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Viewpoint

Insufficient considerations of seasonality, data selection and validation lead to biased species–climate relationships in mountain birds

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Linking organism distribution to climate is key to understanding factors determining species occurrence and evaluating the potential impacts of ongoing climate change. A common analytical tool to assess the link between species and climate is represented by ecological niche modelling and by the tightly related species distribution models (SDMs). Those approaches have been widely used to explain key features related to species occurrence in relation to current climatic and other environmental variables, or as a response to past colonization and extinction events (Pons et al. 2021), as well as to predict the future distribution of target species (Scridel et al. 2021). Moreover, the link between climatic changes and niche evolution, i.e. niche changes (or conservatism) over time and especially across phylogenies remains complex and fascinating.

In the context of change, the rise of community science ('citizen science') data provides an invaluable opportunity to expand our knowledge on species distribution. While much attention has been given to aspects related to the statistical approaches and algorithm settings adopted in distribution or niche modelling (Engler et al. 2017, Ortega-Huerta and Rivera 2017, Kozma et al. 2018), less attention has been paid to validate very fundamental features which can greatly impact models performance, such

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as the quality of data for a given species, its spatial and temporal congruence with the climatic and environmental data used, and the risks associated with the inclusion of records of occasional vagrant individuals observed outside of their usual environment (but see Engler et al. 2017, Eyres et al 2017, Andrew and Fox 2020, Taheri et al. 2020).

Mountain birds and their ecological niche

Modelling the ecological niche of mountain bird species is particularly challenging. As they depend on dynamic habitats subject to large variation in local climate over small spatio-temporal scales (Scridel et al. 2018), they often show strong seasonal preferences during their annual cycle (Engler et al. 2014, Peña-Peniche et al. 2018). Moreover, they use a high diversity of movement strategies (e.g. elevational migration, nomadic or erratic movements), which are related to the very unpredictable seasonality of alpine environments (e.g. climate conditions and resource availability; Borrás et al. 2010, Henry 2011, Boyle 2018, Novoa et al. 2020, Resano-Mayor et al. 2020, Barras et al. 2021). Even for species thought to be largely resident or to move over short distances, there is some evidence of relatively long movements of individuals during the non-breeding season (Resano-Mayor et al. 2020), which might increase the chances of finding some transient individuals outside what could be regarded as the species' niche. Our knowledge of mountain bird movement strategies during the non-breeding period is still very limited and highlights the need to be particularly careful when assessing a species' ecological niche across the annual cycle. For these reasons, separate modelling of breeding versus non-breeding distribution should be required for mountain birds. Otherwise, model outputs may lead to misleading evaluations of species' ecological niches.

A worked example: the thermal niche of the white-winged snowfinch *Montifringilla nivalis*

The white-winged snowfinch *Montifringilla nivalis*, a well-known inhabitant of high alpine zones in Eurasia, is one of the species breeding at the highest elevations in the Western Palearctic (Cramp and Perrins 1994). In a recent paper, Cobos and colleagues (2021) implemented a framework to evaluate niche evolution and related range expansion in the so-called 'snowfinches' (Passeridae), a group of species specialized to high-elevations. They suggested that, while snowfinch species exhibit a cold thermal niche (i.e. average annual temperature from -8 to 7°C), the white-winged snowfinch, the only species that also occurs in Europe, exhibits a much broader thermal niche (i.e. average annual temperature from -9 to 20°C). According to the authors, such a wider niche should be related to a 'dramatic niche evolution event', leading to a niche expansion dated perhaps 2.6 mya ago, which allowed this species to occupy warmer areas in the western Palearctic,

such as southern Europe. However, we are convinced that the reason for such a finding is not an effective niche expansion in the species, but a question of methods – the inclusion of non-representative occurrence records in the analyses of the species' thermal niche –, neglecting crucial facts about the species' ecology.

There is striking evidence that white-winged snowfinches are strictly associated with cold alpine environments, in terms of their distribution (Brambilla et al. 2017a, 2020, Brambilla and Delgado 2020, BirdLife International 2021, de Gabriel Hernando et al. 2021), foraging areas (Antor et al. 1995, Brambilla et al. 2017b, 2018), social behaviour (Delgado et al. 2021), survival rates (Strinella et al. 2020) and habitat and nest-site selection (Heiniger 1991a, b, Brambilla et al. 2017b, Bettega et al. 2020, Niffenegger 2021). The dependence of this species on cold environments is particularly strong during the breeding season (Brambilla et al. 2019, 2022, Resano-Mayor et al. 2019, Schano et al. 2021, Alessandrini et al. 2022, de Gabriel Hernando et al. 2022): the breeding distribution of the species in European mountains is associated with low values of annual average temperature (Brambilla et al. 2017a, 2020, 2022, de Gabriel Hernando et al. 2021), suggesting a thermal niche much narrower than that suggested by Cobos et al. (2021). Similarly, during winter the species appears almost invariably tied to mountain sites above the treeline (Heiniger 1991a, Bettega et al. 2020, Resano-Mayor et al. 2020, Delgado et al. 2021, de Gabriel Hernando et al. 2021; see also the wintering distribution according to BirdLife International 2021), with season-specific distribution models showing how suitable areas during the cold season extend only partly to lower mountain ranges (de Gabriel Hernando et al. 2021). In fact, unlike other typical alpine species like wheatears, water pipits and alpine choughs, observations in warmer areas at low elevation are extremely rare despite the potential suitability of habitat (Knaus et al. 2018) and are more likely to occur in the case of prolonged, exceptionally cold or snowy periods and mostly linked to food shortage at higher elevation (Cramp and Perrins 1994, Glutz von Blotzheim and Bauer 1997). Such evidence contrasts with Cobos et al. (2021) conclusions about the thermal niche of white-winged snowfinches.

In the work of Cobos et al. (2021), seasonality has not been taken into account, and there is a lack of phenological concordance between records and climate data. The authors have pooled community science records related to different time of the year, and used climate data over the period 1979–2013 without considering inter-seasonal climatic variability, but showing results based only on annual average temperature. For mobile species inhabiting highly seasonal environments, such as the white-winged snowfinch in European mountains, this could be strongly misleading (Engler et al. 2017, Andrew and Fox 2020, de Gabriel Hernando et al. 2021). The same set of annual climatic variables could be used to model species distribution in different seasons, but records need to be split as the relationship between species occurrence and the same climatic predictor would be different when considering different periods of the annual cycle

(de Gabriel Hernando et al. 2021). For example, by including occasional observations in warm location, most likely to occur in winter, the annual mean temperature would be overestimated. This likely happened for snowfinch records in Europe and Western Asia (Supporting information) used by Cobos et al. (2021). In this line, we noticed that the authors included a relatively large number of unusual records located in lower and warmer areas (approx. 10% of records were below 1000 m), which we believe are most likely attributable to vagrant birds occasionally visiting areas outside the species' range, if not to incorrect identification/reporting (e.g. records in central and southwestern Iberian Peninsula and southern Italy). We acknowledge that community science data are an emergent, increasingly important tool contributing to ecological research and conservation, and they have been frequently used (also by many of us) for snowfinches as well as for other mountain species (Delgado et al. 2021, de Gabriel Hernando et al. 2021, Schano et al. 2021, Scridel et al. 2021, Brambilla et al. 2022). However, an accurate filtering of observations to remove potentially biased records, based not only on spatial locations and species identification but also on the basic ecology of the species, is crucial to improve model performance and outcome reliability (Steen et al. 2019, Johnston et al. 2021, Scridel et al. 2021, Brambilla et al. 2022).

Although we recognize the important aims of Cobos et al. (2021), we find their conclusions about the broad thermal niche of white-winged snowfinches inconsistent with the species' ecology and distribution. This overestimation of the species' thermal niche and distribution is potentially detrimental for a proper appreciation of the conservation status of the species and its sensitivity to global warming. The white-winged snowfinch is currently classified as a species of 'least concern' in the European and Global IUCN Red Lists and only Spain and Switzerland have recently changed its status to 'nearly threatened' (Knaus et al. 2021, Laiolo et al. 2021). Such an underrated status for a species highly threatened by climate change is likely partly due to the poorly known population trends. In fact, the ongoing range contraction (Scridel et al. 2017, Patrinat 2019, Brambilla and Delgado 2020), the evidence for regional declines (Knaus et al. 2018), the sensitivity to warming (Strinella et al. 2020) and the habitat changes it induces (Brambilla et al. 2018), as well as the forecast dramatic decline that could take place in the next decades (de Gabriel Hernando et al. 2021), suggest this to be one of the species most threatened by climate change in Europe (Brambilla et al. 2018, Knaus et al. 2021, Laiolo et al. 2021, Schano et al. 2021).

Conclusion

Modelling the ecological niche of organisms with seasonal distributions and/or high mobility requires integrating complex ecological aspects, and for many bird species a season-specific approach (Martínez-Meyer et al. 2004, Engler et al. 2014, Eyres et al. 2017). Thanks to their extraordinary mobility, birds

can use different habitats to track suitable climate or resources across seasons (Engler et al. 2017, and references therein), thus occasionally occur outside their usual environments. Species–climate relationships may hence vary across time and space, or according to the climate parameters considered (e.g. annual versus seasonal temperature): neglecting these potential dynamics could lead to wrong conclusions regarding distribution and niche characteristics, as well as to overpredicted ranges (Reside et al. 2010). The careful selection of reliable, spatially accurate records, and the use of accurate information about climate and life history stages is key to model the actual species–climate relationship, while properly considering its seasonality, especially in mountain regions, where abrupt changes may occur over limited spatial and temporal spans.

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Author contributions

Mattia Brambilla, Chiara Bettega, Maria Delgado, Davide Scridel: Conceptualization (lead); Writing – original draft (lead); Writing – review and editing (lead). **M. De Gabriel-Hernando, M. Päckert, S. Hille, F. Korner-Nievergelt, C. Schano, R. Arlettaz, S. Dirren, P. Fontanilles, J. A. Gil, M. Herrmann, P. Pedrini, J. Resano-Mayor:** Writing – review and editing (supporting).

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This paper contain no original data.

Supporting information

The Supporting information associated with this article is available with the online version.

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