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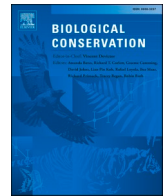
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Fragile plant-frugivore interaction networks in tropical forest edges

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ABSTRACT

Current incessant threats of environmental changes, such as habitat fragmentation, may disrupt vital mutualistic plant-frugivore networks, threatening the whole ecosystem. To advance our knowledge of the magnitude of the impacts of such disruption, we need a better understanding of its structure and robustness. We addressed this by comparing several aspects of plant-frugivore networks in the forest edge and interior habitats of a fragmented forest, using field data on fruit removal by a community of frugivorous birds and lemurs from 40 tree species over 30 months. While the plant-frugivore networks in both habitats were significantly less nested than random expectations, the network in the forest edge habitat had higher value of nestedness compared to the network in the forest interior. Also, the networks in both habitats were highly modular compared to random expectations, with a dominance of species that are highly interactive within its modules. We also found that fruit size, weight, and color as well as tree height predicted the structural role of plants in the networks and their degree of specialization. Finally, the removal/loss of best-connected plants or animals resulted in a weak robustness of the networks in both habitats; this vulnerable pattern is more pronounced in forest edges than interior habitats. Interestingly, the loss of large-bodied seed dispersers from either habitat did not affect much the robustness of the networks; in contrast, when small-sized species were eliminated first, the network became less robust, especially for the edge community. These findings highlight the need to preserve species interactions in forest edges to avoid the collapse of the network, mitigating the impacts of species extinctions on ecosystem equilibrium.

1. Introduction

The mutualistic interactions between frugivorous animals and their food plants constitute a vital ecological process, influencing the structure, dynamics, and maintenance of diversity within ecological communities in natural environments. Plants provide vital resources for the frugivores and, in return, these animals provide them with key seed dispersal services that are fundamental to their life cycle (Gautier-Hion et al., 1985; Howe and Miriti, 2000; Howe and Smallwood, 1982; Wang and Smith, 2002). Frugivore-mediated seed dispersal can also help plants reach and establish in certain environments, such as disturbed communities in forest edges (Muscarella and Fleming, 2007; Razafindratsima et al., 2021). These plant-frugivore mutualistic interactions are often complex and involve multiple interacting species, forming a network of interactions (Bascompte and Jordano, 2007; Donatti et al., 2011). Characterizing the structure of these networks could provide

important insights into our understanding of how they operate and the magnitude of the impacts of their disruption. Understanding the robustness of a network in the face of increasing anthropogenic threats can have implications for designing strategies for preserving species interactions, an important aspect of biodiversity conservation that is often overlooked, but is also critical for self-sustaining ecosystems (Heinen et al., 2020).

Among these anthropogenic threats, habitat fragmentation has been reported to alter plant-frugivore interaction networks and ecological functions (Donoso et al., 2022; Emer et al., 2019). Since fragmentation reduces the available habitats and decreases the area in the core interior of the forest, the diversity of plants can also decrease, and the communities of seed-dispersing frugivores might be downsized, leading to a collapse in the interactions (Cramer et al., 2007; Emer et al., 2018). Also, forest edges are often subject to harsher environmental conditions than the forest interior habitats (Murcia, 1995); this situation can impede

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seed germination and seedling recruitment (Laurance, 2001), creating a different set of plant assemblage. Furthermore, because the abundance of seed dispersers may decrease with the size and quality of fragments and along edge-interior gradient, there could be an increase in the dispersal of small-seeded plant species in the forest edges compared to the interior (de Melo et al., 2006; Razafindratsima et al., 2021; Uriarte et al., 2011). Such ecological filtering can set a gradual selection against large-seeded plants (Albert et al., 2015). Even though generalist seed dispersers may be able to replace the dispersal services of the other dispersers that may be absent at the forest edges, the magnitude and frequency of the services might not be the same and might lead to a functional degradation over time (Fricke et al., 2018; McConkey and O'Farrill, 2016). Thus, characterizing the basic aspects and consequences of network disruption can provide critical insights for understanding the impacts of habitat fragmentation on fragile ecosystems.

Analyzing the structure of plant-frugivore interactions using a network approach can provide ways to identify and characterize the patterns of the organization of the interacting species (Bascompte and Jordano, 2007; Ings et al., 2009). In these networks, each species may have a specific role that may make them more important than others, in terms of the stability of the networks. For example, a few frugivore species with generalist diets may interact with more plant species in the network than specialists, forming a relaxed interaction pattern (Mala-notte et al., 2019; Vázquez et al., 2009). Similarly, some plant species can act as a hub attracting a wide range of frugivores (Carlo et al., 2007). These roles in the network could also influence the rates of seed dispersal. For example, plants that establish highly specialized interactions with certain frugivores may rely on a subset of frugivores that may have unique traits (Moran and Catterall, 2010; Blendinger et al., 2016).

The structure of these plant-frugivore interaction networks and specialization of species within the networks may be determined by certain ecological attributes of the plants, such as their functional traits (Vázquez et al., 2009; Muñoz et al., 2016; Aslan et al., 2019), i.e. aspects of species that can influence its growth, survival, and reproduction (Caruso et al., 2020). Indeed, certain plant functional traits can influence frugivore foraging behavior and fruit selection, ultimately affecting their decisions regarding with which plant species to interact (Blendinger et al., 2008; Muñoz et al., 2016). For instance, dispersal-related traits, such as fruit color, fruit and seed size, and crop size can influence frugivore attraction to a plant (Eriksson, 2016). Fruit color can display information about its quality, location, and ripeness; therefore, it may enhance their visibility in attracting potential seed dispersers (Wheelwright and Janson, 1985; Schaefer et al., 2004). Fruit and seed size are also critical for plant-frugivore interactions because frugivores are often constrained in their fruit removal activity by the size of their gape (Jordano, 1995; Albrecht et al., 2018). In addition to these dispersal traits, some productivity-related traits, such as tree height and fruit crop, can also affect the interactions of frugivores with their food plants. In fact, different frugivore species forage in different forest strata depending on their habitat preference; and depending on their body size and arboreal activity, certain frugivores may favor interacting with certain plant species that can support them over others (Schleuning et al., 2011). Crop size can also influence frugivore attraction to fruits: the larger the crop size, the more likely they might be visited (Ortiz-Pulido and Rico-Gray, 2000). Given the tight links between plant functional traits, frugivore attraction and selection of fruits, it is important to examine how these traits might influence the structure of the network.

Network structure may vary between different habitat types, especially along disturbance gradients, such as in fragmented forests, because certain species may be absent from the highly disturbed community at the forest edges (Fortuna and Bascompte, 2006; Cramer et al., 2007). This is, for instance, the case for certain large-bodied primates and birds that are key seed dispersers in tropical ecosystems (Eppley et al., 2020; Lenz et al., 2014; Razafindratsima et al., 2021). In fact, habitat change and perturbation resulting from fragmentation could

lead to the loss of critical, but vulnerable, seed dispersers that may not tolerate the environmental conditions in the modified landscapes or the matrices (Murcia, 1995; Lenz et al., 2014; Haddad et al., 2015; Pfeifer et al., 2017; de Almeida-Rocha et al., 2021). Thus, characterizing the structure and robustness of the networks in fragmented landscapes could provide important insights into our understanding of the maintenance of an ecosystem in a changing world. When certain frugivores are absent in an area, their ecological functions may also be lost or missing (Rodríguez-Pérez and Traveset, 2010; Aslan et al., 2013). The disruption of the network can also harm the source of nutrition for the frugivores and reduce the likelihood of the plants to be dispersed (McConkey and O'Farrill, 2016; Rogers et al., 2021). Therefore, the extinction of one species could lead to the extinction of the other species that depend on it, triggering a cascade of biodiversity loss (Dunn et al., 2009; Rogers et al., 2021).

In this paper, we investigated the ability of a network of plants and seed dispersers in a human-modified rainforest landscape in Madagascar to withstand species extinction as a result of habitat fragmentation. To reach this goal, we first characterized the structure of the plant-frugivore network in forest edge vs. interior habitats. We hypothesized that the network in the forest edge would be more nested than the network in the forest interior habitat. We also expect that most species would interact more with species within their own modular groups because of the low diversity of faunal and floral communities in forest edges that can lead to fewer interactions in which the species can engage. Then, we assessed which plant traits influence the structural roles and degree of specialization of the plant species in the network. We predicted a positive relationship of fruit size, color, and crop with plant connectivity and degree of specialization because of their influence on frugivore attraction to fruits. Finally, we focused on the seed-dispersing frugivores only to test the robustness of the network in the face of species loss as a result of habitat fragmentation. We expected that the networks involving seed dispersers would become less robust if the best connected (generalist) and large-bodied animals are lost from the system. Indeed, generalist species tend to interact with diverse plant species and large-bodied frugivores tend to have frequent interactions with a wide range of species. Also, given that the majority of the threatened species in Madagascar tend to be large-bodied (data from Razafindratsima et al., 2018, 2019), we also expect to find a similar pattern if the Critically Endangered (CR) seed dispersers are lost first. Similarly, a low robustness in the network is expected if the best-connected plants are lost. The loss of plant species that act as hub in the network (super generalists) is also expected to lead to less robust networks because they connect species in different groups and are important in maintaining a coherence within their groups. We expect these patterns of low robustness to be stronger in the edge than interior habitat.

2. Materials and methods

2.1. Study sites and systems

We conducted this study in the rainforest of Ihofa (18°45' S and 48°24' E), located in the eastern part of Madagascar, through several field periods between 2017 and 2021, encompassing different seasons, as logistics and funding permitted: January–November 2017, October–December 2018, January 2019–January 2020, and January–May 2021. These different periods allowed observations of various species that are fruiting at different times within and across years. Ihofa is an evergreen dense forest within the Mantadia-Zahamena Corridor. This forest is home to 14 lemur species, 60 bird species, and >140 plant species (Razafindratsima et al., 2021). Among these lemur and bird species, 11 and 21, respectively, have fruits in their diet (Razafindratsima et al., 2021), although the percentage and diversity of fruits in the diet may vary among species. Local communities currently manage the natural resources in Ihofa forest landscape. Unfortunately, intense anthropogenic pressures, such as slash-and-burn agriculture, logging,

mining, and hunting, have led to the creation of forest edges that adjoin small expanses of successional fields and a matrix of small-scale agricultural fields and/or open areas (Razafindratsima et al., 2021). Ihofa forest is characterized by a high density of adult trees and shrubs with diameter at breast height (dbh) of <25 cm and an average tree height of 10 m with some emergent trees of >15 m tall (Razafindratsima et al., 2021). Fruits occur year-round, but some different plant species are fruiting at different times of the year. The peak with the most abundant species fruiting and the highest fruiting intensity occurs in June (Razafindratsima et al., 2021). The average monthly temperature in the area is 19.2 °C (range: 10.8° - 34.7 °C) and rainfall is 76.97 mm (range: 6–333 mm) (Razafindratsima et al., 2021).

2.2. Observations of plant-frugivore interactions

We examined plant-frugivore interactions in the forest edges, i.e. <500 m from the border of the forest, and in interior habitats. We considered individuals as being in the edge habitat when they were located at 179 m from the forest edge on average ($\pm$ SD 143, range: 1–480 m) and those in the interior habitats were at 1027 m from the edge on average ($\pm$ SD 714, range: 500–6220 m). For most of the species, the distance between individuals in the two habitat types were at least 255 m on average (see Supplementary materials Table 1). In each of these two habitat types, we carried out direct observations on 40 tree species, with 3–7 individuals per species per habitat type (393 individuals in total; Supplementary Table 2) to determine animal visitors and their feeding behavior (Bollen, 2003; Ramos-Robles et al., 2018). We observed each plant individual for four consecutive days at 07:00 h to 13:00 h, and then at 18:00 h to 22:00 h. We selected these time windows because most fruit-eating lemurs and birds, which are known to be seed dispersers in Madagascar's rainforests (Razafindratsima et al., 2022), tend to be most active during these periods (Overdorff, 1993). Some trees were also observed at 14:00 h to 16:00 h mainly because of their remoteness from our camp and because we observed animals visiting the species around that time. During each observation, one or two people hid in bushes at a distance of at least 10 m from an assigned tree to watch for its animal visitors. We recorded the species identity and activity (such as sleeping, grooming, or feeding) of all vertebrates visiting the tree. Whenever an animal consumed fruits, we recorded their fruit-handling behavior – i.e., eating the fleshy part of the fruit only, eating the seed only, or swallowing the whole fruits. We also recorded the number of fruits consumed and/or dropped under the tree. We used the fruit-handling behavior to define an animal species as seed disperser or not: we assumed an animal was a seed disperser when it eats and/or swallows the fruit/seed and/or transport fruit on its beak (for the case of birds). These behaviors correspond to the common traits of animals performing endozoochory and synzoochory (Schupp et al., 2019). If an animal defecated during our observation, we pay close attention to where the feces landed, then when the animal leaves, we also checked the feces for seeds on the ground to determine its seed-dispersal ability. We acknowledge that fruit bats also play an important role in seed dispersal services in Madagascar (Andrianainjato et al., 2012; Racey et al., 2010; Razafindratsima et al., 2022); however, in recent animal surveys we conducted in this study site, we did not see any fruit bats (Razafindratsima et al., 2021). Thus, our research focuses only on birds and lemurs.

To supplement our direct observation data and maximize our data collection efforts, we deployed camera traps overlooking the branches of fruiting trees that were not being directly observed (Prasad et al., 2010) – camera used were HCO Scout Guard and Bushnell Essential E3 Brown Model 119,837. We used camera traps for a total of 15 species with one individual tree observed per species (Supplementary Table 2). As one camera trap cannot cover the crowns of the fruiting tree at 100 %, we set it up in a way that it can cover the part of the tree with the greatest density of fruits. We left a camera on the same tree for up to ten nights; however, some cameras recorded for shorter periods as they became

non-functional before retrieval dates. In total, the cameras were set-up for a total of 546 nights but they recorded activities for only 154 nights. Each camera trap took either three photos or one video of 15 s long when triggered. We used these photographs and videos to identify the species and determine their behavior, in the same way as with the direct observations. We observed only one species that were eating fruits from the camera trap data, *Coracopsis nigra*. Since this species was also observed through the direct observations, thus, not affecting the composition of the networks, we did not include these data into the interaction matrix.

2.3. Measurement of plant functional traits

We collected data on plant functional traits for each individual fruiting tree that we observed (Supplementary Table 3). For each tree, we collected 1–10 fruits, depending on fruit availability, to measure the following traits: length, width, weight, and color. We used caliper to measure the length from stem to tip and width from the largest part of the fruit to the nearest millimeter; and a small precision scale (0.1 - 600 g) to measure the weight. We averaged the data across individuals to get values for each species. We described fruit color with three attributes, using a Munsell Color chart for plant tissues (Baltimore, 1972; Wheelwright and Janson, 1985; Villafuerte and Villafuerte, 1998): Hue, Lightness and Chroma. "Hue" corresponds to 17 subdivisions of the four principal chromatic colors: red, yellow, blue, and purple. Each subdivision of hue included either the principal color or a combination of these principal hues and a 2.5 step relative to the intensity of color; for example: 2.5 Yellow-Red, 5 Yellow-Red, 7.5 Yellow-Red, 10 Yellow-Red, etc. (Baltimore, 1972). Color "Lightness" (0–10) indicates the level of lightness or darkness of a color relative to a neutral grayscale, and "Chroma" (or saturation) indicates the degree of departure of a given Hue from a neutral gray of the same value (zero for a neutral gray to 14 for more saturation). Since the values of each of these three color-attributes may vary by individual fruit or time of fruit collection, we used the most representative value among the individual fruits (Supplementary Table 4).

In addition to these fruit traits, we measured tree height and fruit crop. We assessed tree height by visual estimation, which we averaged across all individuals for each species. We determined fruit crop by counting the total number of fruits on each tree. We used the maximum fruit crop size in the analysis.

2.4. Description of network structure

We characterized the structure of the plant-frugivore network in each habitat type using three metrics: nestedness, modularity, and degree of specialization. Nestedness describes the pattern of the interactions in the network, i.e. whether specialist species interact with a subset of species interacting with generalists (Bascompte et al., 2003; Burgos et al., 2007; Ulrich and Almeida-Neto, 2012). We organized the data as a matrix of interaction between each plant species and each frugivore, where rows represent plant species and columns represent animal species, with the number of interactions (represented by number of visitations) in each case. We analyzed nestedness using the metric wNODF (Nestedness based on the Overlap and Decreasing Fill, weighted by the number of interactions; Almeida-Neto and Ulrich, 2011), calculated using the R-package *bipartite* (Dormann et al., 2008, 2009). wNODF value ranges from 0 to 100, where 100 indicates perfectly nested network (Almeida-Neto and Ulrich, 2011).

Modularity analyzes the extent to which the interactions are organized into "modules" or groups. In the module, the species interact more with each other than with species in other modules (Olesen et al., 2007; Donatti et al., 2011; Mello et al., 2011). In our case, this metric described the extent to which each plant species interacts with a distinct subset of animal frugivores. We computed modularity *M* by applying the Beckett algorithm (Beckett, 2016) in the function *computeModules* in the R-

package *bipartite* (Dormann et al., 2008, 2009). This algorithm can optimize weighted modularity in bipartite networks, especially for large networks such as in this study (Beckett, 2016). We used the computed values of the number of links that a plant species has with other species within its own module (within-module interaction z) and its connectivity among modules (c) to assign an ecological role in the network for each species as follow: peripheral, connector, module hub, or network hub (Olesen et al., 2007). Peripheral species have low $z \leq 2.5$ and low $c \leq 0.62$ and interact with the species within its own module; they are also referred as specialists. Connector species have low $z \leq 2.5$ and high $c > 0.62$ and connect with several species in different modules. Module hub species have high $z > 2.5$ and low $c \leq 0.62$ and are highly connected with several species in its module; they are important for the coherence of their module. Network hub or super generalist species have high $z > 2.5$ and high $c > 0.62$ and are acting as both a module hub and a connector species.

We measured the degree of specialization of the network at species level (d'), characterizing the focal species, and at community or network level (H_2'), characterizing interaction in the whole network (Blüthgen et al., 2006). d' refers to the number of links or partners and is calculated as the standardized Kullback-Leibler distance, which is a measure of the deviation of species from an expected interaction distribution (Blüthgen et al., 2006). The value of d' ranges from 0 to 1, where 0 indicates the most generalist species and 1 indicates the most specialist species. H_2' quantifies the overlap in animal species among different plant species and vice versa (Blüthgen et al., 2006). The values of H_2' range from 0 to 1, where 0 indicates the most generalized network and 1 indicates a completely specialized network (Watts et al., 2016). Both indices were calculated using the R-package *bipartite* (Dormann et al., 2008, 2009).

We assessed the significance of the network metrics (nestedness: wNODF, modularity: M and degree of specialization H_2') by comparing their observed value in the given matrix against expectation from null models generated with the Patefield's algorithm (Patefield, 1981). This approach considers that all species are interacting with each other and the total numbers of interactions remains constant (Blüthgen et al., 2006). We computed the null model using the function *nullmodel* in the *bipartite* package, with 1000 iterations. We then transformed the observed values of wNODF, M and H_2' into z-scores calculated as [observed – null mean] / null standard deviation (Correa et al., 2016; Dormann and Strauss, 2014). Values of $-2 < z\text{-scores} \geq 2$ mean significantly less or highly, respectively, nested, modular and specialized compared to random expectations (Dormann and Strauss, 2014).

2.5. Influence of plant functional traits on the network.

We performed a stepwise regression model (Mundry and Nunn, 2009), using the function *stepAIC* in the R-package MASS (Ripley et al., 2022) to select the best fit for our data, predicting which plant trait (fruit length, width, weight, and color, tree height, and crop size) explain the structural roles and degree of specialization of the plant species in the plant-frugivore network. This function selects the model with the lowest value of Akaike Information Criteria (AIC) as the best model among all possible models that consider different combinations of the predictor variables. We considered as response variables the ecological role of each species, as represented by z (connectivity within the module) and c (connectivity among module) obtained from the modularity analysis, as well as the degree of specialization represented by d' described above. We treated plant traits as predictor variables and included habitat type (edge and interior) as covariate.

2.6. Robustness of the seed dispersal network in the face of species extinctions

With a focus on seed-dispersing frugivores, we tested how robust the network would be following species extinctions of either seed disperser or plant, by simulating secondary extinction, i.e., the likelihood of a

species going extinct in the event that the species interacting with it goes extinct (Mémott et al., 2004), using the *second.extinction* function in the R-package *bipartite* (Dormann et al., 2008, 2009). Following previous studies (Burgos et al., 2007; Mello et al., 2011; Ramos-Robles et al., 2018), the simulation procedure was based on cumulative removals of species from the network under certain extinction scenarios. For each procedure, we first removed a species from one side of the network (e.g., seed disperser) and then removed the species from the other side (e.g., plants) that was connected only to the first-removed species (i.e., secondary loss), through 1000 randomizations.

We had six scenarios of seed-disperser extinction, in which we removed seed disperser species in a sequence based on three attributes: (1) connectedness in the network – from best-to-least connected, i.e., the most generalist species goes extinct first, and vice versa; (2) threat status – from Critically Endangered (CR) to Least Concern (LC), and vice versa; (3) and body size – from largest to smallest, and vice versa. We obtained data on animal body size from the Malagasy Animal trait Data Archive (Razafindratsima et al., 2018, 2019) and data on threat status from IUCN Red List (IUCN, 2021). For plants, we had four extinction scenarios, in which we removed plant species in a sequence based on two attributes: (1) connectedness in the network – from best-to-least connected, i.e., the most generalist species go extinct first, and vice versa; and (2) ecological role from the modularity analysis – eliminating the module hub species first, followed by peripherals and finally the ultra-peripherals, and vice versa.

Each simulation generated a secondary extinction curve with the cumulative proportion of the remaining species in the network on the y-axis and the cumulative proportion of species removed on the x-axis. The area below each curve, called R , represents a measure of the robustness of the network in the face of species loss. $R = 1$ corresponds to a very slow decrease, indicating that most of species of one side of the interactions remain after removal of most species from the other side and $R = 0$ corresponds to a very fast decrease, indicating a vulnerable system (Burgos et al., 2007; Ramos-Robles et al., 2018).

3. Results

3.1. Structure of the plant-frugivore networks in forest edge and interior habitats

Each of the observed trees was visited by fruit-eating animals at least once during our observations. In total, we had nine species of birds and nine species of lemurs consuming fruits from these 40 tree species (Fig. 1). Among these, seven bird species and all lemurs were considered as “seed dispersers” as they were observed eating and swallowing fruit/seed, transport fruit, and/or we found intact seeds in their feces. In both habitats, the animal assemblages interacting with the plants are dominated by four bird species (*Alectroenas madagascariensis*, *Coracopsis nigra*, *Hypsipetes madagascariensis*, and *Zosterops maderaspatanus*) and three lemur species (*Eulemur fulvus*, *Cheirogaleus major*, and *Microcebus lehilahytsara*) – Fig. 1. However, the frequency of visits on each tree species varies among animal species and between habitat types (Fig. 1; Supplementary Table 5).

3.1.1. Nestedness

In both habitats, the plant-frugivore networks had significantly lower nestedness than random expectations ($z\text{-score} < -2$); however, the network in forest edge had higher wNODF value than that in the forest interior (forest edge: wNODF = 16.55, $z\text{-score} = -9.51$; forest interior: wNODF = 15.54, $z\text{-score} = -9.81$). When looking at a subset of the network that involves the seed-dispersing frugivores only, we found that the network was significantly less nested than random expectations (Supplementary Table 6); the same pattern is also observed when looking at seed-dispersing birds and lemurs separately (Supplementary Table 6).

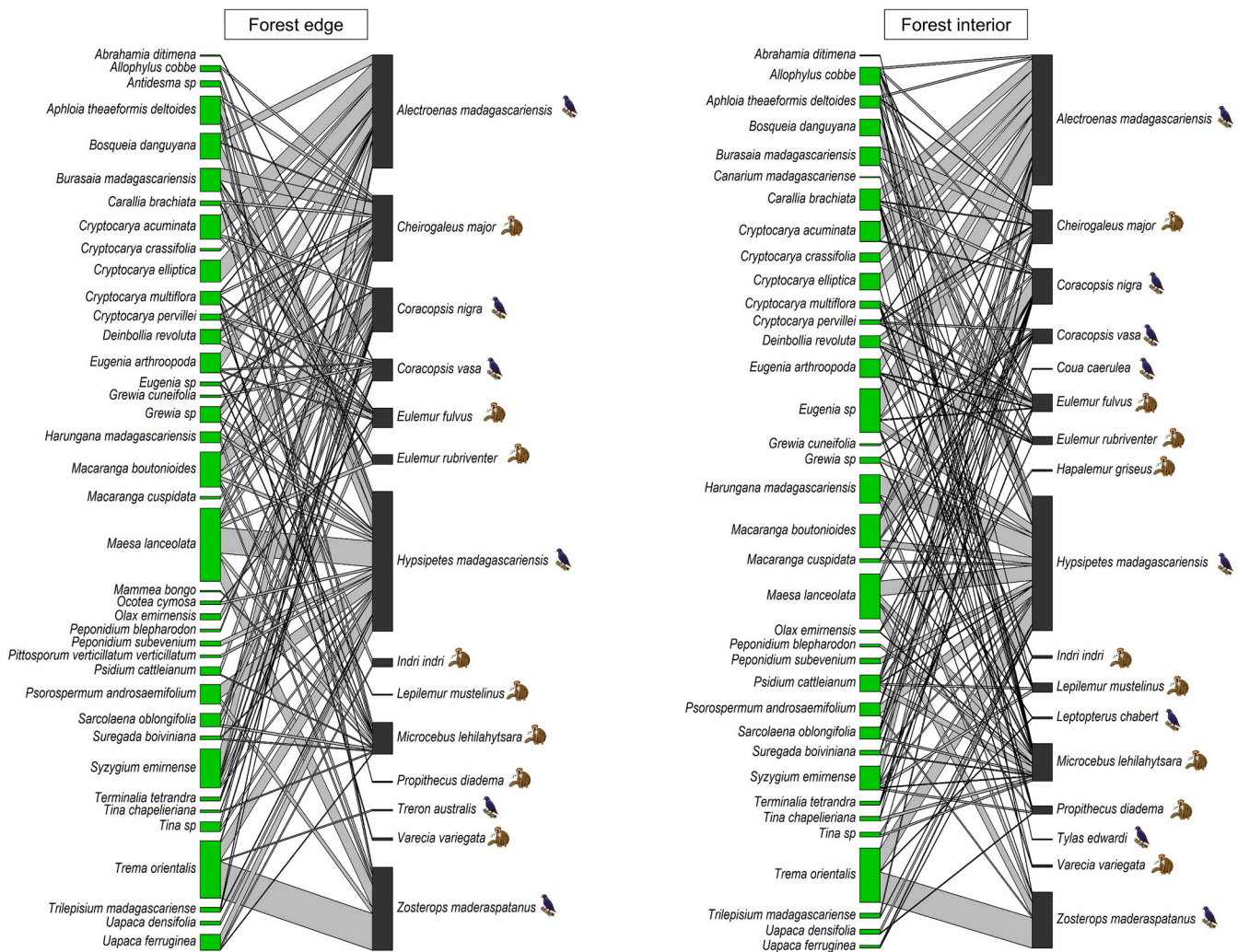


Fig. 1. Plant-frugivore network in forest edge and interior habitats in Ihofa forest. The width of the connecting lines between animals and plants indicates the frequency of the visitation to the tree. Lemur and bird illustrations by Finaritra Randimbiarison.

3.1.2. Modularity

The networks in forest edge and interior habitats were organized into different modules, in which species interact more with each other than with species in other modules. In both habitat types, the plant-frugivore networks were highly modular compared to random expectations (forest edge: $M = 0.49$, $z\text{-score} = 29.03$; forest interior: $M = 0.49$, $z\text{-score} = 34.66$). The plant-frugivore network in the forest edge had a high proportion of plant species that were mostly peripheral (Fig. 2; Supplementary Table 7), i.e., they mainly interact with species within their own modules. Three plant species acted as connector that connect with several species in different modules (*Grewia* sp., *Maesa lanceolata*, and *Trilepisium madagascariense*); and two plant species acted as module hub that connected several species in their own module (*Macaranga boutonioides* and *Trema orientalis*). For the network in the forest interior, the majority and five species were connector (*Eugenia* sp., *Grewia* sp., *Maesa lanceolata*, *Olax emirnensis*, and *Suregada boiviniana*; Fig. 2; Supplementary Table 7). The networks composed of seed dispersers only were also significantly highly modular than random expectations (Supplementary Table 6) with large proportions of peripheral species (Supplementary Figs. 1–3, Supplementary Table 7).

3.1.3. Degree of specialization

Specialization of plants on frugivores (d') ranged from 0.061 to 0.604 at the forest edge and 0.080–0.582 at the forest interior, indicating that most of the plant species in this system were highly generalists

(Supplementary Table 8). The long-lived canopy trees, *Cryptocarya multiflora*, had the highest value of d' at the forest edge habitat (0.60), and *Burasaia madagascariensis* and *Grewia cuneifolia*, at the forest interior (0.58). At the community level, the degree of specialization H_2' was significantly higher than the null model, i.e., the plant-frugivore network was specialized ($H_2' = 0.52$, $z\text{-score} = 40.36$ in forest edge and $H_2' = 0.52$, $z\text{-score} = 45.12$ in forest interior).

3.2. Influence of plant functional traits on the structural roles and degree of specialization of species in the network

The best fit models predicting structural roles of the plant species in the networks (represented by z and c) included fruit width, color, crop, and tree height (Table 1, Supplementary Table 9). However, we found no significant associations of the species connectivity within modules (z) with any of the plant functional traits. Connectivity with other species in other modules (c) was negatively associated with fruit color and tree height, suggesting that species having fruits with lighter and less saturated color and shorter individuals have a tendency to connect more among modules. For the case of degree of specialization d' , we found that fruit width and tree height had positive relationships with d' , suggesting that taller species with wider fruits have a tendency to be specialists. However, species that are heavier in weight were less specialized as indicated by the negative relationship between fruit weight and degree of specialization (d'). Fruit crop did not influence the structural roles and

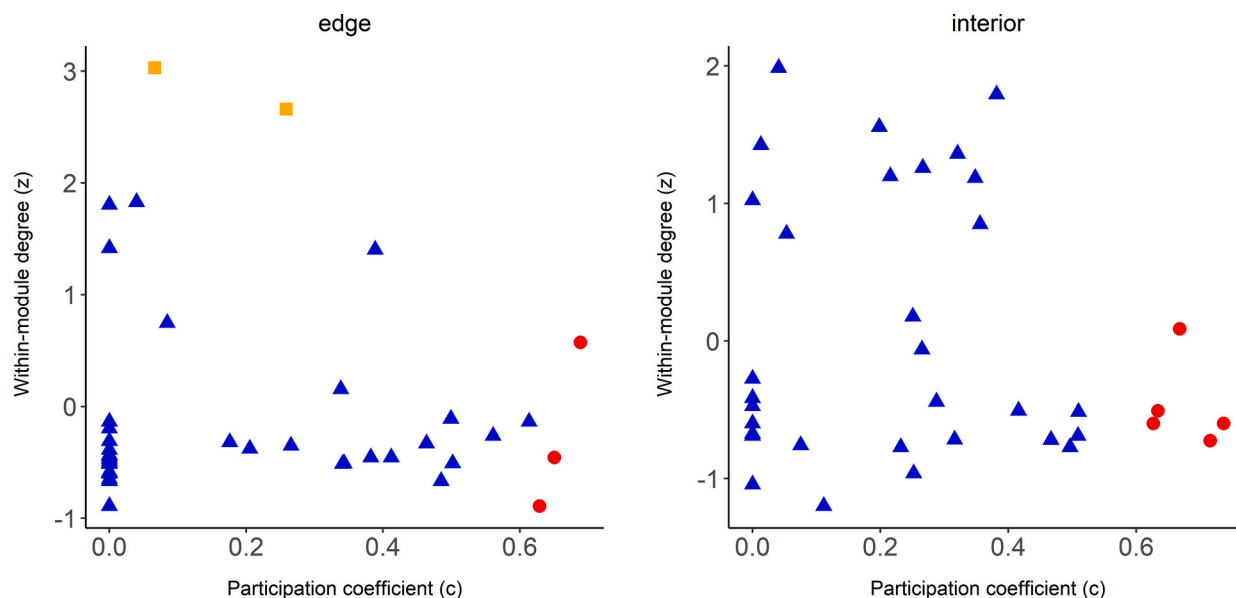


Fig. 2. Role of each plant species in the modules in plant-frugivore interaction network in forest edge and interior habitats. Each species is assigned a role based on the value of its interaction within its module (z) and among modules (c), following Olesen et al. (2007): peripheral (blue triangles; low $z \leq 2.5$ and low $c \leq 0.62$), connector (red circles; low $z \leq 2.5$ and high $c > 0.62$), module hub (yellow squares; high $z > 2.5$ and low $c \leq 0.62$). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Table 1

Results of the stepwise regression model testing how plant functional traits influence network structure using three species-level metrics: connectivity within module (z) and connectivity among module (c) from modularity analysis and degree of specialization d' . Values of the degree of specialization for each plant species in the network are detailed in Supplementary Table 8.

Metric of the network structure	Variable in the best fit model	AIC	Estimate	Standard error	t value	P
z	Fruit length	-20.900	-0.020	0.014	-1.602	0.113
	Fruit crop		-0.000	-0.000	-1.563	0.122
	Fruit color		-0.008	0.003	-2.217	0.029
c	Tree height	-220.350	-0.034	-0.010	-3.335	0.001
	Fruit width		0.017	0.004	4.831	<0.001
d'	Fruit weight	-302.290	-0.011	0.003	-3.597	<0.001
	Tree height		0.012	0.005	2.228	0.029

Bold values highlight statistical significance.

degree of specialization of the plant species in the plant-frugivore network.

3.3. Robustness of the plant-disperser network to species extinction

When looking at the robustness of the network of plants and their seed dispersers in the face of animal extinctions (Fig. 3), we found that the extinctions of the most generalist species first result in a fast decrease in the number of remaining plant partners in both habitats. However, the edge community appeared to be more vulnerable than the community in the interior habitat with a lower value of R (Fig. 3a & c). Switching the order of extinctions, in which we removed the less generalist (less connected) seed dispersers first, we found a slow decrease of remaining plant species in both habitats (Fig. 3b & d). In the extinction scenario based on body size of the seed dispersers, the networks in both habitats remain robust when eliminating the large-sized species first (Fig. 3e & g); however, when the sequence of species removal is reversed, the network became less robust, especially for the edge community. When we removed the seed disperser species from Critically Endangered to Least Concern, the network seems robust, with a very slow decrease in the number of remaining plant species (Fig. 3i & k). When this scenario was reversed, the community in the edge habitat became more vulnerable than the one in the interior habitats (Fig. 4j & l).

When considering plant extinctions in the network, we found that, overall, there is a fast decrease in the number of animal partners when we removed species from best connected to less connected, especially in the edge habitat (Fig. 4a & c). However, when the order of species removal was reversed, the robustness decreases slowly (Fig. 4b & d). In the scenario based on the ecological role of plant species, the networks also remained robust with high values of R in both habitats and regardless of the sequence of species loss (Fig. 4e-h).

4. Discussion

Habitat fragmentation remains one of the most threatening pressures on forest ecosystems, affecting critical ecological processes such as species interactions. As some key species become absent from certain habitats, such as forest edges resulting from fragmentation, the overall integrity and equilibrium within the ecosystem may become at risk of disruption (Rodríguez-Pérez and Traveset, 2010; Aslan et al., 2013, 2019). In this study, we investigated the magnitude of the impacts of the disruption of a network of plants and seed dispersers in a Malagasy rainforest in the face of species loss due to habitat fragmentation, by examining secondary extinctions. We first compared several aspects of the structure of plant-frugivore networks in the forest edges and interior habitats of a fragmented forest. We found that the plant-frugivore networks in both habitats were significantly less nested than random

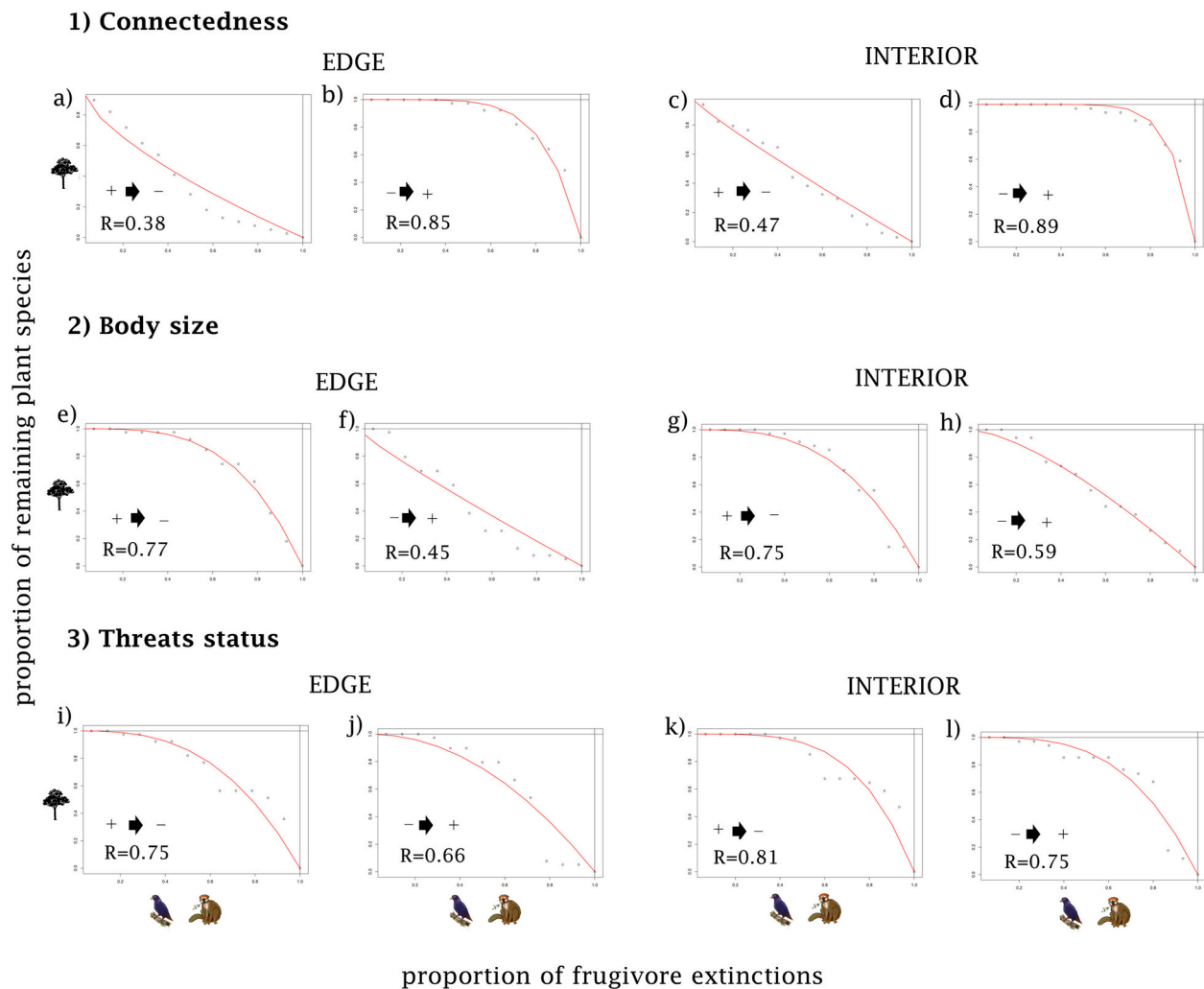


Fig. 3. Robustness of plant-disperser networks in forest edge and interior habitats to simulated extinctions of seed dispersers. In each habitat, the figure shows six sequences of species extinctions based on three attributes: connectedness, threat status, and body size. The minus and positive signs with a pointing arrow refer to the direction of the extinctions at each scenario: from best (+) to least connected (–) and the inverse, from large-sized (+) to small-sized (–) and the inverse, and from Critically Endangered (+) to Least Concern (–) and the inverse. Lemur and bird illustrations by Finaritra Randimbiasison.

expectations; however, the network at the forest edge showed a higher nestedness pattern. Also, the networks in both habitats were highly modular and more specialized compared to random expectations, with a dominance of species that are peripheral in terms of their modular interaction role (*i.e.*, interacting more with species within its modules). In addition, our results show that fruit size (width), weight, and color as well as tree height predicted the structural role of plants in the network and their degree of specialization. Finally, the loss of best-connected seed-dispersing frugivores in the system, especially in the forest edge, led the networks to become less robust and more vulnerable. We observed the same patterns when eliminating plant species from best to least connected, especially in the edge habitat. Contrary to common observations that the loss of large-bodied frugivores in the system leads to a collapse of the ecosystem equilibrium (Pérez-Méndez et al., 2016; Vidal et al., 2019), the loss of large-bodied frugivores in our system from either habitat type did not affect much the robustness of the network; instead, when small-sized species were eliminated first, the network became less robust, especially for the edge community. These findings highlight the critical needs for the management of disturbed communities, such as forest edges, to preserve and restore essential but vulnerable, ecological networks. Also, the community-level impacts of the disruption of such vital interactions could be important in predicting the resilience of the degraded forest communities to anthropogenic

disturbances, which may help in biodiversity conservation and management.

We found that the plant-frugivore networks in this system were less nested than random expectations; however, the value of nestedness was higher for the network in the forest edge than in the forest interior. The pattern of low nestedness compared to random may be related to lower network connectance (Fortuna et al., 2010), which may be as a result of a low fruit availability during the sampling season and, therefore, decrease plant-frugivore interactions. The higher nestedness in the forest edge support the findings in other tropical systems (*e.g.*, Chaves et al., 2022; Menke et al., 2012). We speculate that this pattern might be mostly driven by the interactions of plants with small- and medium-sized animals. In our study system, these species (*e.g.*, *Hypsipetes madagascariensis*, *Microcebus lehilahytsara*, and *Zosterops maderaspatanus*) are highly generalist as they consume a wide range of plant species and have higher frequency of interactions with the plants in the network than other species (Supplementary Table 5); they may, therefore, dominate the network. In contrast, the interior habitats may have more opportunistic frugivore species than the forest edges (*e.g.*, *Coua caerulea*, *Tylas edwardi*, and *Leptopterus chaberti*), each of them interacting with only one plant species in the habitat. Such interactions could result in low nestedness, which can be explained by a low number of interactions (Bascompte et al., 2003). Additionally, the local disturbance

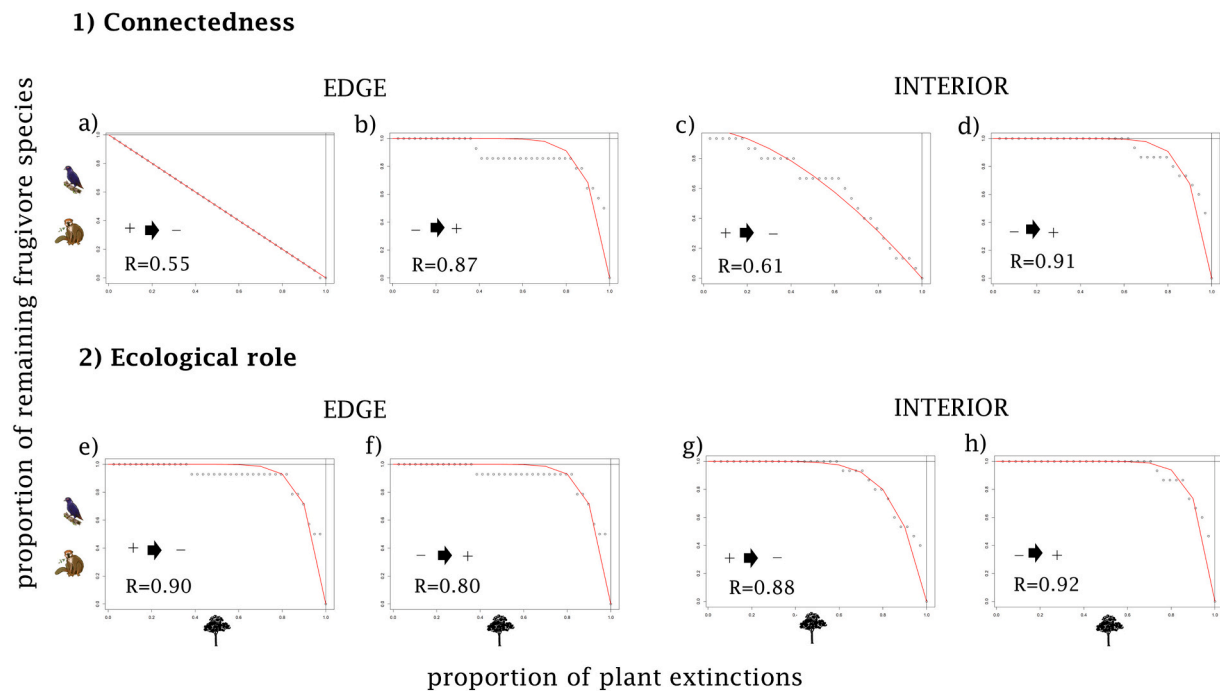


Fig. 4. Robustness of plant-disperser networks in forest edge and interior habitats to simulated plant species extinction. In each habitat, the figure shows four sequences of species extinctions based on two attributes: connectedness and ecological role. The minus and positive signs with a pointing arrow refer to the direction of the extinctions at each scenario: from best (+) to least connected (–) and the inverse, and from Module hub (+) to Ultra peripheral (–) and the inverse. Lemur and bird illustrations by Finaritra Randimbiarison.

resulting from habitat fragmentation in our system may have affected the interactions among frugivores and plants as it may have had an impact on the composition and diversity of both faunal and floral communities (Farwig et al., 2017; Murcia, 1995). These community-level effects at the forest edge could have limited the frequency of interactions that the occurring plants may have with other key organisms. The higher nestedness in the forest edges may also suggest that this habitat could maintain an important plant-frugivore networks, highlighting the urgent need for management strategies to preserve species interactions, seed dispersers, and plant community diversity.

Similar to other plant-frugivore networks in other systems (Ramos-Robles et al., 2018; Vollstädt et al., 2022), the networks in both habitat types in our system were highly modular compared to random expectations, i.e., organized into modules or groups, in which the species interacted more with each other than with species in other modules (Olesen et al., 2007; Donatti et al., 2011; Mello et al., 2011). However, the value of modularity was the same for the networks in the forest edge and interior habitats. Since modular networks may experience lower disruption than non-modular networks (Bascompte et al., 2003; Tylianakis et al., 2008; Grilli et al., 2016), the networks in this system may become more stable over time. The higher modularity in these habitats may also be related to the distinct structural roles of the different plant species that are important for the organization of the interactions and the persistence of the networks (Vidal et al., 2013). We found that most of the plant species in both habitats acted as peripheral in the networks, i.e., they only interacted with species within their own modules. Only a few species were found to be connectors (three at the edge and five at the interior), which links several species in different modules. Two species at the forest edge acted as module hubs, which have high connectivity to multiple nodes in the networks. Some of the connector and hub species are tall canopy trees (up to 12 m) and have large-sized fruits (up to 20 mm). These traits may confer a tendency to connect several groups as they might attract both the most frugivorous large-bodied and generalist lemur and bird seed dispersers in this system.

We also found that the networks in both habitats were more

specialized than random expectations; and the values of the degree of specialization were similar between the two habitat types. The high specialization may indicate complementary functions among the animal species interacting with the plants given that they use the same resources (Blüthgen et al., 2007). Nevertheless, our observations do not support the finding of other studies in other tropical ecosystems where low specialization was observed in plant-frugivore interaction networks (Blüthgen et al., 2007; Menke et al., 2012). The similarity in specialization between the networks in the two habitat types may be a result of the overlap in species composition between plant communities in forest edge and interior habitats in this system (Razafindratsima et al., 2021).

We also found that certain functional traits influenced the structure of the plant-frugivore networks in our system, corroborating the findings in other systems (e.g., Crestani et al., 2018; Malanotte et al., 2019). Specifically, fruit width, fruit color, and tree height were associated with different aspects of the network structure. Plant species with larger fruit size might be more specialized because they need specific consumers with certain traits, such as large-bodied frugivores that are able to ingest large-sized fruits. We also found that species with low fruit weight had higher specialization. Also, the positive relationships of fruit width and tree height with the degree of specialization d' may be a result of the differences in diet and habitat use among different animal species that are dominating different strata of the forest. For instance, the forest edges in this system are dominated by small-bodied frugivores such as *Microcebus lehilahytsara* and *Hypsipetes madagascariensis* (Razafindratsima et al., 2021) that are mostly found foraging in forest under- and mid-story (personal observations), and therefore may be dominated by shorter tree species with small-sized fruits that they can easily handle. Our findings suggest that functional traits may play a vital role in determining the structure of the network in a way that they can change the patterns of interaction between partners by modifying the probability of visitation (Junker et al., 2013; Schleuning et al., 2015).

Finally, our simulations of plant-disperser network disruptions show that the loss of plant species or animal species affected the robustness of the networks in both habitats when the best-connected species in the

network were removed; however, the networks in forest edges were less robust and more vulnerable. The important role of generalist species in maintaining resilience and stability of the network (Fontúrbel et al., 2021) might explain its high robustness when these species are removed first. The loss of large-bodied frugivores from either habitat did not affect much the robustness of the network; however, when small-sized species were eliminated first, the network became less robust, especially for the edge community. The small-bodied species may be critical in the network as they visited the fruiting trees more often than the large-bodied ones (Supplementary Tables 5 & 10), and as also found in other systems (e.g., Carreira et al., 2020). For the case of the scenario considering the threat status, we found that the network would be less robust when Least Concern (LC) species were extinct first, especially in the forest edge. This low robustness might be because most of the animal species in the network are classified as LC (Supplementary Table 10), especially in the forest edge. This pattern of low robustness is more pronounced in forest edges because *Alectroenas madagascariensis* (LC), *Hypsipetes madagascariensis* (LC), and *Microcebus lehilahytsara* (VU) dominated the network in forest edges than other dispersers. When considering the ecological roles of plant species in our simulation of secondary extinction, we found that the networks remained robust in both habitats regardless of the sequence of species removed. However, the loss of hub plant species may affect the disruption of the network resulting from the breakage of the module as they connect different species across modules (Olesen et al., 2007); thus, we should pay more attention in these species to avoid the collapse of the network in this fragile system.

4.1. Conservation implications

Our results suggest that generalist plant species (best connected species) can have important role in the network and their loss might have cascading impacts to the whole system. Therefore, it is important to include these species in reforestation and restoration programs because these species can ensure the maintenance of vital biotic interactions, community diversity and resilience, and ecosystem functioning. Additionally, the loss of small-bodied seed dispersers might have a detrimental effect on plant communities and the integrity of forest ecosystems since their persistence may ensure specific role in the maintenance of plant diversity and distribution. Overall, although our study focused on one site, which restricted the number of species and individuals observed, we showed that habitat fragmentation can alter the structure and robustness of plant-frugivore networks. Nevertheless, fragile habitats can still sustain vital interactions, which, with adequate conservation actions, can favor the persistence of key species, their ecological roles, and the services they provide in the long term. We, thus, strongly advise considering plant-frugivore networks and prioritizing forest edges when designing conservation actions to prevent and mitigate species extinctions and functional loss in forest ecosystems in Madagascar.

Data availability statement

Data relevant to this project have been summarized in the Supplementary Information materials.

CRediT authorship contribution statement

Nancia Raoelinjanakolona: Conceptualization, Methodology, Formal analysis, Investigation, Data curation, Writing – Original draft, Visualization, Project administration, Funding acquisition. **Veronarin-dra Ramananjato:** Methodology, Formal analysis, Writing. **Aristide Andrianarimisa:** Methodology, Writing. **Angelo Andrianaiaina:** Investigation, Visualization, Writing. **Rindra Nantenaina:** Investigation, Writing. **Onja Razafindratsima:** Conceptualization, Methodology, Validation, Formal analysis, Investigation, Resource, Writing – Original

draft, Project administration, Funding acquisition.

Declaration of competing interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.biocon.2022.109822>.

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