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From structure to function in mutualistic interaction networks: Topologically important frugivores have greater potential as seed dispersers

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Abstract

1. Networks of mutualistic interactions between animals and plants are considered a pivotal part of ecological communities. However, mutualistic networks are rarely studied from the perspective of species-specific roles, and it remains to be established whether those animal species more relevant for network structure also contribute more to the ecological functions derived from interactions.
2. Here, we relate the contribution to seed dispersal of vertebrate species with their topological role in frugivore–plant interaction networks. For one year in two localities with remnant patches of Colombian tropical dry forest, we sampled abundance, morphology, behaviour and fruit consumption from fleshy-fruited plants of various frugivore species.
3. We assessed the network topological role of each frugivore species by integrating their degree of generalization in interactions with plants with their contributions to network nestedness and modularity. We estimated the potential contribution of each frugivore species to community-wide seed dispersal, on the basis of a set of frugivore ecological, morphological and behavioural characteristics important for seed dispersal, together with frugivore abundance and frugivory degree.
4. The various frugivore species showed strong differences in their network structural roles, with generalist species contributing the most to network modularity and nestedness. Frugivores also showed strong variability in terms of potential contribution to seed dispersal, depending on the specific combinations of frugivore abundance, frugivory degree and the different traits and behaviours.
5. For both localities, the seed dispersal potential of a frugivore species responded positively to its contribution to network structure, evidencing that the most important frugivore species in the network topology were also those making the strongest contribution as seed dispersers. Contribution to network structure was correlated with frugivore abundance, diet and behavioural characteristics. This suggests that the species-level link between structure and function is due to the fact that the occurrence of frugivore–plant interactions depends largely on the characteristics of the frugivore involved, which also condition its ultimate role in seed dispersal.

KEYWORDS
frugivore traits, generalization, modularity, nestedness, seed dispersal, tropical dry forest

1 | INTRODUCTION

Mutualistic interactions between animals and plants, such as pollination and seed dispersal, play a crucial role in shaping ecological communities and in providing ecosystem functions (Bascompte & Jordano, 2007, 2014). Ecological networks, where species are represented as nodes and interactions between species as links, enable the global quantification of the structure of animal–plant relationships (Bascompte & Jordano, 2014; Dáttilo & Rico-Gray, 2018). In this sense, three general topological patterns have been recognized in mutualistic networks: (a) nestedness, which reflects that the various species that interact with specialists are a typical subgroup of species that also interact with generalists (Bascompte, Jordano, Melián, & Olesen, 2003; Tylianakis, Laliberté, Nielsen, & Bascompte, 2010); (b) modularity, which refers to the network being structured in modules, or groups of species that interact more among themselves than with the species of other modules (Olesen, Bascompte, Dupont, & Jordano, 2007) and (c) heterogeneity, which describes the high frequency of species with few interactions but the low frequency of species with many interactions (Bascompte & Jordano, 2014).

Although the structural generalities of animal–plant mutualistic interactions are well known, we are still far from understanding the functional consequences of variability in network structure (Fricke, Bender, Rehm, & Rogers, 2018; García, Donoso, & Rodríguez-Pérez, 2018). Theoretical studies have found that both network nestedness and modularity affect a network's robustness against species extinction (Bastolla et al., 2009; Rohr, Saavedra, & Bascompte, 2014; Tylianakis et al., 2010). In addition, empirical studies show that the degree of specialization within interaction networks affects the magnitude of their derived ecological functions (e.g. pollination, Fründ, Dormann, Holzschuh, & Tscharntke, 2013; Kaiser-Bunbury et al., 2017; and seed dispersal, García et al., 2018). However, the link between structure and function has been scarcely addressed at levels below that of the global network (e.g. interacting species or individuals). In this sense, individual plants with central positions in pollination networks are known to have greater functional relevance in their populations through their improved fitness (Gómez & Perfectti, 2012; Gómez, Perfectti, & Jordano, 2011). Despite such progress in understanding, it remains to be established whether the species with greater relative contributions to network topology are also those contributing the most to the ecological functions derived from mutualistic interactions (but see Lázaro, Gómez-Martínez, Alomar, González-Estévez, & Traveset, 2019, for pollination networks).

Frugivore–plant relationships, whose complexity is frequently studied through network approaches, underlie a major ecological function (i.e. plant community-wide seed dispersal) in temperate and tropical ecosystems (e.g. García et al., 2018; Jordano, 2014; Jordano et al., 2011). Contribution to the process of seed dispersal, and to the concomitant plant recruitment, varies widely among frugivore species, depending on the species and the quantity of fruit consumed, and the type of handling of fruits and seeds during consumption (with some frugivores destroying seeds while feeding on fruits, whereas others drop them intact after regurgitation or defecation; Jordano, 2014; Simmons et al., 2018). More importantly, the ultimate roles of frugivores depend largely on seed fate after dispersal, which is contingent on the environmental features of seed deposition sites (Schupp, Jordano, & Gómez, 2010; Traveset, Heleno, & Nogales, 2014).

Estimating frugivore-specific contributions to community-wide seed dispersal function requires comprehensive observations of not only plant–frugivore interactions but also of plant recruitment. To date, this sort of integrative information has been gathered in systems of moderate species richness (e.g. Donoso, García, Rodríguez-Pérez, & Martínez, 2016; González-Castro, Calviño-Cancela, & Nogales, 2015) but not in species-rich systems such as tropical forest. There, alternatively, the ecological characteristics of frugivore species may be used as surrogates of their contribution to plant recruitment (Dennis & Westcott, 2006; Naniwadekar, Chaplod, Datta, Rathore, & Sridhar, 2019). For example, frugivore species abundance and the proportion of fruit in an animal's diet have been found to be good indicators of the quantity of fruits consumed by animals in frugivory networks (e.g. García, Martínez, Stouffer, & Tylianakis, 2014; Rother, Pizo, & Jordano, 2016; Ruggera, Blendinger, Gomez, & Marshak, 2016). Moreover, frugivore traits, such as body size, have been found to positively affect the recruitment of plants of different fruit sizes (Chen & Moles, 2015; Muñoz, Schaefer, Böhning-Gaese, & Schleuning, 2017), with larger frugivores retaining seeds in their gut for longer, thus dropping seeds in sites that increase their likelihood of escaping density-dependent mortality factors (Howe, Schupp, & Westley, 1985; Wotton & Kelly, 2011). Finally, frugivore behaviours, such as the likelihood of using forest habitat, may also benefit recruitment expectancies of forest plant species (Wenny & Levey, 1998) through avoiding unsafe landscape patches for seeds such as deforested land (Holl, Loik, Lin, & Samuels, 2000; Zahawi, Holl, Cole, & Reid, 2013).

In the present work, we study interaction networks between vertebrate frugivores and fleshy-fruited woody plants, in two remnant patches of species-rich, tropical-dry forest embedded in deforested matrices of agricultural and cattle rearing lands in northern Colombia. Our main objective was to determine whether frugivore species contributing the most to network structure also show a higher potential to provide seed dispersal for the plant community. Specifically, based on fruit consumption observations, we estimated different measures of species contribution to network heterogeneity, nestedness and modularity to assess an integrative measure of species role in global network structure. Similarly, we combined field-sampled ecological, morphological and behavioural features to estimate an integrative measure of the potential of frugivores to operate as seed dispersers.

2 | MATERIALS AND METHODS

2.1 | Study area

This study was conducted in two localities (Guacamayas and El Pino) in the department of Córdoba in northern Colombia (09°25′–07°15′N, 75°26′–75°10′W; see Appendix S1; Figure S1 for detailed description). This area of the Colombian Caribbean region has average temperatures of 28°C, rainfall of 1,300 mm/year with a unimodal distribution, the dry season being from December to March and the rainy season from April to November. Forests (Tropical Dry Forest type) in this region have been drastically reduced and fragmented by agriculture and livestock ranching (Ballesteros-Correa & Linares-Arias, 2015; Racero-Casarrubia, Ballesteros-Correa, & Perez Torres, 2015). This habitat loss, along with poaching and wildlife trafficking, has resulted in a drastic degree of defaunation.

2.2 | Sampling of frugivore–plant interactions

In each locality, eight 5-day sampling sessions were conducted at 2-month intervals between April 2017 and June 2018. Two complementary methods were used to record interactions between vertebrate frugivores and fleshy-fruited plants: direct observation along walking transects and camera trapping.

Four 1-km transects were established per locality, covering different types of vegetation (open areas, riparian forests, woodland pastures, forest edges, forests; Figure S1). Two observers simultaneously walked two separate transects to detect frugivory events using binoculars. We considered a frugivory event to be any visit by a frugivore to an individual plant in which at least one fruit was consumed. To increase the probability of detecting infrequent interactions, observation while walking was combined with focal watching of individual fruiting plants (Jordano, 2016). Thus, once an event was detected in a given plant, a 4-min focal watch was conducted, and the species involved and number of frugivore individuals consuming fruits was recorded. Surveys were conducted between 6:00 and 11:00 a.m., and between 4:00 and 6:00 p.m., over five consecutive days, alternating the order of transects on the different days. Between 10 and 12 surveys were conducted per transect, yielding a total of 312 hr of observation time. Sampling effort was calculated as the total time invested in both walking transects and focal watching by the two observers. Interaction frequency was measured as the number of times that a frugivore species consumed fruits from a specific plant species.

Camera trapping was used to detect frugivory by cryptic, or difficult to record, animals, such as large birds and nocturnal mammals and reptiles. Between 3 and 7 camera traps (Bushnell Trophy Cam) were used per locality and were positioned either 50 cm off the ground near piles of fallen fruits, or in the woody canopy, at a height of 10–15 m, near bunches of ripe fruits. Cameras were configured to record 30-s videos with 20-s intervals between recordings. Camera locations varied across the study site depending on fruit availability, with the aim of sampling as many fruiting species as possible. From viewings of each video, the species involved and number of frugivore individuals were recorded. To calculate interaction frequency, all video footage relating to the same animal species consuming fruits, and recorded on the same camera during the same period (1 hr), were considered a single frugivore visit (Acevedo-Quintero & Zamora-Abrego, 2016). Sampling effort was calculated as the sum of days in which each camera trap was active.

2.3 | Frugivore abundance

The abundance of a frugivore species was estimated as its frequency of occurrence in observation stations. For birds, we established observation stations in four 50-m radius areas centred on various points, separated by at least 500 m, along transects (Figure S1). Bird censuses, where all individuals detected (visual sightings and vocalizations) over a 15-min period were identified at the species level, were conducted at each point, making between 7 and 12 repetitions. Frequency of occurrence of each bird species was calculated as the proportion of census points where a given species was recorded with respect to the total number of observation stations in each locality. For mammals and reptiles, observation stations were established in each of nine 0.16 km^2 cells in a grid that covered each study site, and camera traps were installed in each cell. All cells were chosen to incorporate at least 20% forest cover (Figure S1). Cameras were, in this case, configured to record for 35 s each time they were triggered, followed by a 10-s pause before the next recording began. The cameras were left in the different locations for a similar amount of time. Each video was later viewed to detect the occurrence of the different species, and the frequency of occurrence for a particular species was calculated as the proportion of observation stations (camera traps) where the species was recorded with respect to the total number of camera traps in each locality (9 in Guacamayas, 8 in El Pino, due to the deactivation of one camera during sampling).

2.4 | Morphological and behavioural characteristics of frugivores

We were interested in sampling frugivore morphological and behavioural characteristics relevant to seed dispersal. Thus, for each frugivory event observed in the field, we recorded the foraging stratum in which each interaction occurred in terms of four height categories (high, medium, low and ground level; Appendix S1). We also classified the type of fruit handling observed in each frugivory event, distinguishing between predation, pulp consumption, fruit transport and endozoochory (Appendix S1). To characterize the range of fruit sizes of the various plant species consumed by each frugivore, we sampled 10 ripe fruits from 10 individuals of each plant species during the period of frugivory observations and measured the width of fresh fruits. Data from the literature were used for some plant species for which field sampling was unfeasible. Lastly, the body size of each frugivore species (median body mass) and frugivory degree (proportion of fruit in the diet of each species) were obtained from the EltonTraits 1.0 database (Wilman et al., 2014).

2.5 | Data analysis

2.5.1 | Interaction networks

We built a quantitative interaction matrix for each locality in which each row represented a frugivore species (*i*), each column represented a plant species (*j*), and the value of the *ij* cell represented interaction frequency, estimated as the number of frugivory events recorded during the entire sampling (Vázquez et al., 2007). Since two different methods were used to record interactions (direct observation and camera trapping), interaction matrices were standardized according to the sampling effort for each method, where interaction frequency was estimated per 24 hr of observation. To evaluate the sampling completeness of interaction networks, we built interaction accumulation curves where the number of interactions (i.e. frugivore–plant species pairs) observed was related to sampling effort (measured as the number of interaction events recorded; Chacoff et al., 2012; Jordano, 2016). The estimated number of expected interactions was calculated using the Chao1 estimator (Chacoff et al., 2012; Chao, Colwell, Lin, & Gotelli, 2009) with EstimateS 9.1.0 software (Colwell, 2013). This analysis showed that the sampling effort applied led to the detection of 80% of expected interactions in both localities (Appendix S2; Figure S2), suggesting a high representativeness for our interaction matrices.

As indicators of global topological patterns of local networks, we calculated nestedness and modularity (Bascompte & Jordano, 2014; Dáttilo & Rico-Gray, 2018). The degree of nestedness (NODF) was calculated using the algorithm proposed by Almeida-Neto, Guimarães, Loyota, and Ulrich (2008). We also evaluated whether the observed value of nestedness differed from that of a situation where interactions emerge randomly, by comparing it to those obtained from a null model which randomized the interactions for 1,000 matrices of the same size as that of the observed matrix (Bascompte et al., 2003). Lastly, the *p* value was defined as the fraction of random matrices with a NODF value equal to or greater than that of the observed matrix. Calculations were made using Aninhado 3.0 software (Guimaraes & Guimaraes, 2006). Modularity was estimated as *Q*, employing the 'QuanBiMo' algorithm, and using the highest *Q* value achieved over five independent runs (Dormann & Strauss, 2014). *Q* values vary from 0 to 1, with values closer to 1 indicating greater modularity. We used the Patefield null model to calculate the significance of the modularity value (difference with respect to random) in 100 matrix randomizations. The *Q* value of each random matrix was calculated, and we transformed the *Q* observed value into a *z* score (*zQ* = (*Q*observed-mean *Q*null)/st dev *Q*null). Since *z* scores were assumed to be normally distributed, networks with *z* above 2 were considered significantly modular, as this meant that observed modularity was 2 standard deviations higher than would be expected from random networks (Dormann & Strauss, 2014). Calculations were made using the BIPARTITE package in R (Dormann, Frund, Bluthgen, & Gruber, 2009).

2.5.2 | Structural relevance of frugivore species in interaction networks

We quantified the contribution that each frugivore species makes to the topological patterns of local networks. We used four species-level metrics which take into account the most important patterns of organization in plant–animal mutualistic networks (i.e. heterogeneity, modularity and nestedness): *degree*, which quantifies the number of links each frugivore species has (i.e. the number of plant species with which it interacts), and represents generalization in that species with high values are considered generalists (Mello et al., 2015); *c* and *z* metrics, which measure, respectively, the level at which a species connects with species from different modules or from the same module (Olesen et al., 2007), estimated using the algorithm described by Dormann and Strauss (2014); *nestedness contribution*, which quantifies each species' contribution to the maintenance of network nestedness (Saavedra, Stouffer, Uzzi, & Bascompte, 2011), calculated using the *nestedcontribution* function from the R package BIPARTITE (Dormann et al., 2009).

These species-level network metrics were used to build a principal component analysis (PCA) with the aim of determining, through PCA axes, global trends of variation across species in the topological parameters of each network (Estrada, 2007; Vidal et al., 2014). Since the first PCA axis (PC1) accumulated a considerable proportion of the variance in both networks and accounted for the covariation of all topological parameters (Appendix S4; Table S4.1), it was used as an estimator of the structural relevance of frugivore species in each interaction network (contribution to network structure, CNS; Dáttilo et al., 2016; Sazima, Guimaraes, dos Reis, & Sazima, 2010).

2.5.3 | Functional relevance of frugivore species: Seed dispersal potential

To represent the functional effect that each frugivore species may provide, through seed dispersal, to community-level plant recruitment, we developed a seed dispersal potential (SDP) index. This index took into account a set of ecological, morphological and behavioural characteristics of frugivore species, which are all considered to affect plant recruitment, by modifying pre- and post-dispersal seed fate as well as seedling establishment (Dennis & Westcott, 2006; Table 1; Appendix S3). Based on previous studies on the effects of frugivore characteristics on seed dispersal and seedling establishment (see rationales in Appendix S3; Table S3), we assumed that high values of these characteristics indicated a greater ability of that frugivore to favour recruitment across plant species in the forest community. The values of each frugivore characteristic within each locality were transformed into *z* scores (with mean 0 and standard deviation 1) for standardization. Then, the standardized values of the different characteristics were summed for each species. By means of

TABLE 1 Ecological, morphological and behavioural characteristics of frugivore species used to calculate species-level seed dispersal potential (SDP) index

Frugivore characteristic	Parameter calculation
Body size	Median body mass (log)
Foraging strata	Diversity of foraging strata, based on frequency of use of high-, medium-, low- and ground-level strata
Forest habit	Use of forest, based on the frequency of occurrence at abundance sampling stations with different canopy cover values (Figure S3)
Handling type	Effect of fruit handling on seed survival, based on the frequency of observed behaviours, and their corresponding effect value (predation, −1; pulp consumption, 0.1; fruit transport, 0.3; endozoochory, 1)
Range fruit size	Coefficient of variation of fruit size of consumed plant species

this sum, we sought to represent the cumulative nature of different recruitment stages surrogated by frugivore characteristics (Herrera, Jordano, Lopez-Soria, & Amat, 1994), as well as the compensatory effect of these characteristics in terms of plan recruitment potential (e.g. a frugivore may demonstrate a high potential to disperse seeds in terms of seed handling behaviour, as a result of its endozoochory, but deposit seeds in an inappropriate habitat, e.g. outside of the forest; Schupp, 1993). To take into account that SDP of frugivore species may also be largely affected by frugivore quantity and/or frugivory magnitude (the degree of frugivory by individual animals), we weighted the contribution of the previous set of frugivore characteristics according to the abundance of the frugivore species and their frugivory degree (i.e. the relative relevance of fruit in the animal's diet; Wilman et al., 2014). Thus, the integrative index of SDP for each frugivore species was estimated as follows:

$$\mathrm{SDP}_j = \left(\mathrm{RA}_j \times \mathrm{FD}\right) \times \sum Z_{ij},$$

where SDP is the SDP index, RA is the relative abundance, FD is the frugivory degree, *j* is the frugivore species, *i* is the frugivore (ecological, morphological and behavioural) characteristics and *Z* is the *z* score of each of the *i* characteristics.

Small mammal species (Rodentia order) that could not be accurately identified and primates for which there was no abundance data (*Saguinus leucopus* and *Cebus capuchinus*) were excluded from this and subsequent analyses.

2.5.4 | Relationship between structural and functional relevance of frugivores

To test the relationship between the topological importance of frugivore species in the local interaction networks and their functional consequences as potential seed dispersers, we fitted a GLMM (Zuur, Ieno, Walker, Saveliev, & Smith, 2009) with SDP as a response variable, considering a Gaussian distribution, with data for frugivore species from both localities. CNS and locality (Guacamayas, El Pino) were incorporated as predictors (fixed effects). Interaction between fixed effects was also incorporated, but removed from the final model after it proved to be statistically non-significant ($p = 0.15$). Frugivore data corresponded to 58 species from 46 genera and 24 families. To control the effect of statistical non-independence due to data for similar taxa in the two localities, we included (as a random effect) frugivore taxonomic identity, which included, with nested categories, species, genus and family (e.g. Dugger et al., 2019). The proportion of variance explained by the fixed effects, and by the combination of the fixed and random effects, was estimated based on the marginal and conditional R^2 values, respectively (Nakagawa & Schielzeth, 2013). All calculations were carried out using R packages NLME (Pinheiro, Bates, & R-core, 2013) and MUMIN (Barton, 2019). Lastly, to verify the occurrence of frugivore matching traits (i.e. characteristics that determine the structural role of a species in interaction networks), for each local network we correlated (using Spearman rank correlation) ecological, morphological and behavioural metrics with CNS.

3 | RESULTS

3.1 | Structure of interaction networks

We recorded 1,396 frugivory events involving 63 animal species and 53 plant species. In both localities, the number of frugivores was greater than that of plants (Table 2), and the proportion of observed

TABLE 2 General descriptors of two frugivore–plant networks in Colombian tropical dry forest

Descriptor	Guacamayas	El Pino
Sampling effort		
Direct observation (hr/observer)	168	144
Camera trapping (days/camera)	298	338
Species richness		
Animals	50	45
Plants	39	25
Interaction richness		
Interactions (links)	208	116
Events	971	425
Nestedness		
NODF	27.52	25.56
p value	<0.001	<0.001
Modularity		
Q	0.37	0.47
z-*Q*	130.6	165.4

interactions in relation to those that were possible was low (connectance = 0.10). The interaction networks of both localities showed similar, and significantly higher than expected by chance, levels of nestedness and modularity ($p < 0.001$, in both localities for both metrics; Figure 1; Table 2). The network from Guacamayas consisted of five modules, and that from El Pino, eight (Figure 1).

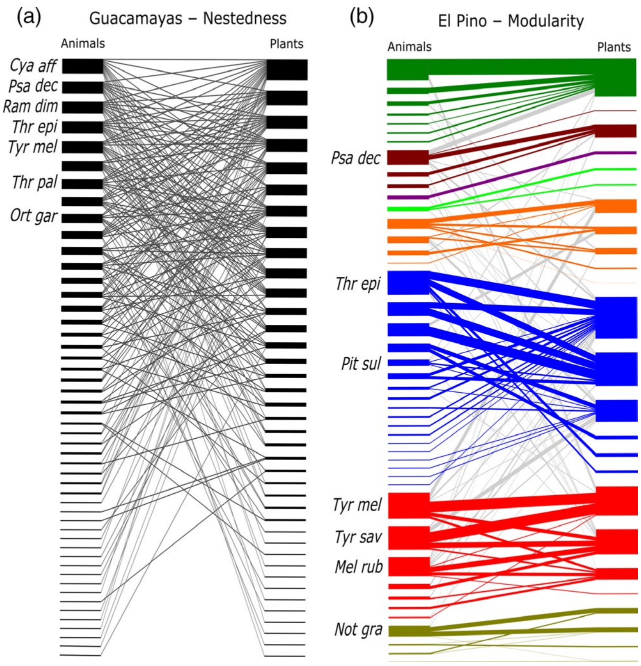

FIGURE 1 Frugivore-plant networks in two Colombian tropical dry forests. (a) Bipartite representation of Guacamayas network highlighting nestedness. Species (animals on the left, plants on the right) are ordered from top to bottom according to degree value. (b) Representation of modularity of El Pino network, each module is a different color. In both networks, the frugivore species making the highest contribution to the network structure (CNS) are shown with abbreviated scientific names. Cya aff, *Cyanocorax affinis*; Psa dec, *Psarocolius decumanus*; Ram dim, *Ramphocelus dimidiatus*; Thr epi, *Thraupis episcopus*; Tyr mel, *Tyrannus melancholicus*; Thr pal, *Thraupis palmarum*; Ort gar, *Ortalis garrula*; Pit sul, *Pitangus sulphuratus*; Tyr sav, *Tyrannus savanna*; Mel rub, *Melanerpes rubricapillus*; Not gra, *Notosciurus granatensis*

3.2 | Structural relevance of frugivore species in the interaction network

The values of species-level network metrics *c*, *z* and *nestedness contribution* were positively correlated with *degree* (Pearson's $r > 0.50$, $p < 0.001$) across frugivore species. This indicates that those frugivores that interacted with many plant species served as connectors both between and within network modules and contributed greatly to nestedness. The first axis (PC1) of the PCA, which considered the four species-level metrics, accounted for 70% of variance in Guacamayas and 54% in El Pino (Table S4.1). Thus, based on PC1 scores, species making the highest contribution to CNS were those which also demonstrated high values for all topological metrics (Figure 1).

3.3 | Functional relevance of frugivore species: SDP

The various frugivore species differed greatly in their SDP values as a result of the different combinations of abundance, frugivory degree, and morphological and behavioural characteristics (Figure 2). For example, species like *Psarocolius decumanus* were abundant and showed high values of frugivory degree as well as of other metrics of potential as seed dispersers, which yielded a high SDP (Figure 2), while species with moderate abundance but with low values for the majority of metrics, such as *Elaenia flavogaster*, had low SDPs and thus were identified as having poor SDP. Intermediate values of SDP were found for species where low abundances were compensated for by high values of other metrics (e.g. *Ortalis garrula*), as well as for spe cies in which compensations occurred among the various ecological and behavioural metrics (e.g. *Ara macao*, a large frugivore that mostly forages, as a seed predator, in the highest forest stratum; Figure 2).

3.4 | Relationship between structural and functional relevance of frugivores

In both localities, frugivore species with high structural relevance (high CNS) showed high potential as seed dispersers (high SDP), while

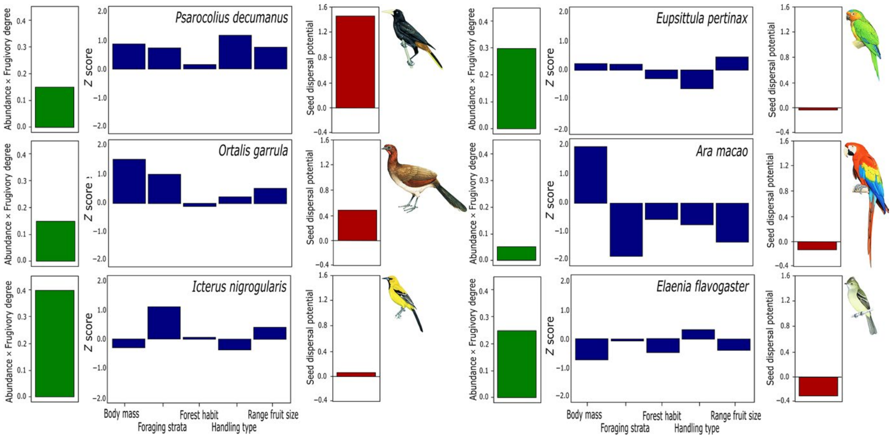

FIGURE 2 Examples of decreasing values of seed dispersal potential (SPD) index (in red; from top to bottom and left to right), for six frugivore species in El Pino. These values were estimated from the sum of values of ecological, morphological and behavioural characteristics (in blue; body size, foraging strata, forest habit, handling type, range of fruit size) weighted by the product of relative abundance and frugivory degree (in green). Illustrations © Lynx Edicions

less topologically important species appeared as poor seed dispersers (Figure 3). However, in El Pino, *Dasyprocta punctata* had a high SDP despite having a very low CNS (Figure 3b), thereby representing an analytical *outlier* as regards the general trend (Bonferroni Outlier Test: *D. punctata* rstudent = 6.54, Bonferonni $p < 0.001$; Appendix S5; Figure S5.1), and was therefore excluded from later analyses. The GLMM revealed that CNS had a statistically significant positive effect on SDP, irrespective of the studied locality (Figure 4; Table 3).

There were significant positive correlations between CNS and frugivore abundance, frugivory degree and frugivore behavioural characteristics in both localities (Table 4; Appendix S3; Figure S6). Body mass, however, showed a quadratic relationship with CNS, indicating that the contribution of medium-sized frugivores was greater than that of very large or very small frugivores (Appendix S3; Figure S6).

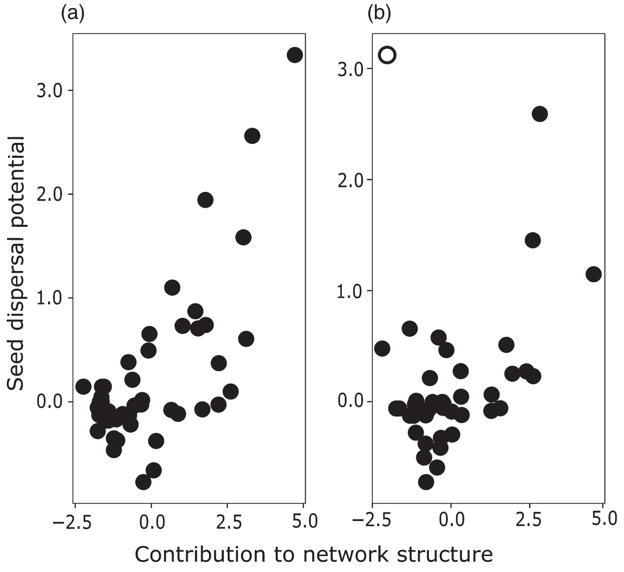

FIGURE 3 Values of seed dispersal potential index in relation to the contribution to network structure of frugivore species in Guacamayas (a) and El Pino (b). White circle in (b) corresponds to *Dasyprocta puntacta*

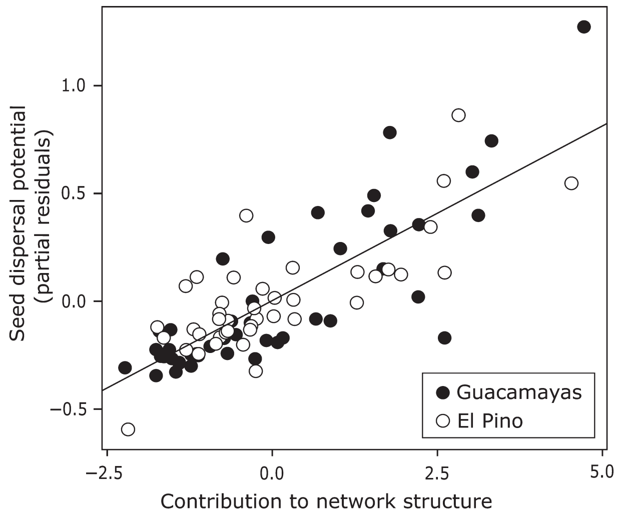

FIGURE 4 Graph of partial residuals representing the net effect of contribution to the network structure on seed dispersal potential. Dots correspond to different frugivore species from different localities. The line represents GLMM fitted values accounting for the effects of locality and taxonomic identity (random factors)

TABLE 3 Generalized linear mixed model for the effect of contribution to network structure (CNS) and locality (fixed effects) on dispersal potential index (SDP). The model includes frugivore taxonomic identity as a random effect. Marginal and conditional (in parentheses) R^2 values are also shown

SDP R^2 = 0.165 (0.814)				
Fixed effects	**Estimate**	***SE***	***t*-Value**	***p* Value**
CNS	0.160	0.030	5.212	<0.001
Locality	−0.089	0.067	−1.330	0.194
Random effects		**Variance**		***SD***
Species[Genus[Family]]		0.393		0.273

TABLE 4 Spearman correlations between frugivore characteristics and contribution to network structure, across different frugivore species in each locality

	Guacamayas (*N* = 47)	**El Pino (*N* = 42)**
Abundance	0.46***	0.44**
Frugivory degree	0.30*	0.17
Body mass	−0.08	0.30
Foraging strata	0.51***	0.31*
Handling type	0.75***	0.53***
Forest habit	0.36*	0.34*
Range fruit size	0.32*	0.38**

*$p \le 0.05$; **$p \le 0.01$; ***$p \le 0.001$.

4 | DISCUSSION

We evaluate here the functional repercussions of the structure of mutualistic interaction networks by measuring the relevance of different species within networks, along with their particular contributions to a given ecological function. We observed that the most important frugivore species in a network topology were also those with higher potential to perform as seed dispersers. We suggest that this link between structure and function is due to the fact that frugivore–plant interactions and the potential outcome of later seed dispersal processes depend largely on the same set of frugivore characteristics.

4.1 | Differential role of frugivore species in network topology and in seed dispersal

Our results show that frugivore species differ in their relative contributions to network structure (Figure 1), as has previously been demonstrated in other animal–plant networks, using similar structural components (Dáttilo et al., 2016; Vidal et al., 2014) or based on centrality measures (Montoya-Arango, Acevedo-Quintero, & Parra, 2019). The differential contribution of frugivores to network structure comes from variability in the frequency and identity of frugivore–plant interactions since some species have the ability to establish more partner plant relationships, or interact selectively with plants of different groups (Dehling, Jordano, Schaefer, Böhning-Gaese, & Schleuning, 2016; Olesen et al., 2011). Our results also show that better connected species (i.e. those with higher *degree* values) do indeed promote greater nestedness and play a more important role in modularity (connectors and hubs; see also: Dáttilo et al., 2016; Vidal et al., 2014). The integrative measure of CNS developed in this work thus represents the role that each species plays in maintaining the global organization of a network (Dáttilo et al., 2016).

The frugivores studied here also presented great variability in their potential role as seed dispersers (Figure 2), as has been previously highlighted in other frugivore assemblages (Rother et al., 2016; Schupp et al., 2010). The variability in SDP observed here could be amplified by positive correlations among the characteristics conditioning SDP. For example, larger and more abundant frugivores used the forest habitat with a higher frequency than small and rare species (Appendix S7; Figure S7). The independence of the methods used to measure the different characteristics suggests an ecological rather than a procedural basis for these correlations. In other words, different frugivore characteristics can represent common responses to a given environmental condition (Mouillot, Graham, Villeger, Mason, & Bellwood, 2013). For instance, habitat loss and hunting exert a filtering effect on frugivore forest habit as well as on body size (Lees & Peres, 2008), leading to the occurrence of positive relationships between the two characteristics across species. Alternatively, some correlations between the components of SDP may actually represent causal concatenations. For example, species with high vertical mobility can potentially access a greater diversity of plants with varying life histories, therefore increasing the range of fruit sizes they consume (Malmborg & Willson, 1988).

4.2 | Relationship between structural and functional relevance of frugivores

Our analysis shows that the topological position of a frugivore species in the interaction network explained its potential contribution as seed disperser in a consistent manner across localities (Figure 4). *Dasyprocta punctata* in the El Pino site did not follow this trend, and its functional contribution was disproportionate to its network role there (Figure 3; Appendix S5). This can be explained by the species having high abundance, large body size and a marked forest habit, but also a locally specialized interactions with large-fruit plants (e.g. *Bactris gasipaes*, *Astrocaryum malybo*). This was probably due to a local, facultative selection toward more profitable fruits because of their nutritional characteristics or their accessibility in low vegetation strata or at ground level (Burns, 2013). Nevertheless, even when this species is included in the global analysis, our results indicate a positive effect of frugivore CNS on potential role as seed disperser (Appendix S5; Tables S5.1 and S5.2).

Previous studies have addressed structure–function relationships in interaction networks by quantifying structural role from single metrics, such as *degree* (number of links of each species) or specificity of interactions (e.g. Coux, Rader, Bartomeus, & Tylianakis, 2016). In this work, we applied an integrative approach to estimate both structural and functional roles: CNS, which involved four metrics directly related to major structural patterns of mutualistic networks (generalization, nestedness and modularity; Dáttilo et al., 2016; Vidal et al., 2014) and SDP, which combined ecological, morphological and behavioural effects of each frugivore on the recruitment potential of the assemblage of zoochorous plants. Our findings suggest that, from a community perspective, plants obtained greater demographic benefits from animals with more responsibility for maintaining nestedness and modularity in interaction networks. This pattern is similar to that found in pollination networks, where centrality in the network was significantly associated with plant fitness (Lázaro et al., 2019).

In both localities, the contribution of frugivores to network structure was associated with frugivore abundance and frugivore diet, as well as with frugivore behavioural characteristics (Table 4). This suggests that the abundance and traits of an animal species determined the identity and the frequency of frugivore–plant interactions. Abundance modulates the occurrence of interactions through neutral effects by which the most abundant species accumulate more interactions as a result of increased probabilities of encounter (Vázquez, Chacoff, & Cagnolo, 2009). Likewise, a species' traits condition the frequency of its interactions through spatial, temporal or morphological matches (or mismatches) between species (López-Carretero, Díaz-Castelazo, Boege, & Rico-Gray, 2014; Olesen et al., 2011). For example, frugivores able to move through different vegetation strata can interact with more plant species (Schleuning et al., 2011). Regarding frugivore body size, we found that both the smallest and the largest frugivores interacted with fewer plant species than medium-sized frugivores, which were better connected within networks (Appendix S6; Figure S6). This quadratic pattern contrasts with the positive linear relationship described in other studies (Correa et al., 2016; García et al., 2014; Palacio, Valderrama-Ardila, & Kattan, 2016), but is in line with cases where the structural role of large frugivores has been found to shrink when they specialize in large fruits inaccessible to small frugivores (Naniwadekar et al., 2019; Sebastián-González, Pires, Donatti, Guimarães, & Dirzo, 2017). That said, the relationship between the characteristics of frugivores and their topological position suggests that the link between frugivore structural and functional roles demonstrated in this work may result from a correspondence between matching traits (i.e. those which determine the identity and frequency of interactions; Dehling et al., 2014; Olesen et al., 2011) and effect traits (i.e. those which determine the magnitude of the ecological function; Dennis & Westcott, 2006) of frugivore species.

5 | CONCLUSIONS

Our study presents a species-based approach to discern the mechanisms that underlie structure–function relationships in ecological interaction networks. We applied an integrative approach which accounted for the various components of the structural and functional roles of the different species. This framework is also applicable to other types of animal–plant mutualistic networks (e.g. plant–pollinator) where the effects of animals on plants fitness depend on ecological, morphological and behavioural traits (Fontaine, Dajoz, Meriguet, & Loreau, 2006; Rosas-Guerrero et al., 2014; Schupp, Jordano, & Gómez, 2017). Finally, we encourage the evaluation of the effects of species decline and extinction on ecosystem stability through studies based on the identification of a species' topological role and on the assessment of ecological functions as a compendium of species contributions. For this goal, species traits emerge as a conceptual target for understanding not only species interactions and functional effects but also species response to extinction drivers (Schleuning, Frund, & García, 2015).

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AUTHORS' CONTRIBUTIONS

J.F.A.-Q., J.G.Z.-A. and D.G. conceived and designed the study; J.F.A.-Q. and J.G.Z.-A. collected the data; J.F.A.-Q. and D.G. analysed the data; J.F.A.-Q. and D.G. wrote the manuscript. All authors revised the manuscript and approved the final version.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository https://doi.org/10.5061/dryad.8pk0p2nk2 (Acevedo-Quintero, Zamora-Abrego, & García, 2020).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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