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Meta-networks for the study of biogeographical traits in ecological networks: the Mexican hummingbird-plant assemblage

Ana M. Martín González[1] · Juan Francisco Ornelas[2] · Bo Dalsgaard[1] · Ubaldo Márquez-Luna[3] · Carlos Lara[4]

Abstract
Recent studies on ecological networks have quantified the contribution of ecological, historical, and evolutionary factors on the structure of local communities of interacting species. However, the influence of species' biogeographical traits, such as migratory habits or phylogeographical history, on ecological networks is poorly understood. Meta-networks, i.e., networks that cover large spatial extensions and include species not co-occurring locally, enable us to investigate mechanisms that operate at larger spatial scales such as migratory patterns or phylogeographical distributions, as well as indirect relationships among species through shared partners. Using a meta-network of hummingbird-plant interaction across Mexico, we illustrate the usefulness of this approach by investigating (1) how biogeographical and morphological factors associate with observed interactions and (2) how species-specific biogeographical characteristics associate with species' network roles. Our results show that all studied hummingbird and plant species in the meta-network were interrelated, either directly or through shared partners. The meta-network was structured into modules, resulting from hummingbirds and plants interacting preferentially with subsets of species, which differed in biogeographical, and, to a lesser extent, morphological traits. Furthermore, migrants and hummingbirds from Nearctic, Transition, and widespread regions had a higher topological importance in the meta-network. Our study illustrates how meta-networks may contribute to our current knowledge on species' biogeographical traits and biotic interactions, providing a perspective complementary to local-scale networks.

Keywords Biotic interactions · Migration · Modularity · Morphology · Phylogeny · Pollination

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Introduction

Species interactions, such as pollination and other mutualistic associations, are widespread and crucial for the functioning of most ecological communities (Rech et al. 2016). An urgent challenge in ecology amidst global change is to quantify the contribution of ecological, historical, evolutionary, and biogeographic mechanisms in the structuring of communities of interacting species (Ricklefs 1987; Cavender-Bares et al. 2009; Martín González et al. 2015; Heilmann-Clausen et al. 2017; Dalsgaard et al. 2018). This is a complex subject, as species typically show a context-dependent behavior reflecting their adaptation to a mosaic of factors present in their local communities, which in turn interplay at different scales. Hence, there is a need of using a wide set of complementary analyses to study the effect of different factors and at different scales (Thuiller et al. 2013; Poisot et al. 2015). For instance, the study of interactions between plants and their pollinators over different seasons and years, including species whose phenophases may not fully overlap, has enabled us to explore the effect of climate, resource seasonality, and species phenophases on community structure and species' roles. Besides a more accurate understanding of community structure and build up, these networks allowed us to characterize the role of species and potential fluctuations over time more accurately (Martín González et al. 2012; Chacoff et al. 2017; Kantsa et al. 2018). Similarly, the study of "meta-networks," i.e., networks of biotic interactions covering large spatial scales, across biomes, or in fragmented habitats, may give new insights into how species' biogeographical traits such as phylogeographical distribution, range dynamics, or migratory habits influence ecological networks, of which there is scarce knowledge (Heilmann-Clausen et al. 2017; Araujo et al. 2018; Emer et al. 2018).

Meta-networks enable us to study indirect interactions among species, that is, relationships between species that do not co-occur spatially or temporally, but which may have an effect on each other through third species. For instance, two consumer species' ranges may not overlap currently but which visit a similar array of resources and hence may prevent the expansion into each other's ranges. Hence, the study of meta-networks may be particularly useful to understand landscape dynamics, such as the effect of biotic interactions on range dynamics (e.g., Araújo and Luoto 2007), and the role and importance of species which, because of large spatial distributions (e.g., migrant species), may appear as peripheral in local networks due to a lower detection probability (Vázquez et al. 2009).

Biogeographical factors may be especially important in areas with a complex geography and topography, in contact zones between biogeographical realms, and in areas with communities containing species with large differences in range distributions or migratory habits. An outstanding combination

of such factors is the Mexican hummingbird-plant assemblage. Mexico is located at the transition between the Nearctic and Neotropical realms (Rzedowski 1965; Halffter 1987) and exhibits a complex topography and geological history (Morrone 2010; Morrone et al. 2017; Fig. 1). Its wide array of ecological conditions has favored population isolation and the action of in situ evolutionary processes (Navarro et al. 2002), enabling to find taxa, largely endemic, with different biogeographical and evolutionary origins. For instance, the Mexican hummingbird fauna appears to have arisen from multiple independent invasions of different phylogenetic lineages and at different times (Stiles 1981; Brown and Bowers 1985; Bleiweiss 1998; Licona-Vera and Ornelas 2017; Appendix 1). Several of the Mexican hummingbirds have very particular biogeographical and ecological restrictions, which entails both processes of diversification and endemism (Rodríguez-Gómez et al. 2013; Malpica and Ornelas 2014; Licona-Vera and Ornelas 2014; Ornelas et al. 2015). For instance, most of the 24 endemic Mexican hummingbirds are restricted to regions of narrow extensions, little landscape connectivity, and complex topography and floral composition. Furthermore, the Mexican hummingbird fauna includes a mixture of sedentary, altitudinal, and short-distance migrants who track nectar availability of local resources and obligate seasonal long-distance migrants who have latitudinally different winter and breeding grounds (e.g., Lara 2006; Licona-Vera and Ornelas 2017).

Hence, given the large differences in phylogeographical history, range distributions, and migratory habits among Mexican species, we expect these biogeographical traits to exert a strong effect on hummingbird-plant interactions and, therefore, on network structure. However, most studies on hummingbird-plant assemblages have focused exclusively on the effect of morphological traits, which have been shown to regulate interactions in some but not all communities (e.g., Maglianesi et al. 2014, 2015; Vizentin-Bugoni et al. 2014; Weinstein et al. 2017; Zanata et al. 2017; Dalsgaard et al. 2018). For instance, in the Brazilian Cerrado, hummingbird traits have been shown to produce modules within local networks with their nectar-food plants (Maruyama et al. 2014). On the other hand, the role of biogeographical traits remains less well-known (Sonne et al. 2016; Araujo et al. 2018). In this study, we investigate the role of hummingbird's biogeographical and morphological traits in structuring a meta-network comprising all available information on hummingbird-plant interaction across Mexico. We expect that the Mexican meta-network will show a strong modular pattern in which modules can be interpreted in terms of species' biogeographical traits, an analogous outcome to the modular pattern of highly seasonal mutualistic assemblages where modules reflect species' staggered phenophases (Martín González et al. 2012). Specifically, we investigate (1) how hummingbird's biogeographical and morphological traits associate with the
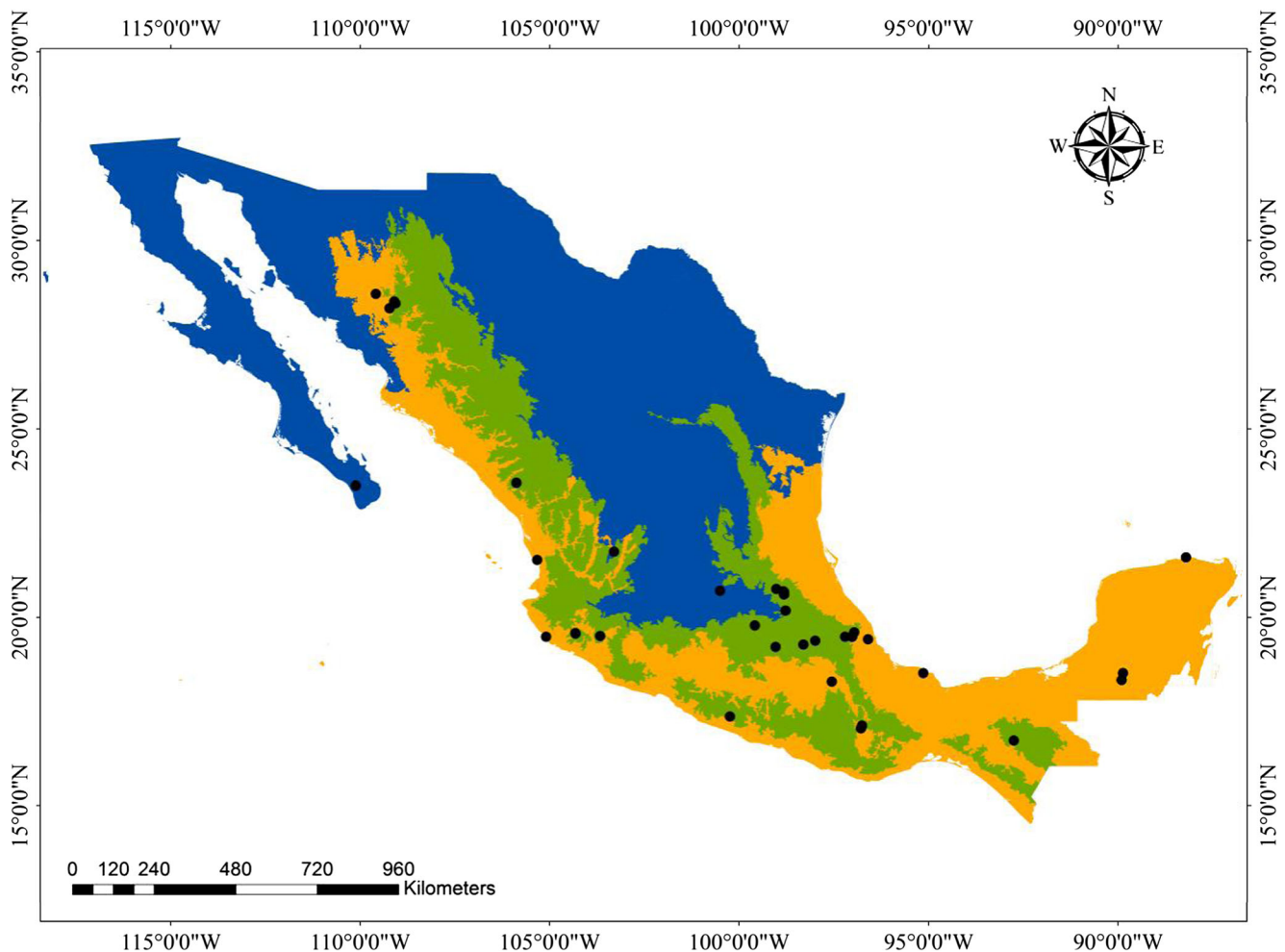
Fig. 1 Map of Mexico showing the different biogeographical regions conforming the Nearctic realm (in blue), the Neotropical realm (in orange), and Transition provinces (in green) as defined by Morrone et al. (2017). Black dots pinpoint the localities where the hummingbird-plant networks were collected. Note that some of the points may overlap slightly

modular partition and (2) how hummingbird's biogeographical and morphological traits may associate with the network role of hummingbirds in the meta-network.

Methods

Study area and study species

Mexico is an outstanding example of complex biogeographical patterns (Morrone 2010; Morrone et al. 2017). The country currently stands out as a mega-diverse country, likely a consequence of its location at the transition between the Nearctic and Neotropical realms (Halffter 1987; Rzedowski 1965, 1992) and the close relationship between geological/climatic and speciation events (Halffter 1987; Luna-Vega et al. 2001). In Mexico, the Nearctic realm comprises the arid subtropical areas that extend from northern to the high plateaus along the Volcanic Belt and the Sierras Madre, where it intermixes

broadly with the Neotropical realm which includes humid and subhumid tropical areas in the central-south part of the country (Morrone and Márquez 2001; Morrone et al. 2017; Fig. 1).

Hummingbirds (Trochilidae) are the most highly specialized nectarivorous birds in the New World, relying almost exclusively on nectar as a food source (Stiles 1981). They distribute from Alaska through Patagonia, and their interactions with plants show strong biogeographical and evolutionary patterns, ranging from generalized to highly specialized (Stiles 1978; Dalsgaard et al. 2009, 2011; Abrahamczyk and Kessler 2014; Martín González et al. 2015; Sonne et al. 2016). Their adaptive radiation manifests them as a highly diverse clade, with more than 338 species (McGuire et al. 2014). With approximately 58 recognized species, Mexico hosts 17% of the described hummingbird species. The Mexican hummingbird fauna is relatively recent and results from various colonization waves from South America (McGuire et al. 2014; Ornelas et al. 2014). The high habitat diversity and abrupt environmental and

climatic changes that characterize Mexico have played a key role on processes of divergence and speciation, resulting in a great level of endemism and varied migratory habits of Mexican hummingbirds (Malpica and Ornelas 2014; Licona-Vera and Ornelas 2017; Appendix 1).

Interaction data and species traits

We compiled 37 hummingbird-plant interaction networks describing feeding relationships between hummingbirds and plants throughout Mexico, spanning over nine different habitats and ten biogeographic provinces (as defined by Morrone et al. 2017), including both Neotropical and Nearctic realms and the Transition zone (Fig. 1, coordinates and references for details on Appendix 2). Overall, we compiled information on hummingbird visitation for 41 hummingbird species and 354 plant species, covering all but three of the nine taxonomically recognized phylogenetic lineages (McGuire et al. 2014) and comprising a wide range of body masses (2.5–11.9 g) and bill lengths (11.3–43.2 mm). Hummingbirds were classified following Escalante et al. (1993) as endemic, when their entire distribution is restricted to Mexico (8 species); semi-endemic, when the entire population is seasonally present in Mexico or in narrowly overlapping adjacent countries (< 35,000 km^2; 9 species); and non-endemic (24 species). Some hummingbirds have long-distance migratory habits (7 species), others migrate locally (9 species), and others are year residents (25 species; Arizmendi and Berlanga 2014). The biogeographical distribution of hummingbirds was categorized as Nearctic, when the hummingbird was reported only in Nearctic or in Nearctic and Transition localities (6 species), as Neotropical when the hummingbird was reported only in Neotropical or in Neotropical and Transition localities (16 species), as Transition, when the hummingbird was reported only in Transition localities (8 species), or widespread if the hummingbird was present in Nearctic, Neotropical, and Transition regions (11 species; Table 1). Plants belonged to 66 different families, were mostly native species (271 species, 92% of total), and included both typical ornithophilous and non-ornithophilous floral morphologies.

Meta-network analyses

To investigate the structure of the Mexican meta-network, we merged all information on the presence/absence of species interactions into a single meta-network describing whether each hummingbird and plant species interacted anywhere in Mexico (data available at the author's homepage).We thereafter examined the potential modularity of this meta-network. Modularity was calculated in MODULAR (Marquitti et al. 2014) using Barber's metric for bipartite networks (Barber 2007), with simulated annealing as the searching algorithm and following the recommended program settings (Marquitti et al. 2014; Appendix 3). Barber's modularity divides the

matrix into an a priori undefined number of modules using matrix eigenvalues, minimizing the number of links between modules while maximizing within-module connectance (Barber 2007). Hence, in the resulting partition, species located in the same module interact more among themselves than with species from other modules. As MODULAR uses an iterative searching algorithm, we investigated the robustness of the resulting modular partition by running the analysis 30 times using different seed set numbers. In addition, we estimated the significance of each run against 100 null matrices obtained with MODULAR's Null Model 2, which creates matrices with the same number of species and interactions as the empirical one, and in which species interaction probability is based on their observed connectivity (Bascompte et al. 2003; Marquitti et al. 2014).

We examined the resulting modular partition in order to understand the underlying mechanisms associated with such pattern of interactions. We performed a non-metric multidimensional scaling (NMDS) of hummingbird morphological and biogeographical traits known or hypothesized to associate with hummingbird-plant interactions, namely bill length, body mass, degree of endemicity, migratory habits, and biogeographical distribution. The NMDS ordination was run 5 times, with a minimum number of 200 iterations and using the previous best solution as starting point, using the *vegan* R package (Oksanen 2017). To the resulting ordination, we fit a secondary matrix, which included group membership (e.g., which groups of hummingbirds were found in the same modules in the different runs of the modularity algorithm) and phylogenetic lineage as factors. Hence, we tested whether species from different groups or from different hummingbird phylogenetic lineages show different morphological or biogeographical traits.

Finally, from the resulting modular partition, we obtained information on the network role of each hummingbird species by computing species' within-module degree (z values) and among-module connectivity (c values) in the cz values function from the *bipartite* R package (Dormann 2012). Connectivity within and among modules are calculated as $z = (k_{is} - ks_{bar}) / SD_{ks}$ and $c = 1 - \Sigma (k_{it}/k_i)^2$, respectively, where k_i is the degree of focal species i; k_{is} is the degree of focal species i to the rest of the species within i's module; ks_{bar} is the average degree of all species in module s; SD_{ks} is the standard deviation of the degrees of species in module s; and k_{it} is the number of links of focal species i to species located in module t (Olesen et al. 2007; Dormann 2012). Hummingbirds can therefore be classified according to how their interactions distributed within and across modules as *hubs* when their z values are high; as *connectors*, when their c values are high; and as *peripherals*, when they are poorly connected and only within their module, and hence both their c and z values are small. As hummingbird traits were a mixture of continuous (bill length and body mass), categorical ordered (degree of

Table 1 Hummingbird species and the traits examined in this study. Phylogenetic lineages were obtained from McGuire et al. (2014), biogeographical species distribution from their observed community location, body mass and bill length from Arizmendi and Berlanga (2014) and from Carlos Lara's unpublished own data (marked with and asterisk *), degree of endemism from Escalante (1993), and species migratory behavior from Arizmendi and Berlanga (2014). Module membership from the modularity analysis (NA for those species with no constant module partners)

Hummingbird species	Phylogenetic lineage	Biogeographical distribution	Bill length (mm)	Body mass (g)	Degree of endemism	Migratory behavior	Module
Amazilia beryllina	Emerald	Widespread	18.71*	4.06*	Non-endemic	Non-migrant	NA
Amazilia candida	Emerald	Neotropical + Transition	17.2	3.6	Non-endemic	Non-migrant	M1
Amazilia cyanocephala	Emerald	Neotropical + Transition	21	5.5	Non-endemic	Non-migrant	M5
Amazilia rutila	Emerald	Neotropical + Transition	21.75	4.75	Non-endemic	Non-migrant	M5
Amazilia tzacatl	Emerald	Neotropical + Transition	21.25	5.35	Non-endemic	Non-migrant	M1
Amazilia violiceps	Emerald	Widespread	22.5	5	Semi-endemic	Local migrant	M4
Amazilia yucatanensis	Emerald	Neotropical + Transition	21.25	3	Semi-endemic	Local migrant	M1
Anthracothorax prevostii	Mango	Neotropical + Transition	27.25	7	Non-endemic	Non-migrant	M1
Archilochus alexandri	Bee	Widespread	18.75	3.65	Semi-endemic	Long-distance migrant	M5
Archilochus colubris	Bee	Widespread	16.04*	5.36*	Non-endemic	Long-distance migrant	M1
Atthis heloisa	Bee	Nearctic + Transition	12.32*	2.53*	Endemic	Non-migrant	M2
Calothorax lucifer	Bee	Nearctic + Transition	21.02*	3.86*	Semi-endemic	Long-distance migrant	NA
Calothorax pulcher	Bee	Transition	17.9	2.85	Endemic	Non-migrant	M3
Calypte anna	Bee	Nearctic	17.25	3.6	Non-endemic	Local migrant	M4
Calypte costae	Bee	Nearctic	17	2.5	Non-endemic	Local migrant	M4
Campylopterus curvipennis	Emerald	Neotropical + Transition	27.3	5.8	Non-endemic	Non-migrant	M1
Campylopterus hemileucurus	Emerald	Neotropical + Transition	27.8	11.9	Non-endemic	Non-migrant	M1
Chlorostilbon auriceps	Emerald	Transition	14	3.25	Endemic	Non-migrant	M3
Chlorostilbon canivetii	Emerald	Neotropical + Transition	14.3	3.25	Non-endemic	Non-migrant	M1
Colibri thalassinus	Mango	Widespread	19.71*	6.03*	Non-endemic	Local migrant	M2
Cynanthus latirostris	Emerald	Widespread	21.25	3.5	Semi-endemic	Local migrant	M4
Cynanthus sordidus	Emerald	Transition	29	4.5	Endemic	Non-migrant	M4
Doricha eliza	Bee	Neotropical + Transition	22.4	2.5	Endemic	Non-migrant	M1
Eugenes fulgens	Gem	Widespread	26.88*	7.65*	Non-endemic	Local migrant	M2
Eupherusa poliocerca	Emerald	Transition	17.8	4.85	Endemic	Non-migrant	M3
Heliomaster constantii	Gem	Neotropical + Transition	34	7.65	Non-endemic	Non-migrant	M5
Heliomaster longirostris	Gem	Neotropical + Transition	34.5	6.8	Non-endemic	Non-migrant	M3
Hylocharis leucotis	Emerald	Widespread	17.03*	3.95*	Non-endemic	Local migrant	M2
Hylocharis xantusii	Emerald	Nearctic	18	3.6	Endemic	Non-migrant	NA
Lampornis amethystinus	Gem	Transition	19.11*	6.98*	Non-endemic	Non-migrant	M2
Lampornis clemenciae	Gem	Widespread	23.92*	8.39*	Semi-endemic	Local migrant	NA
Lamprolaima rhami	Gem	Transition	21.9	6.35	Non-endemic	Non-migrant	NA
Lophornis brachylophus	Coquette	Transition	13	2.7	Endemic	Non-migrant	M1
Lophornis helenae	Coquette	Neotropical	11.3	2.7	Non-endemic	Non-migrant	M3
Phaethornis longirostris	Hermit	Neotropical + Transition	43.2	5.75	Non-endemic	Non-migrant	M3

Table 1 (continued)

Hummingbird species	Phylogenetic lineage	Biogeographical distribution	Bill length (mm)	Body mass (g)	Degree of endemism	Migratory behavior	Module
Phaethornis striigularis	Hermit	Neotropical + Transition	21.55	2.65	Non-endemic	Non-migrant	M1
Selasphorus calliope	Bee	Nearctic + Transition	14.5	2.5	Semi-endemic	Long-distance migrant	M2
Selasphorus platycercus	Bee	Widespread	17.74*	3.73*	Semi-endemic	Long-distance migrant	M2
Selasphorus rufus	Bee	Widespread	16.68*	3.65*	Non-endemic	Long-distance migrant	M2
Selasphorus sasin	Bee	Neotropical + Transition	16.71*	3.59*	Semi-endemic	Long-distance migrant	M2
Tilmatura dupontii	Bee	Transition	13.6	2.85	Non-endemic	Non-migrant	M3

endemicity and migratory habits), and categorical unordered variables (biogeographical distribution), we used a non-parametric multiple regression with kernel estimation to examine whether their z and c values associate with any of these traits, using the *np* R package (Hayfield and Racine 2017). All statistical analyses were performed in R 3.3.1 (R Development Core Team 2014).
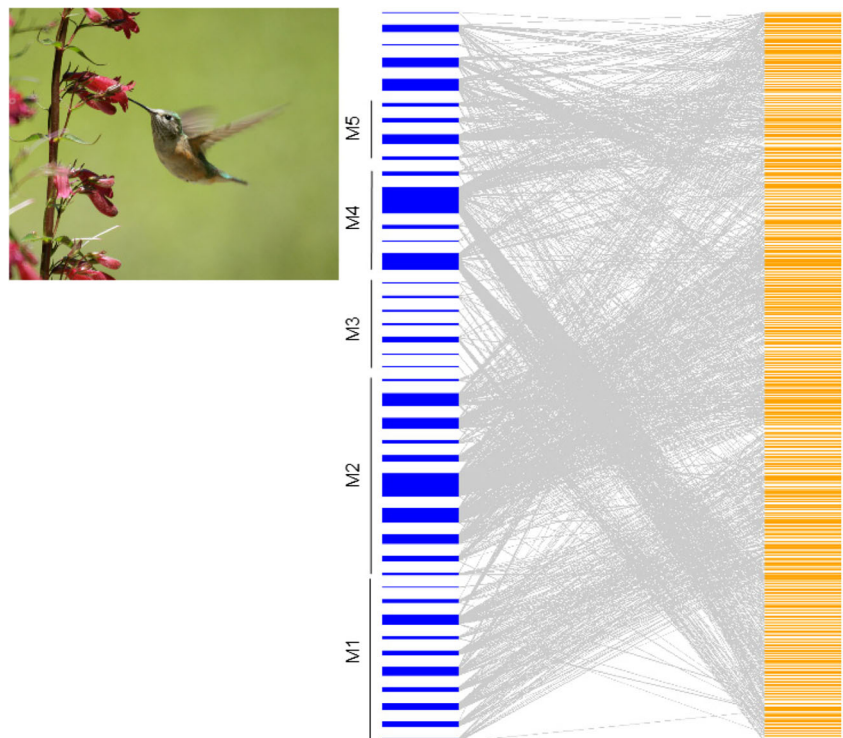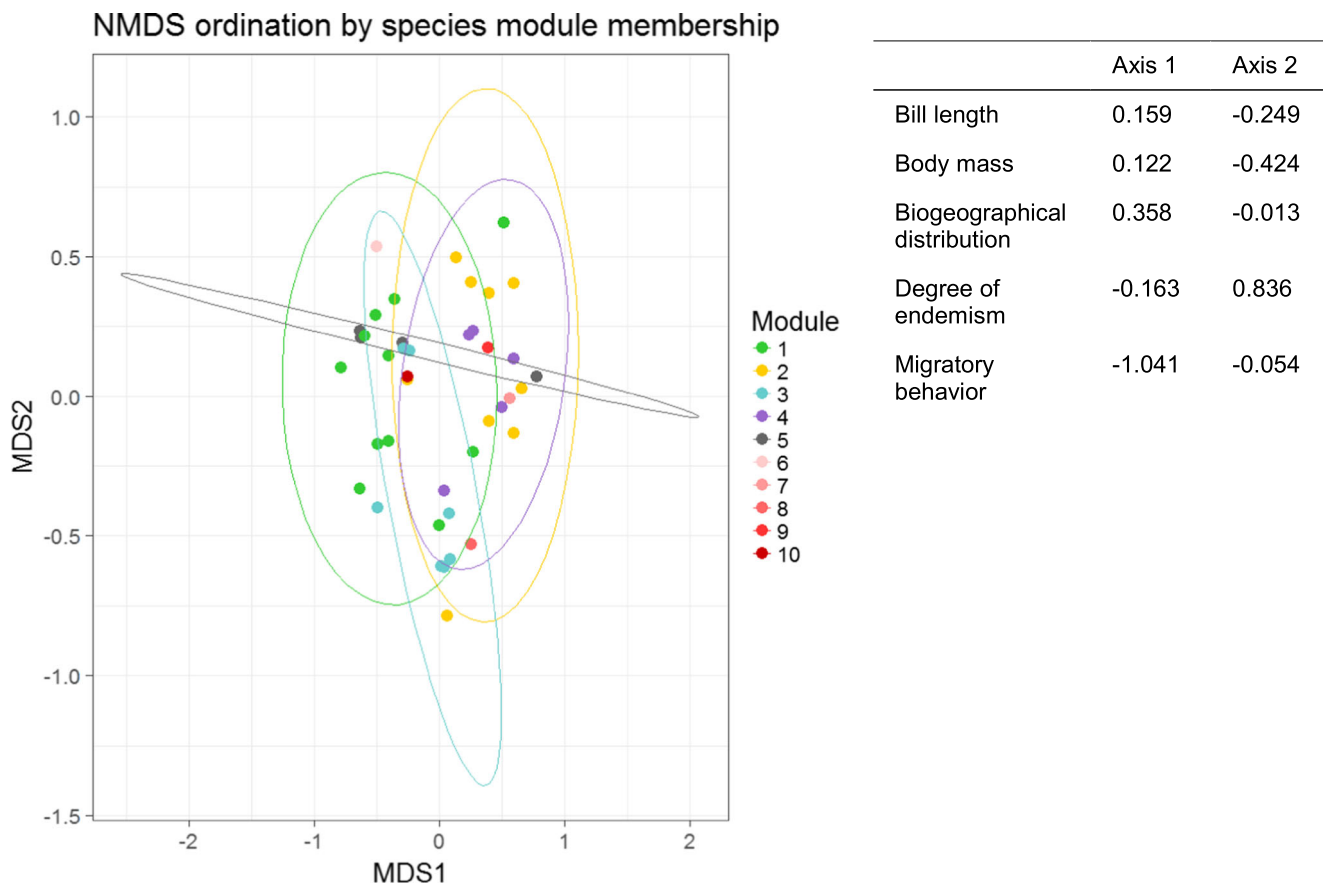
Results

The meta-network consisted of 395 species and 1128 interactions and had a connectance of 8%. All species conformed the giant component, that is, there were no separate subnetworks of species. The two most distant species in the meta-network were seven edges apart, while the average number of shortest paths between any two species in the meta-network was 3.389. Different runs of the MODULAR algorithm yielded different though relatively constant modularity values ($M = 0.466 \pm 0.004$), all of which were highly significant when compared to null models (all p values < 0.001; Appendix 3). Despite resulting partitions varied between five and eight different modules, species composition of modules was relatively constant, with all but five of the hummingbird species being placed over 87% of the runs together in the same module (that is, in 26 out of the 30 runs of the modularity algorithm; Fig. 2; group species compositions are given in Table 1; results from the modularity analysis are given in Appendix 3).

The NMDS analysis on the morphological and biogeographical traits of the 41 hummingbird species of the meta-

Fig. 2 Illustration of the Mexican bipartite meta-network. Hummingbirds are in blue, plants are in orange, and the interactions between them in gray. The width of the species' bars represents species' number of interactions. Hummingbirds are also divided according to their resulting modules. The picture shows a female *Selasphorus platycercus* visiting a flower of *Penstemon roseus*. Photo by Carlos Lara

Fig. 3 Results of the non-metric multidimensional scaling ordination (NMDS) of five hummingbird species traits (bill length, body mass, biogeographical distribution, degree of endemism, and migratory behavior). Ellipses in the NMDS indicate 95% confidence intervals around the centroids of each group. Note that modules 6–10 (colored in different shades of red) are conformed of only one hummingbird species. These are the hummingbird species which had no constant partners in the different runs of the modularity algorithm. Notice also that these hummingbirds do not show biogeographical or morphological differences from hummingbirds with constant module partners

network resulted in a two-dimensional solution with a stress value of 0.132 (Fig. 3). In axis 1, morphological traits and biogeographical distribution had positive scores whereas degree of endemism and migratory behavior had negative scores. The strongest associations were, in this order, with hummingbird migratory behavior and biogeographical distribution. All variables were negatively associated with axis 2 except for endemism, which was also the trait with the highest score, followed by bill length and body mass. Moreover, the resulting ordination was significantly correlated with hummingbird module composition ($R^2 = 0.426$, $p = 0.001$), that is, modules differed in the traits analyzed in the NMDS.

The two non-parametric multiple regressions performed between the z and c values and hummingbird traits resulted in strong and statistically significant associations (Table 2, Appendix 3). The z and c values were averaged across runs as different runs of the modularity algorithm yielded different partitions as species z and c values differed: range SD = 0.038–0.94 and 0.00–2.36 for z and c values, respectively. Migratory behavior and biogeographical distribution showed a highly significant association with both z and c values

(Table 2, Fig. 4), with migratory and Nearctic/Widespread species showing higher within and among-module connectivity values than non-migrants and Neotropical hummingbirds. Hummingbird z values also correlated negatively with bill length and body mass, that is, large and long-bill hummingbirds tend to have a peripheral position in the meta-network (Table 2, Fig. 4).

Discussion

In this study, we explore the usefulness of meta-networks to investigate the effect of biogeographical traits on species interactions. In order to do so, we chose a study system of high geological complexity such as Mexico and a bird group model, which is broadly distributed and shows a wide array of biogeographical and morphological traits that may influence their interaction pattern with plants. By studying the Mexican hummingbird-plant assemblage at a macroecological scale, we included direct and indirect interactions among species. The resulting meta-network was fully connected; this

Table 2 Results from the non-parametric multiple regression with kernel variable estimation between species within and between module connectivity (z and c values, respectively) and their morphological and biogeographical traits. Regression was performed with the 41 hummingbird species and using the 5 studied variables. We used a local-linear kernel regression estimator, using a second-order Gaussian kernel function for the two continuous explanatory variables (bill length and body mass), an Aitchison and Aitken kernel function for the unordered categorical variable (biogeographical distribution) and a Li and Racine kernel function for the two ordered categorical variable (degree of endemism and migratory behavior). Bandwidths were computed using an adaptive k-nearest neighbor algorithm and selected through a least squares cross-validation (Hayfield and Racine 2008, 2017). Significance tests were performed with 399 bootstraps. Significant variables are marked in italic

	z value		c value	
Goodness of fit (R^2)	0.730		0.699	
Standard error	0.101		0.039	
	Bandwidth	p value	Bandwidth	p value
Bill length	*36*	*0.040*	36	0.719
Body mass	*19*	*0.018*	28	0.276
Biogeographical distribution	*$4.40e^{-07}$*	*$2e^{-16}$*	*0.135*	*0.008*
Degree of endemism	0.589	0.155	1.000	0.145
Migratory behavior	*0.075*	*$2e^{-16}$*	*0.516*	*0.010*

indicates that all studied species had the capacity of influencing each other, even when not co-occurring at the same localities. Moreover, the average shortest path length of 3.389 indicates that indirect interactions may exert relatively strong influences across the entire network. The meta-network was also highly modular, with modules reflecting differences in the migratory habits and degree of endemicity of hummingbirds.

Our results highlight the large importance of migratory hummingbird species in the structure of the meta-network. Migration in Mexican hummingbirds appears to be a highly labile and relatively recent trait, occurring repeatedly and independently on several species from basal sedentary ancestors (Licona-Vera and Ornelas 2017). Migratory hummingbirds have significantly higher c values, that is, a relatively high proportion of their interactions are with plant species from other modules, increasing overall network cohesiveness (Olesen et al. 2007; Tylianakis et al. 2010; Stouffer and Bascompte 2011) and the potential importance of indirect interactions. In highly seasonal pollination networks, this role is achieved by pollinator species with long phenophases, who connected species with much more restricted activity periods (Martín González et al. 2012; Kantsa et al. 2018). Modular networks are expected to be highly resilient, as disturbances are less likely to spread beyond modules (Olesen et al. 2007; Tylianakis et al. 2010;

Stouffer and Bascompte 2011). However, at the same time, this particular topological configuration renders connectors a foremost importance, as they are able to affect rapidly the rest of the species in the network. Migratory Mexican hummingbirds show an interaction behavior relatively robust to changes in habitat conditions and in plant distributions and phenologies. By experimentally simulating changes in the environment, Ornelas and Lara (2015) showed that some migratory Mexican hummingbird species included in this study (i.e., Emerald *Amazilia beryllina* and Bee *Selasphorus rufus*) are able to quickly change and adjust their color preferences of the flowers they visit due to the short time spent in a given novel environment, whereas resident hummingbirds also included in this study (i.e., Emerald *Hylocharis leucotis* and Gem *Lampornis amethystinus*) usually prefer visiting their natural red flower type and they take longer to change their color preferences. This apparent neophilia in the migratory hummingbirds could favor the easy incorporation of non-familiar resources, such as invasive plant species, into their interaction networks. Moreover, as the importance of species may depend on the quantity and not just the presence-absence of pollination interactions, a weighted analysis could further illuminate the relative ecological importance of migratory pollinators.

The biogeographical distribution of species was strongly associated with the role of species in the network. Nearctic, Transition, and widespread hummingbirds showed a higher within-module and among-module connectivity. Most of these hummingbirds are also migrants (Table 1) and hence have wider range distributions and habitat preferences. Another possible explanation for the higher importance of Nearctic and widespread hummingbirds involves the divergence time of hummingbirds and their floral preferences. For example, hummingbird species from the Bees and Mountain Gems clades are distributed particularly in North America and Central America (mostly in the Nearctic realm), being the only lineages that expanded and diversified in these regions (~ 12 million years ago, McGuire et al. 2014; Licona-Vera and Ornelas 2017) and show a significantly higher mean c value (Appendix 4). Altogether, these species seem to be more evolutionary and ecologically dynamic. In contrast, Neotropical clades such as Hermits (e.g., *Phaethornis* spp.) and Emeralds (e.g., *Amazilia* spp.) had more recent invasions from South America and a subsequent diversification in the Mesoamerican zone (Ornelas et al. 2014), and have a more peripheral role in the meta-network.

The most common ancestral condition for the hummingbird flowers of North America is a bee-pollinated system (Grant and Grant 1968), promoting hummingbirds to be particularly generalist in their interactions with plants in the Nearctic realm. North-American hummingbirds have a closer phenotype than other hummingbird assemblages (Stiles 1981; Brown and Bowers 1985), which also translates

a)

b)

c)

d)

e)

f)
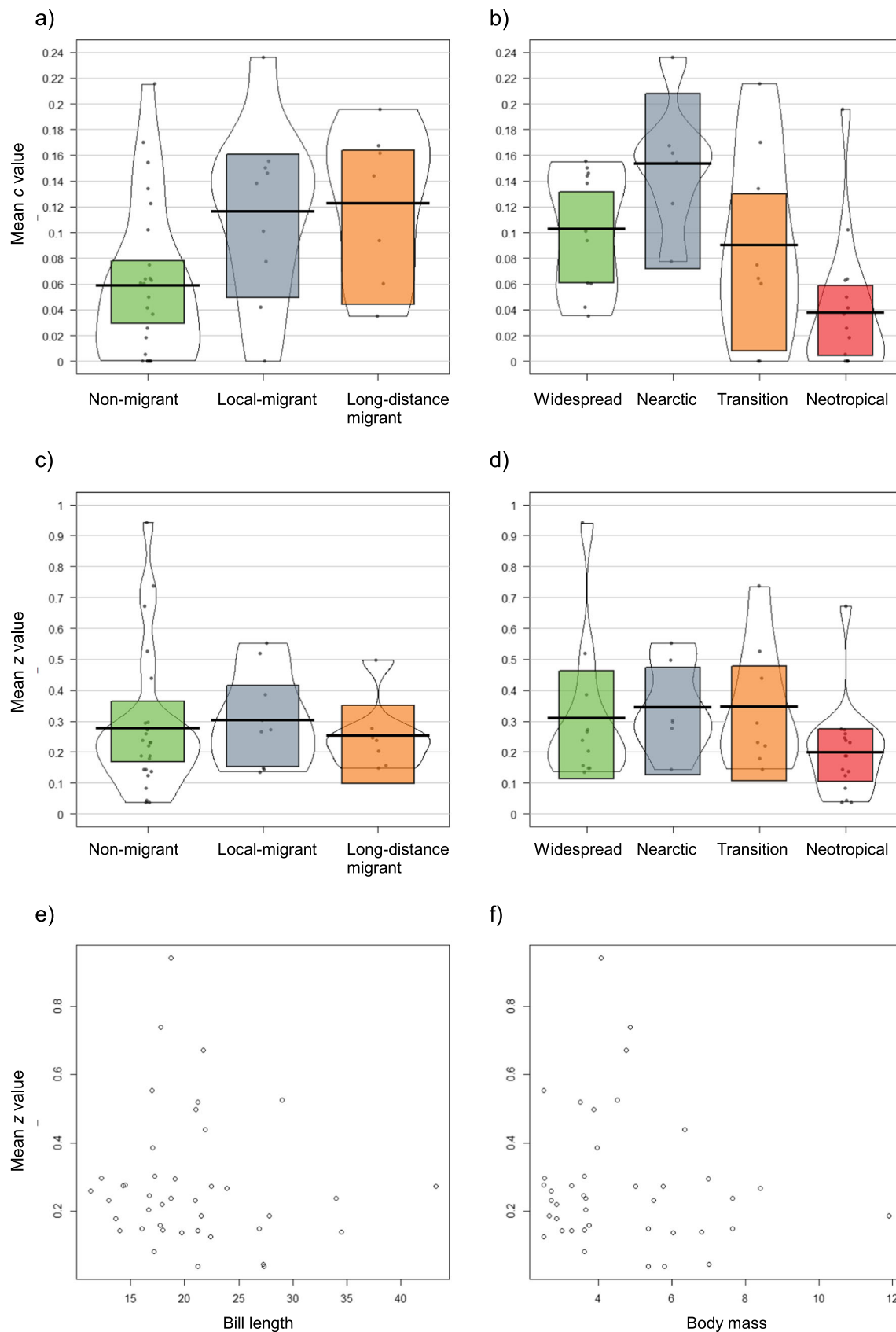
Fig. 4 Plots illustrating the significant associations between z and c values and migratory behavior (**a**, **b**), biogeographical distribution (**c**, **d**), bill length (**e**), and body mass (**f**) of hummingbirds. Pirate plots show raw data as points, the median as a horizontal line surrounded by a Bayesian 95% inference highest density interval as a horizontal bar, and a smoothed density bean surrounding the raw data points

into a higher congruence in the floral phenotypes. By contrast, ornithophilous genera of plants are centered in subtropical or tropical America, where hummingbird-plant interactions show higher levels of specialization and morphological complementarity (Stiles 1978; Dalsgaard et al. 2011). Hence, in Mexican hummingbird-plant assemblages, morphological traits may be, a priori, not as important as other mechanisms in structuring interactions at the community level. Our results show that both the length of the bill and the body mass of the hummingbirds affect the number of interactions hummingbirds establish within their module, with short-bill and smaller species showing a tendency to interact with a higher number of plants within their modules than long-bill and larger hummingbirds. Long bills restrict the number of plants from which a hummingbird can effectively extract nectar, while larger hummingbirds have higher energetic demands which constrain their available floral choices to flowers providing mid-high amounts of nectar, of which the North American flora is relatively scarce (Stiles 1981; Brown and Bowers 1985). Hence, in the Mexican hummingbird-plant assemblage, there seems to be a preference for not establishing strong morphological or energetic barriers between hummingbirds and their nectar plants.

Taken together, our study of the Mexican hummingbird-plant meta-network illustrates how meta-networks may provide a more complete view on the dynamics of ecological communities, particularly as the importance and behavior of migrant species may not be fully characterize when studying only local-scale networks. Notably, through a meta-network, we have been able to capture the direct and indirect interactions between hummingbirds and their nectar plants across Mexico, resulting in relevant insights on the importance of biogeographical traits for such assemblages. This emphasizes the usefulness of meta-networks for the characterization of the factors shaping species communities and how they interact across large spatial scales. This approach may be extended to other taxa and biogeographical regions and may prove valuable in order to assess the effects of mechanisms that operate at large spatial scales such as habitat fragmentation, species invasions, the effect of biotic interactions on range dynamics, and changes in species phenophases (Araújo and Luoto 2007; Araujo et al. 2018; Emer et al. 2018).

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