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Spatial distance and climate determine modularity in a cross-biomes plant–hummingbird interaction network in Brazil

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Abstract

Aim: We examined the effects of space, climate, phylogeny and species traits on module composition in a cross-biomes plant–hummingbird network.

Location: Brazil, except Amazonian region.

Methods: We compiled 31 local binary plant–hummingbird networks, combining them into one cross-biomes metanetwork. We conducted a modularity analysis and tested the relationship between species' module membership with traits, geographical location, climatic conditions and range sizes, employing random forest models. We fitted reduced models containing groups of related variables (climatic, spatial, phylogenetic, traits) and combinations of groups to partition the variance explained by these sets into unique and shared components.

Results: The Brazilian cross-biomes network was composed of 479 plant and 42 hummingbird species, and showed significant modularity. The resulting six modules conformed well to vegetation domains. Only plant traits, not hummingbird traits, differed between modules, notably plants' growth form, corolla length, flower shape and colour. Some modules included plant species with very restricted distributions, whereas others encompassed more widespread ones. Widespread hummingbirds were the most connected, both within and between modules, whereas widespread plants were the most connected between modules. Among traits, only nectar concentration had a weak effect on among-module connectivity.

Main conclusions: Climate and spatial filters were the main determinants of module composition for hummingbirds and plants, potentially related to resource seasonality, especially for hummingbirds. Historical dispersal-linked contingency, or environmental variations not accounted for by the explanatory factors here evaluated, could also contribute to the spatial component. Phylogeny and morphological traits had no unique effects on the assignment of species to modules. Widespread species showed higher within- and/or among-module connectivity, indicating their key role connecting biomes, and, in the case of hummingbirds, communities within biomes. Our results indicate that biogeography and climate not only determine the variation of modularity in local plant–animal networks, as previously shown, but also affect the cross-biomes network structure.

KEYWORDS

biogeography, module composition, ornithophily, phylogeny, pollination, range size, species roles, traits

1 | INTRODUCTION

Knowledge about how biotic interactions are distributed within and between communities is crucial for understanding both species interdependence and community dynamics. For instance, biotic interactions are typically not evenly distributed within communities (Vázquez, 2005). Several tools have been used for the detection of community structure, with modularity being one of the most widespread techniques for describing network clustering (Alzahrani &

Horadam, 2016; Fortunato & Hric, 2016). Indeed, modularity appears as a common feature across a wide variety of ecological and biogeographical networks, i.e. networks based on species occurrence across large areas (Dalsgaard et al., 2013; Kougioumoutzis, Simaiakis, & Tiniakou, 2014; Martín González et al., 2015; Olesen, Bascompte, Dupont, & Jordano, 2007). In modular networks species tend to interact intensively within subsets of species (modules), so that species in a given module interact more frequently with species in the same module than with species outside of it (Olesen et al., 2007).

Several factors such as current and historical climate, species' distributional ranges, morphological traits and phylogenetic relationships may show associations with the level of modularity and module composition, and hence, with the specialization of plant–hummingbird interactions (Dalsgaard et al., 2013; Martín González, Allesina, Rodrigo, & Bosch, 2012; Martín González et al., 2015). However, the importance of these factors seems to vary according to network type and scale of the study (Allen, 2006; Gilarranz, Hastings, & Bascompte, 2015; Martín González et al., 2015; Schleuning et al., 2014). For instance, current climate may shape biotic interactions through the phenologies, range distributions and abundances of plants and hummingbirds (Dalsgaard et al., 2009, 2011; Martín González, Dalsgaard, Ollerton, & Timmermann, 2009), whereas historical climate instability could alter species' phenologies or geographical distributions, causing a decrease in interaction specificity and modularity (Dalsgaard et al., 2011, 2013). If such associations are strong, species with overlapping phenologies and/or similar climatic requirements are expected to occur in the same module (e.g. Martín González et al., 2012; Tur, Olesen, & Traveset, 2015). Species with similar evolutionary histories and phenotypes are likely to interact with the same set of partners, thus forming modules of similar phenotypes (Aizen et al., 2016; Danieli-Silva et al., 2012; Gómez, Verdú, & Perfectii, 2010; Maruyama, Vizentin-Bugoni, Oliveira, Oliveira, & Dalsgaard, 2014; Rezende, Lavabre, Guimaraes, Jordano, & Bascompte, 2007). Altogether, numerous studies reveal that spatiotemporal overlap, phylogenetic relationships, morphology and interspecific competition are associated with module membership and/or variation in modularity in plant–hummingbird networks (Dalsgaard et al., 2013; Martín González et al., 2012, 2015; Maruyama et al., 2014).

Recent studies have addressed the effects of climate (past and contemporary), phylogeny and traits on the modular structure of *local* mutualistic plant–animal interaction networks (e.g. Dalsgaard et al., 2013; Martín González et al., 2015; Schleuning et al., 2014). However, little is known about the determinants of *cross-biomes* networks (Mello, Bezerra, & Machado, 2013), i.e. regional networks of species built from combining many local networks, spanning large spatial areas and including different habitat types. In these, species distributions over a large spatial extent are likely to exert a strong influence on the modular pattern, as turnover in species composition tends to increase with greater geographical distance from a source (McCoy & Heck, 1987; Vilhena & Antonelli, 2015). Therefore, considering communities spanning large areas, species occurring in geographically close locations would experience more chances to interact with each other and occur in the same module, resulting in modules representing the spatial distribution of species (Gilarranz & Bascompte, 2012; Gilarranz et al., 2015). In addition, co-evolutionary histories and the existence of dispersal barriers could also affect patterns of interactions (Dupont & Olesen, 2009; Kougioumoutzis et al., 2014).

Brazil is a large country (8,516,000 km²), which encompasses diverse vegetation domains including open grasslands, savannas and dense forests. Accordingly, patterns of interactions between hummingbirds and their food plants should vary across this almost continental scale. In this study we evaluate the major drivers of plant–hummingbird interactions at the cross-biomes scale, examining how interactions are distributed across space and which factors may explain observed interaction patterns. We ask: (a) whether the organization of a cross-biomes plant–hummingbird network is better explained by climate, geographical and evolutionary constraints or traits related to pairwise interactions; (b) whether drivers of module composition vary between hummingbirds and plants; and (c) whether species with a greater importance in the network have greater range sizes and generalist behaviour and traits. For instance, we expect that hummingbirds less central in the network would be long-billed and large-sized species that visit specialized flowers (Dalsgaard et al., 2009).

2 | MATERIALS AND METHODS

2.1 | Data set

We compiled a data set consisting of 31 local binary plant–hummingbird interaction networks from six different Brazilian biomes (vegetation domains), covering 1,860,700 km² (Figure 1; Appendix S1, Table S1.1). These domains represent areas with low climatic seasonality such as (a) Atlantic forest (14 networks): rain forest spread through the Brazilian coast, including both lowland and highland formations and (b) Pampas (one network): grasslands occurring in Southern Brazil; domains with markedly seasonal climates such as (c) Caatinga (three networks): xeric shrublands occurring mostly in the Northeastern region; (d) Pantanal wetland (two networks): a mosaic of shrublands, grasslands and forests subjected to seasonal flooding occurring in Southwestern Brazil; and savanna formations occurring mainly in central and Southeastern Brazil represented by (e) Cerrado (nine networks): woody grasslands including distinct phytophysiognomies (Eiten, 1978) and (f) Rupestrian Fields (two networks): a savanna subtype occurring on rocky outcrops with grasslands, herbaceous vegetation and shrubs, in mountain areas (>900 m a.s.l.).

We only included studies with sampling periods that span at least 1 year and sampled the entire community of plant species legitimately visited by hummingbirds, i.e. we excluded studies that restricted sampling only to plants conforming to the classical ornithophilous syndrome, and larceny interactions (i.e. visits with no potential to result in pollination). Larceny interactions were excluded because they are antagonistic.

As we aimed to test for the effect of evolutionary history on hummingbird–plant interactions, we excluded exotic plant species from the analysis. We prepared one binary matrix of interactions with rows and columns as plant and hummingbird species. Each cell was filled with 1 when an interaction between that plant and hummingbird species was recorded, and 0 otherwise. We also built two matrices with morphological traits, range sizes, phylogenetic, climatic and geographic information of plants and hummingbirds.

For plants, the used floral/morphological traits were growth form, corolla shape, colour and length, and nectar concentration.
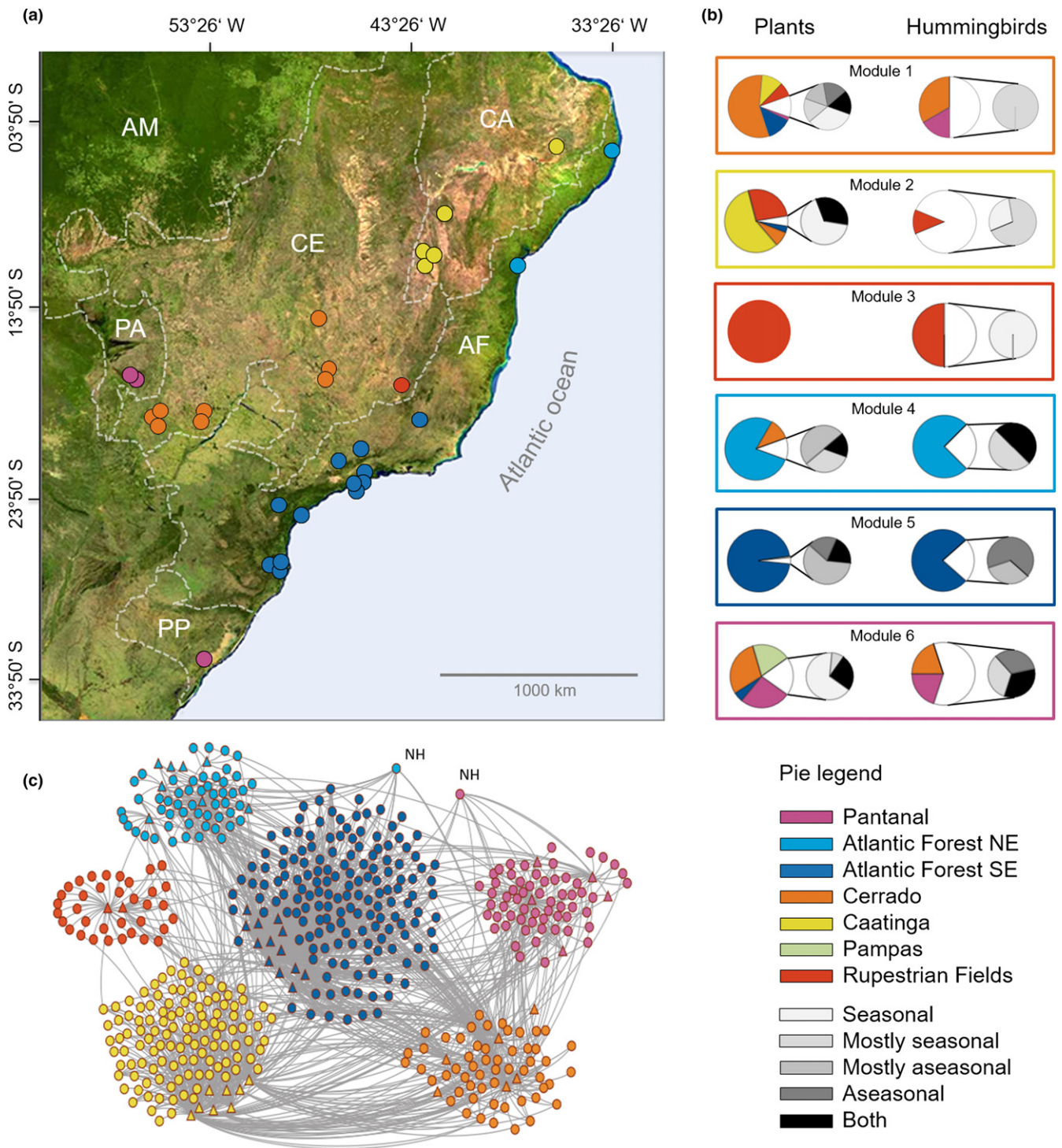
FIGURE 1 (a) Location of the 31 networks in the Brazilian biomes (CA: Caatinga; CE: Cerrado; AF: Atlantic forest; PA: Pantanal; PP: Pampas; AM: Amazon). Dots indicate the 31 networks included, and their colours denote the module that most of their constituent species were assigned to, as displayed in the frames of coloured boxes in (b) and in the network in (c); (b) Proportions of plant and hummingbird species in the six modules according to their domains of origin. White slices in colourful pies represent proportion of species occurring in more than one domain, which were classified according to their seasonality (Seasonal—more than one seasonal area, Aseasonal—more than one less seasonal area, Both—equal proportions of seasonal and less seasonal areas); (c) Cross-biomes network showing the six modules. Circles represent plants and triangles the hummingbirds. Note network hubs (NH) in modules four and six [Colour figure can be viewed at wileyonlinelibrary.com]

Growth form categories were *herb*, *epiphytic* (including hemiparasites), *shrub* (including subshrub), *tree* (including treelets), *lianas* and *cacti* (all Cactaceae species, due to their generally succulent growth form). We also defined six types of corolla shapes (modified from Ramírez, 2003), *dish* (open flowers, including open and disc types), *bell* (including funnel type), *tube*, *brush*, *gullet* and *flag*. We followed

Dalsgaard et al. (2009) for classes of corolla colour, ranging from less specialized to more typical ornithophilous colours: blue/violet (a), purple/yellow/green/white (b), pink/salmon or bi-coloured yellow and red (c), and red/orange (d). Morphological traits included for hummingbirds were bill length (measured as exposed culmen, in mm) and body mass (measured in g). Range size measures the commonness or extension of occurrence of the plant or hummingbird in the network (described below).

A plant phylogeny was obtained from the compiled tree in Phylomatic (see phylodiversity.net/phylomatic). Branch lengths were estimated using the *bladj* function from Phylocom (Webb, Ackerly, & Kembel, 2008), using calibration dates from Wikström, Savolainen, and Chase (2001). The hummingbird phylogeny was obtained from a Bayesian phylogenetic tree calibrated by time, constructed from DNA samples of 284 hummingbird species (McGuire et al., 2014). In order to describe the phylogenetic relationships among species, we calculated phylogenetic eigenvectors (Diniz-Filho, Sant'Ana, & Bini,1998) and kept the first 20 eigenvectors for each phylogeny. These eigenvectors reflect deep-to-moderate structure of the phylogeny, with the first eigenvector reflecting the earliest divergence within the clade.

Information on historical and current climate was obtained from WorldClim (www.worldclim.org) with a spatial resolution of 1×1 km. For the 31 studied networks, we extracted the following data regarding contemporary climate: mean annual temperature (MAT, °C), temperature seasonality (TSN, standard deviation of monthly temperature $\times$ 100), mean annual precipitation (MAP, mm) and precipitation seasonality (PSN, coefficient of variation of monthly precipitation). To describe past climate, we obtained data on temperature (T_{lgm}, °C) and precipitation (P_{lgm}, mm) at the Last Glacial Maximum. To evaluate the impact of climatic instability, we included temperature velocity (T_{veloc}, m/year) and precipitation velocity (P_{veloc}, m/year), which were calculated following Loarie et al. (2009) and illustrate the speed of climatic change between the Last Glacial Maximum (LGM) and preindustrial times. Means for climatic data, topography and elevation for each network were extracted for a 10 km radius around each network. For species occurring in more than one network, we calculated the means of these values.

Finally, using the geographical coordinates of each of the 31 networks, we conducted a principal coordinate analysis (PCoA; Griffith & Peres-Neto, 2006). The resulting first 10 eigenvalues for each species were included as spatial filters in the model (described below; see Appendix S1, Figure S1.1). For species occurring in more than one network, we calculated means for the eigenvalues obtained for each network. These filters describe the spatial distribution of species in the region under study at different scales, and can be used as predictors of a response variable (Diniz-Filho & Bini, 2005). This approach has the advantage of minimizing residual spatial autocorrelation because any remaining spatial structures in regression residuals are taken into account (Diniz-Filho & Bini, 2005).

Only species with information on all the traits were included in the statistical model where we evaluated the drivers of module composition (81.4% of plants and 97.6% of hummingbirds; see below).

2.2 | Data analysis

2.2.1 | Network modularity

Modularity analysis was conducted in MODULAR (Marquitti, Guimarães, Pires, & Bittencourt, 2014), using the Barber's metric (2007) and simulated annealing maximization algorithm for bipartite networks and the recommended settings. To examine whether matrix modularity differs from randomness, we calculated modularity on 100 null matrices of the same size and connectance as the empirical matrix, and where species interact proportionally to their observed number of interactions (Bascompte, Jordano, Melián, & Olesen, 2003). After this first analysis, we computed modularity within each resulting module independently to test for the occurrence of submodules inside modules. As a sensitivity test, we also analysed modularity using the recently implemented LPAb+ algorithm (Beckett, 2016; Liu & Murata, 2010) (see Appendix S2).

Species roles for hummingbirds and plants were calculated following Olesen et al. (2007). The within-module degree (z) is a measure of the number of connections a species has within its own module relative to other species in that module, whereas the among-module connectivity (c) informs about how well a given species is connected to species from other modules (Olesen et al., 2007). According to their c and z-values, species were classified as: *peripherals* (low values of both c and z), *connectors* (high c and low z-values), *module hubs* (high z and low c values) or *network hubs* (high values of both c and z). We tested for effects of species' traits (corolla length and nectar sugar concentration for plants, and bill length and body mass for hummingbirds) and range sizes (RS1 and RS2, see below) on c and z-values separately, using forward stepwise General Linear Models, with partial alpha <0.05 to enter variables. Only one final model included more than one predictor variable and the path diagram is then presented to it.

To test whether vegetation domains explain module composition, we used Contingency Analysis to evaluate if the proportion of species from the same (or similar) vegetation domain in a given module was higher than expected by chance.

2.2.2 | Range size

We calculated two measures of range size to describe how widespread the hummingbird and plant species are across the studied areas: "Range size 1" (RS1), represents the number of networks (out of 31 total) in which a given species occurred, and "Range size 2" (RS2) represents the maximum geographical distance between the networks within which a species was recorded.

2.2.3 | Statistical model

We explained species' module memberships from their phylogeny, traits, spatial positions resulting from the PCoA, climatic conditions and range sizes. For this purpose, we employed Random Forest models as implemented in the R package 'randomForest' (Liaw &

Wiener, 2002). We fitted two Random Forest models (one for plants and one for hummingbirds) with 500 randomizations each. Classification trees and Random Forest models are appropriate tools for the analysis of such complex ecological data sets, being able to model high-order interactions, multicollinearity and nonlinear responses (De'ath & Fabricius, 2000) with easy interpretability (Loh, 2014).

The focal unit of analysis in the statistical model was the species. To evaluate the effects of climate, geography, phylogeny and traits on the assignment of species to modules, we first examined the correlations among the climatic variables. When a variable pair was highly correlated, we kept the variable showing the highest importance in determining module membership (assessed using Random Forest), and kept both variables if they were both of high importance. Thus, we only included the following climatic variables in the model: mean annual temperature (MAT), temperature seasonality (TSN), mean annual precipitation (MAP), precipitation seasonality (PSN), temperature velocity (T_{veloc}) and precipitation velocity (P_{veloc}), along with topography and elevation. For species traits, no strong correlations were observed, and thus all traits were kept in the analysis. As RS1 and RS2 were correlated ($r_s = 0.69$, $p < 0.0001$ for hummingbirds; $r_s = 0.70$, $p < 0.0001$ for plants), we kept only RS1 in the model.

In addition, we fitted reduced models containing groups of related variables (climatic, spatial, phylogenetic and trait variables) and combinations of groups to partition the variance explained by these sets into unique and shared components, which we visualized with Venn diagrams (Legendre, 2008; Moritz & Faith, 1998).

3 | RESULTS

3.1 | Modularity and species traits

The resulting cross-biomes network was composed of 479 plants and 42 hummingbird species (See Appendix S3), was significantly modular ($M = 0.512$, $\bar{M}_{null1} = 0.3967$, z-score = 12.715; $\bar{M}_{null2} = 0.3879$, z-score = 15.105) and formed by six modules containing between 35 and 157 plants and 2 and 13 hummingbird species. These modules differed significantly regarding domains of origin for both hummingbirds (Contingency coefficient $c = 0.82$, Cramér's $v = 0.82$, $p < 0.001$) and plants ($c = 0.82$, $v = 0.64$, $p < 0.001$), and included up to three different vegetation domains. Modules 1 and 2 included species from seasonal areas (Caatinga, Cerrado and Rupestrian Fields), Module 3 included mostly species from Rupestrian Fields, Modules 4 and 5 presented mostly species from Atlantic forest, and Module 6 included species from Cerrado, Pantanal and Pampas (Figure 1).

There were no differences between modules regarding hummingbird morphological traits (bill length and body mass; all p-values >0.05). In contrast, plant habit ($\chi^2 = 183.58$, $df = 25$, $p < 0.0001$), flower shape ($\chi^2 = 69.59$, $df = 25$, $p < 0.0001$), colour ($\chi^2 = 72.90$, $df = 15$, $p < 0.0001$) and corolla length ($H = 38.56$, $p < 0.0001$, Kruskal–Wallis) varied between modules, although flowers in all modules were mostly tubular and of colour classes 2 (purple/yellow/

green/white) or 3 (pink/salmon or bi-coloured yellow and red; Figure 2). Average corolla length was relatively long in Module 5 ($\bar{X} = 28.98 \pm 1.21$) and relatively short in Module 3 (($\bar{X} = 15.58 \pm 2.59$).

3.2 | Distribution extents of species in the modules

Both measures of range size (RS1 and RS2) differed among modules for plants (RS1 $p < 0.0001$; RS2 $p < 0.0001$). Plants in Module 1 (mostly from the Cerrado) and Module 5 (mostly from Southeastern Atlantic forest) occurred in several local networks (RS1 = 0.055 ± 0.004 and RS1 = 0.055 ± 0.004 of the networks, respectively) and species in Module 1 also occurred in networks more distant from each other (RS2 = 329.76 ± 73.7 km). In contrast, plants assigned to Modules 2 and 3 (from Caatinga and Rupestrian Fields in Northeastern/Rupestrian Fields in Central Brazil, respectively) had narrower distributions (RS2 = 116.99 ± 37.62 km and RS2 = 20.81 ± 20.81 km, respectively) and were less represented across modules (RS1 = 0.036 ± 0.002 and RS1 = 0.031 ± 0.0009 of the networks, respectively). There were no differences between modules regarding RS1 ($p = 0.37$) or RS2 ($p = 0.55$) for hummingbirds.

3.3 | Species roles and traits

Most species acted as "peripherals" (92.5% of plants and 90.4% of hummingbirds), followed by "connectors" (5.4% of plants and 9.5% of hummingbirds) and "module hubs" (1.7% plants; Figure 3). "Connector" and "peripheral" plants were shrubs or herbs, mostly with tubular corollas of various colours except blue/violet, whereas "module hubs" were mainly epiphytes with specialized flowers (tubular red/yellow or pink). Only two plant species acted as "network hubs", the non-ornithophilous tree *Inga vera* (Fabaceae) and the ornithophilous epiphyte *Vriesea procera* (Bromeliaceae) (Figure 4), both widely distributed in Brazil (CNC Flora, 2012; Pennington, 1997). Among hummingbirds, there were no "supergeneralists" (i.e. "network hub" or "module hub"), and only four species were connectors (*Amazilia fimbriata*, *Eupetomena macroura*, *Phaethornis pretrei* and *Aphantochroa cirrochloris*) (Figure 4). These four hummingbirds were widespread, with distributions ranging from 2,280,000 km² (*Aph. cirrochloris*) to 12,700,000 km² (*Ama. fimbriata*; Birdlife International 2016). In the stepwise GLM for hummingbirds, only RS2 entered in the final model explaining c and z ($r^2 = 0.39$ and $r^2 = 0.24$ respectively; $p < 0.001$). For plants, only RS2 explained z ($r^2 = 0.213$; $p < 0.001$), but three variables (RS1, RS2 and nectar concentration) were included in the model explaining c ($r^2 = 0.229$, $p < 0.001$), although nectar had only a weak and negative effect (See Appendix S4, Figure S4.2).

3.4 | Drivers of module composition

According to the classification trees, space and climate were the main factors associated with plants' and hummingbirds' module membership. Spatial filter 2 (a longitudinal filter that mostly
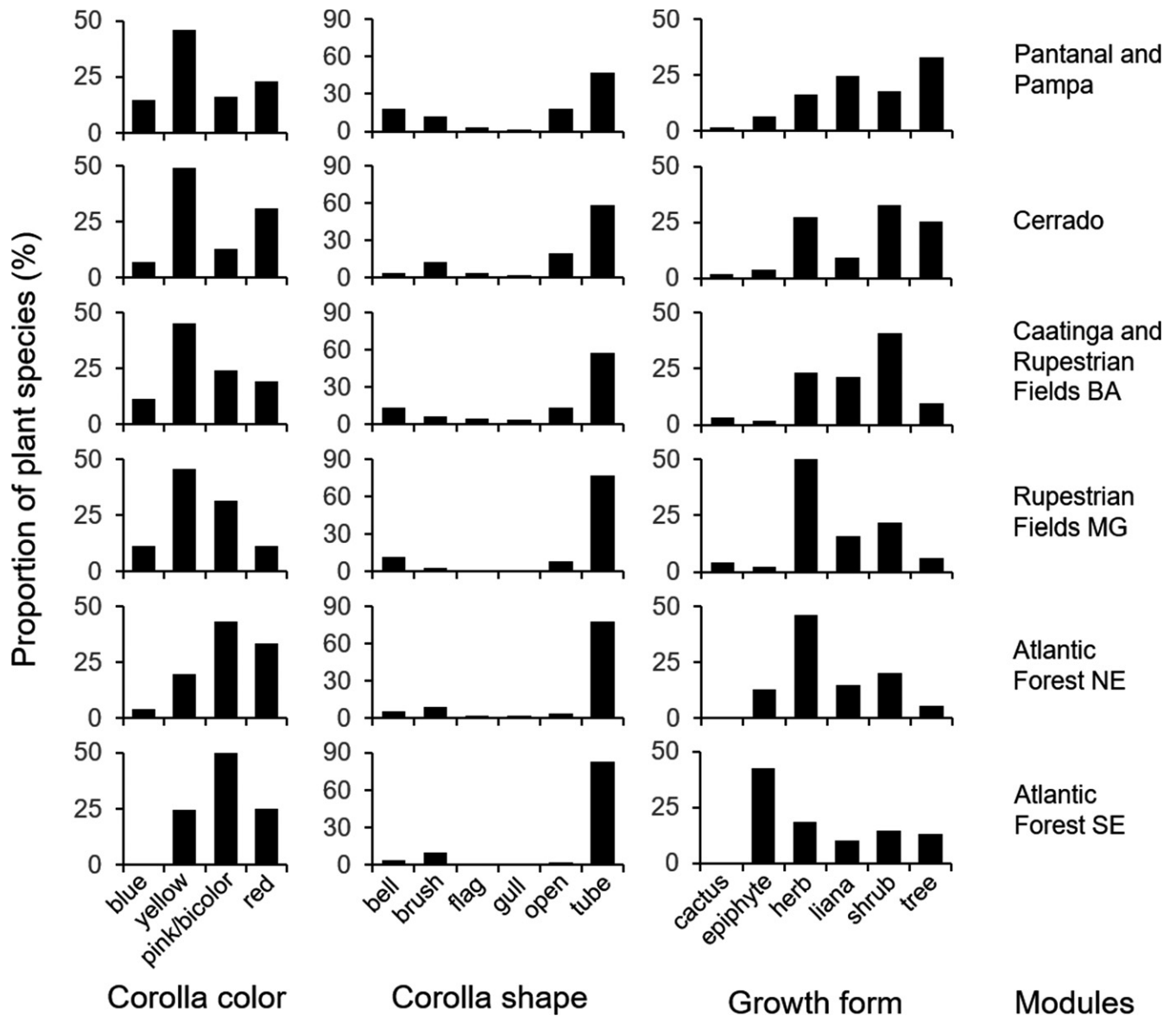
FIGURE 2 Proportion of plant species in each module bearing different traits regarding to corolla colour, corolla shape and growth form (BA: Bahia state; MG: Minas Gerais state; NE: Northeastern; SE: Southeastern)

separated areas of the Brazilian inland from the coast) was associated with the first division and, within each subgroup, climatic and other spatial variables further separated the modules (Figure 5).

Based on the correct prediction rates, it was possible to quantify the accuracy of each model in terms of predicting the module assignment for plants and hummingbirds. For plants, for example, climate alone and a combination of climate and spatial filters gave a correct prediction rate of 0.83. A model including traits, climate and phylogenetic filters also resulted in a high accuracy (0.82). For hummingbirds, a model including space and climate gave the highest rate of correct prediction (0.78), and climate alone gave a rate of 0.76. Overall, climate and spatial filters emerged as the most relevant predictors (Table 1).

However, different predictors exert overlapping effects on module assignment for both plants and hummingbirds, as observed for

spatial filters and climate (Table 1). Phylogeny and traits had virtually no unique effect, that is, climate and spatial filters already accounted for all the explanation produced by these predictors (Figure 6). These results indicate that climate had the strongest association with module composition, with additional effects of spatial filters and a negligible effect of phylogeny and traits.

4 | DISCUSSION

Our study confirms the importance of climate and space for structuring mutualistic interactions, as these factors appeared as main determinants of modularity in the cross-biomes Brazilian plant–hummingbird network. Climate alone had the same effect as a mix of climate and space for plants, whereas for hummingbirds the joint
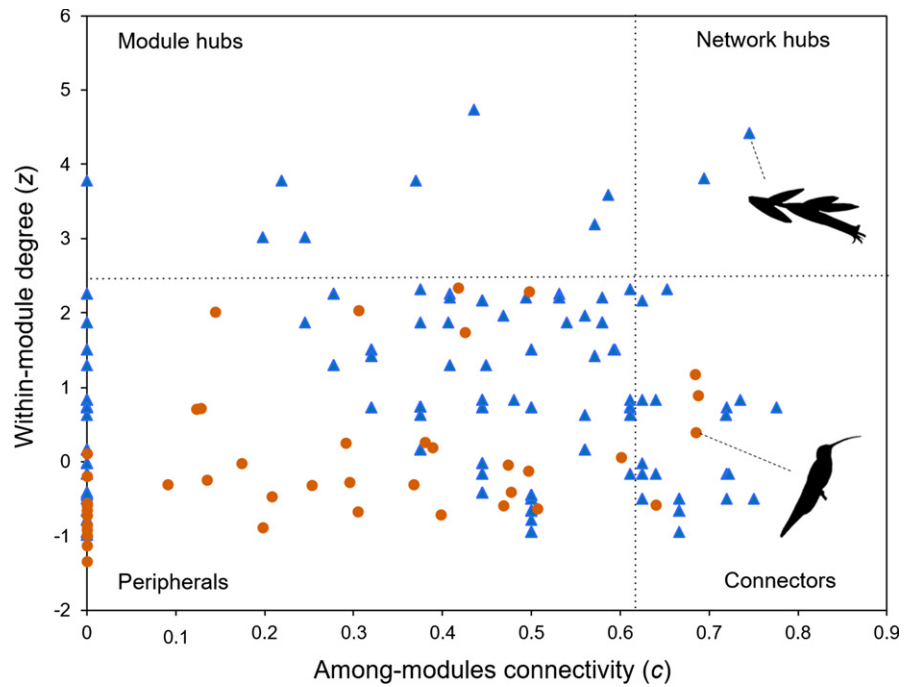
FIGURE 3 Distribution of plant (blue triangles) and hummingbird (red circles) species according to their values of "among-module connectivity" (c) and "within-module degree" (z) in the Brazilian cross-biomes network. The threshold value of $z = 2.5$ and $c = 0.62$ followed Guimerá and Amaral (2005). The illustrated silhouettes are the network-hub *Vriesea procera* (plant) and the connector *Phaethornis pretrei* (hummingbird) [Colour figure can be viewed at wileyonlinelibrary.com]

FIGURE 4 Two of the four connector hummingbirds reported in this study: (a) the traplining Planalto Hermit *Phaethornis pretrei* and (b) the territorial Swallow-tailed Emerald *Eupetomena macroura*. Both hummingbirds are widespread in Brazil. The network-hubs *Vriesea procera* (c) and *Inga vera* (d). Photo credits Ivan Sazima (a, b), Licléia C. Rodrigues (c), Andréa C. Araujo (d) [Colour figure can be viewed at wileyonlinelibrary.com]

effect of climate and spatial filters provided higher predictive performance. In marked seasonal areas, floral availability is unexpected to be regularly distributed through time. For instance, in areas like Cerrado, Pantanal and Caatinga, hummingbirds tend to use non-ornithophilous species as resources with greater frequencies than the ornithophilous species (Araujo & Sazima, 2003; Araújo, Sazima, & Oliveira, 2013; Las-Casas, Azevedo Júnior, & Dias Filho, 2012; Maruyama, Oliveira, Ferreira, Dalsgaard, & Oliveira, 2013; Rodrigues &
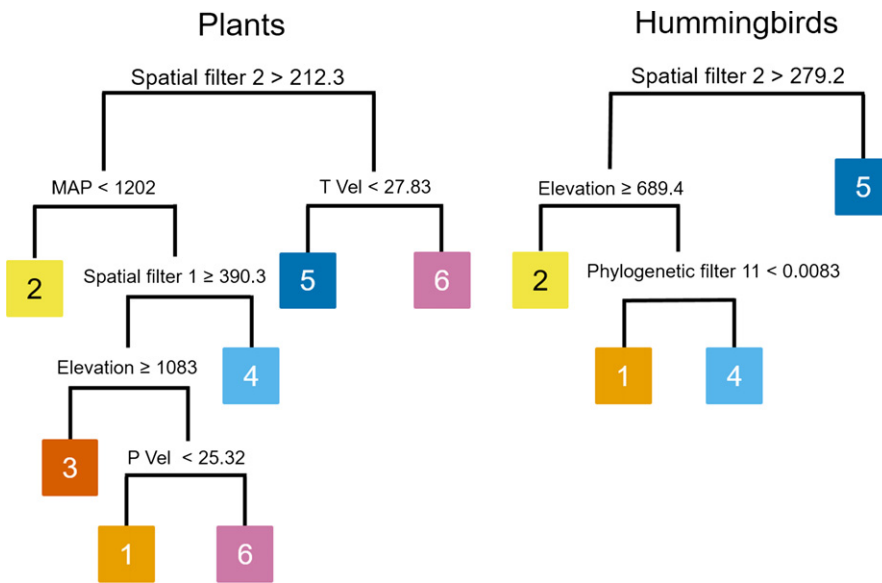
Plants

Spatial filter 2 > 212.3

MAP < 1202

T Vel < 27.83

2

Spatial filter 1 ≥ 390.3

5

6

Elevation ≥ 1083

4

3

P Vel < 25.32

1

6

Hummingbirds

Spatial filter 2 > 279.2

Elevation ≥ 689.4

5

2

Phylogenetic filter 11 < 0.0083

1

4

FIGURE 5 Classification trees to identify the roles of climate, space, phylogeny and traits on assigning plants and hummingbirds to modules (numbers and colours in boxes) in the Brazilian cross-biomes network. *P* Vel: Precipitation velocity; *T* Vel: Temperature velocity; MAP: Mean Annual Precipitation. Boxes colours denote modules membership, as used in Figure 1 [Colour figure can be viewed at wileyonlinelibrary.com]

Araujo, 2011), often in periods of scarcity of the latter (Araujo & Sazima, 2003). On the other hand, Atlantic forest sites, characterized by a less seasonal climate, both in terms of temperature and rainfall, may offer a more constant array of floral sources and, in general, include plants more specialized for hummingbird pollination (Buzato, Sazima, & Sazima, 2000; Vizentin-Bugoni, Maruyama, & Sazima, 2014). In fact, the greater corolla length recorded for these modules indicates a higher phenotypic specialization of the plant–hummingbird assemblages in the Atlantic forest.

Although modular partitioning was consistent with the main vegetation domains included in this study, geographical distance also played an important role in determining module composition. Historical dispersal-linked contingencies (i.e. differences in species arrival history during community assembly), could vary across space, and might correspondingly affect the resulting different sets of interacting species identified in our analyses (Fukami, 2015). For instance, this mechanism might explain the separation of modules including more inland communities from those comprising coastal sites. This could also relate to the savanna corridor that separated the continuous forest that occurred between the Amazonian region and Paraná during the Neogene, and may reflect dispersion limitation due to the

dry barrier between the moister biomes of either side. This corridor, comprising the *Chacoan subregion* (Morrone, 2006, 2014), could have resulted in different evolutionary histories as a consequence of a dynamic vicariant effect (Morrone, 2006). In addition, networks from the Southern and Northern Atlantic forests were assigned to different modules. Historical biogeography could explain this result, as the Northeastern Atlantic forest includes two centres of endemism, one in Bahia and another one in Pernambuco (Carnaval & Moritz, 2008). Furthermore, forest contractions in the Southern portion of the Atlantic forest are suggested to have occurred around the Last Glacial Maximum, approximately 21 ka BP (Carnaval & Moritz, 2008). These historical events have probably resulted in distinct contemporary plant assemblages. Similar effects were recorded for Rupestrian Fields from the Espinhaço Range, which is characterized by a high representation of endemic species (Giulietti & Pirani, 1988; Giulietti, Pirani, & Harley, 1997; Rapini, Ribeiro, Lambert, & Pirani, 2008), resulting in low floristic similarities even within neighbouring localities (Rapini et al., 2008).

A notable finding here is that of the congeneric hummingbirds *Augastes scutatus* and *A. lumachella*, possibly exemplifying a case of vicariance (Vasconcelos, 2009). The former is endemic to Serra do Cipó (Module 3) and the second is endemic to Chapada Diamantina and neighbouring areas of Caatinga (Module 2). Rupestrian Fields from Serra do Cipó present floristic affinities with Atlantic forest, whereas vegetation of Rupestrian Fields from Chapada Diamantina present more affinities with Caatinga (Eiten, 1978), and most of its species were indeed assigned to the module representing this latter domain.

The identified spatial effect could also to some extent describe environmental variations not accounted for by the explanatory factors here evaluated, such as, for example, human disturbance. If anthropogenic impacts vary among the studied areas, their effects on species composition and on the resulting patterns of species interactions in communities also will likely differ (e.g. Stout, 2014;

TABLE 1 Proportion of species of plants and hummingbirds assigned to the observed modules by Random Forest models in a cross-biomes plant–hummingbird interaction network from Brazil

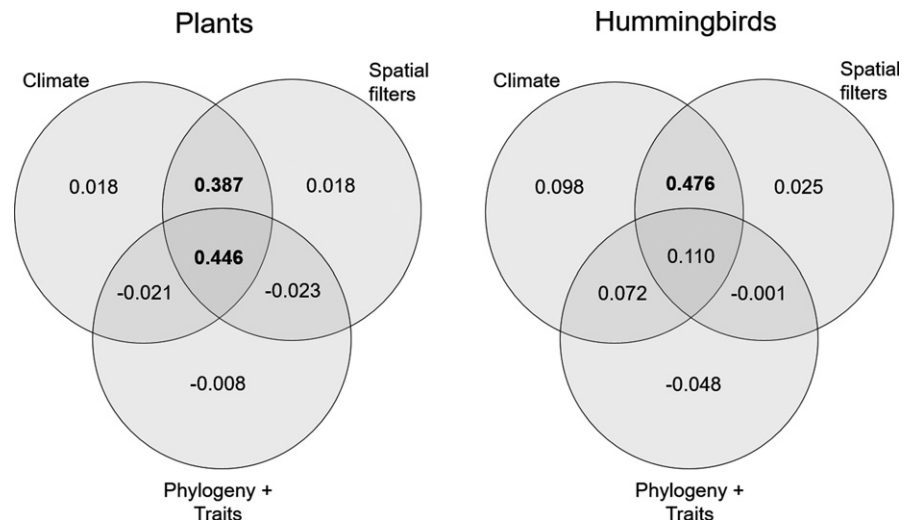|	Plants	Hummingbirds
Traits + Phylogenetic filters (TPF)	0.39	0.15
Climate	0.83	0.76
Spatial filters (SF)	0.81	0.61
TPF + Climate	0.80	0.71
TPF+ SF	0.80	0.63
Climate + SF	0.83	0.78
TPF + Climate + SF	0.82	0.73

FIGURE 6 Venn diagrams showing the partitioning of the variance explained into components accounted for by unique and shared effects of the predictor variable sets in assigning species of plants and hummingbirds to modules, in the Brazilian cross-biomes network. Most important sets are in bold

Valiente-Banuet et al., 2015), with subsequent effects in the structure of interacting networks in the different biomes (Sebastián-González, Dalsgaard, Sandel, & Guimarães, 2015).

Although some modules included species recorded in only a single site, or included species recorded in sites very close to each other, modules did not differ regarding the distributional extents of their hummingbird constituent species. The presence of exclusive species could be expected, such as discussed above for the hummingbirds *Augastes lumachella* and *A. scutatus*, in modules representing Rupestrian Fields, in the region they are endemic to. Similarly, plant species occurring in Rupestrian Fields, which reach 30% of endemic plants in some localities (Alves, Cardin, & Kropf, 2007), also presented more restricted distributions. However, differences in range size between modules recorded for plants may also be an artefact, simply reflecting the number of networks represented per module, with more widespread species being recorded in modules including more networks (e.g. Cerrado and Southeastern Atlantic forest).

In spite of a relatively large geographical distance between the Pampas and Pantanal domains, most of their local plant and hummingbird species were assigned to the same module, constituting an apparent exceptional case. This result could reflect the high importance of the hummingbird *Hylocharis chrysura* in these regions highly dominated by grasslands and shrubby vegetation (Roesch et al., 2009; Silva, Mauro, Mourão, & Coutinho, 2000). The region of Chaco in Paraguay and Argentina, with phytophysiognomies similar to Pampas and Pantanal, might propitiate a route for species sharing between these domains.

Regarding species traits, within all six modules a major proportion of plants have flowers with attributes typically related to hummingbird pollination, namely tubular red/pink or yellow flowers. However, some modules such as the ones from Southeastern and Northeastern Atlantic forest include an even higher proportion of plant species with ornithophilous flowers, suggesting more functionally specialized interactions than other modules. Differences in growth form were also recorded, and are probably related to dominant ornithophilous families in each domain. In Southeastern Atlantic forest (mostly represented in Module 5), Bromeliaceae is the most

diverse ornithophilous family (e.g. Buzato et al., 2000; Vizentin-Bugoni et al., 2014) and, thus, most of the recorded species in this domain are epiphytic. In contrast, in Rupestrian Fields, where Bromeliaceae remains an important family, the hummingbird-pollinated plants are mostly terrestrial, and thus more strongly feature shrubby/herbaceous habits such as those in the families Asteraceae and Ericaceae (Rodrigues & Rodrigues, 2014). Thus, the terrestrial growth form was most prominent in this module.

We found that species traits and phylogeny had no exclusive effect on assignment of hummingbird and plant species to modules. This contrasts with the finding that hummingbird phylogenetic signal observed in local plant–hummingbird networks is correlated with levels of modularity across most of the Americas (Martín González et al., 2015), as well as the finding that traits were important in structuring modules in hummingbird–plant networks in a Neotropical savanna system (Maruyama et al., 2014). However, it corresponds to a recent finding that niche partitioning (i.e. specialization) in insular Caribbean plant–hummingbird networks is determined by topographical and climatic conditions rather than by hummingbird traits (Dalsgaard et al., 2018). Thus, it is likely that traits have a stronger role in structuring hummingbird–plant interactions within local communities/networks rather than in cross-biomes and island systems (Dalsgaard et al., 2018). Especially as species with similar traits are assembled in different modules and thus there is no strong difference on trait distribution across cross-biomes modules. In accordance, with the exception of a weak negative effect of nectar concentration on among-module connectivity (c), we did not observe any relationship between species traits and species roles (i.e. c and z-values), suggesting that traits here evaluated are not good predictors of species roles in cross-biomes networks.

The finding that only plants fulfilled central roles in this cross-biomes network could either be genuine, reflecting differences between plants and animal groups, or be related to sampling, as network data are usually collected by observing the visitors to focal plants, rather than by following focal animals (e.g. Watts, Dormann, Martín González, & Ollerton, 2016). The more connected species, both within and between modules, presented wider geographical

occurrence, which agrees with the finding that hummingbirds' range size is negatively related to ecological specialization (Sonne et al., 2016). Indeed, hummingbirds that acted as connectors and plant species that acted as hubs are well distributed throughout almost whole Brazil (BirdLife International, 2016; CNCFlora, 2012; Pennington, 1997). Although it is expected that species with wider ranges have increased opportunities to interact with a greater array of partners, this result indicates that widespread species nevertheless play an important role in the maintenance of cross-biomes modularity. In addition, it indicates that such effects are largely independent of traits regarded to be important in structuring local plant–hummingbird networks (e.g. Vizentin-Bugoni et al., 2014). This contrasting result reinforces the notion that factors affecting the organization of interactions in small scale, i.e. local interaction networks, differ from those concerning interactions in large scale, cross-biomes networks (Bartomeus et al., 2016).

In conclusion, our results show that the cross-biomes plant–hummingbird Brazilian network is shaped by climate and space, with overlapping effects of traits/phylogeny only for plants. Furthermore, they show that species range size is a major determinant of species roles in networks at this large spatial scale, as species that were present in more networks and/or have wider distributions were more connected both within and between modules. Altogether, our results indicate that biogeography and climate are not only relevant drivers of modularity level in local mutualistic plant–animal networks, as previous macroecological studies have shown, but also structure cross-biomes networks. Evaluating the structure of cross-biomes networks in the light of human disturbance and associated effects of introduced species on module composition would be interesting foci for future studies.

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REFERENCES

Aizen, M. A., Gleiser, G., Sabatino, M., Gilarranz, L. J., Bascompte, J., & Verdú, M. (2016). The phylogenetic structure of plant-pollinator networks increases with habitat size and isolation. *Ecology Letters*, *19*, 29–36. https://doi.org/10.1111/ele.12539

Allen, C. R. (2006). Discontinuities in ecological data. *Proceedings of the National Academy of Sciences of the United States of America*, *103*, 6083–6084. https://doi.org/10.1073/pnas.0601668103

Alves, R. J. V., Cardin, L., & Kropf, M. S. (2007). Angiosperm disjunction "Campos rupestres - restingas": A re-evaluation. *Acta Botanica Brasilica*, *21*, 675–685. https://doi.org/10.1590/S0102-33062007000300014

Alzahrani, T., & Horadam, K. J. (2016). *Community detection in bipartite networks: algorithms and case studies*. In J. Lu, X. Yu, G. Chen, & W. Yu (Eds.), *Complex Systems and Networks* (pp. 25–50). Berlin Heidelberg: Springer. https://doi.org/10.1007/978-3-662-47824-0

Araujo, A. C., & Sazima, M. (2003). The assemblage of flowers visited by hummingbirds in the "capões" of southern Pantanal, Mato Grosso do Sul, Brazil. *Flora*, *198*, 427–435. https://doi.org/10.1078/0367-2530-00116

Araújo, F. P., Sazima, M., & Oliveira, P. E. (2013). The assembly of plants used as nectar sources by hummingbirds in a Cerrado area of Central Brazil. *Plant Systematics and Evolution*, *299*, 1119–1133. https://doi.org/10.1007/s00606-013-0783-0

Barber, M. J. (2007). Modularity and community detection in bipartite networks. *Physical Review*, *76*, 066102.

Bartomeus, I., Gravel, D., Tylianakis, J. M., Aizen, M. A., Dickie, I. A., & Bernard-Verdier, M. (2016). A common framework for identifying linkage rules across different types of interactions. *Functional Ecology*, *30*, 1894–1903. https://doi.org/10.1111/1365-2435.12666

Bascompte, J., Jordano, P., Melián, C. J., & Olesen, J. M. (2003). The nested assembly of plant-animal mutualistic networks. *Proceedings of the National Academy of Sciences of the United States of America*, *100*, 9383–9387. https://doi.org/10.1073/pnas.1633576100

Beckett, S. J. (2016). Improved community detection in weighted bipartite networks. *Royal Society Open Science*, *3*, 140536. https://doi.org/10.1098/rsos.140536

BirdLife International (2016). *IUCN Red List for birds*. Retrieved from http://www.birdlife.org

Buzato, S., Sazima, M., & Sazima, I. (2000). Hummingbird-pollinated floras at three Atlantic forest sites. *Biotropica*, *32*, 824–841. https://doi.org/10.1111/j.1744-7429.2000.tb00621.x

Carnaval, A. C., & Moritz, C. (2008). Historical climate modelling predicts patterns of current biodiversity in the Brazilian Atlantic forest. *Journal of Biogeography*, *35*, 1187–1201. https://doi.org/10.1111/j.1365-2699.2007.01870.x

CNCFlora (2012). *Vriesea procera in Lista Vermelha da flora brasileira version 2012.2 Centro Nacional de Conservação da Flora*. Retrieved from http://cncflora.jbrj.gov.br/portal/pt-br/profile/Vriesea procera

Dalsgaard, B., Kennedy, J. D., Simmons, B. I., Baquero, A. C., Martín González, A. M., Timmermann, A., ... Rahbek, C. (2018). Trait evolution, resource specialization and vulnerability to plant extinctions among Antillean hummingbirds. *Proceedings of the Royal Society B: Biological Sciences*, *28*, pii: 20172754 https://doi.org/10.1098/rspb.2017.2754

Dalsgaard, B., Magård, E., Fjeldså, J., Martín González, A. M., Rahbek, C., Olesen, J. M., ... Svenning, J. C. (2011). Specialization in plant-hummingbird networks is associated with species richness, contemporary precipitation and quaternary climate-change velocity. *PLoS ONE*, *6*, e25891. https://doi.org/10.1371/journal.pone.0025891

Dalsgaard, B., Martín González, A. M., Olesen, J. M., Ollerton, J., Timmermann, A., Andersen, L. H., & Tossas, A. G. (2009). Plant-

hummingbird interactions in the West Indies: Floral specialization gradients associated with environment and hummingbird size. *Oecologia*, *159*, 757–766. https://doi.org/10.1007/s00442-008-1255-z

Dalsgaard, B., Trøjelsgaard, K., Martín González, A. M., Nogués-Bravo, D., Ollerton, J., Petanidou, T., Olesen, J. M. (2013). Historical climate-change influences modularity and nestedness of pollination networks. *Ecography*, *36*, 1331–1340. https://doi.org/10.1111/j.1600-0587.2013.00201.x

Danieli-Silva, A., Souza, J. M. T., Donatti, A. J., Campos, R. P., Vicente-Silva, J., Freitas, L., & Varassin, I. G. (2012). Do pollination syndromes cause modularity and predict interactions in a pollination network in tropical high-altitude grasslands? *Oikos*, *121*, 35–43. https://doi.org/10.1111/j.1600-0706.2011.19089.x

De'ath, G. & Fabricius, K. E. (2000). Classification and regression trees: A powerful yet simple technique for the analysis of complex ecological data. *Ecology*, *81*, 3178–3192. https://doi.org/10.1890/0012-9658(2000)081[3178:CARTAP]2.0.CO;2

Diniz-Filho, J. A. F., & Bini, L. M. (2005). Modelling geographical patterns in species richness using eigenvector-based spatial filters. *Global Ecology and Biogeography*, *14*, 177–185. https://doi.org/10.1111/j.1466-822X.2005.00147.x

Diniz-Filho, J. A. F., Sant'Ana, C. E. R., & Bini, L. M. (1998). An eigenvector method for estimating phylogenetic inertia. *Evolution*, *52*, 1247–1262. https://doi.org/10.1111/j.1558-5646.1998.tb02006.x

Dupont, Y. L., & Olesen, J. M. (2009). Ecological modules and roles of species in heathland plant-insect flower visitor networks. *Journal of Animal Ecology*, *78*, 346–353. https://doi.org/10.1111/j.1365-2656.2008.01501.x

Eiten, G. (1978). Delimitation of the cerrado concept. *Vegetatio*, *36*, 169–178. https://doi.org/10.1007/BF02342599

Fortunato, S., & Hric, D. (2016). Community detection in networks: A user guide. *Physics Reports*, *659*, 1–44. https://doi.org/10.1016/j.physrep.2016.09.002

Fukami, T. (2015). Historical contingency in community assembly: integrating niches, species pools, and priority effects. *Annual Review of Ecology, Evolution and Systematics*, *46*, 1–23. https://doi.org/10.1146/annurev-ecolsys-110411-160340

Gilarranz, L. J., & Bascompte, J. (2012). Spatial network structure and metapopulation persistence. *Journal of Theoretical Biology*, *297*, 11–16. https://doi.org/10.1016/j.jtbi.2011.11.027

Gilarranz, L. J., Hastings, A., & Bascompte, J. (2015). Inferring topology from dynamics in spatial networks. *Theoretical Ecology*, *8*, 15–21. https://doi.org/10.1007/s12080-014-0231-y

Giulietti, A. M., & Pirani, J. R. (1988). Patterns of geographical distribution of some plant species from Espinhaço range, Minas Gerais and Bahia, Brazil. In P. E. Vanzolini & W. R. Heyer (Eds.), *Proceedings of a workshop on Neotropical distribution patterns* (pp. 39–69). Rio de Janeiro: Academia Brasileira de Ciências.

Giulietti, A. M., Pirani, J. R., & Harley, R. M. (1997). *Espinhaço Range region, eastern Brazil*. In S. D. Davis, V. H. Heywood, O. Herrera-Mac-bryd, J. Villa-Lobos, & A. C. Hamilton (Eds.), *Centres of plant diversity: A guide and strategy for their conservation* (pp. 397–404). Oxford: Information Press.

Gómez, J. M., Verdú, M., & Perfectii, F. (2010). Ecological interactions are evolutionarily conserved across the entire tree of life. *Nature*, *465*, 918–921. https://doi.org/10.1038/nature09113

Griffith, D. A., & Peres-Neto, P. R. (2006). Spatial modeling in ecology: The flexibility of eigenfunction spatial analyses. *Ecology*, *87*, 2603–2613. https://doi.org/10.1890/0012-9658(2006)87[2603:SMIETF]2.0.CO;2

Guimerà, R., & Amaral, L. A. N. (2005). Functional cartography of complex metabolic networks. *Nature*, *433*, 895–900. https://doi.org/10.1038/nature03288

Kougioumoutzis, K., Simaiakis, S. M., & Tiniakou, A. (2014). Network biogeographical analysis of the central Aegean archipelago. *Journal of Biogeography*, *41*, 1848–1858. https://doi.org/10.1111/jbi.12342

Las-Casas, F. M. G., Azevedo Júnior, S. M., & Dias Filho, M. M. (2012). The community of hummingbirds (Aves: Trochilidae) and the assemblage of flowers in a Caatinga vegetation. *Brazilian Journal of Biology*, *72*, 51–58. https://doi.org/10.1590/S1519-69842012000100006

Legendre, P. (2008). Studying beta diversity: Ecological variation partitioning by multiple regression and canonical analysis. *Journal of Plant Ecology*, *1*, 3–8. https://doi.org/10.1093/jpe/rtm001

Liaw, A., & Wiener, M. (2002). Classification and regression by randomForest. *R News*, *2*, 18–22.

Liu, X., & Murata, T. (2010). An efficient algorithm for optimizing bipartite modularity in bipartite networks. *Journal of Advanced Computational Intelligence and Intelligent Informatics*, *14*, 408–415. https://doi.org/10.20965/jaciii.2010.p0408

Loarie, S. R., Duffy, P. B., Hamilton, H., Asner, G. P., Field, C. B., & Ackerly, D. D. (2009). The velocity of climate change. *Nature*, *462*, 1052–1055. https://doi.org/10.1038/nature08649

Loh, W. Y. (2014). Fifty years of classification and regression trees. *International Statistical Review*, *82*, 329–348. https://doi.org/10.1111/insr.12016

Marquitti, F. M. D., Guimarães, P. R., Pires, M. M., & Bittencourt, L. F. (2014). MODULAR: Software for the autonomous computation of modularity in large network sets. *Ecography*, *37*, 221–224. https://doi.org/10.1111/j.1600-0587.2013.00506.x

Martín González, A. M., Allesina, S., Rodrigo, A., & Bosch, J. (2012). Drivers of compartmentalization in a Mediterranean pollination network. *Oikos*, *121*, 2001–2013. https://doi.org/10.1111/j.1600-0706.2012.20279.x

Martín González, A. M., Dalsgaard, B., Nogués-Bravo, D., Graham, C. H., Schleuning, M., Maruyama, P. K., ... Martinez, N. D. (2015). The macroecology of phylogenetically structured hummingbird-plant networks. *Global Ecology and Biogeography*, *24*, 1212–1224. https://doi.org/10.1111/geb.12355

Martín González, A. M., Dalsgaard, B., Ollerton, J., & Timmermann, A. (2009). Effects of climate on pollination networks in the West Indies. *Journal of Tropical Ecology*, *25*, 493–506. https://doi.org/10.1017/S0266467409990034

Maruyama, P. K., Oliveira, G. M., Ferreira, C., Dalsgaard, B., & Oliveira, P. E. (2013). Pollination syndromes ignored: Importance of non-ornithophilous flowers to Neotropical savanna hummingbirds. *Naturwissenschaften*, *100*, 1061–1068. https://doi.org/10.1007/s00114-013-1111-9

Maruyama, P. K., Vizentin-Bugoni, J., Oliveira, G. M., Oliveira, P. E., & Dalsgaard, B. (2014). Morphological and spatio-temporal mismatches shape a Neotropical savanna plant-hummingbird network. *Biotropica*, *46*, 740–747. https://doi.org/10.1111/btp.12170

McCoy, E. D., & Heck, K. L. (1987). Some observations on the use of taxonomic similarity in large-scale biogeography. *Journal of Biogeography*, *14*, 79–87. https://doi.org/10.2307/2844788

McGuire, J. A., Witt, C. C., Remsen, J. V., Corl, A., Rabosky, D. L., Altshuler, D. L., & Dudley, R. (2014). Molecular phylogenetics and the diversification of hummingbirds. *Current Biology*, *24*, 910–916. https://doi.org/10.1016/j.cub.2014.03.016

Mello, M. A. R., Bezerra, E. L. S., & Machado, I. C. S. (2013). Functional roles of Centridini oil bees and Malpighiaceae oil flowers in biome-wide pollination networks. *Biotropica*, *45*, 45–53. https://doi.org/10.1111/j.1744-7429.2012.00899.x

Moritz, C., & Faith, D. P. (1998). Comparative phylogeography and the identification of genetically divergent areas for conservation. *Molecular Ecology*, *7*, 419–429. https://doi.org/10.1046/j.1365-294x.1998.00317.x

Morrone, J. J. (2006). Biogeographic areas and transition zones of Latin America and the Caribbean Islands based on panbiogeographic and

cladistic analyses of the Entomofauna. *Annual Review of Entomology*, 51, 467–494. https://doi.org/10.1146/annurev.ento.50.071803.130447

Morrone, J. J. (2014). Biogeographical regionalisation of the neotropical region. *Zootaxa*, *3782*, 001–110. https://doi.org/10.11646/zootaxa.3782.1.1

Olesen, J. M., Bascompte, J., Dupont, Y. L., & Jordano, P. (2007). The modularity of pollination networks. *Proceedings of the National Academy of Sciences of the United States of America*, *104*, 19891–19896. https://doi.org/10.1073/pnas.0706375104

Pennington, T. D. (1997). *The genus Inga. Botany*. Kew: Royal Botanic Gardens.

Ramírez, N. (2003). Floral specialization and pollination: A quantitative analysis and comparison of the Leppik and the Faegri and van der Pijl classification systems. *Taxon*, *52*, 687–700. https://doi.org/10.2307/3647344

Rapini, A., Ribeiro, P. L., Lambert, S., & Pirani, J. R. (2008). A flora dos campos rupestres da Cadeia do Espinhaço. *Megadiversidade*, *4*, 16–24.

Rezende, E. L., Lavabre, J. E., Guimaraes, P. R., Jordano, P., & Bascompte, J. (2007). Non-random coextinctions in phylogenetically structured mutualistic networks. *Nature*, *448*, 925–928. https://doi.org/10.1038/nature05956

Rodrigues, L. C., & Araujo, A. C. (2011). The hummingbird community and their floral resources in an urban forest remnant in Brazil. *Brazilian Journal of Biology*, *71*, 611–622. https://doi.org/10.1590/S1519-69842011000400005

Rodrigues, L. C., & Rodrigues, M. (2014). Flowers visited by hummingbirds in the open habitats of the southeastern Brazilian mountaintops: Species composition and seasonality. *Brazilian Journal of Biology*, *74*, 659–676. https://doi.org/10.1590/bjb.2014.0097

Roesch, L. F. W., Vieira, F. C. B., Pereira, V. A., Schünemann, A. L., Teixeira, I. F., Senna, A. J. T., & Stefenon, V. M. (2009). The Brazilian Pampa: A fragile biome. *Diversity*, *1*, 182–198. https://doi.org/10.3390/d1020182

Schleuning, M., Ingmann, L., Strauß, R., Fritz, S. A., Dalsgaard, B., Dehling, D. M., ... Dormann, C. F. (2014). Ecological, historical and evolutionary determinants of modularity in weighted seed-dispersal networks. *Ecology Letters*, *17*, 454–463. https://doi.org/10.1111/ele.12245

Sebastián-González, E., Dalsgaard, B., Sandel, B., & Guimarães, P. R. Jr (2015). Macroecological trends in nestedness and modularity of seed-dispersal networks: Human impact matters. *Global Ecology and Biogeography*, *24*, 293–303. https://doi.org/10.1111/geb.12270

Silva, M. P., Mauro, R., Mourão, G., & Coutinho, M. (2000). Distribuição e quantificação de classes de vegetação do Pantanal através de levantamento aéreo. *Revista Brasileira de Botânica*, *23*, 143–152.

Sonne, J., Martín González, A. M., Maruyama, P. K., Sandel, B., Vizentin-Bugoni, J., Schleuning, M., ... Dalsgaard, B. (2016). High proportion of smaller ranged hummingbird species coincides with ecological specialization across the Americas. *Proceedings of the Royal Society B: Biological Sciences*, *283*, 20152512. https://doi.org/10.1098/rspb.2015.2512

Stout, J. A. (2014). Anthropogenic impacts on pollination networks and plant mating systems. *Functional Ecology*, *28*, 1–2. https://doi.org/10.1111/1365-2435.12220

Tur, C., Olesen, J. M., & Traveset, A. (2015). Increasing modularity when downscaling networks from species to individuals. *Oikos*, *124*, 581–592. https://doi.org/10.1111/oik.01668

Valiente-Banuet, A., Aizen, M. A., Alcántara, J. M., Arroyo, J., Cocucci, A., Galetti, A., ... Zamora, R. (2015). Beyond species loss: The extinction of ecological interactions in a changing world. *Functional Ecology*, *29*, 299–307. https://doi.org/10.1111/1365-2435.12356

Vasconcelos, M. F. (2009). Mountaintop endemism in eastern Brazil: Why some bird species from campos rupestres of the Espinhaço Range are not endemic to the Cerrado region? *Revista Brasileira de Ornitologia*, *16*, 348–362.

Vázquez, D. P. (2005). Degree distribution in plant-animal mutualistic networks: Forbidden links or random interactions? *Oikos*, *108*, 421–426. https://doi.org/10.1111/j.0030-1299.2005.13619.x

Vilhena, D. A., & Antonelli, A. (2015). A network approach for identifying and delimiting biogeographical regions. *Nature Communications*, *6*, 6848. https://doi.org/10.1038/ncomms7848

Vizentin-Bugoni, J., Maruyama, P. K., & Sazima, M. (2014). Processes entangling interactions in communities: Forbidden links are more important than abundance in a hummingbird-plant network. *Proceedings of the Royal Society B: Biological Sciences*, *281*, 1–8.

Watts, S., Dormann, C. F., Martín González, A. M., & Ollerton, J. (2016). The influence of floral traits on specialization and modularity of plant–pollinator networks in a biodiversity hotspot in the Peruvian Andes. *Annals of Botany*, *118*, 415–429. https://doi.org/10.1093/aob/mcw114

Webb, C. O., Ackerly, D. D., & Kembel, S. W. (2008). Phylocom: Software for the analysis of phylogenetic community structure and trait evolution. *Bioinformatics*, *24*, 2098–2100. https://doi.org/10.1093/bioinformatics/btn358

Wikström, N., Savolainen, V., & Chase, M. W. (2001). Evolution of the angiosperms: Calibrating the family tree. *Proceedings of the Royal Society B: Biological Sciences*, *268*, 2211–2220. https://doi.org/10.1098/rspb.2001.1782

BIOSKETCH

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.