RESEARCH ARTICLE

Climate or diet? The importance of biotic interactions in determining species range size

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Abstract

Aim: Species geographical range sizes play a crucial role in determining species vulnerability to extinction. Although several mechanisms affect range sizes, the number of biotic interactions and species climatic tolerance are often thought to play discernible roles, defining two dimensions of the Hutchinsonian niche. Yet, the relative importance of the trophic and the climatic niche for determining species range sizes is largely unknown.

Location: Central and northern Europe.

Time period: Present.

Major taxa studied: Gall-inducing sawflies and their parasitoids.

Methods: We use data documenting the spatial distributions and biotic interactions of 96 herbivore species, and their 125 parasitoids, across Europe and analyse the relationship between species range size and the climatic and trophic dimensions of the niche. We then compare the observed relationships with null expectations based on species occupancy to understand whether the relationships observed are an inevitable consequence of species range size or if they contain information about the importance of each dimension of the niche on species range size.

Results: We find that both niche dimensions are positively correlated with species range size, with larger ranges being associated with wider climatic tolerances and larger numbers of interactions. However, diet breadth appears to more strongly limit species range size. Species with larger ranges have more interactions locally and they are also able to interact with a larger diversity of species across sites (i.e. higher β-diversity), resulting in a larger number of interactions at continental scales.

Main conclusions: We show for the first time how different aspects of species diet niches are related to their range size. Our study offers new insight into the importance of biotic interactions in determining species spatial distributions, which is critical for improving understanding and predictions of species vulnerability to extinction under the current rates of global environmental change.

KEYWORDS
biotic interactions, climatic niche, dietary niche, Hutchinsonian niche, null models, species range size

1 | INTRODUCTION

Predicting species vulnerability to extinction under rapid environmental change is a pressing challenge for ecologists (Bellard et al., 2012; Pacifici et al., 2015). A major determinant of species vulnerability to extinction is geographical range size (i.e. the number of sites at which a species occurs; Gaston & Fuller, 2009; Manne et al., 1999; Staude et al., 2020). Species with limited ranges are more exposed to stochastic or deterministic variations in their population sizes making them disproportionately sensitive to the effects of large population crashes on their long-term viability. However, before becoming rare they tend to go through a process of population decline. Other species, in contrast, might be naturally rare (Caughley, 1994). Thus, identifying predictors of species range size is paramount to understand and estimate species extinction risk.

It has long been hypothesized that species geographical range sizes are related to their niche breadth, both in terms of the variety of resources they can use, and the diversity of habitats they can inhabit. Intuitively, one would expect that the wider the niche breadth a species has, the larger its range size (Brown, 1984). This hypothesis has been tested on several occasions, mostly reporting a positive relationship between species range size and environmental niche breadth (e.g. Boulangeat et al., 2012; Brown, 1984; Gaston et al., 1997, 2000; Ohlemüller et al., 2008; Slatyer et al., 2013). Yet, there are several issues that have hindered the finding of a robust and universal relationship (Gaston & Blackburn, 2000; Slatyer et al., 2013). A prominent issue is the multidimensional nature of the Hutchinsonian niche, where the dimensions include the environmental conditions and resources that define the requirements of a species to persist (Colwell & Futuyma, 1971; Hutchinson, 1957). Thus, given that niche breadth can be measured in multiple ways (e.g. diet breadth, set of suitable habitats, climatic tolerance), the relationship between niche breadth and range size is likely to be dependent on the dimension of niche under consideration and on whether range size is affecting or related to the measurement of niche. Although this issue has been previously identified and some progress has been made (see Slatyer et al., 2013), understanding the independent contributions of the different dimensions of the niche on species range size remains challenging.

Many of the studies investigating the niche breadth–range size hypothesis have included multiple dimensions of the niche in their analyses (Slatyer et al., 2013). However, the level of detail captured in each of the dimensions varies considerably. While environmental dimensions of the niche, such as climatic tolerance or habitat suitability, have been prominently investigated using sophisticated quantitative analysis, the diet dimension of the niche has traditionally been explored as a categorical variable classifying species as either diet specialists or generalists (see Slatyer et al., 2013 for a review). This coarse diet categorization does not capture the complexity associated with species diet specialization. For instance, biotic specialization can be highly scale dependent, such that specialists at the local scale can

be generalists at regional scales if they switch food resources across locations (Galiana et al., 2019; Gaston et al., 1997; Hughes, 2000). Similarly, species can have different levels of diet specialization along their distribution range given that different aspects of biotic specialization have been shown to vary geographically (Dalsgaard et al., 2017; Galiana et al., 2019; Roslin et al., 2017). Accounting for all these complexities is challenging due to the difficulties involved in collecting detailed data on biotic interactions across large geographical scales (Morales-Castilla et al., 2015).

The lack of information on species interactions across large spatial scales might be one of the reasons that led to the idea that biotic interactions are important for determining species spatial distributions mostly at local scales (Boulangeat et al., 2012; Pearson & Dawson, 2003; Thuiller et al., 2004). The generality of this assumption has been challenged by simulations showing that different types of biotic interactions would play different roles across scales, with interactions involving positive dependencies (e.g. mutualism) being more likely to affect large-scale distributions of species than negative interactions (Araújo & Rozenfeld, 2014). Empirical and modelling studies have also shown that interactions can influence species distributions and community composition across spatial scales through commensalism, competition, parasitism, predation or facilitation (Araújo & Luoto, 2007; Heikkinen et al., 2007; Lemes et al., 2022; Wisz et al., 2013). Yet the influence of interactions on species range size is still generally assumed to decrease as the spatial scale increases (Brändle et al., 2002; Slatyer et al., 2013). The recent acquisition of knowledge on biotic interactions across large geographical scales (Albouy et al., 2019; Kopelke et al., 2017; Maiorano et al., 2020) provides a new means by which to test this assumption.

Here we analysed the relationship between species range size and the two classic dimensions of the niche, namely the trophic and the climatic dimensions, using a continental data set documenting the spatial distribution and biotic interactions of 96 herbivorous insects and 125 parasitoids across Europe (Kopelke et al., 2017). Explicit information about the spatial distribution of these species, together with a detailed information on all the biotic interactions among them across the entire geographical study area, makes this data set uniquely suited to address our question. We used different measures of biotic specialization to quantify the dietary dimension of the niche and coupled sampling site locations with their climatic conditions to define the climatic dimension of the niche. Moreover, to understand the importance of each dimension of a species' niche on its range size, we generated null expectations based on species occupancy that allowed us to assess whether the relationships observed were only an inevitable consequence of species range size (i.e. species with larger ranges are intuitively bound to have wider niche breadths, which could lead to spurious correlations). Our study offers new insight into the importance of biotic interactions in determining species range size, which is critical for improving understanding and predictions of species vulnerability to extinction.

2 | METHODS

2.1 | Data set

The data set used to perform the analyses was published by Kopelke et al. (2017), and describes a single community type of three trophic levels (willows, gall-inducing sawflies and their parasitoids) sampled across central and northern Europe (Figure 1). In particular, this data set includes spatially explicit snapshots of gall-inducing sawflies (Hymenoptera: Tenthredinidae: Nematinae: Euurina) and their diverse natural parasitoids (hymenopteran parasitoids and coleopteran, lepidopteran, dipteran and hymenopteran inquilines) encountered on willows (*Salix* spp.) across 374 sampling sites. The sampling sites covered a latitudinal range of >30°, among which mean annual temperature ranged from −4.7°C in the coldest site to 17.3°C in the warmest site.

At each site, a set of galls was collected from practically all willow specimens supporting galls of focal species within an area of about 0.1–0.3 km². Sampling was conducted during the later stages of larval development (i.e. June/July), and galler species were identified on the basis of willow host species and gall morphology, as these are distinct for each sawfly species (Kopelke, 1999). Then galls were opened to score the presence of galler or parasitoid/inquiline

larvae. Note that this procedure is crucial to diminish the potential number of non-observed (but existent) interactions. Parasitoid larvae were classified to preliminary morphospecies, and the identity of each morphospecies was determined by connecting them to adults emerging after hibernation. In most cases, parasitoids were identified to the species level. Yet, some individuals could only be assigned to genera or (super)families (Braconidae, Ichneumonidae and Chalcidoidea) when only remains of faeces, vacant cocoons of parasitoids, and/or dead host larvae were found. As a result, the largest taxon in the original data set, 'Chalcidoidea indeterminate', represents a superfamily of very small parasitoids that are hard to distinguish from each other. For this reason, in the current study, we removed this superfamily from the analyses to avoid any potential bias. Given that some sites were originally sampled more than once, we checked that the results were not affected by the difference in sampling effort across sites. We performed the analyses considering the full data and compared them with the analyses performed with only one sampling year per site, and we observed no qualitative differences. Further details on the study system can be found in Kopelke et al. (2017).

In summary, the data include information about the location of each site, the *Salix* and galler species inspected, the number of galls
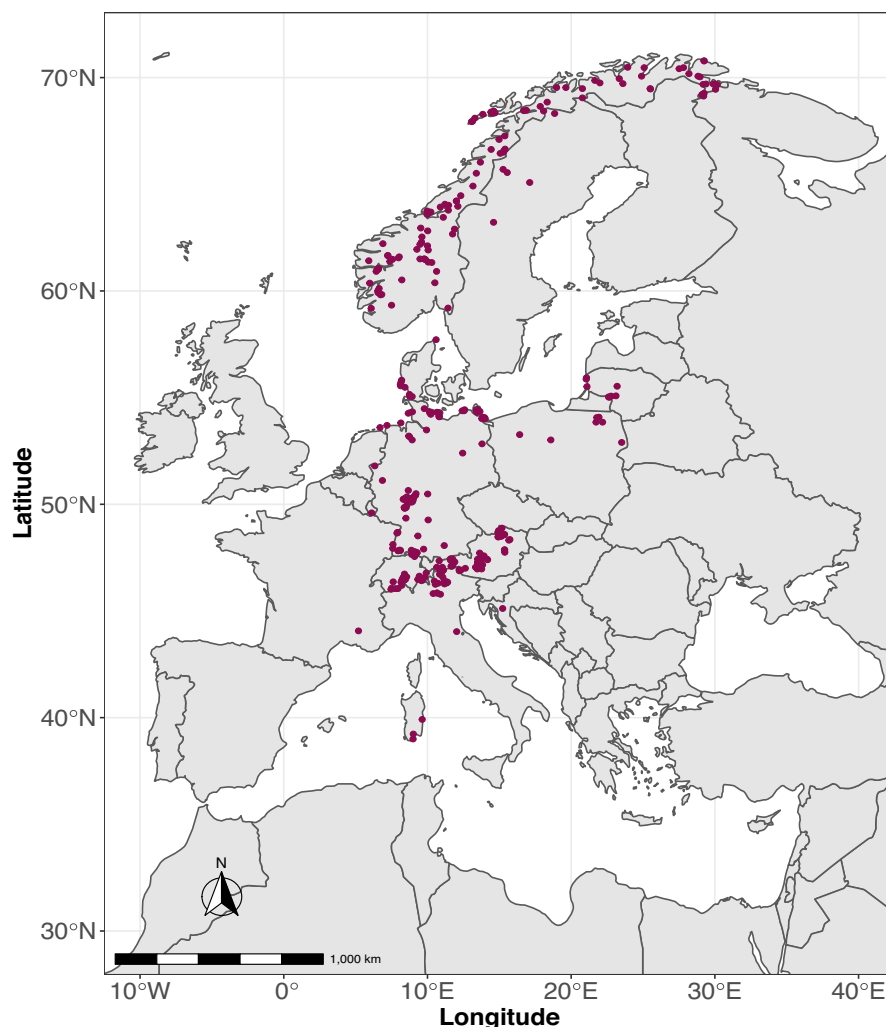
FIGURE 1 Distribution of sampling sites across central and northern Europe. Each point represents a sampling site for which gall-inducing sawflies and their diverse natural enemies were sampled in Kopelke et al. (2017).

collected and dissected or reared, and the parasitoids encountered on them. Given that we were interested in the relationship between diet niche and range size, we focused our analyses on the two upper trophic levels (i.e. gall-inducing sawflies and their natural enemies) because the sampling of the lower trophic level was exclusively focused on the *Salix* spp. and thus, it was not representative of the actual diversity of the trophic level. Our analyses are therefore based on the occupancy (i.e. the number of sites in which the species were identified) and interactions between 96 herbivores and 125 parasitoids (excluding the superfamily 'Chalcidoidea indeterminate') across Europe. In particular, we focused on the relationship between parasitoid occupancy and the breadth of their climatic and diet niches. Sites where no parasitoid species were sampled were therefore not included in the analyses. Note that we use species occupancy to define the species range size and thus the terms occupancy and range size can be used interchangeably throughout the text. Although the species ranges considered may not represent the full range of the species, this data set represents, to our knowledge, the largest spatial scale across which species interactions have been empirically sampled in a comprehensive way. Given that the analysis is based on species characteristics (occupancy, interactions and climatic niche) at the continental scale, rather than by site, spatial autocorrelation cannot play an important role in our results.

2.2 | Climatic niche measures

To obtain a comprehensive picture of the variability of climatic conditions among sampling sites, and hence the climatic niche available to the sample species across the study area, we considered all the biologically relevant bio-climatic variables available from WorldClim (http://worldclim.org). These bio-climatic variables provide a holistic picture of the local climatic environment at different localities (Supporting Information Table S1). Bio-climatic data at each sampling site were obtained from WorldClim version 2.0 (Fick & Hijmans, 2017) using the raster package in R (Hijmans et al., 2014). To define a multidimensional space on which to project species based on their climatic niche requirements, while at the same time reducing the dimensionality of the niche, these bio-climatic variables were analysed using principal component analysis (PCA) using the prcomp function in R (R Core Team, 2023). To define the breadth of the climatic niche of each species, we matched each site where a given species was observed with the corresponding climatic conditions of the site. These points were then projected onto the space defined by the climatic PCA. The climatic niche breadth of each species was then quantified as the area of the smallest convex hull polygon that enclosed all points corresponding to the environments associated with that species on the 2-dimensional space defined by the first two principal components (PCs). Together, these two PCs explain 73.3% of the variance of climatic conditions across sampling sites. Thus, a single metric for each species summarizing the breadth of its climatic niche was obtained.

2.3 | Diet niche measures

2.3.1 | Total number of interactions at the continental scale

The simplest measure we considered to analyse each species' diet niche is the number of interacting partners it has across all sampling sites. Because galler parasitoids have to penetrate a protective wall of modified plant tissue in order to gain access to their victims, gall morphology has been inferred to strongly affect the associations between parasitoids and hosts (Nyman et al., 2007). The interactions between gallers and parasitoids are thus potentially constrained by the location, form, size and thickness of the gall, and by the habitat in which the willow host grows (Nyman et al., 2015). A parasitoid that is able to attack a more diverse variety of galls will therefore have a larger number of interacting partners and a wider diet niche. All interactions among species described in the data set at the continental scale (i.e. across all sampling sites) were summarized into a network of ecological interactions between species called the metaweb.

2.3.2 | Local interactions

A complementary measure to the total number of interactions at the continental scale is the number of interactions each species has locally. While the total number of interactions gives us information about the diet breadth at the continental scale, the number of local interactions informs us about the degree of local qualitative specialization where environmental conditions are the same for all species. We calculated the average number of local interactions for each species across all sites accounting for the total number of potential resources present in each site.

Besides the presence/absence of an interaction, an important feature to consider when characterizing a species' diet niche is the dependency it has on each interaction. This can distinguish strong interactions from weak or occasional ones. To determine this dependency we used the specialization index d' developed by Blüthgen et al. (2006), which considers interaction frequencies to describe quantitatively the degree of species specialization. In each sampling site, each species has a value of quantitative specialization (d') ranging from 0 to 1, where 0 indicates no diet specialization (i.e. no preference for any given prey) and 1 indicates maximum specialization (i.e. absolute preference for a given prey). Thus, d' can be interpreted as the deviations of the actual interaction frequencies from a null model that assumes that all partners are used in proportion to their availability (Blüthgen et al., 2006). Given that the specialization index (d') is measured at the local scale, we calculated for each species the mean d' across all sites to be able to relate it to species range size. A species that uses all resources in the same proportions as their availability in the environment (low d') should be considered more opportunistic than a species that uses rare resources disproportionately more (high d').

2.3.3 | β-diversity of resources

We analysed the change in resource diversity across sites (i.e. β-diversity of resources or turnover in resource use) for each parasitoid species using the beta.multi function of the betapart package in R (version 1.5.4; Baselga & Orme, 2012). This function ranges β-diversity between 0 and 1, where 0 represents no turnover in resource use across sites (i.e. the analysed species interacts with the same resources across all sites in which it is present) while 1 represents a complete turnover in resource use. β-diversity measures give us information about the species' diet niche at the regional scale.

2.4 | Null model analyses

Species that are present at more sites are very likely to have wider climatic niches and larger numbers of interacting partners, simply by virtue of inhabiting a larger variety of the sampled communities. To address this we developed a null model to assess whether the relationship between climatic and diet niches with range size would emerge only as a consequence of species occupancy. The null model thus tests the extent to which the climatic and dietary niche breadths of the parasitoid species in these communities can be explained by a random sampling of the range size covered by their distributions. If we would obtain the same patterns by randomly sampling the number of sites in which the parasitoids are present, we could conclude that the relationship between climatic and diet niches and range size are spurious correlations.

Our null model used the observed site-level occurrences (i.e. occupancy) of each parasitoid species across the spatial extent studied (Figure 1), but randomly distributed these occurrences across all the sampling points. In this way, a random set of locations, equal to the number of locations occupied by each parasitoid species, was chosen. The climatic niche encompassed by these random locations was quantified using a hull polygon over the climatic PCA as described in the previous section. This procedure was repeated 100 times and the distribution of climatic niche values thus obtained was calculated and compared to the original size of the species' climatic niche. The number of replicates was chosen based on the variability observed among replicates measured with the standard error of the mean.

Species diet breadth (i.e. the number of interactions a species has) can be influenced by the distribution of the parasitoid species itself and/or its potential interacting partners. To assess the extent to which resource availability is determined only by the parasitoid species' ranges, we used a null model similar to the one described above but this time quantifying the potential number of resources a parasitoid species might encounter by chance alone based on their occupancy. As above, 100 replicates of this null model were performed, and the resulting distribution was compared to the number of co-occurring resources each species has in the original sites.

2.5 | Statistical analyses

The PCA used to quantify climatic niche breadth for each species was used to determine the proportion of the variance in the climatic niche explained by each PCA axis.

The relationship between species occupancy and diet breadth (i.e. the number of total interactions at the continental scale) was quantified using linear regressions with the variables log-transformed to comply with the linear regression assumptions. For the nonlinear relationships, such as the relationship between occupancy and climatic niche, occupancy and mean number of local resources, and the relationship between occupancy and resources' β-diversity, we used generalized additive models both for visualization purposes and for the statistical tests. To analyse the relationship between occupancy and the mean number of local resources relative to the potential ones, we applied quantile regression since the relationship seemed to differ among quantiles. To analyse the differences between mean specialization index d' across occupancy categories we used the non-=parametric Kruskal–Wallis test given that there was a significant difference in the variance across the occupancy categories. We then used pairwise Wilcoxon rank sum tests to analyse the specific differences between categories.

To analyse the differences between the original data and the null model results, we compared the value of each species' climatic niche and the number of co-occurring resources with the bootstrapped distribution of values obtained from the replicates of the null models using one-sample t tests with a Bonferroni correction. We thus calculated the proportion of the values predicted with the null models that significantly differed from the original data and also the proportion of values that were predicted to be higher or lower than the original data. We subtracted the values of climatic niche and co-occurring resources obtained with the null models from the original values (i.e. residuals of the null model) to test whether the residuals were uniformly distributed across species with different levels of occupancy (Supporting Information Figure S2). All analyses were performed in R. 2023

3 | RESULTS

3.1 | Climatic niche–range size relationship

To tease apart the relationship between environment and occupancy we looked at the climatic niche of species as a collection of 19 climatic variables and collapsed this dimensionality using a PCA, where species were classified according to the breadth of their climatic niche (Figure 2a, Table 1). The two main components of this PCA (explaining 73.3% of the variance) were correlated (i.e. PCA loading > .25) with most of the bio-climatic variables related to precipitation (except for its seasonality) and temperature (Table 1). This indicates that both temperature and precipitation play a key role in determining the climatic niche of the species.

We found a strong positive relationship between climatic niche breadth, measured as the area of the smallest convex hull polygon containing all data points of sites corresponding to each species on the
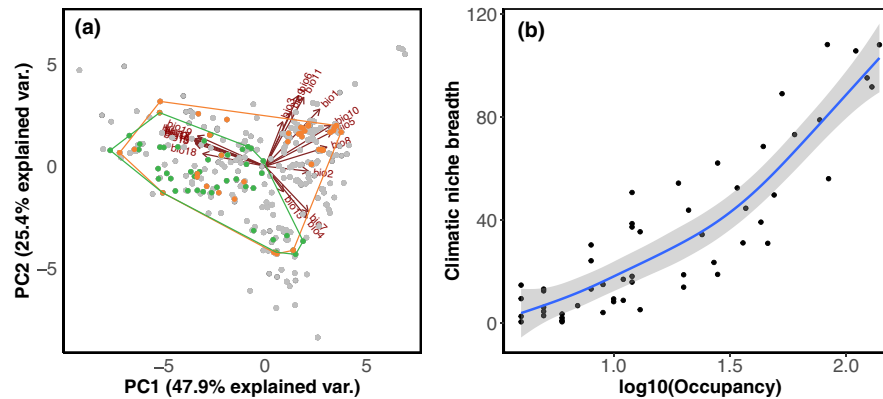
FIGURE 2 Relationship between species range size (i.e. occupancy) and their climatic niche. (a) Principal component analysis (PCA) of the climatic niche determined by the local climatic conditions at each sampling site. Grey points represent all species across their climatic range. Green and orange points and polygons exemplify the climatic niche of two species. Green: *Hydriomena ruberata*; orange: *Adelognathus pusillus*. The bio-climatic variables associated with the two main components of the PCA can be found in Table 1. (b) Relationship between climatic niche breadth and occupancy. Climatic niche breadth is calculated as the area, on the 2-D plane defined by the two main principal components of the climatic niche (a), of the smallest convex hull polygon that enclosed all points defining each species' climatic niche. The area is bounded by the straight lines connecting the outermost points of a polygon containing all sites corresponding to that species (i.e. the hull area). Each point thus represents a species. Blue line represents the mean trend and shaded areas represent 95% confidence intervals.

TABLE 1 Bio-climatic variables correlated with the two main components of the climatic principal component analysis (PCA).

Bio-climatic variables associated with PC1	Bio-climatic variables associated with PC2
Annual precipitation (.30)	Min. temperature of coldest month (.40)
Precipitation of wettest quarter (.29)	Mean temperature of coldest quarter (.39)
Precipitation of driest quarter (.29)	Annual mean temperature (.32)
Precipitation of driest month (.29)	Mean temperature of driest quarter (.31)
Precipitation of wettest month (.29)	Temperature seasonality (.29)
Max. temperature of warmest month (.28)	Temperature annual range (.26)
Precipitation of coldest quarter (.28)	Isothermality (.25)
Mean temperature of warmest quarter (.27)	
Mean temperature of wettest quarter (.26)	
Precipitation of warmest quarter (.26)	

Note: Listed variables display loadings equal to or greater than .25 in the principal component. The loading of each variable is presented in parentheses.

ordination, and the size of the range of the species (i.e. occupancy; adjusted $R^2 = .81$, $p < .001$; Figure 2b and Supporting Information Table S2). As expected, species with wider climatic niches have larger ranges.

3.2 | Diet niche–range size relationship

To analyse the relationship between the species diet dimension of the niche and its range size, we used multiple measures of the

species diet (see Methods). We observed a positive relationship between the total number of interacting partners at the continental scale and species range size. The relationship was linear in log–log with a slope of 0.79 and an adjusted $R^2 = .93$ (Figure 3a and Supporting Information Table S2). Similarly, species with larger ranges (i.e. higher occupancy) had on average more interactions locally (Figure 3b and Supporting Information Table S3), even when accounting for the fact that they could be present in sites where the number of available resources was larger (Figure 3c). Note, however, that at low occupancy the variability in the mean relative number of local interactions is large, which generates a non-significant relationship for the upper quantile (Supporting Information Table S4). Additionally, species resource turnover across sites (i.e. β-diversity of resources) was higher for species with larger ranges (Figure 3d and Supporting Information Table S3). At the same time, some species with small ranges showed high β-diversity due to the fact that they had very few interactions locally that differed among sites. In terms of quantitative diet specialization, species with larger ranges (i.e. high occupancy) showed a weakly significant *higher* mean specialization (d') across sites than species with *intermediate* and *low* occupancy (Supporting Information Figure S1a and Table S5). Yet, the differences in mean d' were small due to the large variation of the species with low occupancy. Moreover, species diet specialization d' decreased as the number of local interactions increased (Supporting Information Figure S1b). Thus, as expected, species with high occupancy showed lower specialization (d') in those sites where they were interacting with more species.

Overall, species with larger ranges not only had more interacting partners at the continental scale, but also locally (Figure 3b,c). Therefore, species with more interacting partners at the continental scale did not have a larger diet breadth only because they were present in more sites, but also because they had a larger number of interactions locally and a higher β-diversity of resources regionally.
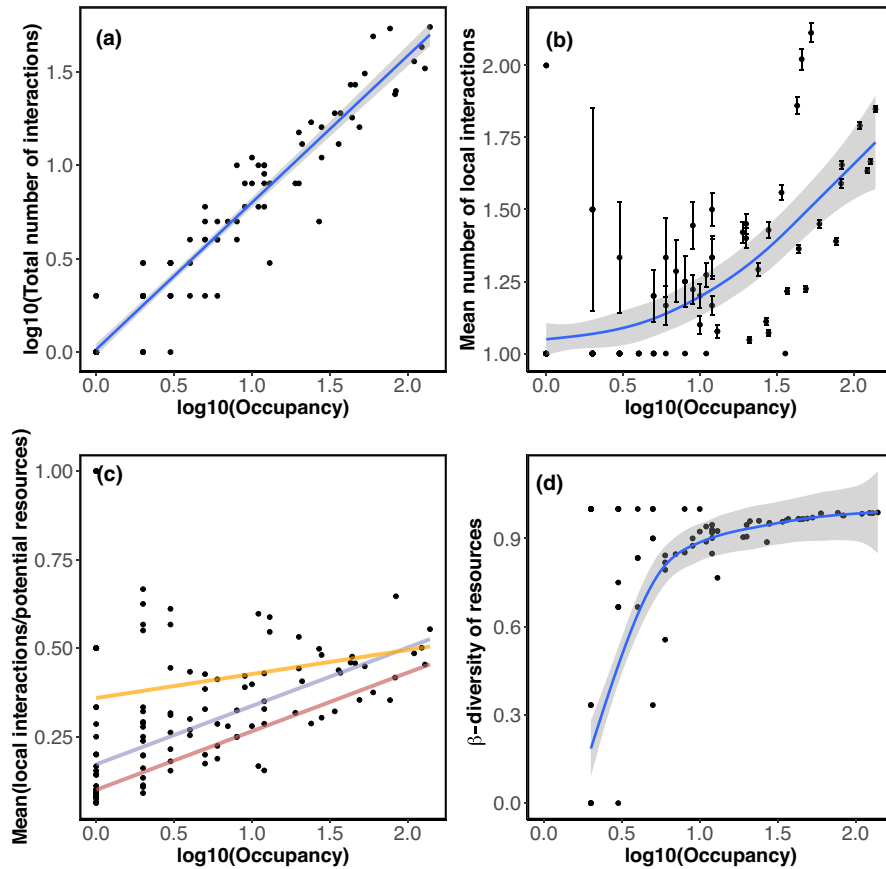
FIGURE 3 Relationship between parasitoid species range size (i.e. occupancy) and their diet niche at different spatial scales. (a) Total number of interactions across their entire continental range. Each point in the plot corresponds to a parasitoid species of the original metaweb. (b) Mean number of local interactions. (c) Mean number of local interactions relative to all the resources available in each site. Notice that the relative use of local interactions almost doubles with occupancy. Line colours represent the regression for different quantiles (red: .25; blue: .5; yellow: .75). (d) β-diversity of resources across all sites occupied by parasitoid species. Blue lines represent the mean trend and shaded areas represent 95% confidence intervals. Vertical black lines in (b) represent the error bars.

This observation supports the hypothesis that generalist species, capable of interacting with a larger number of partners, have larger geographical ranges.

## 3.3 | Are these patterns explained by random associations?

To assess whether species climatic and diet niches are a mere consequence of species occupancy, we used null models of species occupancy across the entire range and analysed the extent of both niches sampled (see Methods). For both niche dimensions, the observations differed significantly from the null models. We found that while species tend to occupy a smaller climatic niche than what would be expected by chance (Figure 4a; 44 out of 55 random distributions significantly different from the values sampled, i.e. 80%; adjusted $p < .05$), the number of potential resources is larger than what would be expected by chance (Figure 4b; 110 out of 126 random distributions significantly different from the values sampled, i.e. 87%; adjusted $p < .05$). In particular, our null model generated wider climatic niches than the original data for 80% of species with intermediate occupancy and for 64% of species with high occupancy (climatic niche cannot be computed for species with low occupancy). Conversely, the number of potential resources was smaller in the null model than in the original data for at least 70% of the species regardless of their occupancy. Note that for species with very high occupancy the original data cannot

differ greatly from the null model expectations because species that were observed in a very large proportion of all sites cover almost the entire climatic range of the study and co-occur with almost all potential resources.

We observed that the residuals of the null models are uniformly distributed across species with different levels of occupancy (Supporting Information Figure S2). The fact that the null models generated wider climatic niches than the original data, while species have a smaller number of potential resources, indicates that species in the original data have a more constrained climatic niche than expected given their range size, while co-occurring with a larger number of potential resources. The narrower climatic niche indicates that there is a constraint in the occupancy of parasitoids. However, the cause of this constraint cannot be unequivocally identified: it could be exclusively a climatic effect but also a consequence of biotic interactions, or a combination of the two. Meanwhile, the resource availability results suggest that the diet dimension of the niche is strongly limiting species range size, such that species in the original data occupy sites with greater diversity of resources than expected by chance.

4 | DISCUSSION

The lack of detailed geographical data on species interactions has hindered the understanding of how the diet dimension of a species' niche influences species range size. Here we used a continental data
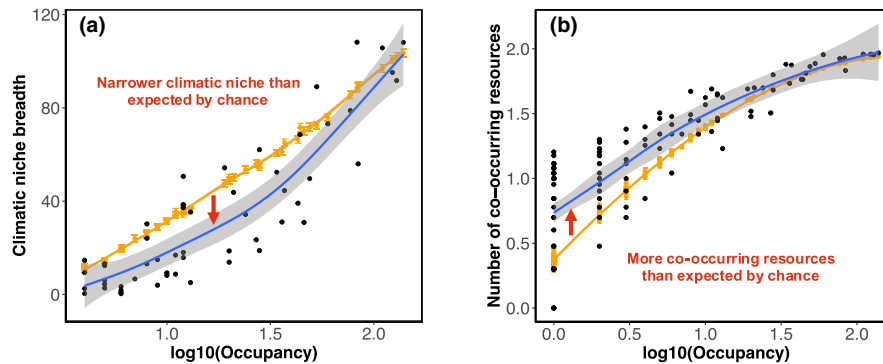
FIGURE 4 Null model expectations. We randomized the location of the sites in which each species is present to test whether the species climatic and diet niche breadths were a mere consequence of their occupancy (i.e. number of sites in which the species was sampled). (a) Null model expectation (orange dots and line) for species climatic niche compared to the observed one (black dots and blue line). (b) Null model expectation (orange dots and line) for species diet niche compared to the observed one (black dots and blue line). Species diet niche is assessed here as the total number of available resources. Orange dots and the corresponding error bars represent the mean value and standard error across 100 replicates. Shaded areas represent 95% confidence intervals. Notice that the x axes slightly differ between the two panels due to the inhability to measure climatic niches for those species that are only present in < 3 sites.

set that describes the spatial distribution and empirically sampled biotic interactions of 96 herbivores and 125 parasitoids across Europe (Kopelke et al., 2017; Figure 1), to analyse the relationship between species range size and two niche dimensions: the climatic and the trophic dimensions.

Our results show that both dimensions of the niche are positively related to species range size (Figures 2 and 3). Species with wider climatic and diet niches had larger ranges. We identified different aspects of diet specialization that are related to species range size. Namely, species with larger ranges have a larger number of interactions locally but also a higher turnover of resources across space, which resulted in a larger number of interactions at the continental scale (Figure 3).

Our null model analyses revealed that, although both dimensions of the niche are positively related to species range size, it is diet breadth that appears to be limiting species range size (Figure 4). In particular, we showed that in the original data species have a more constrained climatic niche than expected by their occupancy alone while they co-occur with a larger number of potential resources. The fact that in the original data species seem to try to maximize the number of potential resources provides evidence in support of the view that biotic interactions are key factors in determining large-scale patterns of species distributions.

4.1 | Biotic interactions and range size

Biotic interactions have been identified as crucial factors underlying large-scale biodiversity patterns, such as the latitudinal gradient in species richness (Dyer et al., 2007; Schemske, 2002; Wisz et al., 2013). Yet, due to the historical lack of information on species interactions across large spatial extents, a full understanding of their influence on the patterns of species geographical range size has been largely missing. Although a few studies have shown that the breadth of the dietary niche is related to the size of a species' range (Brändle

et al., 2002; Slatyer et al., 2013), it has been widely accepted that its influences are less predominant than those determined by the species' capacity to persist in different environments (i.e. environmental or climatic niche) (Boulangeat et al., 2012; Pearson & Dawson, 2003; Slatyer et al., 2013; Thuiller et al., 2004). Moreover, the influence of species diet breadth on range size has been considered to diminish as the spatial scale considered increases (Brändle et al., 2002; Slatyer et al., 2013), while species environmental niches have been related to their range sizes regardless of the spatial scale of observation (Slatyer et al., 2013).

Here we were able to show for the first time in a well-constrained observational system, that species with larger ranges have wider diet breadths at all spatial scales (Figure 3). That is, they have a higher number of interacting partners at local scales but they also interact with a larger diversity of resources across sites (i.e. higher resource turnover), which results in wider diet breadth at the continental scale. Therefore, species with larger ranges are able to be more generalist in terms of their biotic interactions across different spatial scales, which is suggestive of a directionality in the relationship between species diet niches and their range size. In other words, if species with larger ranges would only have a larger number of interacting partners at continental scales but not at local scales, it could indicate that the number of interactions is a mere consequence of their higher occupancy. However, having a larger number of interactions locally (even when accounting for the number of potential resources) shows the capacity of a species to have a more generalist diet. Yet, in terms of quantitative diet specialization, our analyses showed that species with larger ranges can have diet strategies at the local scale that are actually more specialized than many species with smaller ranges. We speculate that this might reflect an ability among successful generalist species to attune to the conditions of different locations by adapting to focus on a subset of prey. This multi-scale perspective thus suggests new insights into the role of species diet breadth in determining range size. Further research could potentially expand quantitative metrics of trophic

specialization across different spatial scales, which could provide more detailed and specific information on the influence of diet specialization upon species distributions.

4.2 | Dietary niche as a strongly range-limiting factor

Given that both dietary and climatic dimensions of species niches were correlated with species range size, we used a null model to determine whether one or both of these are likely to play a causal role. By randomly sampling the same number of sites in which each species was present we generated random expectations for the relationship between both dimensions of the niche and species range size. The comparison of these random expectations and the patterns observed revealed that while the climatic niche occupied by the species was smaller than expected by chance, the diet dimension of the niche was greater than expected by chance (Figure 4). The fact that species occupy sites that have a larger number of resources present than average highlights the importance of biotic interactions for species distributions.

Although the null model showed that species seemed to have more constrained climatic niches than expected by chance, this does not mean that the climatic niche is unimportant in determining species range size, as shown in previous studies (Boulangeat et al., 2012; Brown, 1984; Slatyer et al., 2013). In fact, a relationship between climatic niche breadth and species range size is practically unavoidable when analysing realized niches, which contain implicit information about species range sizes. Hence the importance of the use of null models to analyse the deviations of the patterns observed from null expectations. The analyses of the null model residuals indicate that the shape of the relationship between both dimensions of the niche and species range size could be obtained from species occupancy alone (Supporting Information Figure S2). However, the systematic differences between the null expectations and the original data generate opposite mean tendencies for the climatic and the diet niche residuals. While for the climatic niche we observed a negative mean value in the residuals, for the number of co-occurring resources we observed a positive mean value, indicating that the null model generated larger values than the original data for the climatic niche and smaller than the original for the diet niche. What our results suggest is that in the data analysed in this study, the dietary dimension of the niche strongly influences species range size. Further studies involving detailed data on different types of biotic interactions across large spatial scales would be needed to extend our study and investigate the influence of different aspects of the dietary niche on species range sizes across interaction types.

4.3 | Range size and extinction risk

Previous studies have shown that the presence of predators can strongly influence the abundance, distribution and range limits of prey species (Estes et al., 2011; Ryberg & Chase, 2007; Wisz

et al., 2013). Our results complement these observations by showing that range sizes of parasitoids are influenced by the presence of hosts. Species with smaller ranges will be more vulnerable to extinction not just because they are more susceptible to population loss owing to habitat loss or drastic changes in environmental conditions, but also because they have a smaller number of resource species they can rely on.

The vulnerability associated with resource availability will, however, depend on how rare or widespread (and thus more or less vulnerable to extinction) the resources themselves are. The relationship between range size of consumers and availability of resources is largely unknown partly due to the lack of large data sets containing information on multispecies interactions across large spatial scales. Nevertheless, there is evidence that the greater the human disturbances, with fewer resources available for organisms in natural ecosystems, the more depauperate the trophic communities are with respect to their potential (Mendoza & Araújo, 2019). Depauperate trophic communities follow from local extinctions of species and extinctions follow from declining populations and restricted ranges. So, the relationship between range size and resource availability found here is expected to hold more widely.

A common limitation in the study of the determinants of species range sizes and, therefore, species vulnerability is the lack of data sets that characterize the full set of environmental or dietary resources used by the species. The data set used here is to our knowledge the largest data set describing empirically sampled interactions across geographical scales. The comprehensiveness of the data set allowed us to describe clear relationships between both dimensions of the niche and species range size, which would not be qualitatively altered by, for instance, the addition of newly described interactions. The completeness of the species interactions data is an important issue to consider when characterizing network structural patterns that might be affected by the absence of non-sampled interactions (Jordano, 2016). Yet, given that the main focus of this study is not the structural patterns of the network, even if some interactions were missed, it is unlikely that those interactions would only involve a specific set of species. Missing interactions would most likely affect all species equally, which implies that the qualitative pattern described here would remain unaltered. The comprehensiveness of the data also allowed us to analyse the relationship between the range size of both trophic levels (i.e. parasitoids and hosts) for each interaction sampled. We found that most consumers tend to have larger ranges than their resources (Supporting Information Figure S3). Yet, consumers with narrow ranges were mostly interacting with widespread resources, and inversely, resources with narrow distributions were mostly consumed by widely distributed consumers. This indicates that interactions between species with reciprocally narrowed ranges are rare and potentially very vulnerable. This novel perspective of analyses can be useful to detect not only vulnerable species but also vulnerable interactions, the loss of which may entail further consequences for the functioning of ecosystems (Galiana et al., 2022; Janzen, 1974).

5 | CONCLUSION

We found that both the climatic and diet dimensions of species niches are positively related to their geographical range size at multiple spatial scales. Contrary to common assumptions, we identified that, for the study taxa, the dietary dimension of the niche strongly influences species' range size. We showed for the first time how different aspects of species' diet niche are related to their range size: species with larger ranges are able to use a larger number of resources at both local and continental scales, which highlights the importance of diet generality for species range size. More generally, our results suggest that biotic interactions might be more important in determining large-scale species distribution patterns than previously recognized. Future studies should therefore take advantage of the newly existing data on biotic interactions across geographical scales to further analyse the relative importance of the different dimensions of the niche for other biogeographical patterns. By analysing the relationship between range size across trophic levels, we provide a novel perspective to identify vulnerable interactions, which coul be fundamental to predict and mitigate the effects of global environmental change.

CONFLICT OF INTEREST STATEMENT
The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT
The data used to perform the analyses are available here: https://doi.org/10.5061/dryad.2rbnzs7sr. The code used to perform the analyses is available here: https://doi.org/10.5281/zenodo.7777030.

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BIOSKETCH

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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