

Structural but not functional resistance of frugivore-plant interaction networks to the defaunation process

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ABSTRACT

Defaunation is the process of sequential loss of larger animal species caused by anthropogenic activities such as deforestation and hunting. This phenomenon has potential to disrupt the ecosystem stability, as well as their functional performance through the disruption of trophic interactions. We evaluated the effect of defaunation on structure and function in frugivore-plant interaction networks. We characterized interaction networks in two areas in northern Colombia and used a simulation model of species extinction in three different scenarios. The first scenario eliminated species based on body size, measured by body mass, according to the progressive effect of non-random species loss (defaunation); the second scenario eliminated species according to their contribution to network structure (CNS); and finally, the third scenario eliminated species according to their seed dispersal potential (SDP). Based on these simulations we evaluated the effect of species loss on the structural patterns (nestedness and modularity) and the functional diversity of the frugivore community, through the indexes of functional richness (FRic) and functional evenness (FEve). The loss of species with larger body sizes increased nestedness and did not affect modularity, whereas in the CNS scenario both patterns were affected. The FRic index decreased in the first stages of extinction by defaunation and by SDP, while the FEve index did not suffer significant variations in any scenario. The combination of interaction network analysis with functional diversity indices allows direct quantification of the robustness of network structural patterns and the vulnerability of the functional capacity of frugivore communities in the face of defaunation.

1. Introduction

Defaunation describes the process of progressive population decline or loss of wildlife animal species (Dirzo and Miranda, 1991; Redford, 1992); as well as the potential effects on the stability, maintenance, and evolution of animal communities (Dirzo et al., 2014; Emer et al., 2020). This phenomenon primarily affects vertebrate species with higher body mass (Ceballos and Ehrlich, 2002) which are much more sensitive to extinction processes (Dirzo et al., 2001). This increased susceptibility is related to traits such as body size, long generation periods, low fertility, slow life cycles, and low population densities (Cardillo et al., 2005; Galetti and Dirzo, 2013). External factors such as hunting also increase pressure and decrease population size, leading in many cases to extinction (Redford and Robinson, 1987).

The progressive loss of animal species and populations not only

represents one of the greatest changes to biodiversity but also directly impacts the functions and performance of their ecosystems (Valiente-Banuet et al., 2015; Donoso et al., 2017). For example, targeted hunting of primary seed dispersers, such as primates, some ungulates, medium-sized rodents, and large frugivorous birds, jeopardizes the regenerative capacity of tropical forests (Peres and Palácios, 2007). Particularly at the community level, the negative effects of defaunation are linked to large frugivore species interacting with multiple species (Bascompte et al., 2003; Strauss and Irwin, 2004; Donatti et al., 2011). The absence of large frugivore impacts other species they interact with, generating changes in their interaction network, and producing cascading effects, which have potential to spread throughout the community and destabilize the entire system (Donatti et al., 2011). Similarly, the loss of species with certain characteristics (e.g., large body size) can generate a rapid decline in the functional capacity of communities (Coux et al.,

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2016; Donoso et al., 2020), since a large part of the functions they perform cannot be replaced by other species with different characteristics (Vidal et al., 2013). In this scenario, the quality of ecosystem functions, such as seed dispersal, may result consequences on long-term forest maintenance (Donoso et al., 2017; Fricke et al., 2022).

Although the response of frugivory interaction networks to the defaunation process has been previously studied, analyzes have been limited to assessing individual structural metrics (number of interactions and secondary extinctions) and functional effects related to long-distance seed dispersal (Donoso et al., 2020). Therefore, an integrative and holistic approach that considers the structural and functional roles of species remains necessary. The structural component can be assessed by a set of metrics that quantify the role of species in network organization patterns (nestedness and modularity). These patterns are related to stability, robustness of systems, and coexistence of species within communities (Bastolla et al., 2009; Rohr et al., 2014; Tylianakis et al., 2010). The effect on the functional capacity of communities can be assessed using functional diversity indices that quantify the amount of functional space occupied by species and the homogeneity of the distribution of species abundances in functional space (Villéger et al., 2010). This approach, which integrates interaction network metrics with functional ecology indices, allows us to generate a comparative framework to evaluate the defaunation process in other contexts, including different types of interactions.

In frugivory interaction networks, the structure-function relationship is determined by the response functional traits of frugivores, which determine the effect of environmental factors (e.g., anthropogenic disturbance) on species presence and abundance (Schleuning et al., 2015; Coux et al., 2016). These traits can act as matching traits, which define the identity and frequency of interactions between species, affecting the structure of the networks (Dehling et al., 2016). Likewise, the traits may mediate ecological functions that, in the case of frugivores, correspond with the qualitative and quantitative components of seed dispersal (Schupp et al., 2010; Schleuning et al., 2015; Acevedo-Quintero et al., 2020a). For example, body size is a trait that can act as a response, matching, and function trait for effective seed dispersal (Wheelwright, 1985; Díaz et al., 2013; Galetti et al., 2013); and therefore, defaunation can be expected to affect network interaction patterns and their functional consequences.

In the present work, we investigated the effect of defaunation on the structure and function of two frugivore interaction networks in the tropical dry forest of northern Colombia. Our main objective was to determine how the loss of larger animals modifies patterns of network structure and affects the functional capacity of frugivore communities. To do this, we combined data from field observations of fruit consumption with species extinction simulation models. For these models, we used three different scenarios in the order of species removal: random extinction and from larger to smaller body size in both, the structural and functional components. The third scenario was used as a baseline for comparison and corresponds to the worst-case scenario according to the component. From highest to lowest contribution to network structure (CNS) in the structural component, and from highest to lowest contribution to seed dispersal potential (SDP) in the functional component. We expected that the loss of the larger-bodied frugivore species would alter interaction patterns and reduce community functional diversity more than the random scenario, but less than the worst-case scenario by component.

2. Methods

2.1. Study area

This study was carried out in two localities (Guacamayas and El Pino) in the Córdoba region, northern Colombia. This region of the Colombian Caribbean is part of the tropical dry forest (Tdf) life zone, with a warm climate and average temperature of 28 °C, and its mean

annual precipitation is 1300 mm in unimodal distribution, with a dry season from December to March and a rainy season from April to November. As in most of the Colombian TdFs, forests in this region have been drastically reduced and fragmented due to cattle ranching and agriculture (Ballesteros-Correa and Linares-Arias, 2015; Racero-Casarrubia et al., 2015).

2.1.1. Guacamayas

Hacienda Betancí - Guacamayas Civil Society Reserve (08° 11' 72"N, 75° 32' 78" W) is located in the municipality of Buenavista, Department of Córdoba, Colombia. The average elevation is 70 m amsl, with an average temperature of 28 °C. The area covered by the reserve is 460 ha and is composed of TdFs fragments connected by corridors that border the streams and are immersed in a grassland matrix where silvopastoral cattle ranching is practiced.

2.1.2. El Pino

Hacienda El Pino (08° 25' 11.33" N, 76° 03' 24.43" W) is located in Las Palomas, in the Municipality of Montería, Colombia, in the middle basin of the Sinú River. El Pino covers an area of 2350 ha, at an average altitude of 35 m amsl and an average annual temperature of 29 °C. The ranch is dedicated to extensive cattle ranching and has an artificial water channel that runs almost entirely through it. The studied area was limited to 150 ha that has been set aside for native forest conservation. This segment is surrounded by a matrix of pastures and is completely isolated from other forested areas.

2.2. Data collection

2.2.1. Record of frugivore interactions

At each location, between April 2017 and June 2018, eight sampling sessions of five days each were conducted at two-month intervals. To record interactions between frugivorous vertebrates (birds, mammals, and reptiles) and plants, we used direct observation and photo-trapping as complementary methods, without restricting sampling to a particular taxonomic group (Acevedo-Quintero et al., 2020b). For a detailed description of each method see Appendix 1

2.2.2. Abundance of frugivores

The abundance of a frugivore species was estimated as its frequency of occurrence in observation stations. For birds, the observation stations were four-count points at each location. Sampling was conducted within a 50 m radius of each point and all bird species were recorded (visual sightings and vocalizations) for 15 min. Between 7 and 12 repetitions were made for each observation station. We calculated the abundance of each species as the proportion of points where that species was recorded with respect to the total number of points in each location (frequency of occurrence). For mammals and reptiles, we used a photo-trapping design with nine sampling stations in 0.16 km² cells randomly chosen in a grid covering each location (Acevedo-Quintero et al., 2020a). The cameras were active for one year and with the information obtained we calculated the frequency of occurrence of each species, as the proportion of observation stations (camera) in which a given species was recorded concerning the total number of cameras in each locality (9 in Guacamayas, 8 in El Pino due to the disabling of one of the cameras during sampling).

2.2.3. Morphological and behavioral traits

For each frugivore species, information was collected on their morphological and behavioral traits for their performance as potential seed dispersers. For each frugivory event observed, in addition to the species involved, we recorded the foraging stratum where the interaction took place, in high, medium, low, and ground level. We also recorded the animal's processing of the fruit during consumption, distinguishing between predation, pulp consumption, fruit transport, and endozoochory (Acevedo-Quintero et al., 2020a). For each species of

frugivore, we collected information on the average fruit size of the plant species that were consumed, from a sample of 10 fruits from 10 individuals of each plant species collected during the observation of interactions. For a small proportion of plant species, it was not possible to obtain field data, so they were analyzed based on literature data. Finally, the body size of frugivore species (median body mass) was obtained from the EltonTraits 1.0 database (Wilman et al., 2014).

2.3. Data analysis

From the observations of the frugivores we constructed a quantitative matrix of interactions for each location, where each row corresponded to a frugivore species (i), and each column to a plant species (j), the value of cell i, j corresponded to the interaction intensity (i.e., number of frugivory events recorded during the entire sampling) (Vázquez et al., 2007). Since two different methodologies were used to record interactions (direct observation vs photo-trapping), the matrixes were standardized according to the sampling effort of each method, estimating the interaction intensity per 24 h of observation (i.e., the number of interactions recorded in the time spent in each method was divided into 24 h periods).

To assess the degree of sampling representation, we constructed interaction accumulation curves, with the number of interactions observed as a function of sampling effort (measured as the number of interaction events recorded) (Chacoff et al., 2012; Jordano, 2016). The estimated number of expected interactions were calculated using the Chao1 estimator (Chao et al., 2009; Chacoff et al., 2012), using EstimateS 9.1.0 software (Colwell, 2013). The ratio of interactions detected in the samplings concerning those expected was close to 80% in both locations. Therefore, it can be concluded that the interaction matrixes obtained in this study were based on a highly representative sampling.

2.3.1. Interaction networks metrics

In response to the structural component, we used the topological organization patterns of nestedness and modularity. These patterns were noted for their influence on the dynamics of community competition, the persistence of processes, and the robustness of networks to species extinctions (Bastolla et al., 2009; Tylianakis et al., 2010; Rohr et al., 2014). For the original matrix, the degree of nestedness was calculated as NODF, following the algorithm proposed by Almeida-Neto et al. (2008). Modularity was estimated as Q , following the “QuanBiMo” algorithm for quantitative matrixes, and using the highest Q value achieved over five independent runs (Dormann and Strauss, 2014). In both cases, we evaluated whether the calculated metric differed from that expected by chance (Bascompte et al., 2003). For this, a Patefield null model was constructed with 1000 matrices of the same size, on which the corresponding metric was calculated and then compared with the value of the original matrix. Finally, the p -value was defined as the fraction of random matrices with a NODF or Q value equal to or greater than that of the observed matrix. All calculations were performed using the *bipartite* package in R (Dormann et al., 2009).

2.3.2. Functional diversity

To evaluate the functional component, we used two multi-traits functional diversity (FD) indexes (Laliberté and Legendre, 2010). The first was functional richness (FRic), which quantified the functional space occupied by species in a community regardless of their abundances (Villéger et al., 2010). A low FRic indicated that some of the potentially available resources were not being exploited (Mason et al., 2013). The second was functional evenness (FEve), which quantified the homogeneity in the distribution of species abundances of a community in a functional space (Villéger et al., 2010). A low evenness would imply that some parts of the functional niche were being occupied, but underutilized (Córdova-Tapia and Zambrano, 2015). Four traits related to the effectiveness of the species as seed dispersers were used to calculate the FD indexes: *i*) foraging stratum, *ii*) fruit manipulation, *iii*)

forest habit, and *iv*) range of fruit sizes consumed. For a detailed description of the calculation of each trait see Appendix 2. Trait values were standardized as z values, i.e., mean 0 and standard deviation 1, prior to calculating functional diversity indices and a species-species Euclidean distance was used. Calculations were performed with *dbFD* from R's FD package (Laliberté et al., 2014).

2.3.3. Species extinction simulation models

To assess the effects of defaunation on the structure and function of interaction networks, we used a species extinction simulation models (Mémott et al., 2004; Donatti, 2011). These models removed species sequentially and cumulatively to evaluate the response of networks under different scenarios in the extinction sequence. After each extinction, network metrics (NODF and Q) and functional diversity indices (FRic and FEve) are recalculated. For each network, 15 extinction steps were generated, equivalent to 30% of the species in Guacamayas and 33% in El Pino. The extinction scenarios determined the order in which species were eliminated. This order simulated different ecological scenarios, and was modified from that proposed by Donatti (2011) as follows:

2.3.3.1. Random scenario. In this scenario, all species had the same probability of disappearing (random extinction) and served as a basis for comparison with the other scenarios. In this case, for each extinction step, the elimination of species was repeated 1000 times, except for the modularity where the number of repetitions was 100.

2.3.3.2. Body size scenario (defaunation). This scenario simulated the loss of species via defaunation. The body size of animals was linked to many other life-history traits (demography, growth rates, reproductive rates, etc.) (Jerzolimski and Peres, 2003; Bodmer et al., 1997; Peres and Palácios, 2007). In addition, these species are much more susceptible to anthropogenic activities such as fragmentation or hunting (Peres, 2000; Michalski and Peres, 2007). Therefore, animal species of larger body size are the elements that are first lost, or decrease in abundance after human intervention in ecosystems, which has been called defaunation (Dirzo and Miranda, 1991; Dirzo et al., 2014).

2.3.3.3. Contribution to network structure (CNS) scenario. Corresponds to the worst-case scenario in the structural component. Contribution to Network Structure (CNS) quantifies the contribution of each species to the nestedness and modularity patterns. In this scenario, species were eliminated from highest to lowest CNS. Therefore, the selective loss of these species was expected to lead to a structural collapse of the network. CNS was constructed from the contribution of each species to the different structural patterns using the *degree* (Mello et al., 2015), the *contribution to nestedness* (Saavedra et al., 2011), and c and z values, related to the modular pattern in terms of the level at which a species connected with species from different modules or from the same module respectively (Olesen et al., 2007). These species-level network metrics were used to build a principal component analysis (PCA) with the aim of determining, through PCA axes, global trends of variation across species in the topological parameters of each network (Acevedo-Quintero et al., 2020a; Estrada, 2007; Vidal et al., 2013). Since the first PCA axis (PC1) accumulated a considerable proportion of the variance in both networks and accounted for the covariation of all topological parameters (Appendix 3), it was used as an estimator of the structural relevance of frugivore species in each interaction network (Appendix 5).

2.3.3.4. Seed dispersal potential (SDP) scenario. Represented to the worst-case scenario in functional component. This index quantified the potential for each animal species to act as seed dispersers for the plant community (Appendix 5). The SDP was based on morphological, ecological, and behavioral traits and attributes related to the potential for the species to act as effective seed dispersers (abundance, body size,

Table 1
General descriptors of the interaction networks and frugivore communities of the Guacamayas and El Pino locations, prior to the species extinction simulation.

Descriptor	Guacamayas	El Pino
<i>Species richness</i>		
Plants	39	25
Animals	50	45
<i>Nestedness</i>		
NODF	27.52	25.56
<i>p</i> value	<0.001	<0.001
<i>Modularity</i>		
Q	0.37	0.47
<i>p</i> value	<0.001	<0.001
<i>Functional diversity</i>		
FRic	30.14	23.72
FEve	0.73	0.75

foraging stratum, fruit manipulation, forest habit, and range of fruit sizes consumed). High values of these characteristics indicated a greater ability of that frugivore to favors recruitment across plant species in the forest community (Acevedo-Quintero et al., 2020a). This scenario only was used in functional component and eliminated the species with the highest to the lowest SDP value. See Appendix 4 for details and rationale.

2.3.4. Evaluation of species extinction models

For each extinction step, we evaluated whether the structural (NODF and Q) and functional (FRic and FEve) metrics in each scenario (defaunation, CNS, SDP) differed from the random scenario. The *p*-value for each extinction step was defined as the probability that a random replicate was greater or less than the value obtained in one of the scenarios. A probability of <5% ($p < 0.05$) was used as the significance level. Finally, we calculated the proportion of extinction steps in each scenario in which the metrics were significantly different from those in

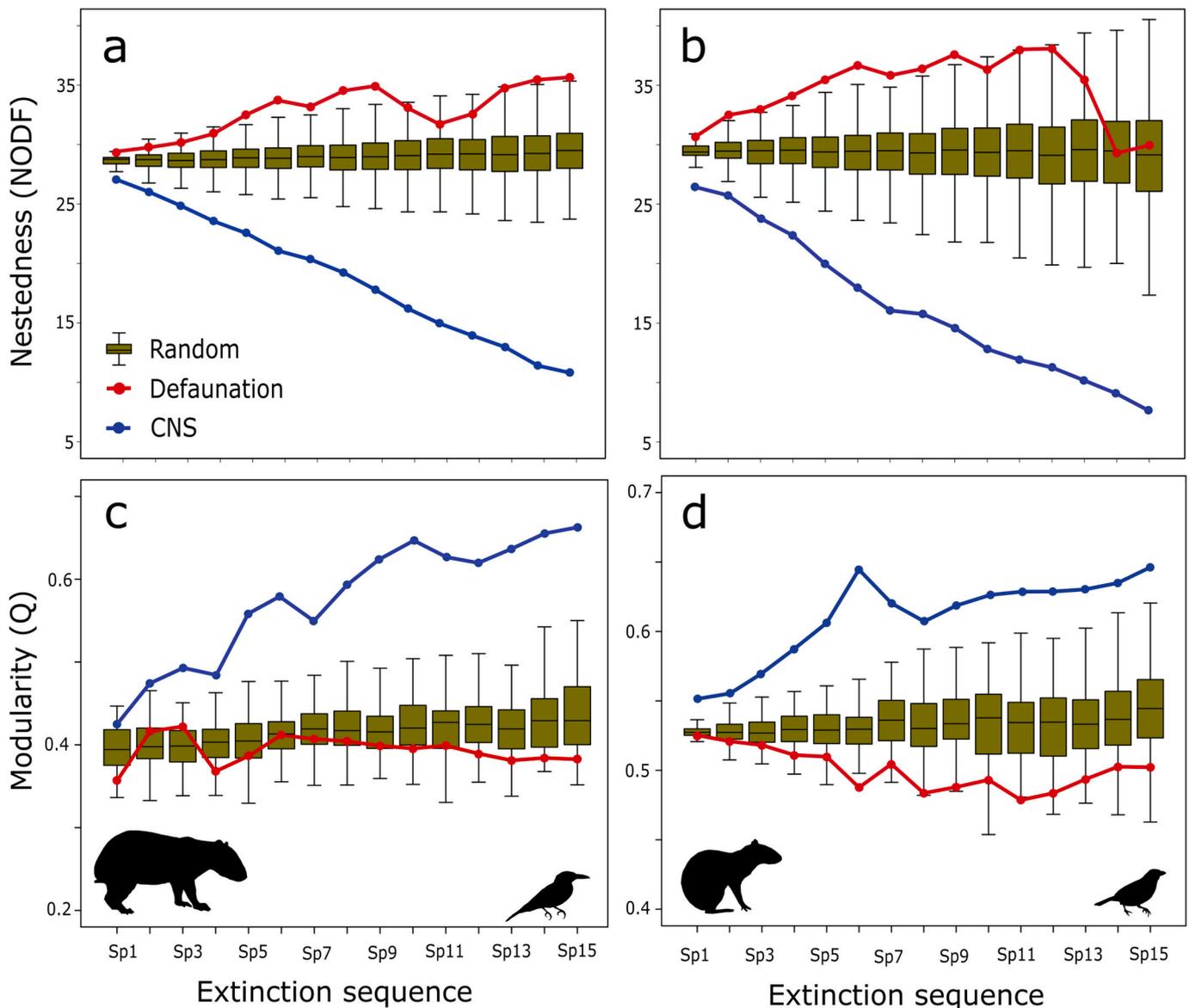


Fig. 1. Nestedness - NODF (a. Guacamayas, b. El Pino) and modularity - Q (c. Guacamayas, d. El Pino) values at each step of the species extinction model. The red line represents the simulation by defaunation, the blue line represents the loss of species according to the contribution to the network structure (CNS), and the green boxes represent the random scenario. The silhouettes represent the largest (*Cuculus paca*, Guacamayas; *Dasyprocta punctata*, El Pino) and smallest (*Megarynchus pitangua*, Guacamayas; *Saltator coerulescens*, El Pino) species eliminated in each defaunation scenario. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 2

Proportion of extinction steps in the Defaunation, Contribution to Network Structure (CNS), and Seed Dispersal Potential (SDP) scenarios in which the metrics of nestedness (NODF) and modularity (Q) for the structural component, and richness (FRic) and functional evenness (FEve) for the functional component were significantly higher or lower ($p < 0.05$) than those in the random scenario.

	Defaunation		CNS	
	Higher than random average	Lower than random average	Higher than random average	Lower than random average
Structural component				
Nestedness (NODF)	0.87	0.00	0.00	1.00
Modularity (Q)	0.00	0.13	0.97	0.00
Functional component			SDP	
Functional richness (FRic)	0.00	0.33	0.00	0.97
Functional evenness (FEve)	0.00	0.00	0.10	0.00

the random scenario.

3. Results

We recorded 1396 frugivory events involving 63 animal species (Appendix 5) and 53 plant species. The interaction networks of both locations showed similar levels of both nestedness and modularity, which were significantly higher than expected by chance (Table 1). The range of frugivore body mass in the Guacamayas location was 7 g – 8172 g and ranged from 7 g – 2674 g in El Pino. Species eliminated in the extinction simulations were >69 g and 52 g, respectively.

3.1. Impact of defaunation on network structural patterns

At both locations, the removal of species in order of their CNS gradually and significantly decreased nestedness (Fig. 1a and b, Table 2). An opposite pattern was observed in the defaunation scenario, where the absence of the larger body size species increased nestedness values significantly in most extinction steps (Fig. 1a and b, Table 2). For both locations, modularity increased significantly through the extinction steps of the CNS scenario (Fig. 1c and d, Table 2). This suggests that a fragmentation of the network into isolated modules occurred after the loss of species with higher CNS values. Though the defaunation scenario decreased modularity values at both locations, this change did not differ from that expected by chance across most extinction steps (Table 2).

3.2. Impact of defaunation on functional diversity patterns in the community

The FRic index decreased gradually in both locations, in both defaunation and SDP scenarios (Fig. 2a and b). The loss of larger body size species only modified FRic values significantly in the early extinction steps (Fig. 2a and b, Table 2). That is, the effect only occurred when species >2000 g were removed from the community at the Guacamayas location and 100 g at El Pino. FEve index was not affected in either location under any scenario (Fig. 2c and d). The highest proportion of values of this index did not differ from the random extinction scenario (Table 2).

4. Discussion

In this work, our predictions were partially fulfilled, since, in the face

of the loss of larger frugivore species (defaunation), the structural patterns of the networks in both locations were maintained. The indexes of functional diversity where abundance was not considered (FRic) responded negatively to defaunation, while the indexes related to the distribution of abundance in the functional space (FEve) were not affected. The Córdoba region, in Colombia, has been subjected to progressive fragmentation and habitat loss (Ballesteros-Correa and Linares-Arias, 2015); especially in the tropical dry forest, which has caused defaunation prior to our evaluation. Therefore, our results suggest that the structural patterns of the interaction networks are resistant to the defaunation process; however, the functional capacity of the communities may be seriously affected by the loss of larger body size frugivores, with potentially adverse repercussions on long term forest regeneration.

Our results show that the response of networks to the loss of larger body-sized species (defaunation) is linked to the current state of frugivore communities, and the distribution of interactions in the network. Particularly, the significant increase in nestedness was related to the loss of specialist species. In disturbed areas, the remaining species of larger body sized frugivores tended to establish interactions with fewer plant species (Montoya-Arango et al., 2019; Acevedo-Quintero et al., 2020a); Therefore, their removal led to an increase in the proportion of generalist species in the network, generating a higher degree of nestedness around the generalist core (Bascompte et al., 2003; Emer et al., 2020). Similarly, specialist species occupy peripheral positions in the modularity pattern of the networks (Ramos-Robles et al., 2018; Montoya-Arango et al., 2019); therefore, their elimination does not have important repercussions at the level of this structural pattern (Ramos-Robles et al., 2018). A contrasting situation is observed when eliminating species according to their contribution to the network structure (CNS), which is highly correlated with the *degree* (number of interactions established by each species) (Acevedo-Quintero et al., 2020a). Evident in this scenario is the loss of the nestedness pattern, as well as a progressive and significant increase in modularity through the extinction steps, which leads to a fragmentation of the networks into isolated modules. Both responses, nestedness, and modularity can be interpreted as the structural collapse of the network.

Previous studies have shown that defaunation has a negative effect on the maintenance of topological patterns of frugivore-plant interaction networks (Donatti, 2011; but see Donoso et al., 2020). In contrast, our study indicates that sequential loss of larger body size animals significantly increases nestedness patterns and has no significant effect on modularity. However, the negative consequences detected by Donatti (2011) are supported by the fact that larger species interact with a greater number of plant species (Vidal et al., 2013). Therefore, the simulation of their loss has repercussions on a structural collapse of the networks (Solé and Montoya, 2001; Memmott et al., 2004; Bastazini et al., 2019). This view omits possible compensatory density effects, i.e., that in the absence of large species, smaller species increase their population densities (Gonzalez and Loreau, 2009). This increase could eventually lead to the replacement of interactors (Costa et al., 2018), where small species occupy topologically important positions within the network. For example, Montoya-Arango et al. (2019), demonstrated that in defaunated environments, smaller species with higher population abundances occupy central and structurally important positions in a frugivore-plant network. Similarly, our results showed that despite the degree of previous defaunation, networks in both locations tended to maintain their modularity and nestedness. Even after simulating continual defaunation processes, these patterns were maintained. Therefore, we suggest that there is a certain degree of structural redundancy, which permits the replacement of important species in the maintenance of topological patterns of the interaction networks.

Our analysis indicate that the structural response is linked to the loss of specialists, which, from a functional point of view, leads to the generalization of networks (García et al., 2018; Emer et al., 2020). This effect and its possible consequences are reflected in changes in the functional diversity patterns of the frugivore community. In both

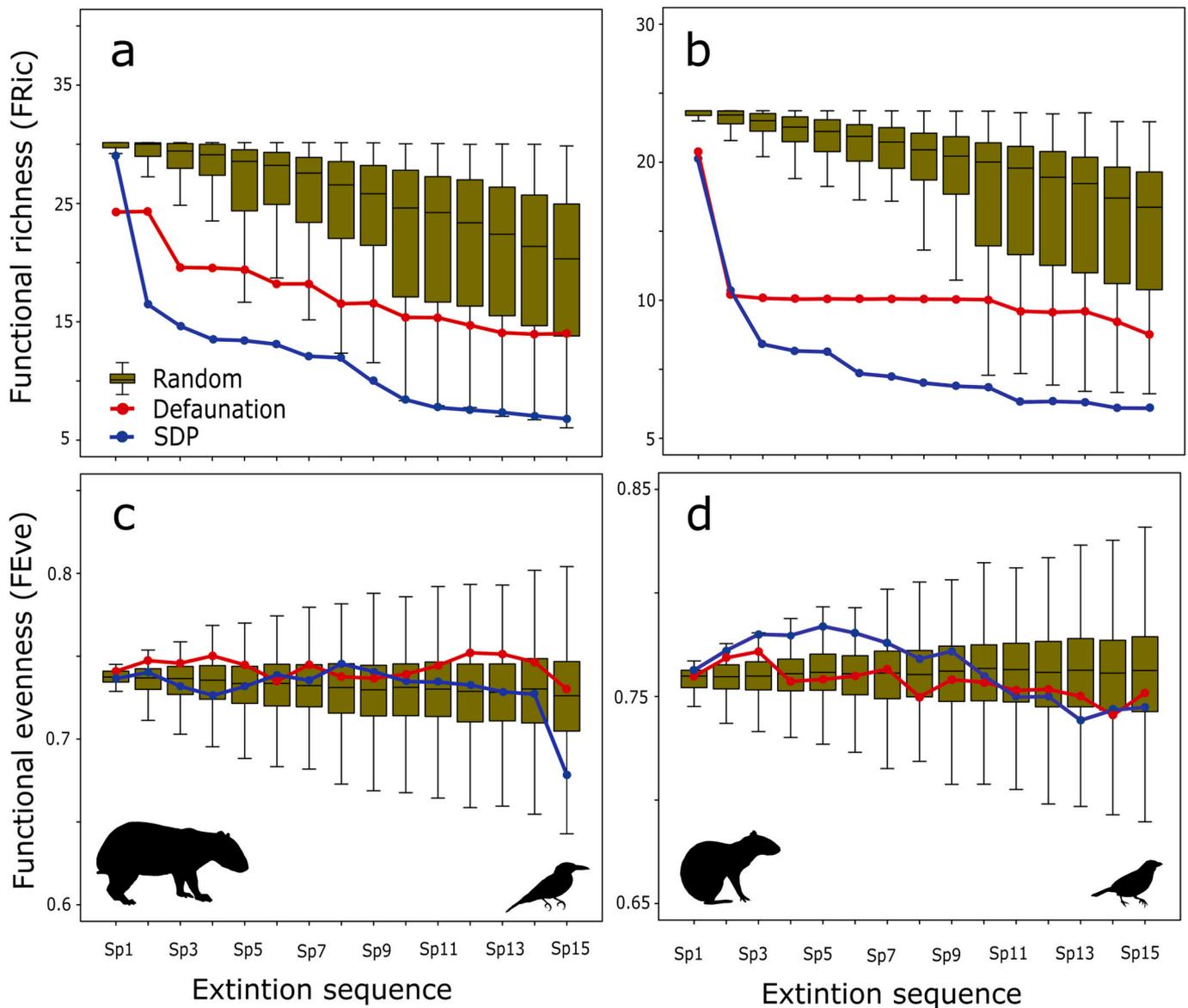


Fig. 2. Functional richness values - FRic (a. Guacamayas, b. El Pino) and functional evenness - FEve (c. Guacamayas, d. El Pino) at each step of the species extinction model. The red line represents the simulation by defaunation, the blue line represents the loss of species according to the seed dispersal potential (SDP), and the green boxes represent the random scenario. The silhouettes represent the largest (*Cuniculus paca*, Guacamayas; *Dasyprocta punctata*, El Pino) and smallest (*Megarynychus pitangua*, Guacamayas; *Saltator coerulescens*, El Pino) species eliminated in the defaunation scenario. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

locations, the FRic index significantly decreases with the loss of the larger body-sized species, which reveals a drastic effect of the defaunation process on the maintenance and functioning of the ecosystem. That is, when mammal species such as *Dasyprocta punctata* (2674 g) at the El Pino location and *Cuniculus paca* (8172 g) at the Guacamayas location are eliminated, part of the potentially available resources (fruits) remain unexploited or can be depredated by small rodent species and invertebrates (Galetti et al., 2006; Galetti et al., 2015). From the point of view of the plants, this means that large-fruited species (e.g., *Pouteria* spp., *Astrocaryum malybo*, *Bactris gasipaes*) lose the last potential effective dispersers. Thus, the roles played by relatively large species are not replaceable, with potentially harmful consequences for the plant community (Bastazini et al., 2019). Moreover, the loss of potential plant dispersers is not only evident after extinction simulations. For example, according to our observations, the *Attalea butyracea* palm at the Guacamayas locality only received visits from the red squirrel (*Notosciurus granatensis*). This plant species can be consumed by a wide variety of

frugivores in conserved areas (Delgado Martinez and Mendoza, 2022), and although the red squirrel can act as a potential disperser (Carvajal and Adler, 2008), in an area affected by defaunation, many of its fruits may remain under the parental canopy.

On the other hand, the stability of FEve index in all extinction scenarios (defaunation and SDP), indicates that even after eliminating a large part of the frugivore species, the distribution of abundances in the remnant functional space is equitable. That is, the remaining dominant species within the community are fulfilling functionally redundant roles as seed dispersers. This effect is associated with patterns of homogenization of interactions that occur in highly impacted areas (Laliberté and Tylianakis, 2010; Emer et al., 2020). The locations evaluated in this study have historically been subjected to high anthropogenic pressures and given that defaunation not only implies local extinction of species but also modification of abundances (Galetti and Dirzo, 2013; Dirzo et al., 2014); it is to be expected that the effects on metrics including abundance are evident even before performing extinction simulations.

The species extinction simulations used in our study showed that the continuation of the defaunation process presented different responses at the structural (stability) and functional (affectation) level of the interaction networks. This result is congruent with and reinforces the findings of Donoso et al. (2020) who, from another perspective, evaluated the structural (in terms of the number of interactions and secondary extinctions) and functional (in terms of dispersal distance) response to defaunation in bird-plant networks. In our work, the record of interactions was not limited to a particular taxonomic group (including birds, mammals, and some reptiles), increasing the representation of the frugivore community, and therefore increasing the variability in traits associated with seed dispersal. In addition, the use of functional ecology indices to quantify the community's functional capacity response allows extending the approach to other contexts or interaction types.

5. Conclusions

Although defaunation does not cause an immediate structural collapse of interaction networks, the loss of larger body-sized species does have the potential to affect regeneration processes in natural forests. Particularly through the loss of potential dispersers of large-fruited plants. Therefore, from the point of view of conservation and maintenance of ecological functions, it is necessary to evaluate the risk of local extinction of medium and large species such as *Dasyprocta punctata* and *Cuniculus paca*, which historically have been subjected to high rates of hunting in the region. Particularly, the tropical dry forest in Colombia is under great pressure from extensive cattle ranching activities. Promoting production systems that combine economic activity with the maintenance of forest cover (e.g. agroforestry systems) could be an important strategy in the Colombian Caribbean.

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Authors statement

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

Declaration of Competing Interest

None.

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Appendix A. Supplementary data

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