Frugivory and seed dispersal in the Cerrado: Network structure and defaunation effects

Rodrigo Béllo Carvalho, Yadvinder Malhi, Imma Oliveras Menor

ORIGINAL ARTICLE

bioTROPICA · ASSOCIATION FOR TROPICAL BIOLOGY AND CONSERVATION · WILEY

Frugivory and seed dispersal in the Cerrado: Network structure and defaunation effects

Rodrigo Béllo Carvalho[1] | Yadvinder Malhi[1] | Imma Oliveras Menor[1,2]

[1]School of Geography and the Environment, Environmental Change Institute, Oxford, UK

[2]AMAP (botAnique et Modélisation de l'Architecture des Plantes et des Végétations), CIRAD, CNRS, INRAE, IRD, Univ. de Montpellier, Montpellier Cedex 5, France

Correspondence
Rodrigo Béllo Carvalho, Environmental Change Institute, School of Geography and the Environment, South Parks Road, Oxford OX1 3QY, UK.
Email: rod_bello@hotmail.com

Associate Editor: Jennifer Powers
Handling Editor: Erin Kuprewicz

Abstract

Seed dispersal is a fundamental process that is highly threatened by the rapid decline of large-bodied frugivores worldwide. The Brazilian Cerrado, the largest savanna in the world, represents an ideal site for investigating seed dispersal because of its bio-diversity, environmental challenges, and knowledge shortfalls. We performed a systematic literature review to analyze the seed dispersal network in the Cerrado and the potential impacts of the defaunation of large-bodied frugivores on it. We considered network metrics, calculated the defaunation index of the frugivore assemblage, and compared traits among different fruit-sized plants and their respective dispersers in the network. We retrieved 1565 interactions involving 193 plant species and 270 animal species. Results show that the Cerrado seed dispersal network is slightly nested and considerably modular, dominated by small- to medium-sized generalist species, such as passerines, marsupials, and mesocarnivores. Nonetheless, large-bodied frugivores like the lowland tapir have a key role in the network due to their great foraging and network integration capacity. The Cerrado frugivore assemblage is moderately defaunated, with possible effects in its interactions with large-fruited plants. The Cerrado's defaunation and functional loss of large vertebrates deserve urgent attention to further understand the impacts on seed dispersal mechanisms and ecosystem functioning.

KEYWORDS
body mass, fruit size, functional-loss, large-bodied vertebrates, savanna, seed dispersal networks, systematic literature review

1 | INTRODUCTION

Seed dispersal is a key process for ecosystem functioning, especially in tropical environments, where it has profound ecological and evolutionary repercussions on the individual (Jordano et al., 2007), population (Galetti et al., 2013), community (Levine & Murrell, 2003), ecosystem (Rogers et al., 2021), and landscape (Villar et al., 2021) levels. One of the key elements for seed dispersal is

the size of the interacting agents. Large plants usually have large seeds (Moles et al., 2005; Moles & Westoby, 2006; Thompson & Rabinowitz, 1989), which are better dispersed by medium- to large-bodied frugivores (Corlett, 1998; Kitamura et al., 2002). However, large-bodied vertebrates represent one of the most highly endangered species groups in the world (Barnosky et al., 2011; Dirzo et al., 2014), commonly threatened by hunting, habitat destruction, fragmentation, selective-logging, and human-wildlife conflicts

(Markl et al., 2012; Peres & Palacios, 2007; Wright et al., 2007). As a consequence, large-bodied animals worldwide are facing sharp declines in their population size (Barnosky et al., 2011; Ceballos et al., 2017; Young et al., 2016). This fast-paced faunal perishing induced by anthropogenic pressure is termed 'defaunation' (Dirzo & Miranda, 1990), and in a forest context has been referred to as a generalized 'empty forest syndrome' (Redford, 1992). An 'empty forest' refers to not only key species being extinguished, but also to the loss of their ecological interactions with different trophic levels, which may cause cascading effects impacting ecosystem functioning (e.g., Beck et al., 2013; Bello et al., 2015; Galetti & Dirzo, 2013; Rogers et al., 2021; Terborgh et al., 2008).

The Brazilian Cerrado is the most biodiverse savanna in the world (Myers et al., 2000; Oliveira & Marquis, 2002). The biome has highly distinctive levels of species richness and endemism (Klink & Machado, 2005), which are reflected in its diverse ecological interactions. More than half of its woody plant species have animal-mediated seed dispersal, being highly reliant on vertebrates (Gottsberger & Silberbauer-Gottsberger, 1983; Kuhlmann & Ribeiro, 2016a, 2016b). The Cerrado vegetation exhibits a heterogeneous and intricate landscape mosaic that ranges from vast grasslands to dense canopy forests within short distances (Oliveira-Filho & Ratter, 2002; Ratter et al., 1997). These formation assortments are essential to maintain the plant-frugivore mutualism in the biome (Kuhlmann & Ribeiro, 2016b). However, almost half of its original territory has already been lost for conversion to pastures and crops for large-scale agribusiness operations (Strassburg et al., 2017; Machado et al., 2004). This fast land conversion, together with other anthropogenic drivers like habitat fragmentation and hunting, has resulted in defaunation rates of nearly 50% in the Cerrado (Bogoni et al., 2020).

Although Brazil is among the best-studied tropical countries in terms of seed dispersal and frugivory (Donoso et al., 2022), the Cerrado remains largely understudied. Despite the pioneering contributions done by Kuhlmann and Ribeiro (2016a, 2016b) on the ecological and phylogenetical relationships of Cerrado fruits and frugivores, Darosci et al. (2017) on the seasonality effects on Cerrado plant-frugivore interactions, and Purificação et al. (2020) on the structure of bird-plant interaction networks in savanna-forest mosaics, our understanding of the dispersal dynamics at community- to ecosystem-level is still emergent. There is evidence of ants complementing seed dispersal along with birds in the Cerrado (Christianini & Oliveira, 2009, 2010), which helps us grasp how such dispersers may flourish when larger animals are extirpated or functionally lost (Christianini et al., 2014). Nonetheless, research explicitly addressing Cerrado dispersal dynamics in defaunation or functional-loss contexts deserves urgent scrutiny.

Comprehending how frugivores and fruited-plants interact at the community-level offers powerful tools to tackle conservation issues and propose management actions (McConkey et al., 2012). For seed dispersal and frugivory research, the interacting network approach is especially useful because it allows analysis of both network structure and properties. It also allows the evaluation of

TABLE 1 Information on the adopted search strings, consulted data bases, and period of search for the systematic literature review.

Search string	Data bases	Search period
("Cerrado" OR "Cerrado Biome" OR "Neotropical Savanna") AND ("Seed Dispersal" OR "Frugivor*") AND ("Network" OR "Defaunation" OR "Frugivore Loss" OR "Functional Extinction"))	Google Scholar SciELO Science Direct Scopus Web of Science	July 2021

species' functional roles (such as seed dispersal effectiveness—Schupp et al., 2010) when enough information on frugivores' natural history and dispersal activity (pre- and post-dissemination stages) is provided (Heleno et al., 2014; Simmons et al., 2018). Moreover, the detection of structural patterns in mutualistic networks allows for a better understanding of communities' ecological and evolutionary dynamics (Bascompte & Jordano, 2007).

Considering the ecological importance of plant-frugivore interactions and the effects of defaunation on them, we ask the following questions: (i) what is the structure of the Cerrado seed dispersal network? (ii) which are the key species and their respective ecological contributions to this network? and (iii) what are the likely effects of the defaunation of large-bodied frugivores on this network?

There is evidence that Cerrado plants are mostly visited by generalist species (Allenspach & Dias, 2012; Francisco & Galetti, 2001, 2002; Paniago & Silva, 2017) that occur in several vegetation types (Kuhlmann & Ribeiro, 2016b). Some studies also report generalization in frugivory interactions (Darosci et al., 2017), as well as considerable overlaps of frugivore assemblages, regardless of habitat or fruiting season (Maruyama et al., 2019). Thus, we hypothesize the Cerrado has a diverse and plural network, predominantly composed of generalist species. Given the ecological-evolutionary relationship between large animals and large-fruited plants in the Cerrado (Guimarães et al., 2008), we also expect the network may be experiencing impacts from large-dispersers' defaunation, affecting interactions of large-fruited plants.

2 | METHODS

2.1 | Experimental design

We performed a systematic literature review (SLR) using the 'Protocol, Search, Appraisal, Synthesis, Analysis, and Report' (PSALSAR) framework (Mengist et al., 2020). The main objective was to obtain secondary data about plant-frugivore interactions to assemble a Cerrado seed dispersal network. Similar methodologies have already been successfully adopted to model other ecosystems' networks (Oliveira et al., 2015; Almeida & Mikich, 2018; Ong et al., 2022). Table 1

presents information about search strings, search period, and data bases used in the SLR. References initially obtained were screened according to the selection criteria of Table 2. The 43 finalist references considered in our study are listed in Table S1.

We covered studies from all Cerrado physiognomies (forest-, savanna-, and grassland-like formations), different locations, and diverse methodologies (Table 3). While the use of different methods with varying sampling efforts can influence the capacity in detecting species interactions (Vitorino et al., 2022), we believe that such limitation was circumvented as most studies used a similar approach.

2.2 | Network analyses

We created a binary (presence [1]/absence [0]) adjacency matrix of plant-frugivore interactions. The matrix consisted of ordering the animal species in rows (i) and the plant species in columns (j). We use a binary approach because of standardization needs, once not all surveyed publications presented additional quantitative information about the interactions (e.g., number of visits per species, number of consumed fruits). Additionally, the binary method is a common method used by other studies because it is practical for detecting general network patterns (such as those expected for a biome) and for making comparisons with the literature (Jordano et al., 2003; Sarmento et al., 2014).

The matrix was graphically represented by bipartite graphs, in which species were designated as vertices (points) and their interactions as edges (lines). Plants were grouped according to the fruit-length categories presented by Kuhlmann (2018a, 2018b): small-fruited (<1 cm), medium-fruited (1–4 cm), and large-fruited (>4 cm). Birds were classified as small (<100 g) or large (>100 g), whereas mammals were grouped into small (<1 kg), midsized (1–10 kg), or large (>10 kg) (Bernardo & Melo, 2013; Chiarello, 2000; Vidal et al., 2013). Given the importance of considering the ecological context to define the largest fauna of an ecosystem (Hansen & Galetti, 2009), we considered 'large-bodied vertebrates' the largest native species acting as seed dispersers in the Cerrado: midsized to large mammals and large birds. Domestic (livestock) species were not included in our analysis. We used the *bipartite* R package v2.16 (Dormann & Strauss, 2014) and the *Pajek* software v5.13 (Batagelj & Mrvar, 1998) to model the network.

We adopted several descriptors to characterize the structure of the Cerrado plant-frugivore network, such as "Nestedness", "Modularity", "Connectance", "Link per Species", "Species Strength", and "Shannon Index for Diversity of Interactions" (Carreira et al., 2020; Silva et al., 2015; Tylianakis et al., 2010). Details on the interpretation and methods of each metric can be found in the Appendix S1.

Lastly, we did proportional analyses considering the total amount of frugivores (*lato* sensu), their biomass (further details about data collection in subsection 2.5), and network interactions. We assessed differences in fruit and seed size among disperser groups with a non-parametric Kruskal–Wallis, followed by a Dunn's *post hoc* test.

2.3 | Network ecological role

Species were classified according to the ecological roles they performed in the network. When a species exhibited a disproportionate number of interactions, especially within its module, it was classified as a "hub". On the other hand, if the species was essential to connect different modules in the network, it was considered to be a "connector". Some species were classified as both when they had many recorded interactions and showed a high capacity to bind modules (Olesen et al., 2007).

2.4 | Seed dispersal potential

Aiming to appraise the ecological contribution of the main frugivores registered in the network, we adapted Kuhlmann's (2018a, 2018b) "Seed Dispersal Potential" classification system, which is based on the combined evaluation of morphological and behavioral attributes exhibited by fauna attracted to fruited-plants. Kuhlmann's system considers body size, feeding capacity, frugivory degree, and fruit processing to rank species accordingly to their dispersal capacity—viz. 1 (low potential), 2 (medium potential), or 3 (high potential). We converted his ranking categories to decimal scale and normalized it to range from 0 (non-existent dispersal potential) to 1 (maximum dispersal potential) after accounting for the network frugivore assemblage. Species that did not originally feature in Kuhlmann's frugivore ranking could not be considered for the seed dispersal potential

TABLE 2 Selection criteria used to include or exclude studies in the systematic literature review.

Selection criteria	Decision
The study addresses the topic of seed dispersal, frugivory, or their related conservation science (e.g., ecological restoration, rewilding, deforestation, defaunation)	Inclusion
The study presents the search string terms, at least, in their title, abstract, or listed keywords	Inclusion
The study provides clear information on interactions of fruited-plant species and frugivores (i.e., which species interact with each other)	Inclusion
The study addresses the subject precisely in the Cerrado biome	Inclusion
Studies that are duplicated within the search documents	Exclusion

(SDP) estimation as there was no available score for them. Hence, we appraised a reduced sample size of frugivores ($n=125$; Table S2) to calculate the SDP for the Cerrado network.

2.5 | Defaunation and frugivore-loss impact

We calculated a defaunation index (DI) (sensu Emer et al., 2020) based on the Bray–Curtis dissimilarity index (Legendre & Legendre, 2012):

$$DI = \frac{\sum_k^s |B_f - B_r|}{\sum_k^s |B_f + B_r|},$$

where "B_f" and "B_r" represent the biomass of species k in the focal 'f' and the reference "r" assemblages, respectively, in a universe of "s" total species. DI ranges from 0, when species in both assemblages are completely similar (non-defaunated), to 1, when all species are absent in the focal assemblage (complete defaunation) (Carreira et al., 2020; Giacomini & Galetti, 2013).

In this study, "Focal Assemblage" referred to the species surveyed in the SLR, and "Reference Assemblage", to the expected frugivores for the Cerrado biome. As a proxy for the biome species pool, we used the list of frugivorous species reported by Kuhlmann (2018a, 2018b) for the Cerrado (Table S2 – 52 mammal species; 167 bird species; 4 reptile species; 4 ant genera). The calculation of DI considered the dissimilarity of animal biomass, calculated as the sum of each species' body mass in the assemblages. Animal mass data were compiled from PanTHERIA (Jones et al., 2009), and from references addressing animal morphology (Dunning Jr., 2007; Herrera & Robinson, 2000; Hölldobler & Wilson, 1998).

We evaluated the possible effects of large-bodied frugivores' defaunation on the network through (i) correlations between fruit and seed size with dispersers' body mass, by simple linear regression and (ii) differences in total disperser body mass among plant groups (small-, medium-, and large-fruited species), using non-parametric Kruskal-Wallis test. Statistical analyses were performed in R Studio (R Core Team, 2021). Data on plant traits were compiled from the literature (Kuhlmann, 2018a, 2018b; Lorenzi, 2010, 2016a, 2016b, 2016c; Silva-Júnior, 2012; Silva-Júnior & Silva Pereira, 2009).

To assess whether large-bodied vertebrates disproportionally comprise the disperser assemblage of large-fruited plants, we compared the species composition of this group with the set of species retrieved in the literature dispersing large-fruited plants, using the "Sørensen similarity index" (Legendre & Legendre, 2012).

3 | RESULTS

3.1 | Network assemblage

We identified 270 animal species interacting with 193 plant species in the Cerrado. There were 179 bird species (66.5% of total animal species) from 29 families of 9 orders; 52 mammal species

(19.5%) from 17 families of 8 orders; 1 reptile species (0.4%), and 38 ant species (13.5%) (Figure S1; Table S3). The most recurrent bird families were Tyrannidae (tyrant flycatchers; $n=39$; 21.8%) and Thraupidae (tanagers; $n=38$; 21.2%), while those of mammals were Phyllostomidae (leaf-nosed bats; $n=12$; 21.4%) and Didelphidae (opossums; $n=9$; 16%). Fruiting plants were represented across 59 families (Table S4), the dominant families being Melastomataceae ($n=29$; 15%) and Myrtaceae ($n=20$; 10.3%). In terms of individual biomass, vertebrates ranged from small species, such as the white-crested tyrannulet (*Serpophaga subcristata* – 6.6 g), to large ones, such as the lowland-tapir (*Tapirus terrestris* – 170 kg).

3.2 | Structure of the cerrado seed dispersal network

We recorded 1565 interactions between plants and frugivores in the Cerrado, with a Shannon diversity index (SDI) of 7.355. Around 70% of interactions were performed by small birds (Figure 1). The seed dispersal network (Figure 2; Figure S2) had low nestedness (NODF = 12.86; NODF$_{EXPECTED}$ = 5.98; $p<.001$) and moderate degree of modularity ($M=0.459$; M$_{EXPECTED}$ = 0.350; $p<.05$), with nine subgroups. The mean number of links per species was 3.344, and the mean connectance was about 3% ($C=0.0294$).

Regarding the number of interactions, species with highest records were the pale-breasted thrush (*Turdus leucomelas*; $n=65$), burnished-buff tanager (*Tangara cayana*; $n=59$), blue-dacnis (*Dacnis cayana*; $n=46$), and helmeted manakin (*Antilophia galeata*; $n=43$; Figure 3). These are mainly low-sized, omnivorous passerines that occur in different physiognomies of the Cerrado, except for *A. galeata*, which is a strict-frugivore of forest areas. Tree species with the greatest amounts of interactions were *Xylopia aromatica* ($n=72$), *Cecropia pachystachya* ($n=45$), and *Schefflera morototoni* ($n=41$).

3.3 | Species ecological contribution and seed dispersal potential

Species strength metric ranged from 0.01 to 13.05 for frugivores (Table S5). The highest scores were obtained for *T. terrestris* (13.04), *T. leucomelas* (8.43), white-eared opossum (*Didelphis albiventris*; 7.70), coati (*Nasua nasua*; 7.20), and burnished-buff tanager (*T. cayana*; 7.02). Dispersers with the strongest influence on the network included large- to mid-sized mammals and passerines (Figure 3). In turn, plant species strength varied from 0.02 to 23.82, with species of pronounced strength being *X. aromatica* (23.82), *Acrocomia totai* (18.19), *Erythroxylum pelleterianum* ($n=16.69$), *S. morototoni* (15.45), and *Miconia rubiginosa* (11.21)—all medium- to small-fruited plants.

Regarding the performed ecological roles in the network, species classified exclusively as hubs included the tree *C. pachystachya* and the passerines *D. cayana* and *A. galeata*. Due to their strong interactions with several modules, dispersers *T. terrestris*, *D. albiventris*,

TABLE 3 Details on location, methods, sampling effort, targeted group, and the number of interactions retrieved from the finalist studies of the systematic literature review used to model the Cerrado seed dispersal network.

Study	Location	Method of study	Sampling effort	Targeted group	Number of interactions retrieved
Marcondes-Machado (2002)	Itirapina Experimental station – São Paulo, Brazil (22°15′ S, 47°49′ W)	Focal observation	10.2h	Birds	11
Francisco and Galetti (2002)	Cerrado fragments in UFSC campus – São Paulo, Brazil (21°25′ S, 47°52′ W)	Focal observation	72h	Birds	13
Melo et al. (2003)	Panga Ecological Station – Minas Gerais, Brazil (19°09–19°11′ S, 48°23′–48°24′ W)	Focal observation	44.5h	Plant	13
Francisco et al. (2007)	Cerrado fragments in UFSC Campus – São Paulo, Brazil (21°58′ S, 47°52′ W)	Focal observation	60h	Birds/Plant	14
Alves-Costa and Eterovick (2007)	Mangabeiras Park – Minas Gerais, Brazil (19°56′ S, 43°54′ W)	Faeces analysis germination test	Weekly visits (2 years)	Mammals	10
Almeida and Galetti (2007)	Jataí Ecological Station – São Paulo, Brazil (21°33′ S, 47°45′ W)	Fruit removal experiment	10–20days	Plant	2
Silva et al.2008)	Cerrado fragments in UFSC Campus – São Paulo, Brazil (21°58′–22°00′ S, 47°51′–47°52′ W)	Focal observation	65h	Plants	15
Melo & Oliveira (2009)	Panga Ecological Station – Minas Gerais, Brazil (19°09–19°11′ S, 48°23′–48°24′ W)	Focal observation	30.2h	Plant	5
Christianini and Oliveira (2010)	Itirapina Experimental Station – São Paulo, Brazil (22°12′ S, 47°51′ W)	Focal observation	109.7h	Birds/Ants	23
Camargo et al. (2011)	Gama Cabeça-de-Veado Protected Area – Federal District, Brazil (15°52′ S, 47°52′ W)	Faeces analysis (Individual capture) germination test	1year (23,040 traps/night)	Mammal	7
Guerta et al. (2011)	Cerrado fragments in UFSC Campus – São Paulo, Brazil (21°58′ S, 47°52′ W)	Focal observation	55h	Birds/Plant	43
Borges & Melo (2012)	Panga Ecological Station – Minas Gerais, Brazil (19°10′ S, 48°23′ W)	Focal Observation	42h	Birds/Plant	7
Allenspach and Dias (2012)	Cerrado fragments in UFSC Campus – São Paulo, Brazil (21°58′ S, 47°51′ W)	Focal observation	156h	Birds/Plant	18
Allenspach et al. (2012)	Cerrado fragments in UFSC Campus – São Paulo, Brazil (21°58′ S, 47°51′ W)	Focal observation	96h	Birds/Plant	19
Oliveira & Leme (2013)	Guariroba Protected Area – Mato Grosso do Sul, Brazil (20°33′ S, 54°23′ W)	Faeces analysis Germination test	51 days	Mammal/Plant	1
Silva & Melo (2013)	Uberlândia – Minas Gerais, Brazil (18°55′ S, 48°17′ W)	Focal observation	300h	Birds/Plants	65
Lessa et al. (2013)	Rio Preto State Park – Minas Gerais, Brazil (18°05′ S, 43°20′ W)	Faeces analysis (Individual capture) germination test	1.8year (24 traps/station)	Mammal	71
Ragusa-Netto (2014)	Emas National Park – Goiás, Brazil (17°19–18°28′ S, 52°39′–53°10′ W)	Focal observation	36h	Bird/Plant	1
Silva & Pedroni (2014)	Clube Caça & Pesca Itororó Reserve – Minas Gerais, Brazil (18°57′ S, 48°12′ W)	Focal observation	196h	Birds	90

(Continues)

TABLE 3 (Continued)

Study	Location	Method of study	Sampling effort	Targeted group	Number of interactions retrieved
Purificação et al. (2014)	Serra Azul State Park – Mato Grosso, Brazil (15°52′ S, 51°16′ W)	Line transect method Focal observation	284 h 36 h	Birds/Plants	187
Farias et al. (2015)	Serra Azul State Par – Mato Grosso, Brazil (15°50′–15°51′ S, 52°16′–52°15′ W)	Focal observation	191 h	Plant	7
Oliveira et al. (2015)	Pirassunga and São Carlos – São Paulo, Brazil Belo Horizonte – Minas Gerais, Brazil	Literature review	9 studies	Birds/Plants	49
Gonçalves et al. (2015)	Uberlândia – Minas Gerais, Brazil (18°57′ S, 48°12′ W)	Focal observation	69 h	Birds/Plant	7
Purificacao et al. (2015)	Destino Farmland – Mato Grosso, Brazil (12°51′ S, 52°04′ W)	Focal observation	31 h	Birds/Plant	23
Paniago and Silva (2017)	Serra de Caldas Novas State Park – Goiás, Brazil (17°46′ S, 48°40′ W).	Focal observation	64 h	Plant	24
Guerra et al. (2017)	Serra do Cipó – Minas Gerais, Brazil (43°35′ W, 19°17′ S)	Focal observation	16 h	Birds/Plant	9
Darosci et al. (2017)	Águas Emendadas Ecological Station – Federal District, Brazil (15°32′ S, 47°34′ W) Água Limpa Experimental Farm, – Federal District, Brazil (15°57′ S, 47°56′ W)	Focal observation	680 h	Birds/Plants	180
Laurindo et al. (2017)	Lagoa and Monte Alegre Farmlands – Minas Gerais, Brazil	Faeces analysis	60 net-nights	Bats/Plants	34
Santos et al. (2017)	Serra do Rola Moça State Park – Minas Gerais, Brazil (20°00′–20°08′ S, 43°96′–44°06′ W)	Focal observation Germination test	242 h	Plants	18
Genrich et al. (2017)	Mangabeiras Municipal Park – Minas Gerais, Brazil (19°56′ S, 43°54′ W) Serra do Rola Moça State Park – Minas Gerais, Brazil (20°55′ S, 44°58′ W) Serra do Curral Municipal Park – Minas Gerais, Brazil (19°57′ S, 43°55′ W)	Faeces analysis (Individual capture) germination test	61 days	Mammals/ Plants	72
Torres et al. (2018)	Dahma Ecological Station – Mato Grosso, Brazil (20°28′ S, 54°32′ W) Prosa State Park – Mato Grosso, Brazil (20°27′ S, 54°33′ W)	Faeces analysis	12 nights/area (6 nets for 6 h per night)	Bats	15
Magalhães et al. (2018)	Mogi-Guaçu – São Paulo, Brazil (22°18′ S, 47°11′ W)	Systematic census	4 monthly census (4 h per census)	Ants/Plant	5
Bezzon (2018)	Clube Caça & Pesca Itororó Reserve – Minas Gerais, Brazil (18°57′ S, 48°12′ W)	Focal observation	60 h	Birds/Plants	40
Camargo et al. (2019)	Itirapina Experimental Station – São Paulo, Brazil (22°12′ S, 47°51′ W)	Focal observation Camera trapping	5072 h	Birds/Ants	19
Blanco et al. (2019)	São Gonçalo da Gurguéia – Piauí, Brazil Exaltación de la Santa Cruz –Yacuma, Bolivia	Direct observation Camera trapping	347 camera-trap days	Mammals/ Birds/ Livestock/ Plants	87
Hannibal et al. (2019)	Córrego do Bandeira Farm – Goiás, Brazil (18°24′ S, 50°43′ W)	Faeces analysis	7 months (18 fortnightly expeditions)	Mammal	18

TABLE 3 (Continued)

Study	Location	Method of study	Sampling effort	Targeted group	Number of interactions retrieved
Purificação & Pascotto (2019)	Serra Azul State Park – Mato Grosso, Brazil (15°52′ S, 51°16′ W)	Focal observation	56 h	Birds/Plant	9
Purificação et al. (2020)	Serra Azul State Park – Mato Grosso, Brazil (15°52′ S, 51°16′ W)	Linear transect method Focal observation	284 h	Birds/Plants	185
Pires & Melo (2020)	Uberlândia – Minas Gerais, Brazil (18°95′ S, 48°20′ W)	Focal observation	260 h	Birds/ Plants	92
Tella et al. (2020)	São Gonçalo da Gurguéia – Piauí, Brazil (10°06′ S, 45°22′ W)	Camera trapping	4080 h	Birds/Plants	1
Campagnoli & Christianini (2021)	Itirapina Experimental Station – São Paulo, Brazil (22°12′ S, 47°51′ W)	Focal observation	784.8 h	Birds/Ants	40
Corral et al. (2021)	São Vicente Institute Properties – Mato Grosso do Sul, Brazil (20°23′ S, 54°36′ W)	Animal and plant survey Direct observation	14 months (5 days monthly)	Birds/Plants	203

and *N. nasua* were regarded as connectors. Angiosperms *A. totai*, *E. pelleterianum*, and *M. rubiginosa* also entered the connector category. Lastly, for having both a high amount of interactions and the ability to interconnect distinct modules in the network, birds *T. leucomelas* and *T. cayana* and trees *X. aromatica* and *S. morototoni* received both classifications. In terms of seed dispersal potential, we found a moderate estimation for the frugivore assemblage (SDP = 0.48; n = 125 spp.).

Fruit size differed among disperser groups (χ^2 = 20.75; df = 5; p < .001; Figure 4a). Large mammals interacted with considerably larger fruits (fruit-width median = 3.9 cm) when compared to mid-sized mammals (fruit-width median = 1.0 cm; p < .01) and small birds (fruit-width median = 1.5 cm; p < .001). A similar pattern was also found for seed size (χ^2 = 26.57; df = 5; p < .001; Figure 4b). Large mammals (seed-length median = 1.0 cm) and large birds (seed-length median = 0.9 cm) interacted with larger seeds compared to small (seed-length median = 0.5 cm; $p_{\text{Large-Mammals}}$ <.01, $p_{\text{Large-Birds}}$ <.01) and midsized mammals (seed-length median = 0.4 cm; $p_{\text{Large-Mammals}}$ <.05, $p_{\text{Large-Birds}}$ <.01).

3.4 | Defaunation and frugivore-loss impact

Comparing the assemblage of frugivores in the network with the expected baseline (Table S2), we found a defaunation index of 0.43. No correlation was observed between fruit size and disperser body mass in the network (F = 1.991, df = 191, p = .16, R^2 = 0.01; Figure S3). The total disperser body mass did not significantly differ among small-, medium-, and large-fruited plants (χ^2 = 0.54; df = 2; p = .76; Figure S4). We found a low similarity between the species composition of the large-bodied frugivore group and the actual dispersers of large-fruited plants in the network (Sørensen index = 0.198).

4 | DISCUSSION

4.1 | What is the structure of the Cerrado seed dispersal network?

Our study demonstrates the heterogeneous structure of the Cerrado seed dispersal network, with a nested topology organized around a modular pattern, as expected for mutualistic networks (Bascompte et al., 2003; Bascompte & Jordano, 2006; Olesen et al., 2007). Compared to neighboring biomes such as the Pantanal (M = 0.42; NODF = 26.27, Donatti et al., 2011) and the Atlantic Forest (M = 0.42–0.51, NODF = 26.27–29.3, Bufalo et al., 2016; Mello et al., 2011; Silva et al., 2015), the Cerrado network was less nested but with a similar degree of modularity.

Although the observed nestedness is considered low for the NODF scale, its value was considerably higher than expected by chance (almost twice as much: NODF = 12.86; NODF$_{\text{EXPECTED}}$ = 5.98). This is an indicator of ecological resilience (Thébault & Fontaine, 2010) because there are alternative routes to respond to disturbances if one or more species become extinct (Bascompte et al., 2003). However,
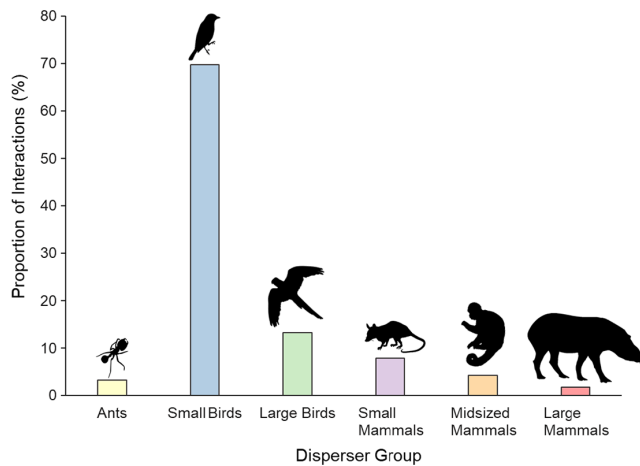
FIGURE 1 Proportion of interactions performed by the major disperser groups in the Cerrado seed dispersal network: ants (yellow bar; 3.1%, $n=49$), small birds (<100 g; blue bar; 69.7%, $n=1086$), large birds (>100 g; green bar; 13.3%, $n=207$), small mammals (<1 kg, non-volant and bats; purple bar; 7.9%, $n=123$), midsized mammals (1–10 kg; orange bar; 4.1%, $n=65$), and large mammals (>10 kg; pink bar; 1.7%, $n=26$). Silhouettes above classes represent a typical species from each disperser group category: an ant (Formicidae; ants), a flycatcher (Tyrannidae; small birds), a macaw (Psittacidae; large birds), a mouse opossum (*Gracilinanus* sp.; small mammals), a capuchin monkey (*Sapajus* sp.; midsized mammals), and a lowland tapir (*T. terrestris*; large mammals). Reptiles were not represented because only one species is interacting in the network (*Tupinambis teguixin*), lacking sufficient group rendition to be plotted in the graph.

the low nestedness of the Cerrado network implies less cohesion than other systems. For example, compared to Afrotropical networks, Neotropical seed dispersal networks are more likely to trigger cascade effects in plant communities if frugivores get extirpated (Dugger et al., 2019). Low nestedness also indicates more interactions between generalist species in the network (Bascompte et al., 2003).

The considerable modular pattern in the Cerrado seed dispersal network encompassed nine subgroups that are more intimately connected with each other than with species from other modules (Olesen et al., 2007). In mutualistic networks, modular topologies are generally associated with complex communities (Silva et al., 2015). Additionally, modular networks ensure robustness and allow greater stability against disturbances because impacts can be retained by a single module, dampening their propagation to the other ones (Thébault & Fontaine, 2010). If cascade effects arise from frugivore loss, a modular network will prevent further extinctions from occurring (Correa et al., 2016; Ramos-Robles et al., 2018).

We must also consider the repercussion of forbidden links (i.e., unobservable connections due to linkage constraints) while determining modules in the seed dispersal network. Restrictions caused by phenological uncoupling (e.g., seasonal availability of fruit and frugivores; interactions of migratory species) or biogeographical mismatches (e.g., species restricted to one of the biome's biodiversity supercentres) prevent our observation of potential links among

species (and consequently modules), regardless of sample efforts (Olesen et al., 2011).

The low connectance found in the Cerrado network seems to reflect a pattern reported for tropical systems. Due to their high species richness, tropical environments have a relatively low number of established interactions in their networks, thus displaying particularly low connectivity (Jordano, 1987). Consequently, if a species were randomly selected, it would have very few interactions with other species, making it more sensitive to the secondary effects of other species' extinctions (Silva et al., 2007). Although the Cerrado network has low connectance, the network may have sufficient robustness to tolerate disturbances, according to its observed modularity pattern. Nonetheless, further evidence is needed to decipher whether the detected modules are influenced by other factors, for example, geography. For a vast biome like the Cerrado, different regions could harbor distinct modules that do not overlap spatially with other modules, and thus they would have little influence on the overall biome resilience.

The predominance of small bird interactions is explained by, first, this group's abundance in the Cerrado (Pinto et al., 2008; Tubelis & Cavalcanti, 2001), and, second, small- and medium-sized birds are highly effective seed dispersers (Godínez-Alvarez et al., 2020), interacting with multiple plants. We also highlight that most seed dispersal research focuses on particular frugivore taxa, often birds (Vidal et al., 2013). Nonetheless, despite birds being the network's most frequent dispersers, the way they handle fruits influences plants' dispersal success (Levey, 1987). For example, Thraupidae (tanagers) are commonly classified as "mashers" (i.e., they crush fruits in their beaks, dropping seeds without ingesting them – Levey, 1987), thus they might only exploit fruit pulp, providing no dispersal away (e.g., *D. cayana*). Conversely, although macaws consume pulps and discard entire seeds on the ground, they commonly handle fruits after flying to distant perches, contributing to long-distance dispersal, forest regeneration, and connectivity (Baños-Villalba et al., 2017). Hence, more information is needed on how the most frequent birds actually contribute to seed dispersal effectiveness to better understand the network dynamics.
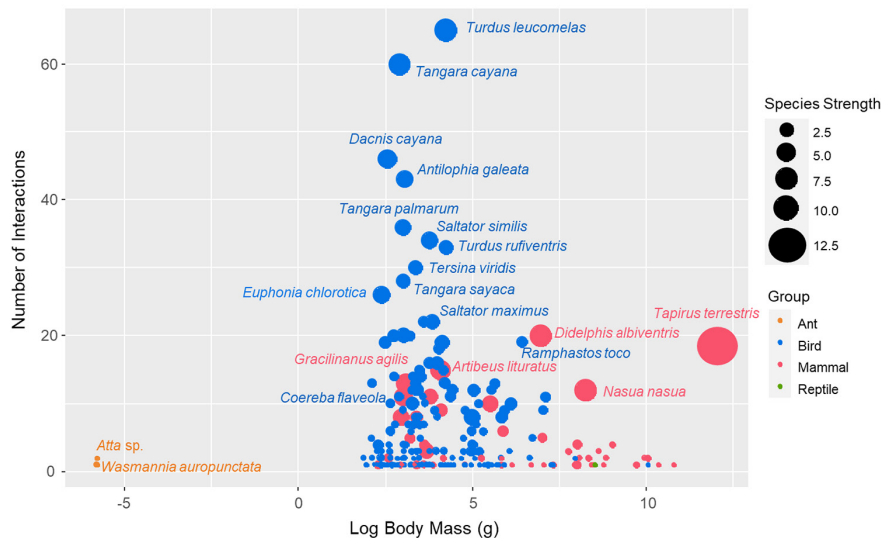
We highlight ants' network participation. Although myrmecochory (ant dispersal) prevails in Cerrado grassland formations and with herbaceous species (Kuhlmann & Ribeiro, 2016b), ants are often neglected in seed dispersal studies in Neotropical vegetation. Current evidence shows how significant these invertebrates are even for the dispersal of woody species from savanna and forest physiognomies. For example, several ant genera (e.g., *Pheidole*; *Pachycondyla*; *Atta*) carry species' secondary dispersal in the Cerrado, complementing vertebrates' performance and assisting plant regeneration (Campagnoli & Christianini, 2021; Christianini & Oliveira, 2009, 2010; Magalhães et al., 2018).

4.2 | Which are the key species and their ecological contribution to the Cerrado seed dispersal network?

The Cerrado network is mainly composed of generalist species, capable of dispersing several plants of varied fruit sizes, confirming our

FIGURE 2 Bipartite representation of the Cerrado seed dispersal network. The graph illustrates the pairwise interactions (lines) between frugivore dispersers (multi-colored boxes, left-hand side, $n=274$ spp.) and fruiting plant species (green boxes, right-hand side, $n=193$ spp.) in the biome. Larger boxes mean species with a greater amount of interactions performed (in the case of dispersers) or received (in the case of plants). Major disperser groups had their boxes and lines color-coded: ants (brown), reptiles (black), small birds (<100 g; blue), large birds (>100 g; turquoise), bats (purple), small mammals (<1 kg, non-volant; light pink), midsized mammals (1–10 kg; orange), large mammals (>10 kg; ruby). The network was modeled by compiling secondary data on plant-frugivore interactions already observed in the biome. All Cerrado vegetation physiognomies were considered (savannah, forest, and grassland formations). Interactions are weighted equally since the network's matrix was binary. The full list of species can be found in Tables S3 and S4 for dispersers and plants, respectively.

FIGURE 3 Performance of frugivores in the Cerrado seed dispersal network – evaluated in the number of interactions (y-axis) and species strength metric (bubble size) – in relation to their body mass. Each point on the graph represents a frugivore species, color-coded according to its main taxonomic group: ants (orange), birds (blue), mammals (pink), and reptiles (green). Point size (bubbles) varies according to species' strength metric (i.e., the larger the bubble, the greater the species' strength metric). Points plotted higher on the chart represent species with the highest number of interactions in the network. Frugivore species with a high number of interactions and a high score of species strength were labeled in the chart (except for *Atta* and *Wasmannia auropunctata*, which were placed to identify the outlier points in the body mass scale). A complete list, detailing species strength metrics for each frugivore of the network, can be found in Table S5.

hypothesis. Most of the network hubs are omnivorous passerines of families Thraupidae and Turdidae (Escribano-Avila et al., 2018). Network connectors included mesopredators and opportunistic frugivores such as *D. albiventris* and *N. nasua*, which disperse a broad range of distinct successional-stage plants' seeds (Alves-Costa & Eterovick, 2007; Cáceres, 2002). The large frugivore *T. terrestris* is also of fundamental importance to the Cerrado network. Besides ingesting different-sized seeds, tapirs have particular relevance for the long-distance dispersal of large-fruited plants since they deposit viable large seeds in places unreachable for other large-bodied dispersers (O'Farril et al., 2013). Moreover, tapirs are important fruit consumers in altered areas of the Cerrado (Hannibal et al., 2019). All these mentioned generalists had distinct network roles and high species-strength metrics, suggesting their relevance as likely-keystone species.

Identifying species' network role is key for conservation. If a connector becomes extinct, the network can fragment into several isolated modules—although their inner structure may be preserved (Donatti et al., 2011). This would be the probable scenario if tapirs, an already vulnerable large-sized mammal (Varela et al., 2019), go extinct: the Cerrado seed dispersal network would become less resilient and more susceptible to subsequent extinctions (Correa et al., 2016; Ramos-Robles et al., 2018). On the other hand, if a hub species disappears, the module it belonged to might fragment, bringing cascade effects on neighboring modules (Donatti et al., 2011). For example, the extinction of the *stricto* sensu frugivore *A. galeata* could disintegrate the core structure of the modules it mostly interacts (Silva & Melo, 2011). Whatever its network role, when a species is lost, disperser richness becomes increasingly important

as disperser abundance declines—meaning the identity of this lost species could greatly impact the number of plants dispersed (Rumeu et al., 2017). It must also be considered indirect or unforeseen impacts caused by disperser extinction on plant communities (Rogers et al., 2021).

In terms of seed dispersal potential, the frugivore assembly in the Cerrado network has a moderate ecological capacity (SDP = 0.48), probably due to the diversity of species acting in the network. Animals interact differently with fruits and seeds: while some frugivores swallow fruits entirely, leaving seeds intact, others destroy seeds when feeding (Levey, 1987; Ragusa-Netto, 2014). In heterogeneous landscapes like the Cerrado, multiple species providing the dispersal service are important to ensure complementary network efficiency (Rother et al., 2016). In fact, a generalized system (i.e., multiple dispersers of contrasting efficiency) can be more advantageous for plants rather than a specialized one (i.e., few but highly efficient dispersers). This is because several dispersal vectors diversify interactions with plants, increase the system's overall seed dispersal efficiency, and ensure plants' maintenance even if their most efficient agents go extinct (Schupp et al., 2010).

In the Cerrado, the synergistic effects of birds and ants help to stabilize temporal fluctuations in the number of seeds dispersed from Cerrado sensu stricto trees (Campagnoli & Christianini, 2021). Likewise, secondary dispersal promoted by different agents is pivotal for the Cerrado vegetation. In Arecaceae species, seeds are dispersed by a rich assemblage of ground- and tree-dwelling frugivores, which assist their short- to medium-distanced dispersal (Blanco et al., 2019).

FIGURE 4 Fruit width (a) and seed length (b) among major disperser groups of the Cerrado seed dispersal network. In boxplots, the median is represented by the bold vertical line, whereas the third and first quartile are represented by whiskers' upper and lower extremities, respectively. Points above whiskers are outliers. Groups assigned the same letter did *not* show statistical differences ($p \leq .05$) in Dunn's *post hoc* test.
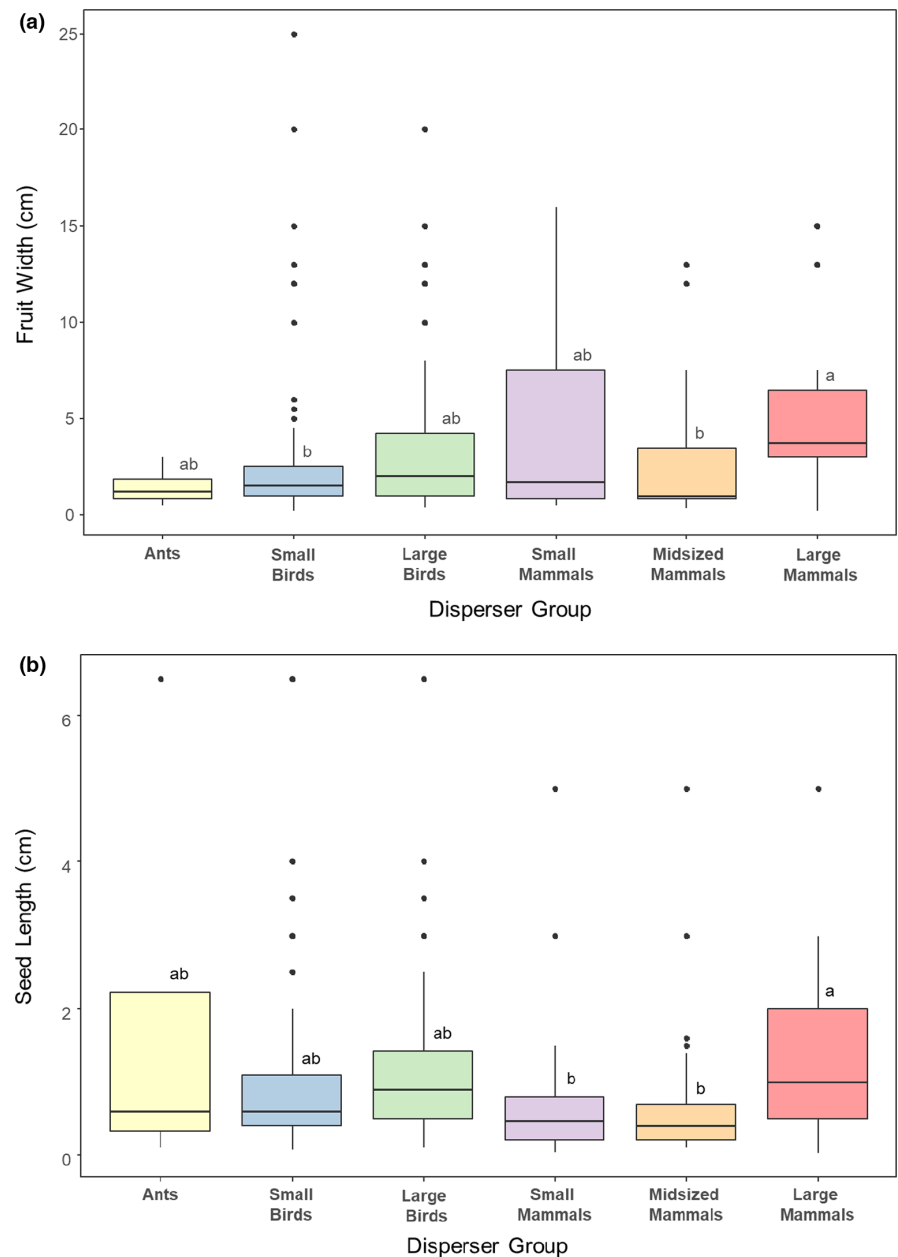
High degrees of generalism—as seen in the Cerrado network—suggest ecological redundancies to seed dispersal, so that a single fruited-plant species can be dispersed by various, distinct agents. Redundancy might even uncover "rescue effects" to the biome's system, in which plants missing their main disperser are unlikely to get extinct due to the "dispersal rescue" exerted by alternative, generalist agents.

Our SDP score represents an initial attempt to numerically evaluate the ecological *potential* of Cerrado frugivores for seed dispersal. Its value is not fixed, however, as it might change if spatially and temporally analyzed. Plant-frugivore interactions usually vary by region and season, susceptible to fruit availability and frugivore abundance (Fleming & Kress, 2013; Howe, 2014). Given Cerrado's extension and seasonality, these factors might also be pondered. SDP is not an estimation of Seed Dispersal Effectiveness (SDE). SDE would

require accounting for quantitative and qualitative aspects of seed dispersal beyond our data availability—for example, amount of seeds removed per species, seed viability after interactions, seed deposition site, and seedlings' fate (Schupp et al., 2010).

4.3 | What are the effects of the defaunation of large-bodied frugivores in the Cerrado seed dispersal network?

We found a DI of 0.43, which means a moderate defaunation intensity (DI = 0.1–0.7) according to Benítez-López et al. (2019)'s defaunation categories. Bogoni et al. (2020) reported a similar DI (=0.50) in their continental-scale analysis of mammal defaunation for the Cerrado. They also found that the Cerrado has one of the

most downsized mammalian faunae among Neotropical biomes (i.e., historical assemblage-wide reductions in species' size structure).

Nevertheless, the defaunation status depicted in our study should be interpreted conservatively. Our frugivore focal assembly was retrieved from secondary data, which may just partially represent the actual situation of Cerrado's largest dispersers. Many studies on seed dispersal networks are conducted in historically-defaunated areas, and large vertebrates occur at low densities (Almeida & Galetti, 2007; Vidal et al., 2013). Investigating, thus, their role as seed dispersers is relatively challenging (Vidal et al., 2013).

Some of our findings suggest the effects of large-frugivore defaunation on the Cerrado seed dispersal network, although more evidence and variables should be considered to verify its comprehensiveness. Nonetheless, by the precautionary principle, we call for urgency to the possibility.

In terms of metrics, the considerably modular pattern of the Cerrado network could be a proximal indication of defaunation. Medium- to large-bodied frugivores disperse a high number of plant species, usually connecting modules. When they are lost, the network could fracture, emphasizing its modular pattern (Donatti et al., 2011). Another sign could be various small-bodied species acting as hubs in the Cerrado network, compensating for the loss of large-bodied species in network topology (Vidal et al., 2013). Some of Cerrado's iconic large-bodied dispersers (Kuhlmann, 2018a, 2018b), like the maned wolf (*Chrysocyon brachyurus*), greater rhea (*Rhea americana*), and white-lipped peccary (*Tayassu pecari*), did not show as much network prominence as expected. We acknowledge, though, they could be underrepresented in our dataset, once recording large dispersers' activity is challenging as many are secretive and nocturnal (Corlett, 2011; Vidal et al., 2013).

Regarding species traits, the lack of correlation between fruit size and disperser body mass is intriguing. Wider fruits are usually associated with larger frugivores (Herrel et al., 2004; Kalko et al., 1996; Lim et al., 2020), and several Cerrado's large-fruited plants exhibit the so-called 'megafaunal syndrome', meaning their main seed dispersers should be large-bodied frugivores (Guimarães et al., 2008). We expected thus these variables would be positively related. Nevertheless, such non-correlation could have other causes rather than defaunation. For example, it could have been influenced by the foraging behavior of tapir, a species capable of ingesting diverse-typed and size-varied fruits (O'Farril et al., 2013). Likewise, Chen and Moles (2015) found a negative relationship between seed size and vertebrates' body size largely due to large ungulates ingesting smaller seeds. Another reason is that we could not isolate the effects of fruit size from other covariates (e.g., morphological traits, chemical components, phylogeny), masking correlation.

Disperser body mass for large-fruited species did not differ from other plant categories. We awaited it would be significantly heavier concerning small and medium-fruited species. A downsizing in the frugivore assemblage, induced by defaunation (Bogoni et al., 2020; Dirzo et al., 2014; Estes et al., 2011), could be an explanation, although this result could stem from limited data availability.

We also saw a low similarity between the network's large-bodied species and the actual dispersers interacting with large-fruited plants. Consequently, Cerrado large-fruited plants could be relying on a greater frugivore diversity for their dispersal as a result of defaunation. We draw a parallel from the recent geological past when Cerrado megafaunal plants (e.g., *Caryocar*, *Hymenaea*, *Annona*) used to be dispersed by massive frugivores—for example, giant ground-sloths, gomphotheres (Guimarães et al., 2008) – and, nowadays, their disperser pool is composed by relatively smaller frugivores (Guimarães et al., 2008). Similarly, in Atlantic Forest areas where large dispersers are declining or functionally extinct, some large-fruited plants have already experienced rapid microevolutionary changes due to selective pressure, exhibiting smaller seeds capable of accommodating a wider—and smaller—range of frugivores (Carvalho et al., 2016; Galetti et al., 2013). Perhaps this could be happening in the Cerrado, yet more data would help test this hypothesis. Information on the number of fruits consumed per species, visitation rate, and population density could help estimate the importance of large-bodied frugivores for Cerrado large-fruited plants' dispersal.

5 | CONCLUSION

The Cerrado seed dispersal network is structured in a slightly nested and considerably modular pattern, conferring some resilience to the plant-frugivore interactions of the biome. Most of the interactions are performed by low body-mass dispersers with opportunistic frugivorous behavior, although large frugivores like the tapir also play a critical role in network maintenance and functionality.

Although we offer an initial description of the Cerrado seed dispersal network, with the type of data available in this study (i.e., incidence records on species interactions), we have considerable restraints to describe a species' functional role or its seed dispersal effectiveness. Future research should gather alike information, which is vital for developing effective conservation policies in the Cerrado.

Our findings on defaunation hint at possible impacts on the Cerrado dispersion network. However, they must be evaluated conservatively, recognizing there are significant methodological limitations (e.g., sampling effort, observation difficulties, number of studies), which limit data about the role of Cerrado large-bodied species in seed dispersal. Further research is urgently needed provided the knowledge shortfall on the subject.

Much remains to be answered regarding the plant-frugivore dynamics in South America's largest savannah, especially at the community and ecosystem levels. Nonetheless, this study represents an initial step toward disentangling such a fundamental topic for Cerrado ecology and conservation.

ORCID

Rodrigo Béllo Carvalho https://orcid.org/0000-0001-8606-4299
Imma Oliveras Menor https://orcid.org/0000-0001-5345-2236

REFERENCES

Allenspach, N., & Dias, M. M. (2012). Frugivory by birds on *Miconia albicans* (Melastomataceae), in a fragment of cerrado in São Carlos, southeastern Brazil. *Brazilian Journal of Biology*, *72*, 407–413.

Allenspach, N., Telles, M., & Dias, M. M. (2012). Phenology and frugivory by birds on *Miconia ligustroides* (MELASTOMATACEAE) in a fragment of cerrado, southeastern Brazil. *Brazilian Journal of Biology*, *72*, 859–864.

Almeida, A. D., & Mikich, S. B. (2018). Combining plant–frugivore networks for describing the structure of neotropical communities. *Oikos*, *127*(2), 184–197.

Almeida, L. B., & Galetti, M. (2007). Seed dispersal and spatial distribution of Attalea geraensis (Arecaceae) in two remnants of Cerrado in Southeastern Brazil. *Acta Oecologica*, *32*(2), 180–187.

Alves-Costa, C. P., & Eterovick, P. C. (2007). Seed dispersal services by coatis (*Nasua nasua*, Procyonidae) and their redundancy with other frugivores in southeastern Brazil. *Acta Oecologica*, *32*(1), 77–92.

Baños-Villalba, A., Blanco, G., Díaz-Luque, J. A., Dénes, F. V., Hiraldo, F., & Tella, J. L. (2017). Seed dispersal by macaws shapes the landscape of an Amazonian ecosystem. *Scientific Reports*, *7*(1), 1–12.

Barnosky, A. D., Matzke, N., Tomiya, S., Wogan, G. O., Swartz, B., Quental, T. B., Marshall, C., McGuire, J. L., Lindsey, E. L., Maguire, K. C., Mersey, B., & Ferrer, E. A. (2011). Has the Earth's sixth mass extinction already arrived? *Nature*, *471*(7336), 51–57.

Bascompte, J., & Jordano, P. (2006). The structure of plant-animal mutualistic networks. In *Ecological networks: Linking structure to dynamics in food webs* (pp. 143–159). Oxford University Press.

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

Bascompte, J., Jordano, P., Melián, C. J., & Olesen, J. M. (2003). The nested assembly of plant–animal mutualistic networks. *Proceedings of the National Academy of Sciences*, *100*(16), 9383–9387.

Batagelj, V., & Mrvar, A. (1998). Pajek-program for large network analysis. *Connections*, *21*(2), 47–57.

Beck, H., Snodgrass, J. W., & Thebpanya, P. (2013). Long-term exclosure of large terrestrial vertebrates: Implications of defaunation for seedling demographics in the Amazon rainforest. *Biological Conservation*, *163*, 115–121.

Bello, C., Galetti, M., Pizo, M. A., Magnago, L. F. S., Rocha, M. F., Lima, R. A., Peres, C. A., Ovaskainen, O., & Jordano, P. (2015). Defaunation affects carbon storage in tropical forests. *Science Advances*, *1*(11), e1501105.

Béllo Carvalho, R., Malhi, Y., & Oliveras Menor, I. (2023). Data from: Frugivory and Seed Dispersal in the Cerrado: Network Structure and Defaunation Effects. *Dryad Digital Repository*. https://doi.org/10.5061/dryad.47d7wm3k4

Benítez-López, A., Santini, L., Schipper, A. M., Busana, M., & Huijbregts, M. A. (2019). Intact but empty forests? Patterns of hunting-induced mammal defaunation in the tropics. *PLoS Biology*, *17*(5), e3000247.

Bernardo, P. V. D. S., & Melo, F. R. D. (2013). Assemblage of medium and large size mammals in an urban Semideciduous Seasonal Forest fragment in Cerrado biome. *Biota Neotropica*, *13*, 76–80.

Bezzon, C. P. S. (2018). *Influência da largura e massa corporal sobre o forrageamento de aves frugívoras no Cerrado sensu lato* [Undergraduate Dissertation, Biological Sciences Course, Universidade Federal de Uberlândia]. UFU Repository. https://repositorio.ufu.br/handle/123456789/27770

Blanco, G., Tella, J. L., Díaz-Luque, J. A., & Hiraldo, F. (2019). Multiple external seed dispersers challenge the megafaunal syndrome anachronism and the surrogate ecological function of livestock. *Frontiers in Ecology and Evolution*, *7*, 328.

Bogoni, J. A., Peres, C. A., & Ferraz, K. M. (2020). Extent, intensity and drivers of mammal defaunation: A continental-scale analysis across the Neotropics. *Scientific Reports*, *10*(1), 1–16.

Borges, M. R., & Melo, C. (2012). Frugivory and seed dispersal of Miconia theaezans (Bonpl.) Cogniaux (Melastomataceae) by birds in a transition palm swamp: Gallery forest in Central Brazil. *Brazilian Journal of Biology*, *72*, 25–31.

Bufalo, F. S., Galetti, M., & Culot, L. (2016). Seed dispersal by primates and implications for the conservation of a biodiversity hotspot, the Atlantic Forest of South America. *International Journal of Primatology*, *37*(3), 333–349.

Cáceres, N. C. (2002). Food habits and seed dispersal by the white-eared opossum, Didelphis albiventris, in southern Brazil. *Studies on Neotropical Fauna and Environment*, *37*(2), 97–104.

Camargo, N. F. D., Cruz, R. M. S., Ribeiro, J. F., & Vieira, E. M. (2011). Frugivoria e potencial dispersão de sementes pelo marsupial Gracilinanus agilis (Didelphidae: Didelphimorphia) em áreas de Cerrado no Brasil central. *Acta Botanica Brasilica*, *25*, 646–656.

Camargo, P. H., Rodrigues, S. B., Piratelli, A. J., Oliveira, P. S., & Christianini, A. V. (2019). Interhabitat variation in diplochory: Seed dispersal effectiveness by birds and ants differs between tropical forest and savanna. *Perspectives in Plant Ecology, Evolution and Systematics*, *38*, 48–57.

Campagnoli, M. L., & Christianini, A. V. (2021). Temporal consistency in interactions among birds, ants, and plants in a neotropical savanna. *Oikos*, *2022*(2), 1–13. https://doi.org/10.1111/oik.08231

Carreira, D. C., Dáttilo, W., Bruno, D. L., Percequillo, A. R., Ferraz, K. M., & Galetti, M. (2020). Small vertebrates are key elements in the frugivory networks of a hyperdiverse tropical forest. *Scientific Reports*, *10*(1), 1–11.

Carvalho, C. S., Galetti, M., Colevatti, R. G., & Jordano, P. (2016). Defaunation leads to microevolutionary changes in a tropical palm. *Scientific Reports*, *6*(1), 1–9.

Ceballos, G., Ehrlich, P. R., & Dirzo, R. (2017). Biological annihilation via the ongoing sixth mass extinction signaled by vertebrate population losses and declines. *Proceedings of the National Academy of Sciences*, *114*(30), E6089–E6096.

Chen, S. C., & Moles, A. T. (2015). A mammoth mouthful? A test of the idea that larger animals ingest larger seeds. *Global Ecology and Biogeography*, 24(11), 1269–1280.

Chiarello, A. G. (2000). Density and population size of mammals in remnants of Brazilian Atlantic Forest. *Conservation Biology*, 14(6), 1649–1657.

Christianini, A. V., & Oliveira, P. S. (2009). The relevance of ants as seed rescuers of a primarily bird-dispersed tree in the Neotropical cerrado savanna. *Oecologia*, 160(4), 735–745.

Christianini, A. V., & Oliveira, P. S. (2010). Birds and ants provide complementary seed dispersal in a neotropical savanna. *Journal of Ecology*, 98(3), 573–582.

Christianini, A. V., Oliveira, P. S., Bruna, E. M., & Vasconcelos, H. L. (2014). Fauna in decline: Meek shall inherit. *Science*, 345(6201), 1129.

Corlett, R. T. (1998). Frugivory and seed dispersal by vertebrates in the Oriental (Indomalayan) Region. *Biological Reviews*, 73(4), 413–448.

Corlett, R. T. (2011). How to be a frugivore (in a changing world). *Acta Oecologica*, 37(6), 674–681.

Corral, A., Valério, L. M., Cheung, K. C., dos Santos Ferreira, B. H., Guerra, A., Szabo, J. K., & Reis, L. K. (2021). Plant-bird mutualistic interactions can contribute to the regeneration of forest and non-forest urban patches in the Brazilian Cerrado. *Urban Ecosystems*, 24(1), 205–213.

Correa, S. B., Arujo, J. K., Penha, J., Nunes da Cunha, C., Bobier, K. E., & Anderson, J. T. (2016). Stability and generalization in seed dispersal networks: A case study of frugivorous fish in Neotropical wetlands. *Proceedings of the Royal Society B: Biological Sciences*, 283(1837), 20161267.

Darosci, A. A. B., Bruna, E. M., Motta-Junior, J. C., da Silva Ferreira, C., Blake, J. G., & Munhoz, C. B. R. (2017). Seasonality, diaspore traits and the structure of plant-frugivore networks in Neotropical savanna forest. *Acta Oecologica*, 84, 15–22.

Dirzo, R., & Miranda, A. (1990). Contemporary neotropical defaunation and forest structure, function, and diversity—a sequel to John Terborgh. *Conservation Biology*, 4(4), 444–447.

Dirzo, R., Young, H. S., Galetti, M., Ceballos, G., Isaac, N. J., & Collen, B. (2014). Defaunation in the Anthropocene. *Science*, 345(6195), 401–406.

Donatti, C. I., Guimarães, P. R., Galetti, M., Pizo, M. A., Marquitti, F. M., & Dirzo, R. (2011). Analysis of a hyper-diverse seed dispersal network: Modularity and underlying mechanisms. *Ecology Letters*, 14(8), 773–781.

Donoso, I., Fricke, E. C., Hervías-Parejo, S., Rogers, H. S., & Traveset, A. (2022). Drivers of ecological and evolutionary disruptions in the seed dispersal process: Research trends and biases. *Frontiers in Ecology and Evolution*, 10, 794481. https://doi.org/10.3389/fevo.2022.794481

Dormann, C. F., & Strauss, R. (2014). A method for detecting modules in quantitative bipartite networks. *Methods in Ecology and Evolution*, 5(1), 90–98.

Dugger, P. J., Blendinger, P. G., Böhning-Gaese, K., Chama, L., Correia, M., Dehling, D. M., Emer, C., Farwig, N., Fricke, E. C., Galetti, M., García, D., Grass, I., Heleno, R., Jacomassa, F. A. F., Moraes, S., Moran, C., Muñoz, M. C., Neuschulz, E. L., Nowak, L., ... Schleuning, M. (2019). Seed-dispersal networks are more specialized in the Neotropics than in the Afrotropics. *Global Ecology and Biogeography*, 28(2), 248–261.

Dunning, J. B., Jr. (2007). *CRC handbook of avian body masses*. CRC press.

Emer, C., Jordano, P., Pizo, M. A., Ribeiro, M. C., da Silva, F. R., & Galetti, M. (2020). Seed dispersal networks in tropical forest fragments: Area effects, remnant species, and interaction diversity. *Biotropica*, 52(1), 81–89.

Escribano-Avila, G., Lara-Romero, C., Heleno, R., & Traveset, A. (2018). Tropical seed dispersal networks: Emerging patterns, biases, and keystone species traits. In W. Dáttilo & V. E. Rico-Gray (Eds.), *Ecological networks in the tropics* (pp. 93–110). Springer.

Estes, J. A., Terborgh, J., Brashares, J. S., Power, M. E., Berger, J., Bond, W. J., Carpenter, S. R., Essington, T. E., Holt, R. D., Jackson, J. B., Marquis, R. J., Oksanen, L., Oksanen, T., Paine, R. T., Pikitch, E. K., Ripple, W. J., Sandin, S. A., Scheffer, M., Schoener, T. W., ... Wardle, D. A. (2011). Trophic downgrading of planet Earth. *Science*, 333(6040), 301–306.

Farias, J., Sanchez, M., Abreu, M. F., & Pedroni, F. (2015). Seed dispersal and predation of *Buchenavia tomentosa* Eichler (Combretaceae) in a Cerrado sensu stricto, midwest Brazil. *Brazilian Journal of Biology*, 75, 88–96.

Fleming, T. H., & Kress, W. J. (2013). *The ornaments of life*. University of Chicago Press.

Francisco, M. R., & Galetti, M. (2001). Frugivoria e dispersão de sementes de *Rapanea lancifolia* (Myrsinaceae) por aves numa área de cerrado do Estado de São Paulo, sudeste do Brasil. *Ararajuba*, 9(1), 13–19.

Francisco, M. R., & Galetti, M. (2002). Aves como potenciais dispersoras de sementes de *Ocotea pulchella* Mart. (Lauraceae) numa área de vegetação de cerrado do sudeste brasileiro. *Brazilian Journal of Botany*, 25, 11–17.

Francisco, M. R., Lunardi, V. O., & Galetti, M. (2007). Bird attributes, plant characteristics, and seed dispersal of Pera glabrata (Schott, 1858), (Euphorbiaceae) in a disturbed cerrado area. *Brazilian Journal of Biology*, 67, 627–634.

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

Galetti, M., Guevara, R., Côrtes, M. C., Fadini, R., Von Matter, S., Leite, A. B., Labecca, F., Ribeiro, T., Carvalho, C. S., Collevatti, R. G., Pires, M. M., Guimarães, P. R., Jr., Brancalion, P. H., Ribeiro, M. C., & Jordano, P. (2013). Functional extinction of birds drives rapid evolutionary changes in seed size. *Science*, 340(6136), 1086–1090.

Genrich, C. M., Mello, M. A., Silveira, F. A., Bronstein, J. L., & Paglia, A. P. (2017). Duality of interaction outcomes in a plant–frugivore multilayer network. *Oikos*, 126(3), 361–368.

Giacomini, H. C., & Galetti, M. (2013). An index for defaunation. *Biological Conservation*, 163, 33–41.

Godínez-Alvarez, H., Ríos-Casanova, L., & 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(12), 6136–6143.

Gonçalves, V. F., Silva, A. M., Baesse, C. Q., & Melo, C. (2015). Frugivory and potential of birds as dispersers of *Siparuna guianensis*. *Brazilian Journal of Biology*, 75, 300–304.

Gottsberger, G., & Silberbauer-Gottsberger, I. (1983). Dispersal and distribution in the cerrado vegetation of Brazil. *Sonderbd Naturwiss Ver Hamburg*, 7, 315–352.

Guerra, T. J., Dayrell, R. L., Arruda, A. J., Dáttilo, W., Teixido, A. L., Messeder, J. V., & Silveira, F. A. (2017). Intraspecific variation in fruit–frugivore interactions: Effects of fruiting neighborhood and consequences for seed dispersal. *Oecologia*, 185, 233–243.

Guerta, R. S., Lucon, L. G., Motta-Junior, J. C., Vasconcellos, L. A. D. S., & Figueiredo, R. A. D. (2011). Bird frugivory and seed germination of *Myrsine umbellata* and *Myrsine lancifolia* (Myrsinaceae) seeds in a cerrado fragment in southeastern Brazil. *Biota Neotropica*, 11, 59–65.

Guimarães, P. R., Galetti, M., & Jordano, P. (2008). Seed dispersal anachronisms: Rethinking the fruits extinct megafauna ate. *PLoS One*, 3(3), e1745.

Hannibal, W., de Jesus, P. R., Oliveira, R. F., & Ragusa-Netto, J. (2019). Frugivory and seed dispersal by the lowland tapir in a fragmented landscape of Cerrado in southern Goiás, Brazil. *Boletim da sociedade Brasileira de Mastozoologia*, 84, 19–22.

Hansen, D. M., & Galetti, M. (2009). The forgotten megafauna. *Science*, 324(5923), 42–43.

Heleno, R., Garcia, C., Jordano, P., Traveset, A., Gómez, J. M., Blüthgen, N., Memmott, J., Moora, M., Cerdeira, J., Rodríguez-Echeverría, S.,

Freitas, H., & Olesen, J. M. (2014). Ecological networks: Delving into the architecture of biodiversity. *Biology Letters*, *10*(1), 20131000.

Herrel, A., Vanhooydonck, B., Joachim, R., & Irschick, D. J. (2004). Frugivory in polychrotid lizards: Effects of body size. *Oecologia*, *140*(1), 160–168.

Herrera, E. A., & Robinson, M. D. (2000). Reproductive and fat body cycles of the tegu lizard, *Tupinambis teguixin*, in the Llanos of Venezuela. *Journal of Herpetology*, *34*(4), 598–601.

Hölldobler, B., & Wilson, E. O. (1998). *Journey to the ants: A story of scientific exploration*. Harvard University Press.

Howe, H. F. (2014). Diversity storage: Implications for tropical conservation and restoration. *Global Ecology and Conservation*, *2*, 349–358.

Jones, K. E., Bielby, J., Cardillo, M., Fritz, S. A., O'Dell, J., Orme, C. D. L., Safi, K., Sechrest, W., Boakes, E. H., Carbone, C., Connolly, C., Cutts, M. J., Foster, J. K., Grenyer, R., Habib, M., Plaster, C. A., Price, S. A., Rigby, E. A., Rist, J., … Purvis, A. (2009). PanTHERIA: A species-level database of life history, ecology, and geography of extant and recently extinct mammals: Ecological Archives E090-184. *Ecology*, *90*(9), 2648.

Jordano, P. (1987). Patterns of mutualistic interactions in pollination and seed dispersal: Connectance, dependence asymmetries, and co-evolution. *The American Naturalist*, *129*(5), 657–677.

Jordano, P., Bascompte, J., & Olesen, J. M. (2003). Invariant properties in coevolutionary networks of plant–animal interactions. *Ecology Letters*, *6*(1), 69–81.

Jordano, P., García, C., Godoy, J. A., & García-Castaño, J. L. (2007). Differential contribution of frugivores to complex seed dispersal patterns. *Proceedings of the National Academy of Sciences*, *104*(9), 3278–3282.

Kalko, E. K., Herre, E. A., & Handley, C. O., Jr. (1996). Relation of fig fruit characteristics to fruit-eating bats in the New and Old World tropics. *Journal of Biogeography*, *23*(4), 565–576.

Kitamura, S., Yumoto, T., Poonswad, P., Chuailua, P., Plongmai, K., Maruhashi, T., & Noma, N. (2002). Interactions between fleshy fruits and frugivores in a tropical seasonal forest in Thailand. *Oecologia*, *133*(4), 559–572.

Klink, C. A., & Machado, R. B. (2005). A conservação do Cerrado brasileiro. *Megadiversidade*, *1*(1), 147–155.

Kuhlmann, M. (2018a). *Frutos e Sementes do Cerrado: Espécies Atrativas para a Fauna* (Vol. *1*). M. K. Peres.

Kuhlmann, M. (2018b). *Frutos e Sementes do Cerrado: Espécies Atrativas para a Fauna* (Vol. *2*). M. K. Peres.

Kuhlmann, M., & Ribeiro, J. F. (2016a). Evolution of seed dispersal in the Cerrado biome: ecological and phylogenetic considerations. *Acta Botanica Brasilica*, *30*, 271–282.

Kuhlmann, M., & Ribeiro, J. F. (2016b). Fruits and frugivores of the Brazilian Cerrado: ecological and phylogenetic considerations. *Acta Botanica Brasilica*, *30*, 495–507.

Laurindo, R. S., Gregorin, R., & Tavares, D. C. (2017). Effects of biotic and abiotic factors on the temporal dynamic of bat-fruit interactions. *Acta Oecologica*, *83*, 38–47.

Legendre, P., & Legendre, L. (2012). *Numerical ecology*. Elsevier.

Lessa, L. G., Geise, L., & Costa, F. N. (2013). Effects of gut passage on the germination of seeds ingested by didelphid marsupials in a neotropical savanna. *Acta Botanica Brasilica*, *27*, 519–525.

Levey, D. J. (1987). Seed size and fruit-handling techniques of avian frugivores. *The American Naturalist*, *129*(4), 471–485.

Levine, J. M., & Murrell, D. J. (2003). The community-level consequences of seed dispersal patterns. *Annual Review of Ecology, Evolution, and Systematics*, *34*(1), 549–574.

Lim, J. Y., Svenning, J. C., Göldel, B., Faurby, S., & Kissling, W. D. (2020). Frugivore-fruit size relationships between palms and mammals reveal past and future defaunation impacts. *Nature Communications*, *11*(1), 1–13.

Lorenzi, H. (2010). *Flora Brasileira: Arecaceae (Palmeiras)*. Instituto Palmarum.

Lorenzi, H. (2016a). *Árvores Brasileiras. Manual de Identificação e Cultivo de Plantas Arbóreas Nativas do Brasil* (Vol. *1*, 7th ed.). Instituto Plantarum.

Lorenzi, H. (2016b). *Árvores Brasileiras. Manual de Identificação e Cultivo de Plantas Arbóreas Nativas do Brasil* (Vol. *2*, 5th ed.). Instituto Plantarum.

Lorenzi, H. (2016c). *Árvores Brasileiras. Manual de Identificação e Cultivo de Plantas Arbóreas Nativas do Brasil* (Vol. *3*, 2th ed.). Instituto Plantarum.

Machado, R. B., Ramos Neto, M. B., Pereira, P. G. P., Caldas, E. F., Gonçalves, D. A., Santos, N. S., Tabor, K., & Steininger, M. (2004). *Estimativas de perda da área do Cerrado brasileiro*. Conservation International.

Magalhães, V. B., Espirito Santo, N. B., Salles, L. F., Soares, H., Jr., & Oliveira, P. S. (2018). Secondary seed dispersal by ants in Neotropical cerrado savanna: Species-specific effects on seeds and seedlings of *Siparuna guianensis* (Siparunaceae). *Ecological Entomology*, *43*(5), 665–674.

Marcondes-Machado, L. O. (2002). Comportamento alimentar de aves em Miconia rubiginosa (Melastomataceae) em fragmento de cerrado, São Paulo. *Iheringia. Série Zoologia*, *92*, 97–100.

Markl, J. S., Schleuning, M., Forget, P. M., Jordano, P., Lambert, J. E., Traveset, A., Wright, S. J., & Böhning-Gaese, K. (2012). Meta-analysis of the effects of human disturbance on seed dispersal by animals. *Conservation Biology*, *26*(6), 1072–1081.

Maruyama, P. K., Melo, C., Pascoal, C., Vicente, E., Cardoso, J. C. F., Brito, V. L. G., & Oliveira, P. E. (2019). What is on the menu for frugivorous birds in the Cerrado? Fruiting phenology and nutritional traits highlight the importance of habitat complementarity. *Acta Botanica Brasilica*, *33*, 572–583.

Melo, C., Bento, E. C., & Oliveira, P. E. (2003). Frugivory and dispersal of Faramea cyanea (Rubiaceae) in cerrado woody plant formations. *Brazilian Journal of Biology*, *63*, 75–82.

Melo, C., & Oliveira, P. E. (2009). Frugivory in *Lacistema hasslerianum* Chodat (Lacistemaceae), a gallery forest understory treelet in Central Brazil. *Brazilian Journal of Biology*, *69*, 201–207.

McConkey, K. R., Prasad, S., Corlett, R. T., Campos-Arceiz, A., Brodie, J. F., Rogers, H., & Santamaria, L. (2012). Seed dispersal in changing landscapes. *Biological Conservation*, *146*(1), 1–13.

Mello, M. A. R., Marquitti, F. M. D., Guimarães, P. R., Kalko, E. K. V., Jordano, P., & de Aguiar, M. A. M. (2011). The modularity of seed dispersal: Differences in structure and robustness between bat– and bird–fruit networks. *Oecologia*, *167*(1), 131–140.

Mengist, W., Soromessa, T., & Legese, G. (2020). Method for conducting systematic literature review and meta-analysis for environmental science research. *MethodsX*, *7*, 100777.

Moles, A. T., Ackerly, D. D., Webb, C. O., Tweddle, J. C., Dickie, J. B., & Westoby, M. (2005). A brief history of seed size. *Science*, *307*(5709), 576–580.

Moles, A. T., & Westoby, M. (2006). Seed size and plant strategy across the whole life cycle. *Oikos*, *113*(1), 91–105.

Myers, N., Mittermeier, R. A., Mittermeier, C. G., Da Fonseca, G. A., & Kent, J. (2000). Biodiversity hotspots for conservation priorities. *Nature*, *403*(6772), 853–858.

O'Farril, G., Galetti, M., & Campos-Arceiz, A. (2013). Frugivory and seed dispersal by tapirs: An insight on their ecological role. *Integrative Zoology*, *8*(1), 4–17.

Olesen, J. M., Bascompte, J., Dupont, Y. L., Elberling, H., Rasmussen, C., & Jordano, P. (2011). Missing and forbidden links in mutualistic networks. *Proceedings of the Royal Society B: Biological Sciences*, *278*(1706), 725–732.

Olesen, J. M., Bascompte, J., Dupont, Y. L., & Jordano, P. (2007). The modularity of pollination networks. *Proceedings of the National Academy of Sciences*, *104*(50), 19891–19896.

Oliveira, D. S. F., Franchin, A. G., & Marçal-Júnior, O. (2015). Rede de interações ave-planta: Um estudo sobre frugivoria em áreas urbanas do Brasil. *Biotemas*, *28*(4), 83–97.

Oliveira, P. S., & Marquis, R. J. (2002). *The Cerrados of Brazil: Ecology and natural history of a neotropical savanna*. Columbia University Press.

Oliveira, A. K., & Leme, F. T. (2013). Didelphis albiventris como indutor de germinação de Rapanea ferruginea (Myrcinaceae) em área de Cerrado, Mato Grosso do Sul, Brasil. *Iheringia. Série Zoologia*, *103*, 361–366.

Oliveira-Filho, A. T., & Ratter, J. A. (2002). Vegetation physiognomies and woody flora of the cerrado biome. In P. S. Oliveira & R. J. Marquis (Eds.), *The Ccerrados of Brazil: Ecology and natural history of a neotropical savana* (pp. 91–120). Columbia University Press.

Ong, L., McConkey, K. R., & Campos-Arceiz, A. (2022). The ability to disperse large seeds, rather than body mass alone, defines the importance of animals in a hyper-diverse seed dispersal network. *Journal of Ecology*, *110*(2), 313–326.

Paniago, L. P. M., & Silva, A. M. (2017). *Partição na Assembleia de Frugívoros em Curatella americana L. (Dilleniaceae) no Cerrado*. [Graduate Field Course Report] (pp. 195–208). Uberlândia Federal University.

Peres, C. A., & Palacios, E. (2007). Basin-wide effects of game harvest on vertebrate population densities in Amazonian forests: Implications for animal-mediated seed dispersal. *Biotropica*, *39*(3), 304–315.

Pinto, M. P., Diniz-Filho, J. A. F., Bini, L. M., Blamires, D., & Rangel, T. F. L. (2008). Biodiversity surrogate groups and conservation priority areas: Birds of the Brazilian Cerrado. *Diversity and Distributions*, *14*(1), 78–86.

Pires, L. P., & de Melo, C. (2020). Seasonal consistency of the assembling rules in a bird-fruiting plant network. *Ecological Complexity*, *44* 100869.

Purificação, K. N., & Pascotto, M. C. (2019). Frugivory by Birds on *Curatella americana* L. (Dilleniaceae) in a Brazilian Savanna area in the East of Mato Grosso, Brazil. *South American Journal of Basic Education, Technical and Technological*, *6*(2), 208–217.

Purificacao, K. N., Pascotto, M. C., Mohr, A., & Lenza, E. (2015). Frugivory by birds on *Schefflera morototoni* (Araliaceae) in a Cerrado-Amazon orest transition area, eastern Mato Grosso, Brazil. *Acta Amazonica*, *45*, 57–64.

Purificação, K. N., Pascotto, M. C., Pedroni, F., Mews, H. A., & Lima-Junior, D. P. (2020). Disentangling the architecture of the frugivorous bird-plant interaction networks in a savanna-forest mosaic in the Neotropical savanna. *Acta Oecologica*, *107*, 103601.

Purificação, K. N., Pascotto, M. C., Pedroni, F., Pereira, J. M. N., & Lima, N. A. (2014). Interactions between frugivorous birds and plants in savanna and forest formations of the Cerrado. *Biota Neotropica*, *14*.

R Core Team. (2021). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing.

Ragusa-Netto, J. (2014). Crop damage of *Eriotheca gracilipes* (Bombacaceae) by the blue-fronted Amazon (*Amazona aestiva*, Psittacidae), in the Brazilian Cerrado. *Brazilian Journal of Biology*, *74*, 837–843.

Ramos-Robles, M., Andresen, E., & Díaz-Castelazo, C. (2018). Modularity and robustness of a plant-frugivore interaction network in a disturbed tropical forest. *Ecoscience*, *25*(3), 209–222.

Ratter, J. A., Ribeiro, J. F., & Bridgewater, S. (1997). The Brazilian cerrado vegetation and threats to its biodiversity. *Annals of Botany*, *80*(3), 223–230.

Redford, K. H. (1992). The empty forest. *Bioscience*, *42*(6), 412–422.

Rogers, H. S., Donoso, I., Traveset, A., & Fricke, E. C. (2021). Cascading impacts of seed disperser loss on plant communities and ecosystems. *Annual Review of Ecology, Evolution, and Systematics*, *52*, 641–666.

Rother, D. C., Pizo, M. A., & Jordano, P. (2016). Variation in seed dispersal effectiveness: The redundancy of consequences in diversified tropical frugivore assemblages. *Oikos*, *125*(3), 336–342.

Rumeu, B., Devoto, M., Traveset, A., Olesen, J. M., Vargas, P., Nogales, M., & Heleno, R. (2017). Predicting the consequences of disperser extinction: Richness matters the most when abundance is low. *Functional Ecology*, *31*(10), 1910–1920.

Santos, A. M., Jacobi, C. M., & Silveira, F. A. (2017). Frugivory and seed dispersal effectiveness in two *Miconia* (Melastomataceae) species from ferruginous campo rupestre. *Seed Science Research*, *27*(2), 65–73.

Sarmento, R., Alves-Costa, C. P., Ayub, A., & Mello, M. A. (2014). Partitioning of seed dispersal services between birds and bats in a fragment of the Brazilian Atlantic Forest. *Zoologia (Curitiba)*, *31*(3), 245–255.

Schupp, E. W., Jordano, P., & Gómez, J. M. (2010). Seed dispersal effectiveness revisited: A conceptual review. *New Phytologist*, *188*(2), 333–353.

Silva, A. M., & Melo, C. D. (2011). Frugivory and seed dispersal by the Helmeted Manakin (*Antilophia galeata*) in forests of Brazilian Cerrado. *Ornitología Neotropical*, *22*, 69–77.

Silva, A. M., & Melo, C. (2013). Overlap and resource sharing in coteries of fruit-eating birds. *Journal of Tropical Ecology*, *29*(5), 409–416.

Silva, G. B. M. D., & Pedroni, F. (2014). Frugivoria por aves em área de cerrado no município de Uberlândia, Minas Gerais. *Revista Árvore*, *38*, 433–442.

Silva, I. A., Figueiredo, R. A. D., & Matos, D. M. D. S. (2008). Feeding visit time of fruit-eating birds in Cerrado plants: Revisiting the predation risk model. *Revista Brasileira de Zoologia*, *25*, 682–688.

Silva, F. R., Montoya, D., Furtado, R., Memmott, J., Pizo, M. A., & Rodrigues, R. R. (2015). The restoration of tropical seed dispersal networks. *Restoration Ecology*, *23*(6), 852–860.

Silva, W. R., Guimaraes, P. R., Jr, Dos Reis, S. F., & Guimarães, P. (2007). Investigating fragility in plant–frugivore networks: a case study of the Atlantic forest in Brazil. In *Seed dispersal: theory and its application in a changing world* (pp. 561–578). CAB International.

Silva-Júnior, M. C. (2012). *100 Árvores do Cerrado sentido restrito: Guia de Campo*. Rede de Sementes do Cerrado.

Silva-Júnior, M. C., & Silva Pereira, B. A. (2009). *+100 Árvores do Cerrado – Mata de Galeria: Guia de Campo*. Rede de Sementes do Cerrado.

Simmons, B. I., Sutherland, W. J., Dicks, L. V., Albrecht, J., Farwig, N., García, D., Jordano, P., & González-Varo, J. P. (2018). Moving from frugivory to seed dispersal: Incorporating the functional outcomes of interactions in plant–frugivore networks. *Journal of Animal Ecology*, *87*(4), 995–1007.

Strassburg, B. B. N., Brooks, T., Feltran-Barbieri, R., Iribarrem, A., Crouzeilles, R., Loyola, R., Latawiec, A. E., Oliveira Filho, F. J. B., Scaramuzza, C. A. M., Scarano, F. R., Soares-Filho, B., & Balmford, A. (2017). Moment of truth for the Cerrado hotspot. *Nature Ecology & Evolution*, *1*(4), 1–3.

Tella, J. L., Hiraldo, F., Pacífico, E., Díaz-Luque, J. A., Dénes, F. V., Fontoura, F., Guedes, N., & Blanco, G. (2020). Conserving the diversity of ecological interactions: The role of two threatened macaw species as legitimate dispersers of "megafaunal" fruits. *Diversity*, *122*(2), 45.

Terborgh, J., Nuñez-Iturri, G., Pitman, N. C., Valverde, F. H. C., Alvarez, P., Swamy, V., Pringle, E. G., & Paine, C. T. (2008). Tree recruitment in an empty forest. *Ecology*, *89*(6), 1757–1768.

Thébault, E., & Fontaine, C. (2010). Stability of ecological communities and the architecture of mutualistic and trophic networks. *Science*, *329*(5993), 853–856.

Thompson, K., & Rabinowitz, D. (1989). Do big plants have big seeds? *The American Naturalist*, *133*(5), 722–728.

Torres, J. M., dos Anjos, E. A., & Ferreira, C. M. (2018). Frugivoria por morcegos filostomídeos (Chiroptera, Phyllostomidae) em dois remanescentes urbanos de cerrado em Campo Grande, Mato Grosso do Sul. *Iheringia. Série Zoologia*, *108*, e2018002.

Tubelis, D. P., & Cavalcanti, R. B. (2001). Community similarity and abundance of bird species in open habitats of a central Brazilian Cerrado. *Ornitologia Neotropical*, *12*(1), 57–73.

Tylianakis, J. M., Laliberté, E., Nielsen, A., & Bascompte, J. (2010). Conservation of species interaction networks. *Biological Conservation*, *143*(10), 2270–2279.

Varela, D., Flesher, K., Cartes, J. L., de Bustos, S., Chalukian, S., Ayala, G., & Richard-Hansen, C. (2019). Tapirus terrestris. *The IUCN Red List of Threatened Species, 2019*, e.T21474A45174127. https://doi.org/10.2305/IUCN.UK.2019-1.RLTS.T21474A45174127.en

Vidal, M. M., Pires, M. M., & Guimaraes, P. R., Jr. (2013). Large vertebrates as the missing components of seed-dispersal networks. *Biological Conservation, 163*, 42–48.

Villar, N., Paz, C., Zipparro, V., Nazareth, S., Bulascoschi, L., Bakker, E. S., & Galetti, M. (2021). Frugivory underpins the nitrogen cycle. *Functional Ecology, 35*(2), 357–368.

Vitorino, B. D., da Frota, A. V. B., Maruyama, P. K., da Silva Nunes, J. R., & Vizentin-Bugoni, J. (2022). Influence of sampling methods on the description of a Neotropical seed dispersal network. *Acta Oecologica, 114*, 103805.

Wright, S. J., Stoner, K. E., Beckman, N., Corlett, R. T., Dirzo, R., Muller-Landau, H. C., Nuñez-Iturri, G., Peres, C. A., & Wang, B. C. (2007). The plight of large animals in tropical forests and the consequences for plant regeneration. *Biotropica, 39*, 289–291.

Young, H. S., McCauley, D. J., Galetti, M., & Dirzo, R. (2016). Patterns, causes, and consequences of anthropocene defaunation. *Annual Review of Ecology, Evolution, and Systematics, 47*, 333–335.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.