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Interindividual variations in plant and fruit traits affect the structure of a plant-frugivore network

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ABSTRACT

Frugivores select their food in a hierarchical way, from plants to individual fruits, to meet their nutritional requirements. According to the optimal diet theory, finding, handling, and digesting fruits is costly, thus plant species that increase attractiveness and reward are usually preferred by frugivores. The same should be expected for individual plants of the same population, which differ from one another in traits related to frugivore attraction. We tested the hypothesis that plant traits that increase attractiveness and reward to frugivores would be strongly selected by birds in a population of *Henriettea succosa* (Melastomataceae). In 20 h of focal observation in 19 individual trees (380 h in total), we measured plant and fruit traits known to influence frugivore attraction and reward: plant height, fruit size, and fruit sugar content. In addition, we recorded bird behaviour during fruit consumption. We built two weighted networks of birds and individual plants: one monolayer network and a multilayer network with four layers, one for each type of behaviour. First, we evaluated three weighted descriptors of network structure: nestedness, modularity, and specialization. Then, we calculated metrics of centrality and correlated them with plant traits. We recorded 271 visits by 22 bird species of eight families. The network is modular and specialized, showing that subgroups of *H. succosa* trees with different trait combinations attract different subsets of bird species, in a way that specialist trees are not connected to a subset of the bird species that visit generalist trees. We also found that centrality metrics reached higher scores in plants with lower height, larger fruits, and intermediate sucrose content. Fruit handling was the predominant foraging behaviour in the multilayer network and represented 90 percent of the interactions. Downscaling a plant-frugivore network to its individual trees showed that the structure of the system is influenced by interindividual variations in the tree population, in which individuals with the best combination of traits occupied central positions in the network.

1. Introduction

Frugivory and seed dispersal are key ecological processes with important consequences for the structure and dynamics of natural environments (Levine and Murrell, 2003). Ultimately, the choices made by frugivores might influence ecological services, such as seed dispersal (Galetti et al., 2013). Those choices are usually hierarchical, from different plants to individual fruits of the same plant (Sallabanks, 1993; Andrade et al., 2013). They are based mainly on plant traits (Eriksson, 2016) and have a large influence on the number of fruits removed and seeds dispersed from each individual species (Carlo and Morales, 2008), ultimately affecting plant fitness (Schupp et al., 2017).

Plant traits, fruit morphology, and nutritional content are very important in determining frugivore foraging behaviour (Blendinger et al., 2008) and fruit removal rates (Muñoz et al., 2017). First, plant size can affect frugivores that have preferences for particular forest strata (Gondim, 2001; Schleuning et al., 2011). Plant size is also generally correlated with crop size, and larger crops attract a larger number of frugivores and so increase fruit removal (Howe and Estabrook, 1977). Second, consumption by animals is also affected by fruit size, for instance fruit size might limit consumption due to frugivore morphological constraint, as suggested by different studies on the relationship between fruit size and selection by frugivores (Jordano, 1995; Mello et al., 2005). Third, groups of frugivorous and nectarivorous birds can visually pre-detect nutritional differences among fruits that differ in their amount of sugars such as sucrose, glucose, and fructose (Levey,

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1987, Martínez Del Rio et al., 1992), which are indicated by low chroma saturation (Cazetta et al., 2012).

The ecological and evolutionary consequences of variations in plant and fruit traits depend on frugivore responses, that is, how strongly those variations affect frugivore foraging behaviour (Guerra et al., 2017; Obeso and Herrera, 1994). According to the optimal diet theory (ODT), individuals make decisions on which food resource should be consumed to maximize energy income (Pulliam, 1974). Thus, individual decisions take into account the energetic value of resources and the search and handling time, related to finding, consuming, and digesting. In this context, trait variation that affects frugivore decisions to optimize energy intake may have consequences for removal rates. Because fruit removal is the first stage of the seed dispersal process, changes in removal rates might influence plant fitness since the number of seeds disseminated is a key component of the seed dispersal cycle (Schupp, 1993; Jordano and Schupp, 2000).

In this context, network analysis helps us understand the relationship between phenotypical traits and frugivore choices in multispecies systems (Dehling et al., 2016). Phenotypical traits might prevent pairwise interactions due to trait mismatch (forbidden links) or promote them when traits match (Dehling et al., 2016; Muñoz et al., 2017). In general, studies on interaction networks focus on the community level (Bascompte and Jordano, 2008), in which interacting species are nodes and each interaction is represented by a link between species. Also, seed dispersal networks focus on particular taxonomic groups (Mello et al., 2011), represented mainly by small birds interacting with plant species sharing similar traits (Rezende et al., 2007). However, a species-based network might overlook important variations at the individual level that might affect interaction outcome. For instance, several generalist populations are composed of specialist individuals (Bolnick et al., 2011). In the past years, a growing number of studies are considering variations between individuals of the same population (González-Castro et al., 2015; Pires et al., 2011). In this approach, each individual is represented as a node of the interaction network. The structural patterns formed by individual-based networks, such as nestedness, modularity, and specialization reveal how individuals use resources. Thus, by downscaling a plant-frugivore network to its individual plants, individual frugivores or both, we might gain further insight on frugivore choices and on the generalization pattern at the population level (Gómez and Perfectti, 2012; Guerra et al., 2017).

So far, the few studies that assessed intrapopulation variations in plant-frugivore networks have focused on animals (Cantor et al., 2013; Benítez-Malvido et al., 2016), and only recently have started to investigate plants (Guerra et al., 2017). In pollination networks, individual plants located in central positions, which are separated from other individuals by only a few steps, have higher fitness than peripheral individuals that cannot easily interact with other individuals (Gómez and Perfectti, 2012). Phenotypic traits may play a key role in determining the position of an individual in a network, as they influence frugivore attraction (Dehling et al., 2016). Centrality, a family of network metrics associated with relative structural importance of the nodes, is a good proxy for the interaction hierarchy within a network (Cirtwill et al., 2018; Mello et al., 2015). Thus, it might be also used as a proxy for the importance of different individuals in a consumer-resource network.

In the present study, we used as a model individual trees of the species *Henriettea succosa* (Aubl.) DC. (Melastomataceae), which is very abundant in the Brazilian Atlantic Forest and whose fruits are consumed by several bird species. Our aim was to evaluate how individual plant and fruit traits might influence fruit choice and consequently affect the network structure of the individual plant-frugivore network. To do this, we built two networks composed of individual trees and the bird species that visit them: one monolayer network with interaction strengths scores and one multilayer network with four layers representing different types of behaviour. First, we calculated the following network structural descriptors: nestedness, modularity, and specialization. Then, we evaluated node level centrality metrics that were further correlated with fruit traits. We hypothesized that plant traits that increase attractiveness and reward to frugivores would be more strongly selected by birds. Thus, we expected the number of interactions (i.e., degree) to increase with plant size, since this trait can increase plant attractiveness for several bird species, regardless of fruit size and nutritional content (Galetti et al., 2013). The higher the sugar content and fruit size of a plant, the higher should be its overlap with other plants in terms of the frugivorous visits (i.e., higher closeness), mainly due to birds preference on large and sweet fruits (Galetti et al., 2011). A combination of high scores of tree size, fruit size, and fruit sugar content in the fruits should lead the plants to be consumed by birds of different modules in the network (i.e., higher betweenness), because those traits are attractive to different bird groups.

2. Material and methods

2.1. Study area

The present study was carried out in an area studied by the Long-Term Ecological Research Program (PELD-Una) of Una Biological Reserve (Rebio Una). Rebio Una is an Atlantic Forest remnant located in Bahia, north-eastern Brazil (15°10′ S and 39°03′ W). It covers 9000 ha of tropical lowland rainforest (Oliveira-Filho and Fontes, 2000), and elevation ranges from 100 to 350 m. The regional climate is humid and hot and is classified as type *Af* in the Köppen system (Gouvêa, 1969). The annual rainfall is approximately 2000 mm (Mori, 1983) evenly distributed throughout the year. The southern Bahia region is notable for the absence of significant seasonal climatic variations (Martini and Dos Santos, 2007). The landscape is characterized by a mosaic of forests at different successional stages, abandoned pastures, and croplands (Faria et al., 2009). Rebio Una harbours a great diversity of species and high level of endemism (Amorim et al., 2008; Pessoa et al., 2012). The study site harbours a high diversity of frugivore species including generalist and forest specialist birds, and important large frugivores such as Toucans and Cracidae (Pardini et al., 2009).

2.2. Study species

Henriettea succosa (Aubl.) DC. (Melastomataceae), locally known as *mundururu*, is a tree species that can reach 5–13 m in height (Baumgratz, 2015). It occurs mainly in secondary forests and *restinga* vegetation (shrubland that grows on coastal sandbanks) and is classified as a pioneer species (Amorim et al., 2008). Its fleshy fruits are ornithocoric, round, have about 1.5 cm in diameter, and contain dozens of 1-mm seeds (Pessoa et al., 2011) (Fig. S1). Fruits are soft and consumed by a wide range of generalist frugivores that are able to swallow parts of the pulp and act as seed disperser due to the tiny size of the seeds present in the pulp. This species produces a large number of fruits per individual tree, fruiting is extended for approximately eight months (Pessoa et al., 2012), and occurs in high densities in the study area. Those characteristics make *H. succosa* a good model for our study, as it produces good sample sizes for behavioural, morphological and nutritional analyses.

2.3. Plant and fruit traits

We selected 19 *H. succosa* trees to assess individual characteristics and fruit consumption by birds. For each individual plant we recorded tree height, fruit diameter, and fruit sugar contents. Tree height was estimated visually, always by the same person. At the end of the focal observation period, we collected ripe fruits for morphological and chemical analyses. Only ripe fruits based on colour, softness, and on previous researcher experience were collected. We measured the diameter of 20 ripe fruits randomly collected per tree to calculate the average fruit size.

Sucrose, glucose, and fructose concentrations were evaluated for each individual tree with a high-performance liquid chromatography (HPLC) system. We focus our analysis on sugar contents because the fleshy fruits of some Melastomataceae species are known to have high amounts of sugar (~85%) compared to other nutrients (Moermond and Denslow, 1985). To perform the chemical analysis, we collected 1 g of pulp of ripe fruits, of each individual tree. We used the same fruits collected for morphological assessment, but more fruits were necessary to obtain the amount of pulp needed for chemical analysis. Fruit pulp was diluted with 100 ml of distilled water and 25 ml of the solution were filtered through a 0.45 μm filter. Twenty μl of the filtered solution were injected into the HPLC system and the individual sugar compounds were identified based on their retention time (Schwan and Souza, 1986). *H. succosa* seeds are numerous and small (less than 1 mm in diameter) and therefore difficult to separate from the pulp. Even so, as seeds were not degraded during the analyses and were retained in the filter, they were unlikely to affect sugar quantification.

2.4. Focal observation

We carried out focal observation on the same 19 individual trees from June 2014 to June 2015, with 20 h of focal observations per tree. Two researchers performed the observations simultaneously, but on different individuals that were randomly selected each time. Observations occurred in 5-h periods and were repeated four times with an interval of about 1–2 months among them, whenever possible, to cover most of the species fruiting period. We performed observations in alternate periods, two in the morning (6 a.m.–11 a.m.) and two in the afternoon (12 p.m.–5 p.m.) (Gondim, 2001; Pizo and Galetti, 2010). The birds were observed with 8 × 50 binoculars and identified using the Birds of Brazil field guide (Perlo, 2009).

During the focal observations, we recorded the bird species, the total number of visits of each species, the number of fruits consumed by each individual bird and the foraging behaviour. Foraging behaviour was classified as dropping, carrying, swallowing, and handling (adapted from Moermond and Denslow, 1985). Dropping was considered when the whole fruit fell beneath the mother plant, carrying when the whole fruit was carried to another plant, swallowing was the behaviour of eating the whole fruit and handling the consumption of parts of the pulp. A visit was considered when at least one fruit was consumed entirely or partially (Cazetta et al., 2002). Foraging behaviour is relevant because it determines the treatment given to fruits and the different roles bird species perform in fruit removal and seed dispersal (Pizo and Galetti, 2010). For instance, legitimate seed dispersers remove seeds by successfully swallowing the whole fruit or carrying it away from the mother plant, whereas pulp thieves handle the fruits to consume the pulp and drop the seeds beneath the mother plant (Jordano and Schupp, 2000). However, particularly for fruits with many and tiny seeds such as *H. succosa*, pulp consumers can also contribute to seed dispersal. Thus, we used the term 'handling' to refer to this behaviour (see Fig. S2). We performed the observations during the entire visit or until the bird was out of sight (Cazetta et al., 2002; Francisco and Galetti, 2001). Only bird species that consumed fruits in at least one visit were included in the analysis.

2.5. Network analysis

We built two individual-based networks of frugivorous bird species and individual *H. succosa* trees (a monolayer and a multilayer network). For the monolayer network, interaction strength was estimated by multiplying the total number of visits by the number of fruits consumed by each species of bird in each individual tree. For the multilayer network, interaction strength was estimated by multiplying the total number of visits by the number of fruits consumed, in which type of behaviour, by each species of bird in each individual tree. We used the interaction strength scores as the link weight in our networks. The networks were analysed using Pajek 4.07 (Batagelj and Mrvar, 1998) and the packages *bipartite* (Dormann et al., 2008) and *igraph* (Csárdi and Nepusz, 2006) for R (R Core Team, 2017). To build the networks we used a quantitative matrix of interactions between plants and frugivores, in which the nodes represent individual trees or bird species, and the links represent the interaction strength between them.

We built the monolayer network using the interaction strength scores for each pair of bird species and individual trees (hereafter "interaction strength network"). The multilayer network was built using each type of behaviour (dropping, carrying, swallowing, and handling) separated into four layers (hereafter "behaviour network"). Each layer represented the number of fruits consumed in which type of behaviour. Foraging behaviour determines the interaction outcome between frugivorous birds and plants, so this multilayer approach helps to tell apart interactions with the potential of resulting in seed dispersal from those without this potential (as in Genrich et al., 2017). Both networks were built from weighted edge lists, which consist of the matrix containing information on bird species and individual trees, used to construct the networks. In the case of the multilayer network, we added information on link type (i.e., behaviours) (following Boccaletti et al., 2014). For tutorials on how to draw and analyse multilayer networks, see https://marcomellolab.wordpress.com/software/.

To describe the structure of the studied systems, we calculated weighted versions of three topological network descriptors for the interaction strength network and the pulp-handling layer of the multilayer network, using the package bipartite for R. We used only this layer because pulp handling was the predominant behaviour observed. These descriptors help us characterize the components of the network quantitatively and qualitatively. Nestedness was calculated using the WNODF metric (Almeida-Neto and Ulrich, 2011). In the context of our individual-based network, a nested structure means that specialist trees are visited by a subset of the bird species connected to generalist trees. Modularity was calculated using the DIRT_LPAwb + algorithm (Beckett, 2016). A modular structure is observed, when subgroups of individual trees are visited by different subsets of bird species. Specialization was calculated using the H_2' metric (Blüthgen et al., 2006). In a specialized network, different individual trees are visited by different subsets of bird species. To estimate the significance of those three metrics, we used a Monte Carlo procedure based on randomization (1000 iterations). To randomize the networks, we used the degree-probable null model, in which the value of each cell (i.e., link) is proportional to marginal totals of the original matrix.

We calculated three node level metrics (i.e. relative degree, betweenness centrality, and closeness centrality) for the interaction strength network and for each layer of the behaviour network, using Pajek 4.07. Centrality metrics were calculated only for individual plants and were used to estimate the relative importance of each *H. sucossa* individual to the structure of the network, considering the number, weight, and patterns of the links they make (Mello et al., 2015). To calculate those metrics, we used the one-mode projections of each original two-mode network. In other words, to calculate a centrality metric for a given individual tree, we considered its position in the one-mode projection of trees. In this one-mode projection, individual trees are connected to one another, when they share at least one common bird species as a visitor. Link weights in those one-mode networks were defined as the number of shared bird species between each pair of individual trees.

Relative degree was measured as the proportion of links made by a given node of the network in relation to the total number of links it could make. Therefore, in our study, relative degree represents the niche breadth of each individual tree in terms of its bird visitors. Closeness was measured as the average distance (measured as number of links) between a given node and all other nodes in the network (Sabidussi, 1966). Thus, it represents the regularity of the niche of each individual tree. Betweenness was measured as the proportion of short paths (geodesics or smallest distances, measured in number of links)

between all pair of nodes in the network, in which a given node is present (Freeman, 1977). Betweenness represents thus the importance of an individual tree in binding different subgroups of birds and plants within the network.

2.6. Statistical analysis

First, we estimated sampling completeness of interactions, estimating the number of expected interactions (I_E) applying a method proposed by Devoto et al. (2012). To calculate the percentage of expected interactions that were actually sampled, first we estimated the number of expected interactions (I_E) (Devoto et al., 2012) using the Chao 2 estimator, which is one of the least biased for small sample sizes (Chacoff et al., 2012), and is based on the concept that rare species carry most information about missing species (Chacoff et al., 2012). This estimator is calculated as follows:

$$I_E = I_O + (f_1^2/2f_2)$$

Where I_E is the number of expected interactions, I_O is the number of observed interactions, f_1 is the number of interactions observed once, and f_2 is the number of interactions observed twice.

Finally, we calculated sampling completeness as follows:

$$\text{sampling completeness} = I_O{*}100/\ I_E$$

Then we performed Spearman correlations to evaluate the pairwise relationships between all explanatory variables. We also calculated Spearman correlations between the response variables, represented by the centrality values calculated for the interaction strength network and all layers of the behaviour network.

To test the relationship between the network metrics (degree, betweenness, and closeness centralities) and individual plant and fruit traits, we used Generalized Additive Models (GAMs) (Zuur et al., 2009). We used GAM because it is indicate for adjusting non-linear relationships and it can also be used for non-normally distributed response variables. We used values of the centrality metrics (relative degree, betweenness, and closeness), calculated using the interaction strength network and the pulp-handling layer from the behaviour network, as response variables. For each response variable, we adjusted a model with the explanatory variables tree height, fruit diameter, sucrose, and fructose concentration. We excluded the glucose values from the analyses because glucose and fructose were highly correlated ($r = 0.87$, $p < 0.001$) (Fig. S3).

We used a Poisson distribution for relative degree centrality and a beta distribution for betweenness and closeness. A Gaussian distribution was used for height, diameter, and sugar content. Only the models that presented a smoothing term with a p-value lower than 0.05 were considered significant and presented in the results. We also based our interpretation on the r^2 values and the Effective Degrees of Freedom (EDF) (Zuur et al., 2009). All analyses were performed in the software R (R Core Team, 2017) using the *gam* [6] and *mgcv* packages (Wood, 2011).

3. Results

The canopy height of the studied trees ranged from 2.8 to 12.0 m (mean ± SD 6.0 m ± 2.47), average fruit diameter ranged from 8.09 mm to 18.33 mm. Sucrose concentration ranged from 3.61 to 18.22 mg/g (mean ± SD: 9.42 ± 3.64), fructose concentration ranged from 36.55 mg/g to 99.38 mg/g (mean = 64.38 ± 14.83), and glucose concentration ranged from 29.92 mg/g to 66.99 mg/g (mean ± SD: 42.17 ± 9.72) (Table S1).

In a total of 380 h of focal observation, we detected 76 interactions (60.3%) and theoretically 126 were expected. In total, 271 visits by 22 bird species of eight families were recorded (Table S2). The most frequent families recorded consuming *H. succosa* fruits were Thraupidae (132 visits) and Fringillidae (85 visits). The species that made a larger number of visits were *Euphonia violacea* (2.47) and *Coereba flaveola* (2.26). Those species consumed most fruits: *Coereba flaveola* consumed 5.1 fruits per tree and *Euphonia violacea* consumed 4.9 fruits per tree (Table S3). The most frequent behaviour observed was pulp handling (528 records), followed by dropping (27), carrying (14) and swallowing (11) (Table S3). The mean number of fruits consumed ranged from 0 to 6.41, and the mean number of visits ranged from 0 to 3.36 (Table 1).

Table 1
Total number of fruits consumed, number of visits, and interaction strength of individual trees of the species *Henriettea succosa* studied in Una Biological Reserve, north-eastern Brazil.

Individual of Henriettea succosa	Number of fruits consumed	Total number of visits	Interaction strength
A	16	6	96
B	27	17	459
C	5	2	10
D	85	43	3655
E	3	3	9
F	15	9	135
G	95	38	3610
H	0	0	0
I	12	7	84
J	5	3	15
K	19	6	114
L	5	4	20
M	141	74	10,434
N	13	7	91
O	3	3	9
P	5	4	20
Q	16	12	192
R	28	13	364
S	44	19	836

The interaction strength scores recorded between individual trees and bird species ranged from 0 to 10,434. The interaction strength network presented low and non-significant nestedness (WNODF = 0.11, P = 0.99), but high and significant modularity (DIRT_LPA = 0.53, P < 0.001) and specialization (H_2' = 0.54, p < 0.001). The same pattern was observed for the pulp-handling layer of the multilayer network: low and non-significant nestedness (WNODF = 0.24, P = 0.10), but high and significant modularity (DIRT_LPA = 0.36, P = 0.004), and specialization (H_2' = 0.44, P < 0.001). Centrality scores for individual trees (Table S4) had varying correlations with one another in both networks (Fig. S4). A high correlation between centrality values was observed between the interaction strength network and the behaviour network considering the pulp-handling layer ($r^2 > 0.8$). This can be explained because handling was the dominant behaviour and represented 90 percent of all interactions (Fig. 1, Fig. S2).

Centrality scores were positively correlated with plant height, fruit diameter, and sucrose content (Fig. 2, Table S5). The GAM analysis of the interaction strength network detected that relative degree decreased with tree height and peaked at intermediate levels of sucrose. Betweenness centrality decreased with tree height, increased with fruit diameter, and peaked at intermediate levels of sucrose (Fig. 2). Closeness centrality was correlated only with fruit diameter (Table S5). Because pulp handling was the predominant behaviour and highly correlated with the interaction strength network (Fig. S4), a similar pattern of relationship among centrality metrics and fruit traits was also found (Table S5).

4. Discussion

In the present study, we downscaled a plant-frugivore network to its individual trees. We observed that a generalist plant population, whose fruits are consumed by a wide range of frugivorous birds, comprises individual trees that differ from one another in terms of frugivore

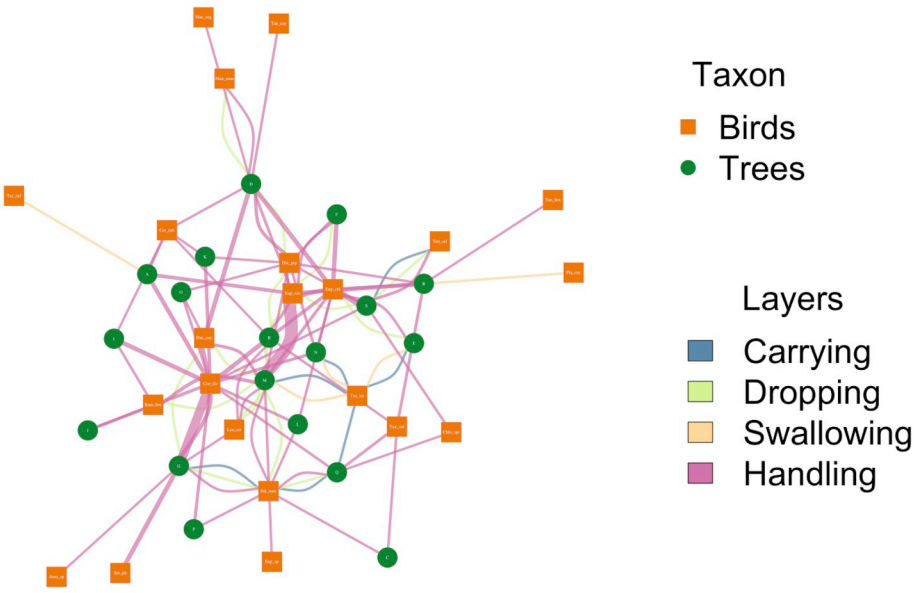

Fig. 1. Behavioural multilayer network of bird species (n = 22) and individual *Henriettea succosa* (Melastomataceae) trees (n = 19, the tree H was excluded from the drawing as it made no interactions) in Una Biological Reserve, north-eastern Brazil. The nodes represent individual trees (circles) or bird species (boxes), and the links represent interactions of frugivory. Link width is proportional to interaction strength (number of visits x number of fruits consumed). Each behaviour (dropping, swallowing, carrying, and handling) has a different potential outcome in terms of seed dispersal. The graph was drawn using the Fruchtermann-Reingold algorithm, so nodes that have higher degree (i.e., number of links) or betweenness (i.e., whose links connect different regions of the network) are drawn closer to the centre.

attraction and reward, as well as fruit consumption. Those inter-individual variations result in a modular and specialized network, in which bird species interact with different subsets of individual trees, and prefer to consume fruits from lower trees that produce larger fruits with intermediate amounts of sucrose. Individual trees with this combination of traits occupied central positions in the network.

Fruit consumers of *H. succosa* include primarily frugivorous birds, such as *Euphonia*, insectivorous birds, such as *Piaya cayana*, and nectarivorous hummingbirds, such as *Amazilia* (Sigrist, 2013). *Euphonia* was the genus that most contributed to seed dispersal of *H. succosa*, since those birds presented the highest number of visits and fruit consumption. Fruit consumption by *Amazilia* hummingbirds was unexpected, as these birds are known to consume flower resources or insects (Parrini, 2015). One possible explanation for this unique interaction is the watery and sugar-rich pulp of *H. succosa*, which often overflows the fruit skin (Fig. S1), and consequently may attract nectarivorous birds. Among those consumers, *Amazilia* is the only one that did not consume fruit pulp and seeds. However, *Amazilia* interact with only eight fruits and the possible negative effect of the species is negligible.

By analysing the multilayer network, it was possible to differentiate the predominant behaviour displayed by each bird species. Furthermore, the most frequent behaviour for *H. succosa* was pulp handling, in which the bird manipulates the fruit to consume the pulp. This foraging behaviour was displayed mainly by small-bodied birds of the family Thraupidae, that cannot swallow the whole fruit. In general, pulp handling results in seed removal failure because birds handle the fruits, but are unable to disperse the seeds, which are dropped beneath the mother plant (Côrtes et al., 2009). However, *H. succosa* produces several small seeds per fruit that can be swallowed by birds during the consumption of the soft pulp. Thus, fruit consumption and, therefore, dispersal of *H. succosa* is not limited by fruit diameter as seeds can be swallowed even by small species. Individual plants benefit from factors that enhance fruit removal with possible consequences on plant fitness because the number of seeds disseminated is an important component of the seed dispersal cycle (Schupp, 1993; Jordano and Schupp, 2000).

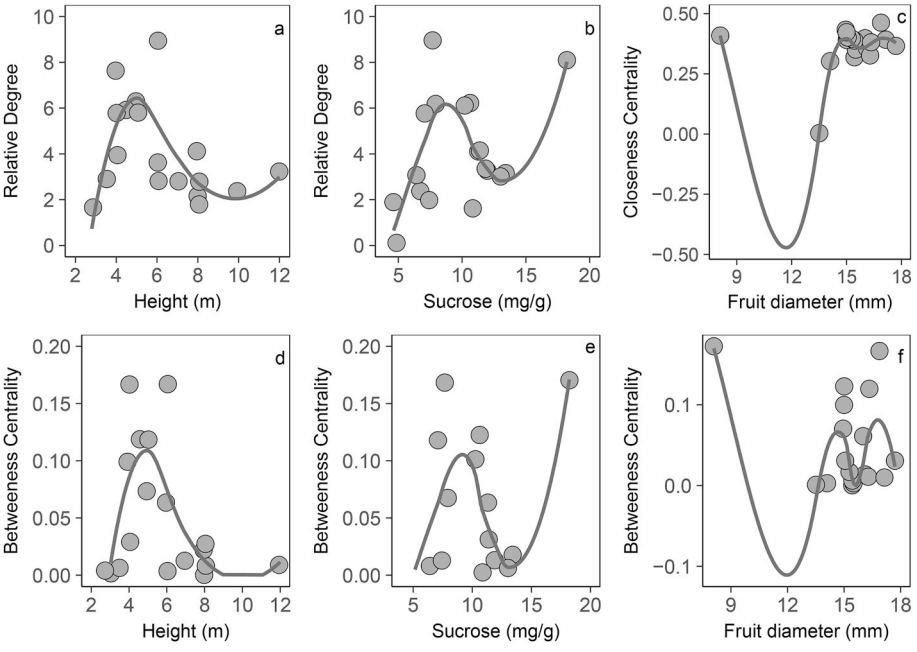

Fig. 2. Generalized additive models calculated to test the relationships between centrality metrics and phenotypic traits in individual *Henriettea succosa* trees in Una Biological Reserve, north-eastern Brazil. Because pulp handling was predominant and highly correlated with the interaction strength network, we correlated plant and fruit traits only with the centrality values calculated in the interaction strength network A: relative degree vs. tree height; B: relative degree vs. sucrose concentration; C: closeness centrality vs. fruit diameter; D: betweenness centrality vs. height; and E: betweenness centrality vs. sucrose concentration; F betweenness centrality vs. fruit diameter.

However, our study only focuses on the quantitative component of the seed dispersal system (*sensu* Schupp, 1993), and the establishment of the new offspring might be limited by several other factors (Schupp et al., 2010).

Consumption of the fruits of *H. succosa* by a wide variety of frugivorous birds indicates that this species has a generalist seed dispersal strategy. However, by downscaling the network to its individual trees, we observed that the generalism observed at the population level results from the interactions made by a few trees. This individual specialization is evidenced from the modular and specialized structure of the network. There is much controversy regarding the predominant topology of interaction networks and other kinds of networks, as conflicting evidence points to nestedness (Bascompte et al., 2003) or modularity (Olesen et al., 2007) as the most common patterns. However, those two topological archetypes are not mutually exclusive (Fortuna et al., 2010), and alternative patterns are also found in some systems. Evidence points out that many interaction networks, in fact, may have a compound topology (*sensu* Lewinsohn et al., 2006), which is modular at the scale of the whole system and nested at the scale of its modules. A compound topology seems to arise from a balance between different processes shaping the network structure at different scales (Flores et al., 2013; Pinheiro et al., 2016; Felix et al., 2017). Our results show that subgroups of *H. succosa* trees with different combinations of plant and fruit traits attract different subsets of bird species, so that specialist trees are not connected to a subset of the bird species that visit generalist trees. This leads to a modular and specialized network structure, instead of a nested structure that has been found in other studies on individual-based interaction networks in other animal populations (Pires et al., 2011) and also in plants of the family Melastomataceae (Guerra et al., 2017).

Our results show that in *H. succosa* interindividual variations in resource use are linked to phenotypic traits, which lead to differential fruit consumption and, possibly, to selective pressures by frugivores (Galetti et al., 2013). In our study, shorter plants with larger fruits and intermediate sucrose content were the most frequently consumed by birds and occupied a central position in the network. This result highlights that this combination of traits is probably the best one in terms of reward to frugivores, according to ODT. On the contrary, higher individual plants, with small fruits and lower or higher levels of sugar are less preferred by frugivores and occupy peripheral positions. The morphological and nutritional traits that influenced consumption by birds might therefore be selected in the next generations of the *H. succosa* population.

Contrary to our expectations, small trees (ranging from 4 to 6 m) were preferred by frugivores. Because plant height is usually related to fruit accessibility or fruit crop (Gondim, 2001), we expected that larger trees would be preferentially selected. In a tropical forest, tree-sized and shrubby plants were visited by different frugivore guilds (Gondim, 2001). However, *H. succosa* individuals were also visited by bird species that predominantly forage in the canopy, such as *Euphonia violacea* (Willis, 1979), which suggests that *H. succosa* is a food source that attracts birds foraging in different strata of the forest. We suggest that the local vegetation structure of the secondary forests where *H. succosa* occurs might increase fruit accessibility or detection of those smaller trees. Larger fruits were also selected by frugivorous birds and this fruit trait influenced closeness centrality in the interaction strength network. Thus, as expected, similar bird assemblages consumed larger fruits. Previous studies have shown that diameter is one of the criteria used by frugivores to select fruits to obtain large amounts of reward (Howe, 1983; Jordano, 1995; Mello et al., 2005). Fruit size is, in general, related to the amount of pulp (Jordano, 1995; Cazetta et al., 2008), and birds are likely to select larger fruits to obtain a greater reward.

Relative degree and betweenness were higher for trees whose fruits contained intermediate levels of sucrose. Thus, those trees were visited by a larger number of bird species that belong to different modules of the network. We suggest that fruit colour might have an important role in sugar recognition because the colour of dark fruits is imparted by anthocyanins and sugar strongly up-regulate the anthocyanin biosynthetic pathway (Solfanelli et al., 2006). It has also been showed that high sugar contents in fruits are indicated by low colour saturation (Cazetta et al., 2012). In general, sugars found in the pulp are an important energy source for frugivorous birds (Martínez Del Rio et al., 1992). However, for some of these animals fruits with high sucrose concentration may not be beneficial, as this complex molecule is hard to break into simpler sugars for absorption (Malcarney et al., 1994). Therefore, we suggest that individuals bearing fruits with intermediate sucrose levels may be more attractive to frugivorous and also to nectarivorous birds.

Among the trees of the studied population, the individual M was the most central. It presented the highest scores of all centralities. In addition to making several interactions with several bird species, this tree was indirectly connected to other individuals visited by a similar bird assemblage. This individual tree thus appears to play a key role in the network structure. It has recently been suggested that certain individuals have extreme phenotypes and can be considered keystone individuals due to the disproportional consequences of these individuals to population ecology and evolution (Start, 2018). Therefore, our findings highlight the importance of downscaling networks from species-level to individual-level to identify the most important nodes. For instance, in case of a disturbance, the loss of the individual tree M could have a higher impact on frugivory and seed dispersal interactions than the loss of other individuals.

To conclude, we provide new insights into how different biological traits, such as canopy height, fruit diameter, and fruit sugar content, help understand intrapopulation variations in frugivory and seed dispersal. It is also interesting to notice that fruit selection can occur at intermediate or low values of some traits, which is counterintuitive, considering the results of previous studies. We highlight that a particular combination of traits determines the position in the network occupied by a plant increasing fruit removal rates and the seed dispersal outcome.

Author contributions

A.C. Crestani and E. Cazetta designed the study, A.C. Crestani conducted the fieldwork, A.C. Crestani and M.A.R. Mello analysed the data, and all authors wrote the manuscript.

Declarations of interest

None.

Data availability

Data will be available on the GitHub https://github.com/marmello77/crestani_etal_2018. DOI https://doi.org/10.5281/zenodo.1487593.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.actao.2018.11.003.

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