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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 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 endemism, migratory habits and biogeographical distribution. The 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 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 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.

206

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 R package *bipartite* (Dormann 2012). Within and among module connectivities are calculated as  $z = (k_{is} - k_{s\bar{a}}) / SD_{k_s}$  and  $c = 1 - \sum (k_{it}/k_i)^2$ , respectively, where  $k_i$  is the degree of focal species  $i$ ;  $k_{is}$  is the degree of focal species  $i$  to the rest of the species within  $i$ 's module;  $k_{s\bar{a}}$  is the average degree of all species in module  $s$ ;  $SD_{k_s}$  is the standard deviation of the degrees of species in module  $s$ ; 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 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).

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362

#### **References**

364 Abrahamczyk S, Kessler M (2014) Morphological and behavioural adaptations to feed on  
nectar: how feeding ecology determines the diversity and composition of  
366 hummingbird assemblages. *J Ornithol* 156:333–347

Araujo AC, Martín González AM, et al. (2018) Spatial distance and climate determine  
368 modularity in a cross-biomes plant-hummingbird interaction network in Brazil. *J*  
*Biogeogr*, in press.

- 370 Araújo MB, Luoto M (2007) The importance of biotic interactions for modelling species  
distributions under climate change. *Glob Ecol Biogeogr* 16:743–753
- 372 Arizmendi MC, Berlanga H (2014) Colibríes de México y Norteamérica / Hummingbirds of  
Mexico and North America. CONABIO Mexico
- 374 Barber MJ (2007) Modularity and community detection in bipartite networks. *Phys Rev E*  
76:066102
- 376 Barber BR, Klicka J (2010) Two pulses of diversification across the Isthmus of Tehuantepec  
in a montane Mexican bird fauna. *Proc R Soc B* 20100343
- 378 Barrier E, Velasquillo L, Chávez M, Gaulon R (1998) Neotectonic evolution of the Isthmus of  
Tehuantepec (southeastern Mexico). *Tectonophysics* 287:77–96
- 380 Bleiweiss R (1998) Origin of hummingbird faunas. *Biol J Linn Soc* 65:77–97
- Brown JH, Bowers MA (1985) Community organization in hummingbirds: relationships  
382 between morphology and ecology. *The Auk* 102:251–269
- Cavender-Bares J, Kozak KH, Fine PV, Kembel SW (2009) The merging of community  
384 ecology and phylogenetic biology. *Ecol Lett* 12:693–715
- Chacoff N, Resasco J, Vázquez DP (2017) Interaction frequency, network position, and the  
386 temporal persistence of interactions in a plant-pollinator network. *Ecology* 99:21–28
- Cotton PA (2007) Seasonal resource tracking by Amazonian hummingbirds. *Ibis* 149:135–  
388 142
- Dalsgaard B, Martín González AM, Olesen JM, Ollerton J, Timmermann A, Andersen LH,  
390 Tossas AG (2009) Plant-hummingbird interactions in the West Indies: floral  
specialisation gradients associated with environment and hummingbird size.  
392 *Oecologia* 159:757–766
- Dalsgaard B, Magård E, et al. (2011) Specialization in plant-hummingbird networks is  
394 associated with species richness, contemporary precipitation and quaternary climate-  
change velocity. *PLoS One* 6:e25891

- 396 Dalsgaard, B, Kennedy, JD, et al. (2018). Trait evolution, resource specialisation and  
vulnerability to plant extinctions among Antillean hummingbirds. Proc R Soc B:  
398 20172754
- Dormann CF (2012) Visualising bipartite networks and calculating some (ecological) indices.  
400 Package "bipartite"
- Emer C, Galetti M, Pizo MA, Guimarães PR, Moraes S, Piratelli A, Jordano P (2018) Seed-  
402 dispersal interactions in fragmented landscapes – a metanetwork approach. Ecol  
Lett 21:484–493
- 404 Escalante P, Navarro AG, Peterson AT (1993) A geographic, historical and ecological  
analysis of land bird diversity in Mexico. In: Ramamoorthy TP, Bye R, Fa J, Lot A  
406 (eds) Biological diversity in Mexico: Origins and distributions. Oxford University  
Press, New York, pp 281–307
- 408 Gómez-Tuena A, Orozco-Esquivel MT, Ferrari L (2005) Petrogénesis ígnea de la faja  
volcánica transmexicana. Bol Soc Geol Mex 57:227–283
- 410 Gómez-Tuena A, Orozco-Esquivel MT, Ferrari L (2007) Igneous petrogenesis of the Trans-  
Mexican Volcanic Belt. Geol Soc Am 422:129–181
- 412 Grant KA, Grant V (1968) *Hummingbirds and their flowers*. Columbia University Press.
- Hayfield T, Racine JS (2008) Nonparametric Econometrics: The np Package. Journal of  
414 Statistical Software 27(5). URL <http://www.jstatsoft.org/v27/i05/>
- Hayfield T, Racine JS (2017) Nonparametric kernel smoothing methods for mixed data types.  
416 Package "np"
- Halffter G (1987) Biogeography of the montane entomofauna of Mexico and Central  
418 America. Annu Rev Entomol 32:95–114
- Heilmann-Clausen J, Maruyama PK, Bruun HH, Dimitrov D, Læssøe T, Frøslec TG,  
420 Dalsgaard B (2017) Citizen science data reveal ecological, historical and evolutionary  
factors shaping interactions between woody hosts and wood-inhabiting fungi. New



Hegland SJ, Nielsen A, Lázaro A, Bjerknes AL, Totland Ø (2008) How does climate warming  
424           affect plant-pollinator interactions? *Ecol Lett* 12:184–195

Hewitt G (2000) The genetic legacy of the Quaternary ice ages. *Nature* 405:907–913

426   Kantsa A, Raguso RA, Dyer AG, Olesen JM, Tscheulin T, Petanidou T (2018) Disentangling  
          the role of floral sensory stimuli in pollination networks. *Nature Comm* 9:1041

428   Lara C (2006) Temporal dynamics of flower use by hummingbirds in a highland temperate  
          forest in Mexico. *EcoScience* 13:23–29

430   Licona-Vera Y, Ornelas JF (2014) Genetic, ecological and morphological divergence between  
          populations of the endangered Mexican Sheartail Hummingbird (*Doricha eliza*).

432           *PLoS ONE* 9:e101870

Licona-Vera Y, Ornelas JF (2017) The conquering of North America: dated phylogenetic and  
434           biogeographic inference of migratory behavior in bee hummingbirds. *BMC Evol Biol*  
          17:126

436   Maglianesi MA, Blüthgen, Böhning-Gaese K, Schleuning M (2014) Morphological traits  
          determine specialization and resource use in plant-hummingbird networks in the  
438           Neotropics. *Ecology* 95:3325–3334

Maglianesi MA, Blüthgen, Böhning-Gaese K, Schleuning M (2015) Functional structure and  
440           specialization in three tropical plant-hummingbird interaction networks across an  
          elevational gradient in Costa Rica. *Ecography* 38:1119–1128

442   Malpica A, Ornelas JF (2014) Postglacial northward expansion and genetic differentiation  
          between migratory and sedentary populations of the broad-tailed hummingbird

444           (*Selasphorus platycercus*). *Mol Ecol* 23:435–452

Marquitti FMD, Guimarães PR Jr., Pires MM, Bittencourt LF (2014) MODULAR: Software  
446           for the Autonomous Computation of Modularity in Large Network Sets. *Ecography*  
          37:221–224

- 448 Martín González AM, Allesina S, Rodrigo A, Bosch J (2012) Drivers of  
compartmentalization in pollination networks. *Oikos* 121:2001–2013
- 450 Martín González AM, Dalsgaard B, et al. (2015) The macroecology of phylogenetically  
structured hummingbird-plant networks. *Glob Ecol Biogeogr* 24:1212–1224
- 452 Maruyama PK, Vizentin-Bugoni J, Oliveira GM, Oliveira PE, Dalsgaard B (2014)  
Morphological and spatio-temporal mismatches shape a Neotropical savanna plant-  
454 hummingbird network. *Biotropica* 46:740–747
- McGuire JA, Witt CC, Remsen JV Jr, Corl A, Rabosky DL, Altshuler DL, Dudley R (2014)  
456 Molecular phylogenetics and the diversification of hummingbirds. *Curr Biol* 24:910–  
916
- 458 Morrone JJ (2010) Fundamental biogeographic patterns across the Mexican Transition Zone:  
an evolutionary approach. *Ecography* 33:355–361
- 460 Morrone JJ, Escalante T, Rodríguez-Tapia G (2017) Mexican biogeographic provinces: map  
and shapefiles. *Zootaxa* 4277:277
- 462 Navarro SAG, Townsend Peterson A, Gordillo-Martínez A (2002) A Mexican case study on a  
centralised database from world natural history museums. *Data Sci* 1:45–53
- 464 Oksanen J (2017) *Vegan: an introduction to ordination*. Package "vegan"
- Olesen JM, Bascompte J, Dupont YL, Jordano P (2007) The modularity of pollination  
466 networks. *Proc Natl Acad Sci USA* 104:19891–19896
- Ornelas JF, Lara C (2015) Differential response to color task on resident and migratory  
468 hummingbirds: a field test. *Ethol Ecol Evol* 27:257–378
- Ornelas JF, González C, Espinosa de los Monteros A, Rodríguez-Gómez F, García-Feria LM  
470 (2014) In and out of Mesoamerica: temporal divergence of *Amazilia* hummingbirds  
pre-dates the orthodox account of the completion of the Isthmus of Panama. *J*  
472 *Biogeogr* 41:168–181

- Ornelas JF, González de León S, González C, Licona-Vera Y, Ortiz-Rodríguez AE,  
474 Rodríguez-Gómez F (2015) Comparative palaeodistribution of eight hummingbird  
species reveal a link between genetic diversity and Quaternary habitat and climate  
476 stability in Mexico. *Folia Zool* 64:245–258
- Ornelas JF, Sosa V, Soltis DE, Daza JM, González C, Soltis PS, Gutiérrez-Rodríguez C,  
478 Espinosa de los Monteros A, Castoe TA, Bell C, Ruiz-Sanchez E (2013) Comparative  
phylogeographic analyses illustrate the complex evolutionary history of threatened  
480 cloud forests of northern Mesoamerica. *PLoS ONE* 8:e56283
- Poisot T, Stouffer DB, Gravel D (2015) Beyond species: why ecological interactions. *Oikos*  
482 124:243–251
- Rech AR, Dalsgaard B, Sandel B, Sonne J, Svenning JC, Holmes N, Ollerton J (2016) The  
484 macroecology of animal versus wind pollination: ecological factors are more  
important than historical climate stability. *Plant Ecol & Div* 9:253–262
- 486 Ricklefs RE (1987) Community diversity: relative roles of local and regional processes.  
*Science* 235:167–171
- 488 Rodríguez-Gómez F, Gutiérrez-Rodríguez C, Ornelas JF (2013) Genetic, phenotypic and  
ecological divergence with gene flow at the Isthmus of Tehuantepec: the case of the  
490 azure-crowned hummingbird (*Amazilia cyanocephala*). *J Biogeogr* 40:1360–1373
- Rzedowski J (1965) Relaciones geográficas y posibles orígenes de la flora de México. *Bol*  
492 *Soc Bot México* 29:121–177
- Stouffer DB, Bascompte J (2011) Compartmentalization increases food-web persistence. *Proc*  
494 *Natl Acad Sci USA* 108:3648–3652
- Sonne J, Martín González, et al. (2016) High proportion of smaller ranged hummingbird  
496 species coincides with ecological specialization across the Americas. *Proc R Soc B*  
283:20152512

- 498 Stiles FG (1978) Ecological and evolutionary implications of bird pollination. *Am Zool*  
18:715–727
- 500 Stiles FG (1981) Geographical aspects of bird-flower coevolution, with particular reference to  
Central America. *Ann Miss Bot Gard* 68:323–351
- 502 Thuiller W, Münkemüller T, Lavergne S, Mouillot D, Mouquet N, Schifffers K, Gravel D  
(2013) A roadmap for integrating eco-evolutionary processes into biodiversity  
504 models. *Ecol Lett* 16:94–105
- Tylianakis JM, Laliberté E, Nielsen A, Bascompte J (2010) Conservation of species  
506 interaction networks. *Biol Conserv* 143:2270–2279
- Vizentin-Bugoni J, Maruyama PK, Sazima M (2014) Processes entangling interactions in  
508 communities: forbidden links are more important than abundance in a hummingbird–  
plant network. *Proc Royal Soc B: Biol Sci* 281:20132397
- 510 Weinstein BG, Graham CH, Parra JL (2017) The role of environment, dispersal and  
competition in explaining reduced co-occurrence among related species. *PloS One*  
512 12:e0185493

## 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 an asterisk \*), degree of  
 518 endemism from Escalante (1993) and species migratory behavior from Arizmendi and  
 Berlanga (2014).

<b>Hummingbird species</b>	<b>Phylogenetic lineage</b>	<b>Biogeographical distribution</b>	<b>Bill length (mm)</b>	<b>Body mass (g)</b>	<b>Degree of endemism</b>	<b>Migratory behavior</b>
<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>Helimaster constantii</i>	Gem	Neotropical + Transition	34	7.65	Non endemic	Non migrant
<i>Helimaster 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	<b>36</b>	<b>0.040</b>	36	0.719
Body mass	<b>19</b>	<b>0.018</b>	28	0.276
Biogeographical distribution	<b>4.40e<sup>-07</sup></b>	<b>2e<sup>-16</sup></b>	<b>0.135</b>	<b>0.008</b>
Degree of endemism	0.589	0.155	1.000	0.145
Migratory behavior	<b>0.075</b>	<b>2e<sup>-16</sup></b>	<b>0.516</b>	<b>0.010</b>

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.

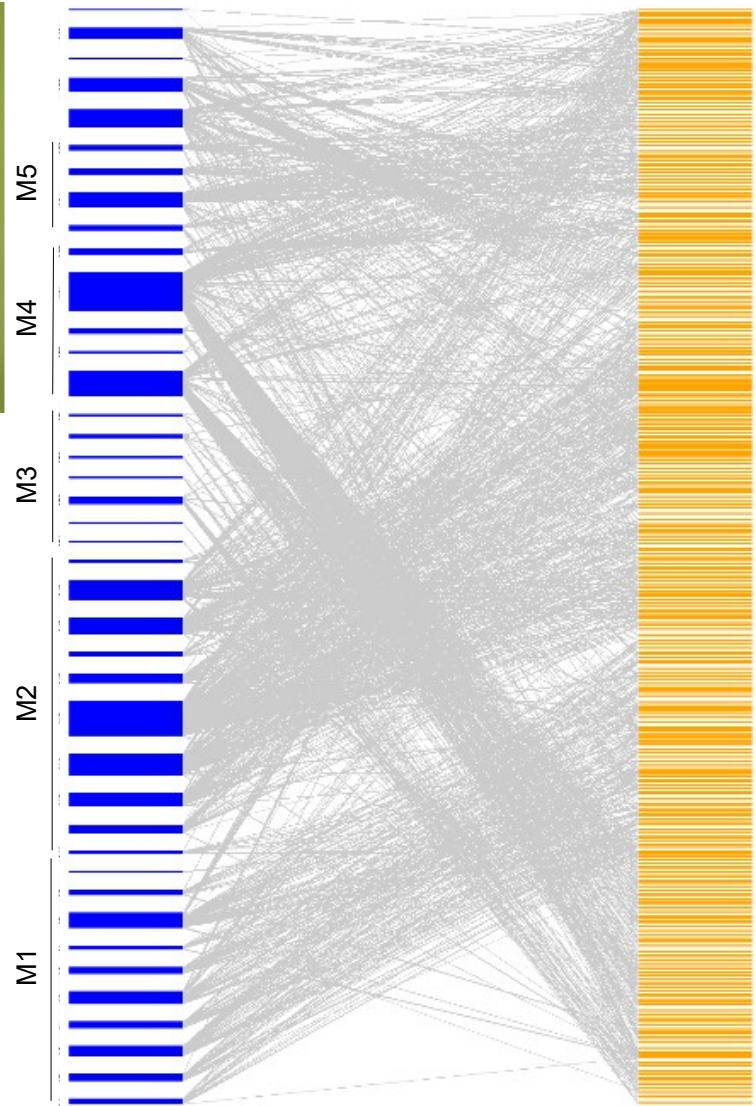
554 **Figure 4.** Plots illustrating the significant correlations between  $z$  and  $c$  values and migratory  
behavior (a,b), biogeographical distribution (c,d), bill length (e) and body mass (f) of  
556 hummingbirds. Pirareplots show raw data as points, the median as a horizontal line  
surrounded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

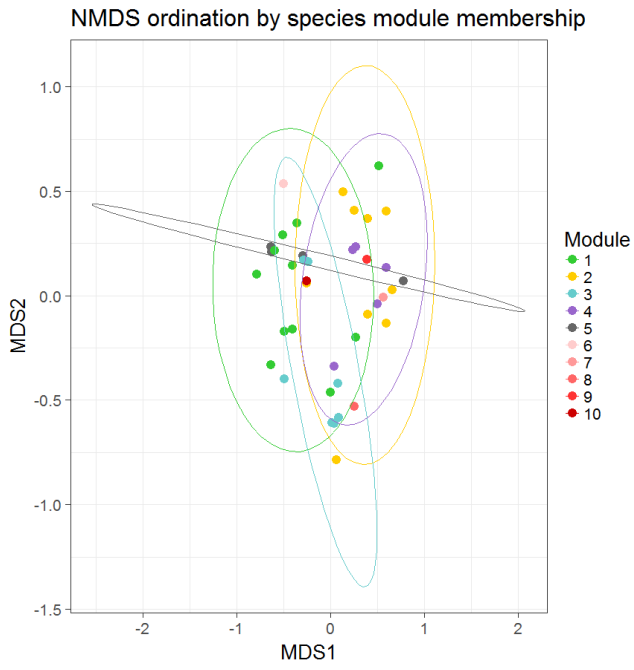


Figure 1

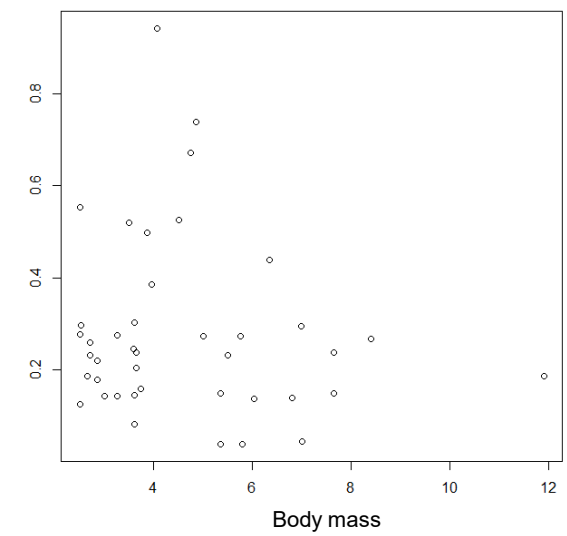
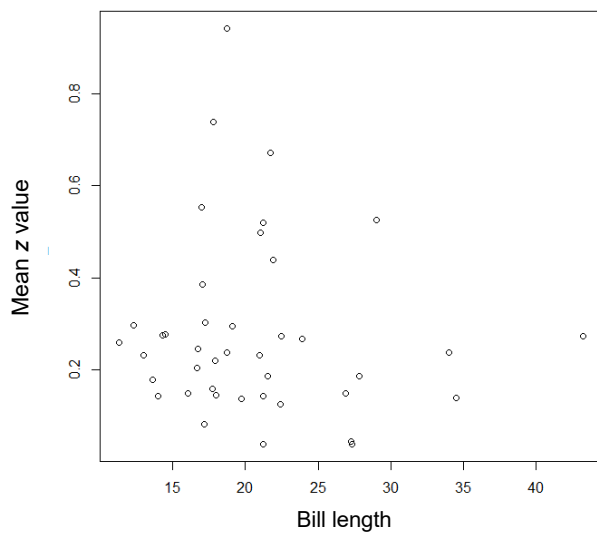
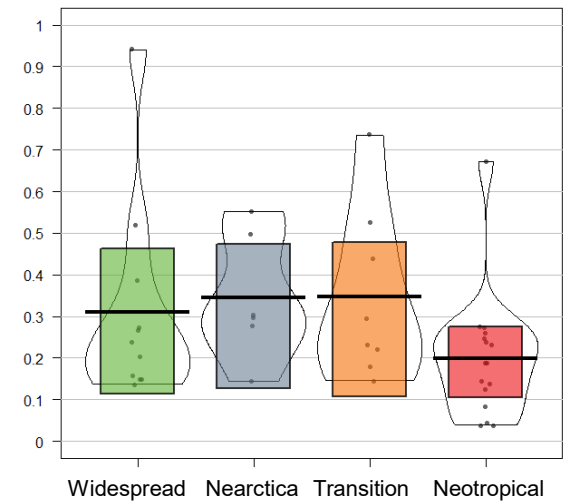
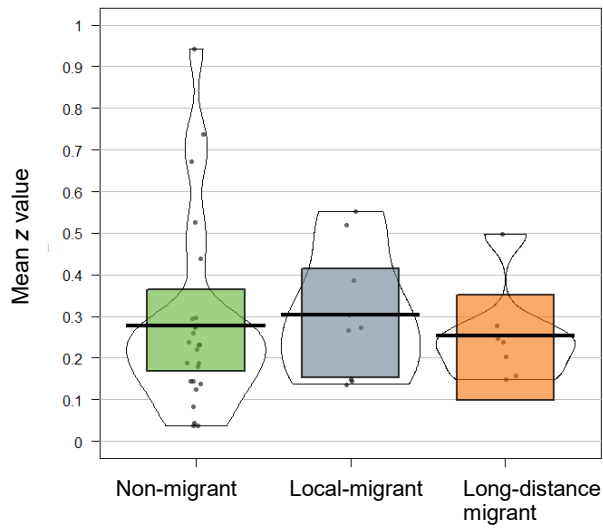
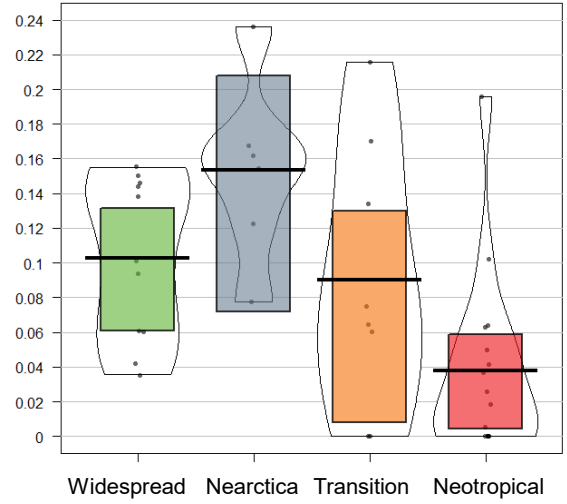
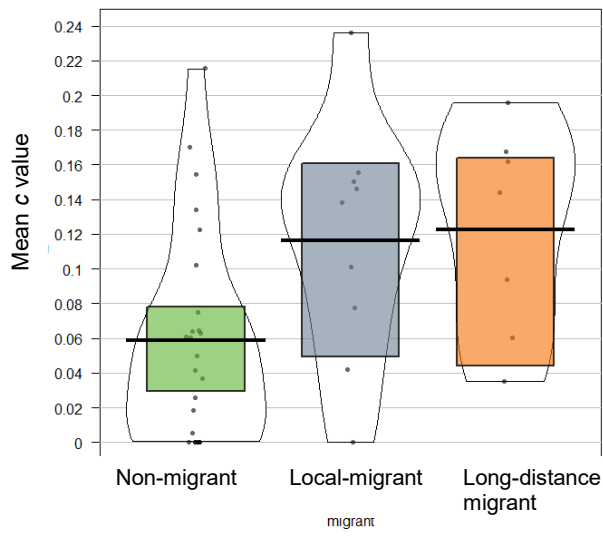
560







	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
1	Rodríguez-Flores CI (2009) Dinámica de las estrategias de forrajeo por néctar en colibríes (Aves: Trochilidae) en la Reserva de la Biosfera Sierra de Manantlán. (Jalisco, México). MSc Thesis, Universidad Nacional Autónoma de México.
2	Ortiz-Pulido R, Díaz R (2001) Distribución de colibríes en la zona baja del centro de Veracruz, México. <i>Ornitol Neotrop</i> 12: 297–317
3	Arizmendi MC (1987) Interacción entre los colibríes y su recurso vegetal en Chamela, Jalisco. BSc Thesis, Universidad Nacional Autónoma de México.
4	Arizmendi MC (1994) Interacciones ecológicas múltiples: el caso del sistema mutualista colibríes-plantas y el ladrón de néctar <i>Diglossa baritula</i> (Passeriformes: Aves). PhD Thesis, Universidad Nacional Autónoma de México.
5	Des Granges JL (1978) Organization of a tropical nectar feeding bird guild in a variable environment. <i>Living Bird</i> 17: 199–236.
6	Lara RP, Enríquez PL, Rangel-Salazar JL, Lara C, Ico, MM (2012) Abundancia de colibríes y uso de flores en un bosque templado del sureste de México. <i>Rev Biol Trop</i> 60: 1621–1630
7	Arizmendi, M. C. Unpublished data.
8	Lyon DL (1976) A montane hummingbird territorial system in Oaxaca, Mexico. <i>Wilson Bull</i> 88: 280–299
9	Arriaga L, Rodríguez-Estrella R, Ortega-Rubio A (1990) Endemic hummingbirds and Madrones of Baja: Are they mutually dependent? <i>Southwest Nat</i> 35: 76–79.
10	Reyna Bustos O (2008) Utilización de los recursos florales por colibríes en el bosque tropical caducifolio de la barranca de Colimilla, Jalisco, México. MSc Thesis, Universidad de Guadalajara.
11	De la Cruz F (2011) Estudio preliminar de la avifauna nectarívora del Jardín Botánico de la Cd. De Oaxaca de Juárez, Oaxaca. BSc Thesis, Universidad Tecnológica del Valle de Oaxaca.
12	Jiménez-Sierra L, Reyes S (2003) Las Cactáceas de la Barranca de Metztitlán. In M.A. Armella, M.L. Yáñez y E. Sandoval (Eds.): <i>Metztitlán: Lugar de la Luna y de las Maravillas</i> . Universidad Autónoma Metropolitana. México. 53–77 p.
13	Toledo VM (1975) La estacionalidad de las flores utilizadas por los colibríes de una selva tropical húmeda en México. <i>Biotropica</i> 7: 63–70.
14 - 17	Van Devender TR, Calder WA, Krehbs K, Reina-G AL, Russell SM, Russell RO, Nabhan GP (2004) Hummingbird plants and potential nectar corridors for the rufous hummingbird in Sonora, Mexico. <i>Conserving migratory pollinators and nectar corridors in western North America</i> . Univ. Arizona Press and Arizona-Sonora Desert Museum, Tucson, pp.96–121
18 - 20	Martínez-García V (2006) Interacciones colibrí-planta en tres tipos de vegetación de la Reserva de la Biosfera Barranca de Metztitlán, Hidalgo, México. BSc Thesis, Universidad Autónoma del Estado de Hidalgo, Pachuca. 58 p.
21 - 23	Díaz-Valenzuela R (2008) Análisis descriptivo del sistema colibrí-planta en tres niveles de las escalas espacial, temporal y en la jerarquía ecológica en un paisaje mexicano. PhD Thesis. Centro Iberoamericano de la Biodiversidad, Alicante. 60 p.
24	Montgomerie RD, Gass CL (1981) Energy limitation of hummingbird populations in tropical and temperate communities. <i>Oecologia</i> , 50(2): 162–165
25	Lara C (2006) Temporal dynamics of flower use by hummingbirds in a highland temperate forest in México. <i>Ecoscience</i> 13: 23–29.
26	Lara, C. Unpublished data
27	Lara, C. Unpublished data
28, 30	Díaz-Fisher A (2002) Determinación de la abundancia y distribución de los colibríes en la Reserva de la Biosfêra Tehuacán-Cuicatlán durante el periodo primavera-verano. BSc Thesis, Universidad de las Américas-Puebla. 42 p.
29	Arizmendi MC, Espinosa de los Monteros A (1996) Avifauna de los bosques de cactáceas columnares del valle de Tehuacán-Cuicatlán. <i>Acta Zoológica Mexicana (nueva serie)</i> 67:25–46
31, 32	Puch-Chávez R (2012) Flora visitada por colibríes en selvas maduras y sitios

- deforestados en Calakmul, Campeche. BSc Thesis, Universidad Autónoma de Campeche. México
- 33 López-Segoviano G (2012) Comportamiento territorial y preferencias de forrajeo del colibrí migratorio *Selasphorus rufus* dentro de un sitio invernal. MSc Thesis, Universidad Nacional Autónoma de México. 50 p.
- 34 Medina-van Berkum P, Parra-Tabla VP, Leirana-Alcocer JL (2016) Recursos florales y colibríes durante la época seca en la Reserva de la Biosfera Ría Lagartos, Yucatán, México. *Huitzil*, 17: 244–250
- 35 Vidal-Hernández, W. J. Unpublished data
- 36 Martínez-Roldan, H. Unpublished data
- 37 Bautista-Salazar, L. Unpublished data
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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

Müllner D (2017) Fast hierarchical clustering routines for R and Python. Package  
658 "fastcluster"  
Zhao S, Guo Y, Sheng Q, Shyr Y (2016) An improved heatmap package. Package  
660 "heatmap3"

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).

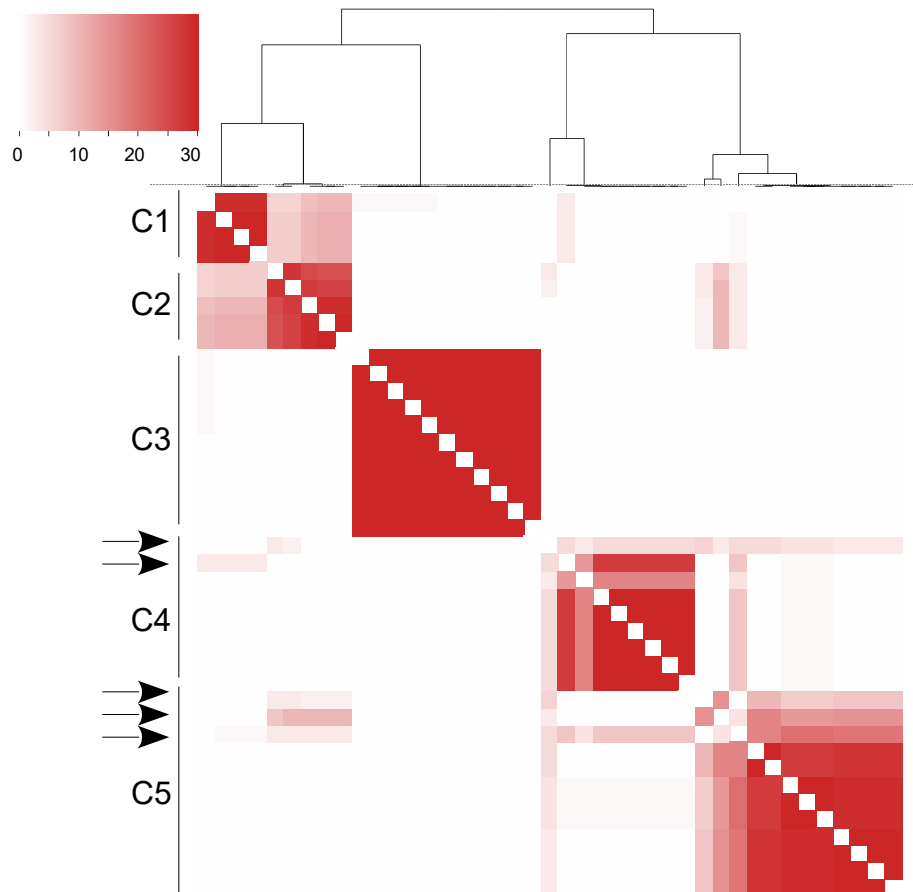
Run ID	Number of resulting modules	Modularity value	NM2 p-value
1	7	0.471	0
2	6	0.467	0
3	5	0.466	0
4	7	0.464	0
5	8	0.464	0
6	6	0.473	0
7	5	0.462	0
8	7	0.471	0
9	7	0.464	0
10	8	0.464	0
11	6	0.463	0
12	6	0.464	0
13	8	0.464	0
14	8	0.464	0
15	6	0.465	0
16	5	0.473	0
17	6	0.461	0
18	8	0.471	0
19	5	0.467	0
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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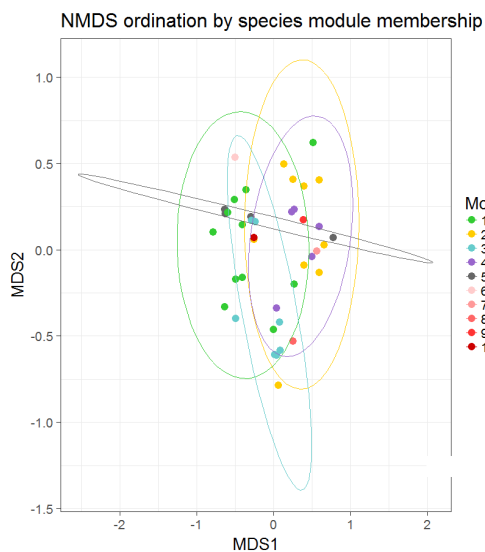
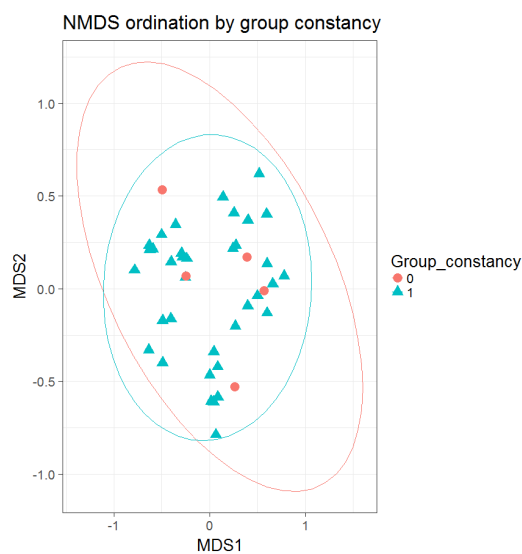
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Figure S4.1. Heatmap illustrating the frequency each pair of hummingbird species was placed  
674 in the same module in each modularity run. The modularity algorithm was run 30 times.  
Clustering analysis was performed with a fast hierarchical and 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).

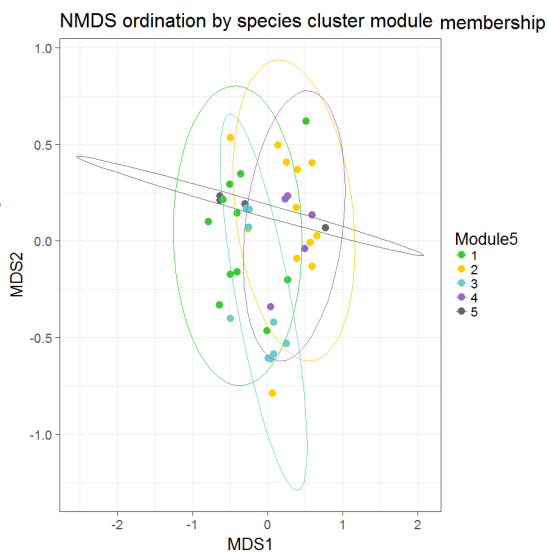


682 Figure S4.2. Results of the non-metric multidimensional scaling ordination of five  
 hummingbird species traits (bill length, body mass, biogeographical distribution, degree of  
 684 endemism and migratory behavior). The illustration shows (a) how hummingbirds without  
 fixed module-partners do 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



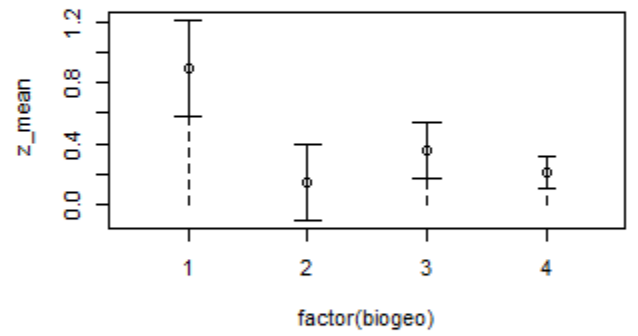
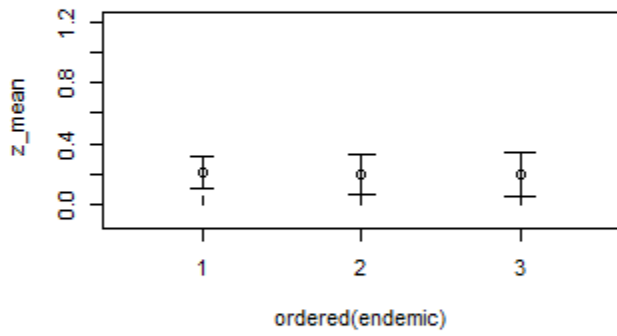
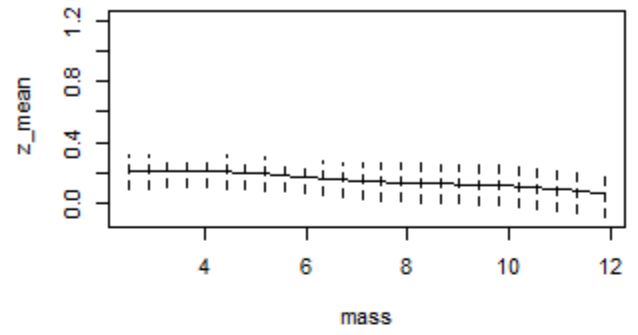
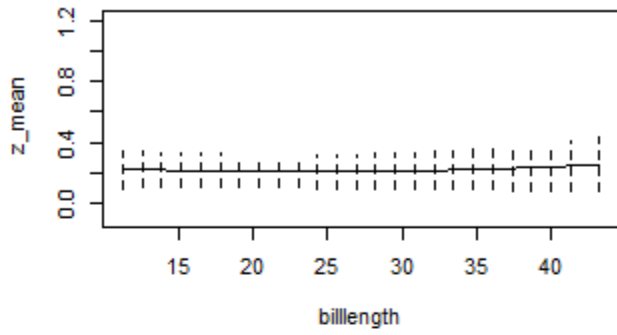
Goodness of fit = 0.426, p-value = 0.001

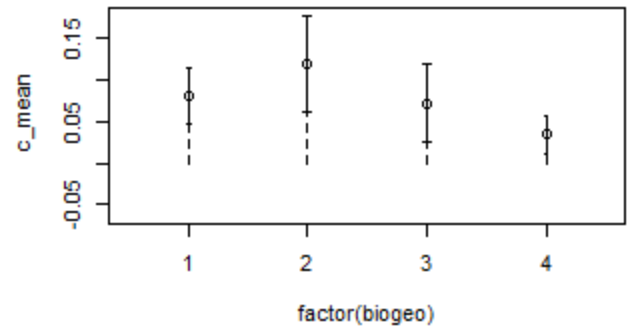
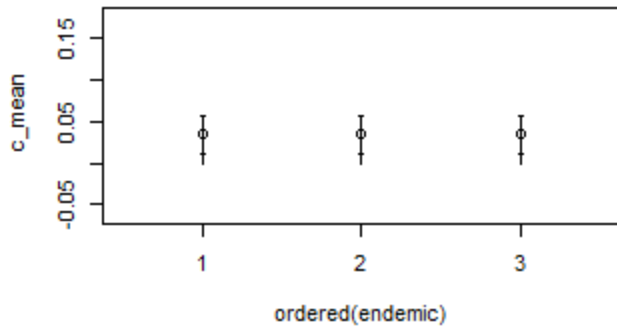
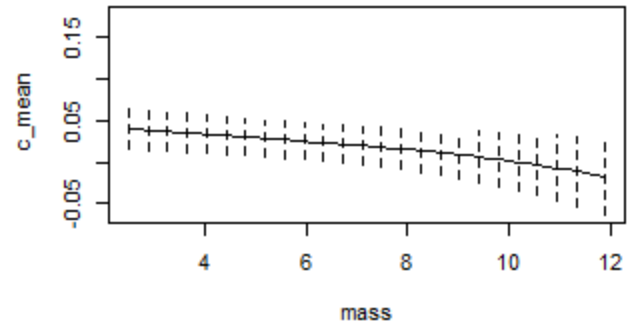
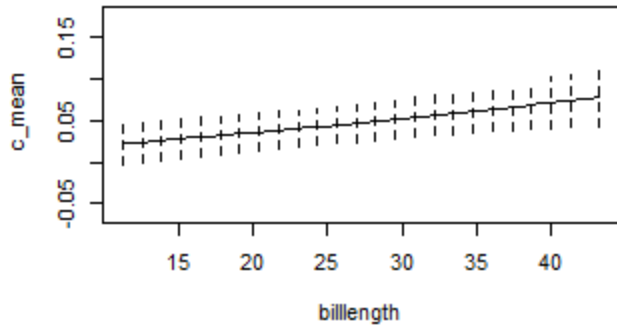


Goodness of fit = 0.345, p-value = 0.001

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

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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).

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