

Research

The individual-based network structure of palm-seed dispersers is explained by a rainforest gradient

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How species interactions change in space and time is a major question in ecology. In tropical forests, plant individuals share mutualistic partners (pollinators or seed dispersers), yet we have little understanding of the factors affecting these individual interaction patterns. We used a seed dispersal individual-based network describing interactions between individuals of a palm species and bird species to investigate how intrinsic and extrinsic characteristics of individual plants influence the network structure. We evaluated if average canopy height, number of fruits, distance to forest gap and habitat type influence the role of palm individuals in the network. From 102 palms, 62 individuals had their seeds dispersed at least once: 17 individual palms in the restinga, 15 in the lowland and 30 in the pre-montane habitat. Twelve bird species were recorded dispersing *Euterpe edulis* seeds. No palm characteristics influenced interaction patterns in the network, characterized by the level of centrality of each palm. At the network level, modularity with qualitative data was reproduced by the null models which consider the variation in the number and distribution across interactions. Three of the seven identified modules were associated with a particular habitat. Indeed, habitat type explained 50% of network modularity. Habitat association with modularity was driven by differences in species composition across habitats. Palm individuals did not differ greatly in central positions, indicating that bird species are not selecting palm individuals by their characteristics. When using the weighted network, modularity level was higher than expected by the number of interactions, and frequency of interactions was positively correlated with canopy height. Our results suggest that the organization of this individual-based network is mostly driven by habitat type. We hypothesize that extrinsic characteristics, such as habitat type, may affect the network organization of populations of sessile organisms with potentially unanticipated consequences to ecological and evolutionary dynamics.

Keywords: Atlantic rainforest, extrinsic characteristics, frugivory, intraspecific variation, intrinsic characteristics, modularity



Introduction

One conspicuous pattern in ecological systems is that some species, such as some parasites and herbivorous insects, interact with a few species, whereas other species, such as some predators and fruiting plants, can interact with a wide range of prey or partners (Thompson 2005). These highly connected species in the community, by exploiting a range of resources, connect otherwise isolated groups of coexisting species and induce a more cohesive system (Bascompte 2009, Albrecht et al. 2014, Mello et al. 2015). Highly connected species in an ecological community are the outcome of how individuals within populations establish ecological interactions at the population level. Theory predicts and empirical evidence supports that there are multiple ways for a highly connected population to emerge from a collection of individuals that vary in their interactions (Van Valen 1965, Thompson 1988, Bolnick 2003, Guimarães 2020). In many empirical systems, highly connected populations are the outcome of nonrandom mixtures of poorly connected and highly connected individuals (Bolnick et al. 2003, Araújo et al. 2008). To advance the understanding of how the community structure can be influenced by individual interactions, it is crucial to consider the distinctiveness in the use of the environment and its resources by these individuals.

Individual variation in interaction patterns can be mediated by two components. Intrinsic characteristics (such as body size) are the first component, governing the way individuals interact with their interacting partners. Examples include individual differences in fruit preferences in a thrush species (*Turdus migratorius*, Jung 1992) or bill size correlated with seed choice by individuals in a species of Darwin's finch (*Geospiza fortis*, Grant et al. 1976). Indeed, detecting interactions that cannot occur due trait mismatching – the forbidden links (sensu Jordano et al. 2003) – can be more accurate when taking trait variation among individuals into account, because averaging trait values can overestimate the incidence of forbidden links (González-Varo and Traveset 2016). Intraspecific variation in traits is especially common in plants (Christenhusz and Byng 2016), which in turn may explain interaction variation among plant individuals and may lead to skewed distributions of interaction strengths according to plant traits (Dupont et al. 2011, Miguel et al. 2018, Jácome-Flores et al. 2020, Arroyo-Correa et al. 2021). Accordingly, resource partitioning among individuals may lead to the formation of modules in individual-species networks (e.g. pollination in Tur et al. 2014; seed dispersal in Miguel et al. 2018, Jácome-Flores et al. 2020), i.e. networks in which there are two sets of elements, one set is composed by individuals and the other set is composed by species.

The second component of the structure of individual-based networks consists of extrinsic characteristics. These are elements and characteristics of the environment, such as different microhabitats used distinctively by specialized foraging fish individuals (Kohda 1994), distinct habitats promoting individual differences in the diet of the Arctic fox *Vulpes lagopus* (Angerbjörn et al. 1994) or differences in how bat

individuals move in the environment (Kerches-Rogeri et al. 2020). In plants, for example, the neighborhood and aggregation of individuals may influence the number of visiting animals (Dupont et al. 2011) and, in seed dispersal systems, patterns of fruit removal by birds and mammals (Carlo and Morales 2008, Miguel et al. 2018). It is expected that extrinsic characteristics may be especially relevant for interactions of plants and other sessile organisms, since they are constrained to experience local environment conditions. If extrinsic characteristics shape patterns of ecological interactions within populations, we may expect these effects to foster spatially heterogeneous interactions within populations (Sallabanks 1993), with potential consequences for the variability, persistence, evolution and diversification of populations and for the organization of ecological communities (van Valen 1965, Thompson 1988, Dieckmann and Doebeli 1999, Bolnick et al. 2003).

Here we analyze the structure of a seed dispersal interaction network between individual *Euterpe edulis* palms and fruit-eating bird species to investigate how individual plant variation in morphological traits, as well as in microhabitat-landscape characteristics, influences interactions with the frugivorous avian assemblage in three different habitats along an elevational gradient. Habitat turnover, such as along elevational gradients, may have a strong influence in structuring plant–frugivore interactions at the community level (Bender et al. 2018), yet how species and interaction turnover affect individuals remains largely unexplored (Miguel et al. 2018). The palm *E. edulis* is one of the dominant plant species in one of the most threatened ecosystems in the world (Hirota and Ponzoni 2019), the Atlantic rainforest (Morellato and Haddad 2000). A variety of birds and mammals consume *E. edulis* fruits and frugivore assemblages may vary across space, time and habitats (Castro et al. 2012, Galetti et al. 2013). Here we explore the contribution of intrinsic (e.g. number of fruits) and extrinsic (e.g. canopy height around and proximity to gap opening in the forest) palm-related characteristics shaping patterns of frugivory interactions. To do so, we characterized individual-based networks consisting of interactions between individual palms and frugivorous bird species (Dupont et al. 2011, 2014, Gómez and Perfectti 2012, Tinker et al. 2012, Miguel et al. 2018). Individual palm variation was characterized by palm traits, microhabitat characteristics surrounding each plant, and habitat type. We aimed at answering two questions by exploring how patterns of interactions, and intrinsic and extrinsic characteristics influence the individual-based network: 1) do highly-connected palm individuals have predictable characteristics? We expect that palm trees with certain characteristics (e.g. more fruits, under taller canopy or proximity to gap opening) attract a wider range of species and occupy central positions in the network. 2) Is the interaction network partitioned in modules (groups) of palm individuals and seed-dispersing birds? If so, are the modules associated with their habitat types (Fig. 1)? We expect that modules in the network are associated with each habitat type and its respective frugivore

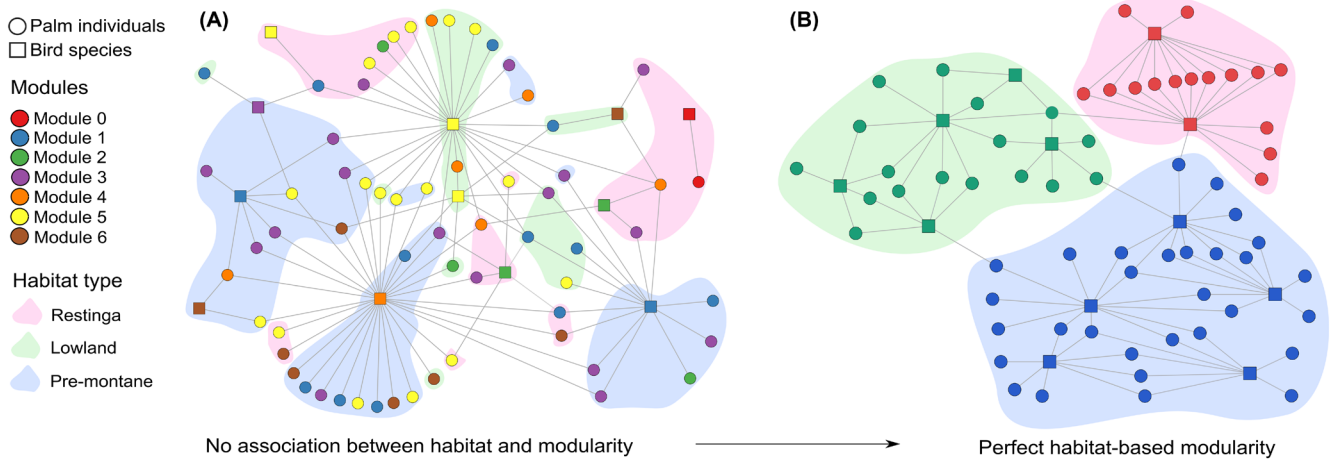


Figure 1. Representation of different scenarios of modular networks: (A) expected modularity if the network is random with no association between habitat and modules, and (B) a perfect habitat-based modular network in case well-delimited modules emerge from different habitat types.

assemblages due to the heterogeneous distribution of bird species among habitats.

Material and methods

Study area

The study was carried out in the Cardoso Island State Park, on the southern coast of the state of São Paulo (25°03'05"S, 48°05'42"W), Brazil, which comprises a protected area of ~151 km² (Bernardi et al. 2005). Palm sampling and frugivory observations were conducted in three different habitats, that correspond to three different forest types distributed along an altitudinal gradient spanning ~5 km: 1) The 'restinga' is a sandy soil-based habitat that occurs at sea level, with a dense herbaceous stratum composed mainly of bromeliads and vegetation reaching up to 15 m with open canopy, allowing passage of sunlight into the forest. The restinga forest habitat is composed of approximately 64 tree species (Sugiyama 1998) and has the lowest relative frequency of *Euterpe edulis* among the three habitat types, presenting around 0.28 individuals per hectare (Sugiyama 2003). 2) The lowland forest habitat occurs 30–50 m a.s.l., with vegetation varying between 8 and 20 m in height, with a much more closed canopy than the restinga. Relative frequency of *E. edulis* in the lowland averages 2.97 adult individuals per hectare (Kojima 2004). 3) The pre-montane habitat covers ~74% of the island's extension, is situated 200 m a.s.l., and consists of inferior (5–10 m), medium (15–20 m) and superior (21–28 m) strata, with closed canopy. The relative frequency of *E. edulis* adults in the pre-montane is lower than in the lowland habitat, with 1.82 individuals per hectare (Kojima 2004).

Euterpe edulis palm

Euterpe edulis can be considered a keystone species (Peres 2000, Galetti et al. 2013) and one of the dominant species

in the Atlantic rainforest (Reis et al. 2000). *Euterpe edulis* populations have been exploited since the beginning of the Brazilian Atlantic forest colonization mainly because of the uncontrolled extraction of palm-heart for human consumption (Galetti and Aleixo 1998). Illegal palm-heart harvesting and habitat loss has led to local extinctions of this species in several areas along the original distribution of the Atlantic forest (Galetti and Fernandez 1998). This species produces fruits with a thin pericarp, but rich in lipids (Galetti et al. 2011). Mean (\pm SD) *E. edulis* fruit diameter and length is, respectively, 13.58 ± 0.86 and 12.60 ± 0.88 mm in the restinga, 13.84 ± 1.13 and 13.01 ± 1.16 mm in the lowland and 13.84 ± 0.68 and 12.93 ± 0.65 mm in the pre-montane habitat (Côrtes unpubl.). Fruit production is annual and seasonal in the three habitats, beginning around February and spanning ~5 months. Fruit ripening occurs between February and June in the restinga, peaking between March and April; in the lowland it extends between January and July, peaking between March and May and in the pre-montane it occurs between February and August, peaking between April and May (Castro 2007). *Euterpe edulis* fruits are consumed by at least 58 bird species (including *Penelope* spp., *Turdus* spp., *Ramphastos* spp. and others; Supporting information) and 21 mammal species (e.g. *Artibeus* spp., *Tapirus terrestris*, *Dasyprocta* spp.) which mostly disperse their seeds (Galetti et al. 2013, Silva and Reis 2019). However, some species are not legitimate dispersers, because they either prey upon the seeds, such as the parakeets *Brotogeris tirica* and *Pyrrhura frontalis*, or only consume pulp, such as tanagers (*Tangara* spp). Therefore, only 32 bird species can in fact act as seed dispersers (Galetti et al. 2013). Frugivorous species seem to rely differently on *E. edulis* fruits. For example, the thrush *Turdus flavipes* tracks available fruits via altitudinal migrations, whereas *T. albicollis* changes its feeding strategy and consumes fruits from other plants during *E. edulis* fruit scarcity (Castro et al. 2012). Understanding how dominant species such as *E. edulis* interact with other bird species is essential, especially because it is an ecologically and economically important plant species.

Seed dispersal sampling

Interactions between birds and palms were considered a seed dispersal event only when the birds swallowed or carried the fruit away, thus ensuring seed deposition at a distance from the maternal plant. We recorded the number of seeds dispersed by each bird species for each individual palm, independent of how many times individual birds visited each palm (hereafter called frequency of interactions). Therefore, besides the presence-absence data of interaction between bird species and palm individuals, our dataset describes how many times a given individual palm had its seeds dispersed by a given bird species. We want to highlight that sampling of interactions is an important concern in network analysis (Jordano 2016), especially because patterns of interactions in networks (as any ecological feature) depend on the temporal scale used (Levin 1992). Consequently, palm individuals without a record of mutualistic partners partially reflect the fixed temporal window we used to sample interactions. However, we want to explore differences in interactions across different habitats and across characteristics (morphological traits and micro-habitat characteristics). Differences in binary and quantitative patterns of interaction across individuals under a fixed temporal window may reveal important aspects of network structure. Seed dispersal events were recorded between March and July 2003 and 2004 according to the fruiting phenology of the palm species in each habitat type (Castro et al. 2007). Different palm individuals were observed in each year in order to better capture the natural between-year fluctuations in fruiting among habitats. This inter-annual variation is discussed in detail by Castro et al. (2007). Focal palm observations of birds consuming *E. edulis* fruits were conducted for a total of 102 palm individuals across all three habitats. We used the number of fruiting palms within a 10 m-radius from the focal palm to estimate the average density of *E. edulis* in each habitat. We estimated that there were approximately 89 ha⁻¹ *E. edulis* reproductive individuals ha⁻¹ in the restinga, 108 ha⁻¹ in the lowland and 87 ha⁻¹ in the pre-montane. A total of 32 palm individuals were observed between April and May in the restinga, with 33 individuals in the lowland between March and May, and 37 individuals in the pre-montane between May and July. We used an area of 1500 m², that contemplates the sampling area, and the average density of reproductive *E. edulis* to estimate the number of palm individuals in each habitat. Then, we estimated the percentage of palm individuals that were observed: 0.15% of individuals in the restinga, 0.14% in the lowland and 0.18% in the pre-montane. Each palm individual was observed for 5 h, starting at dawn. The observer kept a distance of at least 15 m from the focal palms to avoid disrupting animal behavior and used an 8 × 32 mm binocular to record visiting species and feeding behavior (i.e. fruit swallowing, pecking, dropping and carrying in the beak). We recorded bird abundance by using the punctual abundance index (IPA; Vielliard et al. 2010), in which the average number of contacts with a given bird species (seen or heard) within a radius of 50 m is divided by the total number of points sampled in

the area per month. Twenty points were surveyed monthly during the fruiting season of *E. edulis* in the same areas where focal-tree observations were conducted. Observation sessions lasted 10 min each, and were conducted between sunrise and 10:00 h (Castro et al. 2012). Each focal palm was characterized by two sets of variables, hereafter called palm characteristics. ‘Intrinsic’ characteristics (palm traits) included palm height, number of infructescences, estimated number of ripe fruits (standing crop of ripe fruits), and estimated total number of fruits (considering unripe, green fruits). ‘Extrinsic’ habitat characteristics associated with each individual palm included average canopy height above the focal palm (hereafter referred to as canopy height), distance to nearest fruiting palm, number of fruiting palms (up to a distance of 10 m), percentage of canopy openness above palm (estimated visually), and distance to nearest gap opening (up to a distance of 50 m, hereafter referred to as distance to gap).

Network structure and palm characteristics

We describe the interactions between palm individuals and bird species as an individual-based network (Tinker et al. 2012, Miguel et al. 2018, Jácome-Flores et al. 2020). The network is described by a biadjacency matrix **A** in which each row depicts a palm individual and each column depicts a bird species. The element a_{ij} of this matrix describes the number of seed dispersal events of palm individual i by bird species j . The biadjacency matrix **A** defines a bipartite graph, in which there are two sets of nodes representing individual palms and bird species. We then computed the number of bird species that interact with each palm individual (degree of each palm individual) and the frequency of interactions (number of dispersed seeds by bird species) log-transformed to characterize the qualitative and quantitative patterns of interaction of individual palms.

Then, we explored the patterns of overlap among palm individuals in their bird species coterie. To do so, we computed the unipartite projection of **A**, defining a niche overlap network (sensu Araújo et al. 2008) in which each node depicts a palm individual and links indicate that at least one seed-dispersing bird species is shared with the connected palms. Next, we computed two centrality descriptors to describe patterns of overlap among palm individuals from a one-mode projection (Supporting information). We computed closeness centrality, in which the higher the value, the shorter (in number of links) are the direct and indirect pathways connecting a given individual palm to the rest of the palms in the network (Freeman 1978). Palm individuals with higher closeness centrality values are those interacting with the partners (frugivores) of palm individuals with different coterie of frugivores in the network. We also computed betweenness centrality, which measures the extent to which a palm lies on paths between other palms in the network. Values close to one are those that often are part of the shortest path between other palm individuals in the network (de Nooy et al. 2005, Costa et al. 2007, Sazima et al. 2010). Palm individuals with higher values of betweenness may connect different groups

of interacting individuals and bird species in the network, such as palms attracting bird species that occur in different habitats and interact with different groups of palm individuals. Both closeness and betweenness centralities describe patterns of niche overlap in the system, i.e. patterns of overlap among palm individuals in their coteries of seed dispersers. All analyses were performed in R ver. 3.6.1 (<www.r-project.org>), using the bipartite package (Dormann et al. 2008, 2009, Dormann 2011).

To evaluate if individual degree, closeness centrality and betweenness centrality of the palm individuals can be explained by variation in palm characteristics we first log-transformed all variables describing palm characteristics. We ended up retaining three of our nine original variables describing palm intrinsic and extrinsic characteristics that are not strongly correlated ($r < |0.3|$): canopy height, total number of fruits and distance to gap. By choosing the three selected palm characteristics we wanted to understand if palm individuals would be interacting with more frugivores if they were more visible in the habitat (higher canopy height), more productive (number of fruits), or were close to forest gaps attracting different frugivores. To evaluate the general differences of palm characteristics between habitat types we performed variance analyses (ANOVAs) for each of the characteristics. Also, we tested the relation between bird species abundance and the frequency of interaction (number of seeds dispersed) in the three habitats by using Pearson's correlation. Then, we used Pearson's correlation and generalized linear models (GLM; Nelder and Wedderburn 1972) to evaluate each response variable (i.e. centrality measures) as a function of the three isolated predictor variables (canopy height, total number of fruits and distance to gap) to characterize the association between palm characteristics and centrality measures. We also performed GLM with multi-predictor variables including the three palm characteristics and habitat types potentially affecting centrality values. Then we used analysis-of-variance tables to extract the outputs of the models fits (car::Anova function).

We also tested the effect of palm characteristics and habitat type on the quantitative descriptor of interactions (i.e. frequency of interactions). We separately modeled the frequency of interactions as a function of canopy height, total number of fruits and distance to gap using GLMs. We also ran a multi-predictor model including all three variables and habitat type. Finally, we used analysis-of-variance tables on the fitted models to extract the output of the models tested.

Network structure and habitat types

We then explored the formation of modules of palm individuals interacting with distinct coteries of seed dispersers. To do so, we calculated the level of Barber's modularity descriptor for bipartite graphs (Q_B , Supporting information) to characterize modularity of the bipartite network defined by the binary matrix **A**. We first estimated the Q_B of the entire network, which includes all three habitats, using the program Modular

(Marquitti et al. 2014). We used a simulated annealing algorithm to maximize the value of Q_B , since there is no algorithm able to analytically find the partition that maximizes Q_B in polynomial time (Barber 2007, Marquitti et al. 2014). We then investigated if the level of modularity was higher than expected by the theoretical benchmark provided by a null model that preserves the number of palm individuals, number of bird species and proportion of realized ecological interactions among all potential interactions in a network ('null model 1'), and the heterogeneity of interactions across nodes (palm individuals and bird species), in which the probability of a pair being connected by an interaction is proportional to the number of interactions in the nodes ('null model 2'). To investigate if patterns of modularity differed when moving from presence/absence of interactions to interaction weights, we used the number of seeds dispersed per individual palm to estimate the weighted modularity, using the QuanBiMo Modularity algorithm (Q_D , Dormann and Strauss 2014) for quantitative bipartite networks. We then computed the z-score of the observed value of Q_D using as a benchmark the expected modularity predicted by a null model in which interaction events are distributed with probability proportional to the total number of interaction events recorded for a given palm individual and a given bird species (Supporting information). As z-scores are assumed to be normally distributed, z-scores above 2 indicate levels of modularity higher than predicted by the theoretical benchmark that assumes a random distribution of interaction events across partners of a given palm individual or bird species (Blüthgen et al. 2008, Dormann and Strauss 2014).

Modularity descriptors only characterize macroscopic aspects of group formation in a network, i.e. the identifying groups of individuals and species that interact more with each other than with other groups of individuals and species. The level of modularity may allow us to uncover the role of specialization in shaping interacting assemblages (Prado and Lewinsohn 2004, Lewinsohn et al. 2006), but modularity indexes do not allow us to infer the factors shaping particular modules. We now turn our attention to the search for associations between intrinsic and extrinsic characteristics and modules (groups) in the network. We investigated if the particular modules identified by our analysis are explained by individual palm variation in canopy height, total number of fruits and distance to gap. We excluded small modules with less than five palms to avoid small-size statistical artifacts. We performed a GLM for each of the three palm characteristics using them as response variables and the module identity as the predictor variable. Then we tested for pair-wise modules differences using post hoc Tukey's test and computed the mean (and SE) of the palm characteristics for each module.

Next, we explored the association between habitat types and modules in the network. We hypothesize that interactions of palm individuals will be shaped by different habitats. If so, we expect that the modules of the network will be partially associated with habitats in which palm individuals of the same habitat interact with a particular bird species, whereas just a few bird species visit individuals from different

habitats. To investigate if habitat type structures the seed dispersal network we recomputed Barber's (Q_B) and QuanBiMo (Q_D) modularity, but now without using an optimization algorithm. Rather, we imposed the three habitats as modules, hereafter referred to as habitat-based modularity, calling this habitat-based level of modularity $Q_{B_{HR}}$. To do so, we assigned the palms and bird species to one of the three habitats, in which bird species were considered part of a given habitat type when they interacted with more palm individuals in that particular habitat. We note that the assignment of bird species to modules based on the number of interactions is strongly associated with bird abundances, since only two (*Trogon viridis* and *Ramphastos vitellinus*) of 12 species are not assigned to the habitat in which the species show higher abundances. After measuring Q_B , $Q_{B_{HR}}$ and Q_D , we randomized the assigned habitat across palms and bird species and recomputed the modularity, recording a randomized version of the habitat-based modularity, $Q_{B_{HR}}$ ($n = 1000$ randomized trials). If the proportion of randomizations showing $Q_{B_{HR}} \geq Q_{B_H}$ is smaller than 5%, there is evidence that habitat heterogeneity is contributing to the modular structure of this individual-based network. This analysis was also performed in R ver. 3.6.1 (<www.r-project.org>).

Finally, we explored the congruence between modules identified by the optimization algorithms and those identified by habitat. To do this we first defined modules as habitats and computed matrix **C**, in which each palm individual and bird species is a row and each module is a column and the element $c_{ij} = 1$ indicates that the palm individual and bird species i was assigned to the module j . Similarly, by using the optimization algorithm we computed a matrix **D**, in which each row is a module and each column is a palm individual and bird species, and the element $d_{ij} = 1$ indicates that the palm individual and bird species j was assigned to module i using the optimization algorithm. The matrix **E** = **CD** defines the congruence between module assignment assuming habitat-based modularity and the degree of modularity recorded using the optimization algorithm. Specifically, e_{ij} indicates the number of palm individuals and bird species that are assigned

to the same modules assuming either habitat-based modularity or modularity based on the optimization algorithm. We ran 1000 trials in which the randomized based-habitat matrix was multiplied by the algorithm's matrices (Q_B and Q_D) and counted the number of times in which the randomized had higher concordance values than the habitat-based matrix (Q_{B_H}).

Results

From a total of 102 observed palm individuals, 62 had seeds dispersed by at least one bird species: 17 palms from the *restinga* (53% of observed palms of this habitat), 15 from the lowland (45%) and 30 from the pre-montane (81%) habitats. Twelve bird species from seven families were recorded swallowing or carrying *Euterpe edulis* fruits away from focal palms. Five species were recorded in all habitat types (*Procnias nudicollis*, *Pyroderus scutatus*, *Turdus flavipes*, *Turdus albicollis* and *Trogon viridis*). Thrushes (*T. flavipes* and *T. albicollis*) were the most frequent visitors and the ones that visited more palms (Table 1). Three bird species were recorded only in the *restinga* (*Pitangus sulphuratus*, *Tachyphonus coronatus* and *Turdus rufiventris*) and two only in the pre-montane (*Selenidera maculirostris* and *Carpornis cucullata*) environments, whereas no species were exclusive to the lowland habitat (pairwise Jaccard's similarity indexes: *restinga*-lowland: 0.66; *restinga*-pre-montane: 0.45; pre-montane-lowland: 0.75). The frequency of interactions differed between habitats ($F_{2,59} = 3.847$, $p = 0.037$), with lower absolute frequency of interactions in the *restinga* (mean \pm SD = 7.7 ± 7.5 interactions) which differed from the pre-montane (mean \pm SD = 20.6 ± 18.9), which were similar to interaction frequency in the lowland (mean \pm SD = 19.7 ± 18.6). Overall bird abundance estimates (all species included together) did not differ among habitats ($F_{2,23} = 0.58$; $p = 0.566$), as indicated by the dominance of the same *Turdus* in all sites. The most abundance species where *T. albicollis*, *T. flavipes* and *T. rufiventris* in the *restinga* (IPA = 1.04, 0.40 and 0.18 contacts

Table 1. Bird species recorded removing seeds from observed palms in the Cardoso Island State Park, the number of palms that had their seeds dispersed at least once, habitats in which the bird species were visualized (in parenthesis are the abundance for each of the bird species in each of the habitats), and the indication of which modules each bird species was assigned to: according to the number of interactions in each habitat type, Q_B (binary matrix) and Q_D (weighted matrix).

| Bird species | No. palms visited | Habitats ^a and abundance | Assigned modules ^a | Modules (Q_B) | Modules (Q_D) |
|---------------------------------|-------------------|-------------------------------------|-------------------------------|-------------------|-------------------|
| <i>Cyanocorax caeruleus</i> | 3 | RE (0.13), LO (0.03) | RE | 6 | 6 |
| <i>Carpornis cucullata</i> | 2 | PM (0.01) | PM | 5 | 1 |
| <i>Procnias nudicollis</i> | 14 | RE (0.01), LO (0.07), PM (0.20) | PM | 1 | 3 |
| <i>Pyroderus scutatus</i> | 3 | RE (0.01), LO (0.07), PM (0.001) | PM | 2 | 2 |
| <i>Turdus flavipes</i> | 32 | RE (0.4), LO (0.25), PM (1.01) | PM | 5 | 3 |
| <i>Turdus albicollis</i> | 27 | RE (1.03), LO (1.18), PM (1.03) | LO | 3 | 3 |
| <i>Turdus rufiventris</i> | 3 | RE (0.175) | RE | 1 | 3 |
| <i>Tachyphonus coronatus</i> | 1 | RE (0.001) | RE | 0 | 0 |
| <i>Ramphastos vitellinus</i> | 7 | LO (0.225), PM (0.331) | LO | 6 | 6 |
| <i>Selenidera maculirostris</i> | 7 | PM (0.159) | PM | 5 | 5 |
| <i>Trogon viridis</i> | 6 | RE (0.150), LO (0.207), PM (0.345) | RE | 4 | 4 |
| <i>Pitangus sulphuratus</i> | 1 | RE (0.043) | RE | 2 | 2 |

^a Habitats and assigned modules: *restinga* (RE); lowland (LO) and pre-montane (PM).

per point sampled, respectively), *T. albicollis*, *T. flavipes* and *Ramphastos vitellinus* in the lowland forest (IPA=1.18, 0.26 and 0.23) and *T. albicollis*, *T. flavipes* and *P. nudicollis* in the pre-montane forest (IPA=1.03, 1.02 and 0.35). More abundant bird species tended to interact more with palm individuals in the restinga ($r=0.60$, $t=2.41$, $df=10$, $p=0.030$), lowland ($r=0.59$, $t=2.18$, $df=10$, $p=0.056$) and pre-montane ($r=0.51$, $t=1.89$, $df=10$, $p=0.080$) habitats.

Palm characteristics differed among habitats (Supporting information). Considering all three habitats, canopy height varied between 5 and 22 m (mean \pm SD = 12.5 ± 3.5), total number of fruits varied across three orders of magnitude, between 55 and 7280 fruits (mean \pm SD = 962 ± 1307) and distance to gap varied between 0 and 50 m (mean \pm SD = 9.1 ± 13.3). Restinga palms had the lowest canopy height (mean \pm SD = 10.6 ± 2.0 ; [min, max] = [18, 15]), the lowest total number of fruits (mean \pm SD = 235 ± 223.6 ; [min, max] = [55, 1000]) and the highest values of distance to gap (mean \pm SD = 14.6 ± 14.1 ; [min, max] = [0, 50]). Lowland palms had intermediate values of canopy height (mean \pm SD = 12.5 ± 1.9 ; [min, max] = [8, 16]), the highest number of fruits (mean \pm SD = 1724 ± 1840 ; [min, max] = [75, 7280]) and average distance to gap was lower than in the restinga (mean \pm SD = 12.5 ± 16.4 ; [min, max] = [0, 50]). Pre-montane palms had the highest average canopy height

(mean \pm SD = 13.6 ± 4.2 ; [min, max] = [5, 22]), an intermediate number of fruits (mean \pm SD = 993 ± 1148 ; [min, max] = [80, 4800]) and the shortest distance to gap (mean \pm SD = 4.2 ± 9.2 ; [min, max] = [0, 50]), which can be an effect of both number and size of openings in the pre-montane habitat. Canopy height differed significantly between habitats ($F_{2,59}=3.66$, $p=0.032$), and was lower in the restinga than in the pre-montane (Tukey's post hoc test: $p=0.025$). Total number of fruits differed between habitats ($F_{2,59}=13.36$, $p<0.001$), and was lower in the restinga than in the pre-montane (Tukey's post hoc test: $p<0.001$) and lowland (Tukey's post hoc test: $p<0.001$). Distance to gap also differed between habitats ($F_{2,59}=11.02$, $p<0.001$), with the pre-montane presenting lower distance to gap than the lowland (Tukey's post hoc test: $p=0.034$) and the restinga (Tukey's post hoc test: $p<0.001$). So, we can characterize the restinga as having shorter palms and lower fruit production, the lowland as providing the highest palm fruit yield, and the pre-montane habitat as having a more complex forest structure, with taller canopies and close to gap openings in the forest.

Interaction degree (mean \pm SD = 1.709 ± 0.837), closeness centrality (mean \pm SD = 0.016 ± 0.003) and betweenness (mean \pm SD = 0.016 ± 0.023) varied little among individuals and did not differ among habitats. Therefore, no palm individuals were highly central in the network. Also,

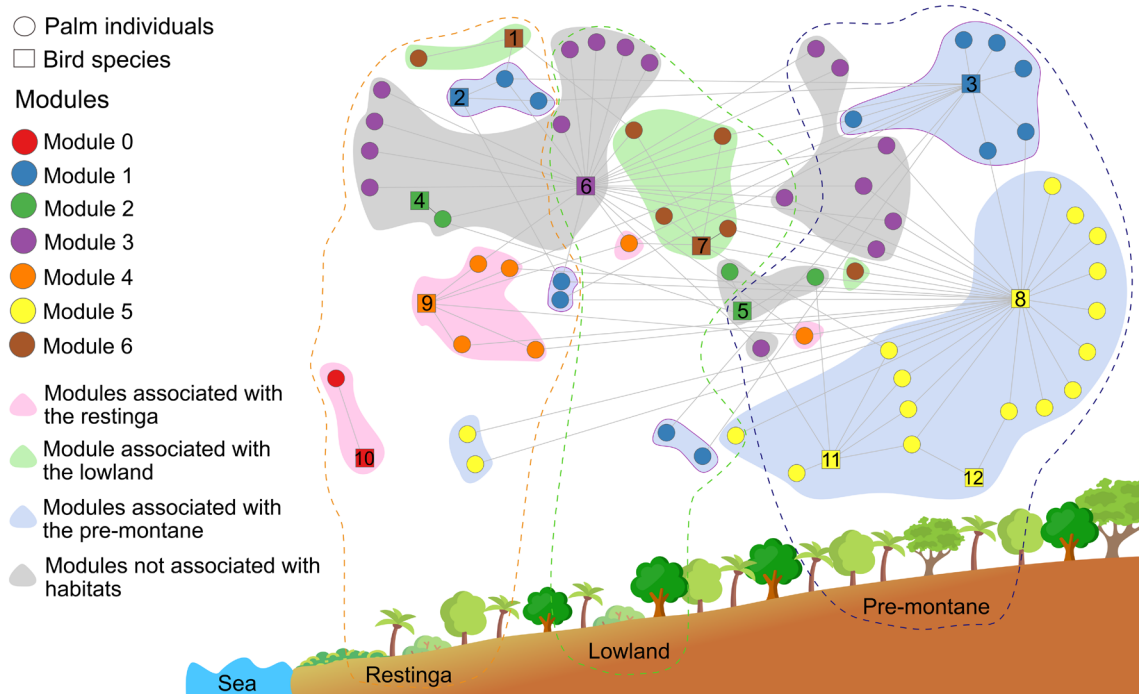


Figure 2. Observed network modularity across all three habitats using presence-absence data. Node colors represent modules resulting from Barber's index of modularity. The three dashed lines indicate the habitat types. Pink, green and blue polygons represent the habitat type that modules were associated with (> than 60% of nodes in concordance). Blue polygons delimited by the dashed purple line indicate module 1, with 50% concordance with the pre-montane nodes. Gray polygons indicate module 3, which had no association with any of the habitats. Numbers inside the squares indicate bird species (1: *Cyanocorax caeruleus*, 2: *Turdus rufiventris*, 3: *Procnias nudicollis*, 4: *Pitangus sulphuratus*, 5: *Pyroderus scutatus*, 6: *Turdus albicollis*, 7: *Ramphastos vitellinus*, 8: *Turdus flavipes*, 9: *Trogon viridis*, 10: *Tachyphonus coronatus*, 11: *Selenidera maculirostris* and 12: *Carpornis cucullata*).

none of the centrality positions were affected by palm characteristics in the isolated models or the multi-predictor model that included combined variables (results of GLM in the Supporting information); so palm characteristics were not correlated with interaction degree (Pearson's correlation for canopy height: $r=0.06$, $t=0.49$, $df=60$, $p=0.62$; number of fruits: $r=-0.17$, $t=-1.33$, $df=60$, $p=0.190$; distance to gap: $r=0.06$, $t=0.516$, $df=60$, $p=0.61$). Characteristics were also not correlated with closeness (canopy height: $r=-0.05$, $t=0.39$, $df=60$, $p=0.710$; number of fruits: $r=-0.09$, $t=-0.71$, $df=60$, $p=0.470$; distance to gap: $r=-0.178$, $t=-1.403$, $df=60$, $p=0.16$). Betweenness was not correlated with palm characteristics (canopy height: $r=0.05$, $t=0.41$, $df=60$, $p=0.680$; number of fruits: $r=0.005$, $t=0.04$, $df=60$, $p=0.960$; distance to gap: $r=-0.05$, $t=-0.36$, $df=60$, $p=0.710$). These results indicate that the centrality of palm nodes in the network is not affected by these intrinsic and extrinsic characteristics. In contrast, the frequency of interactions was positively and marginally significantly associated with canopy height ($r=0.25$, $t=1.98$, $df=60$, $p=0.052$; GLM results in the Supporting information), but was not correlated with number of fruits ($r=0.19$, $t=1.48$, $df=60$, $p=0.140$) or distance to gap ($r=-0.08$, $t=-0.67$, $df=60$, $p=0.500$).

The observed modularity of the presence/absence of interactions was not higher than predicted by the null model that incorporates heterogeneity in the number of interactions across bird species and individual palms ($Q_B=0.48$, $Q_{Null\ model\ 1}=0.51$, $p=0.81$; $Q_{Null\ model\ 2}=0.49$, $p=0.61$). Therefore, modularity at the network level can be viewed as a consequence in the variation of the number of interactions across individual palms and bird species (Fig. 2). In this sense, a fundamental problem is what generates variation in the number of interactions across individuals, because partial association of the seven detected modules with habitats could not be reproduced by the null model ($Q_{B_H}=0.24$, $Q_{B_{HR}}=0.04$, $p < 0.001$). Indeed, half of the modular structure observed in the network can be attributed to habitat types ($Q_{B_H}/Q_B=0.5$). The congruence analysis between modules identified by the algorithm (Q_B) and habitat modules (Q_{B_H}) indicated that three modules obtained through the optimization algorithm were congruent with the three habitats (Supporting information), meaning that palm individuals and bird species were assigned to the same modules assuming either habitat-based modularity or modularity based on the optimization algorithms. One module including a single palm individual and one bird species was associated with a single environment (module 0, restinga), whereas the other modules had members from all habitats, but varied in the proportion of palms and species of distinct habitats. For instance, three modules (modules 1, 3 and 5) were formed primarily by pre-montane palm individuals: 50, 41.2 and 82.3%, respectively, whereas two modules (4 and 6) were represented by 66.6% of palm individuals from the restinga and lowland habitats, respectively. Indeed, only a single module (2) was formed by a similar contribution from all habitats: for the three palm individuals of module 2, each palm was recorded in a single

habitat. The generalized linear model indicated that palm individuals from different modules varied in number of fruits, whereas canopy height and distance to gap did not differ among modules (detailed GLM values in the Supporting information).

The analyses of modularity patterns using interaction frequencies led to similar results as the presence/absence analysis, identifying seven modules that are partially associated with habitat types. Nevertheless, there were two important departures between the two modularity analyses. First, the modularity of the weighted network was much higher than predicted by the null model assuming interaction events were randomly distributed across partners ($Q_D=0.42$, $z\text{-score}=40.11$, Supporting information). Second, a single large module was detected containing 60% of nodes (palms and birds) in the network. This large module detected using the weighted network was not associated with any habitat type. Generalized linear models were built including only three modules with more than five palm individuals to evaluate if modules presented differences in palm characteristics. Modules (from the QuanBiMo algorithm) did not vary in canopy height, number of fruits and distance to gap (GLM results detailed in the Supporting information). In addition, three modules were associated with specific habitats: module 6 was associated with the lowland (71% of palms are from this habitat type), module 5 was associated with the pre-montane (100% of palms are from this habitat type), and module 4 had all three palms from the restinga forest (Supporting information).

Discussion

The way *Euterpe edulis* individuals interact with bird partners is influenced by both intrinsic and extrinsic characteristics (Grant et al. 1976, Angerbjörn et al. 1994). The solid body of empirical work on intrapopulation variation in patterns of interactions is rooted in the niche variation theory (van Valen 1965, Thompson 1988, Bolnick et al. 2003). Such variation may have a myriad of ecological and evolutionary consequences: potentially fueling speciation (Dieckmann and Doebeli 1999), changing the conditions for species coexistence within ecological communities (Bolnick et al. 2011), affecting the average fitness in populations (Gómez and Perfectti 2012), and providing the raw material for coevolution (Thompson 2005). Intrapopulation variation, however, may also be a fingerprint of neutral processes, such as genetic drift and ecological stochasticity (Hubbell 2001). In the last decades, by exploring the network structure of patterns of interaction among individuals and their resources, we began to uncover niche patterns within populations, and candidate ecological factors shaping these patterns, such as higher density of conspecific fishes and addition of new prey in the diet of individuals (Araújo et al. 2008), number and height of inflorescences (Dupont et al. 2011), geographic variation in the local structure of individual plant–pollinator networks having influence on mutualistic interactions (Gómez et al.

2011), and the role of landscape changes in structuring the diversity of interactions at the population scale for plants and frugivorous animals (Miguel et al. 2018, Jácome-Flores et al. 2020). Thus, we are just beginning to understand the network structure of intrapopulation variation in interaction frequency and strength (Guimarães 2020). In this sense, our study contributes to understanding the structure of individual networks in three different ways.

First, we unexpectedly found that individual palm characteristics were not associated with network structure when considering only the presence or absence of interactions. Our dataset included two sampling years to account for interannual variation in fruiting (Castro et al. 2007) and suggests that actual visitation to some palm individuals might be very infrequent or even not occurring. Indeed, only 50% and 45% of the palm trees were visited and had their seeds dispersed in the restinga and lowland, respectively, indicating that other characteristics may be affecting visitors and seed dispersers. Yet, these results may indicate that even if there is an association between plant characteristics and patterns of interaction, this association is weak over short temporal scales, at least for a sizeable fraction of the palm population. Such conditions may occur, for example, in years of extremely high fruit availability that may ‘satisfy’ the frugivore assemblage (Gorchov 1988, Hampe 2008) and result in just sporadic visits or no interaction at all for some individual palms. However, when analyzing the quantitative networks based on the frequency of interactions, canopy height emerged as an important factor attracting more frugivorous birds, suggesting that number of seeds dispersed are, indeed, at least partially affected by palm characteristics. The result is partially consistent with hierarchical models of foraging decisions by avian frugivores (Sallabanks 1993) where selection of habitat patches, individual plants within patches and fruits within plants interact in a hierarchical way generating interindividual variation in interaction outcomes. Correlations between traits and interaction patterns were reported for a variety of organisms, including fish (Araújo et al. 2008), seed-dispersing birds (Dehling et al. 2016, Jácome-Flores et al. 2020) and plants (Guerra et al. 2017). For example, Foster (1990) found that some groups of frugivores birds visited more trees with higher number of fruits, but feeding visits were not influenced by other traits. In particular, interactions between some plants and their floral visitors (Rumeu et al. 2018, Arroyo-Correa et al. 2021) or their frugivorous consumers (Miguel et al. 2018, Crestani et al. 2019, Jácome-Flores et al. 2020) were partially associated with trait variation across individuals. However, in our study system neither individual traits nor microhabitat structure affected variation across the study site in 1) the number of bird species visiting individuals or 2) patterns of overlap in bird assemblages visiting individuals. Individual-based pollination networks seem to result in ecological networks in which individuals in central positions are visited by several species and individuals (Gómez and Perfectti 2012, Arroyo-Correa et al. 2021). However, in *E. edulis*, individuals have their fruits consumed by several bird species, but the interaction among palm individuals and bird species occurred

somehow homogeneously in the network, in which no palm characteristics were especially attracting more frugivore bird species. Therefore, the environment may partially swamp the effects of traits in shaping the structure of individual-based networks, but not necessarily the number of interaction events. Alternatively, the high homogeneity in centrality values across individuals might be a consequence of the failure to sample central individuals due to the fact that any study on patterns of interaction only samples a small proportion of the individuals in the environment (in our case, we estimate these figures as 0.15% of individuals in the restinga, 0.14% in the lowland and 0.18% in the pre-montane). Indeed, in many networks, central nodes represent a small fraction of interacting elements of the system (Barabasi and Albert 1999, Jordano et al. 2003). Having said that, spatially-distributed networks usually also show high homogeneity in centrality and number of interactions across nodes (Watts and Strogatz 1998, Crucitti et al. 2006), as we observed in our network.

Second, palm individuals did not differ greatly in the number of bird species composing the coterie of seed dispersers. We observed no association between individual characteristics of *E. edulis* (i.e. number of fruits) and individual centrality in the network. Accordingly, individuals did not vary in their degree of closeness and betweenness centrality, so the shortest distance from the palm individuals to other individuals did not differ greatly in the network, indicating that no individual palm was considered a strong connector in the network or that we did not obtain sufficient sampling power, which may be a potential limitation of individual-level network analyses. This small variation across palms in the number of mutualistic partners may have swamped the effects of individual characteristics that otherwise could generate differences in the number of mutualistic partners, as observed in some pollination (Rumeu et al. 2018) and seed dispersal systems (Miguel et al. 2018, Crestani et al. 2019, Tonos et al. 2021). Theoretically, homogeneity in patterns of interaction is expected in systems that are primarily structured by spatial characteristics (e.g. habitat types, spatial distribution of food resource) (Watts and Strogatz 1998, Amaral et al. 2000, Albert and Barabási 2002, Carlo and Morales 2008), with the potential for facilitation effects among neighborhood conspecifics (i.e. sharing seed dispersers among closely-growing individuals; Sargent 1990) or neighborhoods of different plant species overlapping in their fruiting season (Albrecht et al. 2015). Both conspecifics and individuals of different species may result in plants species sharing frugivorous species and changing the seed removal rate and interaction strength. Low variation in the number of species dispersing seeds and centrality (e.g. vertices at a short distance to others or with multiple interaction partners) may be a consequence of spatial distribution of palm individuals which, being a dominant subcanopy species, are well distributed across habitats and not restricted to microhabitats in the island.

Third, out of twelve bird species recorded dispersing *E. edulis* seeds, only five species were detected in all habitats in our site. Indeed, we only observed a portion of the species

that were already recorded feeding on *E. edulis* fruits on Cardoso Island (Supporting information). The different habitat types in our site are contiguous and occur along an elevation gradient, and the bird species are prone to occur along both forest and altitudinal gradients, which results in habitats sharing several bird species and palm individuals being distributed across environments abundantly and not restricted to microhabitats in the island. However, even birds that were recorded in all habitats may interact more in one of the three habitats. For example, *Turdus flavipes* was recorded in the three habitat types, but interacted with a higher number of individuals in the pre-montane habitat ($n=22$) compared to the restinga ($n=7$) and lowland ($n=3$) habitats. This result is expected because it is the most abundant palm frugivore in the pre-montane habitat during *E. edulis* fruiting. This bird species is described as naturally occupying higher elevations, migrating to lower elevations during winter while possibly tracking *E. edulis* fruiting (Castro et al. 2012). Also, *Carpornis cucullata* occurs almost exclusively in montane forests (Snow and Sharpe 2020) and was only recorded in the pre-montane habitat. Consequently, the potential richness of mutualistic partners, as well as the centrality of individuals, are limited by habitat-specific bird richness. In this sense, we should expect that habitat types may provide the template shaping interactions of *E. edulis* and seed-dispersing bird species in the study site, leading to a distinct signal of habitat characteristics on modularity. In addition to species richness, individual abundance of frugivorous birds influence, for example, visitation rate (Côrtes 2006) and the interaction patterns with palms.

By using modularity to describe network structure, we were able to assess the modular pattern of the entire network and the partial association of modules with different habitat types. At the level of the entire network, the observed value of modularity was reproduced by a theoretical benchmark provided by a null model that takes into account the number and distribution of interactions in the binary network. This result indicates that, at the level of the entire network, even random networks with similar variation in number of interactions per individual palm and bird species show similar levels of modularity. This suggests an overall high level of cohesion throughout the entire elevational gradient in the identity of frugivore species interacting with the palms: a few bird species were involved in interactions with palms actually growing in each of the three habitats and we may think of these species as ‘connectors’ across habitat types in ecological functions such as long-distance seed dispersal, source-sink dynamics and meta-population integration. In this sense, we hypothesized an association between habitat types and module assignment to individuals. By exploring the relationship between modules and habitat we showed that modules are at least partially associated with habitats. Our results indicate that habitat types create a template for interactions (Fig. 1), contributing to the formation of semi-isolated groups of palm individuals and bird species, meaning that the spatial structure of the palm population affects patterns of interaction, with

potential habitat-biased seed dispersal patterns (Schupp et al. 2010). For example, spatial variation of fruiting plants that are a food resource for frugivorous birds and mammals may impose patterns of interaction, in which both plant phenology and aggregation can have a strong influence on seed dispersal (Carlo and Morales 2008, Miguel et al. 2018). In a broader perspective, there is increased evidence that modularity is associated with spatial distribution in individual-based networks describing the interactions of individual plants and their animal visitors (Fortuna et al. 2009, Dupont et al. 2014, Tur et al. 2014, Miguel et al. 2018, Crestani et al. 2019).

When studying the emergence of modules in individual-based networks especially in an environment in which habitats occur in a gradient and seed-dispersing birds are not restricted to these habitats, it is crucial to partition the effects of intrinsic and extrinsic characteristics on individual-species interactions. The small variation among palm trees regarding centrality positions may have consequences for the demographics and genetics of *E. edulis* (Carvalho et al. 2021) and these patterns may contribute to explain the distribution of this species in the Atlantic rainforest. In a relatively well-preserved rainforest, as in Cardoso island, our results suggest extensive seed dispersal with the presence of interactions with frugivorous species whose activity extends across the entire elevational gradient and may contribute to high cohesiveness at a meta-population (among habitats) scale. Even though palm individuals presented no association between their intrinsic and extrinsic components and centrality measures, there are other aspects that could be addressed. For example: in the restinga larger frugivores interacted more with palm trees that are in areas of higher average canopy height in the forest (Côrtes 2006). Indeed, we observed similar results for individual palms across habitats in our analysis, in which palms with higher canopy show higher frequency of interactions. Then, by partitioning, for instance, the effects of functional groups of seed-dispersing birds, we may even encounter different patterns (Vázquez et al. 2005). Indeed, by exploring interaction frequencies, we added crucial information on *E. edulis* individual variation in seed dispersal. Specifically, we detected a strong modular structure in the patterns of interaction of individual palms that are partially associated with habitats, suggesting that local habitats reshape the frugivore assemblage yielding a distinct, habitat-specific signal to the interaction patterns in the whole network. As evaluated here, the type of interaction registered (binary or weighted interaction data) may provide different perspectives on the system under study. Future studies could explore the interindividual variation in patterns of interaction across frugivorous birds. This variation may show relevant consequences for ecological processes. For example, individuals may vary in regard to competitive strategies (Tinker et al. 2012), efficiency as seed dispersers (Schupp et al. 2010) and differences in individual selectivity of fruits (Cantor et al. 2013). Regarding these seed dispersal networks, we know how difficult it is to sample bird individuals. However, we highlight the importance of associating the seed dispersal events with individual variation in both sides, animals and/or plants, to have a deeper

understanding of the ecology of populations and communities (Bolnick et al. 2003, 2011, Jordano 2016, Melián et al. 2018, Guimarães 2020).

We have shown that interactions between *E. edulis* individuals and their seed-dispersing birds form modules along the altitudinal gradient in Cardoso Island. A potential next step is to explore how interactions of individual birds are structured and organized around visitation to specific palm individuals. The organization of individual-based interactions of frugivores may contribute to our understanding of spatial (Miguel et al. 2018, Jácome-Flores et al. 2020) and temporal variation (Cantor et al. 2013, Machado-de-Souza et al. 2019), and individual preferences (Pires and de Melo 2020) in resource use by seed dispersers. Thus, by exploiting individual variation in both animals and plants we may have a better understanding of the consequences of frugivory for population dynamics and ecological systems. Future studies should explore if this modular pattern may contribute to ecological processes operating at the population level. For example, modules may generate semi-independent dynamics in complex systems (Watson and Pollack 2005). In the studied system, modularity indicates that habitat-specific modules may respond differently to environmental change, such as reduction or expansion of a particular habitat or local extinction of habitat-specific bird species. Moreover, central frugivorous bird species that are more resistant to environmental disturbance (e.g. habitat loss) could restrict the impacts of environmental disturbance on the entire network by interacting with other palm individuals in different habitats, maintaining seed dispersal of palms (Carvalho et al. 2021) and stabilizing the system structure. Along this line, analyses such as the present one, revealing how individuals, neighborhoods and local stands shape plant–frugivore interactions over ample ecological gradients may help to improve the design of restoration initiatives. For example, our results suggest that restoration actions for this palm species should take into account not just the positions of individually restored palms but also the composition of local neighborhoods, spatial aggregations and habitat type. Accordingly, habitat variation in patterns of interaction across individuals may fuel evolutionary dynamics mediated by ecological interactions (Thompson 2005), by preserving the natural diversity of conditions that generate variation in the occurrence of interactions. For now, our study illustrates how habitats shape ecological interaction networks within populations, by potentially constraining the role of individual traits in shaping patterns of interactions within species.

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Author contributions

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Data availability statement

Data are available from the Dryad Digital Repository: <<https://doi.org/10.5061/dryad.stjqc2c4j>> (Friedemann et al. 2021).

Supporting information

The supporting information associated with this article is available from the online version.

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