

Functional roles of frugivores and plants shape hyper-diverse mutualistic interactions under two antagonistic conservation scenarios

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Abstract

Disentangling the structure of plant–animal mutualisms shed light on how species are organized, and allow us to infer about resilience, specificity, and ultimately the consequences of the loss of functions to the ecosystem. Here we gathered fruit–frugivore interactions for all the major vertebrate taxa interacting with plants in two conservation states in the Brazilian Atlantic forest: a small patch and a continuous forest. Using a network approach, we identified individual roles played by vertebrates and plants, as well as the most relevant functional traits determining the network structure. The most important vertebrates in the continuous forest were the frugivorous characterized by the ability to swallow fruits containing small to large seeds, but they also were the first to be vanished from the small patch decades ago. Animal gape/gullet size, but not body mass, together with the greatest degrees of frugivory contributed to structure the conserved community. In the forest patch, where specialization degrees (in terms of number of interactions performed) were lost, small generalist birds and the only still living primate, along with small lipid-rich fruits, were central in maintaining community structure. This study brings insights on the potential of conserved forests to hold important species-rich interactions, at the same time that small patches count on small birds and small fruits with increased energetic rewards to maintain structuring under human degradation threats. Our results reemphasize the importance of

preserving large continuous forest remnants to support important mutualistic interactions subjected to functional traits already lost in small degraded patches.

Abstract in Portuguese is available with online material.

KEYWORDS

Atlantic Forest, defaunation, functional traits, habitat loss, key species, seed dispersal, specialization

1 | INTRODUCTION

Ecological interactions are the major fuel for coevolution between animals and plants, especially in tropical forests (Jordano et al., 2010). Patterns of interactions, how species are organized and relate among each other, have been the focus of empirical and theoretical studies, and the architecture of mutualisms within species-rich communities has received growing attention (e.g., Bender et al., 2018; Carreira et al., 2020; Donatti et al., 2011; Emer et al., 2020; Escribano-Avila et al., 2018; Rumeu et al., 2020; Schleuning et al., 2012; Timóteo et al., 2018). Despite that, assessing community structure accounting for several taxa remains understudied (but see Carreira et al., 2020; Donatti et al., 2011; Timóteo et al., 2018). In the mutualistic context, species should not be considered in isolation, as they participate in a complex of interactions (Bascompte & Jordano, 2014). Individuals depend upon each other for resources and processes, such as dispersal and reproduction, to the point that the loss of single species may drive not just co-extinctions (Colwell et al., 2012) but also pervasive effects on the community stability (Campbell et al., 2012; Sheikhali et al., 2019), and even ecosystem functions derived from that loss (Rogers et al., 2021).

The relative importance of species structuring communities has long been a central topic in ecology, especially from the animal perspective (see e.g., Acevedo-Quintero et al., 2020), but quantifying this importance is challenging (Cottee-Jones & Whittaker, 2012). Distinct sets of traits allow species to play important roles, which has been inferred from natural history, without experimental verification or quantification (Cottee-Jones & Whittaker, 2012). In many cases, the evidence for interactions relies on numerical models, including simulations based on species co-occurrence and morphological matching (e.g., Marjakangas et al., 2019). The dissociation between theoretical and empirical approaches limits strong conclusions about the individual importance of animals and plants (Blanchet et al., 2020; Blüthgen, 2010), and the drivers and consequences of the loss of functions. Therefore, our knowledge about factors holding the architecture of frugivory mutualisms within empirical functionally diverse communities remains limited (but see Schleuning et al., 2011, Grass et al., 2014 and Kaiser-Bunbury et al., 2017). The interacting actors forming a web-like architecture can be explored by the network approach (Bascompte & Jordano, 2014). The description of plant-animal interactions through networks disentangles how species are organized within populations

and communities, and inferences can be made about individual roles, heterogeneity in specificity degrees (Bascompte & Jordano, 2007; Dormann et al., 2017) and, ultimately, the consequences of the loss of functions (Sheikhali et al., 2019; Vieira & Almeida-Neto, 2014).

The interest in investigating the contributions of frugivory to the structure of functionally diverse communities is raising (e.g., Donatti et al., 2011; Dugger et al., 2019; Rumeu et al., 2020; Timóteo et al., 2018), and original approaches have been introduced (e.g., Dehling & Stouffer, 2018). However, a persistent gap still lies in the shortage of sufficiently resolved data for multiple groups. Undiversified networks result mainly from animal-oriented studies focusing on sampling particular taxa (e.g., birds or bats), or their absence due to ongoing depletion, as is the case of large frugivores (Carreira et al., 2020). Important efforts have been dedicated to recover populations (e.g., Correia et al., 2016). However, despite their importance, large vertebrates are often absent either because they have already disappeared in studied areas, or due to sampling limitations to describe interactions of naturally rare and secretive species (Jordano, 2016; Vidal et al., 2014). Therefore, building a complete network based on empirical data and compare traits from different taxa is particularly challenging in mega-diversified communities, such as tropical ecosystems.

Tropical forests are amongst the most threatened environments, and consequences of the loss of functions due to human activities are gaining attention (Allesina et al., 2009; Rezende et al., 2007). Understanding and predicting the effects of losses of key species to ecosystem structure and derived consequences to function is a major goal of ecological research (Campbell et al., 2012; Vieira & Almeida-Neto, 2014). Identifying functional traits defining mutualisms still lacks comparative empirical and theoretical studies, especially for the case of fruit-consuming vertebrates. A persistent challenge in the analysis of diversified frugivory networks is to examine dependence on central species while including multiple functional groups beyond, for example, just frugivorous birds, coexisting and interacting in both conserved and degraded habitats, the central goal of this study.

Here, we (1) use a comprehensive frugivory network, considering several disperser taxa with different functional traits to delineate plant-frugivore interactions in a hyper-diverse tropical ecosystem, (2) identify central species, and (3) evaluate how functional traits structure communities, using both animal and plant perspectives, under two empirical antagonistic conservation scenarios: a

preserved continuum and a small forest fragment where most of the large vertebrate species have been lost due to human activities. Data from highly preserved tropical habitats, such as the one studied here, may be used as a “benchmark” to compare network descriptors from disturbed areas, to establish goals for restoration of interaction diversity (Kaiser-Bunbury et al., 2017) and network function (Genes et al., 2019) in forest restoration programs.

2 | METHODS

2.1 | Study sites

We collected data in two areas, with distinct conservation scenarios in the Atlantic Forest domain (“AF,” hereafter): the most conserved continuous massif of the ombrophilous phytophysiology named “Serra de Paranapiacaba” (“Continuum,” hereafter) in São Paulo state (24°20’S, 48°15’W); and a 250-ha patch of the semi-deciduous phytophysiology (*sensu* Morellato & Haddad, 2000), surrounded by urbanization and agriculture named “Reserva de Santa Genebra” (“Fragment,” hereafter), in São Paulo State (22°49’16’’S, 47°06’41’’W). A complete description of the study sites, including vertebrate assemblage, is available in Appendix S1.

2.2 | Frugivory interactions

One of the main challenges in seed dispersal studies is the combination of plant–animal interactions recorded from different methodologies (e.g., Quintero et al., 2021). To deal with this shortcoming, we pooled binary data on frugivory for vertebrates living in both Continuum and Fragment. To optimize records, we compiled published data with our own records to perform the analysis of observed interactions. Data sources, sampling period, sampling effort, and references are listed in Appendix S2. Vertebrates were categorized according to their taxonomic groups: large birds, small birds, bats, carnivores, marsupials, primates, rodents, and ungulates.

Analyses were performed in the bipartite package in R (Dormann, 2011).

2.3 | The network structure

We organized our dataset as unweighted qualitative matrices for Continuum and Fragment, since interaction frequency was unavailable for most frugivores. Then, to evaluate complexity, we calculated connectance (C, the ratio between the total number of realized links relative to the number of possible interactions), and linkage density (LD, the average number of links per species). Higher values of C and LD designate higher complexity. Then, based on the interaction degree of animals and plants (i.e., the number of interactions performed), we calculated the specialization asymmetry (SA). To calculate SA, specialization values for animals are subtracted from the

values from plants, so a negative SA indicates higher specialization of animals, and positive SA indicates higher specialization of plants.

To assess structural interaction patterns, we calculated nestedness (NODF, Almeida-Neto et al., 2008). A nested network is organized such that species performing the lowest number of links tend to interact only with a subset of the species performing the highest number of links. We also calculated modularity (Q, Olesen et al., 2007; Dormann & Strauss, 2014). Modular networks have dense links between nodes within a certain group of interacting species, defined as modules, but sparse connections between nodes in different groups (Olesen et al., 2007). Nestedness and modularity are inherently related (Fortuna et al., 2019), and given that NODF and Q are sensitive to network size, we extracted z-scores to standardize metrics between Continuum and Fragment.

To evaluate significance of C, LD, SA, NODF, and Q we calculated expected values of each metric with respect to 999 binary null matrices. We set the value of α to 0.05 and selected the “Bascombe probabilistic null model” (mgen) for binary matrices (Vázquez et al., 2009).

2.4 | The role of individual species

To classify species role within the modular structure, we considered the algorithm by Olesen et al. (2007). It assigns, for each species, the number of links with other modules (c) and the number of links within the same module (z). According to the combination of c and z , species are classified as (i) peripheral, if both c and z are low; (ii) connector, if c is high, but z is low, thus the species act connecting modules; (iii) module cores, if c is low, but z is high, thus the species act maintaining connection within modules; and (iv) network cores, if both z and c are high, and species act maintaining connections among and within modules. To determine the thresholds that define roles, we used the 95th percentile of the z and c (Olesen et al., 2007).

To characterize degrees of specialization, we used the following descriptors: species strength (SS), the sum of species dependencies on each other, in order to quantify relevance across all partners; and specialization degree (d'), the specialization based on the discrimination of a species from a random selection of partners. To calculate specialization degree, if a frugivore feeds on a single, most connected plant (i.e., plant species with the highest number of partners), the evidence for specialization is limited, so the frugivore receives a value close to 0. In contrast, a frugivore feeding only on the least connected plant (i.e., the one with the lowest number of partners) indicates higher degrees of specialization, so that it will receive a value close to 1 (Blüthgen et al., 2006).

2.5 | Individual trait correlates

Plant and animal morphologies are a surrogate to evaluate function in ecological assemblages (Dehling et al., 2016). We obtained plant and animal traits from literature (Bello et al., 2017; Gonçalves

et al., 2018; Rodrigues et al., 2019). For animals, we included variables influencing the potential of fruit consumption: body mass (in g), gape/gullet sizes for bats, birds and non-flying mammals (in mm), and the degree of frugivory. Although body mass and gape/gullet sizes presented a moderate degree of correlation ($R = 0.65$, $p < .01$, Appendix S3a), body mass informs us of the amount of fruit a vertebrate is able to consume, whereas gape/gullet sizes inform us of the seed sizes that a vertebrate is able to swallow. The degree of frugivory is a meristic variable where, for each vertebrate, we assigned a value ranging from 1 to 3, based on the degree of dependence on fruits within the overall diet. Animals were divided into the following categories (Bello et al., 2017): (1) occasional consumer, (2) frequent consumer, but also consuming other foods, (3) strict frugivore. For plants, we included variables defining consumption by frugivores: fruit length (in mm), seed width (in mm) and lipid score. Fruit length and seed width presented low degrees of correlation ($R = 0.43$, $p < .01$, Appendix S3b). Lipid score is also a meristic variable where, for each plant species, we assigned a value ranging 1–3 based on the concentration of lipids present in the fruit pulp in terms of percentage relative to pulp dry mass (Bello et al., 2017): (1) <10%, (2) 10%–20%, (3) >20%.

We used exponential random graph models (ERGMs; Kolaczyk & Csárdi, 2014; Lusher et al., 2013) to analyze individual traits of animals and plants that might have shaped each plant–frugivore network. ERGMs are analogous to general linear models and test hypotheses about mechanisms shaping networks by modeling how the

likelihood of edge formation (i.e., the presence of interaction links between a frugivore species and a plant species) is affected by endogenous and exogenous variables. Further details on ERGMs are available on Appendix S4.

3 | RESULTS

3.1 | Overall network topology

We observed 1588 interactions for the Continuum among 133 animals and 315 plants, with a linkage density of 22.52 ($p = 0$) and a connectance of 0.04 ($p = 0$). For the Fragment, we observed 221 interactions among 54 animals and 58 plants, with a linkage density of 8.99 ($p = 0$) and connectance of 0.07 ($p = 0$; Figure 1, Table 1).

Continuum presented, on average, 5.06 interactions per plant and 12.03 interactions per animal, but animals tended to be more specialized than plants ($p = .006$). For the Fragment, we observed an average of 3.81 interactions per plant and 4.09 interactions per animal, with no SA ($p = .15$). Both Continuum and Fragment were nested ($p_{\text{CONT}} < .0001$, $p_{\text{FRAG}} < .0001$) and modular ($p_{\text{CONT}} < .0001$, $p_{\text{FRAG}} < .0001$), although the Continuum was proportionally more nested and modular relative to the Fragment (see z-scores, expected, and observed values in Table 1). Continuum presented eight modules, while fragment had six modules (Appendix S5).

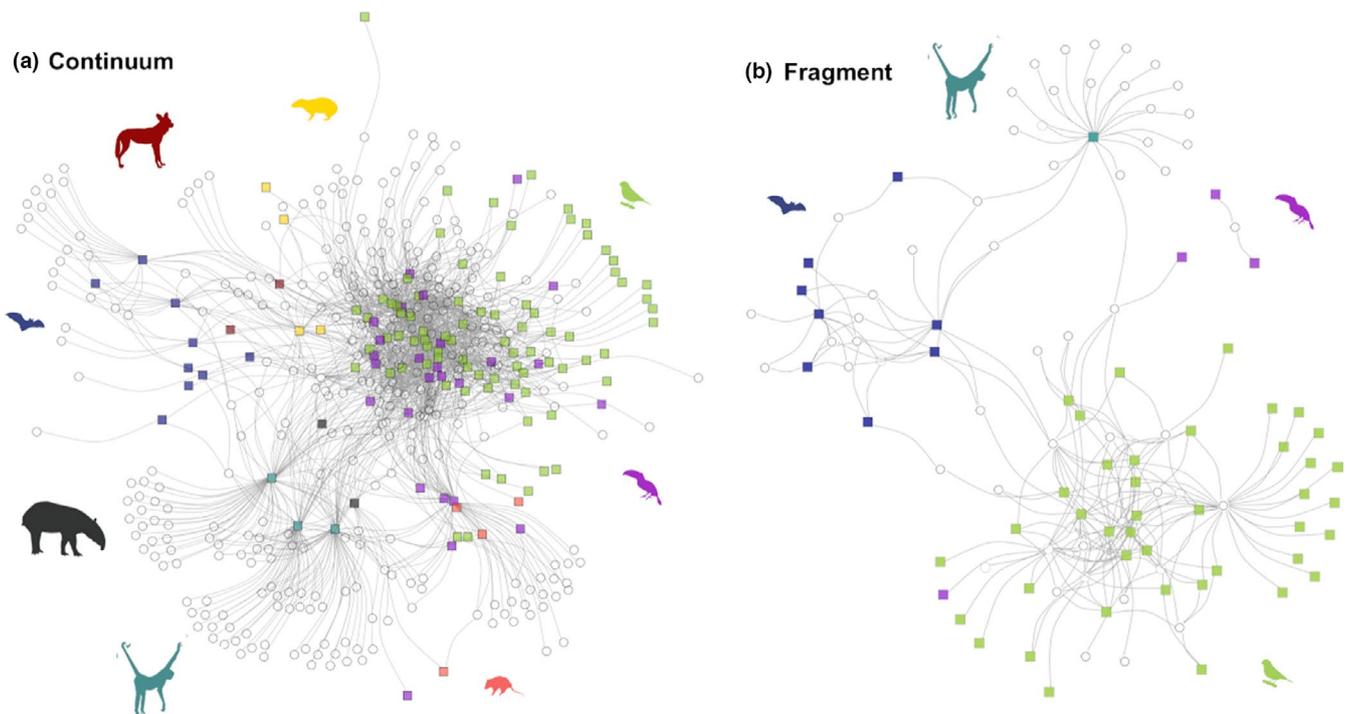


FIGURE 1 Plant–frugivore interaction networks at Continuum (a) and Fragment (b). Circles indicate plant nodes, and squares indicate animal nodes. The arrangement of nodes follows a Fruchterman–Reingold energy-minimization algorithm, locating nodes with similar connectivity patterns at closer distances. Node color for animals indicates the higher-order taxonomic groupings: dark red, carnivorous mammals; dark blue, bats; light blue, primates; dark grey, ungulates; yellow: rodents; orange, marsupials; purple, large birds, and light green, small birds

TABLE 1 Summary of the network descriptors for each study area

Descriptor	Continuum	Fragment
# Plant species	315	58
# Animal species	133	54
# Frugivory events	1588	221
Int./plants	5.06	3.81
Int./animals	12.03	4.09
LD _{obs} /LD _{exp}	22.52/16.91	8.99/6.42
C _{obs} /C _{exp}	0.04/0.03	0.07/0.06
SA _{obs} /SA _{exp}	-0.19/-0.16	-0.04/-0.03
NODF _{obs} / NODF _{exp} /z-score	16.96/7.46/36.73	20.07/9.51/14.68
Q _{obs} /Q _{exp} /z-score	0.4/0.32/15.65	0.52/0.46/4.87
# Modules	8	6

Note: Numbers in bold stand for significance (obs) when compared to 999 binary null matrices (exp). Int./plants and int./animals are the average number of interactions performed for each plant and animal species respectively. Linkage density (LD), connectance (C), specialization asymmetry (SA), Nestedness (NODF), and modularity (Q).

3.2 | Species-specific roles

Based on *c* and *z* values, the great majority of animals and plants within Continuum and Fragment were peripherals (Figure 2). Despite that, a greater proportion of species at Fragment were peripherals when compared with Continuum: about 78% of animals at Fragment against 67% at Continuum, and 90% of plants at Fragment against 81% at Continuum. On the other hand, proportionally, many more animals and plants tended to be connectors at the Continuum compared to the Fragment: about 20% of animals and 14% of plants at Continuum, against 10.5% of animals 0.07% of plants at Fragment.

The severely endangered *Pipile jacutinga* was a network core at Continuum due to its importance in interconnecting the whole network. As for plants, the threatened palm *Euterpe edulis* showed the same role, together with another large-seeded species, *Virola bicuhyba*, well known as a relevant local food resource to frugivores, and other small-seeded and recognized generalist plants: *Cecropia* and *Ficus* species.

Some small birds with the highest degrees of frugivory, such as *Tachyphonus coronatus* and *Trichothraupis melanops* were also key-species at the Continuum, acting as connectors. These two small-bodied birds were the only animals classified as network-cores at the Fragment, together with the plant *Cecropia pachystachya*. The role of connectors was shared among birds with the highest degrees of frugivory, such as the common piprids *Chiroxiphia caudata* and *Manacus manacus*, and the thraupid *Dacnis cayana*. As for plants, the large-seeded *Trichillia clausenii* and the medium-seeded *Magnolia ovata*, both considered important lipid resources, and the small-seeded *Trema micrantha*, played connector roles in the Fragment.

The three primate species inhabiting the Continuum and the largest Cracidae bird were, by far, the animals with highest SS (*Alouatta guariba*: 32.25, *Brachyteles arachnoides*: 28.94, *Sapajus nigritus*: 28.06, and *Pipile jacutinga*: 24.71). They were followed by the bat *Carollia perspicillata* (11.44) and the large Cracidae *Penelope obscura* (11.35). On the other hand, at Fragment the highest SS was shown by the only still living primate *A. guariba* (19.87), followed by two generalist small birds *Chiroxiphia caudata* (3.82) and *Manacus manacus* (3.81), and the two bats *Sturnira liliium* (3.58) and *Artibeus lituratus* (3.41) (Tables S5).

As for the specialization degree (*d'*), the most specialized species at Continuum were mammals. The highest *d'* values were shown by bats (0.72–0.56), primates (0.59–0.54), the carnivore *Cerdocyon thous* (0.56), the Sigmodontinae (0.56) and Sciurinae (0.55) subfamilies of rodents, and the large ungulate *Tapirus terrestris* (0.53). In contrast, at Fragment, where most of the assemblage of large mammals no longer inhabits, the most specialized species were the only primate *Alouatta guariba* (0.91) followed by the largest remaining birds: *Cyanocorax cristatellus* (0.79) and *Ramphastos toco* (0.79), and the bat *Glossophaga soricina* (0.70). Complete results for SS and *d'* can be found in Appendix S5.

3.3 | Individual trait correlates

Our ERGMs showed that animal and plant functional traits played an important role in structuring both Continuum and Fragment communities. At Continuum, the probability of a link to occur was modulated by the interaction patterns generated by animal and seed traits. Depending on the animal taxonomic group, an increment in every unit in the degree of frugivory and in gape/gullet size increased by 0.32 and 0.06 the log-odds likelihood of interactions with plants, respectively, although no effect of animal body mass was detected. Also, a reduction of one unit in seed width, would result in an increase of 0.11 in the log-odds likelihood of being ingested by animals within the Continuum community. On the other hand, neither changes in fruit sizes nor in lipid content modified significantly the odds of interactions (Figure 3; Table S4).

Within Fragment we observed an important shift. An increase in one unit in the degree of frugivory in animals would result in an increase of 0.50 in the log-odds likelihood of interactions with plants. Vertebrate taxonomic groups, body mass and gape/gullet size had no effect on the odds of interactions. On the other hand, smaller fruits and those with larger lipid content (regardless of seed size) tended to be more prone to interactions by increasing 0.21 and 0.50 the odds of interactions, respectively.

4 | DISCUSSION

Our study yielded three main outcomes: (1) we delineated the topology of two species-rich tropical communities under distinct

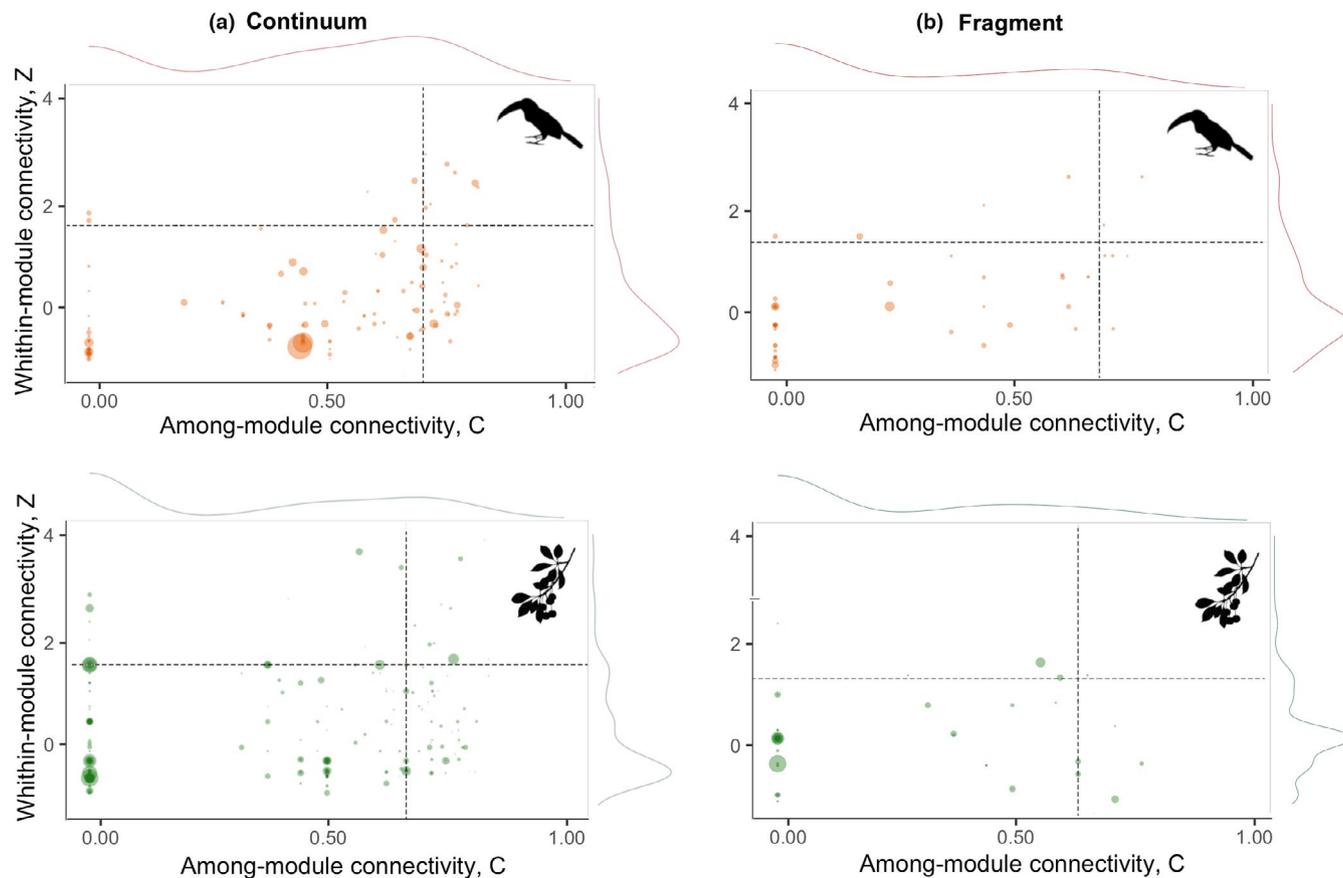


FIGURE 2 Distribution of animal (orange) and plant (green) species according to their role within the modular structure of (a) Continuum and (b) Fragment. Each circle represents a species, and circle sizes reflect gape/gullet size, in the case of animals and seed width, in the case of plants. Red and green lines represent the density distribution (not weighted by species abundances) of data for animals and plants, respectively. Vertical and transversal grey lines represent thresholds sorting species according to their role within the modular structure. To determine the thresholds that define roles, we used the 95th percentile of the z and c values (Olesen et al., 2007)

conservation contexts based on frugivory and observed a loss of complexity in terms of the number of species, connectance, linkage density, and specificity within the disturbed context; (2) the central species working as potential seed dispersers at the preserved context were the largest and the most endangered bird and mammal species in the Atlantic forest, also the first to be historically lost at the disturbed Fragment; (3) the largest degrees of frugivory and gape/gullet sizes in animals, and the smallest seed sizes in plants were the main functional traits structuring the community within the conserved scenario, while body mass, fruit size and lipid score held community structure in the disturbed scenario.

Facing the absence of data on species abundance and interaction frequency, we did not intend to perform an exhaustive comparison between conserved and fragmented forests, or to evaluate effects of habitat fragmentation on mutualistic interactions. Our results limit our conclusions to the ecological meaning of the topological organization of multiple taxonomic groups living in two opposite conservation scenarios interacting among each other, considering variation in functional traits from both animal and plant perspective. Predicting potential trajectories for topological and structural alterations driven by interaction losses still requires an extensive effort

(Domínguez-García et al., 2019), and we encourage new research in this field.

To date, most studies on mutualistic interactions assessed frugivory by a single vertebrate taxa (mammals or birds), and focused on the animal perspective (see e.g., Acevedo-Quintero et al., 2020). Here we bring novel outcomes, which align with the increasing interest of including the plant's perspective and potential bottom-up effects of resources in seed dispersal studies (e.g., Vollstädt et al., 2018; Peña et al., 2020), and show how plant species with specific functional traits have the potential to be central in maintaining community structure.

The Atlantic forest covers only 12% of its original distribution (Rezende et al., 2018; Ribeiro et al., 2009; Zwiener et al., 2017), which encompasses 1.5 million km² along the Brazilian coast and interior (Stehmann et al., 2009). As such remnant areas are represented mainly by small patches (Ribeiro et al., 2009), the patterns described in the Fragment are likely to parallel empirical conditions found in many sites. However, further conclusions depend on resolved data of a myriad of functional groups inhabiting Atlantic forest patches ranging in intensity of disturbance, added to collective effort encompassing complementary sampling techniques (Jordano, 2016; Vidal et al., 2014).

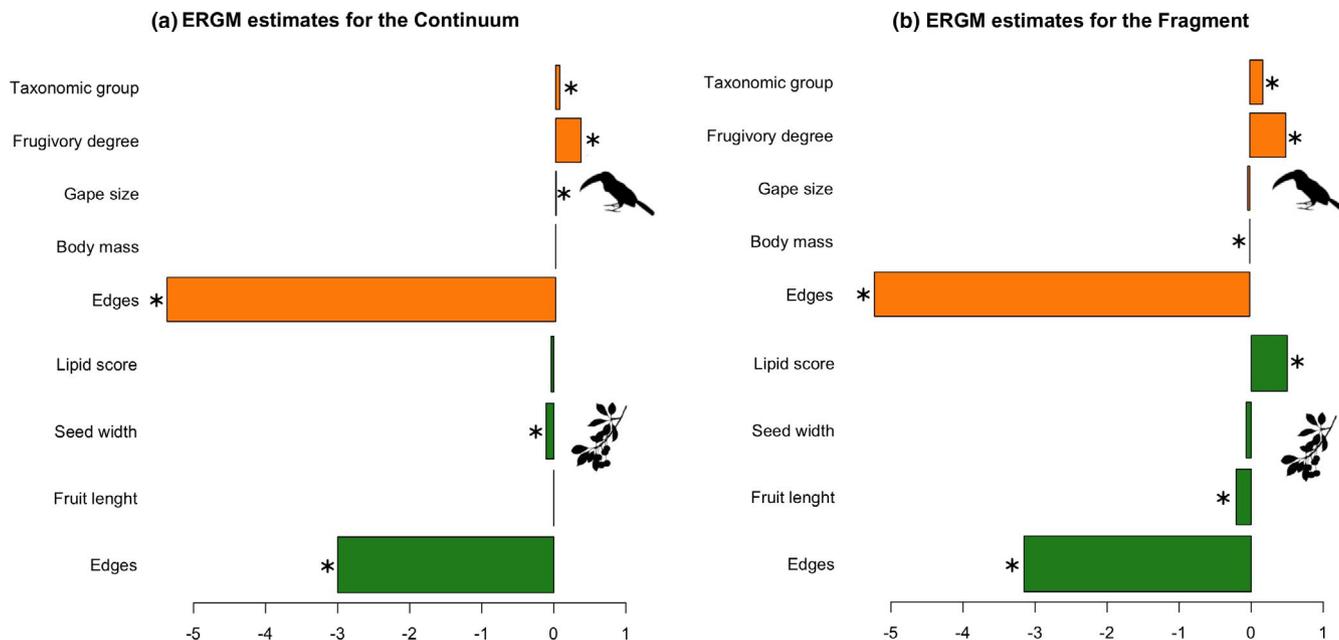


FIGURE 3 Estimates obtained from exponential random graph models showing the change in the log-odds likelihood of an interaction for a unit change in each individual trait of animals (orange bars) and plants (green bars) that produced the structure of (a) the Continuum network and (b) the Fragment network. The edges effect, analogous to the effect of the intercept term in a regular glm, evaluates the influence of just the number of links among animals and fruits, excluding any other parameter. * $p < .05$

4.1 | Overall network topology

Plant–frugivore interactions, especially Neotropics, are characterized by low degrees of specialization like those encountered here, a pattern related to diverse interacting partners (Dalsgaard et al., 2017; Schleuning et al., 2012). It might be yielded by the dominance of highly frugivore vertebrates feeding on a diversity of fruits (Dugger et al., 2019; Emer et al., 2018). Although weak specialization may drive lower degrees of modularity, hyper-diverse fruit–frugivore networks are shown to be modular in conserved scenarios (Carreira et al., 2020; Donatti et al., 2011), a trend reinforced by our results. Distinct subsets of animals and plants interacted more among them than with others at Continuum, and sets of plants sharing a combination of traits matching frugivore morphologies and feeding behaviors contributed to attract assemblages of vertebrates varying in degrees of frugivory and body sizes.

The structure of the preserved Continuum was proportionally more modular than the degraded Fragment, when controlling for network size. Despite the lack of knowledge on the implications of modular structures to mutualism resilience, modularity enhance stability in food webs. Modular food webs better tolerate disturbances and are resilient to species loss (Thébault & Fontaine, 2010). In this case, species extinctions affect only isolated modules, thus negative effects are not easily spread (Stouffer & Bascompte, 2010). Yet, for mutualisms, within the context of the diversity–stability debate (van Altena et al., 2016), highly modular mutualistic networks tend to show lowest connectance (Thébault & Fontaine, 2010), a typical feature from large networks—irrespective of modularity—a pattern also observed in this study.

Our results revealed an enhanced degree of nestedness in the Fragment. Highly human-affected and transformed environments, where interactions have been lost due to local extinctions, may suffer important shifts in architecture, and networks tend to be less modular but more nested (Sebastián-González et al., 2015), a pattern differing from that observed here. At the Continuum, frugivores feeding on a strict fruit assemblage, either due to morphological constraints and/or nutritional requirements, consumed subsets of plants that frugivores feeding on a variety of fruits, regardless of traits, consumed. This kind of highly nested architecture might minimize competition and, therefore, help to support the Continuum biodiversity (Bastolla et al., 2009). At the same time, the shorter degrees of nestedness at Fragment might have been emerged as a consequence of the loss of the most specialized interactions within human-affected communities, as shown by the outcomes that we better discuss below.

4.2 | Species-specific roles

The individual roles played by animals and plants were more balanced at Fragment than at Continuum. This trend emerged by species positions in the modular structure and by the absence of SA at Fragment. Animals performed more than two-fold interactions than plants at Continuum, while at Fragment this number was almost equal. In communities exhibiting substantial reciprocal degrees of specialization, such as observed in Fragment, the extinction of one species may have fatal consequences for its specialist interacting partners (Ollerton et al., 2006), at the same time that well-connected generalists tend

to resist. In this context, ground-dwelling mammals such as rodents, small birds and bats become key actors in defaunated environments (Carreira et al., 2020; Galetti et al., 2015; Mendellin & Gaona, 1999).

The importance of a given species according to the specialization degree is not a simple measure of the number of interactions performed. Instead, it accounts for species importance in terms of partner diversity. For instance, frugivores feeding on plants performing the lowest number of interactions receive the highest degrees of specialization (Blüthgen et al., 2006). Species showing the highest degrees are those from whom the largest number of interacting partners depend upon, owing to a limited number of other partners. Thus, plants depending on frugivores with the highest specialization degrees tend to be more prone to co-extinctions.

In this sense, we found that the most specialized species at Continuum corresponded to distinct groups of mammals. Large mammals are the main groups threatened by extinction in Atlantic forest patches (Galetti et al., 2015; IUCN, 2019), and our results reinforce this trend. At Fragment, where most of the assemblage of large mammals no longer inhabit, we detected a reduced diversity of interacting animals and plants. The only still living primate and two of the three still-living large birds were the most important species in terms of specialization degrees, owing to their ability to swallow a large diversity of fruits regarding seed sizes. Thus, the loss of the few frugivores able to consume large seeds at Fragment, may drive large-seeded plants, all performing interactions with a single frugivore, to local co-extinctions.

In terms of SS, the most relevant animals at Continuum were also those playing the most important roles in maintaining the modular structure. They were represented by the Cracidae *Pipile jacutinga*, and the primates *Brachyteles arachnoides*, *Sapajus nigritus*, and *Alouatta guariba*. We referred to them as central species, due to their underlying importance in delineating the structure of the whole community.

Most central species corresponded to the first to be vanished under disturbance pressures throughout the Atlantic forest, added to the large *Tapirus terrestris* (Galetti et al., 2015; IUCN, 2019). For instance, *B. arachnoides* (critically endangered, IUCN, 2019) and *P. jacutinga* (endangered, IUCN, 2019) are restricted to only a few remnants of the Atlantic forest, and the Continuum holds the largest remaining populations. On the other hand, at Fragment, where most of the referred central species has been locally extinct (Carvalho et al., 2013), the strongest species was the only still living primate *A. guariba*, followed by small generalist birds and bats. Howlers (*Alouatta* species) are recognized for their tolerance to habitat disturbance, as they survive in patches where no other primate are able to persist (Arroyo-Rodríguez et al., 2014). Our results reemphasize their importance as resilient frugivores since *A. guariba* was the only species identified as central at Continuum who persisted and interacted with a range of fruits at Fragment.

4.3 | Individual traits correlates

The outcomes of our ERGM models corroborated the patterns observed for the specific roles of animals and plants in structuring both

Fragment and Continuum. Despite the lack of information on frugivory events by rodents, carnivores, and marsupials for the Fragment, we were able to depict the consequences of the loss of important functional roles due to the lack of the largest and strongest frugivores.

As expected, the degree of frugivory, the proportional amount of fruit in the overall diet, was important to define the odds of interactions. However, the Fragment community tended to rely mostly on birds with the smallest body sizes to maintain structure, as well as in small lipid-rich fruits. Birds are known to eat fruits with a wide range of lipid content in the Atlantic forest (Galetti et al., 2011), and highly frugivorous birds normally require a variety of fruits to be able to reach their daily nutritional requirements (Moermond & Denslow, 1985). As a likely consequence, small lipid-rich fruits tended to be more prone to interactions in the Fragment, where small birds are acknowledged as one of the main agents of dispersal (Grombone-Guaratini & Rodrigues, 2002). The results reinforce the idea of trait-matching processes inherent to frugivory networks influencing the assemblages of interacting partners (see Schleuning et al., 2015).

Lipids and carbohydrates are important nutritional components of fleshy fruits, and are negatively correlated to each other (Herrera, 1987). Their distinct molecular structures require different metabolic pathways for absorption, which may filter distinct sets of frugivores (Levey & Martínez del Rio, 2001). Fruits typically consumed by mammals are chemically more homogeneous than those consumed by birds in the Atlantic forest (Galetti et al., 2011), and mammals tend to prefer large lipid-poor fruits rather than highly energetic ones (Sebastián-Gonguerrázal et al., 2017), as expected by Optimal Foraging Theory (MacArthur & Pianka, 1966). At Fragment, where *A. guariba* is the only persisting large mammal, large and lipid-poor fruits usually dispersed by mammals, performed fewer interactions.

At Continuum we observed an opposite trend. Although larger body sizes are frequently related to enhanced potential of seed dispersal due to the number of fruits consumed (Wotton & Kelly, 2012; but see Godínez-Alvarez et al., 2020), we found no effects of body size on the chances of interactions to occur. Instead, and despite the moderate correlation between body size and gape/gullet sizes, Continuum structure was strongly modulated by the animal capacity to swallow large fruits (measured as the gape/gullet size), and also by the size of seeds. According to each taxonomic group and regardless of body mass, the most frugivorous vertebrates and those with the largest gape/gullet sizes were more prone to interact with plants, since they were able to swallow a large diversity of fruits regarding seed sizes.

From the plant point of view, as expected, the smaller the seed, the greater the chances of being ingested by animals. Seed size may act as a constraint to vertebrate consumption (Sebastián-Gonguerrázal et al., 2017), since animals with smaller gapes and gullets are not able to swallow large seeds. Our results showed a similar trend only to the diverse context of the Continuum, where resource availability does not limit food acquisition and large-seeded species still occur in abundance. Consequently, a small set of vertebrates were shown to consistently benefit from both small- and large-seeded plants, while a wider diversity of frugivores were able to consume fruits containing smaller seeds.

Although information on plant features other than fruit traits are not extensively available, there are plant traits not assessed in our study that are worth to be considered. For instance, plant height, forest strata, fruiting crop and neighboring have been shown to be relevant in determining species interactions, and we encourage future research also to consider them in their assessments (see e.g., Acevedo-Quintero et al., 2020; Guerra et al., 2017; Peña et al., 2020).

5 | CONCLUSIONS

Present and future expansion of economy and agriculture are predicted to impose unprecedented levels of global extinctions in thousands of species, especially vertebrates inhabiting tropical regions. In the context of the ongoing human pressures, our results reinforce the need to maintain large conserved forest fragments as they potentially hold key interactions between animals and plants and might act as important exchanging sources of species and functions for the surrounding fragmented landscape. Under present and past overexploitation, we showed that the small fragment suffered important shifts in structure and loss of functions due to the defaunation of large-bodied frugivores.

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CONFLICT OF INTEREST

There is no conflict of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in the Dryad Digital Repository: <https://doi.org/10.5061/dryad.k3j9kd591> (Fuzessy et al., 2022).

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

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