Journal of Tropical Ecology

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Research Article

Cite this article: Goebel LGA, Vitorino BD, Frota AVB, and Santos-Filho M (2023). Body mass determines the role of mammal species in a frugivore-large fruit interaction network in a Neotropical savanna. *Journal of Tropical Ecology*. **39**(e12), 1–8. doi: https://doi.org/10.1017/S0266467422000505

Received: 19 October 2021
Revised: 3 October 2022
Accepted: 10 December 2022

Keywords:
Cerrado; ecological networks; frugivory; seed dispersal; *Tapirus terrestris*

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Body mass determines the role of mammal species in a frugivore-large fruit interaction network in a Neotropical savanna

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Abstract

Frugivorous mammals play an important role in maintaining biodiversity and are considered one of the main dispersers of large seeds. In this study, we describe the structure of the interaction network between non-flying mammals and seven plant species with large fruits in a megadiverse savanna-forest mosaic in the Brazilian Cerrado. We also evaluated the individual contribution of each species to the organization of the interaction network and tested whether body mass determined the mammals' role in the network. To record frugivory events of mammals with arboreal and terrestrial habits, camera traps were installed at ground and canopy levels. We identified 18 mammal species interacting with seven plant species in 515 frugivory events. Our observations highlight an interaction network with a modular and non-nested topology and the important role of large mammals in the network structure, which reflects the importance of the group in potential seed dispersal. The extinction of large frugivorous mammals can cause several damages to ecosystem services in the Brazilian Cerrado through changes in network structure, especially threatening the survival of plant species with large fruits.

Introduction

Animal-plant interactions are important for maintaining biodiversity and ecosystem functions (Jordano *et al.* 2011). Among vertebrates, mammals receive special attention given their important role in pollination and seed dispersal, which provides gene flow and helps in the proliferation of many plant species (Jordano *et al.* 2007, Golin *et al.* 2011). Interactions between animals and plants are influenced by biological attributes, such as fruit biomass, that shape species interactions (Fuzessy *et al.* 2018). At the same time, several biological characteristics of the species may constitute morphological or spatiotemporal barriers that limit some types of pairwise interactions, which are described as the 'forbidden links' hypothesis (Jordano *et al.* 2003). Therefore, large fruits tend to be dispersed by large mammals, as they could not be dispersed by other animal groups due to the morphological restrictions inherent to small dispersers (Jordano *et al.* 2007, Lim *et al.* 2020).

Interaction networks have been used as tools to understand the complexity of ecological interactions and the influence of morphological traits and have been considered a powerful methodology that maps interactions, characterizes the functional roles of species within communities, the diversity of relationships established between frugivores and plants, and the importance of the species involved (Bascompte & Jordano 2007). Network analyses include interactions between species as an additional layer in ecological evaluations, resulting in great advances in understanding the establishment of biological communities in different ecosystems (Delmas *et al.* 2019). Recently, this approach has provided important information on the ecological role of vertebrates in seed dispersal (Vidal *et al.* 2013), in addition to revealing the drastic reduction in the abundance of the dispersers and changes in the functional roles of species (Galetti *et al.* 2013, Carreira *et al.* 2020).

The use of the interaction network approach can help in conservation and restoration strategies, ensuring the best functioning of ecosystems (Harvey *et al.* 2017, Raimundo *et al.* 2018) and avoiding species extinctions (Carreira *et al.* 2020). In this sense, the investigation of legally protected areas that can serve to define conservation strategies emerges as part of environmental planning for the maintenance of biodiversity and ecological processes in threatened ecosystems. These protected areas have remnants of natural vegetation that are important for the maintenance of biodiversity due to the existing complex structure (Sukma *et al.* 2019, Magioli *et al.* 2021a, Magioli *et al.* 2021b) and serve as stepping stones for connection with smaller fragments (Wintle *et al.* 2019). The low degree of human intervention in these areas allows for the occurrence of several groups of animals and plants, including a high diversity of mammals, which play an important role in seed dispersal, especially of plants that produce large fruits, that, due to morphological restrictions, have their seeds dispersed only by a specific set of mammals (Bello *et al.* 2015, Magioli *et al.* 2021a).

Herein, we aim to describe the structure of the interaction network between frugivorous non-flying mammals and seven plant species that produce large fruits, in a protected savanna-forest mosaic in the Brazilian Cerrado, and to evaluate the individual contribution of the species involved. Our hypothesis is that the interaction network will present a modularity and non-nested structure, due to the existing biodiversity in the area (Santos-Filho & Silva 2002, Santos-Filho *et al.* 2012) and the presence of morphological barriers that restrict consumption of the large fruits evaluated, which can form a set of species closely linked within modules (Almeida-Neto *et al.* 2008, Donatti *et al.* 2011). We also expect a positive relationship between mammalian biomass and its relevance in the context of mutualistic interactions, since larger and heavier species tend to have less morphological restrictions concerning the ingestion of large fruits, besides needing a greater energy demand, which drives the consumption of fruits (Donatti *et al.* 2011, Galetti & Dirzo 2013).

Materials and methods

Study area

The study was carried out at the Serra das Araras Ecological Station (hereafter SAEE), a Federal Integral Protection area that occupies an area of 28.700 hectares, between the municipalities of Porto Estrela and Cáceres in the State of Mato Grosso, Brazil (15° 38’32.0” S 57°11’27.3” W) (Brasil 2016). The predominant climate is of the semi-humid hot tropical type, classified as megathermal Aw with two seasons: dry, which extends from May to October, and rainy from November to April, with annual precipitation around 1.500 mm and maximum average temperature of 30º C and minimum 20º C (Alvares *et al.* 2013). From a biogeographic perspective, the SAEE is located in an ecotone area with high biodiversity, inserted in the Cerrado and in contact with two other Brazilian biomes, the Amazon Forest and Pantanal wetland (Vitorino *et al.* 2018). Inside the SAEE, the samples were taken in a vegetation mosaic of semi-deciduous seasonal forest, savanna woodland (cerrado *sensu stricto*) and gallery forest.

Data collection

In the SAEE, we collected data between September 2019 and September 2020, totalling 13 months of consecutive field expeditions. We used the photographic trapping methodology to record frugivorous mammal-fruit interactions because this method is efficient for sampling interactions between mammals and plants, and it is a minimally invasive methodology (Bogoni *et al.* 2018). To record information about the interactions, camera traps were installed about 50 cm above the ground and attached to the trunks of the trees (Raíces *et al.* 2017, Carreira *et al.* 2020). To record the frugivorous species with arboreal habits and their ecological interactions established there (Zhu *et al.* 2021, Moore *et al.* 2021), a wooden structure was created, in the centre of which the camera was fixed and hoisted so that it could be placed on the branches with the greatest abundance of fruits (Figure S1). The cameras remained active for 24 hours each day and were configured to record 10-second videos after motion detection, with intervals of five seconds between videos.

The criteria for selecting the trees to be sampled were to be in the fruiting period of the focal plant species (Table S2), to have fleshy and/or attractive fruits for frugivorous species with a size greater than 40 mm (Table S2), as described by Kuhlmann (2018), and presenting a minimum distance of 200 metres from the other individuals sampled. Thus, the cameras were installed focusing on seven species, viz., *Hymenaea courbaril* L. (Fabaceae), *Genipa americana* L. (Rubiaceae), *Pouteria ramiflora* (Mart.) Radlk. (Sapotaceae), *Cordiera macrophylla* (K.Schum.) Kuntze (Rubiaceae), *Dipteryx alata* Vogel (Fabaceae), *Diospyros hispida* ADC. (Ebenaceae), and *Attalea speciosa* Mart. ex Spreng. (Arecaceae).

We used 79 camera traps operating an average of 30 days on each individual of the seven plant species, in which we carried out a sampling effort of 28,344 hours of monitoring with the camera traps on the canopy and 68,288 hours on the ground, totalling 97,632 hours of sampling. The sampling effort conducted for each species was based on the number of individuals present in the area, as well as on species phenology (*i.e.*, availability of fruits over time), so that the most representative species were sampled for a longer time (Table 1).

We defined an interaction event (*i.e.,* frequency) every time a mammal ingested or carried a fruit with its seed. We consider as independent records all interactions that were separated from each other by an interval equal to or greater than 30 seconds (*sensu* Carreira *et al.* 2020). The taxonomic classification for plants and mammals followed Brazilian Flora (Brazil Flora 2020) and List of Mammals of Brazil (Abreu-Jr *et al.* 2020), respectively. Non-flying mammals were separated into three categories: small mammals, with a body mass of up to one kilogram, medium-sized mammals, with body mass between one and seven kilograms (Chiarello 2000), and large mammals with a body mass greater than seven kilograms (Emmons & Feer 1997). Information on the body mass of mammal species was obtained from Wilman *et al.* (2014).

Data analysis

For the analysis of interaction networks, we created a matrix weighted by the frequency of interactions collected in the field. All subsequent analyses were performed in the R software (R Development Core Team 2019). The completeness of our sampling was obtained by dividing the total number of observed links (which quantifies the pairing between species) by the estimated number via *Chao* 1 (Chao 1984), using the *iNEXT* R-package (Hsieh *et al.* 2020). We used the bipartite R-package (Dormann *et al.* 2020) to assess the network metrics: species richness of both mammals and plants (network size); number of interactions; number of links; nestedness, using NODF (Nestedness metric based on Overlap and Decreasing Fill, Almeida-Neto *et al.* 2008) and wNODF (Weighted Nestedness metric based on Overlap and Decreasing Fill (Almeida-Neto & Ulrich 2011), that describes the pattern of interaction in which specialist species interact with a subset of generalist species; and modularity (Q_w), which identifies the presence of subsets of species that tend to interact more often with each other than with species from other subsets (Olesen *et al.* 2007). Specifically, for NODF, wNODF, and Q_w, we evaluated the level of significance by comparing the results obtained with those of 1,000 random networks generated according to null models using the *vaznull* function, which maintains the same patterns of connectance and total marginals in relation to the observed matrix (Vázquez *et al.* 2007, Dormann *et al.* 2020).

To determine the role of species in the network, we calculated the metrics Species Strength (SS), which quantifies the importance

https://doi.org/10.1017/S0266467422000505 Published online by Cambridge University Press

Table 1. Number of camera traps installed and sampling effort in hours per fruit plant species in the Serra das Araras Ecological Station.

Taxon	Sampled individuals	Number of cameras (ground)	Effort in hours (ground)	Number of cameras (canopy)	Effort in hours (canopy)
Hymenaea courbaril L.	11	11	11,952	4	936
Genipa americana L.	5	5	6,984	5	1,848
Pouteria ramiflora (Mart.) Radlk	6	6	4,440	3	1,632
Cordiera macrophylla (K.Schum.) Kuntze	10	10	8,424	9	8,064
Diospyros hispida A.DC.	5	5	5,976	3	840
Dipteryx alata Vogel	7	6	23,928	5	15,024
Attalea speciosa Mart. ex Spreng	6	7	7,584	0	0
Total	50	50	68,288	29	28,344

of each species based on the sum of the dependencies of their respective partners, and Closeness Centrality (CC), which measures the proximity of a species to all others, indicating the capacity of a species to act as a hub and increase the cohesion of the network (Martín González *et al.* 2010, Delmas *et al.* 2019). Also, we verified the role of species in the modular structure, calculating the standardized pattern and connectivity of species between modules (*c*-score) and within their respective module (*z*-score). In this approach, species can be classified as *peripheral*, when they present low values of *c*- and *z*-score; *connector*, with high *c*-score and low *z*-score; *module hub*, with high *z*-score and low *c*-score and; network hub, with high *c*- and *z*-score values (Olesen *et al.* 2007). We determined the cut-off values of *c*- and *z*-score from 100 null matrices, following Dormann & Strauss (2014), which in our case was $c_{\text{critical}} = 0.71$ and $z_{\text{critical}} = 1.86$. Next, we performed a non-parametric Wilcoxon test to assess whether there was variation in the metrics at the species level (Species Strength, Closeness Centrality, *c*- and *z*-score) concerning different trophic levels (mammals and plants).

Additionally, we used a principal component analysis (PCA) to synthesize the role of mammals according to the metrics Species Strength, Closeness Centrality, and *c*- and *z*-score. The first principal component (PC1) explained 67% of the variation of the metrics and was used as the descriptor of the contributions exerted by the species. Thus, the higher the value of PC1, the greater the relevance of the species in the structuring of the network. Finally, we tested the mammals' body mass (logarithmized for better fit) as a possible predictor to determine the role of these species in the network, using a linear model (LM).

Results

We identified 18 mammal species, grouped according to their body size into small ($n = 5$), medium ($n = 9$) and large ($n = 4$), interacting with seven plant species. Moreover, we recorded 515 frugivory events distributed into 48 links. The number of estimated links was 76, resulting in a sampling completeness of 63%. The interaction network evaluated was not significantly nested (NODF = 54.95, $p > 0.05$; wNODF 23.45, $p > 0.05$) but significantly modular (Qw = 0.43, $p < 0.05$). The mammal species that consumed fruits the most were *Tapirus terrestris*, *Dicotyles tajacu,* and *Cuniculus paca*, with 130, 69, and 66 frugivory events, respectively. Among the plant species with the largest number of interactions, *Diospyros hispida* ($n = 164$), *Pouteria ramiflora* ($n = 129$), and *Dipteryx alata* ($n = 60$) stand out (Figure 1). When evaluating the Species Strength metric, among the mammals *Tapirus terrestris* (2.15), *Cuniculus paca* (1.17), and *Cerdocyon thous* (0.76) had the highest ones, while among the plants the highest values were of *Dipteryx alata* (5.10), *Cordiera macrophylla* (3.45), and *Diospyros hispida* (3.32). Regarding the Closeness Centrality measure, the species that had the highest values were *Tapirus terrestris* (0.06), *Mazama* sp. (0.06), and *Cerdocyon thous* (0.06) among the mammals, and *Dipteryx alata* (0.14), *Cordiera macrophylla* (0.14), and *Diospyros hispida* (0.14) among the plants (Tables 2 and 3). By checking the role of species in the modular structure of the network, the mammals *Tapirus terrestris* (2.18), *Cerdocyon thous* (1.78) and *Dicotyles tajacu* (1.78) and the plants *Cordiera macrophylla* (0.90), *Pouteria ramiflora* (0.70), and *Genipa americana* (0.16) showed higher *z*-score values, while the mammals *Tayassu pecari* (0.67), *Dicotyles tajacu* (0.66), and *Proechimys longicaudatus* (0.64) and the plants *Pouteria ramiflora* (0.55), *Hymenaea courbaril* (0.38), and *Diospyros hispida* (0.36) showed higher *c*-scores. *Tapirus terrestris* was the only species in the network classified as a module hub, while the others were peripheral (Figure 2).

Using the Wilcoxon non-parametric test, we verified that there was significant variation between the two trophic levels for Closeness Centrality ($W = 0$; $p < 0.001$) and Species Strength ($W = 8$; $p < 0.001$), with plants assuming more central positions and having greater strength of interactions (Figure 3), but we did not observe significant variation for *c* and *z*-scores. We did not observe variation between the different trophic levels for *c* and *z*-scores ($p > 0.05$). In addition, we also identified that the body mass of mammalian species acts as an important predictor of the role that these species play in the network, with mammals with higher biomass being the most relevant ($R^2_{adj} = 0.40$; $p < 0.01$) (Figure 4).

Discussion

Our findings evidenced a modular but non-nested interaction network, with a high number of frugivorous mammals acting as potential dispersers for several plant species that produce large seeds. Furthermore, we found that disperser biomass was a good predictor of the role that these mammals play in the network. In the evaluated interaction network, the largest (heaviest) mammals were also the most important in the modular structure, assuming a central position and with a high value in the species strength.

We observed significant modularity values of the interaction network of mammals with large fruits in the Cerrado, as previously observed in the Atlantic Forest and Pantanal (Donatti *et al.* 2011,

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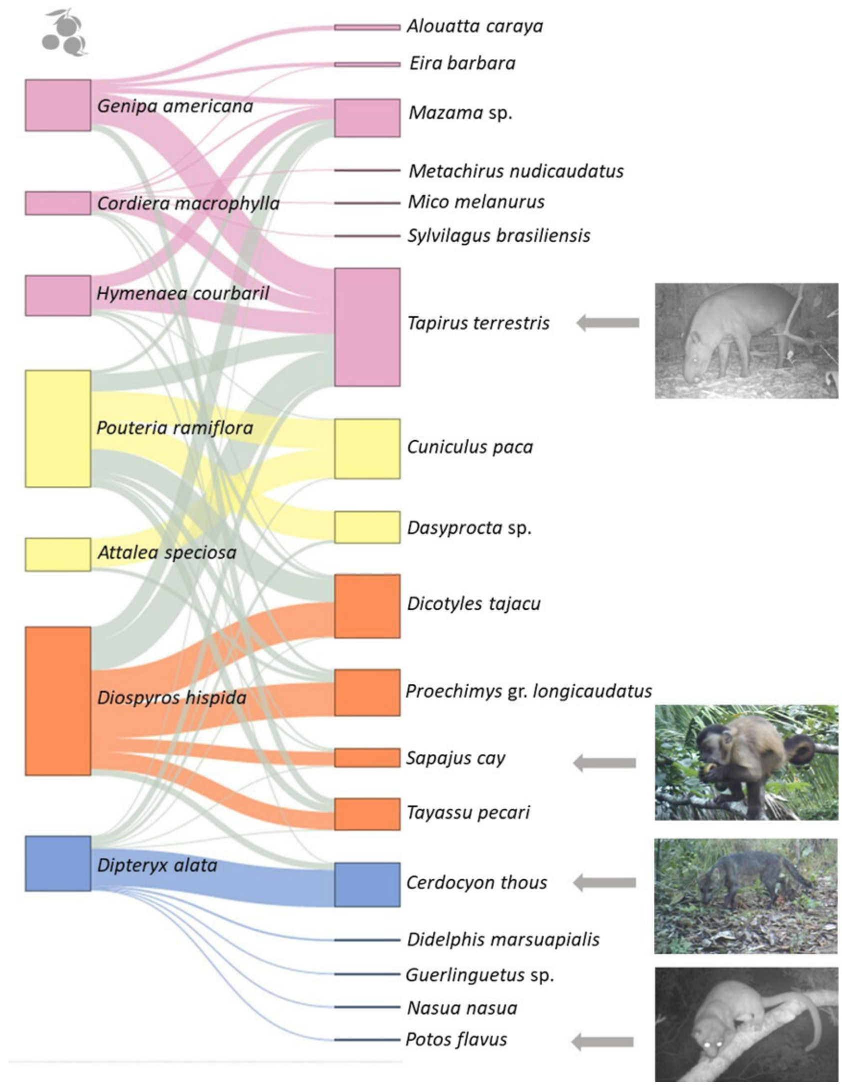

Figure 1. Interaction network between frugivorous mammals and plants that produce large fruits, in a Neotropical savanna in the Serra das Araras Ecological Station, Brazil. Modules are highlighted in the network by different colours, and the grey lines represent the interactions established between species of distinct modules.

Carreira *et al.* 2020), and a non-nested pattern, which was in accordance with our expectations. However, environmental variables such as phenology and plant abundance observed may have influenced the structuring of the interaction network, such as grouping into modules (Vázquez *et al.* 2007, Encinas-viso *et al.* 2012, Machado-de-Souza *et al.* 2019). Regarding modularity, still in line with what was observed for other megadiverse areas, we identified a system in which a set of species tends to interact more with each other than with species from other sets (Olesen *et al.* 2007), which results in a more robust and resilient system in the presence of possible indirect and direct impacts (Carreira *et al.* 2020). In non-modular networks, as observed, for example, by Queiroz *et al.* (2021) and Naniwadekar *et al.* (2019), environmental impacts are felt more intensely and can result in a cascade effect if a species disappears from the system, compromising the network of interactions (Olesen *et al.* 2007). Neotropical interaction networks tend to be less nested (Dugger *et al.* 2019), as we have observed, which may indicate that large-fruited plants attract different subsets of frugivorous species so that interactions are not necessarily occurring with more generalist mammals (Almeida-Neto *et al.* 2008, Crestani *et al.* 2019, Naniwadekar *et al.* 2019).

Using species-level metrics, we highlight three important fruit trees for maintaining the structure of the interaction network: *D. alata*, *C. macrophylla,* and *P. ramiflora*. In addition, we showed that plants have greater strength of interaction and act as connectors in the system. In this sense, this group increases the connectivity and cohesion of the network, suggesting that it is the species that act to maintain the existing biodiversity and the dynamics of the ecosystem, thus avoiding extinctions (Cagua *et al.* 2019, Ramos-Robles *et al.* 2018). These large-seeded plant species are categorized as attractive to fauna due to their high nutritional value (Kuhlmann 2018) and make potential contributions to carbon storage (Bello *et al.* 2015). Also, they are important for the maintenance of the mammal community, including rare species for the region where the study was carried out, such as the Kinkajou (*Potos flavus*), which was recorded interacting with *D. alata*, this being the first record with documented evidence for the species in the SAEE (see Figure 1).

Our results demonstrate the importance of medium and large mammals in the evaluated interaction network with large fruits. Among the species, we can highlight three *T. terrestris*, *C. thous* and *T. pecari*, two of which are categorized as Vulnerable to Extinction at the national and international level (IUCN 2022) and considered important in other studies of ecological interactions (Donatti *et al.* 2011, Vidal *et al.* 2013, Bogoni *et al.* 2018). Specifically, the tapir (*Tapirus terrestris*), identified as module hubs, as explained by Donatti *et al.* (2011), interacts with a high diversity of plant species and stands out for the quality of seed

Table 2. Network metrics evaluated at the species level (Species Strength, Closeness Centrality, *c* and *z*-score) of an interaction network between frugivorous mammals and plants that produce large fruits in a Neotropical savanna in the Serra das Araras Ecological Station, Brazil. Mammal body mass was obtained from Wilman *et al.* (2014). The species were separated into small mammals (weighing up to 1 gg), medium-sized mammals (1 to 7 kg) (Chiarello 2000), and large mammals (more than 7 kg) (Emmons & Feer 1997).

Taxon	English name	Species strength	Closeness centrality	*C*-value	*Z*-value	Body mass (g.)	Group
Carnivora							
Canidae							
Cerdocyon thous (Linnaeus, 1766)	Crab-eating Fox	0.76	0.06	0.19	1.78	5239.98	Medium
Mustelidae							
Eira barbara (Linnaeus, 1758)	Tayra	0.10	0.05	0	−0.40	3910.03	Medium
Procyonidae							
Nasua nasua (Linnaeus, 1766)	South American Coati	0.01	0.05	0	−0.46	3793.85	Medium
Potos flavus (Schreber, 1774)	Kinkajou	0.01	0.05	0	−0.46	3000	Medium
Artiodactyla							
Cervidae							
Mazama sp. (Rafinesque, 1817)	Red Brocket	0.64	0.06	0.36	0.22	22799.75	Large
Tayassuidae							
Dicotyles tajacu (Link, 1795)	Collared Peccary	0.57	0.06	0.66	0.89	21266.69	Large
Tayassu pecari (Link, 1975)	White-lipped Pecarry	0.31	0.06	0.67	−0.69	32233.69	Large
Didelphimorphia							
Didelphidae							
Didelphis marsuapialis (Linnaeus, 1758)	Common Opossum	0.03	0.05	0.03	−0.40	1091.16	Small
Metachirus nudicaudatus (Geoffroy, 1803)	Brown Four-eyed Opossum	0.03	0.04	0	−0.51	375	Small
Lagomorpha							
Leporidae							
Sylvilagus brasiliensis (Linnaeus, 1758)	Tapeti	0.38	0.04	0	−0.51	949.99	Small
Perissodactyla							
Tapiridae							
Tapirus terrestris (Linnaeus, 1758)	Lowland Tapir	2.07	0.07	0.35	2.18	207500.91	Large
Primates							
Atelidae							
Alouatta caraya (Humboldt, 1812)	Black-and-gold Howler Monkey	0.08	0.04	0	−0.44	5862.46	Medium
Cebidae							
Sapajus cay (Illiger, 1815)	Azara's Capuchin	0.16	0.05	0.61	−1.02	2687.21	Medium
Mico melanurus (Geoffroy, 1812)	Black-tailed Marmoset	0.03	0.04	0	−0.51	335.61	Small
Rodentia							
Cuniculidae							
Cuniculus paca (Linnaeus, 1766)	Paca	1.17	0.05	0.06	0.70	8172.55	Medium
Dasyproctidae							
Dasyprocta sp. (Illiger, 1811)	Agouti	0.29	0.05	0.27	−0.70	2492.48	Medium
Echimyidae							
Proechimys longicaudatus (Rengger, 1830)	Rodent	0.50	0.05	0.64	0.81	205	Small
Sciuridae							
Guerlinguetus sp. (Gray, 1821)	Squirrels	0.01	0.05	0	−0.46	384.875	Small

Table 3. Network metrics evaluated at the species level (Species Strength and Closeness Centrality) for the group of plants of an interaction between frugivorous mammals and plants that produce large fruits, in a Neotropical savanna in the Serra das Araras Ecological Station, Brazil.

Taxon	Species strength	Closeness centrality	C-value	Z-value
Arecales				
Arecaceae				
Attalea speciosa Mart.	0.56	0.13	0.23	−0.70
Ericales				
Ebenaceae				
Diospyros hispida A.DC.	3.32	0.14	0.36	NA
Sapotaceae				
Pouteria ramiflora (Mart.) Radlk.	2.46	0.14	0.55	0.70
Fabales				
Fabaceae				
Dipteryx alata Vogel	5.10	0.14	0.09	NA
Hymenaea courbaril L.	0.68	0.14	0.38	−1.07
Gentianales				
Rubiaceae				
Genipa americana L.	2.40	0.13	0.15	0.16
Cordiera macrophylla (K. Schum.) Kuntze	3.45	0.14	0.05	0.90

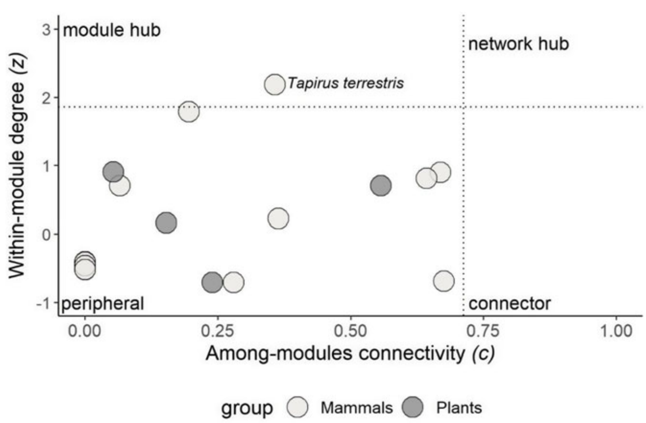

Figure 2. Species' role in the modular structure of an interaction network between frugivorous mammals and plants that produce large fruits in a Neotropical savanna at the Serra das Araras Ecological Station, Brazil.

dispersal over long distances (O'Farrill *et al.* 2013, Jordano *et al.* 2007, Fuzessy *et al.* 2018). These results demonstrate the need for identifying the ecological functions performed by the species, such as frugivory and seed dispersal, given that extinctions can cause cascading effects in the system and compromise these ecosystem services (O'Farrill *et al.* 2013, Vidal *et al.* 2013, Godínez-Alvarez *et al.* 2020). Regarding *C. thous*, this species was also mentioned as relevant in ecological interaction studies, especially in degraded ecosystems, due to its tolerance to environmental changes and ability to disperse seeds over long distances (Bogoni *et al.* 2018).

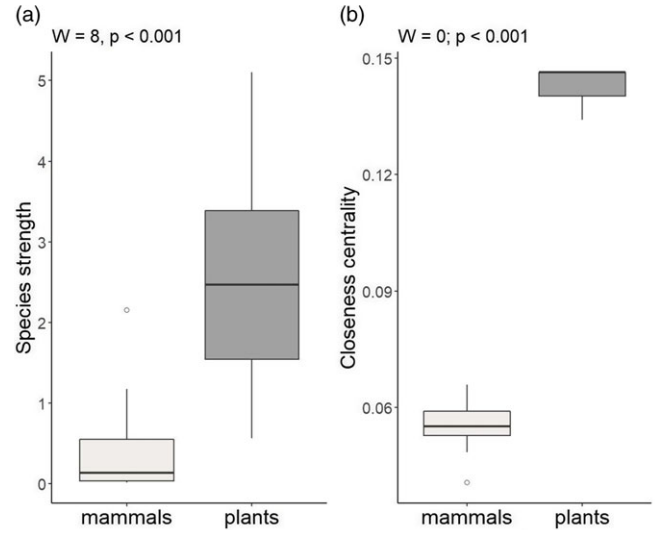

Figure 3. Significant variation in the species roles of an interaction network between frugivorous mammals and plants that produce large fruits, in a Neotropical savanna in the Serra das Araras Ecological Station, Brazil.

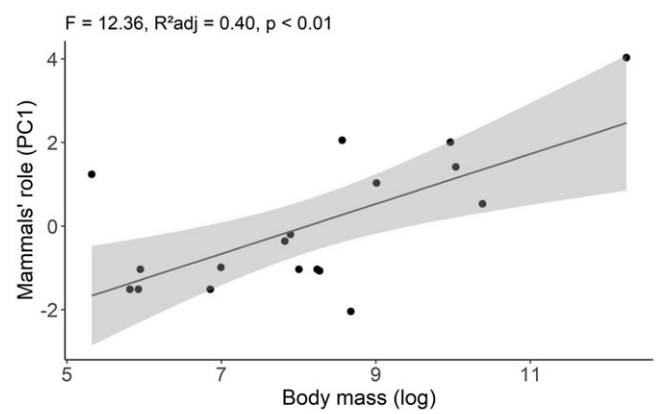

Figure 4. Body mass as a predictor of the role of mammals in the network structure. PC1 Index reflects the species-level metrics Species strength, Closeness centrality, and *c*- and *z*-scores.

Besides verifying the important species in the evaluated interaction network, we also showed that mammal biomass is an ecological determinant of the role that these species play in the network, with a positive and significant relationship with the metrics used in this study. These results support our hypothesis that large mammals provide a major contribution to network structure and fruit removal. Other studies observed similar results, as highlighted by Donatti *et al.* (2011) in a system evaluated in the Pantanal, in which large frugivores interacted with many plants with fruits of different sizes. Therefore, large mammals are essential elements in the structure of frugivory networks (Palacio *et al.* 2016) and play a fundamental role in the processes of seed dispersal and recruitment (Donatti *et al.* 2011, Fuzessy *et al.* 2018), including those of plants that produce large seeds, as shown in our study.

The disappearance of large mammals is one of the current problems of the Anthropocene and is the result of fragmentation, habitat loss, and hunting (Dirzo *et al.* 2014, Ripple *et al.* 2015). Defaunated ecosystems, where the large fauna is extinct, present showchanges in ecological processes (Young *et al.* 2016, Lim *et al.* 2020) and in functional roles (Carreira *et al.* 2020). This favours mesocarnivores and generalists at small scales (Ripple *et al.* 2015), increases seed predation (Galetti *et al.* 2015, Lacher *et al.* 2019), and changes the carbon and nitrogen cycles (Bello *et al.* 2015, Villar *et al.* 2020).

Body mass and species richness are related to ecosystem services and ecological function. Thus, the presence of large mammals in large remnants indicates the importance of preserving these areas (Magioli *et al.* 2021a, Magioli *et al.* 2021b). Therefore, our results emphasize the importance of conserving areas of Cerrado, to preserve species and promote the stability of ecological interactions (Ferreira *et al.* 2020). Researches carried out in this context provide data that enable the implementation of efficient measures to keep communities viable and prevent extinctions (Carreira *et al.* 2020), ensuring better ecological functioning (Harvey *et al.* 2017, Raimundo *et al.* 2018).

Conclusions

In summary, we highlight the importance of a protected environment in the savannas of the Neotropical region for the maintenance of interactions between species of the fauna and flora. In general, the seven observed plant species strongly contribute to the structure of the interaction network with non-flying mammals. We emphasize the importance of large mammals in this process, especially *Tapirus terrestris*, which is a threatened species. The disappearance of large mammals can harm the structure of interaction networks, mainly compromising the maintenance of plant species that have large fruits and, consequently, other ecosystem services. Thus, our results demonstrate the importance of the large fauna, indicating that the absence or loss of large frugivores will have negative consequences on ecological dynamics.

Supplementary material. To view supplementary material for this article, please visit https://doi.org/10.1017/S0266467422000505

Acknowledgments. We are grateful to the postgraduate programme in Environmental Sciences at Universidade do Estado de Mato Grosso, campus of Cáceres. The Chico Mendes Institute for Biodiversity Conservation and the Serra das Araras Ecological Station. We thank Carlos de Souza Ferreira, Marcelo Andrade, Felipe Mendes, Erinalda Mendes, Vicente da Costa, Victor Hugo de Oliveira Henrique and Derick Victor de Souza Campos for their support and field logistics, Daiane Cristina Carreira and Leticia Prado Munhoes for the valuable discussions about the work, Dandara Sebastian for identifying the plant species, Edson Fiedler de Abreu-Jr for identifying species of Sciurini and Márcio Leite de Oliveira for identifying species of Cervidae.

Financial support. This study was partially funded by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior – Brazil (CAPES) – Financing Code 001, and the Fundação de Amparo à Pesquisa do Estado de Mato Grosso (FAPEMAT): LGAG received a CAPES scholarship; BDV and AVBF received a scholarship from FAPEMAT/CAPES 007/2018.

Competing interests. The authors declare none.

References

Abreu-Jr EF, Casali DM, Garbino GST, Loretto D, Loss AC, Marmontel M, Nascimento MC, Oliveira ML, Pavan SE and Tirelli FP (2020) *Lista de Mamíferos do Brasil 2020*. Comitê de Taxonomia da Sociedade Brasileira de Mastozoologia (CT-SBMz). Available at: <https://wwwsbmzorg/mamiferos-do-brasil>. Access on 29 September 2020.

Almeida-Neto M, Guimaraes P, Guimaraes Jr PR, Loyola RD and Ulrich W (2008) A consistent metric for nestedness analysis in ecological systems: reconciling concept and measurement. *Oikos* **117**, 1227–1239.

Almeida-Neto M and Ulrich W (2011) A straightforward computational approach for measuring nestedness using quantitative matrices. *Environmental Modelling & Software* **26**, 173–178.

Alvares CA, Stape JL, Sentelhas PC, Moraes Gonçalves JL and Sparovek G (2013) Köppen's climate classification map for Brazil. *Meteorologische Zeitschrift* **22**, 711–728.

Bascompte J and Jordano P (2007) Plant-animal mutualistic networks: the architecture of biodiversity. *Annual Review Ecology Evolution and Systematics* **38**, 567–593.

Bello C, Galetti M, Pizo MA, Magnago LFS, Rocha MF, Lima RAF, Peres CA, Ovaskainen O and Jordano P (2015) Defaunation affects carbon storage in tropical forests. *Science Advances* **1**, 1–11.

Bogoni JA, Graipel ME and Peroni N (2018) The ecological footprint of *Acca sellowiana* domestication maintains the residual vertebrate diversity in threatened highlands of Atlantic Forest. *PLoS One* **13**, 1–24.

Brasil (2016) *Plano de Manejo Estação Ecológica da Serra das Araras. Ministério do Meio Ambiente*. Brasília, 252 pp. Available from: <https://www.icmbio.gov.br/portal/images/stories/plano-de-manejo/dcom_plano_de_manejo_Esec_Serra_das_Araras.pdf> Access on 15 de September 2020.

Brazil Flora (2020) *Brazilian Flora 2020 project - Projeto Flora do Brasil 2020*. v393.261. Instituto de Pesquisas Jardim Botanico do Rio de Janeiro. Dataset/Checklist. Available at: <https://floradobrasil.jbrj.gov.br/>. Access on 05 January 2020.

Cagua EF, Wootton KL and Stouffer DB (2019) Keystoneness, centrality, and the structural controllability of ecological networks. *Journal of Ecology* **107**, 1779–1790.

Carreira DC, Dáttilo W, Bruno DL, Percequillo AR, Ferraz KMPMB and Galetti M (2020) Small vertebrates are key elements in the frugivory networks of a hyperdiverse tropical forest. *Scientific Reports* **10**, 1–11.

Chao A (1984) Nonparametric estimation of the number of classes in a population. *Scandinavian Journal of statistics* **11**, 265–270.

Chiarello AG (2000) Density and population size of mammals in remnants of Brazilian Atlantic Forest. *Conservation Biology* **14**, 1649–1657.

Crestani AC, Mello MAR and Cazetta E (2019) Interindividual variations in plant and fruit traits affect the structure of a planta-frugivore network. *Acta Oecologica* **95**, 120–127.

Delmas E, Besson M, Brice MH, Burkle LA, Dalla Riva GV, Fortin MJ, Gravel D, Guimarães Jr PR, Hembry DH, Newman EA, Olesen JM, Pires MM, Yeakel JD and Poisot T (2019). Analysing ecological networks of species interactions. *Biological Reviews* **94**, 16–36.

Dirzo R, Young HS, Galetti M, Ceballos G, Isaac NJ and Collen B (2014) Defaunation in the Anthropocene. *Science* **345**, 401–406.

Donatti CI, Guimarães PR, Galetti M, Pizo MA, Marquitti FMD and Dirzo R (2011) Analysis of a hyper-diverse seed dispersal network: modularity and underlying mechanisms. *Ecology Letters* **14**, 773–781.

Dormann CF, Fruend J and Gruber B (2020) *Visualising bipartite networks and calculating some (ecological) indices*. R package version 2.15.

Dormann CF and Strauss R (2014) A method for detecting modules in quantitative bipartite networks. *Methods in Ecology and Evolution* **5**, 90–98.

Dugger PJ, Blendinger PG, Böhning-Gaese K, Chama L, Correia M, Dehling DM, Emer C, Farwig N, Fricke EC, Galetti M, García D, Grass I, Heleno R, Jacomassa FAF, Moraes S, Moran C, Muñoz MC, Neuschulz EL, Nowak L, Piratelli A, Pizo MA, Quitián M, Rogers HS, Ruggera RA, Saavedra F, Sánchez MS, Sánchez R, Santillán V, Schabo DG, Silva FR, Timóteo S, Traveset A, Vollstädt MGR and Schleuning M (2019) Seed-dispersal networks are more specialized in the Neotropics than in the Afrotropics. *Global Ecology and Biogeography* **28**, 248–261.

Emmons L and Feer F (1997) *Neotropical rainforest mammals: a field guide*. Chicago: The University of Chicago Press, 392 p.

Encinas-Viso F, Revilla TA and Etienne RS (2012) Phenology drives the structure and diversity of the mutualistic network. *Ecology Letters* **15**, 198–208.

Ferreira GB, Collen B, Newbold T, Oliveira MJR, Pinheiro MS, Pinho FF, Rowcliffe M and Carbone C (2020) Strict protected areas are essential for the conservation of larger and threatened mammals in a priority region of the Brazilian Cerrado. *Biological Conservation* **251**, 108762.

Fuzessy LF, Janson C and Silveira FAO (2018) Effects of seed size and frugivory degree on dispersal by Neotropical frugivores. *Acta Oecologica* **93**, 41–47.

Galetti M, Bovendorp RS and Guevara R (2015) Defaunation of large mammals leads to an increase in seed predation in the Atlantic forests. *Global Ecology and Conservation* **3**, 824–830.

Galetti M and Dirzo R (2013) Ecological and evolutionary consequences of living in a defaunated world. *Biological Conservation* **163**, 1–6.

Galetti M, Guevara R, Cortes MC, Fadini R, Von Matter S, Leite AB, Labecca F, Ribeiro T, Carvalho C S, Collevatti RG, Pires MM, Guimaraes PR, Brancalion PH, Ribeiro MC and Jordano P (2013) Functional extinction of birds drives rapid evolutionary changes in seed size. *Science* **340**, 1086–1090.

Godínez-Alvarez H, Ríos-Casanova L and Peco B (2020) Are large frugivorous birds better seed dispersers than medium-and small-sized ones? Effect of body mass on seed dispersal effectiveness. *Ecology and Evolution* **10**, 6136–6143.

Golin V, Santos-Filho M and Pereira MJB (2011) Dispersal and predation of araticum seeds in the Cerrado of Mato Grosso, Brazil. *Ciência Rural* **41**, 101–107.

Harvey E, Gounand I, Ward CL and Altermatt F (2017) Bridging ecology and conservation: from ecological networks to ecosystem function. *Journal of Applied Ecology* **54**, 371–379.

Hsieh TC, Ma KH and Chao A (2020) *iNEXT: Interpolation and Extrapolation for Species Diversity*. R package version 2.0.20. Available at: <http://chao.stat.nthu.edu.tw/wordpress/software_download>. Access on 30 January 2021.

IUCN (2022) The IUCN Red List of Threatened Species. Version 2021-3. Available at: <https://www.iucnredlist.org/>. Access on 14 de February 2022.

Jordano P, Bascompte J and Olesen JM (2003) Invariant properties in coevolutionary networks of plant-animal interactions. *Ecology Letters* **6**, 69–81.

Jordano P, Forget PM, Lambert JE, Böhning-Gaese K, Traveset A and Wright SJ (2011) Frugivores and seed dispersal: mechanisms and consequences for biodiversity of a key ecological interaction. *Biology Letters* **7**, 321–323.

Jordano P, Garcia C, Godoy JA and García-Castaño JL (2007) Differential contribution of frugivores to complex seed dispersal patterns. *Proceedings of the National Academy of Sciences* **104**, 3278–3282.

Kuhlmann M (2018) *Frutos e Sementes do Cerrado: Espécies Atrativas Para A Fauna*. Brasília, Brazil: Ipsis Gráfica e Editora, pp. 1–464.

Lacher TE, Davidson AD, Fleming TH, Gómez-Ruiz EP, McCracken GF, Owen-Smith N, Peres CA and Vander Wall SB (2019) The functional roles of mammals in ecosystems. *Journal of Mammalogy* **100**, 942–964.

Lim JY, Svenning JC, Göldel B, Faurby S and Kissling WD (2020) Frugivore-fruit size relationships between palms and mammals reveal past and future defaunation impacts. *Nature Communications* **11**, 1–13.

Machado-de-Souza T, Campos RP, Devoto M and Varassin IG (2019) Local drivers of the structure of a tropical bird-seed dispersal network. *Oecologia* **189**, 421–433.

Magioli M, Barros KMPM, Chiarello AG, Galetti M, Setz EZF, Paglia AP, Abregoi O, Ribeiro MC and Ovaskainen O (2021a) Land-use changes lead to functional loss of terrestrial mammals in a Neotropical rainforest. *Perspectives in Ecology and Conservation* **19**, 161–170.

Magioli M, Rios E, Benchimol M, Casanova DC, Ferreira AS, Rocha J, Melo FR, Dias MP, Narezi G, Crepaldi MO, Mendes LAM, Nobre RA, Chiarello AG, García-Olaechea A, Nobre AB, Devids CC, Cassano CR, Koike CDV, Bernardo CSS, Homem DH, Ferraz DS, Abreu DG, Cazetta E, Lima EF, Bonfim FCG, Lima F, Prado HA, Santos HG, Nodari JZ, Giovanelli JGR, Nery MS, Faria MB, Ferreira PCR, Gomes PS, Rodarte R, Borges R, Zuccolotto TFS, Sarcinelli TS, Endo W, Matsuda Y, Camargos VL, Morato RG (2021b) The role of protected and unprotected forest remnants for mammal conservation in a megadiverse Neotropical hotspot. *Biological Conservation* **259**, 109173.

Martín González AM, Dalsgaard B and Olesen JM (2010) Centrality measures and the importance of generalist species in pollination networks. *Ecological Complexity* **7**, 36–43.

Moore JF, Soanes K, Balbuena D, Beirne C, Bowler M, Carrasco-Rueda F, Cheyne SM, Coutant O, Pierre-Michel F, Haysom JK, Houlihan PR, Olson ER, Lindshield S, Martin J, Tobler M, Whitworth A and Gregory T (2021) The potential and practice of arboreal camera trapping. *Methods in Ecology and Evolution* **2021**, 1–12.

Naniwadekar R, Chaplod S, Datta A, Rathore A and Sridhar H (2019) Large frugivores matter: insights from network and seed dispersal effectiveness approaches. *Journal of Animal Ecology* **88**, 1–13.

O'Farrill G, Galetti M and Campos-Arceiz A (2013) Frugivory and seed dispersal by tapirs: an insight on their ecological role. *Integrative Zoology* **8**, 4–17.

Olesen JM, Bascompte J, Dupont YL and Jordano P (2007) The modularity of pollination networks. *Proceedings of the National Academy of Sciences* **104**, 19891–19896.

Palacio RD, Valderrama-Ardila C and Kattan GH (2016) Generalist species have a central role in a highly diverse plant-frugivore network. *Biotropica* **48**, 349–355.

Queiroz JA, Diniz UM, Vázquez DP, Quirino ZM, Santos FA, Mello MA and Machado IC (2021) Bats and hawkmoths form mixed modules with flowering plants in a nocturnal interaction network. *Biotropica* **53**, 596–607.

Raíces DSL, Ferreira PM, Mello JHF and Bergallo HG (2017) Smile, you are on camera or in a live trap! the role of mammals in dispersion of jackfruit and native seeds in Ilha Grande state park, Brazil. *Nature Conservation Research* **2**, 78–89.

Raimundo RLG, Guimarães PR and Evans DM (2018) Adaptive networks for restoration ecology. *Trends in Ecology & Evolution* **33**, 664–675.

Ramos-Robles M, Andresen E and Díaz-Castelazo C (2018) Modularity and robustness of a plant-frugivore interaction network in a disturbed tropical forest. *Ecoscience* **25**, 209–222.

R Development Core Team (2019) R: A language and environment for statistical computing. R Foundation for Statistical Computing. Available at <https://www.r-project.org/>. Access on 10 December 2020.

Ripple WJ, Newsome TM, Wolf C, Dirzo R, Everatt KT, Galetti M, Hayward MW, Kerley GIH, Levi T, Lindsey PA, Macdonald DW, Malhi Y, Painter LE, Sandom CJ, Terborgh J and Valkenburgh BV (2015) Collapse of the world's largest herbivores. *Science Advances* **1**, 1e1400103.

Santos-Filho M, Frieiro-Costa F, Ignácio ÁRA and Silva MF (2012) Use of habitats by non-volant small mammals in Cerrado in Central Brazil. *Brazilian Journal of Biology* **72**, 893–902.

Santos-Filho M and Silva, MNF (2002) Uso de habitats por mamíferos em área de Cerrado do Brasil Central: um estudo com armadilhas fotográficas. *Revista Brasileira de Zoociências* **4**, 57–73.

Sukma HT, Di Stefano J, Swan M and Sitters H (2019) Mammal functional diversity increases with vegetation structural complexity in two forest types. *Forest Ecology and Management* **433**, 85–92.

Vázquez DP, Melián CJ, Williams NM, Blüthgen N, Krasnov BR and Poulin R (2007) Species abundance and asymmetric interaction strength in ecological networks. *Oikos* **116**, 1120–1127.

Vidal MM, Pires MM and Guimarães PR (2013) Large vertebrates as the missing components of seed-dispersal networks. *Biological Conservation* **163**, 42–48.

Villar N, Paz C, Zipparo V, Nazareth S, Bulascoschi L, Bakker ES and Galetti M (2020) Frugivory underpins the nitrogen cycle. *Functional Ecology* **35**, 357–368.

Vitorino BD, da Frota AVB, Castrillon SKI and Nunes JRS (2018) Birds of Estação Ecológica da Serra das Araras, state of Mato Grosso, Brazil: additions and review. *Check List* **14**, 893–922.

Wilman H, Belmaker J, Simpson J, de la Rosa C, Rivadeneira MM and Jetz W (2014) EltonTraits 1.0: species-level foraging attributes of the world's birds and mammals. *Ecology* **95**, 2027–2027.

Wintle BA, Kujala H, Whitehead A, Cameron A, Veloz S, Kukkala A, Moilanen A, Gordon A, Lentini PE, Cadenhead NCR and Bekessy SA (2019) Global synthesis of conservation studies reveals the importance of small habitat patches for biodiversity. *Proceedings of the National Academy of Sciences* **116**, 909–914.

Young HS, McCauley DJ, Galetti M and Dirzo R (2016) Patterns, causes, and consequences of anthropocene defaunation. *Annual Review of Ecology, Evolution, and Systematics* **47**, 333–358.

Zhu C, Li W, Gregory T, Wang D, Ren P, Zeng D, Kang Y, Ding P and Si X (2021) Arboreal camera trapping: a reliable tool to monitor plant-frugivore interactions in the trees on large scales. *Remote Sensing in Ecology and Conservation* **8**, 92–104.

https://doi.org/10.1017/S0266467422000505 Published online by Cambridge University Press