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Research

The geographical variation of network structure is scale dependent: understanding the biotic specialization of host–parasitoid networks

Núria Galiana, Bradford A. Hawkins and José M. Montoya

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Research on the structure of ecological networks suggests that a number of universal patterns exist. Historically, biotic specialization has been thought to increase towards the Equator. Yet, recent studies have challenged this view showing non-conclusive results. Most studies analysing the geographical variation in biotic specialization focus, however, only on the local scale. Little is known about how the geographical variation of network structure depends on the spatial scale of observation (i.e. from local to regional spatial scales). This should be remedied, as network structure changes as the spatial scale of observation changes, and the magnitude and shape of these changes can elucidate the mechanisms behind the geographical variation in biotic specialization. Here we analyse four facets of biotic specialization in host–parasitoid networks along gradients of climatic constancy, classifying the networks according to their spatial extension (local or regional). Namely, we analyse network connectance, consumer diet overlap, consumer diet breadth, and resource vulnerability at both local and regional scales along the gradients of both current climatic constancy and historical climatic change. While at the regional scale none of the climatic variables are associated to biotic specialization, at the local scale, network connectance, consumer diet overlap, and resource vulnerability decrease with current climatic constancy, whereas consumer generalism increases (i.e. broader diet breadths in tropical areas). Similar patterns are observed along the gradient of historical climatic change. We provide an explanation based on different beta-diversity for consumers and resources across the geographical gradients. Our results show that the geographical gradient of biotic specialization is not universal. It depends on both the facet of biotic specialization and the spatial scale of observation.

Keywords: beta-diversity, biotic specialization, ecological network, host–parasitoid food web, spatial scale

Introduction

Biotic specialization has long fascinated biogeographers and ecologists. Historically, biotic specialization has been thought to be higher in more constant environments. Hypotheses for this pattern include the supposition that greater stability and lower seasonality in e.g. the tropics, lead to more stable population dynamics than those at higher latitudes, allowing for narrower (and more specialized) feeding niches (MacArthur 1955, 1972). Similarly, more historically constant environments reflect the available time for potential species coevolution due to temporal stability of local communities, which increases local adaptation and favours biotic specialization (Jansson and Dynesius 2002, Dalsgaard et al. 2011, 2013, Schleuning et al. 2012). However, recent network studies have addressed the geographical variation in biotic specialization, showing non-conclusive and highly idiosyncratic results (Moles and Ollerton 2016). While some authors showed an increase in network specialization and higher predation risk towards the tropics (Olesen and Jordano 2002, Dalsgaard et al. 2011, Trøjelsgaard and Olesen 2013, Roslin et al. 2017), others found the opposite (Schleuning et al. 2012). Yet some others found distinct trends for each hemisphere (Pauw and Stanway 2015) and for each measure of biotic specialization considered (Dalsgaard et al. 2017), or no latitudinal trend at all (Ollerton and Cranmer 2002, Morris et al. 2014).

Yet, all biogeographical studies to date analysing the geographical variation in biotic specialization focused on specialization across local communities, ignoring how specialization at larger spatial extents (e.g. regional scale) varies along the same biogeographical gradient. This is crucial, as several spatial processes, such as dispersal or species sorting, generate changes in network structure as the spatial scale of observation changes (Gravel et al. 2011, Pillai et al. 2011, Roslin et al. 2014, Montoya and Galiana 2017, Galiana et al. 2018). For instance, given that landscape configuration has different effects on each species depending on their dispersal abilities, (Ewers and Didham 2006), differences in the slopes of the species–area relationships (SAR) across trophic levels can emerge, promoting changes in network structure across spatial scales (Holt et al. 1999, Holt 2009, Roslin et al. 2014, Galiana et al. 2018). These differences in the slope of SARs across trophic levels can reflect differences in β -diversity (i.e. site-to-site variation in community composition) across trophic levels, when the total extent of area and the size of the regional pool of species are accounted for (Storch et al. 2012, Lazarina et al. 2013). If β -diversity is different across trophic levels (Soininen et al. 2007a), and therefore there is an unbalanced increase in the number of species per trophic level as the area sampled increases, network biotic specialization can change across spatial scales. For example, if consumers' β -diversity is higher than resources' β -diversity, the mean number of consumers per resource might increase from local to regional spatial scales due to the larger increase in the richness of consumer species than resource species. Importantly, if differences in beta-diversity across trophic levels are not

universal, the changes in biotic specialization across spatial scales might vary geographically. Changes in biotic specialization across scales can be thus intimately linked to β -diversity patterns in multitrophic communities.

β -Diversity provides a direct link between biodiversity at local scale (α -diversity) and the broader regional pool of species (γ -diversity) (Whittaker 1960, 1972). However, not only species composition can differ among environments. The realization of an interaction between two species that co-occur in space is directly influenced by the surrounding environment and how this environment affects each species (Thompson 2005, Vázquez 2005, Poisot et al. 2011). Species interactions can thus experience spatial turnover independent from species occurrences (Thompson 2005, Poisot et al. 2012a). Scaling up in space allows capturing the variation of species interactions in space and the potential mechanisms driving this variation. For instance, if species richness remains constant from local to regional spatial scales but there is an increase in the number of links, this indicates that two species that co-occur locally do not interact in every location they both occupy. Indeed, a regional network (or metaweb) characterizes all potential interactions among all species that are susceptible to both co-occur and interact at the scale considered (Dunne 2006, Gravel et al. 2013, Morales-Castilla et al. 2015, Redhead et al. 2018). Similar to variations in regional species diversity across geographical gradients, variation in regional network structure can occur, for example, because of the presence of more specialized species in certain regions or due to habitat heterogeneity that can promote the emergence of network modules at the regional scale (Araujo et al. 2018). The motivation for comparing local and regional networks is thus similar to the motivation for comparing local and regional diversity: what and how spatial processes affect the changes of network properties.

Here we focus on how the geographical gradient of biotic specialization depends on the spatial scale of observation (i.e. local versus regional). Specifically, we aim to investigate how biotic specialization changes along the gradients of annual temperature range (i.e. difference between the warmest and the coldest temperature within the year) and historical climatic change (i.e. difference between current mean annual temperature and mean temperature in the Last Glacial Maximum 21 000 yr ago) at both local and regional spatial scales. While annual temperature range indicates how constant the current climate is, historical climatic change indicates the maximum historical temperature range, given that the Last Glacial Maximum is the most recent point at which the global ice extent was at its greatest. Therefore, both measures account for the temperature range experienced in a given location over short and long temporal scales respectively, allowing us to investigate the relationship between biotic specialization and climatic constancy. Even though climate constancy is a multifaceted concept, maximum temperature range establishes the boundaries within which fluctuations through time occur. As such, it is the most fundamental facet of constancy.

The idea that the degree of specialization increases towards the tropics has been rarely explored beyond niches becoming narrower, that is, beyond specialization from the consumers' perspective (MacArthur 1955, Vázquez and Simberloff 2002, Vázquez and Stevens 2004; but see Schleuning et al. 2012, Moles and Ollerton 2016, Dalsgaard et al. 2017). However, specialization is a multifaceted concept. There are other metrics of biotic specialization beyond diet breadth, such as network-based metrics that reflect the general level of specialization of the community (Devictor et al. 2010, Poisot et al. 2012b, Dalsgaard et al. 2017). This is important since different facets of specialization can reveal different patterns across environmental gradients (Dalsgaard et al. 2017).

We use 74 host (resource)–parasitoid (consumer) networks described at the local scale and 99 described at the regional scale (Fig. 1) to analyse how four facets of biotic specialization change along the two environmental gradients depending on the spatial scale of observation. Namely, we analyse network connectance, consumer diet overlap, consumer diet breadth (or generality), and resource vulnerability. We also analyse the number of species at each trophic level to determine the contribution of host and parasitoid β -diversity to the spatial scaling of biotic specialization along the environmental gradients. Following the biotic specialization hypothesis (MacArthur 1955, 1972), we would expect networks to be more specialized in more constant climates, both historically and contemporaneously. That is, less connected networks, with consumer diets being narrower and less overlapped and resources being attacked by fewer consumers. Yet, we expect the patterns of biotic specialization to be affected by the spatial scale of observation due to different β -diversity across trophic levels. Specifically, if the β -diversity of hosts is larger than that of parasitoids, we would expect an increase of

consumers' generality and decrease of host vulnerability from local to regional spatial scales.

Methods

Data set

We compiled and analysed 173 host (resource)–parasitoid (consumer) bipartite networks occurring in a globally extensive range of habitat types extracted from a parasitoid assemblage diversity database initiated by Hawkins (1990, 2005) and extended into the present (Fig. 1). In these networks, species correspond to taxonomic species (i.e. we avoid aggregation into trophic species), and links always correspond to direct observations of a larval parasitoid insect feeding and developing within or on its herbivorous insect host. Only networks composed of more than 10 species (hosts and parasitoids altogether) were considered given that the network properties used are very sensitive to the addition or loss of one or few species in small networks. Additionally, we considered networks with a minimum of 2 species within each trophic level to avoid studies focusing only on one host or one parasitoid. We only considered binary data (i.e. the presence or absence of an interaction) given that data on interaction strengths for regional networks were not available.

Environmental variables

We focused our analyses on the effect of temperature variability, both contemporary and historical, on network biotic specialization. For that, we used the annual range in temperature and the historical climatic change of the location

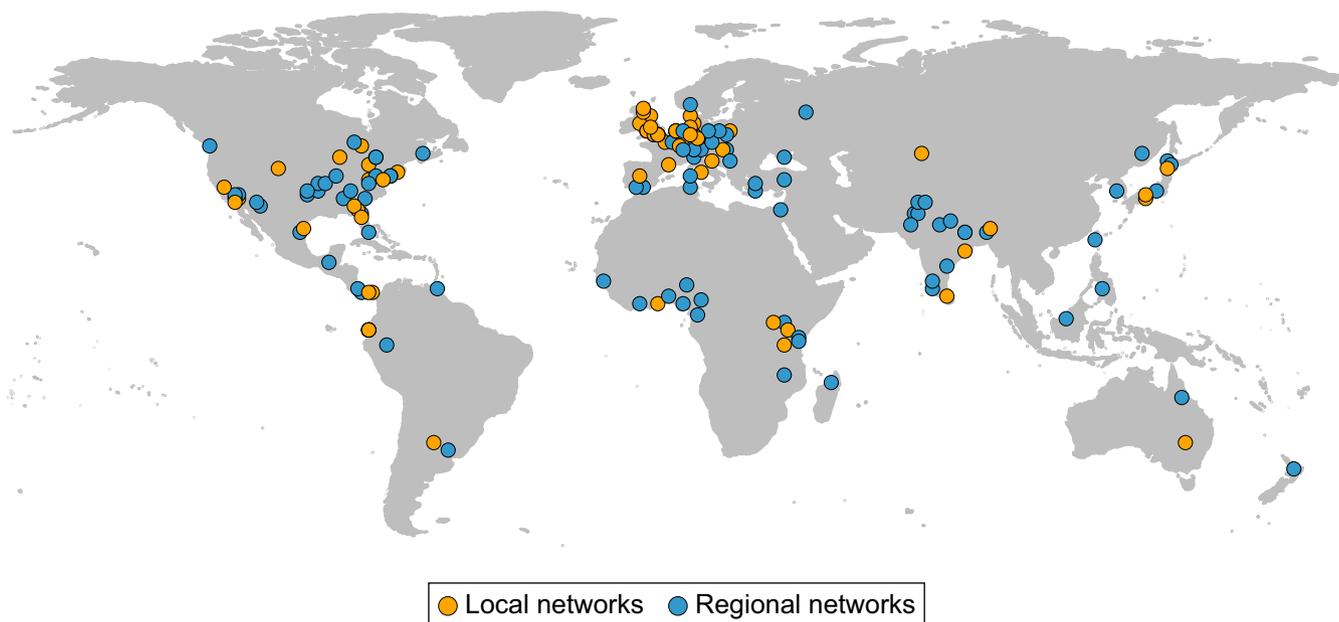


Figure 1. Localization of the 173 host (resources)–parasitoid (consumers) bipartite networks analysed. Each point corresponds to a network, with orange and blue for local and regional respectively.

of each network as predictor variables. For regional networks, we considered a central location within the extension of the regional scale (i.e. average latitude and longitude between all sampling sites used to compose the regional network) to extract the climatic variables. For those regional networks where the exact coordinates of all sampling sites were not provided in the original paper, we extracted the climatic variables for one of the locations described. Annual temperature range was extracted for each location from the WorldClim database (Fick and Hijmans 2017), corresponding to bio7 (max temperature of warmest month – min temperature of coldest month). Although traditionally the geographical gradient of biotic specialization has been tested using latitude as the predictor variable, here we used temperature range because it provides more direct measures of local climatic conditions and allows us to directly test the effect of climatic constancy on biotic specialization (Hawkins and Sheehan 1994). Historical climatic change was calculated using the mean annual temperature 21 000 ybp for each location, provided by the tool PaleoView (Fordham et al. 2017), and the mean annual temperature from WorldClim (i.e. difference between current mean annual temperature and mean annual temperature 21 000 ybp).

Spatial scale: local versus regional networks

To test the influence of the spatial scale on network biotic specialization, we distinguished between local and regional networks. From the 173 host–parasitoid networks used, 74 were classified as local networks and 99 were classified as regional networks. The spatial scale of each network was determined based on the area covered during the data collection of each study described in each publication analysed. In all cases, we considered the original network described in each publication and the spatial scale addressed originally, i.e. we did not build any network, neither local nor regional, from the aggregation of other published local webs or inferred interactions between species. Local webs are those collected from a single sampling site or from multiple sampling sites covering an area smaller than 1000 km². Regional webs are those collected from multiple sampling locations distant from each other covering areas larger than 1000 km². Therefore, while local networks represent the realised interactions between species of the local assemblage, regional networks represent the combination of all the interactions between species that have been observed in at least one of the locations sampled within the scale considered, which does not entail that they are necessarily realized in every single location within the area covered by the regional network. Thus, regional networks represent all potential interactions among species from the regional pool that are susceptible to both co-occur and interact at the scale considered (Dunne 2006, Gravel et al. 2013, Morales-Castilla et al. 2015). We considered the threshold commonly used in the literature for local versus regional species diversity (Willis and Whittaker 2002, Pearson and Dawson 2003) to also determine local and regional spatial scales for biotic interactions. We considered spatial scale as a

categorical variable because accurate estimations of the area sampled were not available in all publications, which makes them not reliable enough across a continuum. We tested the robustness of our results by varying the threshold used from 1000 km² to 500 km² and by using a subset of the data to test the patterns with both extremes of the spatial scale range (i.e. using networks with areas < 100 km² for the local, and areas > 100 000 km² for the regional category). Both analyses demonstrated the robustness of the results showing no differences in the patterns observed (Supplementary material Appendix 1 Table A1, A2). Similarly, given that within the regional scale category we had a wide range of areas, we subdivided it in two categories to validate the robustness of the patterns observed. The threshold used to subdivide the regional networks was set to 100 000 km². We observed no significant differences between the two sub-categories (Supplementary material Appendix 1 Table A3).

Specialization facets and beta-diversity

In our bipartite host–parasitoid networks, species richness (S) is the sum of the number of species of resources (S_R) and consumers (S_C). We measured four facets of network specialization:

Connectance (C) is the number of actual links (L) divided by the number of possible links in the bipartite network ($S_R \times S_C$).

Consumer diet overlap (O), is the connectance of the consumer overlap graph, where a link between two consumers exists if they share, at least, one resource species (Cohen 1978, Sugihara 1984). Consumer overlap is thus the actual number of links among consumers (L_C) divided by the possible links between them ($S_C \times (S_C - 1) / 2$). This property describes the extent and pattern of resource-use overlap amongst consumers.

Diet breadth or *generality* is the mean number of resources per consumer species, that is, L/S_C . It is a measure of the degree of specialization in the web from the consumer perspective.

Vulnerability is the mean number of consumers per resource species, L/S_R , and represents the degree of specialization found in the network from the resource perspective.

We analysed all these network specialization metrics at each spatial scale along the gradient of environmental constancy. Additionally, we measured the number of species at each trophic level (i.e. number of parasitoids and hosts) and consumer:resource ratios. We hypothesize that changes in the consumer:resource ratios across spatial scales can be caused by differences in β -diversity across trophic levels. These changes in the consumer:resource ratios can in turn generate changes in network specialization across spatial scales.

Given that our dataset is composed by independent local and regional networks (i.e. our local networks are not subsets of our regional networks) and the information on species presences and interactions for each local site used to construct the regional networks is not available in most of the original

papers, we cannot directly test this hypothesis with the data. However, to theoretically understand how β -diversity influences the increase in species richness from local to regional spatial scales and how it can generate changes in biotic specialization across spatial scales, we built three identical random local networks to exemplify the process. These networks have the same number of species and links, with species equally distributed across trophic levels, which results on a consumer:resource ratio equal to 1. Interactions between species were randomly assigned from a uniform distribution between 0 and 1, where network connectance determined the probability for a consumer–resource link. We then defined β -diversity as the percentage of species co-occurring within each trophic level across local webs, reflecting their spatial turnover (Koleff et al. 2003). This gives two values of β -diversity, one for each trophic level: β_{consumer} - and β_{resource} -diversity (Fig. 2).

To determine the effect of having unbalanced values of spatial turnover (β -diversity) between trophic levels on the changes in network specialization across spatial scales, we assigned values of β_{consumer} -diversity, ranging from 0.1 to 0.8 with an increase of 0.1, while we kept β_{resource} -diversity equal to 0 (Fig. 2A). On a different scenario, we varied simultaneously β -diversity across trophic levels. That is, we assigned values of β -diversity ranging from 0.1 to 0.8 with an increase of 0.1 to both trophic levels at the same time (Fig. 2B). We then analysed network properties at both local and regional

(i.e. the metaweb resulting from the aggregation of the three local networks) spatial scales.

Control by species richness

Some of the specialization metrics considered can be sensitive to differences in species richness (S) among networks (Bengtsson 1994, Baiser et al. 2012, Poisot and Gravel 2014, Wood et al. 2015). Therefore, comparative analyses of networks need to control for variation in species richness across webs given that conclusions on the variability of network specialization might simply result from variation in species richness across webs. Controlling for S is particularly relevant in biogeographical studies given the latitudinal gradient in species richness: S increases towards the tropics in most taxa (Hawkins and Diniz-Filho 2004, Hillebrand 2004). We thus controlled all the analyses for species richness S ($S = S_r + S_c$) including it as a fixed effect in our statistical analyses, and this should partially correct for different sampling efforts among studies since it has been shown that observational effort and species richness correlate strongly (Magurran 1988, Martinez et al. 1999). Due to the lack of quantitative data, further analyses to control for sampling effort were not possible. However, sampling effort bias are unlikely to affect our results given that we observed opposite patterns for hosts and parasitoids, which indicates that the biases in sampling effort would need to be very specific and directed to underlie the results.

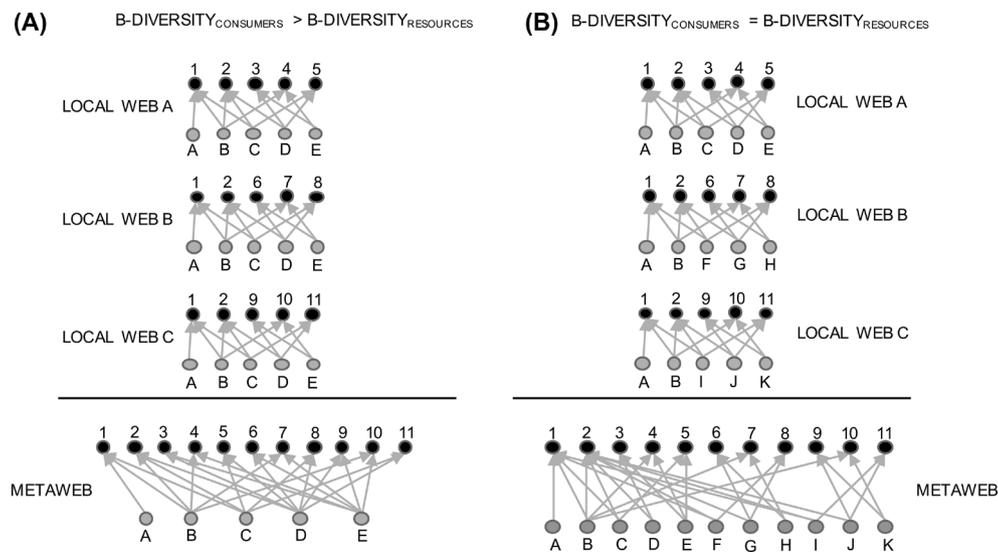


Figure 2. Beta-diversity as a mechanism for the variation on network structure across spatial scales. Black nodes represent consumer species and grey nodes resource species. Species identities are represented with numbers for consumers and letters for resources. Arrows correspond to species interactions. All local networks have the same number of species and identical structure. Properties of the local networks: connectance = 0.48; consumer overlap = 0.8; consumer diet breadth = 2.4; resources vulnerability = 2.4; consumer:resource ratio = 1. In (A) β_{consumer} -diversity = 0.6 and β_{resource} -diversity = 0. That is, 3 out of the 5 species of consumers are replaced in each local network while resource species have the same identity in the three local networks. The regional network (or metaweb) is built from the aggregation of the three local networks, where species maintain their identity and their interactions. Properties of the regional network (metaweb) in (A): connectance = 0.43; consumer overlap = 0.78; consumer diet breadth = 2.18; resources vulnerability = 4.8; consumer–resource ratio = 2.2. In (B) β -diversity = 0.6 for both trophic levels. Properties of the regional network in (B): connectance = 0.247; consumers’ overlap = 0.47; consumers’ diet breadth = 2.72; resources vulnerability = 2.72; consumer–resource ratio = 1.

Statistical analyses

We used GLMs (Family = Gaussian, Link = identity) to analyse differences in network properties depending on both environmental variables (dependent variables: network connectance, consumer overlap, consumer diet breadth, prey vulnerability, number of hosts and number of parasitoids; independent variables: annual temperature range and historical climatic change). Because our independent variables suffered from collinearity (adjusted- $R^2=0.38$, $p < 0.001$), we could not perform a meaningful multiple regression analyses to partition the predictive power of the two environmental variables. Number of species was included into de GLMs as a fixed effect given that all network properties, including the number of hosts and parasitoids independently, were correlated with species richness (separate GLMs were performed to analyse the correlation between species richness and the network properties using spatial scale as a fixed effect) (Supplementary material Appendix 1 Table A4, Fig. A1). Additionally, we also performed the GLMs including the number of hosts and parasitoids individually (instead of species richness) as fixed effects, except for the analyses where they were considered as dependent variables. We performed all the analyses with every network variable and the environmental predictors log-transformed. Given that we expected the relationship of the dependent variables (i.e. network properties) and the environmental variables to be affected by the spatial scale of observation, we included spatial scale as an additional fixed effect with an interaction term with the dependent variables. We used type III sum of squares in our analyses due to our unbalanced data (local networks = 74; regional networks = 99). Following the statistical analysis, we confirmed that none of the network metrics contained significant spatial autocorrelation in the model residuals using Moran's I across 13 distance classes, (all $p > 0.05$), which indicates that significance tests are unbiased. All analyses were performed in R (R Core Team).

Data deposition

Data available from the Dryad Digital Repository: <<https://doi.org/10.5061/dryad.kk75k1p>> (Galiana et al. 2019).

Results

Effects of environmental constancy on biotic specialization

At the regional scale, changes in biotic specialization were not well predicted neither by current climatic constancy nor by historical climatic change. Network connectance, consumer diet overlap, consumer diet breadth, and resource vulnerability showed no significant changes along the gradients of annual temperature range and historical climatic change, except for a slight decrease of consumer diet breadth along the gradient of historical climatic change (Fig. 3, Table 1).

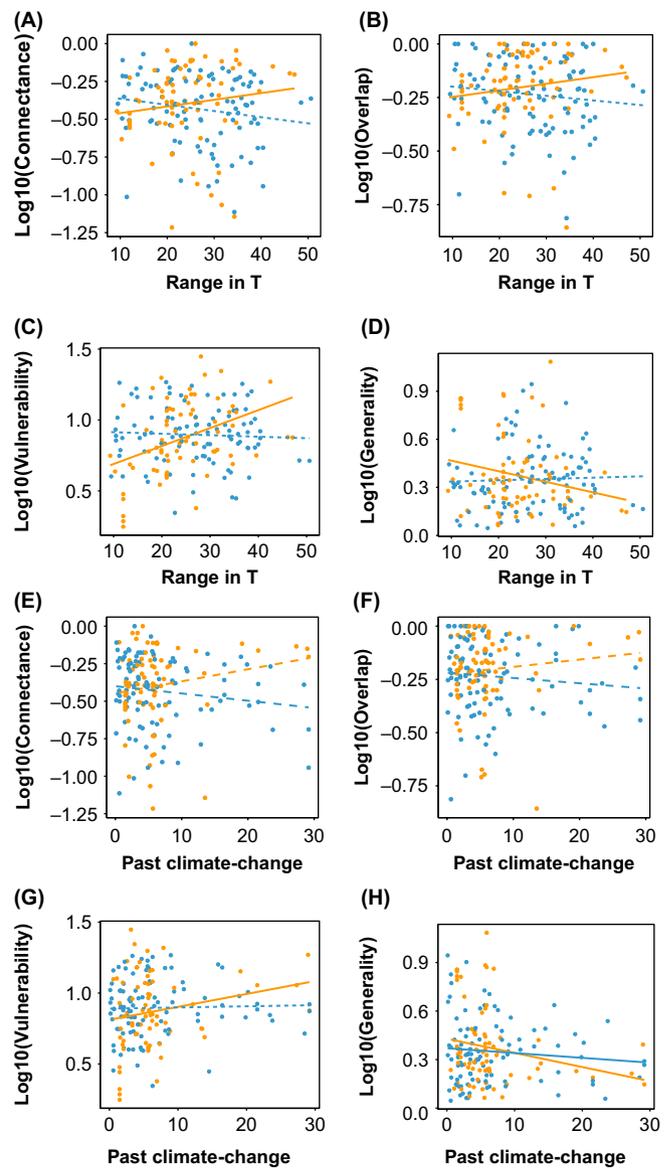


Figure 3. Geographical variation in network structure along the gradient of (A–D) annual temperature range and (E–H) historic climatic change (i.e. change in mean annual temperature for the last 21 000 yr). Relationship between network connectance, consumer overlap, resource vulnerability and consumer diet breadth with both environmental variables at local (orange) and regional (blue) spatial scales. Notice that the tendency line in blue for regional spatial scales does not indicate a significant relationship.

On the contrary, for local webs, both environmental variables were good predictors of biotic specialization. All network properties were significantly correlated with species richness at both spatial scales (Supplementary material Appendix 1 Table A4, Fig. A1). Even though there was no significant difference in the relationship of the number of species with the network properties across spatial scales (Supplementary material Appendix 1 Table A4, Fig. A1), the mean number of species was significantly smaller at local than at regional scales, as expected. We found no significant

Table 1. GLM results for the relationship of each network property with annual temperature range and historical climatic change. Estimates, T values and statistical significances (***) for p-values <0.0001; ** for p-values <0.01; * for p-values <0.05; ° for p-values <0.1) are indicated for the relationship at each spatial scale—local (n=74) and regional (n=99)—and for the interaction term of spatial scale with both environmental variables taking local spatial scale as the reference. Multiple R-squared are provided as an indicator of the explained variation of each model.

| | Connectance | | | Overlap | | | Generality | | | Vulnerability | | | Parasitoids | | | Hosts | | | |
|---------------------|-------------|----------|----------------|----------|---------|----------------|------------|----------|----------------|---------------|-----------|----------------|-------------|-----------|----------------|----------|-----------|----------------|--|
| | Estimate | T-value | R ² | Estimate | T-value | R ² | Estimate | T-value | R ² | Estimate | T-value | R ² | Estimate | T-value | R ² | Estimate | T-value | R ² | |
| Range in T | | | | | | | | | | | | | | | | | | | |
| Local | 0.42 | 3.115** | | 0.28 | 2.653** | | -0.48 | -3.170** | | 0.68 | 4.383*** | | 0.32 | 4.644*** | | -0.65 | -3.675*** | | |
| Regional | -0.12 | -1.237 | 0.53 | -0.05 | -0.684 | 0.38 | 0.02 | 0.223 | 0.23 | -0.09 | -0.810 | 0.26 | -0.03 | -0.489 | 0.88 | 0.12 | 0.936 | 0.52 | |
| Interaction term | -0.54 | -3.237** | | -0.34 | -2.536* | | 0.51 | 2.675** | | -0.77 | -3.998*** | | -0.35 | -4.016*** | | 0.77 | 3.506*** | | |
| Past climate change | | | | | | | | | | | | | | | | | | | |
| Local | 0.09 | 1.476 | | 0.03 | 0.633 | | -0.17 | -2.516* | | 0.17 | 2.421* | | 0.11 | 3.469** | | -0.17 | -2.198* | | |
| Regional | -0.03 | -0.805 | 0.51 | -0.01 | -0.543 | 0.35 | -0.07 | -2.077* | 0.23 | 0.009 | 0.221 | 0.20 | 0.01 | 0.838 | 0.87 | 0.03 | -0.722 | 0.49 | |
| Interaction term | -0.12 | -1.681° | | -0.05 | -0.818 | | 0.09 | 1.167 | | -0.16 | -1.997* | | -0.09 | -2.606** | | 0.14 | 1.557 | | |

relation of species richness with neither of the environmental variables (Supplementary material Appendix 1 Table A5, Fig. A2). Yet, all results described in this section refer to the patterns observed after accounting statistically for the effect of the number of species. Additionally, we performed the analyses controlling by the number of species in each trophic level as two separate covariates and we obtained the same results for the gradient of annual temperature range while losing the trend for resource vulnerability at the local scale with the historical climatic change gradient (Supplementary material Appendix 1 Table A6).

Specifically, network connectance, consumer diet overlap and resource vulnerability increased along the gradient of annual temperature range, while consumer diet breadth decreased (Fig. 3, Table 1). Therefore, local webs in more currently constant environments were less connected, their consumers overlapped less their diets and, in turn, prey vulnerability decreased, as expected from the biotic specialization hypothesis. However, consumer diet breadth (i.e. generality) showed the opposite pattern; it decreased in more climatic fluctuating environments. Historical climatic change predicted similar patterns for prey vulnerability and consumer diet breadth than annual temperature range. That is, the larger the change in climate over the last 21 000 yr, the larger the number of predators attacking a given prey and the fewer the mean number of prey a predator has (Table 1, Fig. 3). However, current climatic constancy was a better predictor of biotic specialization at the local scale than historical climatic change (cf. R² values and significances in Table 1 and Supplementary material Appendix 1 Table A6). Therefore, local networks in more climatically constant environments, both historically and contemporaneously, show opposite results for resource and consumer species. From the resource perspective, local networks are more specialized (i.e. resources have lower vulnerability) in climatically constant environments but, from the consumer perspective, they are less specialized (i.e. consumers are more generalist) (Table 1, Fig. 3).

These contrasting results can be explained by changes observed in the number of parasitoids and the number of hosts in the local webs along both environmental gradients. While the number of parasitoids increased with temperature range and historical climatic change, the number of hosts decreased (Table 1, Fig. 4). For regional networks, neither parasitoid nor host richness changed across the gradients (Table 1, Fig. 4). These opposite tendencies for the number of parasitoids and the number of hosts at the local scale indicate that the distribution of the number of species across trophic levels (i.e. consumer:resource ratio) is changing along both gradients of environmental constancy. Thus, in more constant environments, fewer consumers attacked resources, but this pattern was reversed in more fluctuating areas where the number of parasitoids per host was higher and, therefore, prey vulnerability was larger.

Given that biotic specialization was not well predicted by our environmental variables at the regional scale, the question that remains is: How can the distribution of species

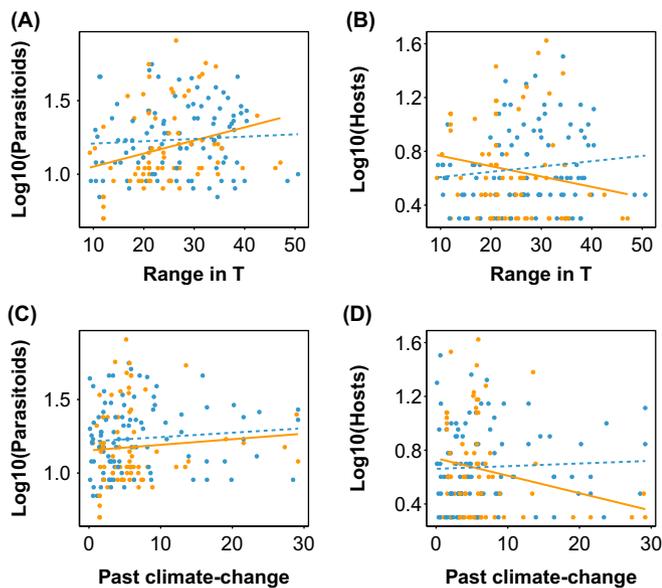


Figure 4. Relationship of the number of parasitoids and hosts with (A–B, respectively) the gradient of annual temperature range and (C–D) the gradient of historic climatic change (i.e. change in mean annual temperature for the last 21 000 yr) at both local (orange) and regional (blue) spatial scales. Notice that the tendency line in blue for regional spatial scales does not indicate a significant relationship.

richness across trophic levels (i.e. consumer:resource ratio), from which the patterns in vulnerability and diet breadth derive, change from local to regional webs along the gradients of environmental constancy?

Beta-diversity as a potential mechanism

We hypothesize that the difference in β -diversity across trophic levels modulates the changes in the patterns of biotic specialization from local to regional spatial scales,

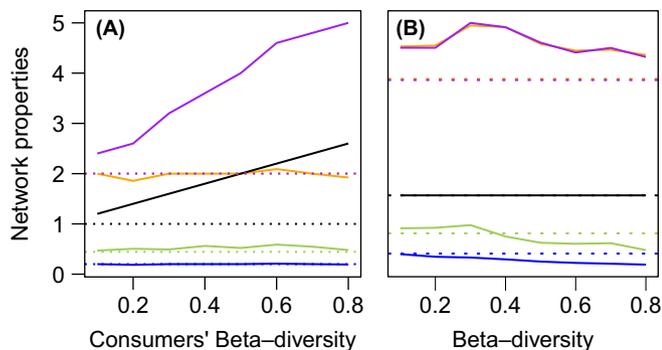


Figure 5. Response of different specialization metrics to increases in (A) consumer beta-diversity (where resource beta-diversity = 0) and (B) beta-diversity at both trophic levels increasing simultaneously (i.e. beta diversity of consumers equals that of resources). Dotted lines represent network properties values at the local scale. Continuous lines represent network property values of the aggregated network (i.e. regional scale) as beta-diversity increases. Blue for connectance, green for overlap, orange for diet breadth, purple for vulnerability and black for consumer:resource ratios.

and that these differences in β -diversity across trophic levels varied along the gradients of environmental constancy. In Fig. 2 we illustrate this mechanism with two specific examples corresponding to the two extremes of the climate constancy gradient, one for more climatically constant regions like the tropics (Fig. 2A) and one for more fluctuating regions (Fig. 2B). If $\beta_{\text{parasitoid}}\text{-diversity} > \beta_{\text{host}}\text{-diversity}$, we observe changes in biotic specialization patterns from local to regional spatial scales (Fig. 2A). In contrast, similar β -diversity in both trophic levels does not generate differences in biotic specialization across spatial scales beyond those changes in network structure produced by the increase in the number of species (Fig. 2B). In Fig. 5 we extend this example to the whole range of β -diversity values to explore systematically the effects of β -diversity in both trophic levels on the patterns of biotic specialization across spatial scales. The larger the difference between $\beta_{\text{parasitoid}}\text{-diversity}$ and $\beta_{\text{host}}\text{-diversity}$, the larger the change expected in the network metrics related to specialization across spatial scales (Fig. 5A). Conversely, assigning similar values of β -diversity between resources and consumers only generates differences in network structure from local to regional webs due to the general increase in species richness (Fig. 5B). In this case, the larger the value of β -diversity, the larger the increase in the number of species as local communities are successively aggregated into the regional network. Our tropical networks appear to display the structural patterns of biotic specialization across spatial scales corresponding to the scenario where $\beta_{\text{parasitoid}}\text{-diversity} > \beta_{\text{host}}\text{-diversity}$. Patterns displayed by networks in more fluctuating environments (i.e. temperate and continental), however, suggest that more balanced values, or even inverted, i.e. $\beta_{\text{parasitoid}}\text{-diversity} \leq \beta_{\text{host}}\text{-diversity}$, are predominant.

Discussion

The gradient of biotic specialization is not universal: it depends on both the facet of biotic specialization analysed and the spatial scale of observation. Indeed, local and regional networks displayed very different patterns along the gradients of contemporary climatic constancy and historical climatic change. At the regional scale, we found little evidence for the biotic specialization hypothesis for any of the specialization facets analysed. In contrast, the biotic specialization hypothesis generally holds at the local scale: networks in more constant environments were less connected, consumers overlapped less their niches, and preys were attacked by fewer predators. The only facet of specialization that showed the opposite pattern was diet breadth: consumers were more generalists in more climatically constant environments, contrary to the hypothesized latitudinal gradient on niche breadth (MacArthur 1955, 1972, Vázquez and Stevens 2004).

Current climatic constancy was a better predictor of biotic specialization at the local scale than historical climatic change. Even though past climate stability has been shown to be a good predictor of the structure of pollination

networks (Dalsgaard et al. 2011, 2013), a meta-analysis showed stronger effects of contemporary climate on pollinators specialization (Schleuning et al. 2012), in agreement with our findings. Our measure of historical climatic change (i.e. difference between current mean annual temperature and mean annual temperature 21 000 ybp) allows for a direct comparison with current climatic constancy, as both measures account for the temperature range experienced over long and short temporal scales, respectively. However, it is a coarse-grained measure that does not account for fine-scale climatic fluctuations within the historical period considered. Because species may respond differently to climate changes, climatic fluctuations can disrupt biotic specialization through phenological mismatches or changes in the geographical distributions of species (Memmott et al. 2007, Tylianakis et al. 2008, Gilman et al. 2010). Thus, the explanatory power of historical climatic change can be relatively smaller than that corresponding to current climatic constancy. Further analyses using finer measures that consider climatic fluctuations in the past might unveil different effects on biotic specialization. Similarly, other environmental variables, such as precipitation, have been related to the geographical variation of network nestedness (Sebastián-González et al. 2015), modularity (Trøjelsgaard and Olesen 2013, Sebastián-González et al. 2015), or to the biotic specialization of plant–hummingbird communities (Dalsgaard et al. 2011, Maruyama et al. 2018). However, our aim was to evaluate the effect of climatic constancy on biotic specialization and, therefore, precipitation was not included in the analyses given that it is not directly related to a region's climatic constancy. Precipitation seasonality, alternatively, has not been identified as a significant predictor of network biotic specialization in previous studies (Dalsgaard et al. 2011).

Our results partially agree with previous findings. Dalsgaard and colleagues (Dalsgaard et al. 2017) analysed the latitudinal gradient in biotic specialization of avian plant–frugivore networks from two different perspectives, namely niche partitioning in the network and consumers' dietary specialization, and found opposite results. They showed that network-derived specialization increases with latitude while bird species were more specialized on specific fruit diet in the tropics. Their results highlight the need of comparing different scales of biotic specialization for a better understanding of a biogeographical pattern. In our case, the analysis of different facets of biotic specialization at different spatial scales was crucial to gain a better understanding of the biogeographical pattern. Interestingly, we found opposite geographical patterns in biotic specialization between consumer (i.e. generality) and resource (i.e. vulnerability) species (Fig. 3). While diet breadth was higher in more climatically constant regions, resource vulnerability was lower. Importantly, the number of consumers and the number of resources also showed opposite trends along both gradients of environmental constancy, which explained the opposite results found between consumer diet breadth and prey vulnerability at the local scale (Fig. 4). Therefore, analysing different facets of biotic specialization

allowed us to have a broader understanding of the geographical variation of biotic specialization.

In a recent study of the macroecology of pollination networks, Trøjelsgaard and Olesen (2013) found that pollinator:plant ratios increased with latitude, indicating that mid-latitudes harboured more pollinators per plants species than communities in the tropics. Our results for antagonistic networks are in agreement with this finding at the local scale where we found that the number of parasitoids decreased with climatic constancy while the number of hosts increased (Fig. 4), indicating a decrease of the consumer:resource ratio with climatic constancy. However, at the regional scale, we did not observe a significant change in the number of consumers and resources along neither of the environmental gradients. This results in opposite patterns between both extremes of the gradients when local and regional networks are compared (Fig. 3, 4). In more constant environments, local networks have a smaller proportion of consumers per resources than regional networks. The opposite is true for more fluctuating environments, where local networks have a larger proportion of consumers per resources than regional networks (Fig. 4).

The importance of spatial turnover across environmental gradients

One key question remains: How can the same 'potential' regional network lead to opposite 'realized' local networks along the climatic constancy gradient? More specifically, how can the distribution of diversity across trophic levels have an opposite trend between spatial scales at both extremes of the gradient?

We propose an explanation based on the differences in spatial turnover (i.e. β -diversity, sensu Whittaker (1972)) of local consumer and resource assemblages along the gradient of climatic constancy. In the tropics (i.e. less fluctuating regions), the spatial turnover of consumers should be larger than that of resources, so that when we aggregate local into regional webs, the number of consumers increases faster than the number of resources (Fig. 2, 5). In contrast, in more fluctuating areas the process should be the opposite: larger spatial turnover of resources results in a faster increase in the number of resources at the regional scale. Empirical evidence partially supports our hypothesis. Consumer assemblages (parasites and parasitoids in particular) tend to be less similar across local communities than resource assemblages (herbivores in particular) (Soininen et al. 2007a). In addition, β -diversity in the tropics tends to be higher than at higher latitudes, at least at relatively small spatial scales (Rodríguez and Arita 2004, Soininen et al. 2007a, b, Kraft et al. 2011).

A number of ecological processes can explain why consumers' β -diversity is larger than resources β -diversity in the tropics, but not in more climatically fluctuating environments. This could simply result from stochastic assembly processes from two species regional pools with different richness. If regional consumer diversity is larger in the tropics than in temperate areas, which it is,

random assembly processes of local communities would lead to larger compositional dissimilarities of consumers in the tropics (Chase 2010, Kraft et al. 2011). However, other non-stochastic ecological processes can also explain this pattern.

Firstly, consumer assemblage similarity tends to decrease with productivity (e.g. for aquatic consumer insects see (Chase and Leibold 2002, Chase and Ryberg 2004)), as environmental heterogeneity and reduced dispersal rates among local communities increase. As productivity tends to be positively correlated with thermal stability (Pianka 1966, Currie et al. 2004), this might explain the increase of consumer β -diversity towards the tropics.

Secondly, diet generalists tend to have wider geographical ranges than specialized species (MacArthur 1972, Gaston et al. 1991, Boulangeat et al. 2012, Slatyer et al. 2013), and consumers tend to have patchier distributions in the tropics (MacArthur 1972, Stevens 1989, Brown et al. 1996, Rodríguez and Arita 2004). This reduces the dissimilarity in the composition of local generalist consumer assemblages. Since generalist species prey upon a wide range of resource species, compositional differences among sites on resource assemblages need to be high. This might explain why diet breadth was not well predicted by the gradients of current climatic constancy and historical climatic change at the regional scale while at the local scale we observed opposite patterns for each extreme of the gradients (Fig. 3). Thus, this suggests that the dissimilarity on the composition of local consumer assemblages is higher in the tropics due to their tendency of having narrower geographical ranges than generalist species (MacArthur 1972, Stevens 1989, Brown et al. 1996, Rodríguez and Arita 2004). This could lead to the isolation of interactions across space if there were reciprocal specializations between consumers and resources, but reciprocal specializations are extremely rare in nature (Joppa et al. 2009) and in our networks isolated links were not taken into account. This suggests that the dissimilarity on the composition of resource assemblages among local sites is low, and resource species thus are attacked by many consumers with narrower and patchier distributions (Fig. 3).

Thirdly, consumer competitive exclusion can be stronger in the tropics than in temperate areas, ultimately determining the patchier distribution of consumers in the tropics (MacArthur 1972). Although supporting evidence is not unequivocal (Terborgh 2015, Ellwood et al. 2016, Gainsbury and Meiri 2017, LaManna et al. 2017), local dynamics in the tropics could exclude different consumers in different habitat patches, resulting in more specialized and less similar consumer communities across patches. Our results show that consumers segregated their dietary niches more in more constant environments (less consumer overlap) (Fig. 3). This could be the consequence of more intense competitive exclusion, so that, locally, for consumers to coexist, they should overlap their dietary niches only weakly (Condon et al. 2014).

Conclusions and perspectives

Our study is not the first attempt to examine network structure across biogeographical scales. However, it is the first to explore the spatial scale-dependency of network biotic specialization across large biogeographical gradients. We found that the difference in the consumer:resource ratio across spatial scales changes along the gradients of current climatic constancy and historical climatic change, which generates further changes in biotic specialization and network structure. Our results thus identify a geographical gradient of biotic specialization that depends both on the spatial scale of observation and on the facet of specialization of interest. They highlight that the spatial patterning of diversity across trophic levels, summarized in β -diversity, is key to understand the geographical gradient of biotic specialization. Similarly, our results show the importance of considering different spatial scales to get a broader understanding of the specialization pattern and their determinants. Additionally, if network structure varies across spatial scales (Pillai et al. 2011, Roslin et al. 2014, Wood et al. 2015, Galiana et al. 2018), then network studies estimating the causes of variation in network structure along any environmental gradient (Dormann et al. 2017, Tylianakis and Morris 2017, Pellissier et al. 2018) might benefit from understanding the spatial scaling of network structure along the gradient. However, caution must be exerted when interpreting the comparison between different spatial scales. Regional networks account for all the interactions between consumers and resources that occur in at least one locality of the area sampled, and thus it does not require that the observed interaction is realized in every location of the area considered. Therefore, network structure at the regional scale must be understood as the structure of the potential network of interactions at a given area, which together with the information on the structure of the realised network at the local scale can help to elucidate the role of different spatial processes in a given region.

Further theoretical and empirical research is needed to determine how general our findings are in regards to the scale-dependency of network structure, and in particular biotic specialization, across large environmental gradients and across different study systems. We focused on host-parasitoid networks which have been described as a particular group of antagonistic interactions that are considered to have higher levels of consumer specialization than other antagonistic networks (Blüthgen et al. 2008, Ings et al. 2009). However, the results presented here and the mechanisms proposed to explain the changes in network structure across spatial scales should hold for any system whose consumers are not super generalists and that it presents a minimum degree of spatial turnover. Regardless of the type of interaction, unbalanced values of β -diversity across trophic levels should generate changes in network structure across spatial scales. Future studies should aim to quantify the spatial scaling of network structure in a continuous way along environmental gradients to better understand what is the

role of β -diversity in determining the possible differences in network structure across spatial scales in different parts of the world.

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Supplementary material (available online as Appendix ecog-03684 at <www.ecography.org/appendix/ecog-03684>). Appendix 1.