

2015-11

The macroecology of phylogenetically structured hummingbird-plant networks

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<http://hdl.handle.net/10026.1/4865>

10.1111/geb.12355

Global Ecology & Biogeography

Wiley

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Article title: The macroecology of phylogenetically structured hummingbird-plant networks

Running title: Macroecology of hummingbird-plant networks

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112 **Type of article:** Research paper

Number of words in abstract: 274

114 **Number of words in main text:** 5263

Number of references: 53

116 **Number of tables in main text:** 1

Number of figures in main text: 3

118 **Number of supplementary appendices:** 5

Number of supplementary tables: 3

120 **Number of supplementary figures:** 1

Keywords: community ecology, current climate, historical climate, hummingbird

122 biogeography, specialization, macroecology, modularity, phylogenetic signal, pollination,
quantitative networks.

124 **ABSTRACT**

126 **Aim** To investigate the association between species richness, species' phylogenetic signal, insularity, and historical and current climate with hummingbird-plant network structure.

128 **Location** 54 communities along a c. 10,000 kilometer latitudinal gradient across the Americas (39°N - 32°S), ranging from sea level to c. 3700 m asl, located on the mainland and on islands, and covering a wide range of climate regimes.

130 **Methods** We measured the level of specialization and modularity in mutualistic plant-hummingbird interaction networks. Using an ordinary least squares multi-model approach, we examined the influence of species richness, phylogenetic signal, insularity, and current and historical climate conditions on network structure (null-model corrected specialization and modularity).

136 **Results** Phylogenetically-related species, especially plants, showed a tendency to interact with a similar array of partners. The spatial variation in network structure exhibited a constant association with species' phylogeny ($R^2=0.18-0.19$); however, network structure showed the strongest association to species richness and environmental factors ($R^2=0.20-0.44$; $R^2=0.32-0.45$, respectively). Specifically, higher levels of specialization and modularity were associated with species-rich communities and communities in which closely-related hummingbirds visited distinct sets of flowering species. On the mainland, specialization also associated to higher levels of warmer temperatures and higher historical temperature stability.

144 **Main conclusions** Our results confirm previous macroecological studies of interaction networks which have highlighted the importance of species richness and the environment in determining network structure. Additionally, for the first time, we report an association between [network structure and species phylogenetic signal](#) at macroecological scale, indicating that high specialization and modularity are associated with high inter-specific

competition among closely-related hummingbirds, sub-dividing the floral niche. This suggests
150 a tighter co-evolutionary association between hummingbirds and their plants than previously
studied plant-animal mutualistic systems.

152 INTRODUCTION

153 An urgent challenge facing contemporary ecologists is to understand how ecological,
154 evolutionary and environmental mechanisms affect the structure and function of ecological
communities. Better understanding of how these processes form and maintain communities
156 should help us to construct more robust theories and accurate models of community
dynamics to predict how species and communities may respond to disturbance (Vázquez *et*
158 *al.*, 2009a; Woodward *et al.*, 2010). For this purpose, the use of network approaches to study
complex communities of interacting species, i.e. networks representing species as nodes and
160 interactions as links between species, has significantly advanced our understanding of
ecological systems (Woodward *et al.*, 2010).

162 For instance, research on mutualistic networks such as plant-pollinator or plant-
frugivore interactions, has revealed that these communities typically exhibit a number of
164 architectural attributes, such as complementary specialization and modularity, which differ
significantly from random interactions among species (Olesen *et al.*, 2007; Blüthgen 2010;
166 Dalsgaard *et al.*, 2011, 2013; Schleuning *et al.*, 2012, 2014; Trøjelsgaard & Olesen, 2013;
Dormann & Strauss, 2014; Sebastián González *et al.*, 2015). Complementary specialization
168 measures the exclusiveness in species' interactions. Specifically, it is a measure of the
deviation from a neutral scenario in which species interact solely according to their
170 availability, measuring species' availability either as its abundance or its interaction frequency
(Blüthgen *et al.*, 2006). Modularity quantifies whether species interact more frequently with
172 subsets of available species within a community, forming modules of densely interacting
species, with loose connections between modules (Olesen *et al.*, 2007). Such modules have
174 been suggested to reflect co-evolutionary units (Olesen *et al.*, 2007), within-network
functional specialization (Maruyama *et al.*, 2014), and phenological units of species in
176 environments with strong climatic seasonalities (Martín González *et al.*, 2012; Schleuning *et*

al., 2014).

178 These architectural attributes have a profound impact on the dynamics of ecological
communities. For example, higher levels of complementary specialization have been linked
180 to higher dependencies between species and, hence, to a higher risk of secondary
extinctions (Blüthgen, 2010); whereas high levels of modularity may at first provide higher
182 network resilience to perturbations, as these are not typically spread across modules, but
ultimately may result into unconnected modules, community fragmentation and rapid species
184 loss (Thébaud & Fontaine, 2010; Stouffer & Bascompte, 2011). Complementary
specialization and modularity are typically related, as some degree of modularity necessarily
186 implies a certain level of complementary specialization on a subset of species from the
available species pool (Dormann & Strauss, 2014). Nevertheless, these metrics measure
188 different aspects of interaction specialization and, hence, may show disparate dynamics and
associations with different ecological, evolutionary and environmental factors.

190 Thus, **comparative** studies at macroecological scales, where differences in network
structure can be associated to varying ecological, evolutionary and environmental factors,
192 may provide valuable insights into the structure and dynamics of ecological networks
(Dalsgaard *et al.*, 2011, 2013; Schleuning *et al.*, 2012, 2014; Trøjelsgaard & Olesen, 2013,
194 Sebastián González *et al.*, 2015). For instance, species richness may promote higher
degrees of complementary specialization and modularity by increasing interspecific
196 competition and providing more species to interact with, i.e. allowing a finer niche partitioning
(e.g. Dalsgaard *et al.*, 2011; Junker *et al.*, 2013). Additionally, evolution may structure biotic
198 interactions via niche conservatism, as closely-related species may display more similar
phenotypes, spatial distributions, and ecological interactions than distantly-related species
200 (Webb *et al.*, 2002; Ives & Godfray, 2006; Rezende *et al.*, 2007; Vázquez *et al.*, 2009a).
Alternatively, closely-related species experiencing strong interspecific competition may

202 undergo niche partitioning, competitive exclusion, or resource-use complementarity (Webb *et*
204 *al.*, 2002; Rezende *et al.*, 2009; Krasnov *et al.*, 2012). Environmental setting may also affect
206 biotic interactions. Historical climatic stability may promote specialization and modularity by
208 providing species more opportunity to co-evolve over longer periods of time compared to
210 species from climatically more unstable areas. **Notably**, large late Quaternary glacial-
212 interglacial climate change is coupled with a decreased modularity in pollination networks
(Dalsgaard *et al.*, 2013), and decreased specialization in hummingbird-plant networks
(Dalsgaard *et al.*, 2011). Likewise, current environmental conditions may influence the identity
214 and strength of species interactions by altering species' spatial distribution, phenophases and
foraging capability (Cruden, 1972; Martín González *et al.*, 2009; Dalsgaard *et al.*, 2011, 2013;
216 Schleuning *et al.*, 2012, 2014). For example, bird pollination has been reported to become
increasingly important and specialized in areas of current high precipitation and low
218 temperatures, possibly because insect pollinator diversity and activity is lower in cold and wet
environments due to thermoregulatory and nesting constraints (Cruden, 1972; Dalsgaard *et*
al., 2009, 2011; Martín González *et al.*, 2009). Finally, insularity may influence pollination
network structure, as insular communities typically show significantly lower levels of
specialization and modularity compared to the mainland (Olesen *et al.*, 2002; Dalsgaard *et*
al., 2013).

220 Despite the recently increasing interest in determining the influence of species
richness, phylogenetic signal and past and current environmental conditions on network
222 structure (Dalsgaard *et al.*, 2011, 2013; Schleuning *et al.*, 2012, 2014; Sebastián González *et*
al., 2015), very little is known about the relative importance of these factors. Only Schleuning
224 *et al.* (2014) studied their combined influence on the modular patterns of mutualistic
networks. Specifically, they used a dataset of 18 frugivore bird-plant networks, reporting a
226 high modularity in areas having low temperatures and high temperature seasonality, whereas

modularity exhibited no detectable association to species' phylogenetic history and historical
228 climate. Here, we likewise examine how [the structure of hummingbird-plant networks,](#)
[another type of mutualistic assemblage, associates to species richness, phylogenetic signal](#)
230 [and environmental conditions](#). To do so, we compiled a dataset consisting of 54 high-
resolution quantitative hummingbird-plant interaction networks, and combined them with
232 complementary data on species richness, state-of-the-art species phylogenies and
simulations of paleo and current climate. In accordance with previous studies on pollination
234 networks, we show that [complementary specialization and modularity are influenced by](#)
[species richness and climatic conditions](#). Additionally, for the first time, we report an
236 association between [network structure and species phylogenetic signal](#) at macroecological
scale. Specifically, communities where closely-related hummingbirds interact with distinct
238 sets of plant species exhibited higher levels of complementary specialization and modularity.

240 **MATERIAL & METHODS**

Hummingbird-plant interaction networks

242 We compiled a large dataset of 54 high-resolution and geographically widely distributed
hummingbird-plant interaction networks from published and unpublished sources (Fig. 1; see
244 Table S1 for full references, and Dalsgaard *et al.*, 2011 for a previous version of this dataset).
This dataset does not include networks which have not sampled the entire floral community,
246 i.e. we discarded studies which had focused only on ornithophilous species or on specific
floral or hummingbird groups. We also discarded illegitimate interactions, i.e. our database
248 focuses exclusively on interactions with potential for pollination. These networks describe the
interaction frequency between plants and hummingbirds, recorded as number of observed
250 visits. In total, our dataset is composed of 141 species of hummingbirds belonging to all
major hummingbird lineages (about 42% of all described species; McGuire *et al.*, 2014) and

252 824 plant species belonging to 79 different plant families (Appendix S1).

Mutualistic hummingbird-plant interaction networks constitute a particularly suitable
254 model system to explore large-scale patterns in network structure as there is ample
knowledge of the historical biogeography of hummingbirds, these assemblages are widely
256 distributed in a variety of ecosystems across the Americas, and they offer examples covering
the entire interaction specialization-generalization spectrum (Bleiweiss, 1998; Dalsgaard *et*
258 *al.*, 2011). Furthermore, our data consists of a single and monophyletic pollinator group
(Brown & Bowers, 1985; McGuire *et al.*, 2014), allowing us to explore the association
260 between phylogeny on overall network structure more precisely.

Finally, the spatial distribution of these networks extend from sea level to c. 3700 m
262 a.s.l. and spans a c. 10,000 kilometer gradient from 39°N to 32°S, from tropical and
subtropical ecosystems in South America to temperate communities in North America. The
264 spatial distribution includes both mainland and insular communities and consists of
communities from various environmental settings (Fig. 1).

266

Network composition and network metrics

268 Network interactions were quantified in terms of the number of interaction events between
hummingbird and plant species at particular locations. For each network we calculated two
270 complementary metrics that describe the degree of specialization or specificity of
hummingbird-plant interactions: complementary specialization (Blüthgen *et al.*, 2006) and
272 quantitative bipartite modularity (Dormann & Strauss, 2014). These metrics were correlated in
our dataset $R^2=0.78$ (Table S2) but were chosen to more fully characterize how evolutionary
274 and environmental factors associate to specialized network structures. For the calculations
we used the R package *bipartite 1.20* (Dormann *et al.*, 2009).

276 (1) *Complementary specialization (H_2')* describes how species restrict their interactions

relative to random expectations based on species' abundances/interaction frequency.

278 Complementary specialization is calculated as $H_2 = - \sum_{i=1}^r \sum_{j=1}^c (p_{ij} \ln p_{ij})$, where p_{ij} reflects the
proportional number of interactions of each species relative to their availability, i.e., for their
280 respective marginal total (in our case total interaction frequency) for r plant and c animal
species. We illustrate this in Figure 1; for instance, from the example community A from Fig.
282 1, $p_{1A}=0.99$ (which results from an interaction frequency of 155 between plant 1 and
hummingbird A, over a marginal total of $155+1=156$ for plant 1) and $p_{A1}=1$ (155 over 155).
284 Hence the interaction A-1 exhibits a high complementary specialization, as hummingbird A
visits exclusively plant 1 and at a high frequency, while plant 1 is only visited, and at a very
286 low frequency, by another hummingbird species. If a community is composed majoritarily by
interactions with such high complementarity, the community will exhibit high values of
288 complementary specialization (Blüthgen *et al.*, 2006). On the other hand, species C and 4
also interact 155 times, but in this case hummingbird C interacts with many other plant
290 species and has a higher marginal total, lowering the complementary specialization of this
pair ($p_{C4}=0.36$, $p_{4C}=1$).

292 We standardized complementary specialization as $H_2' = \frac{H_{2\max} - H_2}{H_{2\max} - H_{2\min}}$, so that H_2'
ranges from minimum ($H_2'=0$) to maximum ($H_2'=1$) link selectiveness, where species establish
294 distinct and highly specific interactions far different than expected interactions (Blüthgen *et*
al., 2006). Thus, H_2' quantifies the deviation of the observed interactions from those expected
296 under a neutral assumption that species' interactions are entirely determined by partner
availability. This assumption minimizes the influence of rare interactions by causing frequent
298 interactions to dominate H_2' .

(2) *Quantitative bipartite modularity* (QuanBiMo) is an algorithm which places species

300 among an *a priori* unespecified number of modules, such that species interact at high
frequencies within their module, and show few links and/or low frequency links with species
302 outside their module (Dormann & Strauss, 2014; Schleuning *et al.*, 2014; Fig. 1). Such
partition is based on a hierarchical representation of interaction frequencies and optimal
304 allocation of species into modules. Specifically, the algorithm maximizes the bipartite version

of Newman's modularity (Q), so that
$$Q = \frac{1}{2N} \sum (A_{ij} - K_{ij}) \delta(m_i, m_j)$$
, where N reflects the total
306 number of interactions, A_{ij} the normalized number of interactions between species i and j , K_{ij}
the expected interaction probability between species i and j drawn from a neutral model of
308 interactions, and the indicator function $\delta(m_i, m_j)$ equals 1 when species i and j are placed in
the same module and 0 otherwise. Modularity ranges from no (Q=0) to maximum (Q=1)
310 modularity. We ran the QuanBiMo algorithm following the methodology established by
Schleuning *et al.* (2014) and the default specifications of the *computeModules* function in
312 bipartite, that is, for each network we chose the partition showing highest modularity from five
independent runs of the algorithm (Dormann & Strauss, 2014; Schleuning *et al.*, 2014).
314 Variations in the likelihood values of modularity were negligible (all SD<0.05).

As raw values for network metrics may be affected by species frequencies and
316 network connectance, network estimates for complementary specialization and modularity
were corrected using null models (Schleuning *et al.*, 2012, 2014; Dormann & Strauss, 2014).
318 Null models simulated matrices with the same number of species and interactions as the
empirical network, with a species' interaction probability distribution drawn from observed
320 species' connectivity (vaznull model in bipartite; Vázquez *et al.*, 2007 – except for network #3
for which we used the r2dtable null model in *bipartite* due to the impossibility of calculating
322 vaznull). Corrected metrics were then calculated as the difference between the value of the
empirical network and the mean value obtained from 1000 and 100 null models for H_2' and

324 QuanBiMo, respectively (as in Schleuning *et al.*, 2012, 2014). As for the calculation of
empirical QuanBiMo values, for each of the 100 null matrices we used the maximum value of
326 five independent runs of the QuanBiMo algorithm (Schleuning *et al.*, 2014). By extracting the
network structure achieved under null conditions, corrected metrics quantify how much an
328 empirical community departs from an average random one with an equivalent set of species,
number of interactions and interaction probability distribution. Notice that for instance, as
330 Figure 1 illustrates, a corrected value of 0.3 gives no information on the uncorrected values,
only that there is a 0.3 difference between observed and null values, e.g. this value can result
332 both from a raw observed value of 0.4 and a mean null value of 0.1 (Fig. 1 community A), or
from a raw observed value of 0.5 and a mean null value of 0.2 (Fig. 1 community B), etc.

334

Analysis of phylogenetic signal in bipartite interaction networks

336 We measured the phylogenetic signal exhibited by hummingbird-plant networks by
quantifying the degree to which closely-related species share more interaction partners than
338 distantly-related species (Ives & Godfray, 2006). Species' interactions are considered to
exhibit a higher phylogenetic signal, when closely-related species share relatively more
340 interaction partners than distantly-related species (Ives & Godfray, 2006; Vázquez *et al.*,
2009b).

342 We used state-of-the-art phylogenies of plants and hummingbirds to create variance-
covariance matrices, which quantify the phylogenetic relatedness of plants or hummingbirds
344 in each community, using the “vcv” function from the R package *ape* (Paradis *et al.*, 2004).
We fitted these vcv matrices to each observed bipartite interaction matrix through a linear
346 model using the “pblm” function from the R package *picante* (Kembel *et al.*, 2010). This
analysis results in two independent measures of the strength of the phylogenetic signal, one
348 for plants (d_{plants}) and another for hummingbirds ($d_{\text{hummingbirds}}$), together with an overall measure

of strength of the model fits for the entire community (measured as mean squared error of the
350 model, MSE). We evaluated three different models, one assuming no phylogenetic signal
($d_{\text{plants}}=d_{\text{hummingbirds}}=0$; Star model), one assuming a maximum phylogenetic signal
352 ($d_{\text{plants}}=d_{\text{hummingbirds}}=1$; Brownian model), and a final one which incorporated the observed
phylogenetic signals combined (estimated d_{plants} and $d_{\text{hummingbirds}}$; Data model). We used the
354 bootstrapping option to calculate confidence intervals for d_{plants} and $d_{\text{hummingbirds}}$. Networks
where these confidence intervals did not overlap zero or when the $\text{MSE}_{\text{Data}} < \text{MSE}_{\text{Star}}$ were
356 considered to exhibit a significant phylogenetic signal (Ives & Godfray, 2006; Vázquez *et al.*,
2009b). For a list of all species included in this study and a detailed explanation of the
358 phylogenetic analysis, refer to Appendices S1 and S2, respectively.

360 *Environmental variables*

We analyzed six variables describing contemporary and historical temperature and
362 precipitation known or hypothesized to affect the structure of pollination networks. Four of the
six variables describe contemporary climatic conditions: *mean annual temperature* (MAT, °C),
364 *temperature seasonality* (TS, standard deviation \times 100), *mean annual precipitation* (MAP,
mm) and *precipitation seasonality* (PS, coefficient of variation). We obtained these
366 measurements from the WorldClim dataset with spatial resolutions of 1 \times 1 km
(<http://www.worldclim.org>; see also Hijmans *et al.*, 2005). The historical climate variables, the
368 *velocity of temperature change* and the *velocity of precipitation change*, reflect the speed of
temperature and precipitation change between the Last Glacial Maximum (LGM) and pre-
370 industrial times (VT, m/yr; VP, m/yr), following the definition of Loarie *et al.* (2009). Projections
of the global climate during the LGM and pre-industry were generated by Hadley Centre
372 Coupled Model Version 3 (HadCM3) with a resolution of 3.75 \times 2.5 arc degrees (Singarayer
& Valdes, 2010), and were downscaled to 0.1 \times 0.1 arc degrees. For each study site, climate

374 estimates were calculated as the average values of all 1 x 1 km grid cells (0.1 × 0.1 arc
degrees for paleoclimate data) within a concentric distance of 10 km from the sampling
376 location. Additionally, we scored whether a network was located on the mainland (0) or on an
island (1).

378

Macroecological models

380 We used a multi-model approach based on information theory as outlined in Diniz-Filho *et al.*
(2008) to simultaneously evaluate the relationships of species richness, phylogenetic signal
382 and environment with hummingbird-plant network structure. First, for each network metric, we
calculated full ordinary least squares (OLS) regression models which included the following
384 ten predictor variables: 1) species richness (network size), 2) the phylogenetic signal in the
interaction pattern of plants' (d_{plants}) and 3) hummingbirds' ($d_{\text{hummingbirds}}$), 4) annual average
386 temperature, 5) temperature seasonality, 6) annual average precipitation, 7) precipitation
seasonality, 8) temperature-change velocity, 9) precipitation-change velocity and 10)
388 insularity. Second, for each network metric, we used the Akaike Information Criterion (AIC_C)
aiming at identifying minimum adequate models (MAMs) among all possible model
390 combinations of our ten predictor variables. MAMs were defined as models exhibiting a
difference in AIC_C of at least two points lower than other models (i.e. a $\Delta AIC_C < 2$; Burnham &
392 Anderson, 2002; Diniz-Filho *et al.*, 2008). As no single MAM was identified, often around 10
models had $\Delta AIC_C < 2$, we instead used a multi-model approach. Specifically, instead of
394 calculating regression coefficients in a single best model (MAM), we calculated the overall
importance of each model (w_i) as the relative likelihood of any given model i over the sum of

$$w_i = \frac{\exp\left(\frac{-1}{2} \Delta_i\right)}{\sum_{r=1}^R \exp\left(\frac{-1}{2} \Delta_r\right)}$$

396 the likelihoods of the entire dataset of models, such that
 398 differences in AIC between the set of R models, so that the relative strength of each model
 depends on the entire set of models. We report the standardized regression coefficients and
 the overall importance ($\sum w_i$) of each variable for an averaged OLS model based on weighted
 400 w_i (Burnham & Anderson, 2002; Diniz-Filho *et al.*, 2008), for which we adopted an importance
 cut-off value of ≥ 0.750 . The standardized regression coefficients were also reported for the
 402 OLS regression model including all ten predictor variables (“full” model). For each network
 metric, we used partial regressions to separate the total, unique and shared variation
 404 explained by species richness, phylogenetic signal and environmental factors in the “full”
 models.

406 The structure of mainland and island hummingbird-plant and pollination networks may
 differ, as previous studies predict higher levels of generalization and less modularity for
 408 insular pollinator communities (Olesen *et al.*, 2002; Dalsgaard *et al.*, 2009, 2013). The
 colonization of the Caribbean by hummingbirds has been considerably more recent than
 410 mainland America (c. 5 million years ago versus 12-22 million years ago for North and South
 America, respectively), and consequently insular hummingbirds have had less time for
 412 specialization and coevolution with their nectar plants than their mainland counterparts
 (Bleiweiss, 1998; McGuire *et al.*, 2014). Moreover, Caribbean communities undergo a high
 414 level of periodic disturbances, which may hinder high levels of specialization on islands
 (Graves & Olsen, 1987; Rivera-Marchand & Ackerman, 2006). Hence, the relationship
 416 between species richness, phylogenetic signal and environmental factors and network
 structure may differ between mainland and insular communities. For instance, the influence
 418 of historical climate change may be weaker on islands than on the mainland (Dalsgaard *et*

420 *al.*, 2013, 2014). As our dataset contains too few island networks (n=9) to allow for a separate
analysis for insular networks, we explored putative differences in mainland and island
networks by analyzing a subset of the dataset composed exclusively by networks from the
422 mainland (Mainland, n=45 networks) and compared these results to those of the entire
dataset (Global dataset, which includes both mainland and insular communities, n=54
424 networks).

For all macroecological models, we log₁₀-transformed species richness, temperature
426 seasonality, temperature velocity, and precipitation velocity, we squared temperature, and
square-root transformed precipitation. All other variables were left untransformed. In all
428 spatial models we tested whether significant positive spatial autocorrelation remained in
model residuals of the “full” models (i.e., whether $p < 0.05$ in all distance classes, tested using
430 10 equally-spaced distance classes and applying a permutation test with 10,000 iterations).
As no positive spatial autocorrelation was observed we did not build more sophisticated
432 spatial models. All regression analyses were conducted using the software Spatial Analysis in
Macroecology, SAM 4.0 (Rangel *et al.*, 2010).

434 To better support our findings, we performed a number of complementary
macroecological models which included sampling effort as a predictor variable (Appendix
436 S3), observed (uncorrected) metrics of network structure instead of null model corrected
metrics (Appendix S4), and climate anomaly as a measure of historical climate stability
438 instead of climate change velocity (Appendix S5).

440 **RESULTS**

Phylogenetic signal on species interaction patterns

442 Values for the independent phylogenetic signals of plants (d_{plants}) and hummingbirds
($d_{\text{hummingbirds}}$) were low but above zero in 85 and 65% of the networks, respectively, suggesting

444 a significant relationship between phylogenetic signal and species interaction patterns. The
confidence intervals (CI) of $d_{\text{hummingbirds}}$ overlapped with zero in a higher number of networks
446 than did CIs of d_{plants} (82 and 57%; Table in Appendix S2), indicating that a significant
association between phylogeny and interaction patterns was exhibited mostly by plant
448 species.

We examined the overall association between phylogeny and the structure of bipartite
450 interaction networks by comparing the mean squared error (MSE) of the model fit among
models adjusted after observed phylogenetic signal (MSE_{data}), models which assumed no
452 phylogenetic signal (MSE_{star}), and models which assume a maximum signal ($\text{MSE}_{\text{Brownian}}$).
Results showed that most networks exhibited a significant phylogenetic signal (in 52
454 networks $\text{MSE}_{\text{data}} < \text{MSE}_{\text{star}}$, in 1 networks $\text{MSE}_{\text{data}} = \text{MSE}_{\text{star}}$, and in 1 $\text{MSE}_{\text{data}} > \text{MSE}_{\text{star}}$; in all
cases $\text{MSE}_{\text{Brownian}}$ had clearly the highest values; Table in Appendix S2), e.g. in most
456 communities the model which fitted best to the data (the one having the lowest error) was
achieved when adjusting the model with observed phylogenetic signals of plants and
458 hummingbirds (MSE_{data}). Nevertheless, most differences between MSE_{data} and MSE_{star} were
small, and much smaller than between MSE_{data} and $\text{MSE}_{\text{Brownian}}$, indicating that in general, the
460 association between phylogenetic signal and species interaction pattern was weak.

462 *Macroecological models*

Full OLS models on corrected network metrics were able to account for 54%-62% of the
464 observed variation in network metrics across the sampled communities (Table 1, Table S3,
Fig. 3). Species richness and environmental factors showed the strongest association with
466 network structure, although with varying strengths across the "Global" and "Only Mainland"
datasets and network metrics (Table 1, Table S3, Figure S1). On the contrary, the
468 associations between phylogenetic signal and network structure remained constant,

exhibiting low regression coefficients in both metrics and datasets (Table 1, Table S3).

470 Collectively, complementary specialization exhibited a stronger association with current
temperature and historical temperature stability, and to a lesser extent with species richness;
472 whereas modularity had the strongest association with species richness (Fig. 3; Table S3).

When the ten predictor variables included in the full OLS models were examined in
474 detail, species richness and hummingbird phylogenetic signal were the only variables
showing an important, spatially consistent and widespread association to network structure,
476 emerging as highly important for both network metrics and datasets. Species richness
showed a strong positive relationship with complementary specialization and modularity
478 (Table 1). On the contrary, a higher phylogenetic signal among hummingbirds was related
with a lower complementary specialization and level of modularity. In other words, despite the
480 association between phylogenetic signal and species' interaction pattern was weak and the
weighted regression coefficients of $d_{\text{hummingbirds}}$ were low, complementary specialization and
482 modularity consistently increased when closely-related hummingbirds visited distinct arrays
of plant species (Table 1, Table S3, Fig. 3).

484 Complementary specialization was also highly associated with the environmental
conditions, as the total variation explained by environmental factors was consistently higher
486 than the variation attributed to species richness and phylogenetic signal in both the "Global"
and "Only Mainland" datasets, and approximated to the variation explained by the full models
488 (Table S3, Fig. 3). The amount of unique variation (i.e. variation explained exclusively by the
predictor-type) explained by environmental factors was similar to the unique variation
490 explained by species richness on the Global dataset (Table S3, Fig. 3). However, when
examining only mainland networks, the unique variation explained by environmental factors
492 was two times greater than the unique variation explained by the other two predictor-types
(Table S3, Fig. 3). Among the seven environmental variables examined, only current

494 temperature and historical temperature stability showed a strong relationship with
complementary specialization, with increasing complementary specialization in communities
496 with current warmer temperatures and with a higher historical temperature stability (Table 1).

Quantitative bipartite modularity showed the strongest association with species
498 richness, particularly in the global dataset, with environmental conditions having a similar
strength association among mainland communities (Table S3, Fig. 3).

500 Shared variability among species richness and phylogenetic signal (i.e. variability
explained by these two predictor types) was non-existent, i.e. richness and phylogenetic
502 signal were distinctly associated to specialization and modularity. Shared variability between
environmental factors and species richness or phylogenetic signal was low (Table S3).

504 The remaining five environmental variables (insularity, temperature seasonality, mean
annual precipitation, precipitation seasonality, and precipitation change velocity) as well as
506 phylogenetic signal in the interaction pattern of plants, showed no important associations with
null model corrected network structure (Table 1).

508

DISCUSSION

510 As previous macroecological studies of interaction networks, we found complementary
specialization and modularity to vary along with environmental conditions and species
512 richness. Additionally, for the first time, we report an association between phylogenetic signal
and network structure at macroecological scale. Specifically, species richness and
514 phylogenetic signal in hummingbird interaction patterns were the two predictor variables that
associated most consistently to network structure, with an association between
516 complementary specialization and current and historical temperature conditions limited to
mainland networks.

518 Hummingbird phylogenetic signal had a constant association with both complementary

specialization and modularity, and on both the Global and Only Mainland datasets, although
520 the variability associated with phylogenetic signal was the lowest of all predictor types. A
weak but significant relationship between phylogenetic signal and species' interaction pattern
522 within ecological networks has also been reported by previous studies on food webs, host-
parasite networks or plant-pollinator networks (Ives & Godfray, 2006; Vázquez *et al.*, 2009b;
524 Krasnov *et al.*, 2012; Rafferty & Ives, 2013). These studies also identified asymmetries in the
phylogenetic signal between trophic levels, with the association between phylogenetic
526 relatedness and species interaction pattern being stronger at lower trophic levels, i.e. plants
in our system (but see Rezende *et al.*, 2007). According to these studies, such asymmetries
528 may stem from a differential relationship between phylogeny and the interaction pattern of
each trophic group, as species from the higher trophic group (“consumer” species) are more
530 likely to adjust their feeding behavior according to local conditions. Our results corroborate
this hypothesis: hummingbird phylogenetic signal showed a weaker relationship with their
532 interaction pattern than plant species ($d_{\text{hummingbirds}}$ tended to be lower than d_{plants} , and CI
 $d_{\text{hummingbirds}}$ overlapped with zero in more networks). Nevertheless, and unlike for plants which
534 showed no association to the spatial variation in network structure, hummingbird
phylogenetic signal was associated to network structure, with higher levels of complementary
536 specialization and modularity consistently achieved when closely-related hummingbird
species visited distinct sets of flowering plant species. This suggests that resource
538 partitioning and inter-specific competition among closely-related hummingbirds might play an
important role in structuring interactions in hummingbird-plant networks. Indeed, inter-specific
540 competition is known to be strong among hummingbirds, and has been noted as a potential
driver of patterns of hummingbird biodiversity (Brown & Bowers, 1985; Bleiweiss, 1998;
542 Cotton, 1998).

Species richness had the strongest association with both metrics, and in both the

544 Global and Only Mainland datasets, except for complementary specialization in the mainland.
Higher species richness may result in a higher niche availability, thus providing ample
546 opportunities for biotic specialization. At the same time, higher species richness may increase
inter-specific competition, which may explain why high species richness lead to higher levels
548 of complementary specialization and modularity (Rezende *et al.*, 2009; Dalsgaard *et al.*,
2011; Krasnov *et al.*, 2012; Junker *et al.*, 2013). Moreover, a higher plant richness may also
550 translate into a temporally-stable availability of floral resources (or the establishment of a
constant minimum local flower supply), enabling a locally constant hummingbird population
552 and, hence, potential for biotic specialization (Montgomerie & Gass, 1981; Stiles, 1985;
Araujo & Sazima, 2003; Cotton, 2007; Abrahamczyk *et al.*, 2011).

554 In the mainland, higher levels of complementary specialization were also found in
warmer areas and in areas with higher historical temperature stability. The former may again
556 be linked to higher inter-specific competition in warmer areas, and particularly in mainland
settings, where hummingbird species and phylogenetic richness is highest (Bleiweiss, 1998;
558 McGuire *et al.*, 2014). This relationship might be stronger on the mainland as insular
pollinator faunas are typically depauperate (Olesen *et al.*, 2002). Moreover, in historically
560 stable climates, hummingbirds may have been able to establish long-term associations with
plants, which may lead to higher levels of local adaptation, interaction specificity and
562 specialization (see Dalsgaard *et al.*, 2011 for a study on a subset of the networks from the
dataset used here). Such long associations may lead to higher complementary specialization
564 in areas with low temperature-change velocity, such as montane habitats and tropical
environments, leaving more generalized interaction patterns to areas with low topography
566 and especially at higher latitudes where changes in temperature velocity have been greatest
(Sandel *et al.*, 2011). Moreover, a higher complementary specialization in areas of high
568 historical temperature stability is consistent with general hummingbird historical biogeography

and speciation patterns, as the core area of hummingbird speciation and diversity occurs in
570 Andean highland and in tropical lowland South-America (Brown & Bowers, 1985; Bleiweiss,
1998; McGuire *et al.*, 2014). We note that complementary macroecological analysis
572 presented in Appendices S3-S5 generally confirmed the importance of species richness and
hummingbird phylogenetic signal, and, additionally, showed that observed (uncorrected)
574 complementary specialization/modularity were associated with insularity and precipitation:
areas of high precipitation and mainland communities showing higher observed
576 complementary specialization and modularity. Precipitation has previously been shown to
influence floral phenotypic specialization and the importance of hummingbird-plant
578 interactions for the entire pollination communities (Cruden, 1972; Dalsgaard *et al.*, 2009;
Martín González *et al.*, 2009). The fact that precipitation and insularity only associated with
580 observed complementary specialization and observed modularity, and not with null model
corrected values of these network metrics, may indicate that insularity and precipitation do
582 not directly influence the interaction pattern of species, but rather associate indirectly with
network structure through species richness and/or interaction probability distributions.

584

CONCLUSIONS

586 Characterizing potential ecological, historical and evolutionary mechanisms associated with
the structure of ecological communities is a critical first step towards understanding the
588 determinants of community assembly and how climate-change may affect biodiversity
(Woodward *et al.*, 2010; Schleuning *et al.*, 2014). By examining null model corrected network
590 metrics, we are investigating how much observed communities depart from random ones with
an equivalent set of species and interactions. Hence, we were able to investigate not only
592 whether a community presents a structure which differs significantly from random, but also to
associate the difference in complementary specialization and modularity to species richness,

594 evolutionary, and environmental conditions.

We have shown that complementary specialization and modularity in hummingbird-
596 plant networks associate to species richness, hummingbird phylogenetic signal and
environmental factors acting at varying spatio-temporal scales and in different aspects of
598 network structure. Notably, species richness and hummingbird phylogenetic signal showed a
consistent association with network structure, with a more restricted but still important role of
600 contemporary temperature and historical temperature stability, which were important among
mainland communities. These results are markedly different to the ones for avian seed-
602 dispersal networks for which species' phylogeny and historical climatic stability were
unrelated to modularity and complementary specialization (Schleuning *et al.*, 2012, 2014;
604 Sebastián González *et al.*, 2015). Such difference suggests that hummingbirds and flowers
engage in tighter co-evolutionary associations than frugivore birds and their plants, and
606 hence, historical and evolutionary factors may have a stronger role in hummingbird-plant
assemblages than for frugivore birds-plant assemblages.

608

ACKNOWLEDGMENTS

610 We kindly appreciate comments given by David Currie, Allen Hurlbert, Robert R. Junker and
an anonymous reviewer on an earlier version of the manuscript. We also thank Carsten
612 Dormann and Matthew Helmus for invaluable help regarding the use of the software bipartite
and the interpretation of the phylogeny results, respectively. AMMG was supported by the
614 Spanish Ministry of Education; BD by the Carlsberg Foundation; ACB by the OTICON
Fonden; PAC by the David Lack studentship from the British Ornithologists' Union and
616 Wolfson College, University of Oxford; CL by the CACyPI-Uatx-2013; MAM by the
Universidad Estatal a distancia (UNED), Costa Rica, and the Biodiversity and Climate
618 Research Centre (BIK-F), Frankfurt, Germany; LRL by FAEP and Unicamp; TTI by Frimodt-

Heineke Foundation, the Knud Højgaard Foundation and Faculty of Natural Sciences

620 University of Aarhus. FAPESP supported ACA and MS; FAPEMIG supported PKM and PEO;
CNPq supported ACA, GMO, LCR, LRL, MS, PKM, PEO, IGV and JV-B; CAPES supported
622 FPA, FMGLC, LRL, PKM and LCR; and FUNDECT supported ACA. SW thanks the National
Institute of Natural Resources (INRENA) for research permits in Perú and LRL the Ministerio
624 del Medio Ambiente de Colombia for permission the entrance to Chiribiquete. AMMG, BD,
DN-B, PKM, ZW and CR thank the Danish National Research Foundation for its support of
626 the Center for Macroecology, Evolution and Climate.

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research and education*. Proceedings of the IS&T/SPIE Symposium on Electronic
760 Imaging, Visualization and Data Analysis, 5295, 124-132.
- 762 **Biosketch:** This work results from an ongoing collaboration among numerous researchers
from different scientific backgrounds and institutions, who have gathered an extensive
764 dataset of hummingbird plant interaction networks and complementary data on species traits,
phylogeny, climate, etc. Such multidisciplinary information is allowing us to study in depth
766 different aspects of hummingbird-plant interaction patterns at macroecological scales, and to
identify potential mechanisms responsible for them. Our ultimate goal is to describe general
768 macroecological patterns in biotic interactions using hummingbird-plant interactions as a
model system.

772 **Table 1.** Relationship between complementary specialization (H_2') and modularity (QuanBiMo) with species richness, phylogenetic signal and environmental
774 factors across the Americas (Global dataset) and the mainland, i.e. when excluding insular communities (Only Mainland). Complementary specialization
776 measures the exclusiveness of the interactions in the community, whereas modularity quantifies whether species interact more frequently with subsets of
778 available species within a community. For each network metric, the standardized regression coefficients are reported for ordinary least squares regression for a
780 model including all variables ("Full") and for a model averaged across all possible models using Akaike Weights (AICc w_i - "Averaged"). For the averaged
models, the relative importance of each predictor variable (" Σw_i ") is given by the Akaike Weights (AICc w_i). Predictors with high importance are marked in bold.
Phylogenetic signal among plants and hummingbirds, d_p and d_h , respectively; Insularity, Ins; Mean annual temperature, MAT; Temperature seasonality, TS;
Mean annual precipitation, MAP; Precipitation seasonality, PS; Velocity of temperature change since the last Glacial Maximum, MAT vel; Velocity of precipitation
change since the last Glacial Maximum, MAP vel. The significance of Moran's I was tested with 10 distance classes and a permutation test with 10,000
iterations. In all models multicollinearity was not an issue, i.e. VIF \leq 3.4, CN \leq 4.0, and there was no positive spatial autocorrelation, i.e. Moran's I was non-
significant.

		Model	AICc	R ²	Species richness	Phylogenetic signal			Environmental factors						
					Network size	d_p	d_h	Ins	MAT	TS	MAP	PS	MAT vel	MAP vel	
Global dataset n=54	H_2'	Full	-54.37	0.54	0.46	-0.09	-0.30	-0.22	0.28	0.18	0.05	-0.21	-0.48	0.19	
		Averaged				0.52	-0.14	-0.36	-0.12	0.14	0.12	0.09	-0.22	-0.27	0.17
		Σw_i				1.00	0.38	0.96	0.28	0.31	0.31	0.26	0.60	0.67	0.29
	QuanBiMo	Full	-99.87	0.64	0.64	-0.15	-0.23	-0.19	0.19	0.08	-0.00	-0.20	-0.13	-0.10	
		Averaged				0.65	-0.18	-0.28	-0.14	0.08	0.06	0.10	-0.18	-0.10	-0.13
		Σw_i				1.00	0.62	0.92	0.34	0.26	0.24	0.29	0.57	0.29	0.39
Only Mainland n=45	H_2'	Full	-55.24	0.58	0.33	-0.04	-0.33	na	0.48	0.13	-0.09	-0.26	-0.71	0.31	
		Averaged				0.32	-0.05	-0.36	na	0.45	0.11	-0.04	-0.24	-0.65	0.36
		Σw_i				0.81	0.20	0.92	na	0.85	0.26	0.23	0.61	0.93	0.78
	QuanBiMo	Full	-76.89	0.57	0.54	-0.17	-0.28	na	0.29	0.05	-0.08	-0.25	-0.29	-0.09	
		Averaged				0.54	-0.18	-0.30	na	0.23	0.02	0.10	-0.23	-0.24	-0.13
		Σw_i				1.00	0.48	0.81	na	0.41	0.20	0.26	0.59	0.43	0.30

782 **Figure 1.** Cartoon illustrations depicting two different communities and the characteristics
and relationship between complementary specialization (H_2') and quantitative bipartite
784 modularity (QuanBiMo). Both communities depict 700 interaction events between 10 plants
and 5 pollinators. Plants are labeled as numbers 1-10 in the matrix and as orange (light tone)
786 nodes in the network representation, and pollinators by letters A-E in the matrix and as blue
(dark tone) nodes in the network. Interaction frequencies between plants and pollinators are
788 illustrated as numbers of interaction events in the matrix format and as varying line widths in
the network illustration. Complementary specialization measures the exclusiveness in
790 species' interactions, whereas modularity quantifies whether species interact more frequently
with subsets of available species within a community. Community A exhibits a moderate
792 complementary specialization, with different species-pairs exhibiting various degrees of
complementary specialization. For instance, species-pair A-1 shows a high complementary
794 specialization, as hummingbird A visits exclusively and with high frequency (155 times) plant
1, which in turn is only visited once by another hummingbird. On the other hand, the
796 complementary specialization of pair E-4 is lower than for the previous pair despite these
species interact with the same frequency because hummingbird E also interacts with other
798 plant species, i.e. the interaction E-4 is less exclusive. Interactions in community B are also
somewhat specialized (species favored interactions with subsets of the available partners),
800 but the exclusiveness of these interactions is lower than for community A. Both communities
show very similar values for corrected modularity and can be divided into three distinct
802 modules, although the modules are composed of a different array of species. By having
different degree of complementary specialization but similar values of modularity, these
804 communities show that although positively correlated, these metrics measure
complementary but different aspects of specialization. Network drawings were created using
806 Network3D and energized with the 3D Force-directed algorithm to enhance visualization of
modularity patterns (Yoon *et al.*, 2004; Williams, 2010).

808 **Figure 2.** Map of the American continent showing the location of the 54 study sites and a
number of example networks located along a species richness gradient. Some networks
810 have been slightly moved horizontally to maximize visualization (exact coordinates of the
localities on Table S1). The grey shading of the background illustrates altitude, with darker
812 shades depicting higher altitudes. Localities with darker shades of green denote networks
with a higher richness. For each illustrated network, the reference number and a concise
814 description of the vegetation type is given, along with a network drawing. For the network
drawings, blue (dark tone) and orange (light tone) nodes depict hummingbird and plant
816 species, respectively, while line width depicts log+1 frequency of interaction among species.
Notice that species-rich networks in general present more complex structures, with networks
818 11, 21 and 50 exhibiting the lowest corrected complementary specialization; networks 50, 11
and 21 the lowest corrected modularity; networks 53, 12 and 4 the highest corrected
820 complementary specialization; and networks 10, 53 and 4 the highest corrected modularity,
respectively. Complementary specialization measures the exclusiveness in species'
822 interactions, whereas modularity quantifies whether species interact more frequently with
subsets of available species within a community. Network drawings were created using
824 Network3D and energized with the 3D Force-directed algorithm to enhance visualization of
modularity patterns (Yoon *et al.*, 2004; Williams, 2010).

826 **Figure 3.** Coefficients of determination (R^2) for complementary specialization and modularity
obtained from partial regression of full models, i.e. in models including all ten predictor
828 variables (see Table 1 for standardized coefficients of each variable and more details of
model fit, and Table S3 for the R^2 values used in this figure). Complementary specialization
830 measures the exclusiveness in species' interactions, whereas modularity quantifies whether
species interact more frequently with subsets of available species within a community. We
832 represent values for all networks in the study (Global dataset; $n=54$) and excluding insular
communities (Only Mainland; $n=45$). Bars illustrate the association between the different
834 "predictor-types" and network structure. Predictor-types refers to (a) species richness (one
variable), (b) phylogenetic signal (two variables: phylogenetic signal in the interaction pattern
836 of plants and hummingbirds), and (c) environmental factors (eight variables: insularity,
average annual temperature, temperature seasonality, total annual precipitation, precipitation
838 seasonality, temperature and precipitation-change velocity between the Last Glacial
Maximum and the present). The amount of variation explained by each pooled predictor-type
840 is color-coded with different shades: bars colored in darkest color depict the overall variation
explained by all factors together; medium colors illustrate the total variation explained by that
842 predictor-type; light colors show the unique variation explained by each predictor-type and
not shared by other variable-types. H_2' , complementary specialization; QuanBiMo,
844 quantitative bipartite modularity.

Figure 1.

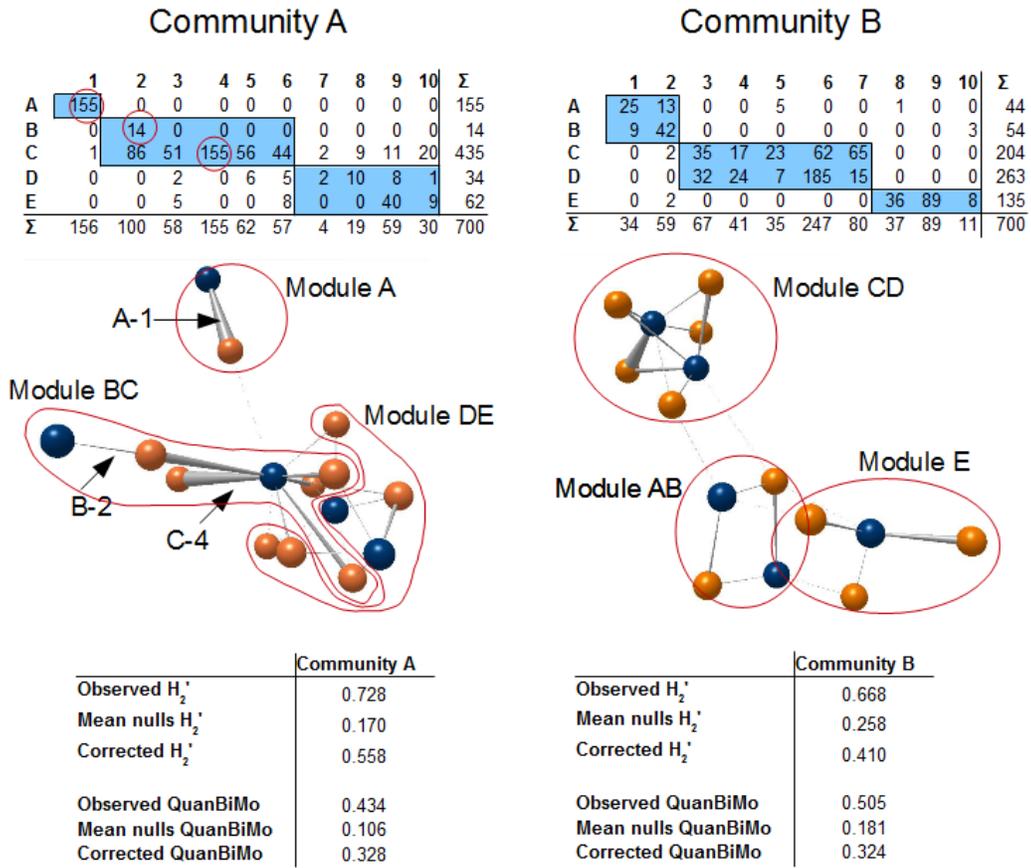


Figure 2.

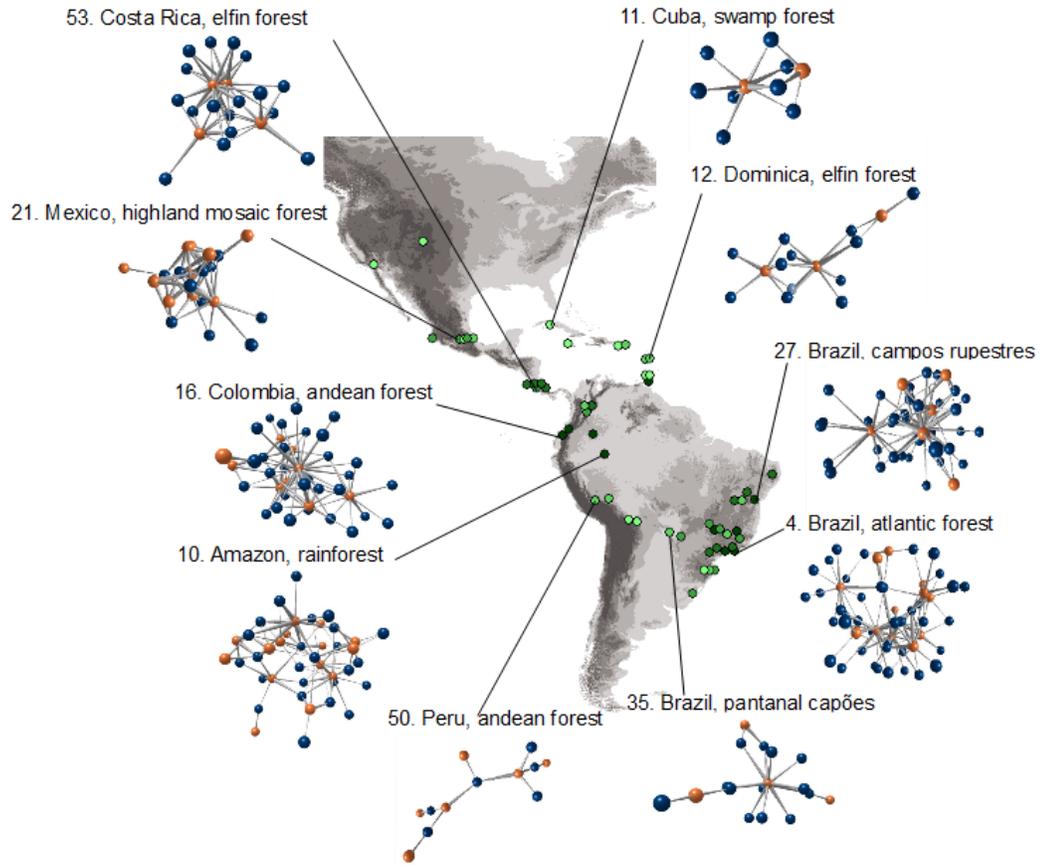


Figure 3.

