted to cold, high-elevation habitats, the link with climatic parameters (especially with temperature) and climate-sensitive habitats and resources may be evident through different spatial scales (Brambilla *et al.* 2019a). In recent years, the white-winged snowfinch is likely one of the species that has gathered the highest interest of ornithologists studying the impacts of climate change on mountain birds in the Old World. Several research initiatives have addressed habitat selection and habitat use over different spatial scales, breeding phenology, demography, social behaviour and distribution at regional and continental (European) scales.

Fine-scaled models describing habitat use during the critical nestling-rearing phase have revealed an association with snow patches (Brambilla *et al.* 2017a, 2019b; Resano-Mayor *et al.* 2019; Schano *et al.* 2021) and other climate-sensitive habitats, such as low-sward alpine grassland (Brambilla *et al.* 2018a, b). Microhabitat selection has also been shown to be affected by micro-climate, with foraging individuals adjusting habitat use according to air temperature (Alessandrini *et al.* 2022). All of these results have provided support for fine-scale associations with rather cold habitats which are perfectly mirrored at a larger scale by consistent effects of temperature on the broad species distribution: models developed at different spatial scales, from a 100 m radius to 2 x 2 km cells, have revealed a consistent link with low temperature (Brambilla *et al.* 2020c; de Gabriel-Hernando *et al.* 2021), which remained constant outside the areas used for model calibration (Brambilla *et al.* 2016, 2017b), to the point that distribution models performed well even when projected to distant areas (Brambilla *et al.* 2022).

Adult survival was also found to be affected by climate, with female mortality increasing during warm and dry summers (Strinella *et al.* 2020). Snowfinch ecology and behaviour also appear to be particularly related to temperature outside the breeding season (Bettega *et al.* 2020; de Gabriel-Hernando *et al.* 2021; Delgado *et al.* 2021). The use of fine-tuned, presence-background models based on heterogeneous data sources (a combination of research data and Citizen Science) proved successful in predicting the white-winged snowfinch distribution across its European range (Brambilla *et al.* 2020c).



Figure B8.2 White-winged snowfinches *Montifringilla nivalis* (Photo: Mattia Brambilla).

For territorial species during the breeding season, the territory scale is likely to be a highly relevant scale, because territory holders need to find many relevant resources within the limited area that they actively defend and exploit (Jedlikowski *et al.* 2016). Studies working at such a scale based on high-resolution records have provided biologically reliable and ecologically relevant results for birds in complex mountain habitats (e.g., Chamberlain *et al.* 2013, 2016; Brambilla *et al.* 2016; Jähnig *et al.* 2018; Barras *et al.* 2021b), but could still miss some potentially relevant ecological patterns taking place at other scales (Lenoir *et al.* 2017). Integrating micro-climate/microhabitat measurements with downscaled macroclimate/macrophabitat patterns would likely provide a definitive perspective for the analysis of species-environment relationships, with relevant implications for modelling distributions and the relative dynamics of communities (Zellweger *et al.* 2019).

The temporally dynamic nature of mountain bird communities and habitats also present a challenge to modelling. Communities vary in their composition and structure not only within the year, but also within the breeding season, because of the progressive settlement of species with different phenologies: as an example, at high elevation in the European Alps, rock ptarmigan *Lagopus muta* may initiate territoriality at the beginning of April, while several songbirds do not occupy their breeding sites before mid-May, or even later in the case of prolonged snow cover. This means that for community studies, it is essential to focus on the most relevant breeding season period, within which all the breeding species are likely to have settled and before species enter their post-breeding phase. The use of data from

multiple years may contribute to overcoming limitations due to dynamic patterns resulting from short-term responses to varying environmental conditions when pairing avian data with climatic predictors. Nevertheless, matching as precisely as possible bird and climate data would provide more accurate and robust insights into the potential effects and importance of climatic predictors (Lembrechts *et al.* 2019; Perez-Navarro *et al.* 2021; Section 8.2.3). The increasing availability of spatially and temporally accurate datasets and methods for local estimation of micro-climate (Hannah *et al.* 2014; Kearney *et al.* 2020) would definitely promote accuracy in distribution modelling (He *et al.* 2015; Lembrechts *et al.* 2018). Scaling-up from fine-scale to regional or even macroecological levels is particularly important for birds in mountain regions, for all the previously mentioned reasons. We likely need to capitalize on the continuous spatio-temporal information that remote sensing provides for many factors key to avian distribution (Randin *et al.* 2020). The occurrence and hence distribution of many mountain bird species is affected simultaneously by climatic, topographic, land-cover and biotic interactions (Braunisch *et al.* 2014; Barras *et al.* 2021b; Chamberlain *et al.* 2016; Brambilla *et al.* 2020a, b). A proper evaluation of relevant environmental predictors is crucial to understand the impact of global change: if a relevant driver is not taken into account, then the importance of the others could be overestimated, and their effect inaccurately modelled.

A first requirement for correctly modelling the effects of determinants of species distribution or abundance in complex mountain environments is therefore to consider simultaneously the potential impact of multiple drivers. More advanced approaches causally link the effect of micro-climate and vegetation by means of structural equation modelling (Duclos *et al.* 2019), disentangling the direct effects of climate from those mediated by the vegetation characteristics, which are largely affected by climate. There are only a few studies that explicitly aim to disentangle the direct impacts of climate on birds (e.g., by effects on habitat selection, phenology or thermoregulatory behaviour) from the indirect impacts, especially through the effect of climate on habitat via an impact on vegetation compositional and structural features. As an example, Ceresa *et al.* (2021) showed the predominant effect of vegetation over temperature for several species along an elevation gradient in the Alps. This approach is important because species distribution changes and shifts in elevation can be due to climate tracking in the case of direct effects, or to habitat tracking in the case of indirect effects. In addition, there may also be synergies between

direct and indirect effects. This has obvious implications for our understanding of ongoing and future changes; studies considering the unique and synergistic effects of climate and land-use changes will better predict variation in abundance of several species than of climate alone (e.g., Betts *et al.* 2019). These synergistic effects could be particularly relevant for mountain birds.

#### **8.4.2 Possible Reasons for Deviations of SDMs from Observed Patterns in the Real World**

SDMs have proved to be an important tool for many real-world applications, providing useful information for fieldwork, conservation, evaluation of potential interactions, and predictions of range variations, among others (Engler *et al.* 2017), and of course this is also the case for mountain birds. However, being models, SDMs may sometimes diverge from the 'true' distribution (i.e., observed patterns in the real world). Thorough model evaluation should be part of any SDM project. Model evaluation regarding realism, accuracy and generality is a broad research field (Araújo *et al.* 2019), which goes beyond the scope of this chapter. We refer the reader to specific literature (Araujo & Guisan 2006; Fourcade *et al.* 2018).

There are several possible reasons why predicted distributions may diverge from observed patterns in the field: inappropriately chosen variables for particular species, both in terms of predictors and responses; the wrong spatial or temporal scale; species that are in a non-equilibrium state with their environment; and, spatial autocorrelation. Such divergence may have implications for the potential use of SDMs for conservation, planning and research, and hence understanding some of the causes of divergence may be useful to improve our ability in modelling mountain bird distributions. In the following, we explore several potential solutions to the above issues, which we consider particularly relevant for mountain birds.

##### *Species-specific environmental variables*

Poor model performance may arise due to inappropriate environmental input variables for a given species, in particular when the same set of variables is applied across all species. Interactions are also important. For predictive studies, information on expected (i.e., modelled) climate change and land-use change needs to be integrated (Sirami *et al.* 2017;

Vincent *et al.* 2019). Direct, physiological effects of climate change may be altered indirectly by (possibly less-responsive) habitat variables (Braunisch *et al.* 2014; Crase *et al.* 2014), such as lagged treeline shifts (Gehrig-Fasel *et al.* 2007; Duclos *et al.* 2019).

The development of species-specific habitat variables has not always received sufficient attention. Sometimes, the selection of habitat variables is driven simply by their availability in (accessible) databases (Araujo & Guisan 2006; Braunisch *et al.* 2013). In most cases, and especially when aiming for an ecological understanding of the distribution rather than for a descriptive pattern, SDMs profit from the inclusion of species-specific variables (Mod *et al.* 2016), and this could be particularly true in the case of mountain birds. As an example, the distribution of ring ouzel in Switzerland is affected not only by climate and land-cover, but also by low-productivity pasture and the number of solitary trees (Barras *et al.* 2021b). Brambilla *et al.* (2020c) found that, depending on species, next to climate and habitat, human management may be important to model species adequately, with red-backed shrike *Lanius collurio* and Eurasian skylark *Alauda arvensis* being sensitive to the occurrence of grazing and ski-pistes, respectively, in mountain grassland in central Italy.

The development of species-specific variables may be challenging, but they are essential to ecologically understand (also in a quantitative way) the factors determining the distribution of species (Fourcade *et al.* 2018). For mountain birds, this can include grassland type (Hotta *et al.* 2019) or the progress of melting of snow fields as a surrogate for food availability (Tipulidae larvae for white-winged snowfinch, Resano-Mayor *et al.* 2019; earthworms for ring ouzel, Barras *et al.* 2021b). Also, environmental variables specific to periods other than the breeding season may be relevant (de Gabriel Hernando *et al.* 2021), including human disturbance in winter (e.g., black grouse and winter outdoor sports; Braunisch *et al.* 2011).

#### *Novel remote sensing environmental data*

Remote sensing has provided new environmental data (e.g., satellite images) that are helpful to distinguish new habitats (He *et al.* 2015; Randin *et al.* 2020), and to model the distributions of mountain birds (e.g., rock ptarmigan in Austria, Zohmann *et al.* 2013), down to very fine scales. As an example, Alessandrini *et al.* (2022) evaluated foraging habitat selection in white-winged snowfinches, highlighting a preference for intermediate vegetation cover, snow patches and higher heterogeneity, and an avoidance of extremely

warm or cold micro-climates. Results matched previous knowledge based on accurate field measurements, and highlighted behavioural buffering against 'hot' conditions. Air-borne lidar-data has great potential to get novel spatial information on habitat structure, and has important explanatory power in SDMs (e.g., in mountain forest birds; Zellweger *et al.* 2013; Huber *et al.* 2016). Such data may also help model three-dimensional habitats, e.g., species breeding in rocky habitats (Brambilla *et al.* 2010). Often, satellite data are provided to global databases, meaning they are particularly helpful for studies encompassing many countries (He *et al.* 2015).

#### *Finer scales of resolution*

Fine-grained, ecologically functional species-habitat relationships are particularly valuable in a mountain context where environmental conditions change markedly over small spatial scales (e.g., Barras *et al.* 2021b). Sun-exposed and pole-facing slopes may be very different, but there are also less evident (but still important) habitat changes for mountain birds induced by topography or geology. Grain size of spatial models can be decisive in determining which environmental variables are important for the distribution of a species (Guisan *et al.* 2007; Brambilla *et al.* 2019a), and modelling may be useful to better understand spatial patterns (Jombart *et al.* 2009; Reverbmann *et al.* 2012). Fine-scaled modelling approaches, e.g., at the territory scale (Hotta *et al.* 2019; Barras *et al.* 2021a), shed additional light on species-environment relationships and species interactions.

#### *Non-equilibrium state with the environment*

SDMs assume that a species occupies its environmental niche wherever this niche is present. However, empirical studies show that this equilibrium state with the environment is the exception rather than the norm (Araujo & Pearson 2005). Species may be in a non-equilibrium state with their environment for multiple reasons (Ewing *et al.* 2020), with some populations in their breeding range limited by drivers other than environmental factors. Populations may be in decline due to deteriorating habitat on migration or overwintering areas (Vickery *et al.* 2014, Zurell *et al.* 2018; Marcacci *et al.* 2020), hunting or persecution (Pernollet *et al.* 2015), diseases or additional factors. On the contrary, species in a non-equilibrium state may have undergone a population decline in the past for any of the above-mentioned reasons and are now recovering, i.e., a species has an expanding population that

has not yet occupied all suitable habitat (e.g., bearded vulture *Gypaetus barbatus*; Hirzel *et al.* 2004; Schaub *et al.* 2009; Margalida *et al.* 2020). Additionally, in many cases, missing important environmental (habitat) variables that describe the spatial patterns of species may also add to a non-equilibrium model.

#### *Spatial autocorrelation*

Spatial autocorrelation is inherent in most ecological data and the effects of ignoring it in SDMs has received considerable attention (Segurado *et al.* 2006; Dormann 2007; Guélat & Kéry 2018). Five categories of factors can drive the presence of spatial autocorrelation in model residuals: ecological data and processes, scale and distance, missing variables, sampling design, and assumptions and methodological approaches (Gaspard *et al.* 2019). Considering spatial variables (e.g., Moran's eigenvectors maps) that account for spatial autocorrelation may be of particular importance when modelling future climate impacts (Cruse *et al.* 2014) and failure to include them may have dramatic effects (Guélat & Kéry 2018). Conditional autoregressive (CAR) models (Besag *et al.* 1991) and ge additive models (Kammann & Wand 2003), which use splines to model spatial structure, have performed well in complex simulations (Guélat & Kéry 2018). Recently, penalized 2D splines were successfully implemented to model spatial autocorrelation both in regional (Knaus *et al.* 2018) and continental (Keller *et al.* 2020) bird distribution atlases that included many mountain birds. Including such spatial variables in modelling may account for missing environmental variables, although whether this is desirable depends on specific study goals. Modelling the spatial structure (i.e., considering spatial autocorrelation) might be a feature required by atlas projects which aim mainly to describe the distributional patterns found in the field. Studies aimed at understanding the spatial ecology of species should possibly try to generate species-specific environmental variables rather than spatial variables for their models. This is especially true when studies are focussed on species conservation and/or the development of management strategies (Hoffmann *et al.* 2015; Brambilla *et al.* 2017b, 2020b). In these cases, model transferability would be highly relevant to ensure likely effectiveness over broader scales.

#### **8.4.3 Implications for Predicting Future Changes**

Climate envelope models (Section 8.2.1) explicitly or implicitly assume niche conservatism (i.e., the ecological niche of the species does not change with time). In addition to the issues relating to distribution modelling already noted (e.g., Sections 8.2.3 and 8.4.2), such an approach is also underpinned by various assumptions about whether or not species will be able to keep pace with niche shifts. Although climate envelope models have been successful to some degree in predicting bird species range shifts in mountains and across latitudes (Illán *et al.* 2014), predictions do not always correlate well with observed trends (Betts *et al.* 2019). These 'fall-downs' in model prediction success may have severe consequences for species conservation planning as the climate changes, thus identification of priority areas or candidate species may be flawed.

How can models that predict the fate of birds in mountain landscapes under climate and land-use change be improved? The sections above have foreshadowed the suggestions here. First, modelling bird responses to climate change will need to include more of the key non-environmental, biological parameters known to influence species distributions and demography. Particularly important will be models that incorporate information about the distributions of competitors, mutualists and other elements of the biotic environment. New jSDMs are now available to incorporate these aspects, but a number of important challenges remain (Poggiato *et al.* 2021). Dispersal and habitat selection are also critical parameters to include in order to enable more accurate forecasting of avian distributions under climate change. 'Process-based' models that incorporate dispersal have been available for some time (Morin *et al.* 2007). Models that account for imperfect detection, including dynamic occupancy models (MacKenzie *et al.* 2003), open-population Dail-Madsen models (Dynamic N-mixture Models; Dail & Madsen 2011; Hostetler & Chandler 2015) and multi-state dynamic occupancy models (MacKenzie *et al.* 2009) are often used to explicitly include population processes. Some of these would allow for the spatially explicit modelling of dispersal processes (Sutherland *et al.* 2014; Broms *et al.* 2016). These models were developed to model dynamic processes in abundance and occurrence of unmarked populations, hence they have their own limitations for estimating demographic parameters that would be available from a marked population study (i.e., true mortality/survival, fecundity, immigration and emigration). More recent developments even enable emigration to be distinguished from survival and reproduction, although restrictive assumptions about dispersal capability remain (Zhao *et al.* 2017). Given the wide range of uncertainty about the



scale(s) and drivers associated with bird dispersal and other demographic processes, such highly parameterized models can still be a challenge to produce for many species, particularly migratory species. Only now are we seeing the first models that incorporate changes in habitat and climate across the full annual cycle (breeding, migration and wintering locations; Culp *et al.* 2017; Rushing *et al.* 2020). The ecology of natal dispersal and breeding dispersal processes of long-distance migrant species remains as a big gap in our knowledge of population processes for many smaller migratory species.

Increasing accessibility to Bayesian approaches, combined with developments in hierarchical, multilevel models, would open more windows for explicitly modelling processes that could improve prediction for occupancy or abundance of mountain birds in the future (Kéry & Royle 2015, 2020). Nevertheless, these 'mechanistic' or 'process-based' models would require well-thought designs that can address the potential biases and errors associated with mountain environments. Additional field data collection is critical for improved analysis of relationships between distributions of mountain bird species and the ecological processes that drive them, and hence better predictions. In this context, elevational gradients are crucial to predict the effect of climate change, as they provide a potential space-for-time substitution, which is frequently needed because of the widespread lack of historical data to determine rates of change in elevational distributions. Of course, such space-for-time data come with the assumption that mechanisms operating across space adequately reflect the same mechanisms over time.

A robust approach must therefore include, as some of its irreplaceable features:

1. elevational gradients and microtopography (i.e., aspect, slope, elevational position), along with other variables of interest, such as vegetation and micro-climate;
2. the temporal gradient, as the phenology of plants and animals in the mountain environment changes along the elevational gradient and across different topographies;
3. stratified sampling to take into account potential biases, elevation and topography;
4. the interactions among species and among biotic and abiotic environmental drivers;
5. a range of climate change and land-cover change scenarios, which would be necessary to predict potential range change and available habitat change in the future.

#### **8.4.4 Implications for Conservation**

Distribution, habitat and community modelling are powerful tools for conservationists. However, as described in this chapter, the complexities and challenges of modelling avian species in mountains make the use of such tools potentially more difficult in these environments and call for additional caution. Evaluating the ecological realism of models and their transferability over independent data (ideally, distant areas) may give indications about their potential reliability and robustness in the face of the complexities that characterize mountain systems. Reliable models should show both realistic evaluations of the species-environment relationships and the ability to predict distributions based on independent data. Such models are likely to be the most useful to predict distributions under different scenarios (e.g., future climates) and hence for conservation, when it comes to identify potential climate refugia (Brambilla *et al.* 2022) or future conflicts with human activities (Brambilla *et al.* 2016). Disentangling the effects of climate and other environmental changes is very important (Ceresa *et al.* 2021), not only for modelling and predicting current and future impacts, but also for conservation-oriented management of mountain environments, because climate change is a particular concern for mountain ecosystems (Nogués-Bravo *et al.* 2007). Long-term monitoring data can help distinguish the effects of climate change from other environmental changes. If birds are tracking habitat rather than climate, then *ad hoc* habitat management (e.g., Brambilla *et al.* 2018a) or targeted habitat conservation or restoration (e.g., Braunisch *et al.* 2016) may greatly enhance their persistence probabilities under a changing climate. However, if birds are mostly affected by climate, modelling trends of relevant climatic variables becomes crucial to conservation because of their direct effect (e.g., impact of heat waves on model species and the non-uniform spatio-temporal patterns at the regional scale, Cunningham *et al.* 2013).

Scales also matter: if micro-climate and microhabitats play a crucial role in driving distributions of mountain species (e.g., Frey *et al.* 2016b; Ceresa *et al.* 2020), fostering generalizable models at fine scales could promote conservation too, by allowing the identification of the characteristics (and their spatial arrangement) that make a site suitable for a species (e.g., Barras *et al.* 2020; Alessandrini *et al.* 2022). On the other hand, at the landscape level, potential climate refugia (Morelli *et al.* 2020), and the main 'corridors' connecting them from current to future occurrence sites (Brambilla *et al.* 2017b), represent key elements for conservation planning at this larger scale (Morelli *et al.* 2017). These

elements provide significant advances compared to static visions of sites of conservation relevance, and can be used to test for the robustness of networks of protected areas in the face of climate change (e.g., Scridel *et al.* 2021). Combining modelling outcomes from multiple scales may allow prediction of local priority areas for conservation, i.e., suitable microhabitats, micro-climates and fine-scale refugia, within landscape units that are, and/or will be, suitable for a target species or community under current and future conditions, i.e., ‘landscape-scale’ refugia (Brambilla *et al.* 2022).

Ideally, such approaches, usually based on (multiple) species-specific models, should be complemented with models describing the likely changes of species diversity and community traits. This would allow development of conservation strategies aimed at maintaining highly diverse and functionally unique species assemblages.

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