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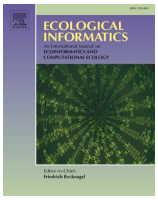

Climatic clues to local distributions: a hierarchical approach to model the distribution of *Miniopterus schreibersii* in Italy

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ABSTRACT

Species distribution models (SDMs) are widely used to understand species-environment relationships and inform conservation strategies. However, when based solely on broad-scale bioclimatic variables, SDMs may fail to capture local environmental heterogeneity relevant to habitat selection. In this study, we modelled the distribution in Italy of the common bent-wing bat (*Miniopterus schreibersii*), a troglophile species of conservation and public health relevance. We compared a traditional bioclimatic SDM (bio-SDM) with a hierarchical SDM (h-SDM) that integrates both coarse-scale climatic predictors and fine-resolution ecological variables.

We used a maximum entropy algorithm to model the species distribution, calibrating the bio-SDM using bioclimatic predictors, while the h-SDM included variables related to roosting (e.g. distance to karstic structures, distance to urban settlements), foraging ecology (e.g. percentage of canopy cover, percentage of agriculture) and climatic suitability derived from the bio-SDM. Both models performed well under cross validation (bio-SDM AUC = 0.80; h-SDM AUC = 0.79), but the h-SDM showed significantly higher maxTSS values (0.81 vs. 0.42) and lower, more variable Boyce Index values (0.26 vs. 0.86), indicating differences in calibration despite similar discrimination ability, and reduced overpredictions in urban and intensively cultivated areas. Climatic suitability and distance to karstic structures proved essential in refining the predicted distribution for the species.

These findings highlight the limitations of climate-only models and demonstrate how integrating local-scale variables can enhance spatial accuracy, providing a more informative tool for conservation planning and epidemiological monitoring in the face of climate and land-use change.

1. Introduction

Species Distribution Models (SDMs) offer a robust framework for estimating species' potential distributions by statistically associating occurrence records of a species (or a group of species) with environmental variables (Elith and Leathwick, 2009; Guisan and Thuiller, 2005). SDMs represent a cornerstone of ecological research, conservation planning, and biodiversity management, especially as ecosystems face increasing anthropogenic pressures and rapid climate change (Mahmoud et al., 2025; Rathore and Sharma, 2023). SDMs are often calibrated considering only bioclimatic variables which are interpolated (e.g., Worldclim; Fick and Hijmans, 2017; https://www.worldclim.org/) or modelled (e.g., Chelsa; Karger et al., 2017); https://chelsa-climate.org/) at spatial resolutions that span hundreds if not thousands km^2. These SDMs are effective at capturing overarching climatic envelopes and delineating potential range boundaries (Guisan and Thuiller, 2005; Hijmans and Elith, 2011), providing useful inputs in biogeographical and macro-ecological studies (e.g., Bellis et al., 2021; Benavides Rios et al., 2024; Dyderski et al., 2025). However, these approaches clearly fail to identify fine-scale habitat features essential for local-scale management and conservation (Chauvier et al., 2022). The misalignment between model resolution and ecological processes can lead to suboptimal conservation planning, as critical habitat patches or microrefugia may not be adequately detected (Pearson and Dawson, 2003; Vicente et al., 2014). Indeed, the finest nuances of habitat selection, such as small-scale land-use or micro-environmental conditions needed for shelter, foraging, or reproduction, might be overlooked by models that rely predominantly on broad scale bioclimatic variables (Briscoe et al.,

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2023; Lembrechts et al., 2019; McGill, 2010).

A possible solution is to consider both small scale, bioclimatic factors and large scale environmental factors, each with its proper scale and resolution. In this way, the same model can incorporate both biogeographical and habitat specific processes. First implemented in early 2000 by Mackey and Lindenmayer (2001), hierarchical species distribution models propose an approach which combines i) broad-scale climatic data to define climatic range limits, ii) regional-scale land use and habitat features to refine habitat suitability, and iii) local-scale microhabitat characteristics to capture ecological specificity. By nesting small scale predictions into large scale models, hierarchical SDMs have the potentiality to produce more ecologically realistic outputs (Guisan and Thuiller, 2005; Pearson et al., 2004) which can guide targeted conservation interventions (Goicolea et al., 2024; Guisan et al., 2025; Pearson et al., 2004).

Hierarchical SDMs have been applied to a few different contexts, ranging from coarse-scale of continental models to fine-scale regional applications (Mateo et al., 2024; Simon et al., 2023), from single-species modelling to multi-species and community-level analyses (e.g., Mateo et al., 2019; Ovaskainen and Soininen, 2011), and even to conservation and restoration strategies spanning forest, marine, and urban ecosystems (Rathore and Sharma, 2023). Their implementation is particularly interesting when focusing on species with huge movement capabilities, migratory behaviours, and at the same time very specific habitat requirements, as in the case of many migratory bird species and bats. While the approach has been tested on multiple bird species (e.g., Fjeld et al., 2024; Keil et al., 2013) very few applications are available for bats (e.g., Bellamy et al., 2020; Neubaum and Aagaard, 2022; Kaminski et al., 2025;). Yet, bats are among the best candidates to get important advantages from hierarchical models. In fact, their distribution is often shaped by an interplay of large-scale climatic constraints and fine-scale ecological drivers such as roost availability, prey dynamics, and anthropogenic pressures (Altringham, 2011; Goicolea et al., 2024; Peixoto et al., 2018). At the same time, bats are affected by huge knowledge gaps (Delgado-Jaramillo et al., 2020; Razgour et al., 2016; Zamora-Gutierrez et al., 2019), and often the only information that is available for many species is a polygon distribution map, which can show broad geographic ranges but would inevitably fail to reflect ecologically important habitat characteristics at the local scale (Herkt et al., 2017).

In this study, we aimed to assess whether integrating both coarse bioclimatic with fine-scale environmental predictors may improve prediction accuracy and inform spatially explicit conservation strategies. To this end, we compared a hierarchical SDM (h-SDM) with a standard bioclimatic SDM (bio-SDM) using the common bent-wing bat (*Miniopterus schreibersii*) as a case study. Specifically, we: i) developed a hierarchical SDM framework that incorporates variables relevant to species ecology at multiple scales; ii) evaluated the relative importance of predictors at different spatial resolutions; iii) quantified the difference in performance and the spatial disagreement between the h-SDM and the bio-SDM.

2. Materials & methods

We modelled the distribution of *M. schreibersii* using a hierarchical approach and focusing on two levels: the global distribution of the species (setting the bioclimatic context that defines the species' bioclimatic niche) and the Italian distribution (setting the local, ecological context; supplementary materials Fig. S1 and S2). At the same time, the bio-SDM was used as a layer into the h-SDM and as benchmark to represent a traditional SDM in the comparison between the h-SDM and the bio-SDM.

2.1. Species occurrences data

Considering the entire distribution range, we obtained a first set of 11,445 occurrences for *M. schreibersii* from GBIF (Global Biodiversity Information Facility, https://www.gbif.org/) and 229 from iNaturalist (https://www.inaturalist.org/). We excluded duplicated records (same date and same location), dubious observations (e.g., visual identification in flight), and all occurrences with a coordinate uncertainty $\geq$1 km, obtaining a final dataset including 991 occurrences from GBIF and 149 from iNaturalist.

To provide a better coverage of species distribution, we also performed a search in the scientific literature for further occurrences with the same token ("MINIOPTERUS" AND "SCHREIBERSII" AND "EUROPE") used in Scopus (https://www.scopus.com/), Web Of Science (https://www.webofscience.com/), and Google Scholar (https://scholar.google.com/). We obtained 6659 references (supplemental materials Table S1) from which we digitized 614 unique occurrences using ArcGis Pro (ESRI ©). After the cleaning process, we obtained a total of 1754 occurrences from all cited sources (citizen-science and literature). To minimize sampling clusters while maintaining a representative sample (Boria et al., 2014; Castellanos et al., 2019), we used a data thinning procedure (SpThin R-package; Aiello-Lammens et al., 2015) based on a user defined threshold distance that is used to identify spatial clusters. To define the threshold, we generated a set of 1754 points randomly located in our study area and measured the nearest neighbour distance for all points. We repeated the procedure for 100 times and found a mean nearest neighbour distance of approximately 5 km. This distance represents the minimum distance that we would expect if the occurrences were not spatially clustered. The data thinning process resulted in a final dataset with 1314 spatially independent occurrences.

To minimize sampling biases, we used a target-group approach for the selection of background points (Ranc et al., 2017). This approach assumes that several species can be pooled considering a common sampling method and observer interest. Therefore, the pool of species is collected with the same sampling intensity and spatial bias that characterize the species occurrences. In our case, we considered all bat species as part of the same target group, assuming that their occurrence records were collected through comparable survey campaigns and detection methods. Consequently, occurrences of other bat species were used as background points to approximate the underlying sampling effort. We downloaded 5,077,988 occurrences for all bat species from GBIF and 6518 from iNaturalist occurring in our study area. These occurrences were merged into a single dataset and thinned with the same approach used for the occurrence data, obtaining a total number of 24,527 occurrences of bats.

The European dataset was used to calibrate the bio-SDM. For the h-SDM, we considered only the 78 occurrences of *M. schreibersii* available for Italy together with 2149 background points (again present in Italy). Given the small sample size available for the h-SDM, we avoided any thinning procedure which could negatively affect model performance when dealing with small occurrence datasets (Ten Caten and Dallas, 2023). A map of the complete set of occurrences and background points for both models is provided in the Fig. S3 in supplementary materials.

2.2. Bioclimatic and environmental variables

To calibrate the bio-SDM, we considered 19 bioclimatic variables from WorldClim v.2.1 (30″ resolution; Fick and Hijmans, 2017). To limit the negative effects of multicollinearity (Araújo et al., 2019), we performed a variance inflation analyses (VIF) (Naimi and Araújo, 2016) and excluded all variables with a VIF $\geq$ 3 obtaining a final dataset with 5 bioclimatic variables: mean temperature diurnal range (e.g. BIO2), mean temperature of wettest quarter (e.g. BIO8), mean temperature of driest quarter (e.g. BIO9), precipitation of warmest quarter (e.g. BIO18), and precipitation of coldest quarter (e.g. BIO19). To calibrate the h-SDM, we focused on variables directly linked to the roosting ecology, feeding grounds, and bioclimatic niche of the species. In particular, we selected five variables: Euclidean distance to karstic structures, Euclidean distance to urban settlements, percentage of canopy cover,

percentage of agriculture, and climatic suitability.

Karstic structures represent the natural and most common roosting habitat (Lanza, 2012) and one of the most important factors in shaping the species distribution at local level. No readily available and comprehensive layer on the presence of karstic structure is available in our knowledge and therefore we combined the information from the Mediterranean Karst Aquifer Map and Database (MEDKAM; Xanke et al., 2024) with those provided by the literature on the distribution of the main karstic systems in Italy (Stoch, 2001). The most recent data on roost ecology for *M. schreibersii* (Guixé et al., 2024; Hoffmann et al., 2016; Leopardi et al., 2021) have shown that species can also use artificial structures. For example, a medium size colony of around 450 individuals has been recently described within the city centre of Arezzo, in Italy, with at least two further reports from the cities of Cesena and Mantova. Therefore, we included distance to urban settlements in the h-SDM. We mapped urban settlements to the highest level possible using the database of the National Italian Institute of Statistics (ISTAT; https://www.istat.it/) updated to 2001 and including at the same time urban and peri-urban areas and isolated buildings.

The most important feeding grounds for *M. schreibersii* correspond to the boundaries between forests or small patches of woods and agricultural areas (Lanza, 2012; Russo and Jones, 2003). Therefore, we included canopy cover (Global 30 m Landsat Tree Canopy Cover v4; Sexton et al., 2013; https://gee-community-catalog.org/projects/global_tcc/) expressed as percentage of coverage per pixel. We also extracted the class agriculture from the ESA WorldCover Global land cover product (Zanaga et al., 2022; https://esa-worldcover.org/en) originally at 10 m resolution. These two layers were resampled at a 100 m resolution calculating the percentage of agriculture and the percentage of canopy cover per pixel (Table 1). Since the bio-SDM was projected at 1 km^2 resolution, its climatic suitability output was resampled to 100 m using bilinear interpolation to match the resolution of the environmental predictors used in the h-SDM. All data manipulation for the environmental layers was done in ArcGis Pro (ESRI ©).

2.3. Model calibration and evaluation

We calibrated both the bio-SDM and h-SDM using the maximum entropy algorithm (Maxent; v. 3.4.1) via the ENMeval R package (Kass et al., 2021; Muscarella et al., 2014).

Specifically, for the calibration of the bio-SDM we included all 1314 occurrences and 24,527 background points collected in Europe. We tuned model parameters following Muscarella et al. (2014) with regularization multiplier ranging from 0.5 to 5.0 (0.5 increments) and with five different combination of feature classes: linear only, linear and quadratic; linear, quadratic, and hinge; linear, quadratic, hinge, and product; linear, quadratic, hinge, product, and threshold. For each combination of feature classes and regularization multipliers, we calculated the corrected Akaike Information Criteria (AICc) based on Li et al. (2020) selecting the model with $\Delta AICc = 0$. To assess variable contribution, we used a k-fold approach, partitioning occurrence localities randomly into 5 bins. We projected the final model (the one with the lowest AICc value) over the entire study area to obtain a map of the European potential bioclimatic distribution of *M. schreibersii* at a 1 km^2 resolution (bio-SDM).

For the h-SDM, we applied the same tuning approach using 78 occurrences and 2149 background points from the Italian peninsula. We selected all models with $\Delta AICc \leq 2$ (Burnham and Anderson, 2004), and we calculated the weighted mean (wAICc; Burnham and Anderson, 2004) to obtain a final model. For all selected models, we assessed variable importance using a jackknife procedure, which evaluates the impact of each predictor by sequentially excluding one variable at a time and measuring the resulting change in AUC. A greater reduction in AUC indicates a higher contribution of that variable to model performance (Peterson et al., 2011; Shcheglovitova and Anderson, 2013). For each variable the result was given by the mean of all selected models, weighted for their AICc weight (wAICc; Burnham and Anderson, 2004). Marginal response curves were generated for each environmental predictor by averaging the curves across jackknife replicates, with all other variables held at their mean values (Muscarella et al., 2014; Phillips et al., 2006). The final prediction was obtained by averaging the outputs of the retained models and projected across the Italian peninsula at 100 m resolution to generate the potential distribution of *M. schreibersii* (h-SDM).

To allow for a visualization and comparative interpretation between the bio-SDM and the h-SDM, we standardized their outputs by rescaling the two maps based on the quantiles of the probability values projected on the occurrences. Specifically, from each model, we extracted the relative probabilities of presence corresponding to all species occurrences and divided the resulting distribution into 10 quantiles. The class boundaries of the quantiles were used to reclassify both SDMs into 10 classes of increasing probability. This step was performed exclusively to facilitate a consistent and interpretable visual comparison between the two models.

To quantitatively assess spatial disagreement between the SDMs, we performed a linear regression analysis using continuous probability values. In this analysis, the h-SDM was used as the response variable and the bio-SDM as the predictor. Prior regression, probability values from both models were transformed using a Yeo-Johnson transformation, *bestNormalize* package in R (Peterson, 2021). Standardized residuals from the regression were then classified into three categories: i) overprediction by the h-SDM (z-scores >1); ii) agreement between the two SDMs ($-1 \leq$ z-scores $\leq +1$); iii) underprediction by the h-SDM (z-score < -1).

We evaluated the predicted performance of the bio-SDM with a k-fold cross validation (5 bins; Peterson et al., 2011; Muscarella et al., 2014) and the h-SDM with a jackknife, leave-one-out cross-validation (Abdi and Williams, 2010; Muscarella et al., 2014). For both models we focused on discrimination (Area Under the ROC Curve, AUC; Maximum True Skill Statistics, maxTSS; Robin et al., 2011) and calibration (continuous Boyce Index; Di Cola et al., 2017). To formally assess performance differences, we compared the distributions of each metric using Wilcoxon rank-sum tests.

Table 1
Summary of spatial resolutions and environmental variables used for model calibration and projection.

Model	Variable type	Data source / layer	Native resolution	Resolution used for calibration	Resolution used for projection
bio-SDM	Bioclimatic variables	WorldClim v2.1 (Fick and Hijmans, 2017)	30 arc-seconds (~1 km^2)	1 km	1 km
h-SDM	Climatic suitability (from bio-SDM)	Output of bio-SDM	1 km	100 m	100 m
h-SDM	Distance to karstic structures	MEDKAM (Xanke et al., 2024); Stoch, 2001	–	100 m	100 m
h-SDM	Distance to urban settlements	ISTAT (2001)	–	100 m	100 m
h-SDM	% canopy cover	Global Landsat Tree Canopy Cover v4 (Sexton et al., 2013)	30 m	100 m	100 m
h-SDM	% agriculture	ESA WorldCover (Zanaga et al., 2022)	10 m	100 m	100 m

3. Results

The bio-SDM achieved an AUC of 0.80 (sd = 0.02; range = 0.72–0.81), a maxTSS of 0.42 (sd = 0.08; range = −0.29-0.48), and a Boyce Index of 0.86 (sd = 0.09; range = 0.74–0.94). The h-SDM showed a comparable AUC (0.79; sd = 0.01; range = 0.79–0.81), but significantly higher values for maxTSS (0.81; sd = 0.21; range = 0.18–1.00). In contrast, the Boyce Index showed greater variability in the h-SDM (mean = 0.26; sd = 0.59; range = −0.63-1.00), reflecting the wider range of suitability values produced by the h-SDM. The h-SDM differed significantly from the bio-SDM in maxTSS (W = 35, $p = 0.0026$) and Boyce Index (W = 295, $p = 0.027$). AUC values also showed a small but significant difference (W = 60, $p = 0.012$).

The bio-SDM (Fig. 1a; supplementary materials Fig. S4a) identified large and continuous areas of high climatic suitability for *M. schreibersii* across the Italian peninsula. These included much of the Tyrrhenian coastal zone, nearly all the region of Puglia, as well as extensive portions of the regions of Sicilia and Sardegna, and several lower elevation areas in the Alpine and pre-Alpine foothills. The model also projected high suitability across some scattered areas in the Po Valley and parts of North western Italy. In contrast, low suitability values were predicted throughout the Alps, almost anywhere in the central Po Valley, inland parts of Campania and Calabria regions, the main peaks in Central Italy, and along the Northern Adriatic coast.

The h-SDM (Fig.1b; supplementary materials Fig. S4b) mirrored the general suitability patterns identified by the bio-SDM but provided a spatially refined prediction. High probability of presence was predicted along the Tyrrhenian coast, South eastern Puglia, Southern Sicilia, North eastern Sardegna, and parts of the Alpine foothills. Low suitability was consistently observed throughout the Alps, in inland parts of Campania and Calabria regions, as well as across much of Central Italy. In contrast to the bio-SDM predictions, the Po Valley and large portions of Northern Italy emerged as areas of very low suitability for the species.

The spatial disagreement between the bio-SDM and the h-SDM (Fig. 2; supplementary materials Fig. S5) highlights a clear pattern of spatial mismatch: large portions of the Northern Apennines, the Po Valley all the way through North western Italy, and parts of Southern Italy show negative residuals, indicating that the h-SDM predicted lower values of suitability in these regions compared to the bio-SDM. Positive residuals (areas where the h-SDM predicted a suitability higher than the bio-SDM) are mainly present in limited areas of the Alps, in the central Apennines, and some small and isolated areas of Sardegna and Sicilia regions.

Precipitation of the warmest quarter (e.g. BIO18; 39.5%) and mean diurnal range (e.g. BIO2; 32.3%) were the strongest contributors, followed by temperature of the driest quarter (e.g. BIO9), temperature of the wettest quarter (e.g. BIO8), and precipitation of the coldest quarter (e.g. BIO19) that collectively accounted for the 28% of variable importance (supplementary materials Table S2). The corresponding response curves (supplementary Fig. S6) shows that probability of presence increases with larger diurnal temperature range (BIO2), rises sharply under high temperatures in the wettest quarter (BIO8), and exhibits a bimodal response to temperature during the driest quarter (BIO9). It is highest under very low precipitation in the warmest quarter (BIO18) and peaks at moderate precipitation in the coldest quarter (BIO19).

Climatic suitability (55.9%) and distance to karstic structures (32.1%) are the main drivers of the distribution of the species for the h-SDM (supplementary materials Table S2). As shown in the response curves (Fig. 3), the probability of presence increases with higher climatic suitability and decreases with greater distance from karstic structures. The remaining predictors as percentage of agriculture, distance to urban settlements, and percentage of canopy cover, collectively account for less than 12% of variable importance, contributing only marginally to the model. Their response curves show weaker effects, with the probability of presence gradually decreasing as the percentage of agriculture and canopy cover increases, and slightly increasing with greater distance to urban settlements.

4. Discussion

Bioclimatic SDMs can be extremely important to broadly outline the

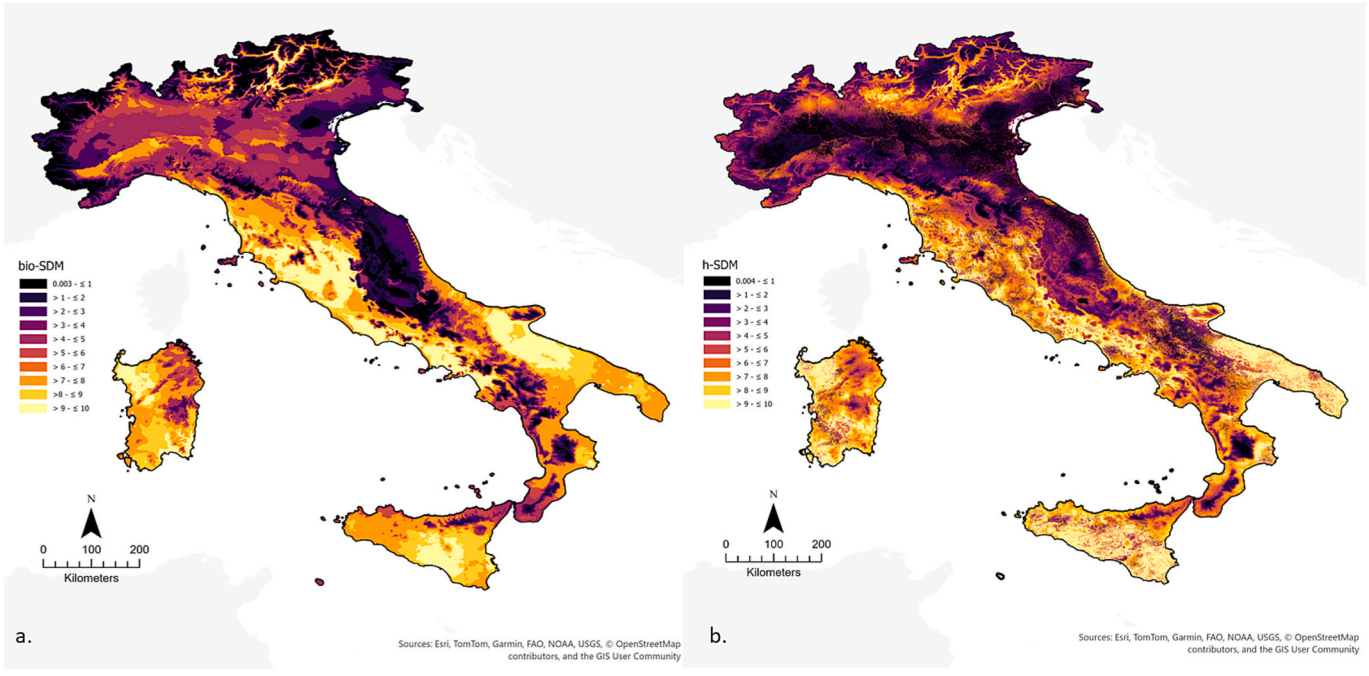

Fig. 1. Predicted probability of presence of *Miniopterus schreibersii* across the Italian territory referring to a) the bio-SDM prediction and b) the h-SDM. Probability values are reclassified in 10 quantiles calculated considering the probability values corresponding to the available occurrences (more details available in the main text). In dark blue are represented values at lowest suitability; in bright yellow are shown highest suitability values. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

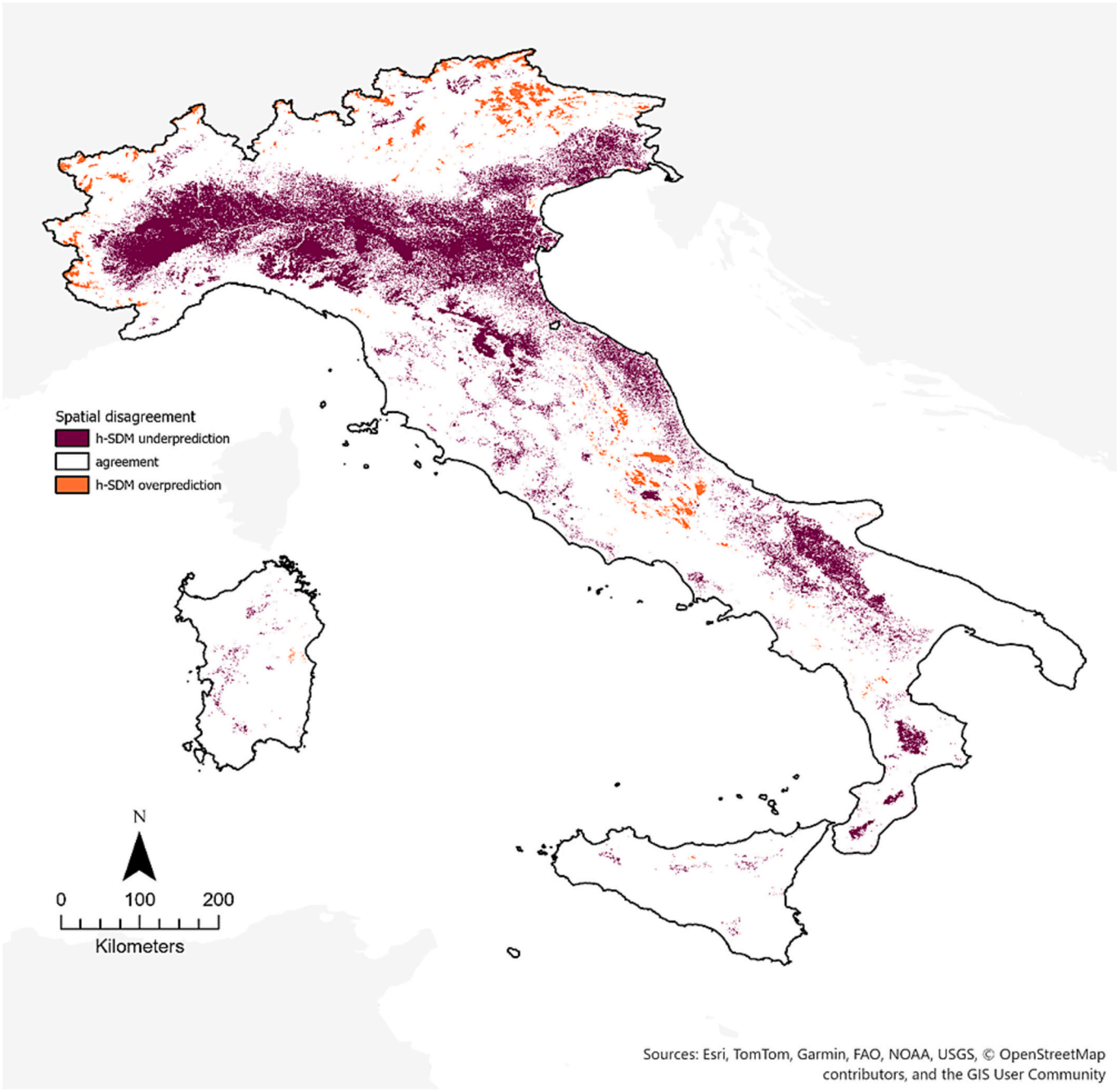

Fig. 2. Map of standardized residuals (z-scores) from the linear regression, comparing the h-SDM to the bio-SDM. Dark purple areas represent negative residuals, where the h-SDM model predicts lower suitability values if compared to those of the bio-SDM. Orange areas show positive residuals, where the h-SDM model predicts higher suitability values if compared to those of the bio-SDM. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

boundaries of a species potential distribution (Thuiller et al., 2004) and predict the responses of species to global changes (Guisan and Zimmermann, 2000; Petitpierre et al., 2016); however they often overlook the fine-grained landscape conditions that govern the actual presences of a species (Chauvier et al., 2022; Franklin, 2023; Pearson and Dawson, 2003). Nevertheless, these models are one of the most widely used tools in ecology and conservation biology, disciplines in which the focus is often oriented towards local contexts and applied research questions (Araújo et al., 2019; Elith and Leathwick, 2009; Guisan et al., 2013; Heikkinen et al., 2006). In the last decade or so, a growing body of research is going beyond broad climatic envelopes, embracing the ecological complexity that unfolds at multiple spatial scales (Chevalier et al., 2021; Fletcher et al., 2019; Simon et al., 2023). This shift is particularly interesting for taxa like bats, whose distribution is certainly linked to large scale bioclimatic factors but their elusive behaviours and fine-scale habitat requirements escape detection by large scale models (Fernandes et al., 2019; Peixoto et al., 2018; Razgour et al., 2016). In fact, the local availability of roosts and foraging habitats shaped by factors such as geology, vegetation, and land-use intensity is extremely important to explain their local occurrence (Bellamy et al., 2020; Razgour et al., 2016). However, while there is an increasing support for hierarchical, multiscale approaches in modelling species distributions (Briscoe et al., 2023; Goicolea et al., 2024; Guisan et al., 2017; Guisan et al., 2025; Mateo et al., 2019), their use in studying bats distributions

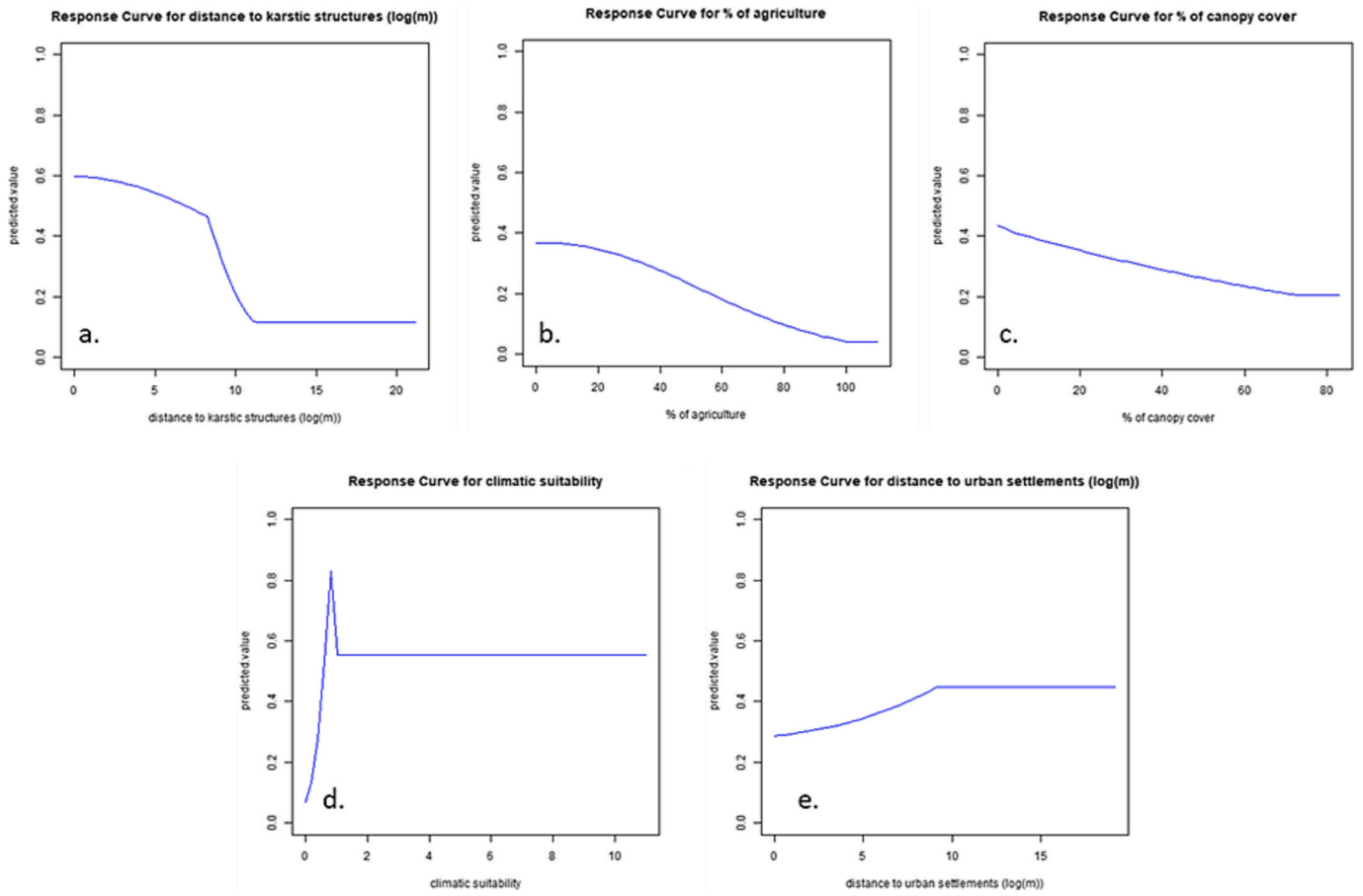

Fig. 3. Response curve for the variables in the h-SDM model for *M. schreibersii*. Plotted curves are relative to (a.) distance to karstic structure (log(m)), (b.) % of agriculture, (c.) % of canopy cover, (d.) climatic suitability, (e.) distance to urban settlements (log(m)).

remains limited.

Our results demonstrate that hierarchical SDMs can be valuable for capturing the local-scale distribution of *M. schreibersii*, revealing ecologically meaningful patterns that may be overlooked at coarser spatial scales. We calibrated a traditional bioclimatic SDM (bio-SDM) and a hierarchical model (h-SDM), and both showed good predictive performance. Consistent with the evaluation metrics, the two models exhibited very similar AUC values (bio-SDM = 0.80; h-SDM = 0.79), while the h-SDM displayed significantly higher maxTSS values (0.81 vs. 0.42), indicating a stronger ability to discriminate between suitable and unsuitable conditions. In contrast, Boyce Index values were more variable for the h-SDM (0.26 vs. 0.86 for the bio-SDM). Overall, these performance metrics suggest a modest but statistically supported improvement in discriminatory capacity for the h-SDM.

Considering what we know on the biogeography of the species (Appleton et al., 2004), the bio-SDM certainly provided a robust baseline of climatic suitability, projecting large portions of the Italian peninsula as climatically suitable, including the Po Valley, large portions of Northern Italy, and basically all coastal regions. These results are consistent with the species thermophilic ecology (Dietz and Kiefer, 2016). However, many of these areas, although climatically suitable, are characterized by intense urbanization and agriculture, therefore lacking critical ecological features such as roosting sites or natural foraging grounds. For example, the Po Valley, one of the areas identified as highly suitable by the bio-SDM, is a vast alluvial plain with few or no karstic systems, minimal topographic heterogeneity, and heavy anthropogenic pressure due to intensive agriculture and farming practices, as well as urbanization. The ecological homogeneity, dominated by large-scale monocultures, urban sprawl, and canalized river systems, offers limited heterogeneity in terms of feeding grounds available for the species. These conditions result in a landscape that is largely inadequate to support the ecological needs of *M. schreibersii*. As a result, the model tends to overpredict the potential distribution, highlighting areas where actual habitat conditions are insufficient to support the species, a limitation also noted in previous studies (Russo and Jones, 2003; Vincent et al., 2011; Russo et al., 2023).

In contrast, the h-SDM produced a more spatially refined output. While including much of the general pattern identified in the bio-SDM (e.g., the Tyrrhenian coast, South Eastern Puglia, Southern Sicilia, and North eastern Sardegna), it predicted patches of suitable habitat in areas such as the Po Valley and North western Italy but excluding areas with intensive land use and without known karstic structures. For example, notable differences between the two models also emerge in scattered areas in the Northern Puglia and South Western Sicily. In Northern Puglia, despite high climatic suitability predicted by the bio-SDM, the h-SDM reduces suitability estimates in areas dominated by agricultural intensification and limited karstic structures. Conversely, in South western Sicily, the h-SDM identifies suitable habitat in areas not emphasized by the bio-SDM, likely due to the presence of localized karstic systems and low-intensity land use. The h-SDM also considered as suitable areas which are not included in the high suitability values of the bio-SDM (e.g. the central Apennines and the South Eastern Alps), areas where karstic structures are widespread and less impacted by urban or agricultural expansion. These refinements are ecologically meaningful and further support the value of hierarchical models to improve the accuracy of bat distribution predictions, highlighting important ecological constraints that go beyond climatic suitability alone. However, it should be noted that part of the spatial refinement observed in the h-SDM output reflects its finer resolution (100 m) compared to the coarser resolution of the bio-SDM (1 km^2). This higher

level of spatial detail should therefore be interpreted cautiously as it could partly derives from the integration of fine-scale predictors and from the projection resolution itself. For this reason, direct spatial comparisons between the two models may be influenced by differences in spatial resolution, and the contrast between bio-SDM and h-SDM predictions should be interpreted with caution. Nevertheless, the improved spatial refinement of the h-SDM does not derive solely from its finer resolution, but from the integration of ecologically meaningful, fine-scale predictors that directly relate to the species' ecological requirements, capturing key aspects of the realised niche that cannot be resolved at coarse climatic scales. In this sense, the hierarchical approach provides a more ecologically grounded representation of species presence, complementing rather than replacing broad-scale climatic suitability. Looking at variable importance, it is clear that climate plays a prominent role in shaping the distribution of the species, but this is coupled with distance to karstic structures. Again, these findings align very well with the known ecological preferences of the species, a Mediterranean, cave-dwelling, thermophilic bat (Lanza et al., 2012; Loy et al., 2025), consistently with evidences from the European range of *Miniopterus schreibersii*, which shows limited population structure (Gürün et al., 2019).

The discrepancies between the bio-SDM and the h-SDM carry important implications for both conservation planning and management. Where the bio-SDM overpredicts climatic suitability, such as in intensively farmed or dense urban areas, it can misdirect resources towards areas lacking essential roosting habitat. At the heart of this mismatch lies the species' dependence on roost availability. While deep, insulated caves remain its preferred refuge, the species routinely exploits artificial subterranean sites, abandoned mines, tunnels, even building cellars, sometimes in regions that, despite being climatically suitable, may not provide natural roosting settings (Aulagnier and Presetnik, 2022; Hoffmann et al., 2016; Presetnik, 2004). These alternative roosts, however, are far more exposed to temperature extremes, heatwaves, and anthropogenic disturbance, and thus offer little buffering against external climatic fluctuations (Johnson and Lacki, 2014; Ruczyński and Bartoń, 2020). Rather than acting in isolation, climate change interacts dynamically with the structural and thermal properties of available roosts: colonies in deep caves may be partially insulated from warming trends, whereas bats in shallow or urban structures could face lethal microclimatic stress. By highlighting areas where vulnerable roosting settings coincide with human-modified landscapes, features entirely invisible to coarse-scale models, the h-SDM enables more precise targeting of conservation actions, from safeguarding natural caves to monitoring and protecting artificial roosting sites. Beyond the spatial refinements observed under current climatic conditions, h-SDMs can also be particularly relevant in the context of global warming. Traditional bio-SDMs may suffer from niche truncation, as they infer a species' climatic tolerance solely from broad-scale macroclimatic surfaces. However, many populations persist in microrefugia where fine-scale environmental features such as cave depth, karst complexity, or local vegetation structure, buffer against climatic extremes. When these microhabitats remain unresolved in coarse-grained models, SDMs tend to underestimate climatic breadth and may project unrealistically severe range contractions under future scenarios. By explicitly integrating fine-scale ecological predictors, the h-SDM captures part of this microclimatic buffering capacity and thus provides a framework that can generate more ecologically plausible projections under warming conditions. This is especially relevant for *M. schreibersii*, whose persistence depends on thermally stable subterranean roosts and whose metapopulation dynamics expose it to climatic-driven problems. Although our study did not include future projections, hierarchical approaches represent a promising tool for future work aimed at identifying potential microrefugia and supporting long-term conservation planning under accelerating climatic change.

Clearly, even our refined and detailed h-SDM has several limitations. *Miniopterus schreibersii* is a partially migratory species, and the occurrence dataset combines records from different ecological contexts, including hibernation sites, transit sites, and summer colonies. These contexts reflect distinct ecological requirements, particularly with respect to microclimatic conditions and roost characteristics. As these differences were not explicitly incorporated into the modelling framework, the SDMs should be interpreted as providing a generalised estimate of probability of presence rather than seasonal-specific distributions. This represents an important caveat when interpreting local predictions. While, in fact, the focus on higher spatial resolutions represents an improvement over coarse biogeographic layers, finer-scale heterogeneity, such as specific roost microclimates or land-use dynamics, are still lacking. These omissions limit the ability of the model to fully resolve habitat suitability at the scale at which *M. schreibersii* selects its roosts and responds to local environmental conditions. One avenue for refinement involves the integration of information associated with roosts, such as structural type, microclimatic stability, or historical occupancy. Adding such features to the h-SDM framework would allow for even more ecologically grounded predictions, particularly in areas where natural and anthropogenic roosts differ in thermal buffering capacity. Such additions would not only improve model accuracy but also support more context-specific conservation actions.

The negative associations observed for the percentage of agriculture and canopy cover reflect the species' preference for heterogeneous, ecotonal landscapes, where open foraging areas are interspersed with linear elements, forest edges, and roosting opportunities, rather than homogeneous agricultural matrices or continuous closed-canopy forests. Distance to urban settlements was included in the h-SDM as a proxy for potential availability of artificial subterranean structures that may function as alternative roosts (e.g. tunnels, cellars, underground infrastructures). Moreover, the response to urban proximity was weakly negative, a pattern that may be ecologically plausible but also partially driven by sampling bias. Indeed, species occurrence datasets often reflect spatial biases in survey effort and citizen science programs (Boakes et al., 2010; Bowler et al., 2022), which can inadvertently influence model outputs. Furthermore, distribution data for bats may be influenced by the species' specific habitat preferences, as well as by the fact that capture efforts often target environments where the species is more likely to occur. In the case of *Miniopterus schreibersii*, which is not considered a synanthropic species, survey efforts, particularly those involving mist-netting or roost search and inspections, are rarely conducted in urban settings. As a result, occurrence records for this species may lack representation from urban environments (Freitag et al., 1998). This under-sampling may lead the model to underestimate the suitability of urban areas, even if these sometimes offer crucial alternative roosting settings such as tunnels and cellars as observed all over Europe (Guixé et al., 2024; Leopardi et al., 2021). While we performed target-group approach to mitigate sampling biases, the substantial presence of synanthropic bat species in major Italian cities recorded in databases like GBIF and iNaturalist suggests that urban bias may persist. Therefore, caution is warranted when interpreting the negative urban response curve as fully reflective of habitat preference. Although urban roosting sites may be considered as suboptimal or alternative settings for *M. schreibersii*, we cannot yet infer habitat shift towards urban environments. In fact, recent declines of urban colonies in some Italian cities (Ancillotto et al., 2024, 2025) suggest that urbanization may exert long-term pressures that reduce local persistence, which aligns with the negative response pattern observed in our model. These conclusions, again, underscore the need for further targeted studies as they carry important implications both for conservation strategies and epidemiological risk assessments.

M. schreibersii represents a species important from many different points of view, with relevance for biodiversity conservation and public health. In fact, the species is a known reservoir for several zoonotic viruses, including *Filoviridae*, *Paramyxoviridae*, and *Rabdoviridae* (Ceballos et al., 2013; Kemenesi et al., 2018; Leopardi et al., 2021; Negredo et al., 2011). Its broad mobility, colonial behaviour, and tendency to form

large aggregations in roosts all contribute to its potential role in pathogen maintenance and transmission (Banyard et al., 2014; Munshi-South and Wilkinson, 2010). In this context, being able to predict its distribution with high spatial resolution, especially in human-dominated landscapes, is crucial for informing disease surveillance, identifying areas of potential contact between bats, humans, and domestic animals, and developing targeted strategies. In conclusion, we showed that a hierarchical modelling framework can be important also for species such as bats, offering a valuable tool to support integrated approaches to wildlife conservation and One Health planning. Although the overall predictive performance of the two models was comparable, the h-SDM provided a more spatially refined and ecologically coherent representation of the potential distribution of *M. schreibersii* across the Italian peninsula. Importantly, this refinement reflects the incorporation of fine-scale environmental predictors and the higher spatial resolution of the h-SDM, rather than a substantial increase in predictive accuracy. The adoption of multiscale modelling frameworks may become increasingly useful, not only to understand where species might persist, but to prioritize interventions where conservation, health, and environmental policy must intersect (Becker et al., 2019; Heidecke et al., 2023).

CRediT authorship contribution statement

Francesca Festa: Writing – review & editing, Writing – original draft, Methodology, Formal analysis, Data curation, Conceptualization. **Stefania Leopardi:** Writing – review & editing, Supervision, Resources, Funding acquisition, Conceptualization. **Luigi Maiorano:** Writing – review & editing, Supervision, Software, Resources, Methodology, Conceptualization. **Francesca Cosentino:** Writing – review & editing, Supervision, Methodology, Formal analysis, Data curation, Conceptualization.

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecoinf.2026.103745.

Data availability

The data sources used in the analysis are all publicly available and their references are given in the supporting information. The data and codes pertaining the analysis are available at the DOI: https://doi.org/10.6084/m9.figshare.31057702

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