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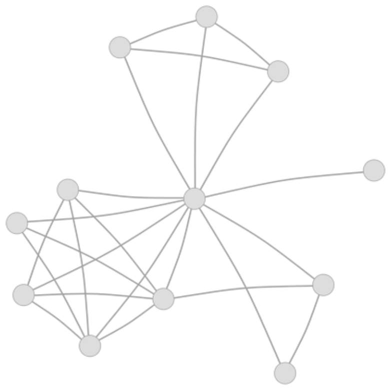

De indivíduos a espécies: a estrutura de redes de dispersão de sementes em diferentes níveis de organização

From individuals to species: the structure of seed dispersal networks in different levels of organization

Pâmela Vanessa Friedemann Tavares

São Paulo

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Orientador: Paulo Roberto Guimarães Jr.

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Dedicatória

Dedico este trabalho à biodiversidade brasileira, que tem sido constantemente ameaçada, e a todas as pessoas que lutam para preservá-la.

Epígrafe

"É perigoso sair porta afora, Frodo", ele costumava dizer, "Você pisa na Estrada, e, se não controlar seus pés, não há como saber até onde você pode ser lavado".

J. R. R. Tolkien – O Senhor dos Anéis: A Sociedade do Anel

"[...] Sei que há tanto pra descobrir
É tudo tão novo para mim
Eu vejo tudo a minha volta
Mas eu sei que há muito mais pra se ver
Quero entender, conte tudo
Quero saber sobre os estranhos como eu".

Phil Collins - Tradução da música *Strangers like me*

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Summary

Resumo geral

Comunidades ecológicas são formadas por organismos que exibem diferentes padrões de interações. Em última instância estes organismos são os indivíduos da comunidade, que quando são considerados em conjuntos, descrevem os padrões de interações das espécies. A dispersão de semente é uma interação potencialmente mutualista que pode envolver diversas espécies, e que é um processo importante para a regeneração das populações de diversas espécies de plantas. As espécies das redes de plantas e dispersores podem apresentar diferentes papéis ecológicos, no qual podemos observar espécies que interagem com muitas outras dentro da rede (e.g., uma espécie de ave que dispersa sementes de várias espécies de plantas) ou espécies que interagem com apenas uma ou poucas espécies dentro da rede. Aqui, nós investigamos as consequências dos padrões de interações na estrutura das redes de interações em diferentes níveis de organização – indivíduos e espécies. Para isso utilizamos redes de dispersão de sementes de aves e plantas. Para o nível de indivíduos, nós avaliamos a estrutura da rede de interação entre indivíduos da palmeira *Euterpe edulis* e as espécies de aves dispersoras de sementes em três tipos de florestas (restinga, planície e encosta) na Ilha do Cardoso. Neste estudo, nós avaliamos se as características dos indivíduos e do micro-habitat de *Euterpe edulis* influenciavam na centralidade dos mesmos (descreve se os indivíduos interagem bastante e/ou conecta grupos dentro da rede). Também analisamos se a rede apresentava uma estrutura modular (grupos de indivíduos e espécies interagindo mais entre si na rede) e se os tipos de florestas influenciavam na emergência destes módulos. Nossos resultados mostraram que as características dos indivíduos e do micro-habitat não influenciaram na centralidade dos indivíduos na rede. Isto pode ser resultado da alta disponibilidade de *Euterpe edulis* na área, pois assim as aves encontram facilmente indivíduos desta palmeira. Acerca da emergência de módulos na rede, nós encontramos que as florestas estavam parcialmente associadas com os módulos na rede. Esta associação das florestas com os módulos mostrou que algumas espécies de aves mesmo interagindo em todos os tipos florestais tendiam a interagir com mais indivíduos em um dado tipo florestal, formando módulos. Para o nível das espécies, nós exploramos papel de espécies do gênero *Turdus* em redes de plantas e frugívoros ao redor do mundo. Para isso nós juntamos 162 redes de plantas-aves frugívoras de sete regiões diferentes no mundo: América do Sul, Europa, África, Ásia, América do Norte, América Central e Oceania. Ao todo foram registradas 342 entradas (registros das espécies de *Turdus* nas redes) de *Turdus*, distribuídas em 36 espécies. Neste estudo, nós avaliamos a variação da centralidade do gênero, das espécies e das populações de *Turdus*. Nossos resultados demonstraram que as espécies de *Turdus* apresentam uma grande variação na centralidade nas redes, mas em média *Turdus* apresentaram maior centralidade do que outras espécies de aves. As espécies que mais tiveram registros apresentaram bastante variação na centralidade nas redes, no qual em determinadas redes a espécies estava em uma posição central, enquanto em outras redes a mesma espécie estava numa posição menos central. Nossos resultados indicam que o papel central dos *Turdus* em redes de interações planta-frugívoros pode ser influenciado pelo contexto da rede, como número de espécies de plantas.

Palavras-chave: mutualismo, redes complexas, dispersão de sementes, centralidade, níveis de organização

Abstract

Ecological communities are formed by organisms that exhibit different patterns of interactions. Ultimately, these organisms are the individuals of the community, which when considered in sets, describe species interaction patterns. Seed dispersal is a potentially mutualistic interaction which is an important process for the regeneration of plant's populations and can involve several species. The species in plant-disperser networks may have different ecological roles, where we can observe species interacting with many others in the network (e.g., a bird species dispersing seeds of several plant species) or species interacting with only one or a few species. Here, we investigate the consequences of interaction patterns on the structure of interaction networks at different levels of organization – individuals and species. For this purpose, we use seed dispersal by birds' networks. At the individual level, we evaluate the structure of the interaction network among individuals of the palm *Euterpe edulis* and seed-dispersing bird species in three types of forests (*restinga*, lowland, and pre-montane) on Ilha do Cardoso. In this study, we assess whether the characteristics of *Euterpe edulis* individuals and micro-habitat influence their centrality (describes whether individuals interact a lot and/or connect groups within the network). We also analyze whether the network exhibits a modular structure (groups of individuals and species interacting more with each other in the network) and if forest types influence the emergence of modules. Our results showed that the characteristics of individuals and micro-habitat did not influence individual centrality in the network. This may result from the high availability of *Euterpe edulis* in the area, as birds can easily find individuals of this palm. Regarding the emergence of modules in the network, we found that forests were partially associated with the network modules. This association of forests with modules showed that some bird species, even though they interacted in all forest types, tended to interact with more individuals in a given forest type, forming modules. At the species level, we explored the role of *Turdus* species in plant and frugivorous bird networks worldwide. For this, we compiled 162 plant-frugivorous bird networks from seven different regions worldwide: South America, Europe, Africa, Asia, Panama, North America, Central America, and Oceania. In total, 342 entries (records of *Turdus* species in all networks) were recorded, distributed among 36 species. In this study, we evaluated the variation in centrality of the genus, species, and populations of *Turdus*. Our results demonstrated that *Turdus* species exhibit a wide variation in centrality in networks, but on average, *Turdus* had higher centrality than other bird species. The species with the most records showed variation in centrality in networks, in which in some networks the species was in a central position, while in other networks, the same species was in a less central position. Our results indicate that the central role of *Turdus* in plant-frugivorous interaction networks may be influenced by network context, such as the number of plant species.

Keywords: mutualism, complex networks, seed dispersal, centrality, organizational levels

Introduction

The ecological interactions between organisms are crucial for the existence of biodiversity in all kinds of environments and taxa (Tilman et al. 2014). The organism's interactions may present a continuum of outcomes, from antagonistic to mutualistic results. In mutualisms, both sets of interacting groups are potentially benefited (Bronstein 1994). Seed dispersal is a fundamental ecological process for the regeneration of plant populations in which seeds can be dispersed in a variety of ways, such as by the action of wind, water, the plant itself, or animals (Howe and Smallwood 1982). Seed dispersal by animals is a potentially mutualistic interaction and can involve several groups, such as ants and crickets (Santana et al. 2016), fish (Galetti et al. 2008), primates (Fuzessy et al. 2017), bats (Mello et al. 2011), and birds (Galetti et al. 2013). Animals, mainly vertebrates, are the main seed dispersers in tropical forests and 70% to 90% of woody plants in these forests depend on vertebrates to disperse their seeds (Jordano 2000). For plants, the benefits of seed dispersal by animals mainly rely on reducing seed mortality due to processes of dispersal far from the origin plant (Janzen 1970). For animals, the main benefit of this interaction is the consumption of fruits as a food resource (Snow 1971). Among vertebrates, birds are usually considered efficient dispersers, as they deposit seeds far from the origin plant (Howe and Smallwood 1982; Loiselle and Blake 1999). However, seed dispersal by birds involves a huge range of species, and these species vary in their efficiency as seed dispersers (Jordano and Schupp 2000) and their dependence on fruits as a food resource (Kissling et al. 2009).

Interactions are established when the organisms involved present characteristics that allow these interactions; for example, the shape, opening, or elasticity of the mouth apparatus allows for resource consumption up to a certain food size (Klumpers et al. 2019; Dehling et al. 2014). These characteristics of organisms can be called traits, such as height and length (Kissling et al. 2018), dispersal (Bonte et al. 2012) and behavior (Gaudreau-Rousseau et al. 2023). Generally, species traits are often described as an average value (e.g., mean body length) and the use of averages as descriptors of morphological traits is based on the simplifying premise that considers individuals of a species as ecologically equivalent. However, the traits of individuals can vary markedly between individuals within the same population (Bolnick et al. 2003) and this variation in traits can influence the resource use by individuals. The consequence for intraspecific variation may results in significant changes on the total niche breadth of a population or species (Van Valen 1965; Bolnick et al. 2011). The interaction patterns may be assessed by looking at different interacting units, such as individuals and species and the organizational level chosen will depend on the ecological question. To build a more complete knowledge about ecological interaction patterns and its implication on ecological and evolutionary processes it is essential to evaluate the interactions at different levels of organization.

The interactions among organisms are established through individuals, which may present significant differences in their traits. For example, the body size of individuals of *Turdus migratorius* is associated with the preference for certain fruits (Jung 1992). The intraspecific variation can occur in different attributes of the natural history of organisms, such as foraging and the use of microhabitats (Kohda 1994). Also, variation between individuals may be observed in the relationship between competitive ability and the use of food resources (Sol et al. 2005) and seasonality in the use of resources (del Rio et al. 2009). Due to this potential intraspecific variation and other components (such as environmental context), individuals could interact differently and the outcomes of this may include implications for community stability (May 1972) and trait evolution (Thompson 2005). In studies that explored the individual differences in the use of resources it is pointed out that sex, age, morphology, and behavior (Tinker et al. 2012), as well as population density (Araújo et al. 2008), and resource diversity may lead to significant individual specialization (Bolnick et al. 2003). Individual niche specialization may emerge from the competition among individuals for resources because it could lead the population to expand the niche breadth through the individual niche expansion (Svanbäck and Bolnick 2005). In pollination, it has already been registered that as the abundance of pollinator's individuals increased, they were more specialized by consuming pollen from different plant species (Tur et al. 2014). In seed dispersal interactions, individuals may present changes in efficiency as seed dispersers (Schupp et al. 2010), and differences in the selectivity of fruits (Cantor et al. 2013). Meanwhile, in predator and prey interactions, the fish individuals in a population may present different ways to deal with high conspecific density, with groups of fishes including new prey items in their diet, while others remain with their preferred prey (Araújo et al. 2008). The myriad of ways that individuals can interact will depend largely on the studied group and the environmental contexts.

Zooming out from the individual to species level, the outcome of individuals interacting in their ecological community will reflect on the general pattern of species interactions. The outcome on the way that species interact in a community can vary along with the continuum of species that establish interaction with only a few partners to species highly-connected in the systems. Thus, in a predator-prey scenario, the coexistence of two competing species may be possible because of the differences in how species are exploiting the resources. So, the generalist species may exploit efficiently the wide range of resources available and present a higher population-level plasticity in resource use (Petroelje et al. 2021), while the less generalist species specialize on a few resources. In a pollination context, the habitat features may drive the interaction pattern; for example, the higher abundance of a conspecific plant species may increase floral visits. Also, the pollinator species may present distinct roles, with some given species mediating long-distance pollen-flow (Santos et al. 2018). Also, the variation in species composition in a community can generate selective pressures and shape evolutionary dynamics. For example, in a seed dispersal system, Galetti et al. (2013) observed that *juçara* palms (*Euterpe edulis*) present smaller seeds in defaunated areas - where there has been functional or complete extinction of their larger seed dispersers. The most plausible explanation for this pattern is the rapid evolutionary change mediated by the change in the composition of bird species in these areas, in which large frugivores became extinct, leaving only small frugivores that are limited to the consumption of small fruits. To deepen the comprehension of how species differ in ecological roles and how the species interactions may change the structure of the community it is essential to understand how species influence - and are influenced – by other species.

The network approach can be a useful tool to study the influence of individuals or species interactions in other biological components of the ecosystem. Networks are defined by nodes or points (which can be individuals, species, genes, proteins) and by lines or edges (ecological interactions, gene regulation) that connect the points (Bascompte and Jordano 2007). The structure of interaction networks constitutes a pattern that varies over time, in which ecological processes that occur locally shape and are shaped by the structure of the network (Pascual and Dunne 2006; Bascompte and Jordano 2007). Studying individuals and species interactions under network approaches allows us to zoom in and out within the organizational levels and understand how the individual's interactions can translate to species' general patterns of interaction in the community. This is especially important to identify important characteristics of the individuals that are driving the structure of the interactions and also to identify the key individuals and species in ecological network.

During my PhD, I decided to develop my thesis within the framework of individuals and species patterns of interactions and the respective ecological outcomes of these interactions. To achieve this, we evaluated plant-frugivore interaction networks at different scales by using bipartite networks, which consist of two sets of nodes representing individuals and species. First, we focused on the seed dispersal of different individuals of the *Euterpe edulis* palm by bird species in three different habitats on Ilha do Cardoso (São Paulo, Brazil). For this, we created individual-species-based network for the palm species (each palm node refers to an individual) and the bird species (each bird node refers to a species). *Euterpe edulis* is an ecologically and economically important plant species in the Atlantic Forest and is locally extinct in several areas (Galetti and Fernandez 1998).

In the individual-based network study of *Euterpe edulis* and its seed dispersers, we explored how intrinsic and extrinsic features may lead to the emergence of modules in the networks. Modules are groups of nodes (individuals and/or species) that interact more with each other than with the rest of the nodes in the network. This means that the nodes are partitioning the resources in the network (e.g., pollination in Tur et al. 2014; seed dispersal in Miguel et al. 2018). We also evaluate if the palm's characteristics influence the individuals' position in the network. For this, we used centrality measures that describe if the node is interacting with numerous partners or if they are interacting with important nodes (which connect several others). In plants, intraspecific variation in traits may lead to skewed distributions of interaction strengths according to the traits (Dupont et al. 2011; Jácome-Flores et al. 2020; Arroyo-Correa et al. 2021). Our results showed that the individuals' intrinsic characteristics (e.g., canopy height and number of fruits available) did not have any effect on the centrality position of the individuals in the seed dispersal network. The modules detected were partially associated with the three habitat types. This study was published at Oikos in 2022 (Friedemann et al. 2022: The individual-based network structure of palm-seed dispersers is explained by a rainforest gradient. https://doi.org/10.1111/oik.08384).

Zooming out to the species level (for both plants and birds), in the second chapter of my thesis, we explored the ecological role of *Turdus* species (Thrushes) as potential seed dispersers in plant-frugivore networks around the world. *Turdus* species vary in the proportion of different food items (as fruits) in their diet, with several species presenting a high consumption of invertebrates. However, even though the diet of most *Turdus* species relies greatly on invertebrate, these species play a central and important role as seed dispersers in different regions of the world (Côrtes et al., 2009; Fadini et al. 2009; Breitbach et al. 2012; Uriarte et al. 2011; Isla et al. 2023). For this study, we gathered a total of 162 plant-frugivore networks around the world which had at least one *Turdus* species present. We measured the ecological role of the species by using three centrality measures to evaluate the position of the *Turdus* species. The centrality measures describe how each species is interacting in the networks and can indicate if that species is central (e.g., a key species) in the given network. We also tested if the frugivory degree (the proportion of fruit in the species' diet) and the size of *Turdus* species predict the general species centrality. The regions with the higher number of plant-frugivore networks in our dataset were from South America (n= 69), followed by Europe (n= 39) and Africa (n= 18). *Turdus merula* was the most common species across the dataset (n= 54), followed by *Turdus philomelos* (n= 45) and *Turdus rufiventris* (n= 29). We found that the *Turdus* species presented a great variation in the centrality position between the networks, but in general, *Turdus* species appeared as central ones when compared with other bird species. Neither the frugivory degree nor the size of the species presented influence on *Turdus* species in the average centrality. We also noted that the centrality of the majority species that appeared in several networks varied in different networks. So, in some networks, those species appeared in a very central position, while in others they were in a less central position. Then, *Turdus* seems to be a key species in several scenarios, and the wide variation in centrality may indicate that the position assumed by *Turdus* species in a given plant-frugivore network could depend on the ecological and environmental context of the community.

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Chapter 1: The individual-based network structure of palm-seed dispersers is explained by a rainforest gradient

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Abstract

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 ther habitat types (Fig. 1)? We expect that modules in the network are associated with each habitat type and its respective frugivore assemblages due to the heterogeneous distribution of bird species among habitats.

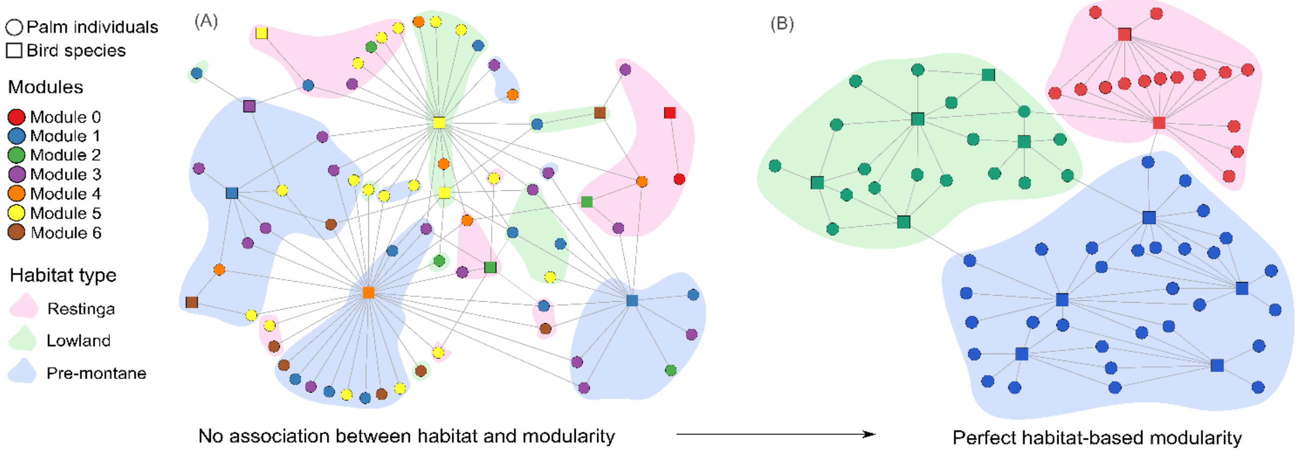

Figure 1. Representation of different scenarios of modular networks: (A) expected modularity if the network is random with no association between habitat and modules, and (B) a perfect habitat-based modular network in case well-delimited modules emerge from different habitat types.

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 (Sugyama 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 (± 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 microhabitat 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 *aij* 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 coteries. 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 coteries 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 (QB, Supporting information) to characterize modularity of the bipartite network defined by the binary matrix **A**. We first estimated the QB 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 QB, since there is no algorithm able to analytically find the partition that maximizes QB 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_H*. 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_H* and

QD, we randomized the assigned habitat across palms and bird species and recomputed the modularity, recording a randomized version of the habitat-based modularity, QB_HR (n = 1000 randomized trials). If the proportion of randomizations showing $QB\_HR \geq QB\_H$ 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 $cij = 1$ 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 $dij = 1$ 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, eij 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 (QB and QD) and counted the number of times in which the randomized had higher concordance values then the habitat-based matrix (QB_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 ($F2,59 = 3.847$, $p = 0.037$), with lower absolute frequency of interactions in the restinga (mean ± SD = 7.7 ± 7.5 interactions) which differed from the pre-montane (mean ± SD = 20.6 ± 18.9), which were similar to interaction frequency in the lowland (mean ± SD = 19.7 ± 18.6). Overall bird abundance estimates (all species included together) did not differ among habitats (F2,23 = 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 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.

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)
Cyanocorax caeruleus	3	RE (0.13), LO (0.03)	RE	6	6
Carpornis cucullata	2	PM (0.01)	PM	5	1
Procnias nudicollis	14	RE (0.01), LO (0.07), PM (0.20)	PM	1	3
Pyroderus scutatus	3	RE (0.01), LO (0.07), PM (0.001)	PM	2	2
Turdus flavipes	32	RE (0.4), LO (0.25), PM (1.01)	PM	5	3
Turdus albicollis	27	RE (1.03), LO (1.18), PM (1.03)	LO	3	3
Turdus rufiventris	3	RE (0.175)	RE	1	3
Tachyphonus coronatus	1	RE (0.001)	RE	0	0
Ramphastos vitellinus	7	LO (0.225), PM (0.331)	LO	6	6
Selenidera maculirostris	7	PM (0.159)	PM	5	5
Trogon viridis	6	RE (0.150), LO (0.207), PM (0.345)	RE	4	4
Pitangus sulphuratus	1	RE (0.043)	RE	2	2

a – Habitats and assigned modules: *Restinga* (RE); lowland (LO) and pre-montane (PM)

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

= 12.5 ± 16.4; [min, max] = [0, 50]). Pre-montane palms had the highest average canopy height (mean ± SD = 13.6 ± 4.2; [min, max] = [5, 22]), an intermediate number of fruits (mean ± SD = 993 ± 1148; [min, max] = [80, 4800]) and the shortest distance to gap (mean ± 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 (F2,59 = 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 (F2,59 = 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 (F2,59 = 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 ± SD = 1.709 ± 0.837), closeness centrality (mean ± SD = 0.016 ± 0.003) and betweenness (mean ± 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, 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 teh 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 ($QB = 0.48$, QNull model 1 = 0.51, $p = 0.81$; QNull 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 ($QB\_H = 0.24$, $QB\_HR = 0.04$, $p < 0.001$). Indeed, half of the modular structure observed in the network can be attributed to habitat types ($QB\_H/QB = 0.5$). The congruence analysis between modules identified by the algorithm (QB) and habitat modules (QB_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).

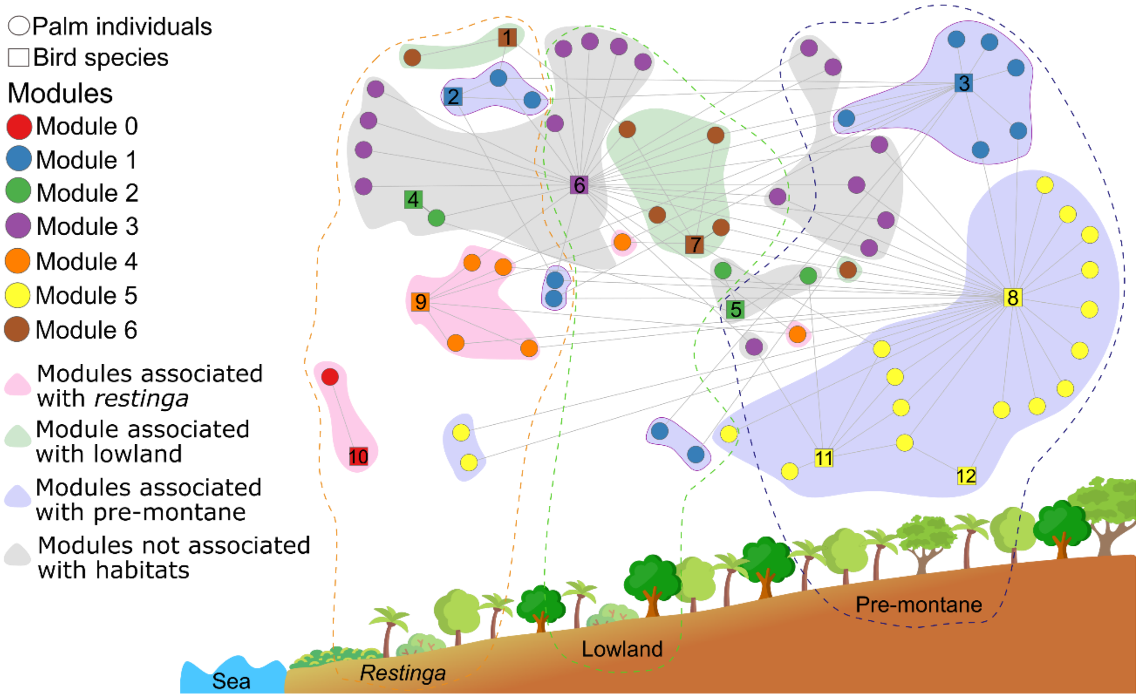

Figure 2. Observed network modularity across all three habitats using presence-absence data. Node colors represent modules resulting from Barber's index of modularity. The three dashed lines indicate the habitat types. Pink, green and blue polygons represent the habitat type that modules were associated 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*).

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 ($QD = 0.42$, z-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 'satiate' 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. 2022). 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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Supporting information

Appendix 1

Individual-level metrics

We used three measures to quantify the centrality of palm individuals in the individual-species network: interaction degree, betweenness and closeness. These metrics were calculated using binary data. The centrality measures were computed from a one-mode projection.

Interaction degree

The degree in the number of interaction partners of individuals, ranging from one to the number of bird species.

Closeness centrality

Measures how close a focal individual i is to all others in the network (Freeman 1978). Individuals with high closeness values have shorter distances (in number of individuals) to other individuals in the network (Martín González et al. 2010). Closeness is calculated as follows:

$$CC_i = \sum_{j=1;i\neq j} \frac{s_{ij}}{n-1}$$

(Eq. 2)

where, in our case, n is the number of individuals, and s_{ij} is the shortest distance between the other palm individuals measured in number of interactions (González et al. 2010, Freeman, 1978).

Betweenness centrality

Indicates the frequency in which the nodes are between pairs of nodes in the shortest path connecting them (Freeman 1978). Individuals with high values of betweenness centrality are at a shorter distance to other palm individuals (González et al. 2010). Betweenness is measured as follows:

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

(Eq. 3)

where n is the number of species and/or individuals in the network, g_{jk} is the number of shortest paths linking any two nodes, and $g_{jk}(i)$ is the number of those shortest paths among g_{jk}, that includes i (Freeman 1978). Individuals with a BC higher than zero are termed connectors (González et al. 2010).

Network-level metrics

Barber’s bipartite modularity

We first describe the binary structure of the seed dispersal network. To do so, we calculated Barber’s bipartite modularity algorithm (Barber 2007):

$$Q_B = \frac{1}{2m}\sum_{ij}(a_{ij} - p_{ij})\delta(g_i, g_j)$$

(Eq. 1)

where m is the number of unique pairwise interactions recorded in the adjacency matrix, a_{ij} is the element of the adjacency matrix **A** in which $a_{ij} = 1$ if there is at least one interaction event between nodes i and j interacts and $a_{ij} = 0$ otherwise; p_{ij} is the probability in a null model that an interaction exists between vertices i and j, and δ indicates if the nodes are on the same module, $\delta = 1$, or if the nodes are in different modules, $\delta = 0$.

Quantitative Bipartite Modularity (QuanBiMo, Dormann and Strauss 2013)

We then used the data on frequency of interactions to evaluate weighted patterns of modularity. This algorithm is a modification of Barber's:

$$Q_D = \frac{1}{2m}\sum_{ij}(w_{ij} - q_{ij})\delta(g_i, g_j)$$

In which, w_{ij} is the expected number of links between nodes i and j, in which in the weighted version the values of abundant species is expected to be higher and rare species to be low edge weights; q_{ij} are the probabilities in a null model that an interaction exists between vertices i and j, and δ indicates if the nodes are on the same module. The main difference for the binary index is that here q_{ij} is proportional to the observed relative frequency of interaction events between species i and j in the pool of all interaction events.

Appendix 2

Table S1 - Twenty-two bird species recorded consuming *Euterpe edulis* fruits in the three habitat types in the Cardoso Island during tree-focal, transect, and *ad libitum* observations (Castro 2003, Côrtes 2006).

Species	*Restinga*	Lowland	Pre-montane
Cyanocorax caeruleus	X	X	-
Carpornis cucullata	-	-	X
Procnias nudicollis	X	X	X
Pyroderus scutatus	X	X	X
Aburria jacutinga	-	-	X
Penelope obscura	-	X	X
Penelope superciliaris	X	-	-

Turdus flavipes	X	X	X
Turdus albicollis	X	X	X
Turdus amaurochalinus	X	X	-
Turdus rufiventris	X	X	-
Amazona brasiliensis	-	-	X
Pyrrhura frontalis	-	-	X
Ramphastos dicolorus	X	X	X
Rampahstos vitellinus	X	X	X
Selenidera maculirostris	-	X	X
Trogon viridis	X	X	X
Tachyphonus coronatus	X	X	-
Tangara cyanocephala	-	X	-
Tangara seledon	-	X	X
Pitangus sulphuratus	X	-	-
Tityra cayana	-	X	-

Table S2 - Correlation matrix of the nine intrinsic and extrinsic palm features.

	Palm height	Number of infructescences	Estimate of ripe fruits	Estimate of total fruits	Average canopy height near focal palm	Distance to nearest fruiting palm	Number of fruiting palms	Canopy openness (%)	Distance to nearest gap opening
Palm height	1	0.21	0.39	0.31	0.61	-0.02	0.16	0.43	-0.11
Number of infructesecences	-	1	0.30	0.56	0.04	0.03	0.13	0.28	0.16
Estimate of ripe fruits	-	-	1	0.85	0.13	-0.19	0.34	0.25	0.11
Estimate of total fruits	-	-	-	1	0.13	-0.21	0.39	0.23	0.27
Average canopy height near focal palm	-	-	-	-	1	-0.07	0.09	0.08	-0.17
Distance to nearest fruiting palm	-	-	-	-	-	1	-0.57	-0.07	0.21
Number of fruiting palms	-	-	-	-	-	-	1	0.25	-0.10
Canopy openness (%)	-	-	-	-	-	-	-	1	-0.28
Distance to nearest gap opening	-	-	-	-	-	-	-	-	1

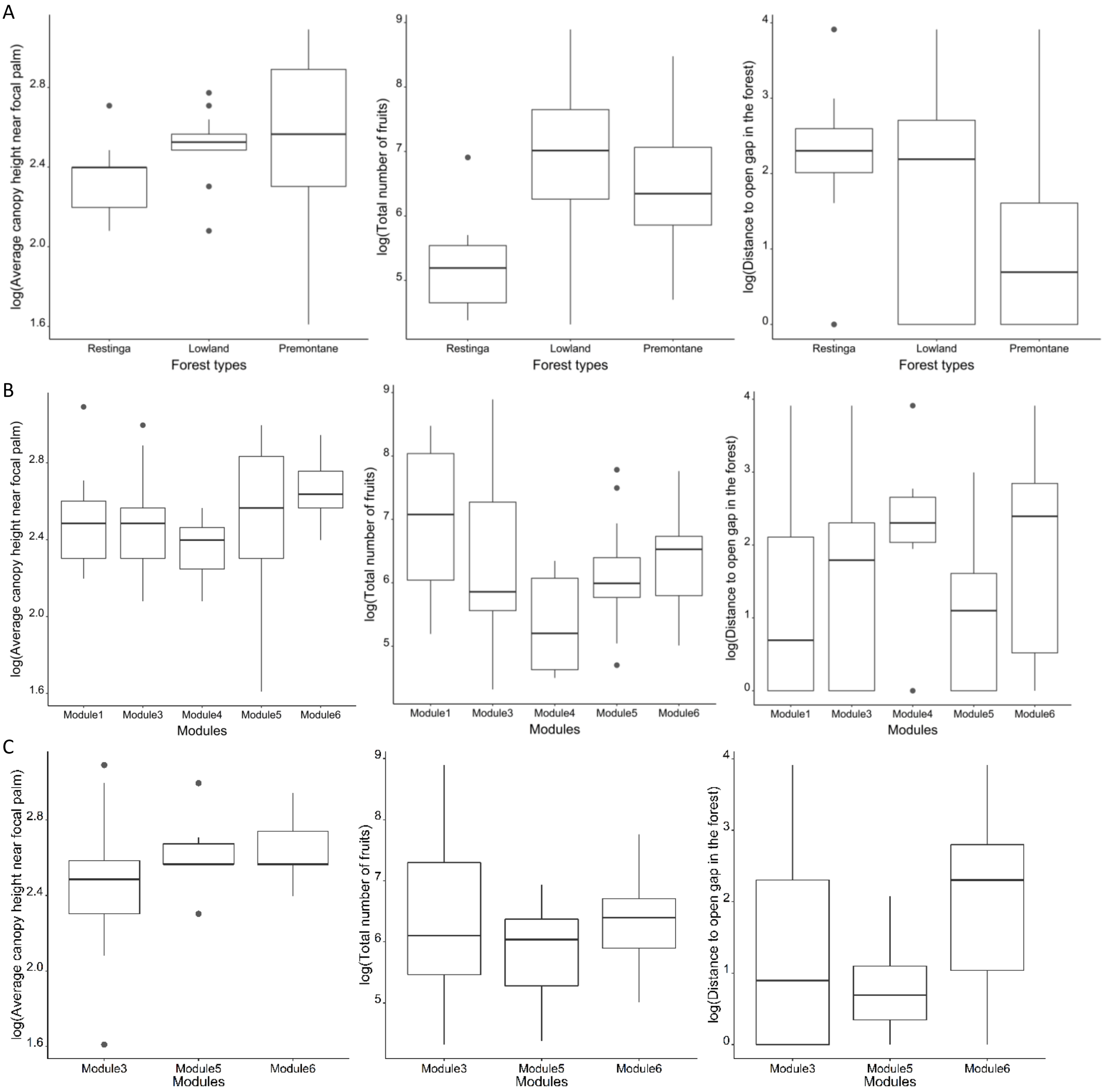

Figure S1 - Variation of canopy height above the focal palm, total number of fruits, and distance to gap opening among (A) habitat types, (B) modules from binary interaction matrix and (C) modules from weighted interaction matrix. Only modules with five or more palm individuals were used in these analyses.

Table S3 – Congruence between modules identified by the optimization algorithms for binary modularity (Q_B) and weighted modularity (Q_D) and those identified based on habitat (Q_{B_H}). Statistically significant (p-value<0.05) combinations (e_{ij}) between habitat-based (matrix **C**) and modularity (matrix **D**) matrices indices are marked with *, meaning that the palm individuals and bird species are assigned to the same modules assuming either habitat-based modularity or modularity based on the optimization algorithms after the 1000 randomization and comparisons.

Modularity algorithm	Habitat-based	M0	M1	M2	M3	M4	M5	M6
Q_B	Restinga	0.07	0.38	0.44	0.87	0.03*	0.99	0.74
	Pre-montane	1	0.54	0.78	0.84	0.9	0.001*	0.9
	Lowland	1	0.90	0.73	0.063	0.8	0.9	0.01*
Q_D	Restinga	0.04*	0.83	1	0.34	1	0.81	0.08
	Pre-montane	1	0.29	< 0.001*	0.93	0.22	1	1
	Lowland	1	0.68	1	0.656	1	0.006*	1

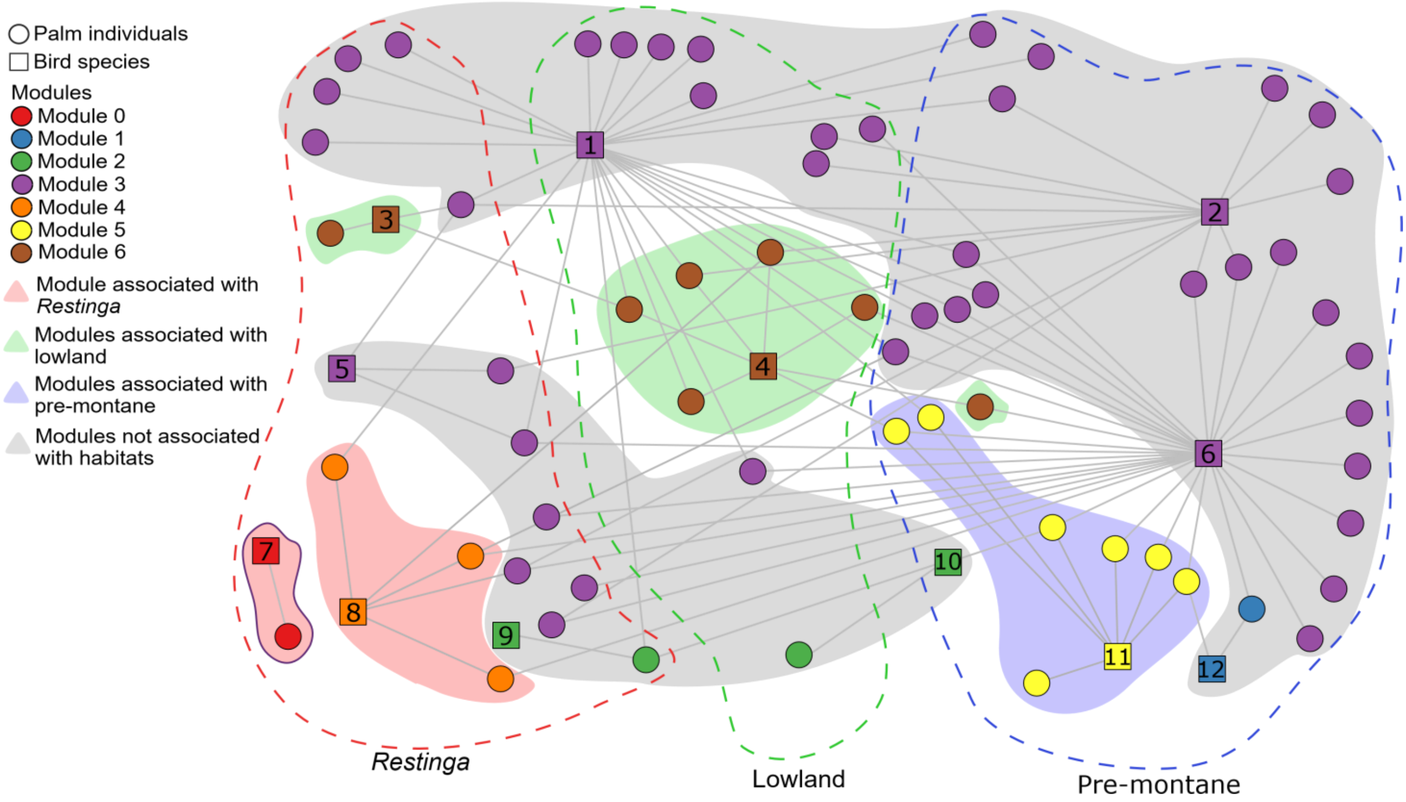

Figure S2 - Modularity found in our observed network across all three habitats using weighted matrix data (number of seeds dispersed). Node colors represent modules resulting from QuanBiMo's algorithm of modularity. The three dashed lines indicate habitat types. Red, green and blue polygons represent the habitat type the modules were associated with it. Numbers inside the squares indicate bird species (1: *Turdus albicollis*, 2: *Procnias nudicollis*, 3: *Cyanocorax caeruleus*, 4: *Ramphastos vitellinus*, 5: *Turdus rufiventris*, 6: *Turdus flavipes*, 7: *Tachyphonus coronatus*, 8: *Trogon viridis*, 9: *Pitangus sulphuratus* , 10: *Pyroderus scutatus*, 11: *Selenidera maculirostris* and 12: *Carpornis cucullata*).

Table S4 – Variance-of-analysis tables of generalized linear models (GLM) evaluating the association of the individual's centrality indices with palm features and habitat type. We used closeness, betweenness and interaction degree as centrality measures. All relationships were not statistically significant (P-value>0.05).

Model	Palm features	Sum squares	F-value	P	df
Closeness ~ Canopy height	Canopy height	0.00000142	0.153	0.697	1
	Residuals	0.00055588			60
Closeness ~ Number of fruits	Number of fruits	0.00000474	0.514	0.476	1
	Residuals	0.00055256			60
Closeness ~ Distance to gap	Distance to gap	0.00001772	1.970	0.165	1
	Residuals	0.00053958			60
Closeness ~ Canopy height + Number of fruits + Distance to gap + Habitat type	Canopy height	0.00000024	0.027	0.870	1
	Number of fruits	0.00002267	2.522	0.118	1
	Distance to gap	0.00000267	0.297	0.588	1
	Habitat types	0.00002601	1.447	0.244	2
	Residuals	0.00050326			56
Betweenness ~ Canopy height	Canopy height	0.000088	0.167	0.684	1
	Residuals	0.031723			60
Betweenness ~ Number of fruits	Number of fruits	0.000001	0.002	0.963	1
	Residuals	0.031810			60
Betweenness ~ Distance to gap	Distance to gap	0.000070	0.133	0.717	1
	Residuals	0.031741			60
Betweenness ~ Canopy height + Number of fruits + Distance to gap + Habitat type	Canopy height	0.0000565	0.100	0.752	1
	Number of fruits	0.0000055	0.010	0.922	1
	Distance to gap	0.0000140	0.025	0.875	1
	Habitat types	0.0001894	0.169	0.845	2
	Residuals				56
Interaction degree ~ Canopy height	Canopy height	0.171	0.241	0.625	1
	Residuals	42.603			60
Interaction degree ~ Number of fruits	Number of fruits	1.232	1.780	0.188	1
	Residuals	41.542			60
Interaction degree ~ Distance to gap	Distance to gap	0.189	0.266	0.608	1
	Residuals	42.585			60
Int. degree ~ Canopy height + Number of fruits + Distance to gap + Habitat type	Canopy height	0.837	1.154	0.287	1
	Number of fruits	1.375	1.896	0.174	1
	Distance to gap	0.107	0.148	0.702	1
	Habitat types	0.041	0.028	0.972	2
	Residuals	40.612			56

Table S5 – Analysis-of-variance tables of the generalized linear model to evaluate if the palm features differed among modules in the binary description (Q_B). Modules with less than 5 palm individuals were removed from analysis. Tests with P<0.05 indicated by (*).

Variance analysis						Mean and SE values of each module			Pair-wise Tukey pos-hoc	
Models	Variable	Sum squares	F	P	df	Modules	Log (Mean)	Log (SE)	Differing modules	P
Canopy height ~ Modules	Modules	0.307	0.987	0.422	4	1	2.50	0.080	-	-
	Residuals	4.118			53	3	2.46	0.067		
						4	2.35	0.114		
						5	2.51	0.067		
						6	2.66	0.114		
Number of fruits ~ Modules	Modules	12.495	2.698	0.040*	4	1	6.99	0.311	4-1	0.026
	Residuals	61.366			53	3	6.14	0.261		
						4	5.34	0.439		
						5	6.06	0.261		
						6	6.36	0.439		
Distance to gap opening ~ Modules	Modules	7.849	1.287	0.287	4	1	1.16	0.356	-	-
	Residuals	80.804			53	3	1.43	0.299		
						4	2.21	0.504		
						5	1.10	0.299		
						6	1.93	0.504		

Table S6 – Analysis-of-variance tables of the generalized linear model to evaluate if the palm features differed among quantitative modules (Q_D). Only included modules with five or more palm individuals.

Models	Variables	Sum squares	F	P	df	Modules	Log (Mean)	Log (SE)
Canopy height ~ Modules	Modules	0.287	1.899	0.160	2	3	2.47	0.043
	Residuals	3.855			51	5	2.62	0.104
						6	2.65	0.104
Number of fruits ~ Modules	Modules	1.678	0.617	0.543	2	3	6.33	0.184
	Residuals	69.301			51	5	5.81	0.441
						6	6.34	0.441
Distance to gap opening ~ Modules	Modules	4.941	1.531	0.226	2	3	1.297	0.201
	Residuals	82.270			51	5	0.809	0.480
						6	1.985	0.480

Table S7 – Analysis-of-variance tables of the generalized linear model analysis evaluating the association of palm features and frequency of interaction

Model	Palm features	Sum squares	F-value	P	df
Frequency of interactions ~ Canopy height	Canopy height	5.635	3.91	0.052	1
	Residuals	86.323			60
Frequency of interactions ~ Number of fruits	Number of fruits	3.265	2.21	0.14	1
	Residuals	88.693			60
Frequency of interactions ~ Distance to gap	Distance to gap	0.694	0.45	0.50	1
	Residuals	91.263			60
Frequency of interactions ~ Canopy height + Number of fruits + Distance to gap + Habitat type	Canopy height	2.398	1.64	0.20	1
	Number of fruits	0.042	0.03	0.86	1
	Distance to gap	0.485	0.33	0.56	1
	Habitat types	3.398	1.16	0.32	2
	Residuals	81.794			56

Chapter 2: Untangling the role of a central avian group in plant-frugivore networks: a case study from genus to populations of *Turdus*

Pâmela Friedemann and Paulo R. Guimarães Jr.

Abstract

The species within an ecological community present a wide range of roles and characteristics. The outcome of these differences may result in a great variation on interaction patterns between species, from species interacting with numerous partners to others interacting with only a few. The highly-connected species may present important key roles in the community in different ecological process, as seed dispersal. Here we explore the role of the *Turdus* genus as potential seed dispersers in 162 plant-frugivore networks around 8 regions of the world. Besides the role of the genus, we also evaluated the variation of the seed disperser role of *Turdus* species and interpopulation. Thrushes species rely differently in fruit as food resource and in different cases they appear as central and important species in seed dispersal interactions. To describe their role in seed dispersal networks we used three centrality measures, which show if the species interact with numerous and/or important partners. The regions presented different number of networks, with South America (*n*= 69) and Eurasia (*n*= 39) presenting more networks. When compared to other bird species, *Turdus* species is, in average, in a more central position in the networks. The species presented a great variation in centrality, then in some networks the species were central while in others they did not appeared in central positions. These results indicate that in general *Turdus* species appear as important and key species in seed dispersal systems, but the highest centrality roles could depend of several other community contexts.

Keywords: seed dispersal; centrality; Thrush; keyspecies

Introduction

A fundamental aspect of ecological interactions is the variability of species in their interaction patterns (Hagen et al. 2012). In an ecological community, one can concurrently observe species engaging with only a limited set of other species (Bolnick et al. 2003; Julliard et al. 2006) and generalist species, whose individuals use a broad range of resources, thereby interacting with numerous other species (Olesen et al. 2007). These generalists serve as highly-connected species, exerting central influence in the structuring interacting assemblages (Guimarães 2020) and potentially influencing system dynamics (Dunne et al. 2002, Palacio et al. 2016). Notably, highly-connected species may diminish coevolutionary events in mutualistic interactions, as the species interacting with them are more likely to undergo evolutionary changes in response, whereas these generalists rarely adapt to their interaction partners (Guimarães et al. 2007; Guimarães et al. 2011). Lastly, highly-connected species may play a crucial role in the reassembly of interactions among organisms within aquatic food webs (Xu et al. 2022).

To explore the interaction patterns of the key species in an ecological community one can use a network approach. A network is composed of nodes, in which each node is a species (or individual, population) and a pair of nodes is connected by a link if they interact (Bascompte 2007). Among the ways of characterizing patterns of interaction of particular species in a network, it is possible to use centrality metrics. If a species presents a higher value of centrality it means that the given species have several interacting partners (Solé and Montoya, 2001) and/or are interacting with (other) highly connected species (Newman 2003, Marchiori and Latora 2000). These type of analytical evaluation aims to identify important nodes may be applied in different ecological systems, as in predator-prey food webs, in which central species appear in different trophic levels from top predators to basal (herbivore) species (Solé and Montoya, 2001). In mutualistic systems, as pollination, central individuals of a plant species that share pollinator species with other individuals may show higher fitness, measured as the number of seeds produced (Arroyo-Correa et al. 2021). Thus, the well-connected species and individuals in communities may appear as key organisms for evolutionary dynamics, since, through interactions, they can exert pressure on other organisms and may benefit in resources consume over time.

The pattern of species interaction may be partially associated with the evolutionary history of interacting species (Rezende et al. 2007, Gómez et al. 2010), in which more related species may present similar patterns of interactions. For example, in a plant-pollinator system, phylogenetic related plant species with similar morphological characteristics attract similar pollinators community, so this way it is possible to identify plant species that are more likely to share a set of pollinators in different scenarios as climate change (Rafferty and Ives 2013). In seed dispersal systems, closely related frugivores that present similar traits may interact with more similar plant species, while distantly related frugivores with distinct traits exhibit less overlap in resource use (Pigot et al. 2016). To advance the understanding of the overall ecological role of a clades, species and populations is necessary to explore how these different levels of evolutionary organization are interacting in their respective ecological contexts (Fig. 1).

In seed dispersal interaction networks the keystone species may present central positions and are usually the species that are strongly frugivores, largely depending on fruits as food resources (Mello et al. 2015). The most common seed disperser agents are birds, which present a lot of variation on the way they consume fruits and disperse seeds. Among birds as seed dispersers, there are only a small number of taxonomic families which are described as strongly frugivorous. For example, only 29 of 194 families (14.9%) are heavily relying upon fruits (>90% their diets are fruits, source: Elton Traits database, Wilman et al. 2014). Hence, in plant-frugivore interactions, most of the bird species involved in these systems will not be strongly frugivorous and, in some cases, the most connected species present a diet relying on invertebrates, fruits, seed and other resources. Among the most conspicuous representatives of the frugivore coterie are the thrushes (*Turdus* spp.), widely distributed clades of birds.

Birds from the Turdidae family appear as key species in different seed dispersal networks around the world (Côrtes et al. 2009, Breitbach et al. 2012, Burns 2012), even if the diet of most *Turdus* species rely more upon invertebrate consumption. In the Atlantic Forest, *Turdus* species are the main seed dispersers of several plant species, such as *Eugenia umbelliflora* (Myrtaceae) (Côrtes et al. 2009). In temperate regions, *Turdus merula* is generally a key species and it may appear as an efficient seed disperser, since in addition to consuming fruits from several plants, they also deposit their seeds in places that are suitable for seedling recruitment (Breitbach et al. 2012).

In this study, our aim is to understand how the role of species varies across different scales, from the general role of one genus to different populations of a given species, using as an example a conspicuous group of frugivores, the *Turdus* genus. Our questions and predictions are: 1) Do the different levels of *Turdus* taxonomy (genus, species, and populations) vary in centrality positions? Since the species vary in key traits (i.e., frugivory degree, migratory or sedentary, aggressive territorial behavior, and others) we expect that some species will appear as key species in their networks, while others may appear as peripherals (Fig. 1B). We also expect interpopulation variation in centrality, since populations of the same species will experience different ecological contexts (Thompson 2005), but we expect that populations of highly central species generally will appear as above the average in their centrality values (Fig. 1C). 2) Does the frugivory degree and body size of *Turdus* species predict their positions in the networks? We expect that species that have a higher frugivory degree could be at central positions in networks, as they would eventually use a greater diversity of fruits than species which do not rely as much on fruits. Regarding the body size, we expect that species in which individuals are larger could be at more central positions, since their larger size would allow them to consume a wider range of fruit sizes and, consequently, more species. 3) Do phylogenetically related species present similar roles in the network? We predict that closer related species could be at similar positions in the networks, since they probably would have similar body size and frugivory degree as well as other traits. To answer our questions, we gathered plant-frugivore networks that contained at least one *Turdus* species from several parts of the world.

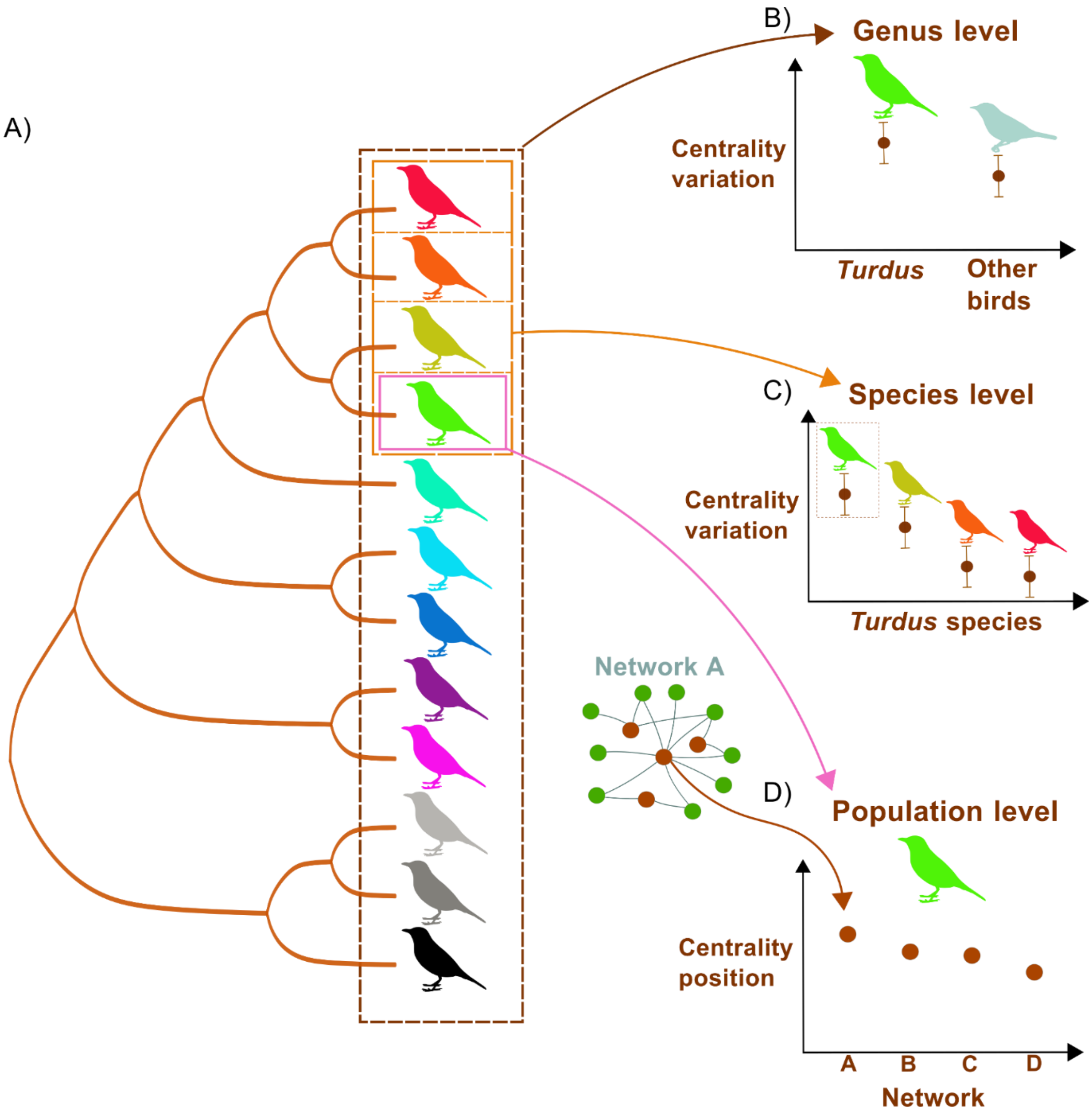

Figure 1 – Conceptual representation of the ecological role across a gradient of organizational levels from the genus to populations of *Turdus* birds within networks of plants and their frugivores. (A) Depiction of a phylogenetic tree illustrating the species relationships (note that this tree serves as a visual aid and does not represent any specific phylogenetic hypothesis). (B) Assessment of the central position of the *Turdus* genus in comparison to other bird species within plant-frugivore networks. If a particular bird species exhibits a high central position, it indicates interactions with multiple plants, wherein their partners also engage in numerous interactions, or the bird species participates in multiple indirect pathways. (C) Examination of the variation in central position among different *Turdus* species. (D) Exploration of central position variations within different populations of a given species. The description of centrality provides a characterization of the nodes' role within the networks.

Material and methods

Study areas

We used 162 plant-frugivore networks worldwide that had at least one *Turdus* species. Since our focus was on bird dispersing plant species, we excluded all other taxa (e.g. mammals, fish, and reptiles) and their exclusive plant interaction partners. The networks were found in networks repositories as Interaction Web Database (http://www.ecologia.ib.usp.br/iwdb), from the data set assembled by Fricke and Svenning 2020 and by web searches. Given the interaction data set used here there was 6471 entries that represent species, genus, morphotypes or unidentified groups, including repeated species across networks. Accounting for all distinct identification levels, 3488 bird and 2983 plant entries were registered. Each entry refers to a row or column depicting a species (or genus, morphotype, etc) in a matrix describing local patterns of interaction. The number of plants and birds per network varied from data sets presenting from 3 to 180 plant species, and 3 to 112 bird species. The data were from 29 different countries from 87 different authors. Some of the authors had more than one network in the data set, in which they registered the plant-frugivore interactions in different sites. The interactions that were collected in the same site, but in different seasons, were merged in the same interaction matrix for this study. The data set included plant-frugivore networks from all continents but Antarctica (Fig. 1S, Supplementary Information) and were distributed as follows: South America (n= 69 networks), Europe (n= 39), Africa (n= 18), Oceania (n= 16), North America (n= 8), Asia (n= 6) and Central America (n= 6).

The genus *Turdus*

According to the Handbook of Birds of the World database the Turdidae family enclose 17 genera and 175 species (Winkler et al. 2020). Almost half of the Turdidae's species belong to the *Turdus* genus, with 86 species. Thrushes (*Turdus* spp.) are long-bodied, strong-legged birds that are comfortable inhabiting the ground, where they often hop after buried invertebrate prey (Winkler et al. 2020). The diet of *Turdus* species includes a wide variety of invertebrates and various small fruits. During the winter months, fruit becomes an especially important food item for species wintering in temperate regions (Winkler et al. 2020). Thrushes may be registered in several types of habitat from dense forests to grasslands and urbanized areas (Gasperin and Pizo 2009, Evan et al. 2010). Habitat destruction by anthropic action is one of the major threats to some species, as *Turdus helleri* which inhabit a few forest fragments in Kenya and *Turdus swalesi* that is restricted to Dominican Republic and Haiti (McFarland et al. 2020).

Interacting *Turdus* species in the networks

We described the interactions between plant and bird species as a rectangular matrix, in which each row depicts a recorded plant species and each column depicts a record bird species. All matrices were binary, so the elements represent the presence or absence of interactions between plant and bird species. In the networks, the nodes (or vertices) represent the plant and bird species, and the edges (or links) represent the interactions between a pair of species. Since the plant species richness substantially varied between networks (n= 3 to 180 plant species), we log transformed the values to perform the analysis. The same was done to the bird richness (n= 3 to 112 birds).

A total of 342 *Turdus* entries were recorded in all networks, which is the sum of all records describing the presence of a *Turdus* species in a network. It was registered a total of 36 thrush species and two other entries of unidentified *Turdus* species in our dataset. From all bird species, the species mostly recorded across the networks were: *Turdus merula* (n= appearing in 54 different networks) and *Turdus philomelos* (n=45), followed by *Sylvia atricapilla* (n=38), *Erithacus rubecula* (n=37), *Thraupis sayaca* (n=37), *Sylvia borin* (n=34), and *Turdus rufiventris* (n=29). From all plants, the most common species were *Sambucus nigra* (n=24) from Adoxaceae family, and three representants of Rosaceae family: *Sorbus aucuparia* (n=23), *Crataegus monogyna* (n=21) and *Prunus padus* (n=18). It is noteworthy that from the 342 entries across 34 *Turdus* species, three species represented 38% of all entries (*T. merula*, *T. philomelos* and *T. rufiventris*).

Role of *Turdus* in the interaction networks

To assess the importance of the *Turdus* species to the network structure we used three network measures: (1) interaction degree, which is the number of interactions each node (bird or plant) has in the network. We standardized the degree by dividing the sums of the number of interaction per node by the plant richness in the network (equation 1 SI); (2) the harmonic centrality, which is a version of closeness centrality to deal with unconnected networks, it is the mean of the reciprocal of the pairwise distance of a given node to all other vertices and indicate how close a node is to all other nodes in the network (equation 2 SI, Golbeck 2013, Newman 2003, Marchiori and Latora 2000). Biologically, high harmonic centrality implies that there are short indirect pathways connecting the focal species to all other species in the network and (3) the Katz centrality, that indicates the influence of the nodes combining the direct and indirect interactions, in which the shorter path lengths are more valued than longer paths (equation 3 SI, Katz 1953). There is a key parameter, α , for Katz centrality that controls the impact of long pathways on the centrality value: the higher the α , the higher the contribution of long pathways. To compute the Katz centrality, we set α= 0.05 and we built a square adjacency matrix (with both animal and plant species in rows and columns) that was normalized by dividing each cell value by the total row sum. Biologically, high Katz centrality values imply that the focal species is connected to other species in the network due to a combination of direct and/or indirect pathways (Guimarães et al. 2017, Maia et al. 2019). The values of bird's interaction degree, harmonic centrality and Katz centrality were also log transformed to reduce the skewedness of the distributions.

We used the resembling bootstrap of the log transformed values of interaction degree, harmonic centrality and Katz centrality to calculate the average per species. Then we compute the relationship of the centrality average of the 36 *Turdus* species with the species median weight and frugivory degree. The species median weight (in grams) was log transformed and varied between 47g and 130g (mean= 77.19g, SD=18.55). Frugivory degree was characterized as the proportion of the diet was transformed by using the logit transformation (Warton and Hui 2011). To compare how the log transformed of the *Turdus* entries' centralities varied between these regions we used the rank-based Kruskal–Wallis test. We then and used a post-hoc test with the Holm-Šidák adjustment as the family-wise error rate.

For each network we calculated the z-scores for all bird and plant species for three the centrality measures, which describes if the organism is above or below the network average for that given measure. In analysis to evaluate the role of species that occurred in more than one network (28 of 36 species, 78% all *Turdus* species) we averaged z-score centrality measure across all networks the species were present. We used the z-scores to perform a Mann-Wilcoxon test aiming to evaluate if *Turdus* species consistently show higher centrality z-score values than other bird species in our data set. We separated the networks in 7 regions: African (n= 18 networks), Eurasian (n= 39), North American (n= 7), New Zealand (n= 16), Oriental (n= 6), Panamanian (n= 7) and South American (n= 69).

We tested if *Turdus* species are more predictable (i.e., show lower variance) in their role as central species than other bird species. To do so, we compared the variance of the centralities between *Turdus* species and other bird species. We used only networks that had three or more *Turdus* species. To investigate if the observed variance in the centralities of co-occurring *Turdus* species was smaller than expected for a randomly sample of local bird species, we used the following algorithm: (1) randomly sampled *n* species, in which *n* is the number of observed *Turdus* species in the network; (2) compute the variance of the centrality measures of the random sample; (3) repeated 1000 times procedures 1 and 2; (4) for each centrality measure, we counted how many times the variance of the randomly selected sample of species was higher than the *Turdus* species in that given network. In total there was 45 different networks with at least 3 *Turdus* species registered interacting with plants, from the following regions: South America (*n*= 24), Eurasia (*n*= 19), Panamanian (*n*= 1) and Oriental (*n*= 1).

Next, we explored if the centrality of *Turdus* species were consistent across networks. We tested if *Turdus* species present less variation in central position across networks than expected by chance. To do so, we used the following algorithm: (1) we identified *Turdus* species that appear in at least four different networks (n= 20 *Turdus* species and 312 entries in total); (2) for each species, we computed the variance in the centrality measures across networks in which the species were present; (3) randomly sampled *m* entries (records of *Turdus* species in a network) across all records of species identified in step (1); (4) compute the variance of the random sample; (5) repeated 1000 times the procedures 3 and 4; (5) varied *m* = [4, 5, 6… to 54] to reproduce the number of records in networks observed for *Turdus* species; (6) compare the empirical variances of the species identified in steps 1 and 2 with the confidence intervals generating by the randomization procedure (steps 3 to 5). The randomization procedure generates the expected variance in the centrality measures for a species assuming there is no consistency in the centrality of a given *Turdus* species, i.e., the variation in intraspecific variation in centrality is similar to the inter-specific variation in centrality.

We used Moran autocorrelation index to quantify whether the proportion of fruits in diet and the distribution of a centrality trait among a set of species is associated or not by their phylogenetic relationships (Moran 1950, Gittleman & Kot 1990). Here we used the centrality measures of *Turdus* species as traits to evaluate if more phylogenetically related *Turdus* species present a similar average position in the networks. Moran index was run 50 times and each time it was selected a random phylogenetic tree out of 1000 trees. The index was calculated in R software, with *Moran.I* function of the “ape” package and the output of this function includes the observed and the expected Moran index, the standard deviation of the index and the p-value of the test. When the observed index is significantly greater than the expected, then the values of *x* are positively autocorrelated, and vice-versa. To calculate the phylogenetic signal, we first select the model that better describes the data among three evolutionary models: Early-burst, Ornstein-Uhlenbeck and Brownian motion models. Used the function “fitContinuous” from “geiger” package, that fits macroevolutionary models to phylogenetic trees, then it extracted the AIC values to evaluate the differences results among the models.

Results

Variation in traits across *Turdus* species

Turdus species varied on the body size and the proportion of frugivory on diet. The species median weight showed almost three-fold variation across *Turdus* species, between 47g and 130g. Four species have 20% of their diet composed of fruits (e.g., *T. merula*, *T. pallidus*). Eighteen species consume fruits between 30% and 40% (e.g., *T. albicollis*, *T. leucomelas*). Twelve species present around 50% and 60% of fruits in their diet (e.g., *T. amaurochalinus*, *T. subalaris*). *T. flavipes* has 80% and *T. serranus* has 100% of fruits composing their diet (Wilman et al. 2014, Collar 2020, Collar et al. 2020a). Thus, most of the species that rely less than 50% of their diet on fruits forage on the ground for earthworms and other invertebrates (Fig. 2S, Collar et al. 2020b).

Turdus species, on average, were more central species than other birds in the networks (Fig. 3S). The comparison of the z-scores of the *Turdus* species and all other birds showed *Turdus* species presented higher z-score of the centrality measures than other bird species in the given network for interaction degree (W = 390.898, $p < 0.0001$), harmonic centrality (W = 407.484, $p < 0.0001$) and Katz centrality (W = 392.864, $p < 0.0001$). In general, we found no association between the three centrality metrics and the frugivory proportion and weight of *Turdus* species. Only species weight has a negative relationship with harmonic centrality (Table 1), indicating, contrary to our expectations, that the larger the *Turdus* species, the less central the species is (for harmonic centrality).

Table 1 – Estimates of the linear regressions testing the relationship of *Turdus* species weight and fruit proportion on diet with three centrality metrics (interaction degree, harmonic centrality and Katz centrality). Only one relationship is significant (bold). We used the average of the log (centrality measures) for each species as response variable, and the log (weight) and the logit (fruit proportion) as predictor variables.

Model	Coefficients	Estimate	Std. Error	t value	*F*- stat	df	*p*
log (average interaction degree) ~ logit (fruit proportion)	Intercept	1.342	0.114	11.73	-	34	$2.58e^{-13}$
	Fruit proportion	-0.017	0.124	-0.14	0.019	34	0.889
log (average interaction degree) ~ log (weight median)	Intercept	2.033	1.945	1.045	-	34	0.303
	Weight median	-0.166	0.447	-0.371	0.137	34	0.713
log (average harmonic centrality) ~ logit (fruit proportion)	Intercept	3.00	0.074	40.41	-	34	$<2e^{-16}$
	Fruit proportion	0.137	0.079	1.732	2.516	34	0.092
log (average harmonic centrality) ~ log (weight median)	Intercept	5.763	1.184	4.867	-	34	$2.55e^{-05}$
	Weight median	**-0.646**	**0.272**	**-2.375**	**5.638**	**34**	**0.023**
log (average Katz centrality) ~ logit (fruit proportion)	Intercept	1.283	0.050	25.63	-	33	$2\ e^{-16}$
	Fruit proportion	-0.006	0.053	-0.13	0.284	33	0.897
log (average Katz centrality) ~ log (weight median)	Intercept	1.043	0.846	1.232	-	33	0.226
	Weight median	0.122	0.448	0.272	0.074	34	0.788

Network characteristics and centrality measures

Among the 162 networks the average of total number of species was 39.9 (SD =30.3). The mean number of bird species was 21.5 (SD=16.3) and plant species = 18.4 (SD=18.2). The network with the largest specie richness was from South America and accounted with 268 species (88 birds and 180 plants). The networks with the smallest richness of birds and plants were from South America (n= 5 birds and n= 4 plants), Eurasian (n= 7 birds and n= 3 plants) and Africa (n= 5 birds and n= 5 plants). The regions varied in the number of *Turdus* representants: African (n= 4 species), Eurasian (n= 6), North American (n= 2), New Zealand (n= 2), Oriental (n= 6), Panamanian (n= 5), and South American (n= 14 and two unidentified). The average of number of interactions per region varied: South America (mean= 4.59, SD= 5.53), Eurasian (mean= 4.17, SD= 3.86), African (mean= 4.54, SD= 4.52), North American (mean= 3.86, SD= 3.94), New Zealand (mean= 3.31, SD= 3.24), Oriental (mean= 6.63, SD= 7.33) and Panamanian (mean= 4.03, SD= 5.16).

The centrality measures of *Turdus* presented a large variation across all the regions and the difference between the 7 regions was weak (Figure 4S). Interaction degree (KW= 9.4967, df = 6, p= 0.1475) did not present any differences among regions. The harmonic centrality (KW= 65.257, df = 6, $p < 0.001$) of New Zealand were smaller than South America, Oriental, African, Panamanian and

Eurasian regions and also South American was higher Eurasian. For Katz centrality (KW= 15.987, df = 6, *p*= 0.01382), the New Zealand region was marginally higher than Oriental region.

The *Turdus* species vary in centrality, so we had *Turdus* presenting negative to positive z-score values of the centrality across all the networks, which was similar to the variation presented by the other bird species (Fig. 5S). Regarding the centrality variation between *Turdus* entries, we had almost half of entries above the average of centrality in the given networks. In more detail, considering the z-scores of the interaction degree of the 342 *Turdus* registered across all networks, we had that more than half (*n*= 174 entries) were higher than the average for the networks (z-score > 0), with the rest of the entries (*n*= 168) presenting z-score lower than 0. However, it is important to notice that the number of records are uneven distributed across species. Three species represent almost 50% of the records for z-score above the average (46 *T. merula*, 23 *T. philomelos* and 15 *T. rufiventris*), and the majority of *Turdus* species show negative z-scores. The harmonic centrality followed the same relationship (z-score > 0 = 212 entries, z-score < 0 = 130) with four species representing more than 50% for z-score above the average (47 *T. merula*, 26 *T. philomelos*, 18 *T. leucomelas* and 18 *T. rufiventris*). Katz centrality followed the interaction degree numbers, with 174 *Turdus* entries with z-score higher than 0 and 168 entries lower than 0 and with three species representing almost half of entries above the average (45 *T. merula*, 23 *T. philomelos* and 15 *T. rufiventris*, Fig. 6S).

We then compared the variance of the centralities between *Turdus* species and other birds for networks that presented three or more *Turdus* species. In some networks more than one species of *Turdus* were present (the maximum was six *Turdus* species in the same network, mean= 2.1 ± SD= 1.23). In total, 62 networks presented 1 *Turdus* species, 55 networks presented 2 *Turdus* species, 24 networks had 3 species, 12 networks had 4 species, 4 networks presented 5 species, and 5 networks had 6 *Turdus* species. Most of the comparisons of networks with three or more *Turdus* species did not show any significant differences between the centrality variance of randomly sampled bird records with *Turdus* variance. This means that, in general, co-occurring *Turdus* species were not more consistent than other bird species in their central position. Only in a few cases (8 networks, 6 from South America and 2 in Eurasia) there was a significant difference, in which the random variance of other bird was significantly smaller than *Turdus* variance. This means that, in these cases, other bird species were more predictable (presented lower variance) in their central roles than *Turdus* species (Tab. 1S).

Regarding the analysis among *Turdus* species only, the simulated variance of centralities tended to decrease when the number of *Turdus* entries selected in the simulation was higher (an expected consequence of increasing the number of records). The comparison of the simulated variance of *Turdus* species with the actual centralities' variance within *Turdus* species showed that the patterns of variance in centrality vary depending on the centrality metric evaluated (Fig. 7S). For interaction degree, three species *(T. pelios*, *T. olivaceus* and *T. leucomelas*) presented the actual variance higher than the random simulated variance. For harmonic centrality, six species (*T. fuscater, T. flavipes, T. albicollis, T. leucomelas, T, amaurochalinus* and *T. rufiventris*) presented an actual higher variance that the simulated variance. Lastly, for Katz centrality, three species (*T. albicollis, T. leucomelas* and *T. rufiventris*) presented an actual higher variance than simulated variance. Since the majority of the species presented less variation in centrality in their given networks than expected by chance for the genus, it seems that most of the species of *Turdus* are predictable regarding their central role in plant-frugivore networks. However, species who presented high variance when compared to the simulated variance for the whole *Turdus* genus seems to play a wide range of roles, which could be an outcome that depends of the ecological community context.

In general, the highest averages for the centrality measures of *Turdus* species occurred in networks with intermediate number of plants (between 15 and 50 plants), but the *Turdus* entries showed a lot of variation in centrality, in which for a similar number of plants species, the entries presented central and non-central positions. *Turdus pelios,* for example, presented the highest centrality in an entry that was in the most species-richer network (25 plants and 48 birds). Meanwhile, the other five entries were in a similar network regarding plant species richness (7 or 8 plant), but presented from high to low centrality positions in the given networks.

The Pearson's correlation between the number of plants and the average of the centrality measure considering all bird species for each network indicated that the greater the number of plant species in the network, the greater the average interaction degree for birds in the network (r= 0.65, p= $2.2e^{-16}$, t= 10.93, df= 160, CI= [0.55, 0.73]). Similarly, the same pattern was observed for the harmonic centrality measure (r= 0.74, p= $2.2e^{-16}$, t= 14.11, df= 160, CI= [0.66, 0.80]) and for Katz centrality (r= 0.48, p = $4.443e^{-11}$, t= 7.07, df= 160, CI= [0.36, 0.59]). We also computed Pearson's correlation between the 20 *Turdus* species centrality measures values and the plant richness of the networks where the species occurred. Here it was computed only the *Turdus* species that were registered at least in 4 different networks. We found that the greater the plant richness in the network, the greater the average interaction degree of *Turdus* species in the given networks (r= 0.44, t = 8.6414, df = 310, p= $3.005e^{-16}$, CI= [0.34, 0.53]) and an even stronger positive relationship was observed for harmonic centrality (r= 0.71, t = 17.835, df = 310, p= $2.2e^{-16}$, CI= [0.65, 0.76]). Katz centrality followed the same positive relationship (r= 0.31, t = 5.8455, df = 310, p= $1.279e^{-08}$, CI= [0.21, 0.41]). A similar pattern was found by using z-scores of the centrality measures: z-scores of interaction degree (r= 0.36, t = 6.9557, df = 310, p= $2.087e^{-11}$, CI= [0.26, 0.46]) and harmonic centrality (r= 0.23, t = 4.1796, df = 310, p = $3.803e^{-05}$, CI= [0.12, 0.33]) were higher in networks more rich in plants, and Katz centrality only showed a weak tendency (r= 0.11, t = 1.9439, df = 310, p= 0.05281, CI= [-0.001, 0.22]). When calculating the relationship between the richness of all birds and the average of the centrality measures considering all bird species in the given networks, the harmonic centrality was strongly positively correlated (Tab. 2S), meanwhile interaction degree was weaker positively correlated; Katz centrality was negatively correlated. Accordingly, when considering the richness of bird species in the network and the average of the centrality value only for *Turdus* species in the given networks, the relationships were similar: the harmonic centrality was strongly positively correlated, interaction degree was positively correlated and Katz centrality tended to be negatively correlated (Tab. 2S).

The Moran index indicated that there is no pattern of higher similarity for species that are closer related across centrality measures (Tab. 3S). Consequently, phylogenetically related species did not exhibit similar roles in the networks regarding the centrality. This trend it was also mapped on the absence of the relationship of phylogeny and frugivory degree. Our findings indicated an absence of phylogenetic signal concerning the proportion of fruits in the diet, implying that closely related species did not demonstrate a similar proportion of fruit consumption in their diets. Then, regarding these two variables, *Turdus* species presented centrality and frugivory degree values less similar than the expected Brownian motion, since the major observed Moran index values were smaller than zero (Tab. 3S, Fig. 8S).

Discussion

In ecological communities are comprised by the collection of species, each assuming diverse ecological roles within the ecosystem, and by the biological interactions established among these species. From the perspective of ecological interactions, species described as central may be a crucial component that connect the community (Olesen 2007, Guimarães et al. 2011). The presence of such central species is especially important in an extinction scenario, wherein the ecological functionality of the species is lost long before the species begins to disappear (Säterberg et al. 2013, Dirzo et al. 2014). Identifying species that play a pivotal biological role within communities is essential, particularly in a context where species significantly influence ecological processes within an ecosystem through interactions, such as seed dispersal. We used several plant-frugivore networks to assess the distinct ecological roles of the *Turdus* clade around the world. Our results emphasize three components that need to be explored when evaluating the ecological role of one clade of species.

First, in various contexts certain groups of species play a crucial ecological role, which may result from their well-connected characteristics in biological networks. Around the world, *Turdus* species emerge as an important seed disperser in disparate regions as Atlantic rainforest in Brazil (Côrtes et al. 2009), Mediterranean shrubland in Chile (Uriarte et al 2011), coniferous forest in New Zealand (Burns 2012), in Germany (Breitbach et al. 2010), in western Mediterranean Spain (Isla et al.

2023). At the genus level, we observed that on average *Turdus* occupies central positions when compared to other groups of birds in plant-frugivore networks. However, this centrality pattern was not directly associated with the two traits that we tested here, which are commonly linked to central and key positions in networks, frugivory degree (Mello et al. 2015, Sebastián-González 2017) and species size (Woodward and Hildrew 2002, Vidal et al. 2013, Genes et al. 2022). Regarding frugivory degree, we had species relying on fruits in different proportion occupying different central position across the networks. Accordingly, no association between centrality and species body size was found; thus, species of different sizes occupied distinct positions. Given that none of these traits appears to predict the ecological role of *Turdus* in these networks, it is possible that these traits alone are not robust enough to explain the position of these bird species within the networks. Other attributes and traits may influence their ecological roles. In addition to variations in diet and body size, *Turdus* species also exhibit considerable diversity in foraging behavior. One aspect that may influence the potential role of a given species within a community is their movement in scenarios of forest cover and fruit abundance. Certain *Turdus* species, such as *T. iliacus* and *T. philomelos*, exhibit a gradual increase in movement, while *T. merula* demonstrates a rapid increase in movement when fruit abundance begins to rise (Morales et al. 2013). Species capable of greater movement across diverse landscapes may explore various ecological contexts, potentially leading to interactions with a wide range of plants. In contrast, other species may be more specialized in the use of resource (such as food and habitat), playing a more specific role on a smaller spatial scale.

Second, variation on interaction patterns may be an important component on the emergence of biological patterns (Butler 1989, Levin 1992, Benedetti-Cecchi 2003). The variation in patterns of ecological interactions may be an outcome of species traits, which could result from the effects of changes in temporal and spatial scales (Butler 1989). The findings regarding the variation of *Turdus'* roles in different networks are in accordance with other studies that described how their ecological role differ in distinct seed dispersal systems (Gasperin et al. 2009). The generalist habits in several biological features seem to allow *Turdus* to adapt very well in several ecological contexts and explore with efficiency the necessary biotic and abiotic resources. Thus, different species of *Turdus* seem to provide different functions to seed dispersal and these responses may present a pattern of complementary in the ecosystem, with species presenting different efficiency in seed dispersal depending the ecological context, such as the forest cover amount and the species sensitiveness on using and exploring less preserved localities (Morales et al. 2013). We observed that, in general, the highest averages for centrality measures occurred in networks with an intermediate size (in terms of the number of plant species), ranging between 15 and 50 plants. However, the different datasets exhibited considerable variation, thus for a similar richness of plants, *Turdus* was positioned very centrally in some instances, while in others, it occupied much less central positions.

Third, when a species exhibits populations distributed across multiple localities, it is plausible that variations in environmental conditions and community composition may impact how species influence one another. This aligns with the postulates of the Geographic Mosaic Theory (Thompson, 2005). Zooming in to the variation of centrality within species recorded in different networks we also observed a great quantity of variation on the centrality position for all species. Concerning the variance of the 20 *Turdus* species in comparison to simulated variance, aimed at assessing the predictability of different species, our study revealed that the majority of *Turdus* species exhibited lower variance in centrality within the networks than anticipated by chance (random *Turdus* species). Only eight species demonstrated higher variance across all three centrality measures in the networks - two from Africa and six from South America. Consequently, these eight species appear to be less predictable due to significant variations in their central positions. *Turdus merula* was the species most registered in distinct networks and because of this higher number of occurrences in different studies is an interesting species to evaluate regarding its role as seed disperser. *T. merula* presented a smaller variation on centrality, which may be an outcome from the higher number of networks with this given species, which allowed a more complete description of the network average position of *T. merula* in plant-frugivore systems. The central position of *T. merula* regarding the number of direct interactions and partners, may be associated with the efficiency of this species on exploring their territories and other bird territories looking for food (Snow 1956). *Turdus philomelos* was another species that occurs in a high number of different networks, but the species was not as central as *T. merula* and is described as being a species that is a good fruit tracker, at least in a Mediterranean wintering context (Rey 1995, Tellería et al. 2008), and this characteristic is attributed especially due to their migrant status (Tellería et al. 2014). The variation in centrality within species could be linked to geographic variations among populations or intrinsic characteristics of the populations, an aspect that cannot be precisely assessed due to the unavailability of readily accessible information at this level of detail. Furthermore, it may be associated with the features of the environment in which they interact with plants.

One noteworthy aspect is the variation in the number of studies conducted across the seven regions, with a higher prevalence in South America and Europe. Also, it is worth noting that less than half of the species within the genus *Turdus*, which comprises 86 species, have been recorded in our dataset. This may also be associated with significant regional data gaps regarding fruit consumption by birds worldwide. These discrepancies are likely influenced by data availability and historical research interests in studying plant-frugivore interactions in specific regions. To gain a comprehensive understanding of the general seed dispersal role within a clade, it is crucial to incorporate as much information as possible. For *Turdus* species in South America, where more than 15 studies are available for certain species (such as *T. rufiventris*, *T. amaurochalinus*, *T. leucomelas* and *T. albicollis*), it is feasible to infer the characteristics that might influence their overall ecological role in these networks. Almost all *Turdus* species in South America exhibit versatility in inhabiting various landscapes, ranging from well-preserved forests to disturbed areas (Billerman et al. 2022). This adaptability to diverse habitat types may allow them to assume distinct roles within plant-frugivore networks.

Numerous components can influence species interactions, spanning from environmental characteristics to competition for resources among species and individuals. Understanding the drivers of variation in the ecological roles played by different species is crucial for advancing knowledge about processes that can alter species interactions patterns. While we observed a tendency for *Turdus* species to generally occupy central positions in communities with higher plant richness, the substantial variation within the species implies that other components are equally important. The pronounced generalism observed in *Turdus* species regarding diet, behavior, and habitat occupancy may be a pivotal factor enabling them to occupy significant positions within these networks. Identifying the variables that influence the role of *Turdus* species in plant-frugivore networks is particularly crucial in the context of human-induced land changes. A more in-depth understanding of this bird group can aid in pinpointing species that could serve as key species in conservation and/or restoration efforts for natural habitats. The adaptability of the *Turdus* clade to various habitat types, ranging from well-preserved natural habitats to heavily anthropized areas, coupled with their generalist diet and behavior, could be significant in such initiatives.

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Supplementary material

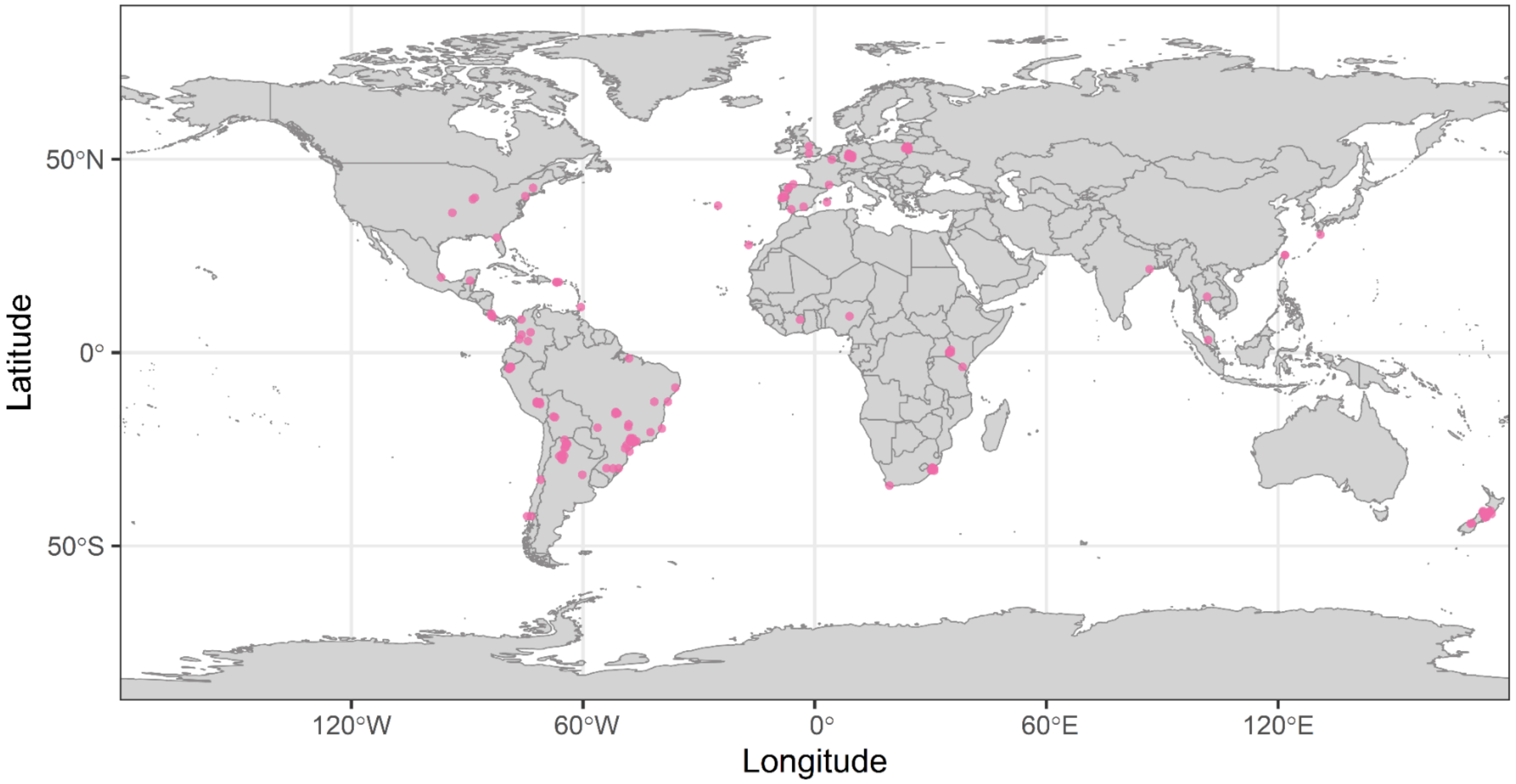


Figure S1 - Data set distribution that included 162 plant-frugivore networks worldwide with at least one *Turdus* species. The data set include networks from seven different regions: South America (n= 69 networks), Europe (n= 39), Africa (n=18), Oceania (n =16), North America (n= 8), Asia (n= 6) and Central America (n= 6).

Centrality measures

Interaction degree: number of interactions of one node (birds or plants) in the given network. Here we divided the number of interactions of birds by the number of plant species in the given networks.

$$A_i = \frac{\sum_{j=1} a_{ij}}{r_p} \qquad \text{Equation 1}$$

A*i* is total number of interactions of bird *i* with plants (a_{ij}) divided by the plant richness (r_p) in the given networks.

Harmonic centrality: measure how close a node is to all other nodes in the network.

$$H_i = \sum_{i \neq j} \frac{1}{\mathrm{dist}(x_i, x_j)} \qquad \text{Equation 2}$$

H is the sum of the reciprocals of the distances (dist) of two given nodes x_i and x_j. If there is no direct or indirect path connecting the two nodes (i.e., the nodes are in different network components) the dist (x_i , x_j) →∞ and therefore 1/ dist (x_i , x_j) → 0.

Katz centrality: measure the influence of the nodes combining the direct and indirect interactions.

$$K_i = I - \left(\frac{1}{\lambda + \alpha}\right) A \qquad \text{Equation 3}$$

In which, K_i is the Katz centrality value of each node. *I* is the identity matrix, λ is the leading eigenvalue, α is scalar (α= 0.05 in our analysis) and *A* is the adjacency matrix.

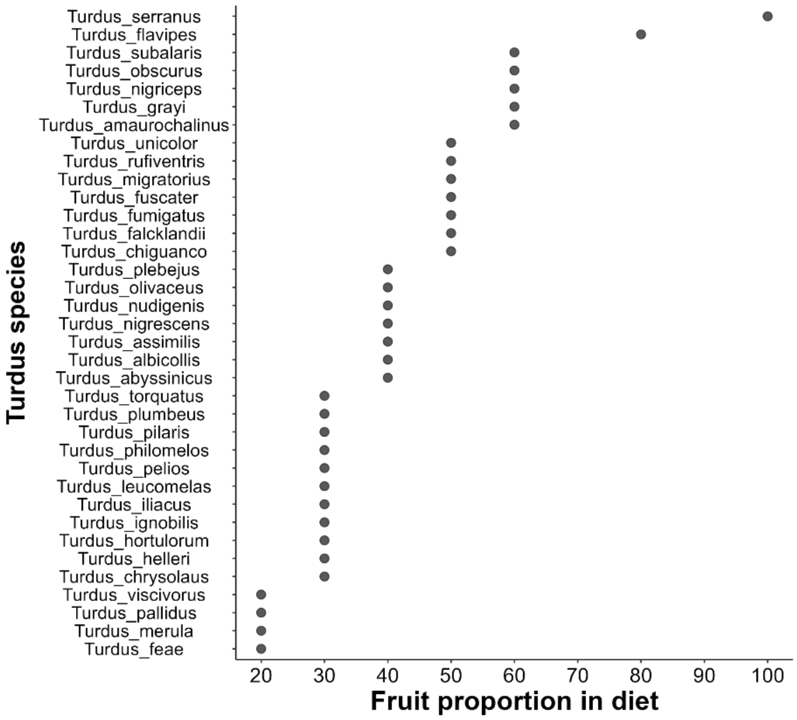


Figure 2S – The dietary composition of fruits was examined across 36 *Turdus* species. Half of the species (n=18) exhibited a dietary fruit proportion ranging between 30% and 40%. Fourteen species displayed a fruit proportion of 50% or more. Notably, *Turdus abyssinicus* is the sole species lacking fruit proportion data, attributed to the absence of this information within the Elton Traits database (Wilman et al., 2014).

Figure 3S – Boxplots of the z-scores of the three centrality measures of other birds and *Turdus* species. The points refer to z-scores values of the bird entries in the networks. Z-scores values refers to the number of standard deviations the entries are above or below the average for the given network; so, if the average z-score values are above zero, it means that in average that group is above the average for the centrality. *Turdus* species were, in average, more central than other bird species.

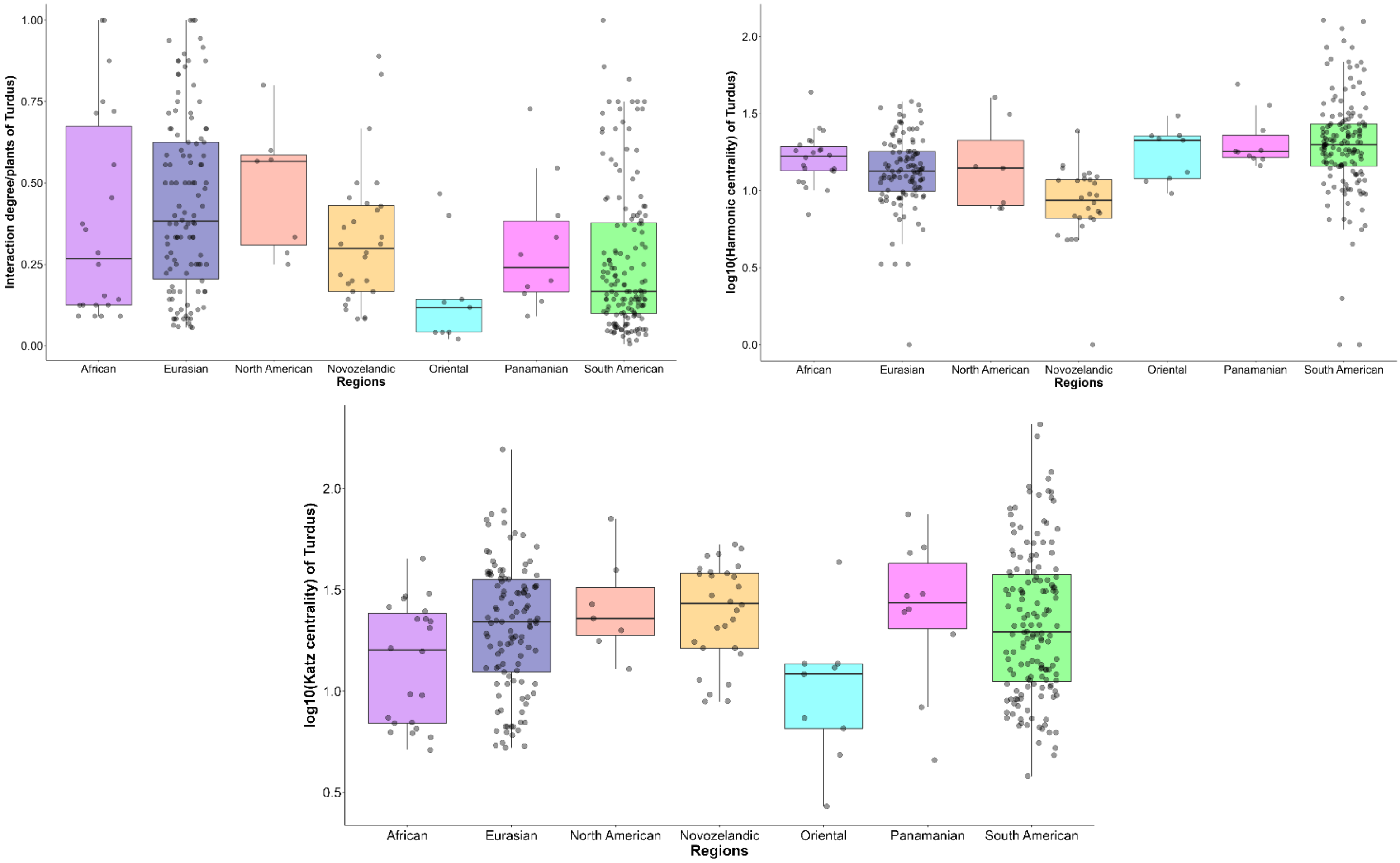


Figure 4S – Boxplots of the centralities per region. Each point is a *Turdus* entry in the given region. To test the differences between the regions we used Kruskal–Wallis and only weak differences were found in some regions (results on the main text).

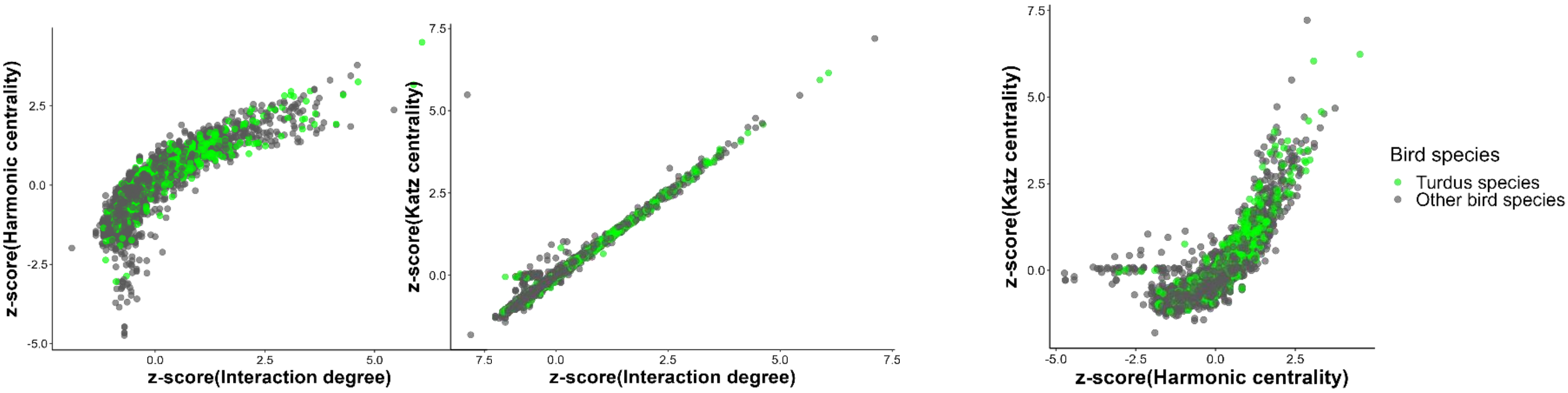
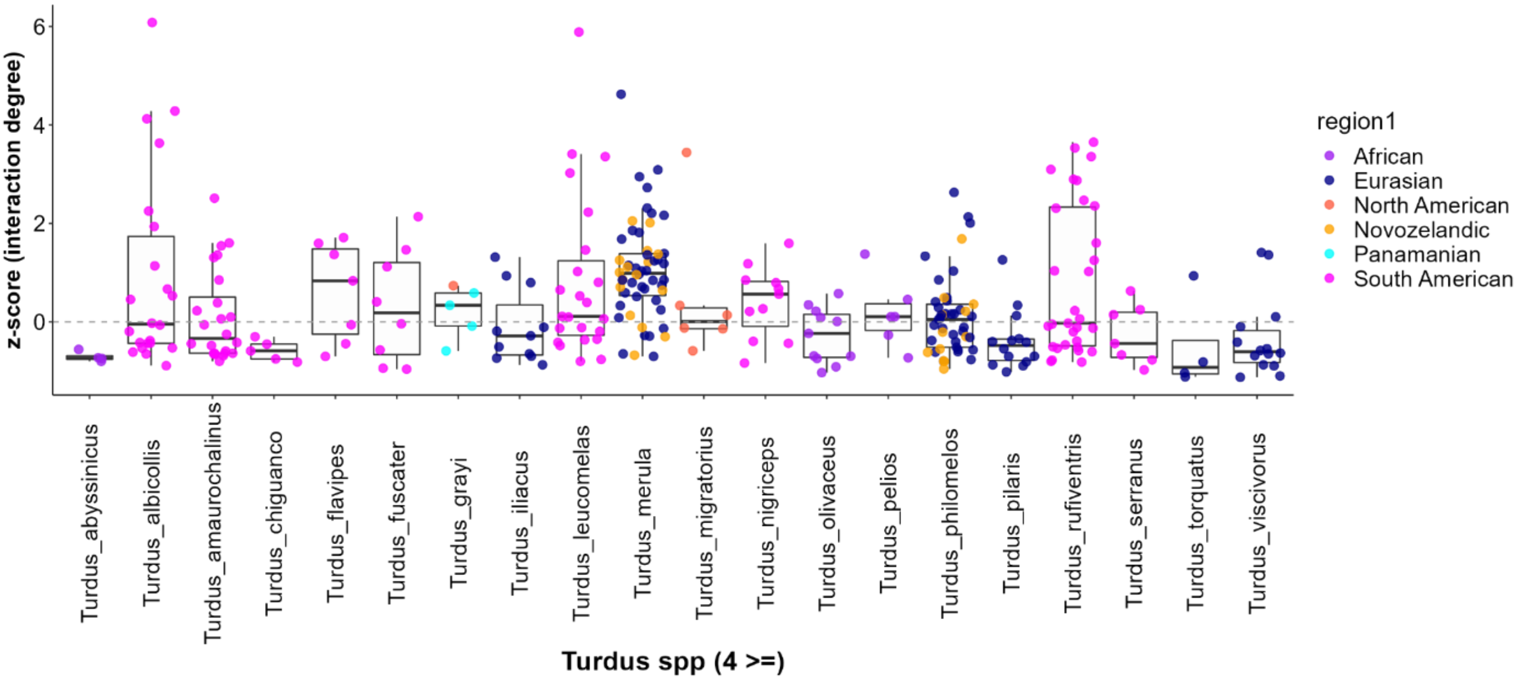


Figure 5S – Distribution of the z-scores of *Turdus* species (green circle) and other birds (gray circles) across the 162 plant-frugivore networks. Each point refers to a z-score of the centrality of one node in the networks. A) The association between values of interaction degree and harmonic centrality, in which the increase of interaction degree the higher harmonic centrality. B) Association of interaction degree and Katz centrality, in which there is a strong positive relationship. C) Relationship of harmonic and Katz centrality, which presented a positive relation, with some data noise.



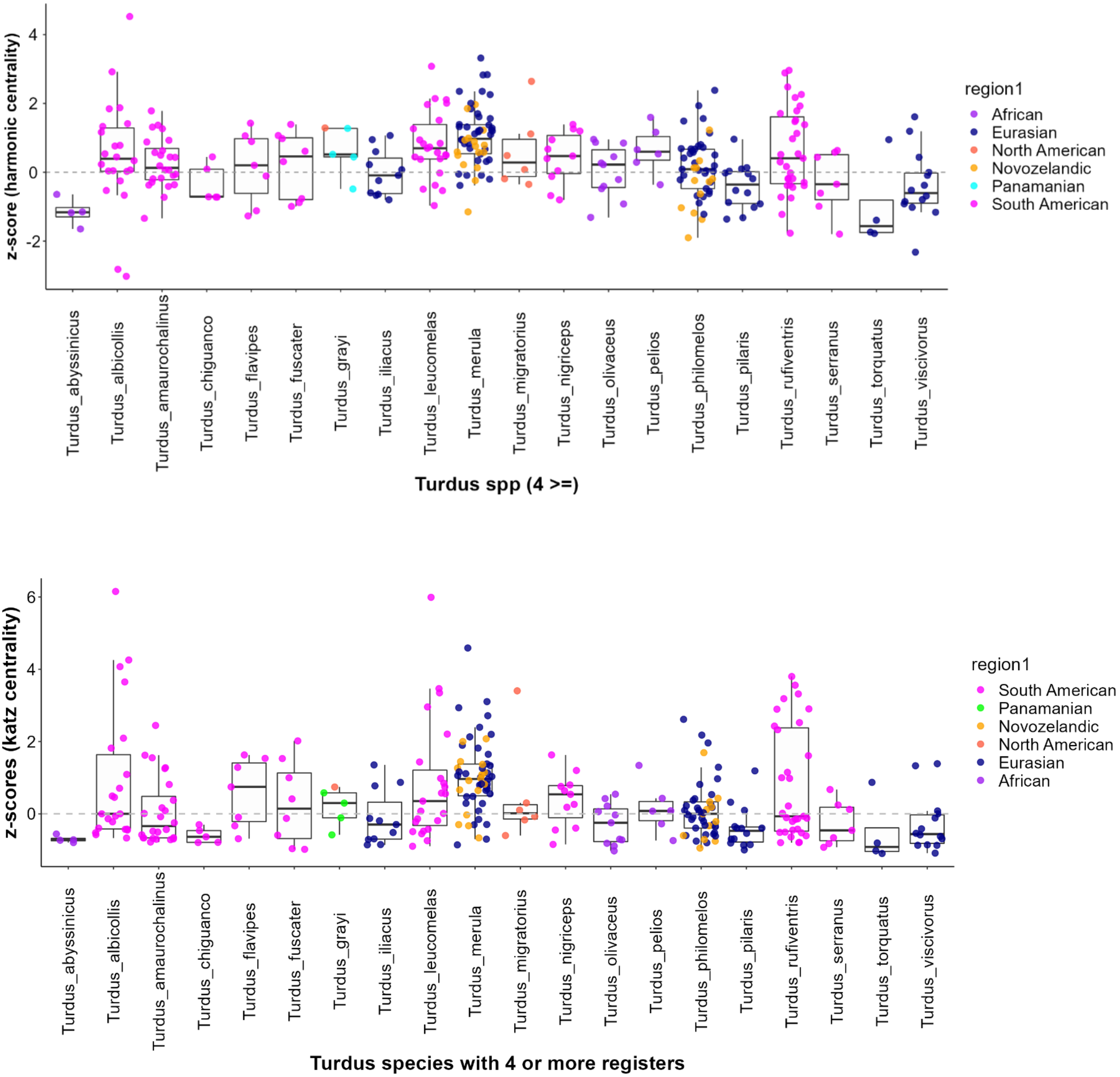
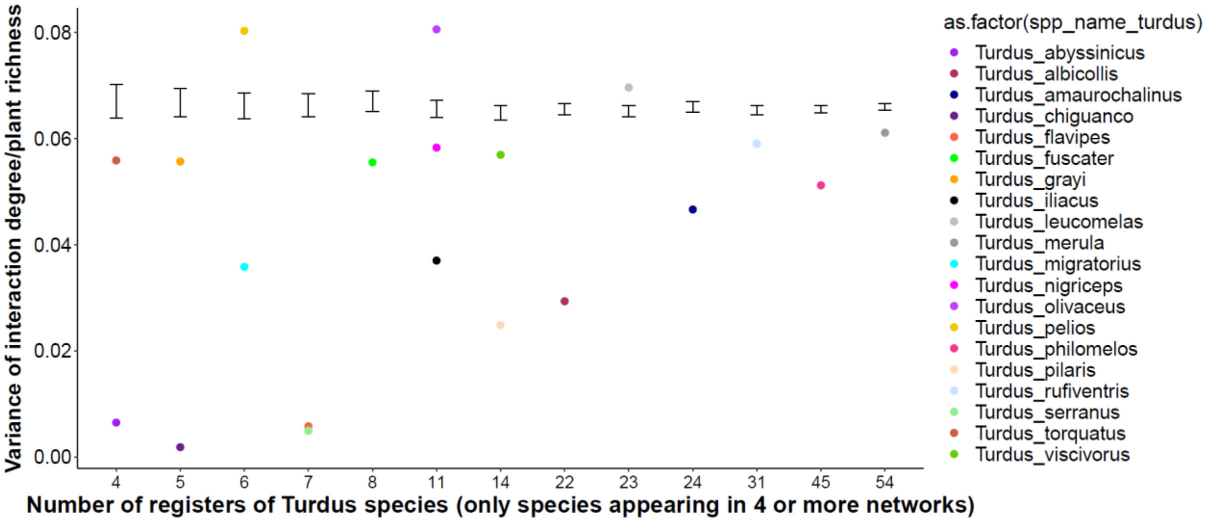
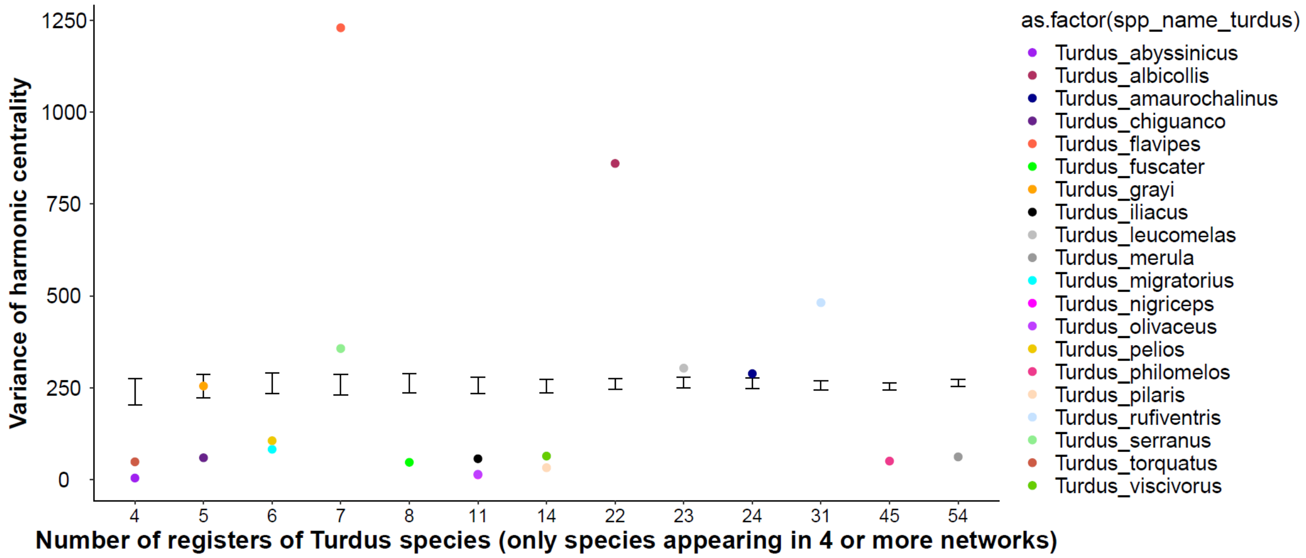


Figure 6S – Distribution of z-scores of centralities of the 20 *Turdus* species that were recorded in at least 4 different networks. Each point refers to one entry of the species; the colors are indicating the regions. The dashed line is z-score= 0; values above zero means that that entry is above the average for the centrality in the given network.

Table 1S - Networks with three or more *Turdus* species in which the variance of *Turdus* centralities were higher when compared to the selection of nodes of random bird species. We simulated 1000 times, in which each time the variance of the *n* randomly selected species was calculated, in networks with *n* number of *Turdus* species in the network. Then, we counted how many times the variance of the randomly selected species was higher than the *Turdus* species in that given network. These are the cases in which the variance of other birds were smaller than *Turdus* species variances.

Network code	**Centrality index**	**Region**	**Num bird species**	**Num of plants**	**Num *Turdus* spp in the network**	***p*-value of random variance >*Turdus spp* variance**
sl	Int. degree	S. American	18	15	3	0
si	Int. degree	S. American	36	5	3	0.05
sb3	Int. degree	Eurasian	10	8	3	0.05
sl	Harmonic	S. American	18	15	3	0.012
sb3	Harmonic	Eurasian	10	8	3	0
ro	Harmonic	S. American	29	6	3	0.016
bz	Harmonic	S. American	12	22	3	0.041
pu	Katz	S. American	43	24	4	0.058





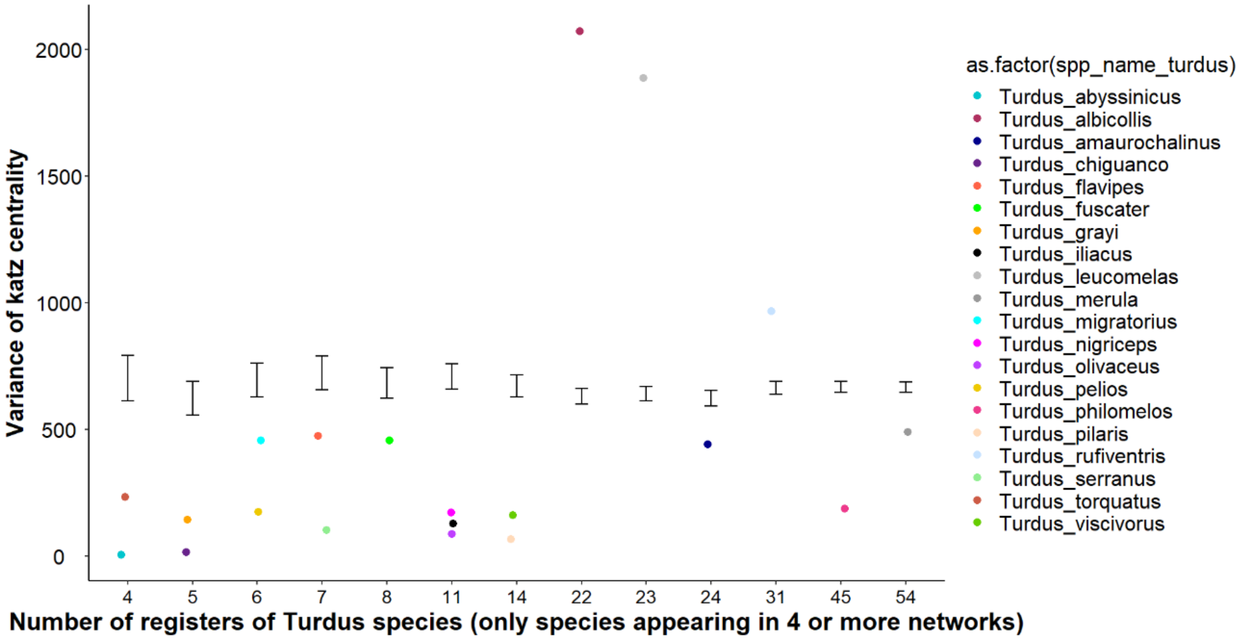


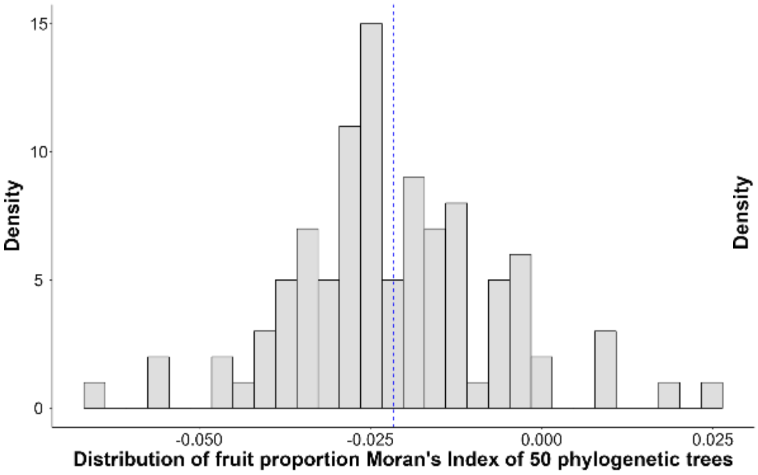
Fig. 7S – Distribution of simulated variance of the 20 *Turdus* species (bars of interval confidence) with the actual centralities' variance (points) among *Turdus* species in a given network showed that the patterns of variance in centrality for species coexisting in a given network is different depending on the centrality metric evaluated.

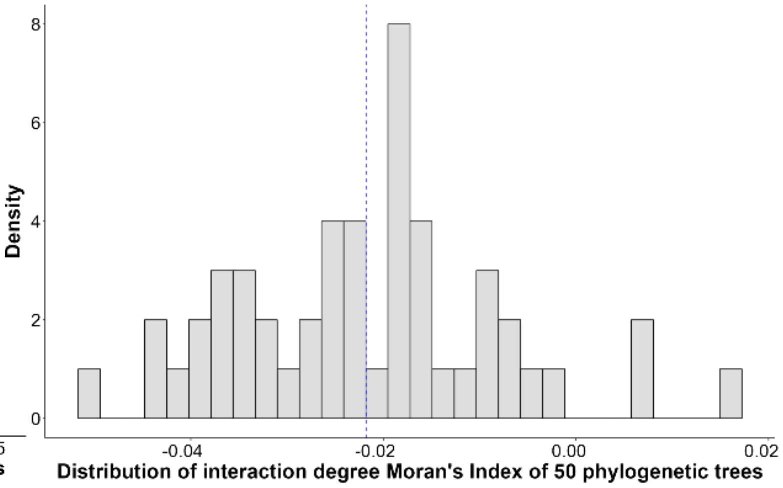
Table 2S – Pearson’s correlation between bird richness in the networks and the average of centrality for all bird species and considering only for *Turdus* species.

Correlation test	***R***	**t**	**df**	**Conf. Interval**	**p-value**
log(network bird richness) ~ log(average of interaction degree of all birds in the network)	0.005	0.069	160	-0.148, 0.159	0.94
log(network bird richness) ~ log(average of harmonic centrality of all birds in the network)	0.781	15.83	160	0.713, 0.834	$2.2e^{-16}$
log(network bird richness) ~ log(average of katz centrality of all birds in the network)	-0.56	-8.62	160	-0.66, -0.45	$5.88e^{-15}$
log(network bird richness) ~ log(average of interaction degree of *Turdus* spp in the given network)	0.12	2.25	310	0.01, 0.23	0.024
log(network bird richness) ~ log(average of harmonic centrality of *Turdus* spp in the given network)	0.71	17.74	310	0.65, 0.76	$2.2e^{-16}$
log(network bird richness) ~ log(average of katz centrality of *Turdus* spp in the given network)	−0.1	-1.691	310	-0.20, 0.01	0.091

Table 3S - Phylogenetical signal tested by Moran index for the three centrality metrics (interaction degree, harmonic and Katz) and for frugivory degree. The results are the average of each analysis that were runed 50 times with random phylogenetic trees.

Variables tested	**Expected**	**Average observed Moran**	**SD**	**p-value**
Interaction degree	-0.0294	-0.0267	0.0168	0.644
Harmonic	-0.0294	-0.0363	0.0170	0.600
Katz	-0.0294	-0.0162	0.0160	0.454
Frugivory degree	-0.0294	-0.0213	0.0175	0.537





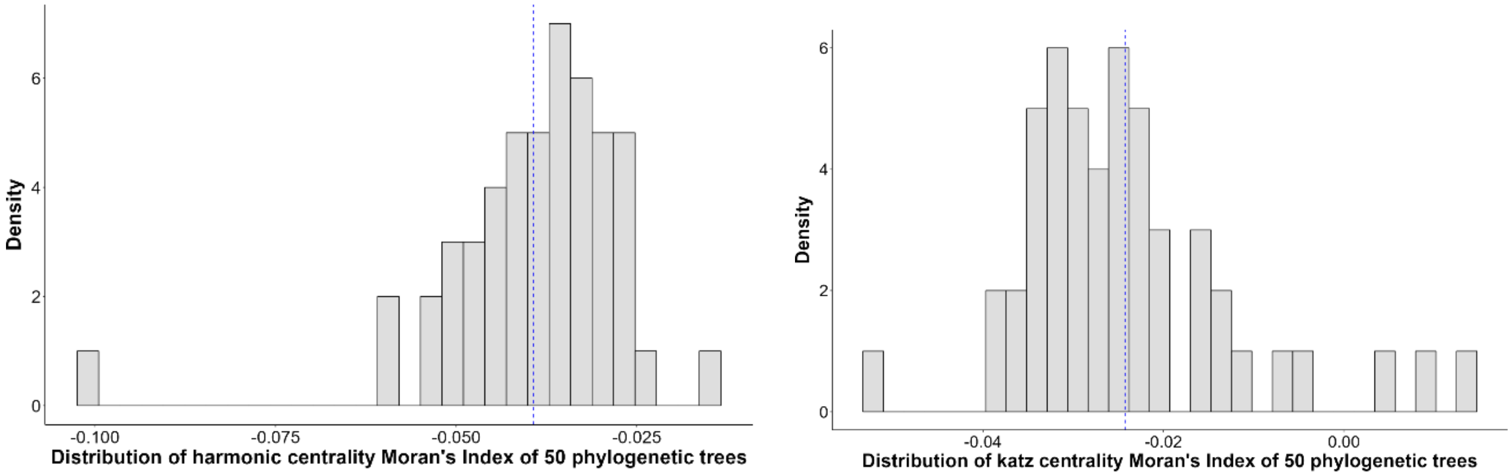


Figure 8S - Distribution of Moran index for each of frugivory degree and the three centrality measures for 50 randomly selected phylogenetic *Turdus* species trees. The blue dashed line indicates the average of Moran index for the given variable tested.

Conclusions

Throughout the writing of this thesis, I wanted to explore how the interactions among different levels of organization (individuals and species) influence, and are influenced by, the network structure. Individuals are the basic unit of ecological interactions, so it is through them that interactions are established. In a population, individuals may consume resources differently, and by presenting this individual niche variation, frequency-dependent interactions may have an effect on population stability and capacity to diversify. Then, in this context, it is crucial to advance the knowledge of the patterns and consequences of individual interactions. Moving towards the species level, it is necessary to understand the role of species that are key in ecological processes and if related species necessarily play similar roles in the same process. To approach these questions, I used seed dispersal systems, focusing on bird as seed dispersers.

First, we studied the seed dispersal of the palm individuals of *Euterpe edulis* and bird species from three different forest types on a continental island in Brazil. We found that the palms' characteristics did not influence the centrality of the individuals in the network. This is possibly explained by the fact that there is a high number of *E. edulis* individuals across all forest types on Cardoso Island, so the bird species may easily find the palm and consume their fruits and seeds. We showed that interactions between *E. edulis* individuals and their seed-dispersing birds form modules which are partially associated with the forest types and altitudinal gradient on Cardoso Island. Then, even though five bird species occur in all three forest types, some of these species seem to strongly interact with palm individuals in only one forest types. So, the local habitat types seem to reshape the frugivore assemblage, yielding a distinct, habitat-specific signal to the interaction patterns in the whole network, which leads to the emergence of modules in this seed dispersal network. This study highlights how habitat context may shape ecological interaction networks within populations by potentially constraining the role of individual traits in shaping patterns of interactions within species, which is essential to have a better understanding of the effect of individuals and species interactions on the ecological community.

Second, zooming out from individual-based to species-based networks, we explored the seed disperser roles played by 36 *Turdus* species around the world. We used three centrality metrics to describe the species' ecological role. We found that there is large variation between *Turdus* species in their average central position in the 162 seed dispersal networks. Moreover, the variation of centrality within the same species was also large, in which, in some networks, a given species presented a high central position (e.g., which indicates that the species is highly interactive and/or is interacting with important partners in the networks). However, in other networks, the same species presented less central positions, which may indicate that the centrality of species may be strongly dependent on community context. The seed dispersal dataset we were able to gather from the literature showed that most studies were from South America and Europe, and the two most common species recorded were *Turdus merula* (n= 54 out of 162) and *Turdus philomelos* (n= 45). Most of the *Turdus* species presented less variance in the centrality measures in their given networks than expected by chance (*Turdus* entries randomly sampled across networks), which indicates that, in general, the species are presenting a consistent centrality when compared to the whole *Turdus* genus. Only 8 species (out of 20) presented higher variance across all three centrality measures in the networks, two species from Africa and six from South America. This indicates that six out of the 11 species that were recorded in South America presented a very high variance in their position in their networks. One of the patterns that were associated with the centrality values (log-transformed) of *Turdus* species (and other bird species) in the networks was the richness of plants in the networks, in which the greater plant richness resulted in higher central values in the given networks. So, in networks richer in resources, it appears that bird species have more possibility to show higher centrality, by interacting with a higher number of plants or by interacting with plants that are interacting with several birds in the systems.

By associating the natural history of individuals and species, and employing a network approach to study the interaction patterns of individuals and species in seed dispersal systems, we learned that habitat may shape the way individuals interact in an environmental gradient context on a continental island. We also showed that the ecological role played by phylogenetically related species may vary significantly. Also, the role played by a unique species vary in different communities, which again may point out to the importance of the ecological scenario in which the interactions are played. In studies examining how interactions between individuals and species shape community structure it is important to incorporate additional information about other types of interactions, such as pathogen effects and predation. From the plant's perspective, other interactions than seed dispersal could have significant effects on plant individuals. For instance, fruit size and chemical composition are known to be important in the selection of fruits by seed dispersers, but these fruits traits are also important for insect oviposition and infestations (Herrera 1986, Nakagawa et al. 1978, Levinson and Levinson 1984). Then, to deepen the understanding about the effects of interaction patterns over the ecological community it would useful, whenever feasible, to include data of other types of interactions and the environment features.

For future studies regarding differences in organizational levels in ecological interactions, I want to highlight the importance of partitioning the effects of extrinsic factors (such as environment, micro and macro habitats, etc) and intrinsic features (such as morphology, productivity rate, etc) on the emergence of interaction patterns (such as modularity). By including the partitioning of effects of characteristics in an ecological pattern could result in a better comprehension of what shapes the individuals (and species) interaction patterns. Another aspect I would like to highlight is the importance of identifying key species in ecological process (such as seed dispersal) and attempting to evaluate why the given species occupy these important positions in networks. This could involve examining whether these positions are driven by morphology, population context (such as abundance), community context (such as resource availability, resource competition) at the individual and species level.

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