Journal of Biogeography

WILEY

Journal of Biogeography

RESEARCH ARTICLE OPEN ACCESS

Variations of Environmental Niche Breadth, Range Sizes and Geographic Exclusion With Bat Species Richness

Julian Oeser[1] | Damaris Zurell[2] | Frieder Mayer[3] | Emrah Çoraman[3,4] | Nia Toshkova[5] | Stanimira Deleva[5] | Ioseb Natradze[6] | Petr Benda[7,8] | Christian Dietz[9] | Panagiotis Georgiakakis[10] | Eran Levin[11] | Amit Dolev[12] | Heliana Dundarova[13] | Astghik Ghazaryan[14] | Sercan Irmak[4,15] | Nijat Hasanov[16] | Gulnar Guliyeva[16] | Mariya Gritsina[17] | Alexander Bukhnikashvili[6] | Tobias Kuemmerle[1,18]

[1]Geography Department, Humboldt-Universität zu Berlin, Berlin, Germany | [2]Ecology and Macroecology, Institute for Biochemistry and Biology, University of Potsdam, Potsdam, Germany | [3]Museum für Naturkunde, Leibniz-Institut für Evolutions- und Biodiversitätsforschung, Berlin, Germany | [4]Department of Ecology and Evolution, Eurasia Institute of Earth Sciences, Istanbul Technical University, Maslak, Istanbul, Türkiye | [5]National Museum of Natural History, Bulgarian Academy of Sciences, Sofia, Bulgaria | [6]Institute of Zoology of Ilia State University, Tbilisi, Georgia | [7]Department of Zoology, National Museum, Praha 1, Czech Republic | [8]Department of Zoology, Faculty of Science, Charles University, Praha 2, Czech Republic | [9]Biologische Gutachten Dietz, Haigerloch, Germany | [10]Natural History Museum of Crete, University of Crete, Irakleio, Greece | [11]School of Zoology, Faculty of Life Sciences, Tel-Aviv University, Tel Aviv, Israel | [12]Science Division, Nature and Park Authority, Jerusalem, Israel | [13]Institute of Biodiversity and Ecosystem Research, Bulgarian Academy of Sciences, Sofia, Bulgaria | [14]Department of Zoology, Yerevan State University, Yerevan, Armenia | [15]Science and Technology Research and Application Center, Balikesir University 10145, Balıkesir, Türkiye | [16]Institute of Zoology, Ministry of Science and Education, Baku, Azerbaijan | [17]Institute of Zoology, Academy of Science of Uzbekistan, Tashkent, Uzbekistan | [18]Integrative Research Institute on Transformation in Human Environment Systems, Humboldt-Universität zu Berlin, Berlin, Germany

Correspondence: Julian Oeser (julian.oeser@gmail.com)

Received: 17 January 2025 | **Revised:** 2 March 2025 | **Accepted:** 16 March 2025

Funding: This work was supported by Leibniz-Gemeinschaft and Istanbul Teknik Üniversitesi.

Keywords: avoidance | bats | competition | distribution modelling | exclusion | niche breadth | range filling | range size | richness

ABSTRACT

Aim: More species-rich communities are often assumed to contain more specialist species with narrower niches and smaller ranges. Stronger interspecific competition in species-rich communities is thought to be a key mechanism explaining these patterns. Yet, the relationship between richness and specialisation has so far only been studied for a few taxa, and characterising the effects of interspecific competition on species distributions is challenging. Here, we assess broad-scale relationships between niche breadth, range sizes and geographic exclusion along richness gradients of bats.

Location: Eastern Mediterranean, Western Asia, and Central Asia.

Taxon: Bats (Chiroptera).

Methods: Based on a novel integrated species distribution modelling approach that combines occurrence information with expert range maps, we assessed how environmental niche breadth and range sizes varied with species richness. In addition, by contrasting species' potential and realised distributions in areas where species pairs overlap, we derived indicators of geographic exclusion to understand how potential interspecific competition is affecting range limits along richness gradients.

Results and Main Conclusions: We found a nonlinear association between environmental niche breadth and richness, with the most specialised species occurring in species-poor regions and niche breadth peaking at intermediate richness. Despite a positive association of niche breadth and range sizes at the species level, range sizes in predicted bat communities declined continuously with species richness. In addition, patterns of geographic exclusion were linked to patterns of niche breadth, with species filling less of their potential range overlaps when overlapping species were more specialised. Our findings suggest that

Journal of Biogeography, 2025; 52:e15125
https://doi.org/10.1111/jbi.15125

small range sizes in species-rich bat communities are better explained by the number of interacting species than by environmental specialisation or stronger exclusion between individual species. More broadly, we show how integrated distribution modelling approaches can shed new light on the interplay of species richness, specialisation and community structure, and caution against generalising relationships between richness and specialisation across taxa and geographies.

1 | Introduction

Increasing species richness is commonly associated with more specialised communities. In this context, specialisation is often understood as a decrease in environmental niche breadth (i.e., environmental specialisation) in more species-rich communities (Belmaker et al. 2012; Chejanovski and Wiens 2014). In addition, in line with the widely observed positive association between niche breadth and range sizes (Slatyer et al. 2013), increasing species richness has also been linked to smaller range sizes (Batt et al. 2017; Eeley and Foley 1999). Whereas traditionally, relationships between richness and specialisation have mainly been studied across latitudinal gradients (Stevens 1989), recent evidence suggests clear direct associations between species richness and specialisation, independent of latitude. For example, meta-analyses on the relationships of niche breadth (Granot and Belmaker 2020) and range sizes (Guo et al. 2022) observed clear trends of specialisation with increasing richness. Yet, associations between specialisation and richness remain unexplored for many taxa, or else have been summarised at broad taxonomic levels (e.g., all birds and mammals; Belmaker et al. 2012; Boucher-Lalonde et al. 2016), which could obscure variation if relationships differ between taxonomic groups. Thus, it remains unclear how general trends of specialisation and range sizes with increasing richness are.

One key mechanism that could explain increased specialisation in more species-rich communities is stronger biotic interactions, particularly increased interspecific competition (Bolnick et al. 2010; Legault et al. 2020). In line with this idea, the meta-analyses by Granot and Belmaker (2020) and Guo et al. (2022) concluded that the observed patterns of decreasing niche breadth and range sizes with increasing richness are best explained by stronger biotic interactions in species-rich communities. Yet, data on the effects of interspecific competition is difficult to obtain, and it has thus rarely been tested whether high species richness coincides with stronger effects of interspecific competition on species ranges. Therefore, open questions remain regarding how niche breadth and range sizes are linked to interspecific competition, and whether decreasing range sizes in species-rich communities are explained by an increasing number of interacting species, stronger competitive interactions or result from environmental specialisation (i.e., narrower niche breadths).

Bats (Chiroptera) provide an interesting case for assessing how species richness relates to patterns of environmental niche breadth and range sizes. Although comprising roughly 20% of all described mammal species (Peixoto et al. 2018), the distribution and niches of bats remain poorly understood, with detailed data on bat species richness lacking for many regions (Herkt et al. 2016). Bats often show high diet overlap (70% of bat species are insectivorous) and high morphological similarity (Salinas-Ramos et al. 2020). Bat species occupying similar trophic and morphological niches have frequently been shown to coexist through fine-scale mechanisms of niche partitioning, such as spatiotemporal partitioning in foraging habitats or echolocation activities (Krüger et al. 2014; Novella-Fernandez et al. 2020; Peixoto et al. 2018; Razgour et al. 2011; Roeleke et al. 2018). Yet, recent evidence suggests that interspecific competition between morphologically similar species can limit bat ranges at broad spatial scales when fine-scale coexistence mechanisms are lacking (Novella-Fernandez et al. 2021). However, it remains unclear how broad-scale patterns of bat species richness relate to variations in environmental niche breadth and range sizes, and whether high bat species richness is associated with specialisation as observed in other mammal taxa (e.g., primates; Eeley and Foley 1999).

Understanding the associations between niche breadth, range sizes, and interspecific competition requires approaches that jointly characterise these phenomena (D'Amen et al. 2018; Novella-Fernandez et al. 2021). Species distribution models (SDM; Elith and Leathwick 2009) are potentially powerful in this regard, allowing to assess species' environmental niches, distributions, and emerging patterns of species richness (Syfert et al. 2018; Zurell, Zimmermann, et al. 2020). However, SDMs typically characterise species' *potential distributions* determined by environmental conditions, rather than species' *realised distributions* that are further constrained by biotic interactions and dispersal limitations (Araújo and Guisan 2006; Soberon and Peterson 2005). In addition, rare species without sufficient reliable occurrence data often need to be excluded from SDM analyses (van Proosdij et al. 2016), which can bias richness patterns obtained from stacking species-level distributions.

Here, we attempt to overcome these limitations through an SDM approach that integrates occurrence observations with expert range maps (Oeser et al. 2024). Adding information on species' range limits makes it possible to contrast realised and potential ranges and assess *range filling* (Svenning and Skov 2004). For highly mobile organisms like bats that are not strongly limited by dispersal, this enables us to evaluate the degree of geographic avoidance and exclusion among overlapping species, which can proxy the importance of interspecific competition as a range-limiting factor (Novella-Fernandez et al. 2021). In addition, we use expert range maps to estimate and correct geographic bias in species richness maps stemming from the exclusion of rare species in stacked SDM predictions. We apply this approach to understand relationships between specialisation and geographic exclusion along richness gradients in a biodiverse but understudied region ranging from the Eastern Mediterranean to Central Asia. Specifically, we ask the following research questions:

1. What are the geographic patterns of bat species richness across our study area?
2. How do environmental niche breadth and range size relate to community richness?

3. How does geographic exclusion relate to niche breadth and community richness?
4. How do niche breadth, species richness and geographic exclusion influence species' range size?

2 | Material and Methods

2.1 | Species Distribution Models

Our study area covers about 6.5 million km^2 and intersects four global biodiversity hotspots (following Myers et al. 2000): the eastern part of the Mediterranean hotspot, the Caucasus hotspot, the Irano-Anatolian hotspot, as well as partially covering the Mountains of Central Asia hotspot. We collected and homogenised a large bat occurrence dataset (9650 records, see Figure 1) from various sources of field data, primarily collected via mist netting, opportunistic sightings and echolocation recordings. These data were available as part of literature sources, national databases (Georgiakakis et al. 2023; Natradze et al. 2023) and fieldwork carried out by the authors and their teams (see Appendix S1 and ODMAP protocol in Appendix S3 for details on the occurrence data and its sources).

We used this occurrence data set alongside environmental predictors characterising climate, land cover, topography, geology and human pressure to build species distribution models (SDMs) for 49 bat species at 1 km resolution (see Appendix S2 for a description and overview of all environmental predictor variables). For each species, we performed cross-validations to select the best-performing variables with pairwise correlations <0.7 (Dormann et al. 2013), limiting the number of variables chosen to 1 per 10 available presence records to avoid overfitting (Moudrý et al. 2024; Reineking and Schröder 2006). The number of selected variables ranged from 2 to 16 (median: 8). We tuned hyperparameters of the modelling algorithms using a grid search in a second cross-validation. To treat sampling bias, we thinned occurrence records (Boria et al. 2014) and performed a target-group background sampling (Barber et al. 2022; Inman et al. 2021; Syfert et al. 2013). We provide an ODMAP protocol (Zurell, Franklin, et al. 2020) in Appendix S3 summarising all key modelling decisions. In addition to a traditional SDM approach (ensemble of SDM algorithms), we integrated SDMs with expert information on range limits (expert range maps provided by the International Union for the Conservation of Nature—IUCN; Oeser et al. 2024).

Specifically, we used the integrated SDM approach developed by (Oeser et al. 2024). In the following, we provide a brief overview of the approach and refer to Oeser et al. (2024) for a full description. The integrated SDM approach is based on an ensemble method called stacked generalisation. In stacked generalisation, the predictions of several input models are used as training data in a meta-learner regression model (Naimi and Balzer 2018). Specifically, we combined three SDM algorithms (Maxent, random forest and boosted generalised additive models) via logistic regression as a meta-learner. By adding the distance of occurrence records to the expert range maps as an additional predictor in this meta-learner, the model fits a *distance term* that characterises how occurrence probability declines outside the expert range map. As a result, the integrated SDMs can capture range limits while accounting for varying accuracy of expert information across species (Oeser et al. 2024).

We generated two outputs based on our SDMs: first, an estimate of the *potential distribution* obtained from a stacked generalisation ensemble of the three SDM algorithms (traditional SDM approach), and second, an estimate of the *realised distribution* obtained by integrating expert range maps into the ensemble. Adding information on species range extents helps to capture distribution limits caused by factors not accounted for in traditional SDM approaches, such as movement barriers or interspecific competition (Merow et al. 2017; Oeser et al. 2024). To convert continuous predictions of relative occurrence

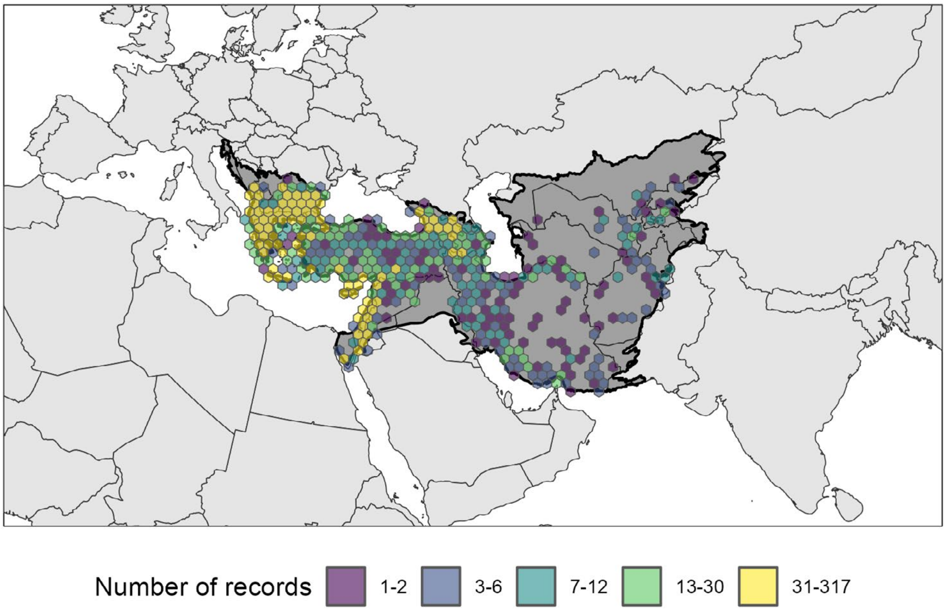

FIGURE 1 | Study area in a wider geographic context. The number of bat occurrence records was counted at the level of 100 km^2 hexagonal grid cells to visualise the distribution of available occurrence records. Map is in Albers equal area projection.

probability into binary distribution maps, we applied a 10% omission threshold for both potential and realised distributions, resulting in maps characterising core distribution areas for each species (Ellis-Soto et al. 2021).

2.2 | Mapping Species Richness

To map bat species richness across the study area at 1-km resolution, we overlaid binary maps of realised distributions for all 49 bat species. While our integrated SDMs included most species occurring in the western parts of our study region, we did not have enough reliable occurrence records for building SDMs for all species occurring in our study area (minimum number of records used: 25), particularly in the east (Figure 1). This meant that raw species richness estimates obtained from stacking integrated SDMs were geographically biased (i.e., underestimating richness in the eastern parts of our study area). To correct this bias, we estimated the geographic bias of our richness map based on IUCN range maps. Specifically, we related species richness patterns calculated with IUCN range maps of the 49 modelled bat species to richness maps obtained when including all bat species with IUCN ranges intersecting our study area ($n = 81$). Assuming that, for any given area, the ratio between species richness estimates for the pool of modelled and the complete pool of species is the same between IUCN ranges and SDMs, we calculated a bias-corrected species richness estimate as:

$$R_{\mathrm{SDMc}} = \frac{R_{\mathrm{SDMm}} \times R_{\mathrm{Ec}}}{R_{\mathrm{Em}}}$$

where R_{SDMc} is the bias-corrected SDM-based species richness estimate, R_{SDMm} the raw richness estimate from stacking SDMs for the modelled pool of species, R_{Em} the richness estimate from IUCN range maps for the modelled pool of species, and R_{Ec} the richness estimate from IUCN range maps for the complete species pool.

2.3 | Variations of Environmental Niche Breadth and Range Size With Species Richness

We calculated niche breadth based on two sets of environmental variables characterising climate and land cover. Specifically, we used (1) 19 bioclimatic variables (Karger et al. 2017) and (2) six land-cover fractions (agriculture, forest, shrubs, herbaceous vegetation, bare and sparse vegetation, water) alongside nine satellite-based metrics further characterising vegetation structure (ESA 2017; Oeser et al. 2020; see Appendix S2 for an overview of variables). We used these data sets to characterise environmental niche breadth regarding (1) bioclimatic conditions and (2) vegetation and land-cover characteristics, both of which are key factors shaping the distributions of bat species (Zamora-Gutierrez et al. 2018). While climate often limits the distributions of bats at broad scales (Festa et al. 2023), land-cover characteristics are important determinants of habitat availability at finer scales (Mehr et al. 2011). To reduce dimensionality, we derived the first three principal components (PCs) of the climate and land-cover datasets, which captured 99% and 98% of the variance, respectively. Then, we built two additional SDMs per species containing only these climate and land-cover PCs as predictors and calculated niche breadth as Levins' B2 metric in the *ENMTools* package in R (Warren et al. 2021). This widely used metric of niche breadth ranges from 0 to 1, with larger values indicating higher niche breadth. We calculated niche breadth in environmental space. In this approach, instead of using model predictions in geographic space (Warren et al. 2008), niche breadth is calculated based on SDM predictions across a range of predictor combinations sampled using Monte Carlo integration (Warren et al. 2019).

We derived range sizes for each species based on the binary predictions of our integrated SDMs (i.e., estimates of species' realised distributions). To understand how niche breadth and range size varied across bat communities with different species richness, we assessed their relationships with species richness in geographic space. To do so, we created raster stacks of niche breadth and range size by assigning environmental niche breadth and range size values to all areas where a species was predicted to be present and then sampled 1000 cells per species richness value. In addition, we summarised niche breadth patterns at the species level. To do so, we calculated the average species richness within the distribution of each species (hereafter: *average richness*) and then related this measure to the species' niche breadth.

2.4 | Geographic Exclusion Between Species Pairs

We contrasted potential distributions predicted by traditional SDMs with realised distributions predicted by our integrated modelling approach to assess patterns of range filling (i.e., the proportion of environmentally suitable habitats occupied by a species; Svenning and Skov 2004). Range filling can be indicative of the role of biotic interactions and dispersal limitations in determining range limits (Svenning and Skov 2004). Based on patterns of range filling, we calculated two indicators that characterise potential broad-scale effects of interspecific competition on species' range limits. Specifically, we identified potential overlaps between species pairs based on the potential distribution maps and calculated how much of this overlap is filled (realised) by each species based on our realised distribution maps. To remove parts of potential distributions located far outside the current, realised distribution of species and focus on areas likely reachable by species, we only considered potential habitats within 500 km of the realised distribution of species. Based on these *reachable potential habitats*, we first calculated a geographic avoidance score following Novella-Fernandez et al. (2021). This avoidance score is calculated by relating the proportions of potential distributions realised by a species pair inside potential overlaps versus outside the overlap (in our case, the reachable potential habitats; see Novella-Fernandez et al. 2021 for details). As a second indicator, we calculated a geographic exclusion score. To do so, we divided the range filling of each species inside the overlap through the species' range filling across the reachable potential habitats (hereafter *overlap filling*). For example, an overlap filling value of 1 would mean that a species showed the same range filling inside the overlap as across the entire reachable potential habitat. The exclusion score of a species pair was then given by the absolute difference in the overlap filling of both species.

Whereas the geographic avoidance score proposed by Novella-Fernandez et al. (2021) is highest when both species fill small parts of potential overlaps, our exclusion score highlights cases in which one species fills a higher proportion of the potential overlap, thus better indicating potential competitive exclusion between species. We limited the calculation of geographic avoidance and exclusion scores to species pairs with potential overlaps of at least 200 km^2 to ensure robust estimates (Novella-Fernandez et al. 2021). We then assessed how avoidance and exclusion between species pairs relate to the niche breadth of overlapping species. In addition, we assessed how average avoidance and exclusion scores per species relate to the average richness inside the species' distribution.

2.5 | Disentangling Effects of Niche Breadth, Richness, and Geographic Exclusion on Range Size

To understand how range sizes of species are influenced by species richness (i.e., the number of potentially interacting species), niche breadth (i.e., environmental specialisation) and geographic exclusion (i.e., the strength of competitive interactions), we additionally performed a regression analysis of range size. For this analysis, we focused on geographic exclusion scores as an indicator of interspecific competition and climatic niche breadths as an indicator of environmental specialisation. Specifically, we modelled log-transformed range size with a Gaussian error distribution and used climatic niche breadth, the average richness inside species' ranges, and the average geographic exclusion score of species as predictor variables. For each predictor, we compared linear effects against nonlinear smooth effects (thin plate regression splines) and performed model selection via AIC in the R-package *mgcv* (Wood 2022).

3 | Results

The integrated SDMs generally performed well (mean cross-validated AUC = 0.85, range 0.67–0.99). Temperature-related variables were generally the most important predictors, followed by precipitation-related variables (see Appendix S4 for a summary of variable importance across all species). Based on stacked SDM predictions and bias correction, our species richness map identified large parts of the Balkan Peninsula, coastal areas in Turkey, as well as the Caucasus and Alborz mountains as key hotspots of bat species richness in the study region. Predicted species richness was highest in more productive mountainous and coastal areas and lowest in arid steppes and deserts. Correcting for bias introduced by excluding species with few occurrence records (< 25) led to an increase in predicted species richness in the eastern part of the study area (Figure 2; see Appendix S5 for a comparison with the uncorrected map).

Environmental niche breadth showed a nonlinear relationship with the richness of bat communities. Species-poor communities were the most specialised and niche breadth was highest in communities with intermediate richness (Figure 3A,B). Towards the high end of the richness gradient, the niche breadth of species decreased. The pattern was consistent across both climate and land-cover variables (correlation between niche breadth values = 0.70). We observed the same nonlinear relationship between niche breadth and the average richness inside species' ranges when summarising patterns at the species level (see Appendix S6). Despite this nonlinear and mostly positive relationship of niche breadth with community richness, range sizes of the predicted bat communities declined with species richness along the entire richness gradient (Figure 3C).

Geographic exclusion between species pairs was lowest for overlapping generalist species (i.e., with wide environmental niche breadth) and tended to be higher for overlapping specialists (Figure 4A). Species' average exclusion score declined with average species richness inside its range (Figure 4B). We observed the same patterns for geographic avoidance scores, although the decrease in avoidance scores with average richness was less pronounced than for exclusion scores (see Appendix S7).

Our regression model of range size explained 84% of the observed deviance in our data set. Nonlinear smooth effects were supported based on AIC for niche breadth and average richness. All predictors showed clear associations with range size, although the relationship with geographic exclusion scores was less pronounced (p values for niche breadth and average richness $\ll 0.01$, for geographic exclusion = 0.024). While climatic niche breadth had a positive effect on range

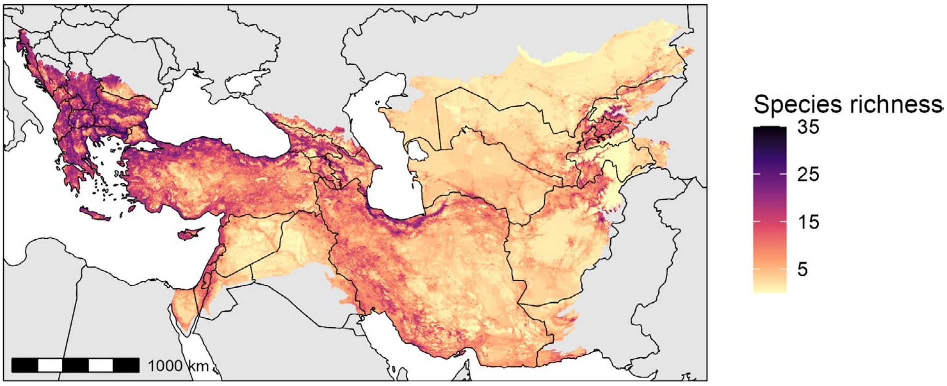

FIGURE 2 | Bat species richness in the study area. The plot shows bias-corrected richness predictions accounting for data-poor species that were not included in the distribution modelling. The map is in Albers equal area projection.

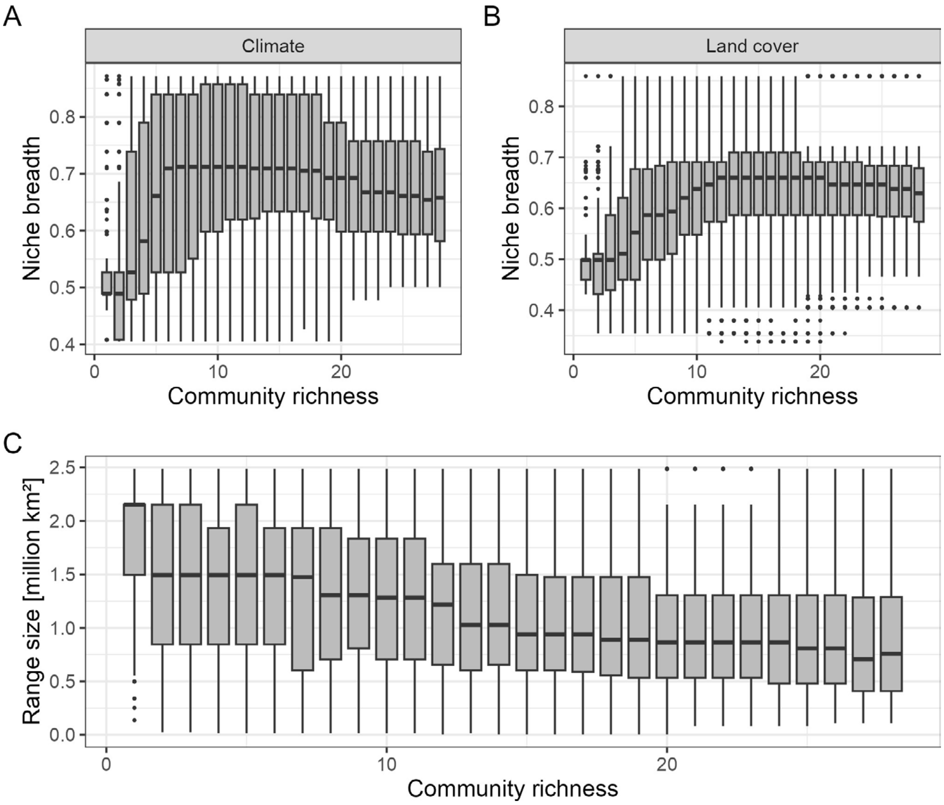

FIGURE 3 | Distributions of environmental niche breadth (Levin's B2; A, B) and range sizes (C) against species richness in bat communities predicted by integrated species distribution models. Distributions were derived from a stratified random sample of richness values ($n = 1000$ per richness value).

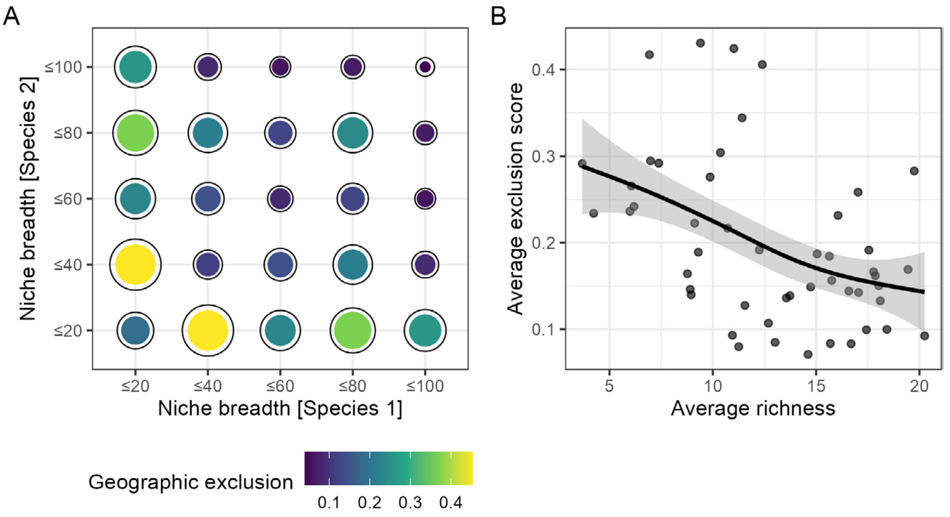

FIGURE 4 | (A) Relationship between geographic exclusion and niche breadth of overlapping bat species, and (B) relationship between average geographic exclusion per species and average species richness found within species ranges. In plot (A), species were binned into five groups based on their niche breadth, with each bin containing 20% of the species (i.e., lowest to highest niche breadth). The sizes and colours of points correspond to the mean geographic exclusion scores between species pairs belonging to the respective niche breadth bin. Black circles surrounding points correspond to one standard deviation added to the mean exclusion score to indicate variance. The trend line and 95% confidence intervals in plot (B) are based on a generalised additive model. Exclusion scores are calculated as the difference between how much two species fill potential overlaps, relative to their range filling across the entire range. Larger values indicate stronger geographic exclusion between species.

size, average richness and geographic exclusion had negative effects (Figure 5). The negative effect of average richness on range sizes was particularly strong at low richness values (note the log-transformed response variable in Figure 5). Similarly, the positive effect of niche breadth on range sizes was strongest at low niche breadth values.

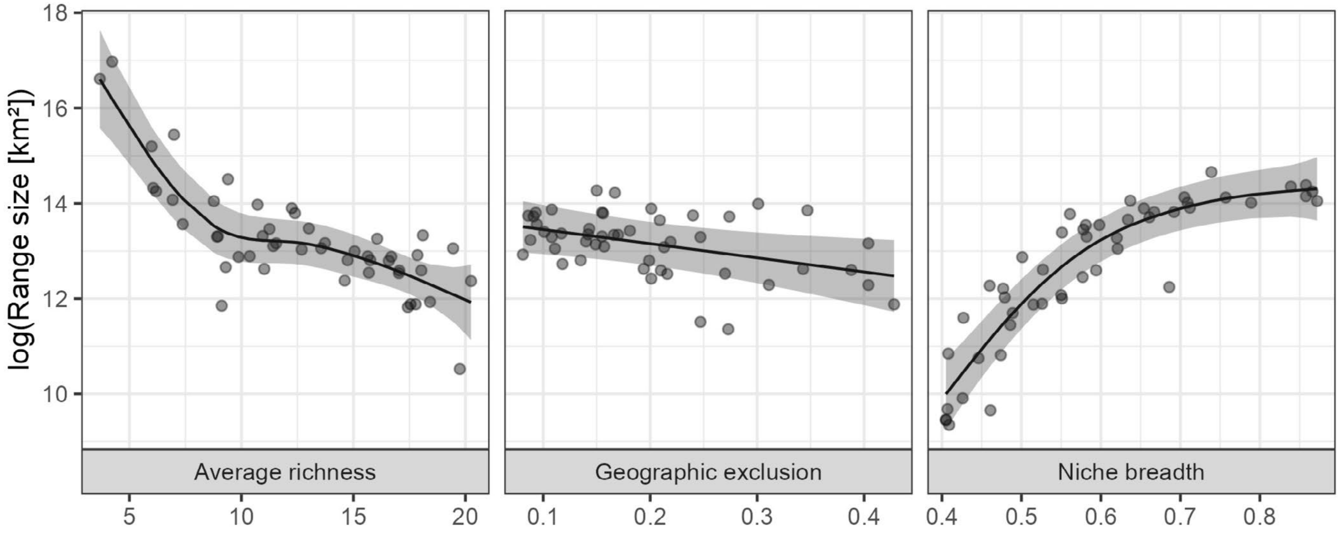

FIGURE 5 | Partial effects of average richness, geographic exclusion, and climatic niche breadth on range sizes of bats based on regression analysis with a generalised additive model. Plots include 95% confidence intervals and partial residuals. Note the log-transformed response variable.

4 | Discussion

Increasing species richness is typically assumed to coincide with a higher number of specialist species, characterised by narrower environmental niches and smaller range sizes (Granot and Belmaker 2020; Guo et al. 2022). Leveraging a rich occurrence data set and a novel integrated species distribution modelling approach, we assessed relationships between species richness, specialisation and geographic exclusion for bats in a biodiverse, yet understudied region. Our fine-scale distribution and richness maps provide new insights into patterns of bat diversity in the study area. While we indeed observed decreasing range sizes in more species-rich communities, this was not linked to increasing environmental specialisation in climate and land-cover niches. Instead, niche breadths were lowest in resource- and species-poor environments, also coinciding with the strongest geographic exclusion between species, which could be indicative of stronger interspecific competition. We demonstrate that integrating SDMs with expert range maps offers a powerful approach that helps assess species richness at high resolution and sheds new light on the interplay between interspecific competition and community structure. More generally, our findings highlight that associations between specialisation and interspecific competition along richness gradients can be complex, cautioning against generalisations across taxa and geographies.

Our study used updated, high-resolution distribution maps for 49 bat species to provide the first fine-scale assessment of bat species richness in the study region, which can serve as a basis for conservation planning. Our richness maps highlighted strong differences between species-rich coastal and mountain areas associated with more productive and climatically stable habitats (e.g., on the Balkan peninsula and in the Caucasus and Alborz mountains), and species-poor arid deserts and steppes characterised by colder winter temperatures (e.g., Middle East steppe and Central Asian deserts). These patterns align with previous research highlighting the importance of water availability, productivity and climate stability as key environmental determinants of bat species richness (Alves et al. 2018; McCain 2007; Tello and Stevens 2010). Since nearly all bat species in our study area are insectivorous, an important underlying factor behind these gradients might be the increasing levels of insect prey availability in more productive environments (Mendes et al. 2017).

We observed a nonlinear relationship between species richness and environmental niche breadth, with niche breadth being lowest in species-poor communities and peaking at intermediate richness. This finding contrasts with results from meta-analyses (Granot and Belmaker 2020; Vázquez and Stevens 2004) as well as previous studies on other mammal taxa (Eeley and Foley 1999), which reported negative associations between niche breadth and richness. Our observation that environmental specialisation is highest in resource-poor, arid environments and that niche breadth peaks at intermediate richness could be explained by a release in interspecific competition due to a higher abundance of resources (e.g., insect prey) in more productive environments (Bolnick et al. 2010; Costa-Pereira et al. 2019; Morningstar et al. 2019). Our results show a trend of environmental specialisation towards the high end of the richness gradient. This indicates that once a certain community size is reached, the high number of interactions with other species might force species to specialise in their environmental niches despite high resource availability. Our results highlight the importance of testing for nonlinear relationships when assessing associations between niche breadth and species richness.

In line with findings on bats (Varzinczak et al. 2020) and other taxa (Slatyer et al. 2013) niche breadth showed a strong positive relationship with range size when assessing patterns at the level of species. Yet, we observed a continuous decrease in range sizes with increasing richness of bat communities, which agrees with more general findings on range size patterns (Guo et al. 2022). This can be explained by a direct negative effect of species richness on range sizes, which outweighs the positive effect of niche breadth and is supported by our regression model indicating a strong negative effect of richness on range sizes at low richness values. Thus, our findings indicate that decreasing range sizes along the richness gradient are not primarily driven by environmental specialisation.

The strength of geographic exclusion and avoidance, as indicated by differences between potential and realised distributions of overlapping species, tended to be highest among specialist species occurring in species-poor environments. Our species-level regression analysis indicated a significant negative effect of our exclusion scores on species' range size, supporting the usefulness of this metric for capturing the impact of species interactions as a range-limiting factor. Despite decreasing range sizes in more species-rich communities, the observed average exclusion score per species declined with increasing richness in their range. Our results therefore also suggest that decreases in range sizes with increasing richness could be primarily driven by the total number of interacting species (i.e., a direct effect of richness), rather than stronger competitive interactions between geographically overlapping species. Although there is growing evidence that interspecific competition can scale up to shape distribution limits (Gotelli et al. 2010; Legault et al. 2020), little is known about bats in this regard (Salinas-Ramos et al. 2020). Novella-Fernandez et al. (2021) found that competition between morphologically similar sister species of bats can limit their distributions when fine-scale mechanisms of niche partitioning are absent. Our results indicate that the number of interacting species and, to a lesser degree, the strength of competitive interactions (itself linked to environmental specialisation), are important determinants of range sizes in bats. In sum, this suggests that interspecific competition could play an important role in shaping macroecological distribution patterns of bats.

We demonstrated that combining correlative SDMs with expert range maps offers a powerful approach to improving species richness mapping (Oeser et al. 2024). In addition, this approach can provide valuable insights into the effects of interspecific competition on species distributions. Correlative SDMs are widely used for characterising global biodiversity patterns but typically neglect the effects of biotic interactions and dispersal (Araújo and Guisan 2006; Soberon and Peterson 2005). Additionally, SDM often rely on opportunistic occurrence datasets that usually exhibit considerable sampling bias (Hughes et al. 2021). These factors reduce the accuracy of mapped distributions, thereby limiting the usefulness of stacking SDMs for assessing species richness (Ellis-Soto et al. 2021). Integrating information on range limits via expert range maps offers a simple but effective way to address these shortcomings (Merow et al. 2017; Oeser et al. 2024). Expert range maps not only improve estimates of realised ranges but, as we have shown here, allow us to correct for biases in stacked SDMs introduced by excluding species due to insufficient occurrence observations required for building SDMs. Given strong regional differences in the availability of occurrence data (Hughes et al. 2021; Yang et al. 2013), bias caused by omitting species is likely common in SDM analyses, yet it is typically overlooked in studies assessing species richness using stacked SDMs. Moreover, by allowing us to contrast between potential and realised ranges, our approach helps to gain insights into factors limiting species' ranges. For sessile species like plants, range filling has mainly been related to dispersal effects on species distributions (Nogués-Bravo et al. 2014; Svenning and Skov 2004). In highly mobile species less limited by dispersal (e.g., birds and bats), assessing species' range filling can help understand the potential effects of interspecific competition in limiting distributions (Novella-Fernandez et al. 2021). Given these advantages for understanding and predicting species distributions, integrated SDM approaches hold great potential for improving our understanding of global biodiversity patterns (Fletcher Jr. et al. 2019; Miller et al. 2019).

Although providing important insights into the potential importance of interspecific competition at macroecological scales, our results need to be interpreted cautiously. Our calculations of niche breadth only describe climate and land-cover niches related to species' environmental habitat preferences at broad spatial scales. Similarly, avoidance and exclusion scores cannot reflect whether species show niche differentiation at finer spatial scales. Several studies have shown that fine-scale partitioning of dietary and foraging niches can be important in bats (Arrizabalaga-Escudero et al. 2018; Peixoto et al. 2018; Roeleke et al. 2018), and might enable the coexistence of species occupying similar climate and habitat niches. In addition, our approach did not allow us to characterise intraspecies variation in niche breadth and range sizes. Assessing variation in habitat and dietary niches and capturing intraspecific variation across communities could be particularly valuable for better understanding how interspecific competition shapes species' niches and range sizes at finer scales. Yet, our findings suggesting signals of interspecific competition in broad-scale distribution patterns of a taxon known for fine-scale niche differentiation can be interpreted as a sign of the general importance of biotic interactions in shaping broad-scale biodiversity patterns. Two factors likely caused some bias in our geographic exclusion and avoidance scores. First, the varying dispersal abilities of bat species, even though we focused on potential overlaps likely reachable by species, and second, the varying accuracy of expert range maps, influencing how strongly expert range maps are weighted in the integrated SDM predictions (Oeser et al. 2024) and thus also affecting estimates of range filling. Finally, since we were limited to occurrence information that did not cover the entire ranges of all modelled species, our results are influenced by niche and range truncation (Chevalier et al. 2021). Thus, our range size and niche breadth estimates do not reflect patterns across the species' entire distributions but are limited to patterns within our study area. However, since we did not perform model transfers to other regions or time periods, the accuracy of our distribution models should not be compromised by this issue (Chevalier et al. 2021).

More broadly, our results demonstrate that associations between species richness and specialisation can be complex, with niche breadths and range sizes following independent trends along the gradient of species richness. Despite decade-long research on global patterns of species richness and specialisation, identifying general trends and attributing patterns to underlying mechanisms that hold across taxa and geographies has been challenging (Carscadden et al. 2020; Cirtwill et al. 2015; Vázquez and Stevens 2004). Thus, achieving a deeper understanding of how and why community structure varies with species richness might require embracing complexity and allowing for explanations that vary across taxa and environmental contexts.

Author Contributions

Julian Oeser: conceptualization (lead); methodology (lead); data curation (lead); formal analysis (lead); writing – original draft (lead); writing – review and editing (lead). **Damaris Zurell:** conceptualization (equal); methodology (equal); writing – original draft (equal); writing – review and editing (equal). **Frieder Mayer:** conceptualization (equal); writing – original draft (equal); writing – review and editing (equal). **Emrah Çoraman:** conceptualization (equal); data curation (equal); writing – original draft (equal); writing – review and editing (equal). **Nia Toshkova:** data curation (supporting); writing – review and editing (supporting). **Stanimira Deleva:** data curation (supporting); writing – review and editing (supporting). **Ioseb Natradze:** data curation (supporting); writing – review and editing (supporting). **Petr Benda:** data curation (supporting); writing – review and editing (supporting). **Christian Dietz:** data curation (supporting); writing – review and editing (supporting). **Panagiotis Georgiakakis:** data curation (supporting); writing – review and editing (supporting). **Eran Levin:** data curation (supporting); writing – review and editing (supporting). **Amit Dolev:** data curation (supporting); writing – review and editing (supporting). **Heliana Dundarova:** data curation (supporting); writing – review and editing (supporting). **Astghik Ghazaryan:** data curation (supporting); writing – review and editing (supporting). **Sercan Irmak:** data curation (supporting); writing – review and editing (supporting). **Nijat Hasanov:** data curation (supporting); writing – review and editing (supporting). **Gulnar Guliyeva:** data curation (supporting); writing – review and editing (supporting). **Mariya Gritsina:** data curation (supporting); writing – review and editing (supporting). **Alexander Bukhnikashvili:** data curation (supporting); writing – review and editing (supporting). **Tobias Kuemmerle:** conceptualization (equal); data curation (equal); writing – original draft (equal); writing – review and editing (equal).

Acknowledgements

We gratefully acknowledge Giorgi Sheklashvili, Andrei Kandaurov, Irina Rakhmatulina, Kursantbek Altybaev, Pirimkul Mamatkalykov, Abdurashit Nizamiev, Alexey Dudashvili, Svetlana V. Baskakova, Georgiy V. Shakula, Kudaibergen Amirekul, Artemis Kafkaletou Diez, Ioanna Salvarina and Eleni Papadatou who have helped with the collection of bat occurrence data. Occurrence data were mainly compiled from published records and from national databases. They are managed by the authors who have the permission to analyse the databases and to publish results. For additional fieldwork, all relevant permissions were obtained (permit number Nr. 8143-5464-fb18-0184-dc97-2324-3005 issued by the Ministry of Ecology, Environmental Protection & Climate Change of Uzbekistan). Open Access funding enabled and organized by Projekt DEAL.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study are openly available in Dryad at http://datadryad.org/stash/share/LxIkaqijO1__mtN9EWgX4crx_W0.

References

Alves, D. M. C. C., J. A. F. Diniz-Filho, K. da Silva e Souza, S. F. Gouveia, and F. Villalobos. 2018. "Geographic Variation in the Relationship Between Large-Scale Environmental Determinants and Bat Species Richness." *Basic and Applied Ecology* 27: 1–8. https://doi.org/10.1016/j.baae.2017.12.002.

Araújo, M. B., and A. Guisan. 2006. "Five (Or So) Challenges for Species Distribution Modelling." *Journal of Biogeography* 33, no. 10: 1677–1688. https://doi.org/10.1111/j.1365-2699.2006.01584.x.

Arrizabalaga-Escudero, A., E. L. Clare, E. Salsamendi, et al. 2018. "Assessing Niche Partitioning of Co-Occurring Sibling Bat Species by DNA Metabarcoding." *Molecular Ecology* 27, no. 5: 1273–1283. https://doi.org/10.1111/mec.14508.

Barber, R. A., S. G. Ball, R. K. A. Morris, and F. Gilbert. 2022. "Target-Group Backgrounds Prove Effective at Correcting Sampling Bias in Maxent Models." *Diversity and Distributions* 28, no. 1: 128–141. https://doi.org/10.1111/ddi.13442.

Batt, R. D., J. W. Morley, R. L. Selden, M. W. Tingley, and M. L. Pinsky. 2017. "Gradual Changes in Range Size Accompany Long-Term Trends in Species Richness." *Ecology Letters* 20, no. 9: 1148–1157. https://doi.org/10.1111/ele.12812.

Belmaker, J., C. H. Sekercioglu, and W. Jetz. 2012. "Global Patterns of Specialization and Coexistence in Bird Assemblages." *Journal of Biogeography* 39, no. 1: 193–203. https://doi.org/10.1111/j.1365-2699.2011.02591.x.

Bolnick, D. I., T. Ingram, W. E. Stutz, L. K. Snowberg, O. L. Lau, and J. S. Paull. 2010. "Ecological Release From Interspecific Competition Leads to Decoupled Changes in Population and Individual Niche Width." *Proceedings of the Royal Society B: Biological Sciences* 277, no. 1689: 1789–1797. https://doi.org/10.1098/rspb.2010.0018.

Boria, R. A., L. E. Olson, S. M. Goodman, and R. P. Anderson. 2014. "Spatial Filtering to Reduce Sampling Bias Can Improve the Performance of Ecological Niche Models." *Ecological Modelling* 275: 73–77. https://doi.org/10.1016/j.ecolmodel.2013.12.012.

Boucher-Lalonde, V., A. Morin, and D. J. Currie. 2016. "Can the Richness–Climate Relationship Be Explained by Systematic Variations in How Individual Species' Ranges Relate to Climate?" *Global Ecology and Biogeography* 25, no. 5: 527–539. https://doi.org/10.1111/geb.12433.

Carscadden, K. A., N. C. Emery, C. A. Arnillas, et al. 2020. "Niche Breadth: Causes and Consequences for Ecology, Evolution, and Conservation." *Quarterly Review of Biology* 95, no. 3: 179–214. https://doi.org/10.1086/710388.

Chejanovski, Z. A., and J. J. Wiens. 2014. "Climatic Niche Breadth and Species Richness in Temperate Treefrogs." *Journal of Biogeography* 41, no. 10: 1936–1946. https://doi.org/10.1111/jbi.12345.

Chevalier, M., O. Broennimann, J. Cornuault, and A. Guisan. 2021. "Data Integration Methods to Account for Spatial Niche Truncation Effects in Regional Projections of Species Distribution." *Ecological Applications* 31, no. 7: e02427. https://doi.org/10.1002/eap.2427.

Cirtwill, A. R., D. B. Stouffer, and T. N. Romanuk. 2015. "Latitudinal Gradients in Biotic Niche Breadth Vary Across Ecosystem Types." *Proceedings of the Royal Society B: Biological Sciences* 282, no. 1819: 20151589. https://doi.org/10.1098/rspb.2015.1589.

Costa-Pereira, R., M. S. Araújo, F. L. Souza, and T. Ingram. 2019. "Competition and Resource Breadth Shape Niche Variation and Overlap in Multiple Trophic Dimensions." *Proceedings of the Royal Society B: Biological Sciences* 286, no. 1902: 20190369. https://doi.org/10.1098/rspb.2019.0369.

D'Amen, M., H. K. Mod, N. J. Gotelli, and A. Guisan. 2018. "Disentangling Biotic Interactions, Environmental Filters, and Dispersal Limitation as Drivers of Species Co-Occurrence." *Ecography* 41, no. 8: 1233–1244. https://doi.org/10.1111/ecog.03148.

Dormann, C. F., J. Elith, S. Bacher, et al. 2013. "Collinearity: A Review of Methods to Deal With It and a Simulation Study Evaluating Their Performance." *Ecography* 36, no. 1: 27–46. https://doi.org/10.1111/j.1600-0587.2012.07348.x.

Eeley, H. A. C., and R. A. Foley. 1999. "Species Richness, Species Range Size and Ecological Specialisation Among African Primates: Geographical Patterns and Conservation Implications." *Biodiversity and Conservation* 8, no. 8: 1033–1056. https://doi.org/10.1023/A:1008831320469.

Elith, J., and J. R. Leathwick. 2009. “Species Distribution Models: Ecological Explanation and Prediction Across Space and Time.” *Annual Review of Ecology, Evolution, and Systematics* 40, no. 1: 677–697. https://doi.org/10.1146/annurev.ecolsys.110308.120159.

Ellis-Soto, D., C. Merow, G. Amatulli, J. L. Parra, and W. Jetz. 2021. “Continental-Scale 1 Km Hummingbird Diversity Derived From Fusing Point Records With Lateral and Elevational Expert Information.” *Ecography* 44, no. 4: 640–652. https://doi.org/10.1111/ecog.05119.

ESA. 2017. “Land Cover CCI Product User Guide Version 2 [Dataset].” http://maps.elie.ucl.ac.be/CCI/viewer/download/ESACCI-LC-Ph2-PUGv2_2.0.pdf.

Festa, F., L. Ancillotto, L. Santini, et al. 2023. “Bat Responses to Climate Change: A Systematic Review.” *Biological Reviews* 98, no. 1: 19–33. https://doi.org/10.1111/brv.12893.

Fletcher, R. J., Jr., T. J. Hefley, E. P. Robertson, B. Zuckerberg, R. A. McCleery, and R. M. Dorazio. 2019. “A Practical Guide for Combining Data to Model Species Distributions.” *Ecology* 100, no. 6: e02710. https://doi.org/10.1002/ecy.2710.

Georgiakakis, P., A. Kafkaletou Diez, I. Salvarina, et al. 2023. “The Bats of Greece: An Updated Review of Their Distribution, Ecology and Conservation.” *Animals* 13, no. 15: 2529. https://doi.org/10.3390/ani13152529.

Gotelli, N. J., G. R. Graves, and C. Rahbek. 2010. “Macroecological Signals of Species Interactions in the Danish Avifauna.” *Proceedings of the National Academy of Sciences of the United States of America* 107, no. 11: 5030–5035. https://doi.org/10.1073/pnas.0914089107.

Granot, I., and J. Belmaker. 2020. “Niche Breadth and Species Richness: Correlation Strength, Scale and Mechanisms.” *Global Ecology and Biogeography* 29, no. 1: 159–170. https://doi.org/10.1111/geb.13011.

Guo, Q., H. Qian, and J. Zhang. 2022. “On the Relationship Between Species Diversity and Range Size.” *Journal of Biogeography* 49, no. 11: 1911–1919. https://doi.org/10.1111/jbi.14477.

Herkt, K. M. B., G. Barnikel, A. K. Skidmore, and J. Fahr. 2016. “A High-Resolution Model of Bat Diversity and Endemism for Continental Africa.” *Ecological Modelling* 320: 9–28. https://doi.org/10.1016/j.ecolmodel.2015.09.009.

Hughes, A. C., M. C. Orr, K. Ma, et al. 2021. “Sampling Biases Shape Our View of the Natural World.” *Ecography* 44, no. 9: 1259–1269. https://doi.org/10.1111/ecog.05926.

Inman, R., J. Franklin, T. Esque, and K. Nussear. 2021. “Comparing Sample Bias Correction Methods for Species Distribution Modeling Using Virtual Species.” *Ecosphere* 12, no. 3: e03422. https://doi.org/10.1002/ecs2.3422.

Karger, D. N., O. Conrad, J. Böhner, et al. 2017. “Climatologies at High Resolution for the Earth's Land Surface Areas.” *Scientific Data* 4, no. 1: 170122. https://doi.org/10.1038/sdata.2017.122.

Krüger, F., E. L. Clare, S. Greif, B. M. Siemers, W. O. C. Symondson, and R. S. Sommer. 2014. “An Integrative Approach to Detect Subtle Trophic Niche Differentiation in the Sympatric Trawling Bat Species Myotis Dasycneme and *Myotis Daubentonii*.” *Molecular Ecology* 23, no. 15: 3657–3671. https://doi.org/10.1111/mec.12512.

Legault, G., M. E. Bitters, A. Hastings, and B. A. Melbourne. 2020. “Interspecific Competition Slows Range Expansion and Shapes Range Boundaries.” *Proceedings of the National Academy of Sciences of the United States of America* 117, no. 43: 26854–26860. https://doi.org/10.1073/pnas.2009701117.

McCain, C. M. 2007. “Could Temperature and Water Availability Drive Elevational Species Richness Patterns? A Global Case Study for Bats.” *Global Ecology and Biogeography* 16, no. 1: 1–13. https://doi.org/10.1111/j.1466-8238.2006.00263.x.

Mehr, M., R. Brandl, T. Hothorn, F. Dziock, B. Förster, and J. Müller. 2011. “Land Use Is More Important Than Climate for Species Richness and Composition of Bat Assemblages on a Regional Scale.” *Mammalian Biology* 76, no. 4: 451–460. https://doi.org/10.1016/j.mambio.2010.09.004.

Mendes, E. S., C. Fonseca, S. F. Marques, D. Maia, and M. J. Ramos Pereira. 2017. “Bat Richness and Activity in Heterogeneous Landscapes: Guild-Specific and Scale-Dependent?” *Landscape Ecology* 32, no. 2: 295–311. https://doi.org/10.1007/s10980-016-0444-0.

Merow, C., A. M. Wilson, and W. Jetz. 2017. “Integrating Occurrence Data and Expert Maps for Improved Species Range Predictions.” *Global Ecology and Biogeography* 26, no. 2: 243–258. https://doi.org/10.1111/geb.12539.

Miller, D. A. W., K. Pacifici, J. S. Sanderlin, and B. J. Reich. 2019. “The Recent Past and Promising Future for Data Integration Methods to Estimate Species' Distributions.” *Methods in Ecology and Evolution* 10, no. 1: 22–37. https://doi.org/10.1111/2041-210X.13110.

Morningstar, D. E., C. V. Robinson, S. Shokralla, and M. Hajibabaei. 2019. “Interspecific Competition in Bats and Diet Shifts in Response to White-Nose Syndrome.” *Ecosphere* 10, no. 11: e02916. https://doi.org/10.1002/ecs2.2916.

Moudrý, V., M. Bazzichetto, R. Remelgado, et al. 2024. “Optimising Occurrence Data in Species Distribution Models: Sample Size, Positional Uncertainty, and Sampling Bias Matter.” *Ecography* 2024, no. 12: e07294. https://doi.org/10.1111/ecog.07294.

Myers, N., R. A. Mittermeier, C. G. Mittermeier, G. A. B. da Fonseca, and J. Kent. 2000. “Biodiversity Hotspots for Conservation Priorities.” *Nature* 403, no. 6772: 853–858. https://doi.org/10.1038/35002501.

Naimi, A. I., and L. B. Balzer. 2018. “Stacked Generalization: An Introduction to Super Learning.” *European Journal of Epidemiology* 33, no. 5: 459–464. https://doi.org/10.1007/s10654-018-0390-z.

Natradze, I., A. Buknikashvili, G. Sheklashvili, and L. Mumladze. 2023. “Bats of Georgia—An Occurrence Dataset From 1835 Through 2022.” *Biodiversity Data Journal* 11: e103181. https://doi.org/10.3897/BDJ.11.e103181.

Nogués-Bravo, D., F. Pulido, M. B. Araújo, et al. 2014. “Phenotypic Correlates of Potential Range Size and Range Filling in European Trees.” *Perspectives in Plant Ecology, Evolution and Systematics* 16, no. 5: 219–227. https://doi.org/10.1016/j.ppees.2014.05.005.

Novella-Fernandez, R., C. Ibañez, J. Juste, E. L. Clare, C. P. Doncaster, and O. Razgour. 2020. “Trophic Resource Partitioning Drives Fine-Scale Coexistence in Cryptic Bat Species.” *Ecology and Evolution* 10, no. 24: 14122–14136. https://doi.org/10.1002/ece3.7004.

Novella-Fernandez, R., J. Juste, C. Ibáñez, et al. 2021. “Broad-Scale Patterns of Geographic Avoidance Between Species Emerge in the Absence of Fine-Scale Mechanisms of Coexistence.” *Diversity and Distributions* 27, no. 9: 1606–1618. https://doi.org/10.1111/ddi.13375.

Oeser, J., M. Heurich, C. Senf, D. Pflugmacher, E. Belotti, and T. Kuemmerle. 2020. “Habitat Metrics Based on Multi-Temporal Landsat Imagery for Mapping Large Mammal Habitat.” *Remote Sensing in Ecology and Conservation* 6, no. 1: 52–69. https://doi.org/10.1002/rse2.122.

Oeser, J., D. Zurell, F. Mayer, et al. 2024. “The Best of Two Worlds: Using Stacked Generalisation for Integrating Expert Range Maps in Species Distribution Models.” *Global Ecology and Biogeography* 33, no. 12: e13911. https://doi.org/10.1111/geb.13911.

Peixoto, F. P., P. H. P. Braga, and P. Mendes. 2018. “A Synthesis of Ecological and Evolutionary Determinants of Bat Diversity Across Spatial Scales.” *BMC Ecology* 18, no. 1: 18. https://doi.org/10.1186/s12898-018-0174-z.

Razgour, O., C. Korine, and D. Saltz. 2011. “Does Interspecific Competition Drive Patterns of Habitat Use in Desert Bat Communities?” *Oecologia* 167, no. 2: 493–502. https://doi.org/10.1007/s00442-011-1995-z.

Reineking, B., and B. Schröder. 2006. "Constrain to Perform: Regularization of Habitat Models." *Ecological Modelling* 193, no. 3: 675–690. https://doi.org/10.1016/j.ecolmodel.2005.10.003.

Roeleke, M., L. Johannsen, and C. C. Voigt. 2018. "How Bats Escape the Competitive Exclusion Principle—Seasonal Shift From Intraspecific to Interspecific Competition Drives Space Use in a Bat Ensemble." *Frontiers in Ecology and Evolution* 6. https://doi.org/10.3389/fevo.2018.00101.

Salinas-Ramos, V. B., L. Ancillotto, L. Bosso, V. Sánchez-Cordero, and D. Russo. 2020. "Interspecific Competition in Bats: State of Knowledge and Research Challenges." *Mammal Review* 50, no. 1: 68–81. https://doi.org/10.1111/mam.12180.

Slatyer, R. A., M. Hirst, and J. P. Sexton. 2013. "Niche Breadth Predicts Geographical Range Size: A General Ecological Pattern." *Ecology Letters* 16, no. 8: 1104–1114. https://doi.org/10.1111/ele.12140.

Soberon, J., and A. T. Peterson. 2005. "Interpretation of Models of Fundamental Ecological Niches and Species' Distributional Areas." *Biodiversity Informatics* 2: 1–10. https://doi.org/10.17161/bi.v2i0.4.

Stevens, G. C. 1989. "The Latitudinal Gradient in Geographical Range: How So Many Species Coexist in the Tropics." *American Naturalist* 133, no. 2: 240–256. https://doi.org/10.1086/284913.

Svenning, J.-C., and F. Skov. 2004. "Limited Filling of the Potential Range in European Tree Species." *Ecology Letters* 7, no. 7: 565–573. https://doi.org/10.1111/j.1461-0248.2004.00614.x.

Syfert, M. M., N. A. Brummitt, D. A. Coomes, N. Bystriakova, and M. J. Smith. 2018. "Inferring Diversity Patterns Along an Elevation Gradient From Stacked SDMs: A Case Study on Mesoamerican Ferns." *Global Ecology and Conservation* 16: e00433. https://doi.org/10.1016/j.gecco.2018.e00433.

Syfert, M. M., M. J. Smith, and D. A. Coomes. 2013. "The Effects of Sampling Bias and Model Complexity on the Predictive Performance of MaxEnt Species Distribution Models." *PLoS One* 8, no. 2: e55158. https://doi.org/10.1371/journal.pone.0055158.

Tello, J. S., and R. D. Stevens. 2010. "Multiple Environmental Determinants of Regional Species Richness and Effects of Geographic Range Size." *Ecography* 33, no. 4: 796–808. https://doi.org/10.1111/j.1600-0587.2009.05991.x.

van Proosdij, A. S. J., M. S. M. Sosef, J. J. Wieringa, and N. Raes. 2016. "Minimum Required Number of Specimen Records to Develop Accurate Species Distribution Models." *Ecography* 39, no. 6: 542–552. https://doi.org/10.1111/ecog.01509.

Varzinczak, L. H., M. O. Moura, and F. C. Passos. 2020. "Strong but Opposing Effects of Climatic Niche Breadth and Dispersal Ability Shape Bat Geographical Range Sizes Across Phylogenetic Scales." *Global Ecology and Biogeography* 29, no. 11: 1929–1939. https://doi.org/10.1111/geb.13163.

Vázquez, D. P., and R. D. Stevens. 2004. "The Latitudinal Gradient in Niche Breadth: Concepts and Evidence." *American Naturalist* 164, no. 1: E1–E19. https://doi.org/10.1086/421445.

Warren, D. L., L. J. Beaumont, R. Dinnage, and J. B. Baumgartner. 2019. "New Methods for Measuring ENM Breadth and Overlap in Environmental Space." *Ecography* 42, no. 3: 444–446. https://doi.org/10.1111/ecog.03900.

Warren, D. L., R. E. Glor, and M. Turelli. 2008. "Environmental Niche Equivalency Versus Conservatism: Quantitative Approaches to Niche Evolution." *Evolution* 62, no. 11: 2868–2883. https://doi.org/10.1111/j.1558-5646.2008.00482.x.

Warren, D. L., N. J. Matzke, M. Cardillo, et al. 2021. "ENMTools 1.0: An R Package for Comparative Ecological Biogeography." *Ecography* 44, no. 4: 504–511. https://doi.org/10.1111/ecog.05485.

Wood, S. 2022. "mgcv: Mixed GAM Computation Vehicle With Automatic Smoothness Estimation (Version 1.8-41)." https://CRAN.R-project.org/package=mgcv.

Yang, W., K. Ma, and H. Kreft. 2013. "Geographical Sampling Bias in a Large Distributional Database and Its Effects on Species Richness–Environment Models." *Journal of Biogeography* 40, no. 8: 1415–1426. https://doi.org/10.1111/jbi.12108.

Zamora-Gutierrez, V., R. G. Pearson, R. E. Green, and K. E. Jones. 2018. "Forecasting the Combined Effects of Climate and Land Use Change on Mexican Bats." *Diversity and Distributions* 24, no. 3: 363–374. https://doi.org/10.1111/ddi.12686.

Zurell, D., J. Franklin, C. König, et al. 2020. "A Standard Protocol for Reporting Species Distribution Models." *Ecography* 43, no. 9: 1261–1277. https://doi.org/10.1111/ecog.04960.

Zurell, D., N. E. Zimmermann, H. Gross, A. Baltensweiler, T. Sattler, and R. O. Wüest. 2020. "Testing Species Assemblage Predictions From Stacked and Joint Species Distribution Models." *Journal of Biogeography* 47, no. 1: 101–113. https://doi.org/10.1111/jbi.13608.

Supporting Information

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