RESEARCH ARTICLE

Broad-scale patterns of geographic avoidance between species emerge in the absence of fine-scale mechanisms of coexistence

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Abstract

Aim: The need to forecast range shifts under future climate change has motivated an increasing interest in better understanding the role of biotic interactions in driving diversity patterns. The contribution of biotic interactions to shaping broad-scale species distributions is, however, still debated, partly due to the difficulty of detecting their effects. We aim to test whether spatial exclusion between potentially competing species can be detected at the species range scale, and whether this pattern relates to fine-scale mechanisms of coexistence.

Location: Western Palearctic.

Methods: We develop and evaluate a measure of geographic avoidance that uses outputs of species distribution models to quantify geographic exclusion patterns expected if interspecific competition affects broad-scale distributions. We apply the measure to 10 Palearctic bat species belonging to four morphologically similar cryptic groups in which competition is likely to occur. We compare outputs to null models based on pairs of virtual species and to expectations based on ecological similarity and fine-scale coexistence mechanisms. We project changes in range suitability under climate change taking into account effects of geographic avoidance.

Results: Values of geographic avoidance were above null expectations for two cryptic species pairs, suggesting that interspecific competition could have contributed to shaping their broad-scale distributions. These two pairs showed highest levels of ecological similarity and no trophic or habitat partitioning. Considering the role of competition modified predictions of future range suitability.

Main conclusions: Our results support the role of interspecific competition in limiting the geographic ranges of morphologically similar species in the absence of fine-scale mechanisms of coexistence. This study highlights the importance of incorporating biotic interactions into predictive models of range shifts under climate change, and the need for further integration of community ecology with species distribution models to understand the role of competition in ecology and biogeography.

1 | INTRODUCTION

The need to forecast shifts in species distributions under global climate change is driving an emerging interest in understanding the factors that shape species ranges (Pacifici et al., 2015). The presence of a species in a given location, and thus the species' range, depends on the abiotic environment (climate, topography and physical environment), biotic interactions and movement factors that relate to species dispersal ability under constraints of its evolutionary history (Poggiato et al., 2021; Soberón & Peterson, 2005). The relative contribution of these factors across spatial scales is, however, still not well understood. Climatic factors are commonly thought to shape the distribution of species at a broad spatial scale, whereas the impact of biotic factors is thought to be more pronounced at the local scale (Willis & Whittaker, 2002). Hence, the role of biotic factors in shaping broad-scale patterns of species ranges remains controversial (Early & Keith, 2019; Wiens, 2011; Wisz et al., 2013), for example, see the Eltonian Noise hypothesis (Soberón & Nakamura, 2009). Among the different types of biotic interactions, interspecific competition can result in competitive spatial exclusion (Gause, 1932). While the effect of competition on local-scale patterns such as ensemble composition is broadly accepted and supported by studies (e.g. Fraterrigo et al., 2014), substantial evidence shows that competition effects on species presence can scale up and drive broad-scale assemblage patterns, as seen in avifauna in Denmark (e.g. Gotelli et al., 2010), and also can shape species broad-scale range limits. There are several documented examples of range patterns being shaped partially by competition (reviewed in Wisz et al., 2013). In their review of the literature, Sexton et al. (2009) found that 39 out of 51 studies supported or partially supported the role of competition in shaping broad-scale species range limits. Our mechanistic understanding of the role of interspecific competition in shaping species ranges is, however, limited, in part because we still lack tools to identify such patterns. Yet recent theoretical studies suggest that the scaling-up of competitive exclusion depends on the development of fine-scale coexistence mechanisms (Godsoe et al., 2015).

The ultimate consequence of interspecific competition in the absence of coexistence mechanisms, such as partitioning of the trophic, spatial or temporal ecological niche, is spatial exclusion (Gause principle: Gause, 1932; Hardin, 1960). Consequently, if competitive exclusion scales up and has an effect on species' geographic distributions, the predicted detectable signal on species' occurrences would be a tendency to be absent from their environmentally suitable area where the competitor is present. Indeed, parapatric ranges between morphologically similar or phylogenetically related species were traditionally interpreted as the result of competitive interactions, especially in the absence of geographical barriers to dispersal and when

sharp edges do not match clear environmental gradients (Bull, 1991). The main difficulty when aiming to infer competition effects using patterns of species presences is separating true avoidance resulting from competition from the effects of differential ecological preferences (Bar-Massada, 2015).

One of the current methodological approaches that consider biotic interactions at macroecological scales is including the geographic range of a potential competitor as an additional predictor layer in species distribution models (SDMs) (Anderson, 2017). Although this approach often improves model performance (e.g. Palacio & Girini, 2018), it cannot be used to separate biotic from environmental effects (Dormann et al., 2018). More recent methodological developments aim to separate biotic from environmental effects at the local community level by using patterns of species co-occurrences (e.g. D'Amen et al., 2018). Among these approaches, joint species distribution models (JSDMs) (e.g. Harris, 2015; Pollock et al., 2014) model simultaneously species presences using environmental variables and identify patterns of residual co-occurrences between species that are not explained by environmental predictors and therefore might reveal a signal of biotic interactions. However, the validity and the interpretation of co-occurrence patterns as inferences on biotic interactions are unclear (see Blanchet et al., 2020; Dormann et al., 2018; Peterson et al., 2020; Poggiato et al., 2021; Zurell et al., 2018). Moreover, the assemblage data that these methods require reduce their applicability for understanding broad-scale species range patterns.

Despite the paucity of available methods to identify broad-scale effects of biotic interactions on species ranges, there is increasing awareness that considering the role of biotic interaction is important for better understanding how climate change will impact diversity patterns (Alexander et al., 2016). Biotic interactions can modify responses towards climate change, for example, through preventing species from being able to maintain or establish populations in predicted future suitable range due to increased overlap with competitors either in existing range or in new suitable areas (HilleRisLambers et al., 2013).

We aim to test whether spatial exclusion between potentially competing species can be detected at the species' range scale, and whether fine-scale mechanisms of coexistence affect broad-scale species distributions. To this end, we develop a measure of geographic avoidance between pairs of species that uses SDM outputs. We apply the measure to four sets of cryptic Palearctic bat species (10 bat species) that show different degrees of ecological similarity and range overlap. Cryptic species are morphologically similar but genetically distinct species and therefore are likely to show high ecological similarity and compete for the same resources, offering an excellent model system for testing competitive interactions

(Novella-Fernandez et al., 2020). We predict that broad-scale geographic avoidance can be detected in pairs of species with higher ecological similarity and in the absence of fine-scale coexistence mechanisms. We expect that species with high geographic avoidance will be less likely to colonize their future suitable range in areas of overlap with their competitors, which will reduce the size of the suitable range available to them under climate change. Therefore, it is important to understand current patterns of geographic avoidance to be able to incorporate the effects of future range overlap with competitors in climate change vulnerability assessments.

2 | MATERIALS AND METHODS

2.1 | Developing a measure of geographic avoidance

While SDMs model species' suitable geographic areas, this predicted environmentally suitable range (herein predicted range) is not entirely occupied by the species, which are restricted to a smaller portion of it (herein realised range). The difference between modelled species predicted and realised ranges can be attributed partially to processes not included in the correlative environmental SDM framework, such as biotic interactions or dispersal limitation (Guisan et al., 2017). A species whose range is negatively affected by the presence of another is expected to realise less of its predicted suitable range in those areas where the competitor is present. Based on this, we present a measure of species geographic avoidance that uses SDM outputs for pairs of potential competitor species i and j with partially overlapping ranges. The measure establishes a relationship between the realised proportion of the range of species i and j in overlapping (sympatric) and non-overlapping (allopatric) areas. To convert this to a measure of avoidance, we take 1 − the ratio between these:

$$GA_{ij} = 1 - \frac{\text{proportion of range realised in overlapping areas between } i \text{ and } j}{\text{proportion of range realised in non–overlapping areas between } i \text{ and } j} \quad (1)$$

See Figure 1 for an overview of the implementation of this methodology.

- P_i **(predicted range): (P_i):** The binary geographic area that is environmentally suitable for species i. Binary suitable areas are generated from SDM outputs using the thresholding method that minimizes the difference between sensitivity and specificity. This thresholding method has been shown to outperform other approaches (Liu et al., 2013).
- **PO_{ij} (predicted range overlap):** The geographic overlap between the predicted ranges of species i and j. This is the expected geographic overlap between species according to their binary model outputs (Gutiérrez et al., 2014).
- R_i **(realised range):** The area of the predicted range where species i is present. A low proportion of predicted range realised suggests

that processes not included in the abiotic model, such as the effects of biotic interactions and/or dispersal limitations (Soberón & Peterson, 2005), are preventing the species from occupying its entire environmentally suitable range. The realised range is estimated by clipping the predicted range of the species by its known range limits (e.g. Marcer et al., 2013). This can be based on detailed occurrence records, when such information is available, or expert-generated distribution maps, such as those available from the IUCN Red List (https://www.iucnredlist.org). The reliability of the measure depends on accurately measuring species realised ranges, and therefore, it should not be applied to data-deficient species or cryptic species that have not been recently assessed if using IUCN red list range maps.

- **RO_{ij} (realised range overlap):** The geographic overlap between the realised ranges of species i and j. It represents the overlap between the two species that occurs at the model resolution (cell size). High values denote species coexistence.

Inserting these parameters into Equation 1 and rearranging gets:

$$GA_{ij} = 1 - \frac{RO_{ij}(P_i + P_j - 2(PO_{ij}))}{PO_{ij}(R_i + R_j - 2(RO_{ij}))} \quad (2)$$

Values of $GA_{ij} = 0$ indicate that for a given pair of species i and j, an equal proportion of predicted range is realised in overlapping areas and in non-overlapping areas. Values of $GA_{ij} < 0$ indicate that a higher proportion of predicted range is realised in overlapping areas. Finally, values of $GA_{ij} > 0$ indicate a lower proportion of predicted range is realised in overlapping areas, as expected if they occupy less of their suitable range in the presence of a competitor. The maximum value of GA_{ij} will tend to 1 in the extreme case where species i and j do not realise any of their predicted range in their overlapping areas. Because the measure is based on ratios, values based on very small proportion of realised range overlap (around less than 0.5%) are prone to high variability and are not reliable, and therefore, the measure is not suitable under these circumstances. Code to implement this measure in R is provided in dryad: https://doi.org/10.5061/dryad.rbnzs7hbq.

2.2 | Testing geographic avoidance with an empirical dataset of cryptic bat species

2.2.1 | Study system

Bats offer good case studies for assessing the role of interspecific competition in shaping species ranges to due their high number of cryptic species (e.g. Ibáñez et al., 2006). To test the performance of the measure with an empirical dataset, we used four sets of potentially competing cryptic bat species (10 species in total): *Eptesicus serotinus, Eptesicus isabellinus, Myotis crypticus, Myotis escalerai, Plecotus auritus, Plecotus austriacus, Plecotus macrobullaris, Plecotus*
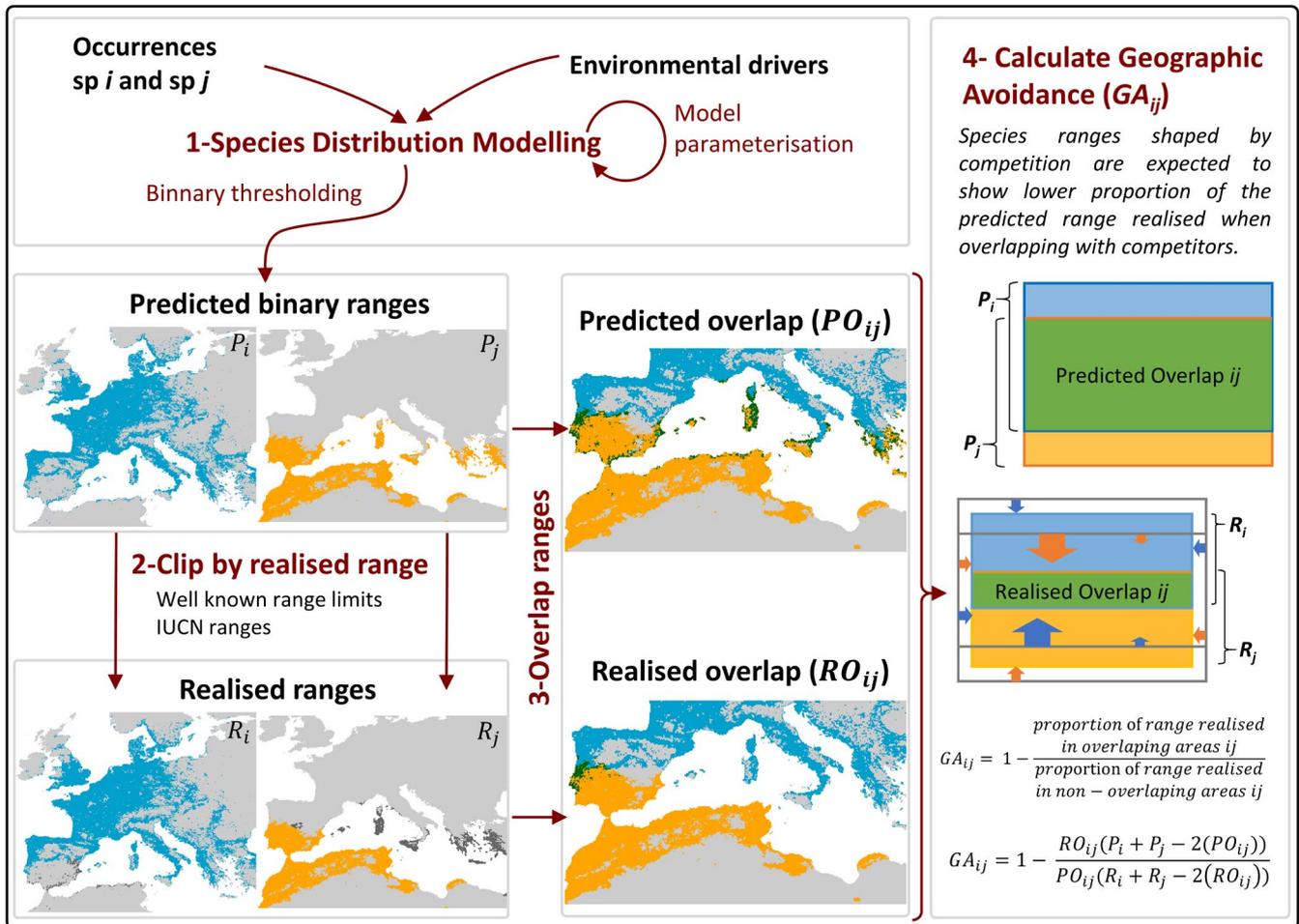
FIGURE 1 Flow chart representing the implementation of the approach to measure geographic patterns of species avoidance expected from macroecological effects of competition. 1—For a given pair of potentially competitor species, occurrence records and species environmental drivers are used to model species' predicted ranges. 2—Binary predicted ranges are cropped by species realised range limits to obtain species' realised ranges. 3—Ranges of both species are combined to estimate extent of overlap in predicted and realised ranges. 4— The measure of Geographic Avoidance (GA_{ij}) is applied. In this example, arrows describe a larger decrease from predicted to realised range in areas that overlap with the competitor (large arrows) than in non-overlapping areas (small arrows). Or, equivalently, a lower proportion of realised range occurs in overlapping areas compared to non-overlapping areas. This pattern is described by GA_{ij} with a value >0

kolombatovici, Rhinolophus euryale and *Rhinolophus mehelyi*. All species within each genus share a very similar morphology but have different degrees of geographic and ecological overlap. Consequently, we expect different levels of potential competition among them. See Table 1 for an outline of geographic, morphological and ecological overlap among these cryptic bat species and Tables S1.1–S1.3 for a more detailed overview of species ecological similarity. In addition to these four sets of potentially competitor cryptic groups, we included seven other bat species (*Myotis cappaccini, Myotis daubentonii, Myotis emarginatus, Myotis myotis, Myotis naterereri, Miniopterus schreibersii, Rhinolophus ferrumequinum*) to compare the GA_{ij} measure outcome between potential competitors to non-competitors. The study area included the western Palearctic and North Africa, extending up to a longitude of 34.5°E. This represents the full range of *E. isabellinus, M. escalerai, M. crypticus, P. austriacus* and *P. kolombatovici* and the majority of the range of the remaining potential competitor species.

2.2.2 | Occurrence and environmental data

In total, we gathered 13,408 species occurrence records. Of these, 6,976 came from five online databases: GBIF (www.gbif.org), BioGIS (www.biogis.huji.ac.il), NBN (nbn.org.uk), Eurobats (www.eurobats.org/) and Laji.fi (laji.fi); 1,892 from 64 publications (see Appendix S2) and 4,540 were unpublished records provided by seven bat researchers. Only records with validated species identification were used. In areas where ranges of similar species overlap, we used records that were confirmed genetically or morphologically by bat experts, considering identification year relative to when the species were split taxonomically. When original published records consisted only of a locality descriptor, geographic coordinates were obtained manually whenever possible (<1% of records). Spatial quality of records was checked, removing low-quality records in terms of spatial resolution and confirmed identification. We accounted for uneven sampling across the study area by removing clustered records in intensively

TABLE 1 The four cryptic bat species groups included in the study with information on their overlap in distribution, morphology and ecology (see Tables S1.1–S1.3 for overview on species ecological similarity). Information taken from Dietz and Kiefer (2016); Juste et al. (2019); Juste et al. (2004); Spitzenberger et al. (2006)

Group	Species	Distribution	Morphology	Ecological similarity
Eptesicus		Parapatric – overlap in a narrow contact zone in Iberia	Highly similar	Very High
	Eptesicus serotinus	Broad Palearctic distribution		
	Eptesicus isabellinus	Restricted to southern Iberia and North Africa		
Myotis[a]		Overlap in northern Iberia	Highly similar	Medium-High
	Myotis crypticus	Italy, southern France, and northern Iberia		
	Myotis escalerai	Restricted to Iberia and French Pyrenees		
Plecotus		Some overlap	Similar	Variable (Medium to Medium-High)
	Plecotus auritus	Broad Palearctic distribution, more northern distribution		
	Plecotus austriacus	Mediterranean and temperate parts of Europe		
	Plecotus macrobullaris	Mountain ranges across the Palearctic		
	Plecotus kolombatovici	Balkans		
Rhinolophus		High overlap	Minor differences	High, but lower when sympatric
	Rhinolophus euryale	Circa-Mediterranean		
	Rhinolophus mehelyi	Circa-Mediterranean		

[a]Another member of the *Myotis* cryptic group, the more northern European *Myotis nattereri*, was excluded from the study due to uncertainty regarding the extent of its range overlap with *M. crypticus* at the south-western part of its range.

sampled areas (Kramer-Schadt et al., 2013), using the ArcGIS toolbox "SDMtools" (Brown, 2014) with unclustering distances between 20 and 60 km based on species' degree of cluttering and range size. Most records used in the models (>95%) had a spatial precision <2 km. We included records with lower precision (up to 10 km) only in regions with very low sampling intensity (Eastern Europe and North Africa). This accounted for <5% of records.

To model the predicted range of each species, we considered 36 environmental variables recognized as ecologically important for bats (16 climatic, six geographic, 13 habitat and three human disturbance variables; Table S3.1). All raster layers were set at a resolution of 30 arc-seconds (~1 km). We tested for correlation among variables using ENMTOOLS v1.3 (Warren et al., 2010) and selected the most ecologically relevant variable or the variable with the stronger effect on model performance on its own among highly correlated variables ($|r| > 0.75$). Additionally, we discarded variables that did not contribute to model gain. Whenever possible, we aimed to select the same variables for species in the same cryptic group (Tables S3.2–S3.5 for final variables included in each model).

2.2.3 | Obtaining predicted and realised species ranges

Ensemble SDMs were generated using the R package biomod2 (Thuiller et al., 2009), including five models (MAXENT v3.4, generalized boosting model, classification tree analysis, random forests and flexible discriminant analysis). For each model, we selected 10,000 random background points and 1,000 maximum iterations. Maxent model parameters (number of features and regularization value) were selected based on Akaike information criterion (AIC) scores using ENMTOOLS v1.3 (Table S3.6 for final model features). To assess model performance, we used tenfold cross-validations, with 75% of records used for training and 25% for model testing. The ability of the models to discriminate between presence locations and background pseudo-absences was evaluated with area under the curve (AUC) of the receiver operator characteristics (ROC) and True Skill Statistic (TSS). The 10 model replicates were combined to obtain a final predictive map for each of the five modelling methods. Ensemble models were obtained by using AUC values to proportionally weight each method according to its predictive power, excluding models with AUC < 0.75. Binary presence–absence maps were generated based on the thresholding criteria that minimizes the difference between sensitivity and specificity because these criteria has been shown to outperform others (Liu et al., 2013). However, we analysed whether using other four commonly used thresholding criteria resulted in changes in the measure. It is important to note that measures of accuracy of thresholded maps in general assume presence–absence data, while our models were generated using presence-only data and background points.

Species' realised ranges were calculated by clipping the SDM output binary maps using a convex hull polygon drawn around occurrence records (R package concaveman, Gombin et al., 2017) and adding a buffer of 30 km. This distance considers a species' home

range (3–10 km depending on species; Boye & Dietz, 2005), and seasonal or reproductive movements that typically occur outside species home range (e.g. Robinson & Stebbings, 1997). Before using these maps to calculate the measure of GA_{ij}, they were projected to the Gall-Peters equal-area projection to allow for area calculations.

2.2.4 | Assessing the performance of the measure

We calculated the measure of GA_{ij} for the pairs of potentially competitor species and tested whether observed values were higher than distributions of null values obtained for pairs of virtual species. For that we created for each species 15–30 sets of virtual ranges (R package *virtualspecies*, Leroy et al., 2015) that follow environmental gradients, using the PCA method. We selected from the resulting virtual species ranges, the areas with highest suitability scores totalling the equivalent size of the realised range of the real species. We distributed within that area the same number of random occurrence records as used in the models of the real species. With this procedure, for each species we obtained different sets of occurrence records with the same number of records and covering the same area as the real species, but following different, though ecologically meaningful, environmental gradients and having different spatial distributions. We used these randomly generated sets of occurrence record to model virtual species' predicted ranges, and we clipped them to obtain their realised ranges, following the same procedures outlined above for the empirical dataset. Finally, we calculated, for each pair of potentially competitor species in the empirical dataset, values of GA_{ij} between all pair combinations of equivalent virtual ranges. These distributions constitute the null expectation of GA_{ij} values between virtual species with the same number of occurrence records and coverage extent, but arbitrary environmental preferences and different spatial distribution from the real species. We only used pairs of sets of virtual ranges whose realised range overlapped by more than 0.5% to reduce inaccuracies due to the calculation of ratios with very small values. We compared for each pair of potentially competing bat species, the observed value of GA_{ij} with at least 100 null values. Observed values of GA_{ij} higher than 95% of null values were considered as significantly higher than null expectations. We also compared GA_{ij} values of potential competitor pairs with GA_{ij} between all combination of non-competitor pairs (115), which includes species pairs from different cryptic groups as well as pairs formed with the additional seven species. GA_{ij} values between potential competitor pairs higher than 95% of the values between non-competitor pairs were considered as significantly higher.

We analysed whether the measure was robust to missing data and spatial sampling biases. For each species, we randomly removed 10, 20 and 30% of the occurrence records across the entire study area. In addition, we divided species' range extents to nine equal quadrats; we randomly selected five and removed from these 10%–30% of the occurrence records to simulate spatial bias in the data. Both thinning processes were repeated 10 times at each of the three data removal percentages. We used these sets of thinned records and the original complete set of records to run SDMs (Table S3.7). We assessed whether GA_{ij} values obtained using the full datasets fell within 95% confidence intervals of GA_{ij} values from thinned datasets.

2.2.5 | Comparing measure outputs to patterns of ecologically similarity

Ecological similarity of potential competitor bat pairs was ranked from 1 (minimum) to 5 (maximum) in terms of foraging habitat, diet and roosting ecology by five bat researchers based on the literature and expert opinion (Appendix S1). Evidence of fine-scale resource partitioning between each pair was determined based on the literature. Values of GA_{ij} between pairs of cryptic bat species were compared to these values of ranked ecological similarity and evidence of resource partitioning.

2.2.6 | Predicting future range losses considering current geographic avoidance

In order to assess whether competition between pairs of species may modify future suitable range predictions, we modelled changes in range suitability for species under climate change projections for 2070. We used the worst-case emission scenario (RCP 8.5) and three different European Global Circulation Models (GCMs: HadGEM2-ES, IPSL-CM5A-LR and MPI-ESM-LR; obtained from www.worldclim.com). We included in the models the same climatic variables as in the main models (Tables S3.2–S3.5), excluding habitat variables because of high uncertainty in land cover change projections, and altitude due to collinearity with climate. We combined the outputs from the three GCMs and considered future suitable areas if identified by two or more GCMs. We estimated range losses through comparing the future models to models generated for present conditions using the same variables. Then, we calculated predicted future geographic overlap between pairs of cryptic bat species within a 500 km buffer around their current range. This distance was selected to represent the maximum distance that these bats are likely to be able to disperse in response to climate change by the end of the century. As none of the studied species are long-distance migrants, they are not likely to reach all suitable future areas projected by the models. Species pairs with high geographic avoidance and an increased future geographic overlap may not realise their future range change predictions due to the effects of competition.

3 | RESULTS

3.1 | Geographic avoidance between cryptic bat species

Ensemble SDMs had good discrimination ability (AUC$_{test}$ range: 0.92–0.99, TSS: 0.65–0.93; Table S3.8). Models predicted different

suitable ranges for members of the same cryptic group, but with some extent of suitable range overlap. *P. auritus* and *E. serotinus* were predicted to have a more northern European distribution, *P. austriacus*, *M. escalerai* and *M. crypticus* a southern European distribution, while *Rhinolophus* spp. and *E. isabellinus* a circa-Mediterranean distribution. The percentage of unrealised range was particularly high (>40%) for *P. kolombatovici*, *M. escalerai*, *M. crypticus* and *P. macrobullaris*, intermediate (15%–30%) for *E. isabellinus*, *R. euryale*, *P. austriacus* and *R. mehelyi* and low (<10%) for *P. auritus* and *E. serotinus* (Figure 2; Figure S3.1).

The extent of geographic avoidance (GA_{ij}) was lowest (<0) in the pairs *P. auritus*–*P. austriacus*, and *P. macrobullaris*–*P. kolombatovici*. Intermediate in *R. euryale*–*R. mehelyi* (0.31), *M. escalerai*–*M. crypticus* (0.35), *P. auritus*–*P. macrobullaris* (0.53) and *P. austriacus*–*P. macrobullaris* (0.57) and highest in *P. austriacus*–*P. kolombatovoci* (0.83) and *E. serotinus*–*E. isabellinus* (0.85). Only in the latter two pairs, GA_{ij} values were higher than 95% of values of 100 null models (Table 2; Figure 3) and also higher than 95% of GA_{ij} values between non-competitor species (Figure S3.2). These two pairs with significantly higher GA_{ij} values than null expectations and non-competitors were also the ones with highest levels of ecological similarity and no known mechanisms of resource partitioning (Table 2).

Measure outputs based on other binary thresholding criteria resulted in very similar values (Figure S3.3). Similarly, thinned sets of occurrence records did not produce different GA_{ij} values compared to the full datasets for four out of the nine bat species pairs under all the thinning methods and all removal percentages. For the other five species, thinned sets tended to produce slightly higher GA_{ij} values, especially at larger percentage of thinning, but not depending on thinning method. Nevertheless, in all cases values were very close and had the same ranking relative to other species pairs, showing that the measure is robust to missing data and geographically biased sampling (Figure S3.4).

3.2 | Future range losses and overlap

Present projections with only climatic variables were very similar in extent to the ones including habitat variables and mostly differed in the fine-grained suitability values. When projected to the future, models predicted losses in climatic range suitability for *E. serotinus*, *M. escalerai*, *M. crypticus*, *P. auritus* and *P. macrobullaris* under future climate change. In contrast, the suitable climatic ranges of *E. isabellinus*, *P. austriacus*, *P. kolombatovici*, *R. euryale* and *R. mehelyi* were predicted to increase by the end of the century (Table S3.9). Under future climate change, range overlap was predicted to decrease in the pairs *E. serotinus*–*E. isabellinus*, *M. escalerai*–*M. crypticus* and *P. auritus*–*P. macrobullaris*. While range overlap in *P. auritus*–*P. kolombatovici*,

P. macrobullaris–*P. kolombatovici* and *R. euryale*–*R. mehelyi* was predicted to increase. For the pairs with high values of GA_{ij}, range overlap between *E. serotinus* and *E. isabellinus* was predicted to decrease
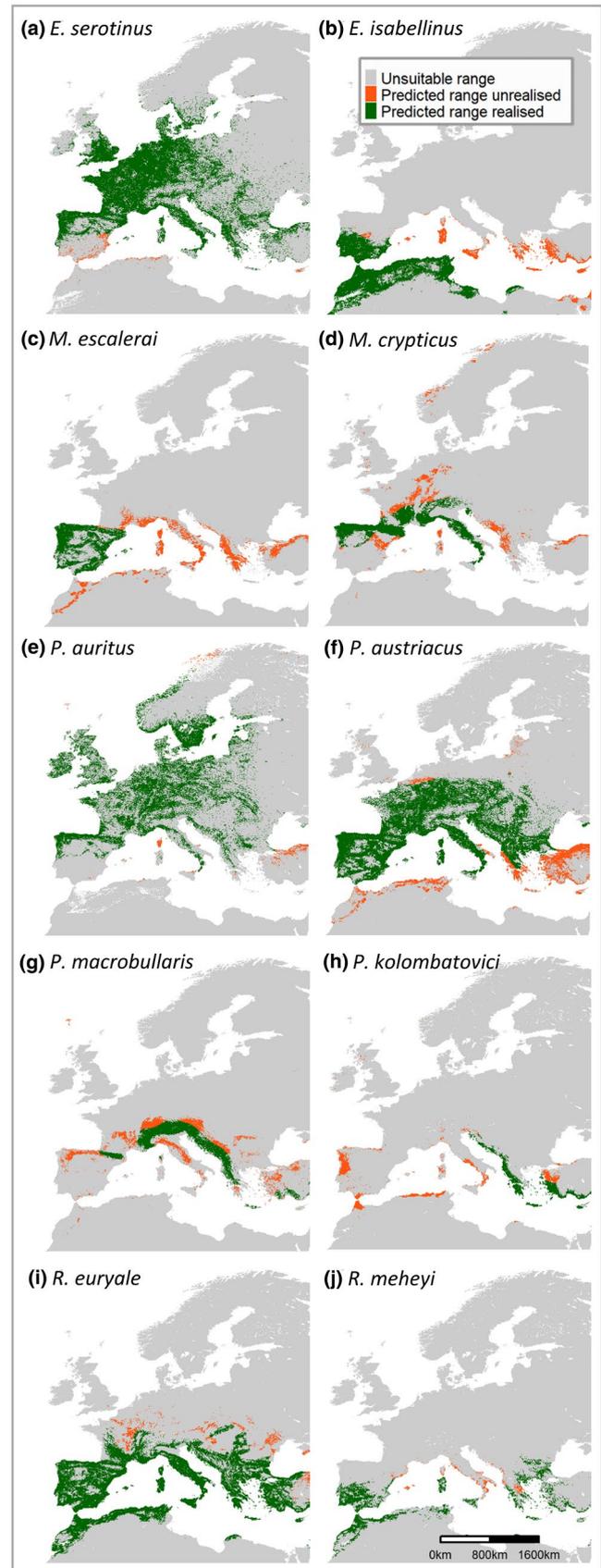
FIGURE 2 Predicted ranges of the four sets of cryptic bat species partitioned into portions that are realised (green) and unrealised (orange). *Eptesicus* group: (a,b), *Myotis* group (c,d), *Plecotus* group (e–h) and *Rhinolophus* group (i,j)

TABLE 2 Results of the measure of geographic avoidance between pairs of cryptic bat species and their level of ecological similarity. Predicted (PO$_{ij}$) and realised range overlap (RO$_{ij}$). Observed geographic avoidance (GA$_{ij}$ Obs). Null distribution of GA$_{ij}$ values using virtual species, including mean (GA$_{ij}$ null mean), and 95% confidence intervals (GA$_{ij}$ null CI). Extent of ecological similarity between species pairs (range 1–5) according to foraging habitat, diet and roost selection and evidence of resource partitioning when sympatric based on expert opinion and the literature (details in Appendix S1, Tables S1.1–S1.3)

Species pair	PO$_{ij}$ (%)	RO$_{ij}$ (%)	GA$_{ij}$ Obs	GA$_{ij}$ null mean	GA$_{ij}$ null CI	Ecological similarity Habitat	Diet	Roost	Resource part.
E. serotinus–E. isabellinus	4.90	0.75	0.85[a]	0.37	0.14–0.63	4.5	4.7	4.5	No
M. escalerai–M. crypticus	29.99	21.76	0.35	0.45	0.06–0.78	3.5	4.5	1.5	Some
P. auritus–P. austriacus	25.54	26.88	–0.07	0.18	–0.03 to 0.50	2.6	3.7	2.6	Yes
P. auritus–P. kolombatovici	2.29	0.23	NA	NA	NA	2.6	3.7	2.6	Yes
P. auritus–P. macrobullaris	15.19	7.73	0.53	0.40	0.23–0.63	2.0	3.5	2.7	Yes
P. austriacus–P. kolombatovici	12.43	2.32	0.83[a]	0.48	0.24–0.66	4.5	3.7	4.0	No
P. austriacus–P. macrobullaris	18.93	9.17	0.57	0.49	0.25–0.77	3.5	3.7	2.7	Some
P. macrobullaris–P. kolombatovici	11.28	11.32	–0.01	0.51	0.05–0.86	3.5	4.7	2.7	Some
R. euryale–R. mehelyi	30.33	23.07	0.31	0.36	0.08–0.67	4.0	4.7	4.8	Yes

[a]Denotes values falling above the 95% CI of 100 null models. Realised range overlap between P. auritus and P. kolombatovici was too small to calculate the measure.

(−27.42%), while overlap between *P. austriacus* and *P. kolombatovici* was predicted to increase substantially (42.27%) (Table 3). Adding the effects of these competitive interactions into projections of future range suitability shows that a large proportion of future climatically suitable areas for *P. kolombatovici* may not be realised due to the presence of *P. austriacus* (Figure 4).

4 | DISCUSSION

Our study suggests, using a new approach based on SDM outputs and empirical data from sets of cryptic Palearctic bat species, that interspecific competition can limit the geographic ranges of morphologically similar species in the absence of fine-scale mechanisms of coexistence. This study provides additional evidence for the potential of competition to shape species' geographic ranges (e.g. Gotelli et al., 2010; Sexton et al., 2009; Staniczenko et al., 2018). Moreover, it supports predictions made by mathematical models that competitive exclusion scales up and impacts species ranges only when coexistence mechanisms, such as trophic or habitat partitioning, are not developed at finer spatial scales (Godsoe et al., 2015). Biotic interactions, and in particular interspecific competition, can slow down climate tracking and prevent species from colonizing new habitats (HilleRisLambers et al., 2013). Yet despite the urgent need to better understand the effect of biotic interactions on species vulnerability to climate change, there is currently no adequate methodology to infer competitive effects at the regional or continental spatial scale.

4.1 | The link between broad-scale geographic avoidance and fine-scale mechanisms of coexistence

Biotic interactions are primarily thought to play a role in driving local assemblages, which are, as a result, often composed of morphologically and functionally different species (Bocher et al., 2014; Codron et al., 2015). However, there is increasing evidence that biotic interactions can affect broader-scale biogeographic patterns (Sexton et al., 2009). Our results suggest that local-scale coexistence mechanisms are key processes preventing biotic interactions from scaling-up and having broader-scale consequences. The two pairs of species found to have higher values of geographic avoidance than expected by chance are the most ecologically similar pairs of species that lack fine-scale mechanisms of resource partitioning. *E. serotinus* and *E. isabelinus* are similar in their habitat use, being both open air foragers, have very similar diets composed mostly by Coleoptera and share similar roosting preferences (Tables S1.1–S1.3). Interspecific competition has been previously suggested to affect these species' ranges (Santos et al., 2014). *P. austriacus* and *P. kolombatovici* use similar semi-open habitats, feed mostly on Lepidoptera and roost in anthropogenic structures or caves (Tables S1.1–S1.3). In contrast, pairs of species with lowest levels of geographic avoidance, including *P. auritus–P. austriacus* and *R. euryale–R. mehelyi*, are known examples of bat
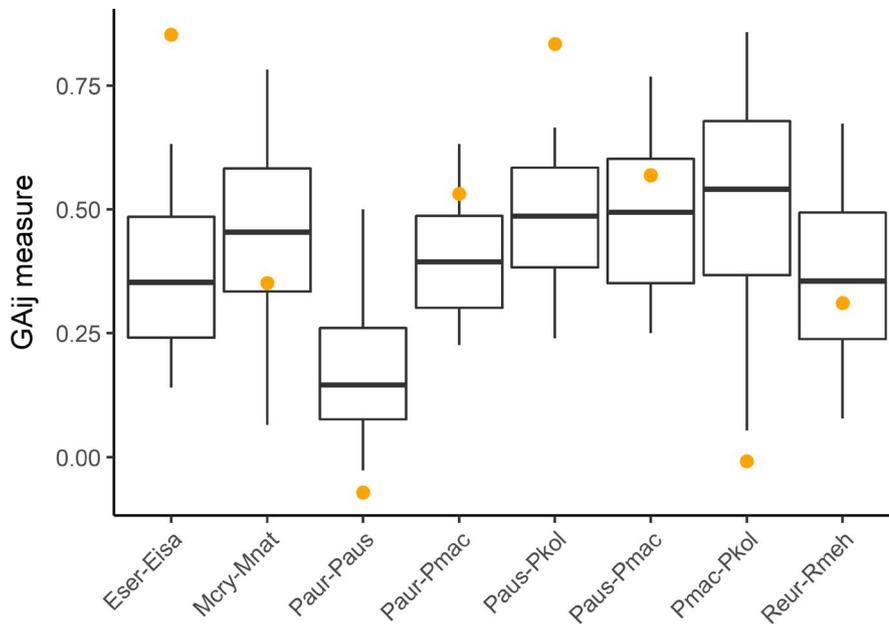
FIGURE 3 Geographic avoidance (GA_{ij}) values for each pair of cryptic bat species (orange large dots) relative to null distributions of values (boxplots). Boxes represent first and third data quartiles. Whiskers represent 95 percentiles. (Eser: *E. serotinus*, Eisa: *E. isabellinus*. Mesc: *M. escalerai*. Mcry: *M. crypticus*. Paur: *P. auritus*. Paus: *P. austriacus*. Pkol: *P. kolombatovici*. Pmac: *P. macrobullaris*. Reur: *R. euryale*. Rmeh: *R. mehelyi*)

Species pairs	Present PO_{ij} (%)	Future PO_{ij} (%)	Change in PO_{ij} (%)
E. serotinus–E. isabellinus	1.08	0.79	−27.42
M. escalerai–M. crypticus	19.54	15.07	−22.84
P. auritus–P. austriacus	25.40	15.71	−38.14
P. auritus–P. macrobullaris	12.16	8.41	−30.87
P. austriacus–P. macrobullaris	12.11	8.03	−33.70
P. auritus–P. kolombatovici	2.53	1.78	−29.91
P. austriacus–P. kolombatovici	9.59	13.65	42.27
P. macrobullaris–P. kolombatovici	8.14	9.89	21.45
R. euryale–R. mehelyi	45.13	45.23	0.21

TABLE 3 Comparison between present predicted overlap between pairs of cryptic bat species and future predicted overlap in 2070 under RCP 8.5 emissions scenario. Differences in PO_{ij} compared to Table 2 are because these models did not include land cover variables

species with similar morphology and broad-scale range overlap that coexist through fine-scale habitat partitioning (Tables S1.1–S1.3).

Broad-scale biogeographic patterns in bats are mainly driven by temperature and water availability (McCain, 2006; Ulrich et al., 2007) especially in areas where access to water can be limiting (Razgour et al., 2018). However, several studies point to biotic interactions and in particular interspecific competition as important processes in the group (see Salinas-Ramos et al., 2020). Competition has been suggested to limit morphological similarity among rhinolophid bats in Malaysia (Kingston et al., 2000) and bat assemblages in southern Africa, where patterns of body size are regularly spaced (Schoeman & Jacobs, 2008). Studies using exclusion experiments in both tropical (Kalka et al., 2008) and temperate forests (Böhm et al., 2011) show that bats can control arthropod abundance, suggesting that exploitative competition may occur between bats due to prey depletion. Competition among bats can also occur through interference when species are attaining prey resources. Large aggregations of bats are thought to forage less effectively as a consequence of echolocation interference (Amichai et al., 2015), and bats can actively use jamming calls to disrupt competitors and make them

miss targets (Corcoran & Conner, 2014). Our study suggests that competition among bats can also scale up to affect their broad-scale geographic distributions in the absence of fine-scale mechanisms of resource partitioning.

4.2 | Performance of the measure of geographic avoidance

No currently available methodology enables direct inference of competitive interactions from analysing co-occurrence patterns at broad spatial scales given the commonly available density of occurrence data. Our measure of geographic avoidance quantifies the expected geographic patterns resulting from broad-scale competitive exclusion and produces inferences consistent with predictions based on ecological information and evidence of coexistence mechanisms. Previous studies using SDM's outputs to identify patterns of geographic exclusion resulting from competitive interactions measured an uneven proportion of occurrence records in the predicted overlapping range or a mismatch in species identity (Anderson et al., 2002; Gutiérrez et al., 2014).

FIGURE 4 Present and future predicted suitable range for *E. serotinus* (a), *E. isabellinus* (b), *P. austriacus* (c) and *P. kolombatovici* (d) and extent of range overlap with their potential competitors. Orange shows current range that will become unsuitable in future. Green shows current range that will still be suitable in future, and blue shows current unsuitable range that will become suitable. Black shows future suitable range that will overlap with future suitable range of a competitor
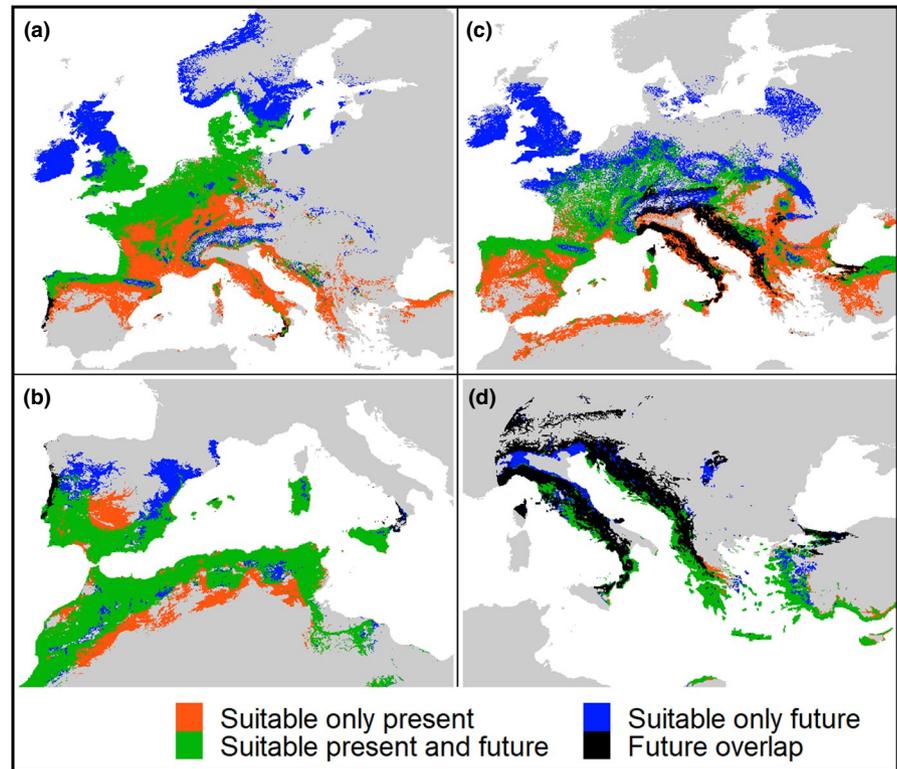
The applicability of these methods is however limited by their assumptions of identical environmental preferences, sampling effort and detectability for both species in the potential predicted overlapping area. The method of including a competitor's realised range in SDMs is thought to primarily suit simple systems (Anderson, 2017) and correlations between environment and competitors make difficult to distinguish the effect of competition from environmental effects (Godsoe et al., 2017). While JSDM approaches directly incorporate biotic interactions into the models, they are most suitable for spatially-discrete community level studies, and the common lack of available representative community data across large spatial extents limits their application in broad-scale studies. The use of JSDMs with insufficient sampling intensity would result in a large amount of false absences that the model may interpret as negative residual correlations.

The approach presented here is based on the assumption that SDMs are able to estimate representatively the predicted and realised ranges of the species, which, equally to any other study based on SDMs, is a function of the quality of the occurrence data used and the inclusion of all the relevant environmental variables in the models (Guisan et al., 2017). While we show that the measure is considerably robust to missing data and spatially biased data, the occurrence data used should offer a good representation of the realised range of both species. The realised ranges for our case study species have been extensively studied by the authors and therefore are best represented by our data. However, whether using either own data or IUCN range maps, uncertainties in realised range and extent of realised overlap among species should always be carefully taken into account. Hence, this approach is not suitable for data-deficient species with under-studied range extents.

Lower ratio of realised range in overlapping areas relative to non-overlapping areas could occur for other reasons than competitive effects, such as dispersal limitations in that area (Guisan et al., 2017; Soberón & Peterson, 2005) or by chance due to inaccuracies in model predictions. Therefore, interpretations of the measure outputs should consider the potential effects of dispersal limitations. Dispersal limitation is less likely to bias the conclusions with volant animals like bats and birds, but more so with dispersal-limited taxa, such as other small mammals, reptiles and amphibians. The comparison between the observed patterns with null models based on virtual species allows to identify the cases where the observed pattern is greater than expected by chance and therefore most likely to be result of competition.

Altogether, this approach is most suitable for pairs of species with well and equally known ranges and little dispersal restrictions. Inferences given by the measure should be taken as a geographic pattern consistent with a process of broad-scale competitive exclusion, and not as a direct inference of the effect of competition. A sensible interpretation of current biogeographical patterns also requires knowledge of evolutionary history to tease-apart biotic and historical effects, in particular for species with limited dispersal and colonization abilities (Dormann et al., 2018; Warren et al., 2014), and information on ecological similarity between species.

4.3 | Including biotic interactions in range shift projections under climate change

Biotic interactions can modify predicted responses of species to climate change (HilleRisLambers et al., 2013), as highlighted

by theoretical models assessing species extinction risk (Norberg et al., 2012). Climate change can lead to changes in the intensity of interactions or the appearance of novel interactions (Alexander et al., 2016). While the outcome of the interaction between biotic interactions and range shift processes is difficult to predict, considering the patterns of species geographic avoidance presented in our study could be of relevance. In species pairs with high geographic avoidance, if future suitable range overlap is predicted to increase, model projections that ignore the impact of strong biotic interactions will overestimate future range suitability. In contrast, a decrease in predicted future suitable overlap could lead to an unexpected larger suitable area due to competitive release. In our study system, among the pairs of species whose current ranges are most likely shaped by competition, future models predict a decrease in range overlap between *E. serotinus* and *E. isabellinus*, which would lead to competitive release effect and larger realisation of their future suitable ranges than at present. Conversely, the ranges of *P. austriacus* and *P. kolombatovici* are predicted to overlap substantially more in the future, which may limit the ability, in particular of *P. kolombatovici* that already has a very restricted range, to shift its range to track future suitable conditions. We show that disregarding biotic interactions can affect our ability to accurately predict species future distributions and their vulnerability to climate change. We also stress the importance of generating future range suitability projections that indicate areas where interspecific competition may limit range shifts.

5 | CONCLUSIONS

Our study suggests that in absence of fine-scale mechanisms of resource partitioning, the effects of interspecific competition can scale up to impact species broad-scale geographic ranges. Therefore, this study highlights the importance of considering the effects of biotic interaction when predicting future range suitability under climate change. While a better comprehension of the operation of biogeographical processes across spatial scales requires better integration of community ecology process with larger-scale species distribution models, the measure of geographic avoidance that we present can be used to identify range patterns compatible to a broad-scale effect of interspecific competition. Its low data and computational requirements allow it to be widely applied as a screening tool to identify cases where biotic interactions could impact future climate change predictions.

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BIOSKETCH

Roberto Novella-Fernandez is interested in to develop comprehensive understanding on the role of ecological processes driving diversity patterns, which is key to increase our ability to predict antropogenic impacts on biodiversity. He currently focuses his research on the operation on environmental and biotic filtering processes across spatial scales, from species ranges to local assemblies by using spatially explicit modelling tools and a functional perspective.

Author´s contributions: RNF and OR conceived the idea and designed the study. RNF carried out all GIS modelling and analyses. HP, OR, LG, and CPD advised on the measure and methods. JJ, CI, HR, AA, DR, AK provided location records data and contributed to the assessment of ecological similarity. RNF led the writing of the manuscript and OR supervised the project. All co-authors contributed to revisions.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.