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ABSTRACT

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

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

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).

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.

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.

INTRODUCTION

152 **INTRODUCTION**

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 (Thébault & 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). Additionaly, 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 al.,* 2002; Rezende *et al.,* 2009; Krasnov *et al.,* 2012). Environmental setting may also affect

204 biotic interactions. Historical climatic stability may promote specialization and modularity by providing species more opportunity to co-evolve over longer periods of time compared to

206 species from climatically more unstable areas. Notably, large late Quaternary glacial-interglacial climate change is coupled with a decreased modularity in pollination networks

208 (Dalsgaard *et al*., 2013), and decreased specialization in hummingbird-plant networks (Dalsgaard *et al.,* 2011). Likewise, current environmental conditions may influence the identity

210 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;

212 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

214 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*

216 *al*., 2009, 2011; Martín González *et al*., 2009). Finally, insularity may influence pollination network structure, as insular communities typically show significantly lower levels of

218 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 39ºN to 32ºS, 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 $H_2' = \dfrac{H_{2max} - H_2}{H_{2max} - H_{2min}}$, 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* unspecified 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 $Q = \frac{1}{2N} \Sigma (A_{ij} - K_{ij}) \delta(m_i, m_j)$, 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 imposibility 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 ($d_{hummingbirds}$), 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

$(d_{plants}=d_{hummingbirds}=0$; Star model), one assuming a maximum phylogenetic signal

352   $(d_{plants}=d_{hummingbirds}=1$; Brownian model), and a final one which incorporated the observed

phylogenetic signals combined (estimated d_{plants} and $d_{hummingbirds}$; Data model). We used the

354   bootstrapping option to calculate confidence intervals for d_{plants} and $d_{hummingbirds}$. Networks

where these confidence intervals did not overlap zero or when the $MSE_{Data} < MSE_{Star}$ 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, ºC),

364   *temperature seasonality* (TS, standard deviation × 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 x 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 × 2.5 arc degrees (Singarayer

& Valdes, 2010), and were downscaled to 0.1 × 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' ($d_{hummingbirds}$), 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

396 the likelihoods of the entire dataset of models, such that $w_i = \dfrac{\exp\left(\dfrac{-1}{2}\Delta_i\right)}{\sum\limits_{r=1}^{R}\exp\left(\dfrac{-1}{2}\Delta_R\right)}$, being Δ_i the

differences in AIC between the set of R models, so that the relative strength of each model

398 depends on the entire set of models. We report the standardized regression coefficients and

the overall importance ($\Sigma\ w_i$) 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*

al., 2013, 2014). As our dataset contains too few island networks (n=9) to allow for a separate

420   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 $\log_{10}$-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

($d_{hummingbirds}$) 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 $d_{hummingbirds}$ 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 ($MSE_{Brownian}$).

Results showed that most networks exhibited a significant phylogenetic signal (in 52

454   networks $MSE_{data}<MSE_{star}$, in 1 networks $MSE_{data}=MSE_{star}$, and in 1 $MSE_{data}>MSE_{star}$; in all

cases $MSE_{Brownian}$ 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 $MSE_{Brownian}$, 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 $d_{hummingbirds}$ 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 ($d_{hummingbirds}$ tended to be lower than d_{plants}, and CI

$d_{hummingbirds}$ 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

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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.

Table 1. Relationship between complementary specialization (H_2') and modularity (QuanBiMo) with species richness, phylogenetic signal and environmental factors across the Americas (Global dataset) and the mainland, i.e. when excluding insular communities (Only Mainland). Complementary specialization measures the exclusiveness of the interactions in the community, whereas modularity quantifies whether species interact more frequently with subsets of available species within a community. For each network metric, the standardized regression coefficients are reported for ordinary least squares regression for a 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 ("$\Sigma\ w_i$") 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 ≤ 3.4, CN ≤ 4.0, and there was no positive spatial autocorrelation, i.e. Moran's I was non-significant.

					Species richness	Phylogenetic signal			Environmental factors					
		Model	AICc	R^2	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
		$\Sigma\ w_i$			**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
		$\Sigma\ w_i$			**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
		$\Sigma\ w_i$			**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
		$\Sigma\ w_i$			**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).

2

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,

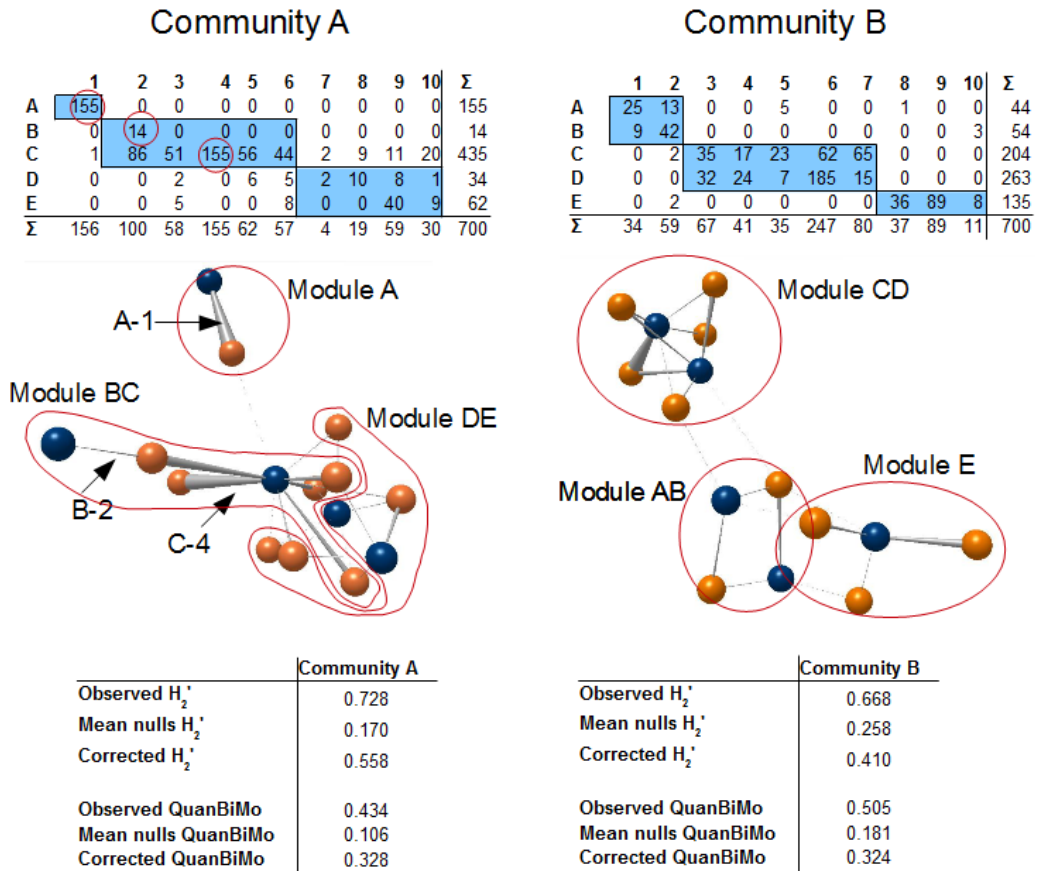844 quantitative bipartite modularity.

Figure 1.

Community A

	1	2	3	4	5	6	7	8	9	10	Σ
A	155	0	0	0	0	0	0	0	0	0	155
B	0	14	0	0	0	0	0	0	0	0	14
C	1	86	51	155	56	44	2	9	11	20	435
D	0	0	2	0	6	5	2	10	8	1	34
E	0	0	5	0	0	8	0	0	40	9	62
Σ	156	100	58	155	62	57	4	19	59	30	700

Community B

	1	2	3	4	5	6	7	8	9	10	Σ
A	25	13	0	0	5	0	0	1	0	0	44
B	9	42	0	0	0	0	0	0	0	3	54
C	0	2	35	17	23	62	65	0	0	0	204
D	0	0	32	24	7	185	15	0	0	0	263
E	0	2	0	0	0	0	0	36	89	8	135
Σ	34	59	67	41	35	247	80	37	89	11	700

	Community A
Observed H_2'	0.728
Mean nulls H_2'	0.170
Corrected H_2'	0.558
Observed QuanBiMo	0.434
Mean nulls QuanBiMo	0.106
Corrected QuanBiMo	0.328

	Community B
Observed H_2'	0.668
Mean nulls H_2'	0.258
Corrected H_2'	0.410
Observed QuanBiMo	0.505
Mean nulls QuanBiMo	0.181
Corrected QuanBiMo	0.324

4

Figure 2.

53. Costa Rica, elfin forest

11. Cuba, swamp forest

12. Dominica, elfin forest

21. Mexico, highland mosaic forest

27. Brazil, campos rupestres

16. Colombia, andean forest

4. Brazil, atlantic forest

10. Amazon, rainforest

35. Brazil, pantanal capões

50. Peru, andean forest

Figure 3.