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Published in:
Science of Nature

DOI:
[10.1007/s00114-018-1578-5](https://doi.org/10.1007/s00114-018-1578-5)

Publication date:
2018

Document version
Peer reviewed version

Citation for published version (APA):
Martín González, A. M., Ornelas, J. F., Dalsgaard, B., Márquez-Luna, U., & Lara, C. (2018). Meta-networks for the study of biogeographical traits in ecological networks: the Mexican hummingbird-plant assemblage. *Science of Nature*, 105(9-10), [54]. <https://doi.org/10.1007/s00114-018-1578-5>

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Meta-networks for the study of biogeographical traits in ecological networks: the

4 **Mexican hummingbird-plant assemblage**

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Abstract

26 Recent studies on ecological networks have quantified the contribution of ecological,
historical and evolutionary factors on the structure of local communities of interacting
28 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.
30 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
32 patterns or phylogeographical distributions, as well as indirect relationships among species
through shared partners. Using a meta-network of hummingbird-plant interaction across
34 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
36 biogeographical characteristics associate with species' network roles. Our results show that
all studied hummingbird and plant species in the meta-network were interrelated, either
38 directly or through shared partners. The meta-network was structured into modules, resulting
from hummingbirds and plants interacting preferentially with subsets of species, which
40 differed in biogeographical, and, to a lesser extent, morphological traits. Furthermore,
migrants and hummingbirds from Nearctic, Transition and widespread regions had a higher
42 topological importance in the meta-network. Taken together, this study illustrates how meta-
networks may contribute to our current knowledge on species biogeographical traits and
44 biotic interactions, providing a perspective complementary to local-scale networks.

46 *Keywords* biotic interactions, migration, modularity, morphology, phylogeny, pollination

INTRODUCTION

48 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
50 challenge in ecology amidst global change is to quantify the contribution of ecological,
historical, evolutionary and biogeographic mechanisms in the structuring of communities of
52 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
54 typically show a context-dependent behavior reflecting their adaptation to a mosaic of factors
presented in their local communities, which in turn interplay at different scales. Hence, the
56 need of using a wide set of complementary analyses to study the effect of different factors and
at different scales (Thuillier et al. 2013; Poisot et al. 2015). For instance, the study of
58 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
60 climate, resource seasonality and species phenophases on community structure and species'
roles. Besides a more accurate understanding of community structure and build up, these
62 networks allow us to characterize more accurate the role of species and potential fluctuations
over time (Martín González et al. 2012; Chacoff et al. 2017, Kantsa et al. 2018). Similarly, the
64 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
66 biogeographical traits such as phylogeographical distribution, range dynamics or migratory
habits influence ecological networks, of which there is scarce knowledge (Heilmann-Clausen
68 et al. 2016; Araujo et al., 2018; Emer et al. 2018).

70 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
72 each other through third species. For instance, two consumer species whose ranges may not
overlap currently but which visit a similar array of resources, and hence may prevent the
74 expansion into each other ranges. Hence, the study of meta-networks may be particularly
useful to understand landscape dynamics, such as the effect of biotic interactions on range
76 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
78 networks due a lower detection probability (Vázquez et al. 2009).

80 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
82 containing species with large differences in range distributions or migratory habits. An
outstanding combination of such factors is the Mexican hummingbird-plant assemblage.
84 Mexico is located at the transition between the Nearctic and Neotropical realms (Halffter
1987; Rzedowski 1965), and exhibits a complex topography and geological history (Morrone
86 2010; Morrone et al. 2017; Fig. 1). Its wide array of ecological conditions has favoured
population isolation and the action of *in situ* evolutionary processes (Navarro et al. 2002),
88 enabling to find fauna, largely endemic, with different biogeographical and evolutionary
origins. For instance, the Mexican hummingbird fauna appears to have arisen from multiple
90 independent invasions of different phylogenetic lineages and at different times (Stiles 1981;
Brown and Bowers 1985; Bleiweiss 1998; Licona-Vera and Ornelas 2017; see more details in
92 methods). Several of the Mexican hummingbirds have very particular biogeographical and
ecological restrictions, which entails both processes of diversification and endemism
94 (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
96 restricted to regions of narrow extensions, little landscape connectivity, and complex
topography and floral composition. Furthermore, the Mexican hummingbird fauna includes a
98 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
100 winter and breeding grounds (e.g. Lara 2006; Licona-Vera and Ornelas 2017).

102 Hence, given the large differences phylogeographical history, range distributions and
migratory habits among Mexican species, we expect these biogeographical traits to exert a
104 strong effect on hummingbird-plant interactions and, therefore, on network structure.
However, most studies on hummingbird-plant assemblages have focused exclusively on the
106 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
108 and Graham 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
110 (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
112 hummingbird's biogeographical and morphological traits in structuring a meta-network
comprising all available information on hummingbird-plant interaction across Mexico. We
114 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
116 modular pattern of highly seasonal mutualistic assemblages where modules reflect species'
staggered phenophases (Martín González et al. 2012). Specifically, we investigate (1) how
118 hummingbird's biogeographical and morphological traits associate with the modular partition,
and (2) how hummingbird's biogeographical and morphological traits may associate with the
120 network role of hummingbirds in the meta-network.

122 **Methods**

Study area and study species

124 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
126 consequence of its location at the transition between the Nearctic and Neotropical realms
(Halffter 1964, 1987; Rzedowski 1965, 1992) and the close relationship between
128 geological/climatic and speciation events (Croizat 1958, 1964; Rosen 1978; Halffter 1987;
Liebherr 1991; Luna-Vega et al. 1999). In Mexico, the Nearctic realm comprises the arid
130 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
132 humid and subhumid tropical areas in the central-south part of the country (Halffter 1964;
Morrone and Márquez 2001; Morrone et al. 2017; Fig. 1).

134

Hummingbirds (Trochilidae) are the most highly specialized nectarivorous birds in the New
136 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
138 biogeographical and evolutionary patterns, ranging from generalized to highly specialized
(Stiles 1978; Dalsgaard et al. 2009, 2011; Abrahamczyk and Kessler 2014; Martín González
140 et al. 2015; Sonne et al. 2016). Their adaptive radiation manifests them as a highly diverse
clade, with more than 338 described species (McGuire et al. 2014). With approximately 58
142 recognized species, Mexico hosts 17% of the described hummingbird species. The Mexican
hummingbird fauna is relatively recent and results from various colonization waves from
144 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
146 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
148 Ornelas 2017; Appendix 1).

150 **Interaction data and species traits**

We compiled 37 hummingbird-plant interaction networks describing feeding relationships
152 between hummingbirds and plants throughout Mexico, spanning over nine different habitats
and ten biogeographic provinces (as defined by Morrone et al. 2017), including both
154 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
156 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
158 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
160 restricted to Mexico (8 species); semi-endemic, when the entire population is seasonally
present in Mexico or in narrowly overlapping adjacent countries ($<35000\text{Km}^2$; 9 species); and
162 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);

164 Arizmendi and Berlanga 2014). The biogeographical distribution of hummingbirds was
categorized as Nearctical, when the hummingbird was reported only in Nearctical or in
166 Nearctical and Transition localities (6 species), as Neotropical when the hummingbird was
reported only in Neotropical or in Neotropical and Transition localities (16 species), as
168 Transition, when the hummingbird was reported only in Transition localities (8 species), or
widespread if the hummingbird was present in Nearctical, Neotropical and Transition regions
170 (11 species; Table 1). Plants belong to 66 different families, are mostly native species (271
species, 92% of total) and include both typical ornithophilous and non-ornithophilous floral
172 morphologies (see Appendix 2 for a list of plants present in the meta-network).

174 **Meta-network analyses**

To investigate the structure of the Mexican meta-network, we merged all information on the
176 presence/absence of species interactions into a single meta-network describing whether each
hummingbird and plant species interacted anywhere in Mexico (Appendix 2). We thereafter
178 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
180 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
182 into an a priori undefined number of modules using matrix's eigenvalues, minimizing the
number of links between modules while maximizing within-module connectance (Barber
184 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
186 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
188 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,
190 and in which species interaction probability is based on their observed connectivity
(Bascompte et al. 2003; Marquitti et al. 2014).

192

We examined the resulting modular partition in order to understand the underlying
194 mechanisms associated with such pattern of interactions. We performed a non-metric
multidimensional scaling (NMDS) of hummingbird morphological and biogeographical traits
196 known or hypothesized to associate with hummingbird-plant interactions, namely bill length,
body mass, degree of endemism, migratory habits and biogeographical distribution. The
198 NMDS was run following the approach recommended in the R package *vegan* (Oksanen et al.
2017), e.g. the ordination was run 5 times, with a minimum number of 200 iterations and
200 using the previous best solution as starting point. To the resulting ordination, we fit a
secondary matrix, which included group membership (e.g. which groups of hummingbirds
202 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
204 from different hummingbird phylogenetic lineages show different morphological or
biogeographical traits.

206

Finally, from the resulting modular partition we obtained information on the network role of
208 each hummingbird species by computing species' within-module degree (*z-values*) and
among-module connectivity (*c-values*) in the *cz-values* function from the R package *bipartite*
210 (Dormann 2012). Within and among module connectivities are calculated as $z = (k_{is} - k_{s\bar{}}) /$
 SD_{k_s} and $c = 1 - \sum (k_{it}/k_i)^2$, respectively, where k_i is the degree of focal species i ; k_{is} is the
212 degree of focal species i to the rest of the species within i 's module; $k_{s\bar{}}$ is the average degree
of all species in module s ; SD_{k_s} is the standard deviation of the degrees of species in module s ;
214 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
216 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
218 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
220 of endemism and migratory habits) and categorical unordered variables (biogeographical
distribution), we used a non-parametric multiple regression with kernel estimation to examine

222 whether their z and c -values associate with any of these traits, using the R package *np*
(Hayfield and Racine 2017). All statistical analyses were performed in R 3.3.1 (R
224 Development Core Team 2014).

226 **Results**

The meta-network consisted of 395 species and 1128 interactions, and had a connectance of
228 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
230 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
232 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
234 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
236 same module (that is, in 26 out of the 30 runs of the modularity algorithm; Fig. 2; group
species compositions are given in Appendix 2; results from the modularity analysis are given
238 in Appendix 3).

240 The NMDS analysis on the morphological and biogeographical traits of the 41 hummingbird
species of the meta-network resulted in a two-dimensional solution with a stress value of
242 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
244 strongest associations were, in this order, with hummingbird migratory behavior and
biogeographical distribution. All variables were negatively associated with axis 2 except for
246 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
248 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 4). 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).

262

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 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 even indirect interactions may exert relatively strong influences across the network. The meta-network was also highly modular, with modules reflecting differences in the migratory habits and degree of endemism of hummingbirds.

276

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

280 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
282 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
284 indirect interactions. In highly seasonal pollination networks this role is achieved by
pollinator species with long phenophases, who connected species with much more restricted
286 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
288 (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
290 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
292 conditions and in plant distributions and phenologies. By experimentally simulating changes
in the environment, Ornelas and Lara (2015) showed that some migratory Mexican
294 hummingbird species included in this study (i.e. Emerald *Amazilia beryllina* and Bee
Selasphorus rufus) are able to quickly change and adjust their colour preferences of the
296 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
298 *Lampornis amethystinus*) usually prefer visiting their natural red flower type and they take
longer to change their colour preferences. This apparent neophilia in the migratory
300 hummingbirds could favor the easy incorporation of non-familiar resources, such as invasive
plant species, into their interaction networks.

302

The biogeographical distribution of species was strongly associated with the role of species in
304 the network. Nearctic, Transition and widespread hummingbirds showed a higher within-
module and among-module connectivity. Most of these hummingbirds are also migrants
306 (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
308 divergence time of hummingbirds and their floral preferences. For example, hummingbird
species from the Bees and Mountain Gems clades are distributed particularly in North

310 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;
312 Licona-Vera and Ornelas 2017) and show a significantly higher mean *c-value* (Appendix 5).
Altogether, these species seem to be more evolutionary and ecologically dynamic. In contrast,
314 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
316 Mesoamerican zone (Ornelas et al. 2014), and have a more peripheral role in the meta-
network.

318

The most common ancestral condition for the hummingbird flowers of North America is a
320 bee-pollinated system (Grant and Grant 1968), promoting hummingbirds to be particularly
generalist in their interactions with plants in the Nearctic realm. North-American
322 hummingbirds have a closer phenotype than other hummingbird assemblages (Stiles 1981;
Brown and Bowers 1985), which also translates into a higher congruence in the floral
324 phenotypes. By contrast, ornithophilous genera of plants are centred in subtropical or tropical
America, where hummingbird-plant interactions show higher levels of specialization and
326 morphological complementarity (Stiles 1978; Dalsgaard et al. 2011). Hence, in Mexican
hummingbird-plant assemblages, morphological traits may be, *a priori*, not as important as
328 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
330 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-
332 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
334 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
336 Bowers 1985). Hence, in the Mexican hummingbird-plant assemblage there seems to be a
preference for not establishing strong morphological or energetic barriers between
338 hummingbirds and their nectar plants.

340 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
342 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
344 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
346 biogeographical traits for such assemblages. This emphasizes the usefulness of meta-
networks for the characterization of the factors shaping species communities and how they
348 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
350 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
352 Luoto 2007; Araujo et al. 2018; Emer et al. 2018).

354 *Acknowledgements* —

We thank Tobias Roth, Sven Thatje and an anonymous referee for helpful comments on a
356 previous version of the manuscript. AMMG is supported through a Marie Skłodowska-Curie
Individual Fellowship (H2020-MSCA-IF-2015-704409). AMMG and BD thank the Danish
358 National Research Foundation for its support of the Center for Macroecology, Evolution and
Climate (Grant number DNRF96). CL thanks the Secretaría de Investigación of Universidad
360 Autónoma de Tlaxcala for the scholarship awarded. Verónica Mendiola-Islas provided
logistical support during the revision of hummingbird-plant networks.

362

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TABLES

514 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
 516 observed community location, body mass and bill length from Arizmendi and Berlanga
 (2014) and from Carlos Lara's own measurements (marked with and asterisk *), degree of
 518 endemism from Escalante (1993) and species migratory behavior from Arizmendi and
 Berlanga (2014).

Hummingbird species	Phylogenetic lineage	Biogeographical distribution	Bill length (mm)	Body mass (g)	Degree of endemism	Migratory behavior
<i>Amazilia beryllina</i>	Emerald	Widespread	18.71*	4.06*	Non endemic	Non migrant
<i>Amazilia candida</i>	Emerald	Neotropical + Transition	17.2	3.6	Non endemic	Non migrant
<i>Amazilia cyanocephala</i>	Emerald	Neotropical + Transition	21	5.5	Non endemic	Non migrant
<i>Amazilia rutila</i>	Emerald	Neotropical + Transition	21.75	4.75	Non endemic	Non migrant
<i>Amazilia tzacatl</i>	Emerald	Neotropical + Transition	21.25	5.35	Non endemic	Non migrant
<i>Amazilia violiceps</i>	Emerald	Widespread	22.5	5	Semi endemic	Local migrant
<i>Amazilia yucatanensis</i>	Emerald	Neotropical + Transition	21.25	3	Semi endemic	Local migrant
<i>Anthracothorax prevostii</i>	Mango	Neotropical + Transition	27.25	7	Non endemic	Non migrant
<i>Archilochus alexandri</i>	Bee	Widespread	18.75	3.65	Semi endemic	Long distance migrant
<i>Archilochus colubris</i>	Bee	Widespread	16.04*	5.36*	Non endemic	Long distance migrant
<i>Atthis heloisa</i>	Bee	Nearctica + Transition	12.32*	2.53*	Endemic	Non migrant
<i>Calothorax lucifer</i>	Bee	Nearctica + Transition	21.02*	3.86*	Semi endemic	Long distance migrant
<i>Calothorax pulcher</i>	Bee	Transition	17.9	2.85	Endemic	Non migrant
<i>Calypte anna</i>	Bee	Nearctica	17.25	3.6	Non endemic	Local migrant
<i>Calypte costae</i>	Bee	Nearctica	17	2.5	Non endemic	Local migrant
<i>Campylopterus curvipennis</i>	Emerald	Neotropical + Transition	27.3	5.8	Non endemic	Non migrant
<i>Campylopterus hemileucurus</i>	Emerald	Neotropical + Transition	27.8	11.9	Non endemic	Non migrant
<i>Chlorostilbon auriceps</i>	Emerald	Transition	14	3.25	Endemic	Non migrant
<i>Chlorostilbon canivetii</i>	Emerald	Neotropical + Transition	14.3	3.25	Non endemic	Non migrant
<i>Colibri thalassinus</i>	Mango	Widespread	19.71*	6.03*	Non endemic	Local migrant
<i>Cyanthus latirostris</i>	Emerald	Widespread	21.25	3.5	Semi endemic	Local migrant
<i>Cyanthus sordidus</i>	Emerald	Transition	29	4.5	Endemic	Non migrant
<i>Doricha eliza</i>	Bee	Neotropical + Transition	22.4	2.5	Endemic	Non migrant

<i>Eugenes fulgens</i>	Gem	Widespread	26.88*	7.65*	Non endemic	Local migrant
<i>Eupherusa poliocerca</i>	Emerald	Transition	17.8	4.85	Endemic	Non migrant
<i>Helioaster constantii</i>	Gem	Neotropical + Transition	34	7.65	Non endemic	Non migrant
<i>Helioaster longirostris</i>	Gem	Neotropical + Transition	34.5	6.8	Non endemic	Non migrant
<i>Hylocharis leucotis</i>	Emerald	Widespread	17.03*	3.95*	Non endemic	Local migrant
<i>Hylocharis xantusii</i>	Emerald	Nearctica	18	3.6	Endemic	Non migrant
<i>Lampornis amethystinus</i>	Gem	Transition	19.11*	6.98*	Non endemic	Non migrant
<i>Lampornis clemenciae</i>	Gem	Widespread	23.92*	8.39*	Semi endemic	Local migrant
<i>Lamprolaima rhami</i>	Gem	Transition	21.9	6.35	Non endemic	Non migrant
<i>Lophornis brachylophus</i>	Coquette	Transition	13	2.7	Endemic	Non migrant
<i>Lophornis helenae</i>	Coquette	Neotropical	11.3	2.7	Non endemic	Non migrant
<i>Phaethornis longirostris</i>	Hermit	Neotropical + Transition	43.2	5.75	Non endemic	Non migrant
<i>Phaethornis striigularis</i>	Hermit	Neotropical + Transition	21.55	2.65	Non endemic	Non migrant
<i>Selasphorus calliope</i>	Bee	Nearctica + Transition	14.5	2.5	Semi endemic	Long distance migrant
<i>Selasphorus platycercus</i>	Bee	Widespread	17.74*	3.73*	Semi endemic	Long distance migrant
<i>Selasphorus rufus</i>	Bee	Widespread	16.68*	3.65*	Non endemic	Long distance migrant
<i>Selasphorus sasin</i>	Bee	Neotropical + Transition	16.71*	3.59*	Semi endemic	Long distance migrant
<i>Tilmatura dupontii</i>	Bee	Transition	13.6	2.85	Non endemic	Non migrant

520 Table 2. Results from the non-parametric multiple regression with kernel variable estimation
 between species within and between module connectivity (z and c value, respectively) and
 522 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
 524 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
 526 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
 528 behavior). Bandwidths were computed using an adaptive k-nearest neighbor algorithm and
 selected through a least squares cross-validation (Hayfield and Racine 2008, 2017).
 530 Significance tests were performed with 399 bootstraps. Significant variables are marked in
 bold.

	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

532

FIGURES

534 **Figure 1.** Map of Mexico showing the different biogeographical regions conforming the
Nearctical realm (in blue), the Neotropical realm (in orange) and Transition provinces (in
536 green) as defined by Morrone et al. (2017). Dots pinpoint the localities where the
hummingbird-plant networks were collected. Note that some of the points may overlap.

538

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

544

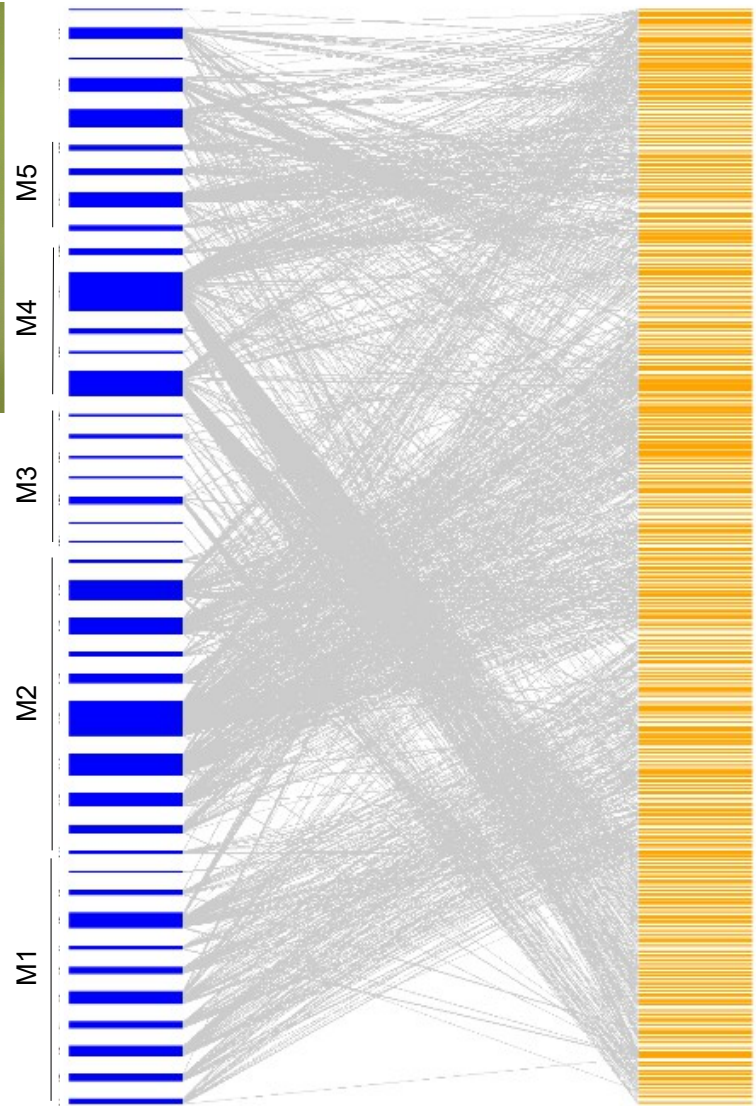
Figure 3. Results of the non-metric multidimensional scaling ordination of five hummingbird
546 species traits (bill length, body mass, biogeographical distribution, degree of endemism and
migratory behavior). Ellipses in the NMDS indicate 95% confidence intervals around the
548 centroids of each group. Note that modules 6-10 (colored in different shades of red) are
conformed of only one hummingbird species, as these hummingbirds appeared in different
550 modules in the different runs of the modularity algorithm. Notice also that these
hummingbirds do not show biogeographical or morphological differences from
552 hummingbirds with constant module partners.

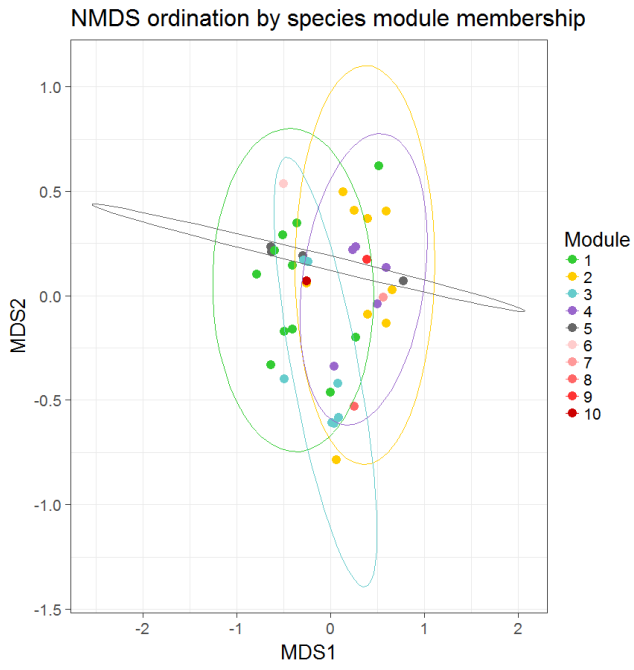
554 **Figure 4.** Plots illustrating the significant correlations between z and c values and migratory
behavior (a,b), biogeographical distribution (c,d), bill length (e) and body mass (f) of
556 hummingbirds. Pirareplots show raw data as points, the median as a horizontal line
surrounded by a Bayesian 95% Inference Highest Density Interval as a horizontal bar, and a
558 smoothed density bean surrounding the raw data points.

Figure 1

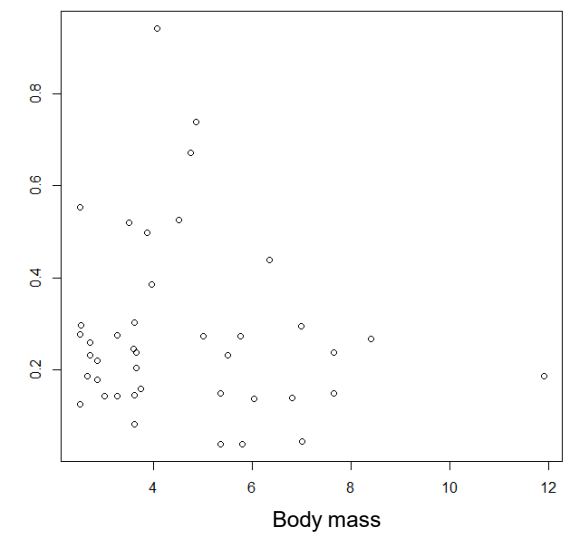
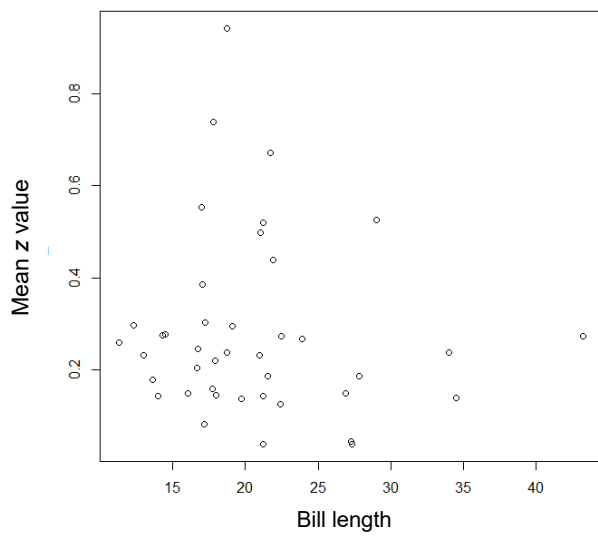
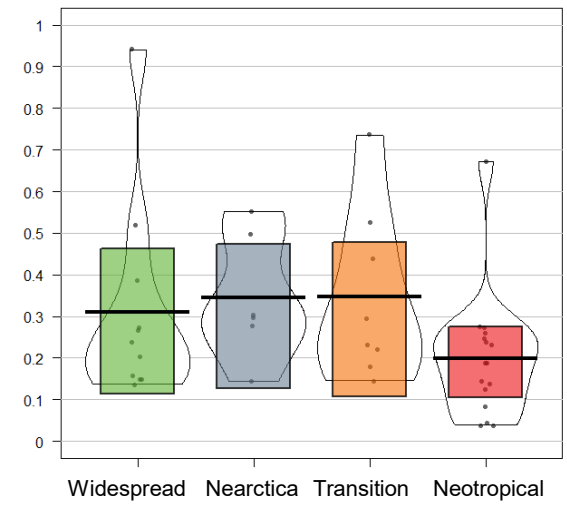
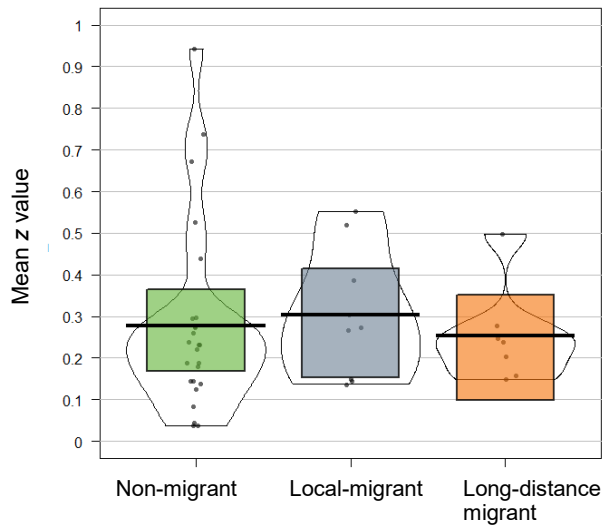
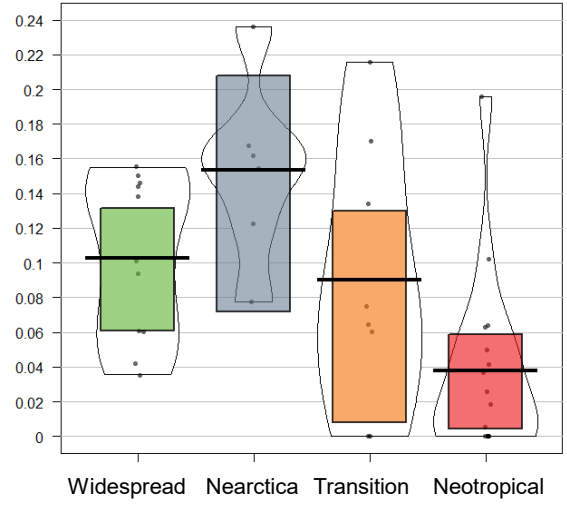
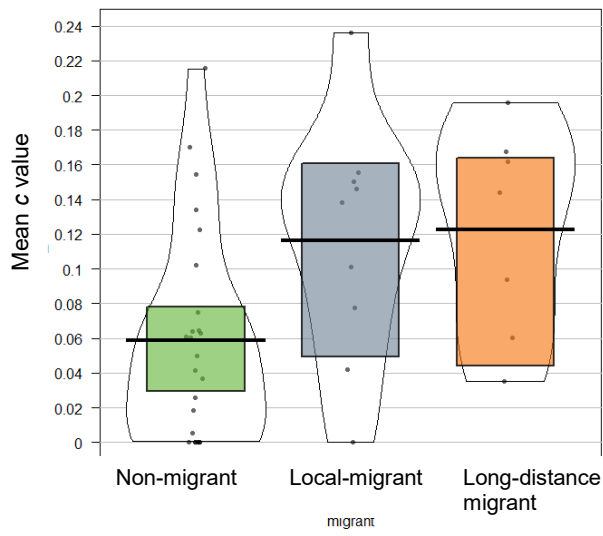
560







	Axis 1	Axis 2
Bill length	0.159	-0.249
Mass	0.122	-0.424
Biogeographical distribution	0.358	-0.013
Degree of endemism	-0.163	0.836
Migratory behavior	-1.041	-0.054



568 **SUPPORTING INFORMATION**

Appendix 1. Details about the Mexican biogeography and hummingbird fauna and
570 biogeographical characteristics.

572 Mexico is an outstanding example of complex biogeographical patterns (Morrone 2010;
Morrone et al. 2017). The Mexican Transition Zone (Halffter 1987), which marks the
574 transition between the Neotropical and the Nearctic biota, is considered a critical area for
understanding not just diversification in the region, but also the evolution of migratory
576 systems of various animal species. This zone includes the Isthmus of Tehuantepec in southern
Mexico, formed c. 3 Ma, and the Trans-Mexican Volcanic Belt (TMVB) across central
578 Mexico, formed c. 10–7 Ma (Gómez-Tuena et al. 2007). The Isthmus of Tehuantepec divides
mountain ranges along the Sierra Madre Oriental and Oaxaca from those in Chiapas and
580 Guatemala. Its formation was followed by changes in sea levels caused by glaciation cycles,
with rising sea levels and marine transgression during interglacials inundating much of the
582 coastal plains and isolating montane habitats on either side (Barrier et al. 1998). At present,
the lowlands in the area are occupied by dry scrubby habitats that are very different from the
584 moist mountainous areas on either side. The TMVB was formed during four main episodes of
volcanic activity from the middle-to-late Miocene to the Holocene (Gómez-Tuena et al.
586 2005), resulting in a continental magmatic arc of nearly 8000 volcanic chain of mountains
(reaching over 4000 m above sea level), extending west to east and virtually cutting Mexico
588 into northern and southern halves. The TMVB acts as an effective geographic barrier to the
dispersal of most hummingbird species, producing abrupt environmental changes, which may
590 explain the existence of such high number of endemic hummingbird species. Recent
phylogeographic studies have shown that species level population divergence of terrestrial
592 species post-dates Pliocene faulting and marine inundations across the Isthmus of
Tehuantepec (Barber and Klicka 2010; Ornelas et al. 2013 and references therein).

594

The Mexican hummingbird fauna (including all North American species) began with a single
596 invasion from South America by the common ancestor of the Bee and Mountain Gem clades
ca. 12–14 million years ago (McGuire et al. 2014; Licona-Vera and Ornelas 2017). After this

598 invasion, there have been multiple independent invasions of North America by Emeralds,
Coquettes, Mangoes, and Hermits and single invasions by Brilliants and Topazes, presumably
600 all of which occurred prior to or after the Panamanian land bridge formation (McGuire et al.
2014; Ornelas et al. 2014). Species accumulation in North America proceeded slowly at first
602 and a rapid increase during the past 7 Ma, which reflects not only in situ diversification of
Mountain Gems and Bees, but also a heterogeneous diversification dynamics during the
604 history of hummingbirds and an extraordinary high rate of net diversification in the Bee clade
(McGuire et al. 2014), potentially linked to the evolution of migratory behavior (Licona-Vera
606 and Ornelas 2017). In the Nearctic-Neotropical migration systems, analyses of molecular data
suggest that many bird species colonized northern areas when they became available after the
608 Last Glacial Maximum (LGM) event (Hewitt 2000). For example, the ancestral sedentary
ranges of the Bee clade (such as *Selasphorus* species) expanded into northern latitudes
610 following the LGM, until they reached limits for residency imposed by the local seasonality
of the floral resources and migration was selectively favoured (Malpica and Ornelas 2014).
612 These migrations were followed by rapid radiations and local adaptations to both xeric and
humid conditions in different regions of Mexico, and produced both sedentary and migratory
614 populations (Licona-Vera and Ornelas 2017). In a phylogenetic framework, the repeated
evolution of long-distance migratory behavior is observed at different times in the radiation of
616 the Bee clade, highlighting the key role of the environment (local topographical features and
climatic changes) on processes of divergence and speciation. These repeated gains of
618 migration at the phylogenetic scale seem to have occurred linked to certain patterns of
climatic change during the Late Pliocene and Pleistocene glaciations, whereas the evolution of
620 long-distance seasonal migration within species seems to have occurred during the last
glacial-interglacial cycles of the Pleistocene (Rodríguez-Gómez et al. 2013; Malpica and
622 Ornelas 2014; Licona-Vera and Ornelas 2017).

Appendix 2. Table S2. Geographical and habitat details for each hummingbird-plant network.

Study #	Author	Mexican state	Main Vegetation type	Latitude	Longitude	Biogeographical province	Biogeographical realm
1	Rodríguez-Flores, C.I.	Jalisco	Cloud forest	19°34'14'' - 19°37'30''	104°14'49'' - 104°18'16''	Sierra Madre del Sur	Transition
2	Ortiz-Pulido, R.	Veracruz	Pine forest	19°29'59.86"	97° 8'12.08"	Trans-Mexican Volcanic Belt	Transition
3	Arizmendi, M.C.	Jalisco	Tropical deciduous forest	19° 30'	105° 03'	Pacific Lowlands	Neotropical
4	Arizmendi, M. C.	Jalisco	Cloud forest	19° 35'	104° 16'	Sierra Madre del Sur	Transition
5	Des Granges, J.- L.	Colima	Pine-oak forest	19°31'3.18"	103°37'5.55"	Trans-Mexican Volcanic Belt	Transition
6	Partida Lara, R.	Chiapas	Cloud forest	16°44'38"	92°40'15"	Chiapas Highlands	Transition
7	Arizmendi, M. C.	Guerrero	Pine-oak forest	17°19'53.1'' - 17°25'47.8''	100° 09' 56.1'' - 100°11'48.5''	Sierra Madre del Sur	Transition
8	Lyon, D. L.	Oaxaca	Pine forest	17° 8'26.67"	96°41'21.55"	Sierra Madre del Sur	Transition
9	Arriaga, L.	Baja California Sur	Oak forest	24°-22°50'	109°60'-110°10'	Baja Californian	Nearctica
10	Reyna Bustos, O.	Jalisco	Tropical deciduous forest	21°45'08'' - 21°44'50''	103°15'	Pacific Lowlands	Neotropical
11	De la Cruz, F.	Oaxaca	Xeric shrubland	17°04'04''	96°43'12''	Sierra Madre del Sur	Transition
12	Jimenez Sierra, L.	Hidalgo	Xeric shrubland	20°45'26''	98°57'08''	Sierra Madre Oriental	Transition
13	Toledo, V.	Veracruz	Evergreen tropical forest	18°32'	95° 04'	Veracruzian	Neotropical
14	Van Devender, T.	Sonora	Foothills thorn scrubs	28°34'40"	109°33'09"	Sonoran	Nearctica
15	Van Devender, T.	Sonora	Tropical deciduous forest	28°25'48"	109°11'31"	Sonoran	Nearctica
16	Van Devender, T.	Sonora	Oak woodland	28°22'18"	109°03'53"	Sonoran	Nearctica
17	Van Devender, T.	Sonora	Pine-oak forest	28°19'31"	109°02'00"	Sonoran	Nearctica

18	Martínez-García, V. 1	Hidalgo	Xeric shrubland	20°36'44"	98°44'54"	Sierra Madre Oriental	Transition
19	Martínez-García, V. 2	Hidalgo	Oak forest	20°40'31.7"	98°45'12.3"	Sierra Madre Oriental	Transition
20	Martínez-García, V. 3	Hidalgo	Pine-oak forest	20°41'45.82"	98°45'55.92"	Sierra Madre Oriental	Transition
21	Díaz-Valenzuela, R. 1	Hidalgo	Pine forest	20°11'11"	98°42'34"	Sierra Madre Oriental	Transition
22	Díaz-Valenzuela, R. 2	Hidalgo	Pine forest	20°41'45.82"	98°45'55.92"	Sierra Madre Oriental	Transition
23	Díaz-Valenzuela, R. 3	Hidalgo	Oak forest	20°41'45.82"	98°45'55.92"	Sierra Madre Oriental	Transition
24	Montgomerie, R. D.	Nayarit	Tropical deciduous forest	21°32'	105°17'	Pacific Lowlands	Neotropical
25	Lara, C.1	Tlaxcala	Pine forest	19°13'49.5"	98° 58' 19.67"	Trans-Mexican Volcanic Belt	Transition
26	Lara, C.2	Tlaxcala	Oak forest	19°17'36"	98° 14' 30"	Trans-Mexican Volcanic Belt	Transition
27	Lara, C.3	Veracruz	Cloud forest	19°30'	96°57'	Trans-Mexican Volcanic Belt	Transition
28	Díaz-Fisher 1	Puebla	Arid tropical scrubland	19°36'45"	96° 53' 45"	Sierra Madre del Sur	Transition
29	Arizmendi, M. C.	Puebla	Arid tropical scrubland	18°18'31"	97° 29' 25"	Sierra Madre del Sur	Transition
30	Díaz-Fisher 2	Puebla	Arid tropical scrubland	19°25'55"	96° 31' 53"	Sierra Madre del Sur	Transition
31	Puch Chávez, R.	Campeche	Evergreen tropical forest	18°21'	89° 49'	Yucatán Peninsula	Neotropical
32	Puch Chávez, R.	Campeche	Evergreen tropical forest	18°32'	89° 47'	Yucatán Peninsula	Neotropical
33	López Segoviano, G.	Sinaloa	Oak forest	23°34'16"	105°50'15"	Sonoran	Nearctica
34	Medina-van Berkum, P. et al.	Yucatán	Xeric shrubland	21°37'23.4" - 21°34'19"	88°07'42.3" - 88°06'00.9"	Yucatán Peninsula	Neotropical
35	Vidal-Hernández, W. J.	Estado de México	Pine-oak forest	19°48'2.8"	99° 31' 15.1"	Balsas Basin	Neotropical

36	Martínez-Roldan, H.	Tlaxcala	Xeric shrubland	19°23'31''	97°55'49''	Trans-Mexican Volcanic Belt	Transition
37	Bautista-Salazar, L.	Querétaro	Xeric shrubland	20° 30' - 20° 55'	100° 17' - 100° 36'	Chihuahuan Desert	Nearctica

ID number	Data Source Reference
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- 37 Bautista-Salazar, L. Unpublished data
-

Appendix 4. Results from the modularity analysis. Modularity was calculated in MODULAR
634 (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
636 settings: an initial temperature of 2.0, a cooling factor of 1.01, and an iteration factor of 1
(Marquitti et al. 2014). Barber's modularity divides the matrix into an a priori undefined
638 number of modules using matrix's eigenvalues, minimizing the number of links between
modules while maximizing within-module connectance (Barber 2007). We estimated the
640 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,
642 and in which species interaction probability is based on their observed connectivity
(Bascompte et al. 2003; Marquitti et al. 2014). As MODULAR uses an iterative searching
644 algorithm, we investigated the robustness of the resulting modular partition by running the
analysis 30 times using different seed set numbers. The resulting 30 partitions showed similar
646 levels of modularity but differed in the resulting number of modules (Table S3.1). Hence, we
further explored the species composition of the modules in the different runs. Species
648 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
650 runs). This threshold value for establishing modules was chosen through a hierarchical
agglomerative cluster analysis of dissimilarity data (Figure S3.1). Supporting this partition,
652 hummingbirds with variable module partners were not randomly scattered but tended to be
placed together with specific modules (Figure S3.1) and showed no differences in any of the
654 studied traits with species forming constant groups (Table 1, Figure S3.2).

656 References

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Zhao S, Guo Y, Sheng Q, Shyr Y (2016) An improved heatmap package. Package
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662 Table S4.1. Results from the 30 runs of the MODULAR (Marquitti et al. 2014) modularity
 analysis. Notice that the resulting number of modules varies between 5 and 8. Modularity
 664 values average $M=0.466$, with a standard deviation of $SD=0.004$. All runs were significantly
 modular when compared against matrices of same number of species and interactions as the
 666 empirical one, and where species have a probability of interaction derived from their observed
 connectivity (NM2).

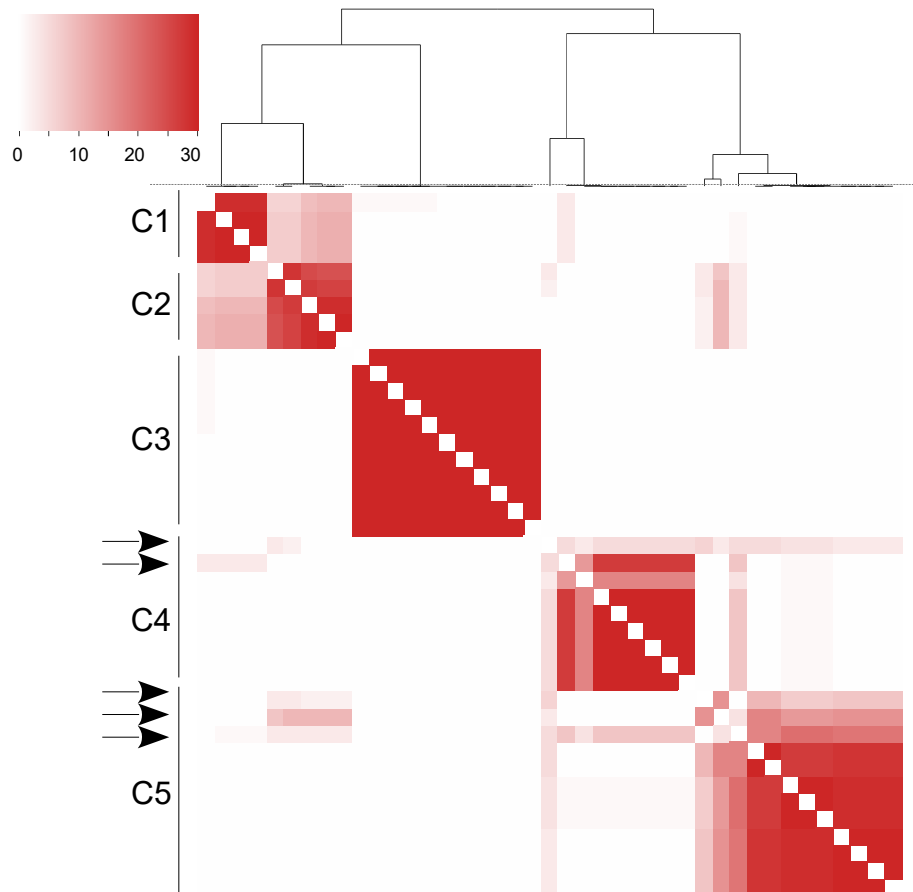
Run ID	Number of resulting modules	Modularity value	NM2 p-value
1	7	0.471	0
2	6	0.467	0
3	5	0.466	0
4	7	0.464	0
5	8	0.464	0
6	6	0.473	0
7	5	0.462	0
8	7	0.471	0
9	7	0.464	0
10	8	0.464	0
11	6	0.463	0
12	6	0.464	0
13	8	0.464	0
14	8	0.464	0
15	6	0.465	0
16	5	0.473	0
17	6	0.461	0
18	8	0.471	0
19	5	0.467	0
20	6	0.474	0
21	7	0.461	0
22	5	0.464	0
23	7	0.464	0
24	6	0.462	0
25	5	0.458	0
26	5	0.471	0
27	7	0.466	0
28	6	0.464	0
29	6	0.466	0
30	6	0.458	0

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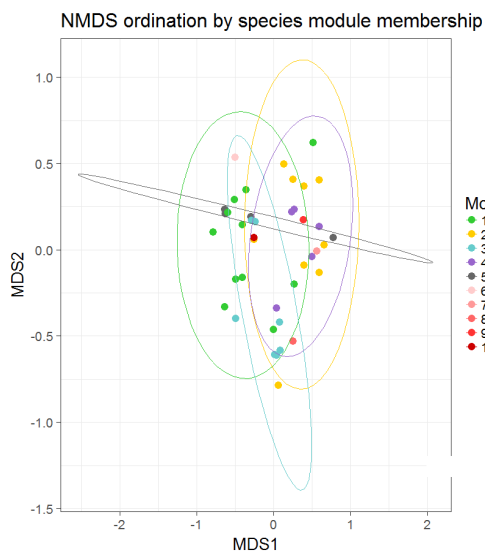
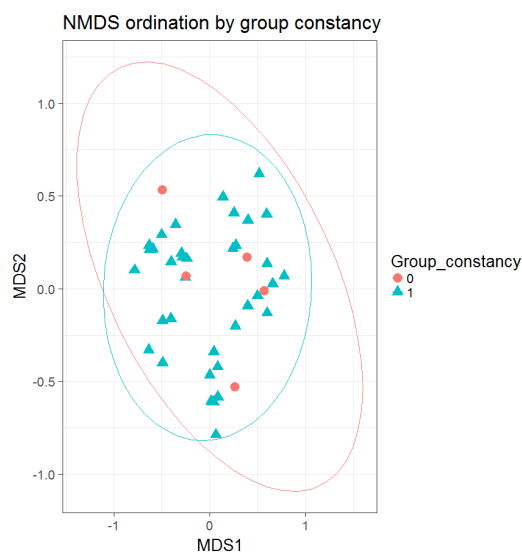
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Figure S4.1. Heatmap illustrating the frequency each pair of hummingbird species was placed
674 in the same module in each modularity run. The modularity algorithm was run 30 times.
Clustering analysis was performed with a fast hierarchical and agglomerative routine of
676 dissimilarity data from the *fastcluster* package in R (Müllner 2017) resulting in five clusters.
Arrows mark the five hummingbird species without constant partners. Heatmap compiled in
678 the *heatmap3* package in R (Zhao et al. 2016).

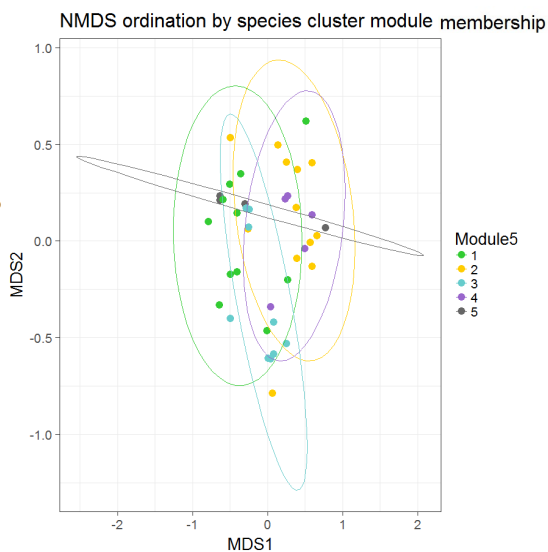


682 Figure S4.2. Results of the non-metric multidimensional scaling ordination of five
 hummingbird species traits (bill length, body mass, biogeographical distribution, degree of
 684 endemism and migratory behavior). The illustration shows (a) how hummingbirds without
 fixed module-partners do not differ in traits from hummingbirds with fixed module partners,
 686 and (b,c) the lack of significant differences when considering modules conformed of only
 constant partners (bottom left, the partition showed in the main text) and when considering
 688 modules derived from the cluster partition (bottom right). Ellipses in the NMDS indicate 95%
 confidence intervals around the centroids of each group. Note that analyzing only constant
 690 groups of partners or clusters result in virtually identical ellipses.

	Axis 1	Axis 2
Bill length	0.159	-0.249
Mass	0.122	-0.424
Biogeographical distribution	0.358	-0.013
Degree of endemism	-0.163	0.836
Migratory behavior	-1.041	-0.054



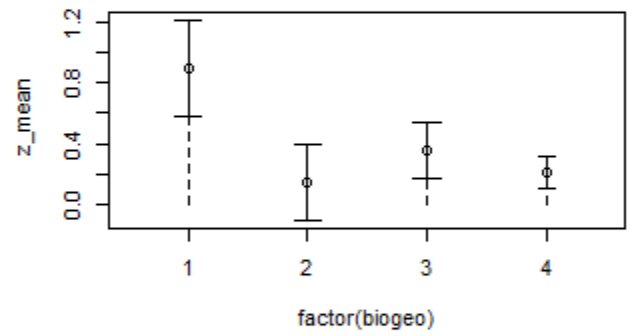
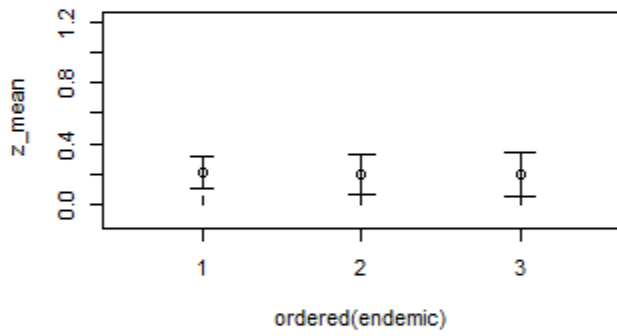
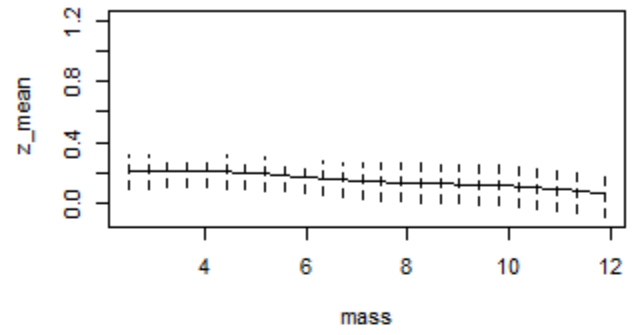
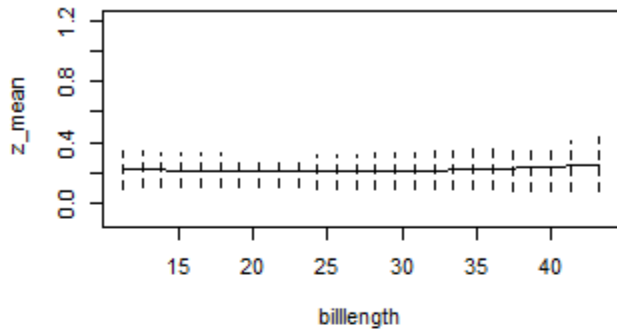
Goodness of fit = 0.426, p-value = 0.001

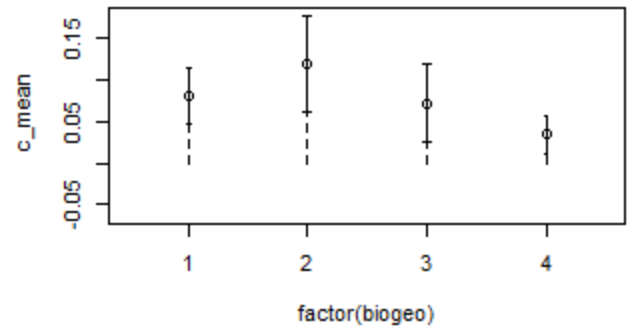
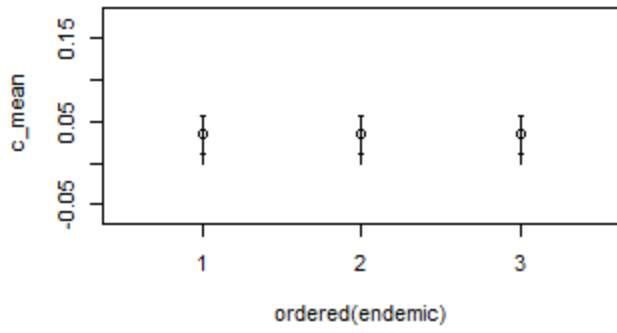
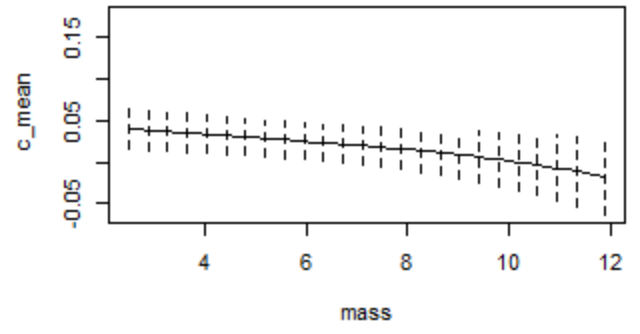
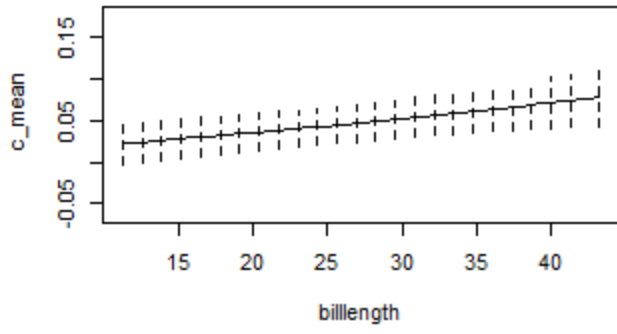


Goodness of fit = 0.345, p-value = 0.001

692 Appendix 5. Partial regression plots for the asymptotic errors of the non-parametric multiple
694 regression with kernel smoothing analysis.

696





700 Appendix 6. Differences in average *c* values in the various hummingbird phylogenetic lineages (KW $X^2 = 13.751$, $df = 5$, p -value = 0.017).

702

