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Drivers of bat roles in Neotropical seed dispersal networks: abundance is more important than functional traits

Rafael de Souza Laurindo[1] · Jeferson Vizentin-Bugoni[2] · Davi Castro Tavares[3] · Matheus Camargo Silva Mancini[1] · Rodrigo de Macêdo Mello[1] · Renato Gregorin[1]

Abstract

While functional traits can facilitate or constrain interactions between pair of species in ecological communities, relative abundances regulate the probabilities of encounter among individuals. However, the relative importance of traits and relative abundances for the role species play in seed dispersion networks remains poorly explored. Here, we analyzed 20 Neotropical seed dispersal networks distributed from Mexico to southeastern Brazil to evaluate how relative abundance and functional traits influence bat species' roles in seed dispersal networks. We tested how bat relative abundance and traits relate to species contribution to between-module (c metric) and within-module connectivity (z metric) and their position and potential to mediate indirect effects between species (betweenness centrality). Our results indicate that relative abundance is the main determinant of the role bats play in the networks, while traits such as aspect ratio show modest yet statistically significant importance in predicting specific roles. Moreover, all seed dispersal networks presented two or three superabundant obligatory frugivore species that interacted with a high number of plants. The modest influence of the functional traits on species' roles is likely related to the low variation of morphological traits related to foraging ecology, which reduces the chances of morphological mismatching between consumers and resources in the system. In this scenario, abundant bats have higher chances of encountering resources and being capable of consuming them which leads such species to play critical roles in the community by acting as module hubs and network connectors.

✉ Rafael de Souza Laurindo
rafaelslaurindo@gmail.com

[1] Departamento de Biologia, Universidade Federal de Lavras, CP 3037, Lavras, Minas Gerais CEP 37200-000, Brazil

[2] Department of Natural Resources and Environmental Sciences, University of Illinois at Urbana-Champaign, Turner Hall, 1102 S Goodwin Avenue, Urbana, IL, USA

[3] Systems Ecology Group, Leibniz Centre for Tropical Marine Research, Fahrenheitstraße 6, 28359 Bremen, Germany

Introduction

In ecological communities, species interact one with another forming complex interaction networks (Bascompte and Jordano 2007). Multiple processes define networks structure, and the role species play in communities (e.g. Vázquez et al. 2009; Vizentin-Bugoni et al. 2014; Sebastián-González 2017). In plant–frugivore mutualistic networks, usually a low number of animal species concentrate a large proportion of the interactions and, therefore, play a pivotal role in the community. Thus, highly connected species disproportionally contribute for the network structure, while most of the species are often poorly connected and tend to play peripheral roles (Mello et al. 2015; Palacio et al. 2016; Laurindo et al. 2019). Distinct factors are associated to such roles, including population abundance and functional traits—here defined as any measurable morphological, physiological, and behavioral characteristics of an organism (Sebastián-González 2017;

Tavares et al. 2019). However, the contribution of each of those factors for structuring distinct mutualistic networks remains poorly understood (Mello et al. 2015; Sebastián-González 2017).

Functional traits (e.g. morphological, physiological, behavioral) influence network by allowing or constraining species pairwise interactions (i.e. niche-based processes, Vizentin-Bugoni et al. 2018). In contrast, abundances regulate the probability of species encounter, where more abundant species tend to interact with more partners and with higher frequencies than rarer species (neutral-based processes, Chamberlain and Holland 2009; Vázquez et al. 2009; Winfree et al. 2014; Vizentin-Bugoni et al. 2018). In this sense, abundance can be considered a null model reflecting interaction patterns expected under no influence of traits associated to species niches (Vizentin-Bugoni et al. 2014). Traits known to be influential on the role that dispersers play in networks include degree of frugivory which describes the percentage of consumed fruits by a species (e.g. obligatory, secondary, or opportunistic frugivores), and body mass which is directly related to daily energetic demands (Chamberlain and Holland 2009; Sebastián-González 2017). Also, phenotypic traits related to food acquisition and processing such as skull shape, mouth gape, and force of bite are important for bat–fruit interactions as they may define, for instance, how large fruits can be in order to be consumed (Nogueira et al. 2009; Sebastián-González 2017). Thus, skull and dentition structure are directly related to diet, with fruit-eating species usually presenting shorter rostrum, and wide and robust skulls and molars (Nogueira et al. 2009).

The role a particular species plays in a mutualistic network may be described based on its contribution to the connectivity within and among different modules. Specifically, *module hubs* are species highly connected within their modules which promotes resistance to species loss due to increased interaction redundancy (Bezerra et al. 2009), and *network connectors* are species connecting distinct modules which consequently play a crucial role for the maintenance of network cohesion (Donatti et al. 2011). Thus, it is relevant to understand which factors determine the role species play in seed dispersal networks to identify keystone species and to predict and mitigate the impacts of species loss on interaction networks (Saavedra et al. 2011; Simmons et al. 2019a).

Species' roles have also been described in terms of the position a species occupy in a network. Betweenness centrality (BC), for example, reflects the role a species plays in connecting pairs of members in the network (Martín González et al. 2010). Species with high BC values have higher potential to mediate indirect interactions such as competition or facilitation between plants for shared dispersers (Cirtwill et al. 2018). Thus, such species play key roles for network structure and robustness to species extinction (Maia et al. 2019).

In the Neotropical region, bats are essential seed dispersers as they interact with thousands of plant species (Lobova et al. 2009) and 23 plant species, on average, rely on bats for seed dispersal in local communities (Laurindo et al. 2019). Furthermore, not only obligatory frugivores disperse seeds, but also species of other trophic guilds (such as omnivores, carnivores, and nectarivores) which may feed on fruits and contribute at some extent to seed dispersal (Kalko et al. 1996; Munin et al. 2012; Sarmento et al. 2014). Therefore, frugivory by both obligatory and opportunistic frugivores may result in ecological and morphological traits variation which could increase the functional diversity in seed dispersal networks, with potentially important consequences for community structure and dynamics (Mello et al. 2015; Sarmento et al. 2014).

Here, we compiled data on seed dispersal for 20 communities in the Neotropical region to investigate how relative abundances and traits influenced the functional role that distinct bats species played in bat–fruit networks. We expected that abundance would be the main factor shaping species' roles in seed dispersal networks as few superabundant bat species usually concentrate most interactions (Mello et al. 2011; Laurindo et al. 2019). We also expected a secondary relevance of behavioral and morphological traits due to low variability of those traits among obligatory frugivorous bats (Murillo-García and De la Vega 2018) in comparison to other frugivorous vertebrates such as birds (Sebastián-González 2017) and terrestrial mammals (Donatti et al. 2011).

Materials and methods

Dataset

We compiled 20 seed dispersal networks throughout the Neotropical region (Appendix 1) distributed from Mexico to Brazil (Fig. 1). Sixteen networks were obtained from online repositories and 4 are primary data we collected. The online search included the following keywords in English, Portuguese and Spanish: bats (morcegos, murciélagos), frugivory (frugivoria), diet (dieta), interaction networks (redes de interação, redes de interacción), and seed dispersal (dispersão de sementes, dispersión de semillas). Searches comprised the period from January 1990 to December 2018 and we used the following repositories: Web of Science (https://webofknowledge.com), Scientific Electronic Library Online (https://scielo.org), Science Direct (https://sciencedirect.com), Scopus (https://scopus.com), SpringerLink (https://link.springer.com), Wiley (https://onlinelibrary.wiley.com), Google Scholar (https://scholar.google.com), and the dissertation and thesis
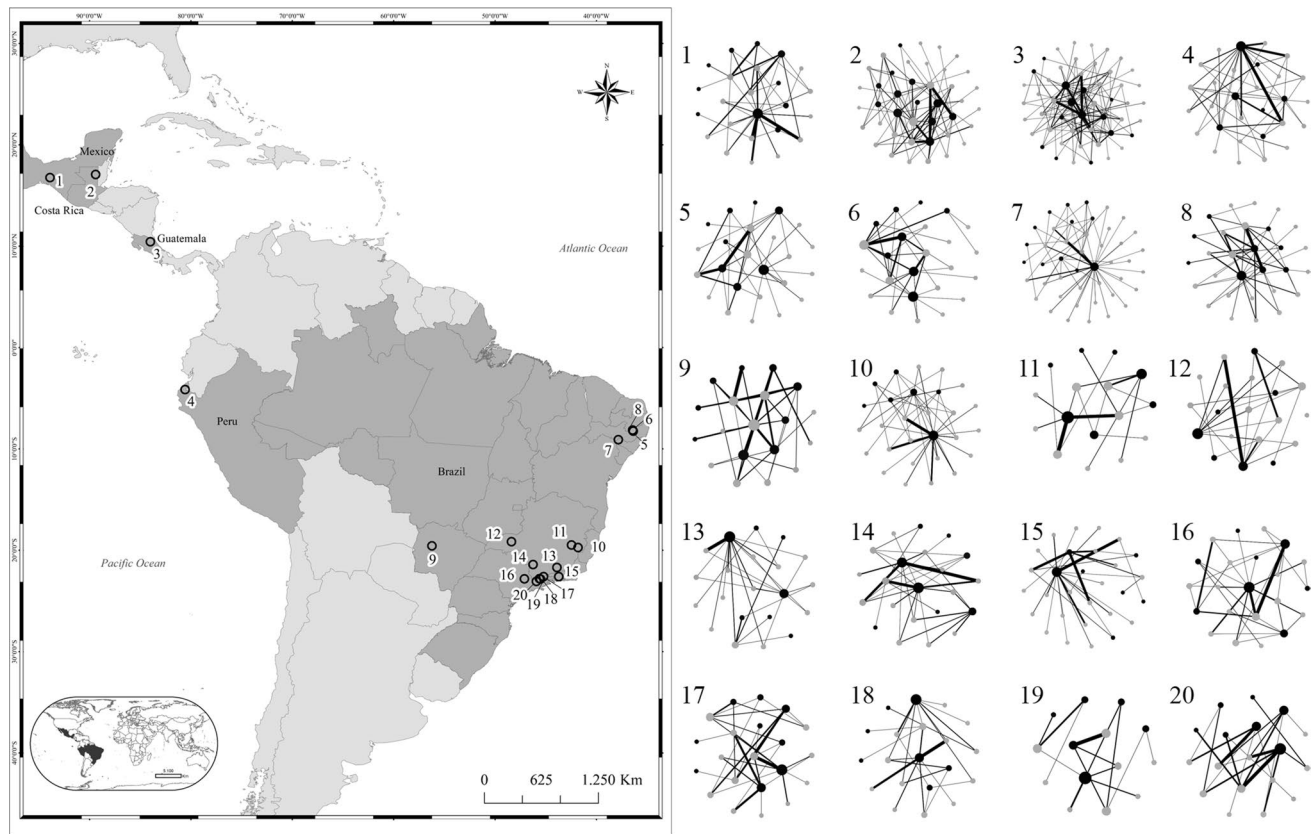
Fig. 1 Geographical distribution of 20 Neotropical bat-fruit mutualistic networks showing bats (black dots) and plants (gray dots) linked by their interactions. Node sizes are proportional to the number of links, and links' thickness indicates interaction frequencies. For details of the localities and species' roles, see Appendices 1 and 5

dataset from CAPES (https://capes.gov.br/servicos/banco-de-teses). The four interactions networks based on primary data result of fieldwork carried out from October 2015 to December 2017 in four sampling sites at the protected area *Área de Proteção Ambiental Serra da Mantiqueira*, São Paulo state, southeastern Brazil (Appendix 2). In each sampling site, two field expeditions were carried out totalizing 12 days (six in rainy season and six in the dry season). Bats were caught using six mist nets with dimensions of 12×3 m. Caught individuals were placed in cotton bags for 30 min to collect fecal samples, which after collected were wrapped in plastic microtubes with glycerin for preservation. Seeds were identified by comparison to material deposited in the Mammals' Diversity and Systematics Laboratory (Laboratório de Diversidade e Sistemática de Mamíferos) at Federal University of Lavras (Universidade Federal de Lavras), Brazil or literature (see Lobova et al. 2009). All datasets analyzed here included interactions detected using fecal samples collected from bats caught using mist-netting, which is

an efficient method of capture for *Phyllostomidae* species (Trevelin et al. 2017).

Quantitative interaction networks

All datasets used in this study report the number of fecal samples in which seeds of each plant species were found as an estimate of frequencies of interactions. Because the number of seeds may vary considerably across species, we considered interactions as the presence of seeds on a fecal sample regardless of the number of seeds. Thus, an interaction matrix is populated with intensities of interactions (I_{ij}) defined as the proportion of samples of a bat species j in which a plant species i. When necessary, proportions were rounded so that interaction frequencies in the matrices were represented by integers. Therefore, this measure of intensity of interactions takes into account differences in sample size across bat species constituting a relative measure comparable among species both within and among communities (Laurindo et al. 2019).

Species' roles in the network

To begin, we considered the recurrent modular structure of bat–fruit networks which often present three or four modules of species that interact more among them than with other species in the network, forming modules of highly connected species frequently phylogenetically related (Laurindo et al. 2019). This modularity promotes robustness to species loss due to the ecological redundancy of bat species within each module (Laurindo et al. 2019). Based on this notion, we chose metrics related to the distinct roles species may play for the cohesion in a modular mutualistic network.

Based on the modularity obtained for quantitative matrices, we calculated the c and z metrics for each network. The metric c, between-module connectivity, represents the contribution of each bat species for the connectivity among modules and is defined as follows:

$$c_i = 1 - \sum_{t=1}^{Nm} \left(\frac{k_{is}}{k_i} \right)^2$$

where k_{is} is the number of links of node i to nodes in module s, and k_i is the total degree of node i. Thus, c_i values are close of 1 when the links are randomly distributed among all modules and 0 if all links are in a single module (Guimerà and Amaral 2005; Olesen et al. 2007).

The z metric, within-module connectivity, is the standardized number of links a species i has within its own module compared to the remaining species in the same module. This metric is defined as:

$$z_i = \frac{K_i - \bar{K}_{si}}{SD_{Ki}},$$

where K_i is the degree of species i in its own module, and $\bar{K}_{si}$ and SD_{Ki} are the mean and standard deviation of the degree of all species composing the module s, respectively (Guimerà et al. 2007; Guimerà and Amaral 2005). Thus, species with high c and z values engage in many interactions in the network and, therefore, play an important role in connecting species both within and among modules. On the other hand, low c and z values indicate peripheral species that contribute little to the network cohesion, while intermediate values of c and z indicate that, relative to the other species in the network, the species play moderate roles for within and among module cohesion.

We also calculated betweenness centrality (BC) which measures the position of a species in relation to each pair of network members and reflects the role of the species for network cohesion (Martín González et al. 2010; Cirtwill et al. 2018) as well its potential to mediate indirect interactions such as competition or facilitation.

$$BC_i = 2 \sum_{j<k;\, i \neq j} \frac{g_{jk}(i)/g_{jk}}{(N-1)(N-2)},$$

where N is the number of species in the network, g_{jk} is number of shortest paths linking any two species, and $g_{jk}(i)$ is the number of those shortest paths among g_{jk}, that pass through i (Martin González et al. 2010). All metrics (c, z and BC) were calculated using the R package *bipartite* (Dormann et al. 2009).

Bat functional traits

We considered behavioral (degree of frugivory) and morphological [body mass, wing shape (here named "aspect ratio"), and skull shape] traits. All these traits may potentially influence feeding performance and, therefore, define seed dispersal interactions (Mello et al 2019) For diet, we used a previous classification of degree of frugivory in the Neotropical bat family Phyllostomidae (Lobova et al. 2009; Fleming and Kress 2013; Mello et al. 2015) which is: (1) animalivore species that occasionally feed on fruits (e.g. phyllostomines, micronycterines), (2) nectar-feeding species which are secondary frugivorous but frequently feed on fruits (glossophagines and lonchophyllines), and (3) obligatory frugivores species which are highly dependent on fruit (carolliines and stenodermatines). Body weight is an important trait for bat–fruit interactions (Soriano 2000), which is related to the energetic demand and range of traits of the consumed fruit (size, hardness, texture). Thus, larger bat species are expected to interact with more plant species and higher frequencies that small body species (Soriano 2000).

We used *aspect ratio* (AR), i.e. the ratio between wingspan and wing area, as the morphological trait related to wing shape. This functional trait is related to habitat use, foraging mode, and diet (Denzinger and Schnitzler 2013), with high values of AR indicating long narrow wings and higher aerodynamic efficiency and low energetic cost during the flight, but low maneuverability to fly within the foliage (Marinello and Bernard 2014). Selected skull dimensions were the greatest length, braincase and zygomatic breadth. Because these tree variables are highly correlated (Appendix 3), we ran a principal component analysis (PCA) to summarize the three measurements in a unique variable (PC1). Differences in skull dimensions have implications on the feeding habits and force of bite among species (Nogueira et al. 2009) which, therefore, influence diet and bat–fruit interactions. High values in the PC1 indicate long and broad skulls that are characteristics of frugivore and omnivore bats that feed on large fruits, while low values in the PC1 reflect shorter and narrower skulls, as found in nectarivores and other species with weak bite.

Some Neotropical bat species have broad ranges and may present geographic variation in morphology. To account for that, skull and weight measures were taken from individuals collected in localities as close as possible from the communities where interactions were sampled. While this approach represents an improvement to previous studies on traits associated to species roles (e.g. Mello et al. 2015; Sebastián-González 2017) which have used average trait measures for species, ideally future studies should measure traits from specimens collected at the same community sampled for interactions. For each species, we used average values obtained for more than one individual of both sexes when available (Appendices 4, 5). For wing measures, we used the same measurement for each species across all networks because such variable is rarely available in the literature and measures from museum specimens may be inaccurate due to variations in the specimen's preservation. Finally, relative abundance was calculated as the proportion of individuals of a species in relation to the total number of individuals caught during a study in a community. Finally, nomenclature and range followed Wilson and Mittermeier (2019) (see Appendix 6).

Data analyses

Before running the statistical tests, we carried out a data exploration to assess data distribution, presence of outliers, collinearity, and correlation among samples (Zuur et al. 2010). The correlation between the species' role metrics c and z and BC was evaluated using Spearman's correlation. Although BC was correlated with c ($r = 0.54$, $p < 0.001$) and z ($r = 0.29$, $p = 0.001$) and c and z were correlated among them ($r = 0.21$, $p = 0.005$), correlations were never higher than 0.55, indicating that metrics are at some extent complementary. Thus, we kept all metrics in subsequent analyses. The collinearity among predictors (bat relative abundance, degree of frugivory, body size, aspect ratio, and skull shape) was evaluated using the variance inflation factor (VIF) and correlograms. VIF values > 3 indicate significant collinearity (Zuur et al. 2010; Tavares et al. 2016). When significant collinearity among predictor was observed, we also fitted models excluding each of the correlated predictors (see below). Regarding correlations among predictor variables, body mass was significantly correlated with skull shape (Pearson's $r = 0.95$, $P < 0.01$, Appendix 7) while abundance showed weak positive correlation with degree of frugivory ($r = 0.23$, $P < 0.01$, Appendix 7) and aspect ratio ($r = 0.20$, $P = 0.01$, Appendix 7). Variance inflation factor (VIF) values indicate that body mass and skull shape are significantly correlated (Appendix 8).

To investigate the association of bat relative abundance, degree of frugivory, aspect ratio, body mass, and skull shape to species' role metrics c, z and BC, we used generalized least square models. We implemented GLS, because this method is less sensitive to model residual distributions and because other techniques such as generalized linear models and generalized additive models did not meet model residual assumptions, i.e. normal distribution of model residuals and heteroscedasticity (Zuur et al. 2009). GLS also allowed us to fit mixed models, thus allowing us to account for the repeated occurrence of the same species across communities by including species identity as a correlation term.

To investigate the association of each of the species' role metrics to the predictors, we fitted different models and selected the best ones to infer effect sizes of predictors. Best models were obtaining step-by-step reducing from a full model that included all predictor variables (Bolker et al. 2009). We considered as best models those with the lowest AIC score (Burnham and Anderson 2002). In some cases, small differences in AIC scores between models prevented us to select one best single model. We adopted a model averaging using a cut-off of 2 AIC, because estimates from models with poor weights tend to be spurious (Tavares et al 2015). We considered the effect of predictors on the response variables significant when $P < 0.05$. The model fit was validated employing a visual inspection of residual normality and homoscedasticity (Zuur et al. 2010).

To determine the most important predictors of each species' role metrics, we calculated the importance score for each predictor as the sum of the Akaike weights in a set of models randomly generated from the full model, i.e. a model that includes all predictors (Tavares et al. 2015). We used the R packages *nlme* for GLS fitting and *MuMIn* for estimating variable importance scores in R 3.4.3.

Results

We analyzed a total of 46 bat species from 20 Neotropical bat–fruit mutualistic networks (Fig. 1). Mean c was 0.32 (range 0–0.77, SD 0.27), mean z was -0.0003 (range -1.37 to 1.30, SD 0.61) and mean BC was 0.12 (range 0–1, SD 0.18).

The variable importance scores obtained from full-models (Generalized least squares) indicate that bat relative abundance is the main predictor of between-module connectivity (c metric), within-module connectivity (z metric) and betweenness centrality (Fig. 2). Aspect ratio and degree of frugivory presented moderate importance on predicting the c and z metrics, respectively (Fig. 2a, b). Notably, bat abundance was at least sixfold more important than other predictors, such as aspect ratio, for predicting metrics c, z and BC (Fig. 2).

The best model predicting the c metric included abundance and aspect ratio. The best two models for predicting the z metric included together bat abundance, degree of frugivory and

Fig. 2 Ranking of importance of the variables predicting bat species' roles in Neotropical bat–fruit mutualistic networks. Importance scores were estimated by Generalized Least Square models (see "Materials and methods"). Species' roles metrics include: between-module connectivity (**a**), within-module connectivity (**b**) and betweenness centrality (**c**)
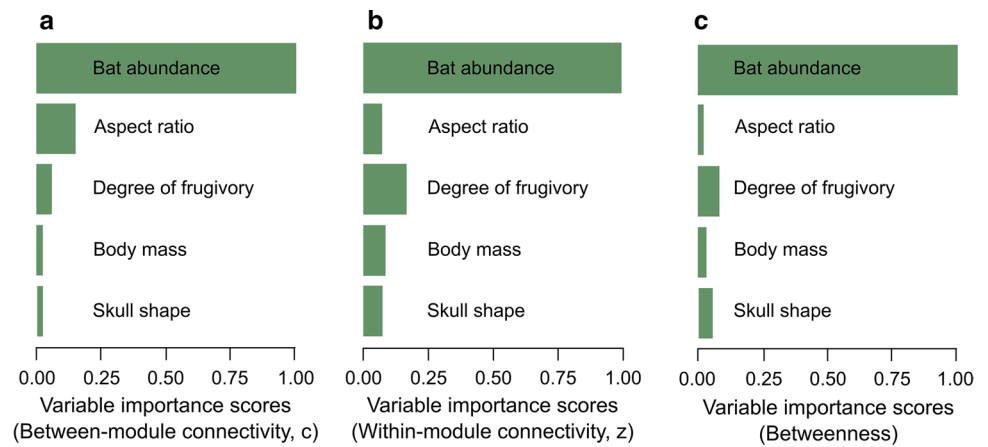

Table 1 Ranking of the best models predicting bat species' roles (c, z and betweenness centrality) in Neotropical bat-fruit mutualistic networks, resulting from Generalized Linear Square analysis

Predictors	AIC	ΔAIC	w_i
Between-module connectivity (c)			
Bat abundance + aspect ratio	33.8	0.0	0.71
Bat abundance * aspect ratio	36.3	2.5	0.20
Bat abundance + aspect ratio + degree of frugivory (DOF)	38.6	4.8	0.07
Bat abundance + body mass + aspect ratio	41.5	7.7	0.02
Within-module connectivity (z)			
Bat abundance + degree of frugivory (DOF)	294.7	0.0	0.67
Bat abundance + aspect ratio	296.6	1.9	0.26
Bat abundance + DOF + aspect ratio	299.6	4.9	0.06
Bat abundance + DOF + skull shape + aspect ratio	304.5	9.8	0.01
Bat abundance + DOF + body mass + aspect ratio	304.7	10.0	0.01
Betweenness centrality			
Bat abundance + degree of frugivory (DOF)	108.7	0.0	0.51
Bat abundance + skull shape	108.1	0.5	0.39
Bat abundance * DOF	104.5	4.1	0.07
Bat abundance + DOF + skull shape	103.097	5.6	0.03

Asterisk (*) indicates interaction between variables

AIC Akaike's Information Criterion score, *ΔAIC* difference in AIC scores between ranked models, w_i AIC weights

aspect ratio (Table 1). The best models for predicting betweenness included bat abundance, degree of frugivory and skull shape (Table 1). Effect sizes and the statistical significance of predictors on species' roles metrics are presented in Table 2. Metrics c, z and betweenness were positively associated to abundance (GLS, $P < 0.01$, Table 2; Fig. 3), while c was negatively correlated with bat aspect ratio (GLS, $P = 0.04$, Fig. 3). Degree of frugivory and skull shape were not significantly associated to any species' role investigated.

Discussion

Our study provides evidence that bat abundances play a major role in comparison to functional traits in the definition of the roles played by bats in seed dispersal networks. This contrasts with previous findings that indicate degree of frugivory as primary driver of the roles played by bats (Mello et al. 2015) and also birds in seed dispersal

Table 2 Summary of the best Generalized Least Squares models for predicting between-module connectivity (*c*), within-module connectivity (*z*) and betweenness centrality (BC) of each bat species in Neotropical bat-fruit mutualistic networks

| Response variables	Predictors	β	Lower CI	Upper CI	P value
c	Bat abundance	0.10	0.06	0.14	<0.01*
	Aspect ratio	− 0.04	− 0.08	0.00	0.04*
z	Bat abundance	0.18	0.09	0.28	<0.01*
	Degree of frugivory	0.06	− 0.01	0.18	0.28
	Aspect ratio	− 0.01	− 0.15	0.05	0.69
BC	Bat abundance	0.08	0.06	0.11	<0.01*
	Degree of frugivory	0.02	0.00	0.05	0.37
	Skull shape	0.01	0.00	0.05	0.48

β indicates slopes and reflect the intensity and direction of the association between predictor and response variables. Asterisks indicate significant predictors

networks (Schleuning et al. 2014; Sebastián-González 2017 but see Montoya-Arango et al. 2019). The contrast between our results and previous studies that reported the primary importance of degree of frugivory (Mello et al. 2015) may be related to the set of predictor variables analyzed in each study. To the best of our knowledge, our study is the first to directly test whether species abundances are associated to bats' roles in seed dispersal networks. According to our results, abundances are more important than other potential predictors of species' roles previously considered, i.e. degree of frugivory and morphological traits (Mello et al. 2015) which highlights the importance of abundant bat species for seed dispersal (Sarmento et al. 2014). These results are also supported by studies on avian seed dispersers, for which degree of frugivory was found to be a major driver of birds' roles when abundance is not among the predictor variables (Sebástian González 2017; Schleuning et al. 2014) but to be less important than abundance when this variable is considered (Montoya-Arango et al. 2019). Mechanistically, abundance is a key driver of interaction between bats and plants because as the number of individuals in the community increases, the chance of encounter and interaction with their food resources also increase. Thus, abundant bat species interact with more plant species and, therefore, play more important roles in the networks.

The high importance of abundances may be related to the existence of few superabundant and widely distributed species which often correspond to 70–80% of the individuals in the bat assemblages, while most other species are rare (Appendix 5). In fact, most bat assemblages throughout Neotropics show similar distribution of abundances

Fig. 3 Predicted and observed relationship for significant predictors of bat species' roles in Neotropical bat-fruit mutualistic networks according to Generalized Least Square models. Circles indicate observations and shaded areas indicate 95% confidence intervals calculated based on predicted values. The confidence intervals, therefore, represent the variability of predicted values rather than the variability in the data
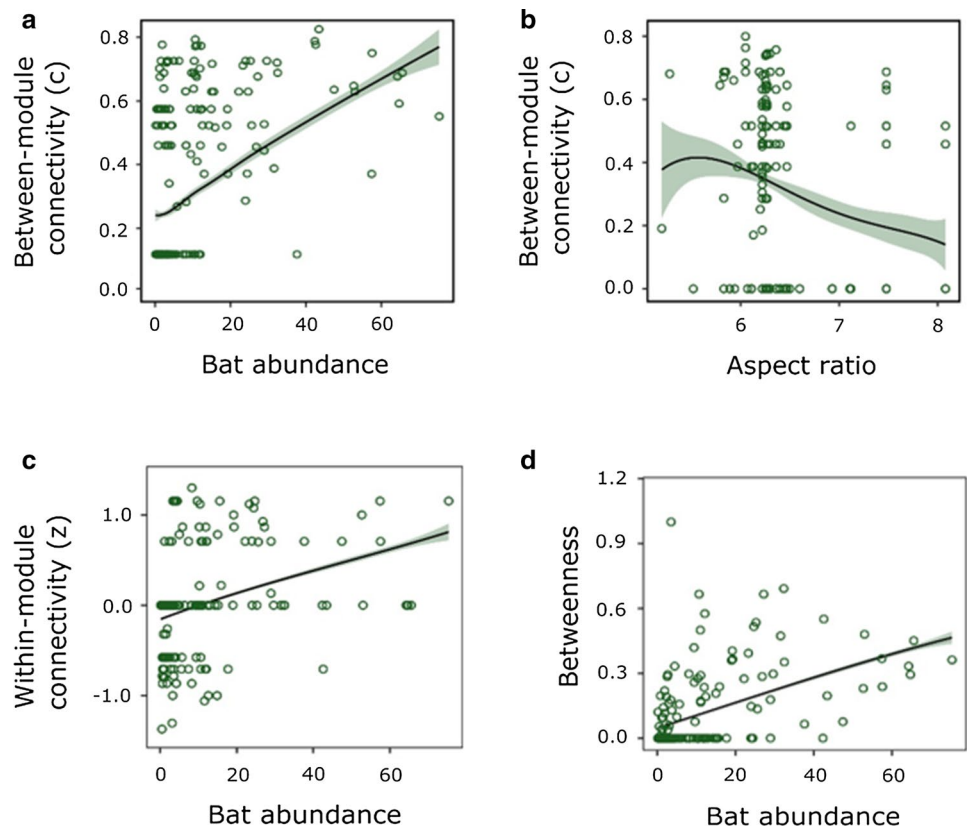
(Bernard et al. 2001; Sánchez et al. 2007; Muylaert et al. 2017). Another reason for the higher importance of abundance may be the low morphological variation among fruit-eating bat species in terms of feeding traits. In comparison to other organisms such as birds, Neotropical fruit-eating bats have low mouth gape variation (Murillo-García and De la Vega 2018) which do not impose important constraints to the interactions once no strong trait matching is required for fruit consumption (Sebastian González 2017). While preferential genus–genus associations exist (*Carollia* feeding mainly on *Piper* fruits, *Sturnira* on *Solanum*, and *Artibeus* on *Ficus* and *Cecropia*) (Laurindo et al. 2019), all species are virtually capable of consuming a broad variety of fruit (Lobova et al. 2009). This is in contrast to other mutualisms such as plant–hummingbird or plant–hawkmoth pollination networks in which interactions are often constrained by morphological barriers or trait matching (Vizentin-Bugoni et al. 2014; Sazatornil et al. 2016; Sonne et al. 2020). Unlike those systems, bats are prone to consume fruits in proportion to their abundances in the landscape, rendering the more abundant and more frugivore species to play key roles in bat–fruit networks.

Although no study has yet investigated the abundance-generalization dilemma (i.e. whether a species is abundant because is generalist or generalist because is abundant) for bat–plant mutualistic interactions, findings for other mutualistic plant–animal interactions indicate that abundance drives generalization (Fort et al. 2016; Simmons et al. 2019b). This is likely the case of bat–fruit interactions because, despite the consistent genus–genus associations which indicates that most bat species present certain level of specialization on specific fruits, only the more abundant species played roles associated to high connectivity which implies in higher generalism (see also 'Caveats and Opportunities'). Specifically, by feeding on more plant species, superabundant bat species play important roles for maintaining cohesion both within (high z) and between (high c) modules and are consequently more central (high BC). Such higher generalism of abundant species reinforces the importance of neutral processes (i.e. abundances governing random chances of encountering resources) as well as the secondary importance of constraints imposed by species morphologies in shaping interactions in this system. Such lack of morphological constraints that allow abundant species to consume a broader variety of fruit may be especially important during periods of shortage of preferred fruits, which ultimately result in increased importance of abundant bats for network connectivity and structure.

Among the morphological traits considered, only aspect ratio influenced species' roles. Specifically, species with low aspect ratio acted as connectors of distinct modules. The wing shape, which is a component of aspect ratio, is considered a good proxy to diet preference and foraging patterns,

directly reflecting habitat use (Kalko et al. 1996; Marinello and Bernard 2014). Some obligatory frugivores such as *Artibeus* and *Sturnira*, that acted as module connectors (high c), present lower aspect ratio when compared with other obligatory (e.g. *Platyrrhinus* spp. and *Chiroderma* spp.), secondary (e.g. *Glossophaga* spp. and *Anoura* spp.), and opportunistic frugivores (*Phyllostomus* spp.) which were present in most networks. Low aspect ratio values imply slow flight and high maneuverability, allowing these species to forage in all forest strata, from forest edge to dense understory and canopy (Gregorin et al. 2017), which may also explain the higher diversity of fruits consumed and, consequently, the higher importance of such species in the networks.

The moderate correlation between the three metrics of species' roles evaluated here indicates that distinct species are important for between-modules connectivity (metrics c and BC) and within-module connectivity (metric z). This suggests the existence of functional complementarity among species which may increase network robustness to species loss (Laurindo et al. 2019). For example, the extinction of a species that connects different modules (high c and BC) can break networks apart by disconnecting modules while having little impact on the structure of each module individually. On the other hand, extinction of a species important for within-module connectivity (high z) may lead to disassembly of the module while having low impact over the overall network structure (Donatti et al. 2011). However, in both cases, the loss of central species may affect network structure with direct consequences on seed dispersers diversity (Laurindo et al. 2019).

Caveats and opportunities

Virtually all networks are influenced by sampling to some extent (Vázquez et al. 2009). In fact, disentangling the influence of species abundances and sampling artifacts on network structure and species' roles is a persistent challenge in network ecology (Vázquez et al. 2009; Dorado et al. 2011; Kaiser-Bunbury and Blüthgen 2015; Dormann et al. 2017). A first caveat concerns rare species. So far, there are no comprehensive studies on the diet of rare frugivorous bats, so that the real diet breadth of most species remains poorly understood. Thus, rare species which are naturally less captured owing to low abundances are likely to have the number of plants they interact with underestimated, as known for rare pollinators (Dorado et al. 2011). A second caveat concerns the sampling techniques used. Using sampling techniques, such as direct observation and search for seeds under feeding perches and roosts, in addition to fecal sampling, increased by 32.7% the number of plants species known to be dispersed by the most widespread Neotropical frugivorous bat *Artibeus lituratus* (Laurindo and Vizentin-Bugoni 2020). This occurs because despite being effectively dispersed, large seeds are not

swallowed and, therefore, are not present in the feces. Thus, both the potential undersampling of rare species' diets and the use of single sampling techniques are likely to influence the patterns observed in interaction networks. We encourage further studies to directly address these gaps by using complementary sampling methods and investigating how distinct methods influence the description of rare species' diets, network structure and species' roles.

Conclusion

In summary, our results highlighted that bat abundance is a more important driver than species traits for the role bats play in seed dispersal networks in Neotropical communities. We argue that the high importance of bat abundances is due to the existence of few superabundant species that interact with a higher number of plant species when compared with rarer species. The low variability in functional traits has been predicted to result in fewer constraints to interactions which consequently decreases the importance of traits in comparison to abundances (Vizentin-Bugoni et al. 2018). The system studied here presented relatively low trait variation compared to other mutualistic systems which may explain the low relative importance of traits in comparison to abundances as driver of species' roles. By studying abundance and traits concomitantly rather than predictor variables in isolation, our study advances the understanding of processes driving interactions in bat–plant seed dispersal networks. Bat abundance and aspect ratio may be useful proxies to identify keystone bat species in this system.

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