RESEARCH PAPER

The macroecology of phylogenetically structured hummingbird–plant networks

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ABSTRACT

Aim To investigate the association between hummingbird–plant network structure and species richness, phylogenetic signal on species' interaction pattern, insularity and historical and current climate.

Location Fifty-four communities along a *c.* 10,000 km latitudinal gradient across the Americas (39° N–32° S), ranging from sea level to *c.* 3700 m a.s.l., 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 multimodel 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 mutualistic 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 with species richness and environmental factors ($R^2 = 0.20$–0.44 and $R^2 = 0.32$–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 was also associated with warmer temperatures and greater historical temperature stability.

Main conclusions Our results confirm the results of 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 a macroecological scale, indicating that high specialization and modularity are associated with high interspecific competition among closely related hummingbirds, subdividing the floral niche. This suggests a tighter co-evolutionary association between hummingbirds and their plants than in previously studied plant–bird mutualistic systems.

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INTRODUCTION

An urgent challenge facing ecologists today is to understand how ecological, evolutionary and environmental mechanisms affect the structure and function of ecological communities. A better understanding of how these processes form and maintain communities 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 al.*, 2009a; Woodward *et al.*, 2010). For this purpose, the use of network approaches for studying complex communities of interacting species, i.e. networks representing species as nodes and interactions as links between species, has significantly advanced our understanding of ecological systems (Woodward *et al.*, 2010).

For instance, research on mutualistic networks such as plant–pollinator or plant–frugivore interactions has revealed that these communities typically exhibit a number of architectural attributes, such as complementary specialization and modularity, which differ significantly from random interactions among species (Olesen *et al.*, 2007; Blüthgen, 2010; Dalsgaard *et al.*, 2011, 2013; Schleuning *et al.*, 2012, 2014; Trøjelsgaard & Olesen, 2013; Dormann & Strauss, 2014; Sebastián González *et al.*, 2015). Complementary specialization 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 availability, measuring a species' availability either as its abundance or its interaction frequency (Blüthgen *et al.*, 2006; Fig. 1). Modularity quantifies whether species interact more frequently with subsets of available species within a community, forming modules of densely interacting species with loose connections between modules (Olesen *et al.*, 2007; Fig. 1). Such modules have 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 environments with a strong climatic seasonality (Martín González *et al.*, 2012; Schleuning *et al.*, 2014).

These architectural attributes have a profound impact on the dynamics of ecological communities. For example, higher levels of complementary specialization have been linked to higher dependences between species and, hence, to a higher risk of secondary extinctions (Blüthgen, 2010); whereas high levels of modularity may at first provide higher network resilience to perturbations, as these are not typically spread across modules, it ultimately may result in unconnected modules, community fragmentation and rapid species loss (Thébault & Fontaine, 2010; Stouffer & Bascompte, 2011). Complementary

specialization and modularity are typically related, as some degree of modularity necessarily implies a certain level of complementary specialization for a subset of species from the available species pool (Dormann & Strauss, 2014). Nevertheless, these metrics measure different aspects of interaction specialization and, hence, may show disparate dynamics and associations with different ecological, evolutionary and environmental factors.

Thus, comparative studies at macroecological scales, where differences in network structure can be associated with varying ecological, evolutionary and environmental factors, 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; Sebastián González *et al.*, 2015). For instance, species richness may promote a higher degree of complementary specialization and modularity by increasing interspecific competition and providing more species to interact with, i.e. allowing finer niche partitioning (e.g. Dalsgaard *et al.*, 2011; Junker *et al.*, 2013). Additionally, evolution may structure biotic interactions via niche conservatism, as closely related species may display more similar phenotypes, spatial distributions and ecological interactions than distantly related species (Webb *et al.*, 2002; Ives & Godfray, 2006; Rezende *et al.*, 2007; Vázquez *et al.*, 2009a). Alternatively, closely related species that experience strong interspecific competition may undergo niche partitioning, competitive exclusion or resource-use complementarity (Webb *et al.*, 2002; Rezende *et al.*, 2009; Krasnov *et al.*, 2012). The environmental setting may also affect biotic interactions. Historical climatic stability may promote specialization and modularity by providing species with more opportunity to co-evolve over longer periods of time compared with species from climatically more unstable areas. Notably, large late Quaternary glacial–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 and strength of species interactions by altering the spatial distribution, phenophases and foraging capability of species (Cruden, 1972; Martín González *et al.*, 2009; Dalsgaard *et al.*, 2011, 2013; 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 temperatures, possibly because the diversity and activity of insect pollinators 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).
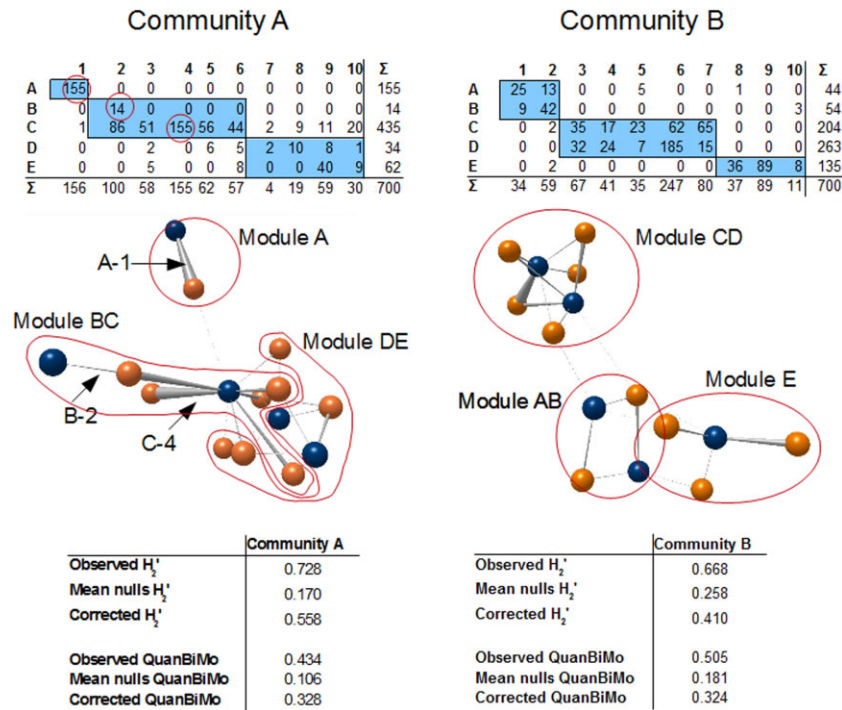
Figure 1 Diagram illustrations depicting two different communities and the characteristics and relationship between complementary specialization (H_2') and quantitative bipartite modularity (QuanBiMo). Both communities depict 700 interaction events between 10 plants and 5 pollinators. Plants are labelled as numbers 1–10 in the matrix and as orange (light tone) 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 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 species interactions, whereas modularity quantifies whether species interact more frequently with subsets of available species within a community. Community A exhibits a moderate complementary specialization, with different species pairs exhibiting various degrees of complementary specialization. For instance, species pair A–1 shows a high complementary 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 complementary specialization of pair C–4 is lower than for the previous pair despite these species interacting with the same frequency because hummingbird C also interacts with other plant species, i.e. interaction C–4 is less exclusive. Interactions in community B are also somewhat specialized (species favoured interactions with subsets of the available partners), 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 modules, although the modules comprise a different array of species. By having different degrees of complementary specialization but similar values of modularity, these communities show that although they are positively correlated, these metrics measure complementary but different aspects of specialization. Network drawings were created using Network3D and energized with the 3D Force-directed algorithm to enhance visualization of modularity patterns (Yoon *et al.*, 2004; Williams, 2010).

Finally, insularity may influence pollination network structure, as insular communities typically show significantly lower levels of specialization and modularity compared with mainland ones (Olesen *et al.*, 2002; Dalsgaard *et al.*, 2013).

Despite the recently increasing interest in determining the influence of species richness, phylogenetic signal and past and current environmental conditions on network 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 *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 high modularity in areas having low temperatures and high temperature seasonality, whereas modularity exhibited no detectable association with species phylogenetic history and historical climate. Here, we examine how the structure of hummingbird–plant networks, another type of mutualistic assemblage, is associated with species richness, phylogenetic signal and environmental conditions. To do this, we compiled a dataset consisting of 54 high-resolution quantitative hummingbird–plant interaction networks and combined them with complementary data on species richness, state-of-the-art species phylogenies and simulations of palaeo- and current climate. In accordance with previous studies on pollination networks, we show that complementary specialization and modularity are influenced by species richness and climatic conditions. Additionally, for the first time, we report an association between network structure and species

phylogenetic signal at a macroecological scale. Specifically, communities where closely related hummingbirds interact with distinct sets of plant species exhibited higher levels of complementary specialization and modularity.

MATERIAL AND METHODS

Hummingbird–plant interaction networks

We compiled a large dataset of 54 high-resolution and geographically widely distributed hummingbird–plant interaction networks from published and unpublished sources (Fig. 2; see 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, i.e. we discarded studies which focused only on ornithophilous species or on specific floral or hummingbird groups. We also discarded illegitimate interactions, i.e. our database focuses exclusively on interactions which have the potential for pollination. These networks describe the interaction frequency between plants and hummingbirds, recorded as the number of observed visits. In total, our dataset comprises 141 species of hummingbirds belonging to all major hummingbird lineages (about 42% of all described species; McGuire et al., 2014) and 824 plant species belonging to 79 different plant families (Appendix S1).

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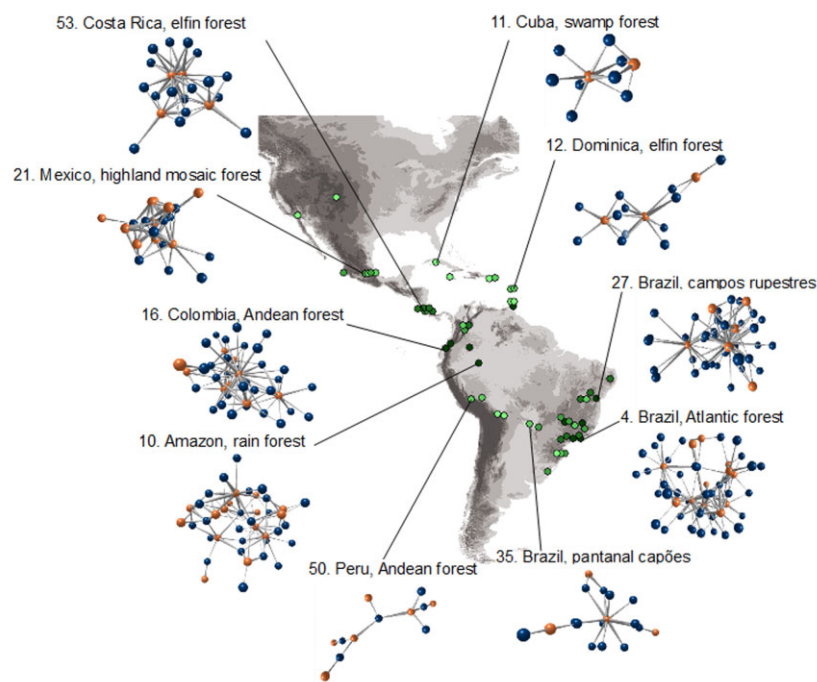

Figure 2 Map of the American continent showing the location of the 54 study sites and a number of example networks located along a species richness gradient. Some networks have been moved slightly horizontally to maximize clarity (the exact coordinates of the localities are given in Table S1). The grey shading of the background illustrates elevation, with darker shades depicting higher elevations. Localities with darker shades (darker green) denote networks with a higher richness. For each illustrated network, the reference number and a concise 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 species, respectively, while line width depicts the log + 1 frequency of interaction among species. Notice that species-rich networks in general present more complex structures, with networks 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 complementary specialization; and networks 10, 53 and 4 the highest corrected modularity, respectively. Complementary specialization measures the exclusiveness in species interactions, whereas modularity quantifies whether species interact more frequently with subsets of available species within a community. Network drawings were created using Network3D and energized with the 3D Force-directed algorithm to enhance visualization of modularity patterns (Yoon et al., 2004; Williams, 2010).

Finally, the spatial distribution of these networks extends from sea level to *c.* 3700 m a.s.l. and spans a *c.* 10,000 km gradient from 39° N to 32° S, from tropical and subtropical ecosystems in South America to temperate communities in North America. The spatial distribution includes both mainland and insular communities and consists of communities from various environmental settings (Fig. 2).

Network composition and network metrics

For each location, interaction networks were quantified in terms of the number of interaction events between hummingbird and plant species. For each network we calculated two complementary metrics that describe the degree of specialization or specificity of hummingbird–plant interactions: complementary specialization (Blüthgen *et al.*, 2006) and 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 and environmental factors associate with specialized network structures. For the calculations we used the R package *bipartite 1.20* (Dormann *et al.*, 2009).

1. *Complementary specialization* (H_2') describes how species restrict their interactions relative to random expectations based on species abundances/interaction frequency. Complementary specialization is calculated as $H_2 = -\sum_{i=1}^{r}\sum_{j=1}^{c}(p_{ij} \cdot \ln p_{ij})$, where p_{ij} reflects the proportional number of interactions of each species relative to their availability, i.e. for their respective marginal total (in our case total interaction frequency) for r plant and c animal species. We illustrate this in Fig. 1; for instance, from the example community A from Fig. 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). Hence the interaction A–1 exhibits a high complementary specialization, as hummingbird A visits plant 1 exclusively and at a high frequency, while plant 1 is only visited, and at a very low frequency, by another hummingbird species. If the majority of a community has interactions with such high complementarity, the community will exhibit high values of 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 species and has a higher marginal total, lowering the complementary specialization of this pair ($p_{C4} = 0.36$, $p_{4C} = 1$).

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

2. Quantitative bipartite modularity (QuanBiMo) is an algorithm which places species 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 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 allocation of species into modules. Specifically, the algorithm maximizes the bipartite version of Newman's modularity (Q), so that $Q = \dfrac{1}{2N}\sum_{ij}(A_{ij} - K_{ij})\delta(m_i, m_j)$, where N reflects the total number of interactions, A_{ij} is the normalized number of interactions between species i and j, K_{ij} is the expected interaction probability between species i and j drawn from a neutral model of 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 ($Q = 1$) modularity. We ran the QuanBiMo algorithm following the methodology established by Schleuning *et al.* (2014) and the default specifications of the computeModules function in bipartite; that is, for each network we chose the partition showing the highest modularity from five independent runs of the algorithm (Dormann & Strauss, 2014; Schleuning *et al.*, 2014). 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 network connectivity, network estimates for complementary specialization and modularity were corrected using null models (Schleuning *et al.*, 2012, 2014; Dormann & Strauss, 2014). 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 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 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 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 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 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 Fig. 1 illustrates, a corrected value of 0.3 in modularity 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 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.

Analysis of phylogenetic signal in bipartite interaction networks

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

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 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 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 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 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 ($d_{plants} = d_{hummingbirds} = 1$; Brownian model) and a final one which incorporated the combined observed phylogenetic signals (estimated d_{plants} and $d_{hummingbirds}$; Data model). We used the 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 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 phylogenetic analysis, see Appendices S1 & S2, respectively.

Environmental variables

We analysed six variables describing current and historical temperature and precipitation known or hypothesized to affect the structure of pollination networks. Four of the six variables describe current climatic conditions: mean annual temperature (MAT, °C), temperature seasonality (TS, SD × 100), mean annual precipitation (MAP, mm) and precipitation seasonality (PS, coefficient of variation). We obtained these measurements from the WorldClim dataset with spatial resolutions of 1 km × 1 km (http://www.worldclim.org; see also Hijmans et al., 2005). The historical climate variables, the velocity of temperature and the velocity of precipitation, reflect the speed of change of temperature and precipitation change between the Last Glacial Maximum (LGM) and pre-industrial times (VT, m/year; VP, m/year), following the definition of Loarie et al. (2009). Projections of the global climate during the LGM and pre-industrial times were generated by the Hadley Centre Coupled Model Version 3 (HadCM3) with a

resolution of 3.75° × 2.5° (Singarayer & Valdes, 2010), and were downscaled to 0.1° × 0.1°. For each study site, climate estimates were calculated as the average values of all 1 km × 1 km grid cells (0.1° × 0.1° for palaeoclimatic data) within a concentric distance of 10 km from the sampling location. Additionally, we scored whether a network was located on the mainland (0) or on an island (1).

Macroecological models

We used a multimodel approach based on information theory as outlined in Diniz-Filho et al. (2008) to simultaneously evaluate the relationships of species richness, phylogenetic signal 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 10 predictor variables: (1) species richness (network size), (2) the phylogenetic signal in the interaction pattern of plants (d_{plants}), (3) the phylogenetic signal in the interaction pattern of hummingbirds ($d_{hummingbirds}$), (4) annual average temperature, (5) temperature seasonality, (6) annual average precipitation, (7) precipitation seasonality, (8) temperature-change velocity, (9) precipitation-change velocity, and (10) insularity. Second, for each network metric we used the Akaike information criterion (AIC_C) aiming to identify minimum adequate models (MAMs) among all possible model combinations of our 10 predictor variables. MAMs were defined as models exhibiting a difference in AIC_C of at least two points lower than other models (i.e. $\Delta AIC_C < 2$; Burnham & 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 multimodel approach. Specifically, instead of 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 the likelihoods of the entire dataset of models, such that

$$w_i = \frac{\exp\left(-\frac{1}{2}\Delta_i\right)}{\sum\limits_{r=1}^{R} \exp\left(-\frac{1}{2}\Delta_R\right)},$$

Δ_i being the difference 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 (Σw_i) of each variable for an averaged OLS model based on weighted w_i (Burnham & Anderson, 2002; Diniz-Filho et al., 2008), for which we adopted an importance cut-off value of ≥ 0.80. The standardized regression coefficients were also reported for the OLS regression model including all 10 predictor variables ('full' model). For each network metric, we used partial regressions to separate the total, unique and shared variation explained by species richness, phylogenetic signal and environmental factors in the 'full' models.

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 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 that of mainland America (*c.* 5 Ma versus 12–22 Ma for North and South America, respectively), and consequently insular hummingbirds have had less time for specialization and co-evolution with their nectar plants than their mainland counterparts (Bleiweiss, 1998; McGuire *et al.*, 2014). Moreover, Caribbean communities undergo a high level of periodic disturbances, which may hinder high levels of specialization on islands (Graves & Olsen, 1987; Rivera-Marchand & Ackerman, 2006). Hence, the relationship between species richness, phylogenetic signal and environmental factors and network structure may differ between mainland and insular communities. For instance, the influence 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 analysis for insular networks, we explored putative differences in mainland and island networks by analysing a subset of the dataset composed exclusively by networks from the mainland (Mainland; *n* = 45 networks) and compared these results with those of the entire dataset (Global dataset, which includes both mainland and insular communities; *n* = 54 networks).

For all macroecological models, we log$_{10}$-transformed species richness, temperature seasonality, temperature velocity and precipitation velocity; we squared temperature and square-root transformed precipitation. All other variables were left untransformed. In all 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 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 spatial models. All regression analyses were conducted using the software Spatial Analysis in Macroecology (SAM) 4.0 (Rangel *et al.*, 2010).

To better support our findings, we performed a number of complementary macroecological models which included sampling effort as a predictor variable (Appendix 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 instead of climate change velocity (Appendix S5).

RESULTS

Phylogenetic signal on species interaction patterns

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 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 than did CIs of *d*$_{plants}$ (82% and 57%; see the table in Appendix S2), indicating that a

significant association between phylogeny and interaction patterns was exhibited mostly by plant species.

We examined the overall association between phylogeny and the structure of bipartite 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 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 networks MSE$_{data}$ < MSE$_{star}$, in one network MSE$_{data}$ = MSE$_{star}$ and in one MSE$_{data}$ > MSE$_{star}$; in all cases MSE$_{Brownian}$ clearly had the highest values; see table in Appendix S2). For example, in most 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 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 association between phylogenetic signal and species interaction pattern was weak.

Macroecological models

Full OLS models on corrected network metrics were able to account for 54–62% of the observed variation in network metrics across the sampled communities (Tables 1 & S3, Fig. 3). Species richness and environmental factors showed the strongest association with network structure, although with varying strengths across the 'Global' and 'Only Mainland' datasets and network metrics (Tables 1 & S3, Fig. S1). On the contrary, the associations between phylogenetic signal and network structure remained constant, exhibiting low regression coefficients in both metrics and datasets (Tables 1 & S3). Collectively, complementary specialization exhibited a stronger association with current temperature and historical temperature stability, and to a lesser extent with species richness, whereas modularity had the strongest association with species richness (Fig. 3, Table S3).

When the 10 predictor variables included in the full OLS models were examined in detail, species richness and hummingbird phylogenetic signal were the only variables showing an important, spatially consistent and widespread association with network structure, emerging as highly important for both network metrics and datasets. Species richness showed a strong positive relationship with complementary specialization and modularity (Table 1). On the contrary, a higher phylogenetic signal among hummingbirds was related to a lower complementary specialization and level of modularity. In other words, despite the association between phylogenetic signal and species interaction pattern being weak and the weighted regression coefficients of *d*$_{hummingbirds}$ low, complementary specialization and modularity consistently increased when closely related hummingbirds visited distinct arrays of plant species (Tables 1 & S3, Fig. 3).

Complementary specialization was also highly associated with the environmental conditions, as the total variation explained by environmental factors was consistently higher than

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. Predictors with high importance are marked in bold.

		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**	n.a.	**0.48**	0.13	−0.09	−0.26	**−0.71**	0.31
		Averaged			0.32	−0.05	**−0.36**	n.a.	**0.45**	0.11	−0.04	−0.24	**−0.65**	0.36
		$\Sigma\,w_i$			**0.81**	0.20	**0.92**	n.a.	**0.85**	0.26	0.23	0.61	**0.93**	0.78
	QuanBiMo	Full	−76.89	0.57	**0.54**	−0.17	**−0.28**	n.a.	0.29	0.05	−0.08	−0.25	−0.29	−0.09
		Averaged			**0.54**	−0.18	**−0.30**	n.a.	0.23	0.02	0.10	−0.23	−0.24	−0.13
		$\Sigma\,w_i$			**1.00**	0.48	**0.81**	n.a.	0.41	0.20	0.26	0.59	0.43	0.30

Phylogenetic signal among plants and hummingbirds, d_p and d_h, respectively; Ins, insularity; MAT, mean annual temperature; TS, temperature seasonality; MAP, mean annual precipitation; PS, precipitation seasonality; MAT vel, velocity of temperature change since the Last Glacial Maximum; MAP vel, velocity of precipitation change since the Last Glacial Maximum; n.a., not applicable.
The significance of Moran's I was tested with 10 distance classes and a permutation test with 10,000 iterations. Multicollinearity was not an issue in any of the models, i.e. Variance Inflation Factor (VIF) ≤ 3.4, Condition Number (CN) ≤ 4.0, and there was no positive spatial autocorrelation, i.e. Moran's I was non-significant.
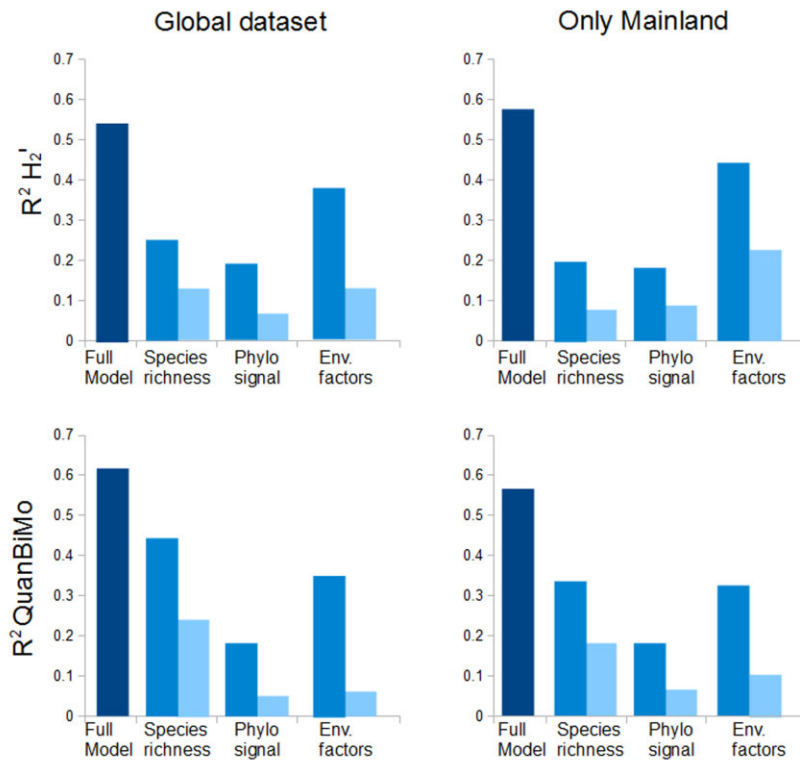
Figure 3 Coefficients of determination (R^2) for complementary specialization and modularity obtained from partial regression of the full models, i.e. models including all 10 predictor variables (see Table 1 for standardized coefficients of each variable and more details of model fit, and Table S3 for the R^2 values used in this figure). Complementary specialization measures the exclusiveness in species interactions, whereas modularity quantifies whether species interact more frequently with subsets of available species within a community. We 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 'predictor types' and network structure. Predictor types refers to (1) species richness (one variable), (2) phylogenetic signal (two variables: phylogenetic signal in the interaction pattern of plants and hummingbirds), and (3) environmental factors (eight variables: insularity, average annual temperature, temperature seasonality, total annual precipitation, precipitation seasonality, temperature and precipitation-change velocity between the Last Glacial Maximum and pre-industrial times). The amount of variation explained by each pooled predictor type is coded with different shades: bars coloured in darkest colour/shade depict the overall variation explained by all factors together; medium colours/shades illustrate the total variation explained by that predictor type; light colours/shades show the unique variation explained by each predictor type and not shared by other variable types. H_2', complementary specialization; QuanBiMo, quantitative bipartite modularity.

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 (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 explained by species richness in the Global dataset (Table S3, Fig. 3). However, when examining only mainland networks, the unique variation explained by environmental factors was twice as much as the unique variation explained by the other two predictor types (Table S3, Fig. 3). Among the seven environmental variables examined, only current temperature and historical temperature stability showed a strong relationship to complementary specialization, with increasing complementary specialization in communities with current warmer temperatures and with a higher historical temperature stability (Table 1).

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

For both complementary specialization and modularity. 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 signal were distinctly associated with specialization and modularity. Shared variability between environmental factors and species richness or phylogenetic signal was low (Table S3).

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

DISCUSSION

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

Hummingbird phylogenetic signal had a constant association with both complementary specialization and modularity, and on both the Global and Only Mainland datasets, although the variability associated with phylogenetic signal was the lowest of all predictor types. A weak but significant relationship between phylogenetic signal and species interaction patterns within ecological networks has also been reported by previous studies on food webs, host–parasite networks and plant–pollinator networks (Ives & Godfray, 2006; Vázquez et al., 2009b; Krasnov et al., 2012; Rafferty & Ives, 2013). These studies also identified asymmetries in the phylogenetic signal between trophic levels, with the association between phylogenetic 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 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 likely to adjust their feeding behaviour according to local conditions. Our results corroborate this hypothesis: hummingbird phylogenetic signal showed a weaker relationship with their 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 showed no association with the spatial variation in network structure, hummingbird phylogenetic signal was associated with network structure, with higher levels of complementary specialization and modularity being consistently achieved when closely related hummingbird species visited distinct sets of flowering plant species. This suggests that resource partitioning and interspecific competition among closely related hummingbirds might play an important role in structuring interactions in hummingbird–plant networks. Indeed, interspecific 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; Cotton, 1998).

Species richness had the strongest association with both metrics, and in both the 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 opportunities for biotic specialization. At the same time, higher species richness may increase interspecific competition, which may explain why high species richness leads to higher levels 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 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 and, hence, the potential for biotic specialization (Montgomerie & Gass, 1981; Stiles, 1985; Araujo & Sazima, 2003; Cotton, 2007; Abrahamczyk et al., 2011).

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 be linked to higher interspecific competition in warmer areas, and particularly in mainland settings, where hummingbird species and phylogenetic richness is highest (Bleiweiss, 1998; 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 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 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 in areas with low temperature-change velocity, such as montane habitats and tropical environments, leaving more generalized interaction patterns to areas with low topography and, especially, higher latitudes where changes in temperature velocity have been greatest (Sandel et al., 2011). Moreover, a higher complementary specialization in areas of high historical temperature stability is consistent with general hummingbird historical biogeography and speciation patterns, as the core area of hummingbird speciation and diversity occurs in the Andean highlands and in tropical lowland South America (Brown & Bowers, 1985; Bleiweiss, 1998; McGuire et al., 2014). We note that complementary macroecological analysis presented in Appendices S3–S5 generally confirmed the importance of species richness and hummingbird phylogenetic signal, and also showed that observed (uncorrected) complementary specialization/modularity were associated with insularity and precipitation: areas of high precipitation and mainland communities showing higher observed complementary specialization and modularity. Precipitation has previously been shown to influence floral phenotypic specialization and the importance of hummingbird–plant interactions for entire pollination communities (Cruden, 1972; Dalsgaard et al., 2009; Martín González et al., 2009). The fact that precipitation and insularity were only associated with observed complementary specialization and observed modularity, and not with null-model-corrected values of these network metrics, may indicate that insularity and precipitation do not directly influence the interaction pattern of species but rather associate indirectly with network structure through species richness and/or interaction probability distributions.

CONCLUSIONS

Characterizing the potential ecological, historical and evolutionary mechanisms associated with the structure of ecological communities is a critical first step towards understanding the 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 metrics, we are investigating how much observed communities depart from random ones with an equivalent set of species and interactions. Hence we are able to investigate whether a community presents a structure which differs significantly from random and also to associate the difference in complementary specialization and modularity with species richness and evolutionary and environmental conditions.

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

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Appendix S1 List of all plant and hummingbird species present in the studied networks.
Appendix S2 Phylogenetic methods.
Appendix S3 Effect of the differences in sampling effort among data sets on network structure.
Appendix S4 Results of macroecological models on observed network metrics.

Appendix S5 Complementary macroecological analyses.
Figure S1 Association between species richness (network size) and hummingbird phylogenetic signal with null model corrected measures of complementary specialization (H'_2) and quantitative bipartite modularity (QuanBiMo).
Table S1 Coordinates, description, location and data references for each studied community.
Table S2 Correlations between corrected and observed indices of network structure and the predictor variables included in the OLS models.
Table S3 Coefficients of determination (R^2) from partial regression local models separating the effect of species richness, phylogenetic signal and environmental factors as predictors of corrected network structure when including climate change velocity as an estimate of historical climate stability.

BIOSKETCH

This work results from an ongoing collaboration among numerous researchers from different scientific backgrounds and institutions who have gathered an extensive 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 different aspects of hummingbird–plant interaction patterns at macroecological scales and to identify the potential mechanisms responsible for them. Our ultimate goal is to describe general macroecological patterns in biotic interactions using hummingbird–plant interactions as a model system.

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