

# Chapter 7

## Tropical Seed Dispersal Networks: Emerging Patterns, Biases, and Keystone Species Traits

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**Abstract** Seed dispersal mediated by animals is a pivotal ecological interaction in the tropics. Despite a long tradition of tropical seed dispersal studies, only recently the drivers of the structure of seed dispersal networks are beginning to be uncovered at macroecological scales. The knowledge on tropical seed dispersal comes mainly from avian dispersal studies in the Neotropics while other frugivores and tropical regions are strongly understudied. The networks sampled with a combination of visitation census and seed recovery from feces seem more reliable of the number of detected links and web asymmetry than networks based on a single method. Our review reveals that keystone species in most networks share a set of functional traits likely influenced by species phylogeny. Woody plants bearing small berries (in the Melastomataceae, Myrtaceae, Moraceae, and Urticaceae families) were the most frequent keystone plants whereas two groups of keystone animals could be identified, namely: small obligate frugivores (Pipridae and Thraupidae) and large animals including a variety of taxonomic groups such as cracids, rodents, monkeys, and megafauna. Large keystone species tend to face a higher extinction risk leading to a concern on the sustainability of the dispersal services they provide, mainly to large-seeded plant species that are essential to ecosystem functioning.

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## 7.1 Introduction

In the tropics, the majority of seeds are contained in fleshy fruits of different shapes and colours, adapted to endozoochory (Wheelwright 1988). When feeding upon fruits, the animals remove the pulp and free the seed that is frequently moved away from its parent's crown, escaping strong competition with siblings and high pressure from shared natural enemies (Janzen 1970; Connell 1971, but see Hyatt et al. 2003). This interaction between frugivorous animals and fleshy-fruited plants is the most relevant mode of seed dispersal in tropical forests and promotes local regeneration and colonization of vacant habitats (Howe and Smallwood 1982). However, it has been identified as one of the biological interactions related to forest dynamics that is most vulnerable to human disturbance (Neuschulz et al. 2016). Seed dispersal mediated by animals contributes to genetic diversity and gene flow at local and regional scales (Jordano et al. 2007) and it also functions as a relevant driver of evolutionary dynamics for fleshy-fruited plants (Jordano et al. 2007; Lomáscolo et al. 2010; Galetti et al. 2013). A large proportion of vertebrates rely on fruits for a living, especially in tropical forests where the extraordinary bird and mammal richness is partly explained by the evolutionary relationship of such species with fleshy-fruited plants (Fleming et al. 1987).

Strictly speaking, seed dispersal events usually involve two individuals: a plant and an animal. Yet, the fruits of each plant are usually dispersed by an array of frugivorous, which in turn consume the fruits and disperse the seeds of many other plants, and consequently seed dispersal is intrinsically a community-level process. Hence, to fully understand the ecological and evolutionary consequences of seed dispersal, it is crucial to consider the inherent complexity of interactions at the level of entire biological communities (Vázquez et al. 2009a). The analytical network approach is the most valuable tool to accomplish such task by providing a holistic viewpoint from where each pairwise plant–disperser interaction can be considered simultaneously and at the same time account for the biological context of the entire community (Bascompte and Jordano 2007).

Some of the classic studies on seed dispersal already embraced such a community-wide understanding for the study of seed dispersal (Snow and Snow 1971; Crome 1975; Wheelwright et al. 1984). However, only with the advent of modern ecological networks analysis, communities started being considered as interaction networks, progressively moving from qualitative to quantitative networks (Heleno et al. 2014). Recent work has already detected some emerging macroecological patterns from tropical seed dispersal networks (Schleuning et al. 2011, 2012, 2014; Sebastián-González et al. 2015; Sakai et al. 2016). For instance, tropical dispersal networks show to be less specialized than temperate ones, which has been attributed to the greater plant diversity and lower relative abundance of resource plants in the former (Schleuning et al. 2012; Chama et al. 2013). Tropical networks also appear to be less modular than temperate ones, which might be due to a lower preponderance of seasonal effects structuring tropical interactions (Schleuning et al. 2014). Yet, such a relationship between modularity and latitude was absent once accounting for spatial autocorrelation, and a nested pattern with latitude was not found either (Sebastián-González et al. 2015).

Probably, the next challenge for researchers working on seed dispersal networks is to build more functional networks, i.e., networks that inform us on how their composition and structure translate into ecosystem functioning. To accomplish such task, it is necessary to move from seed dispersal to recruitment networks (Schleuning et al. 2015) and also from community to intra-population level. Yet, only recently has seed fate begun being incorporated in networks by quantifying the proportion of intact seeds present in animal droppings (Heleno et al. 2013). Studies that quantify seed dispersal effectiveness (sensu Schupp et al. 2010) and estimate seedling recruitment are still very rare (González-Castro et al. 2015; Donoso et al. 2016) with only some attempts in tropical ecosystems (Muñoz et al. 2016; Pigot et al. 2016).

Despite the progress made over the last decades, our understanding of tropical seed dispersal networks is still in its infancy and is currently limited by the quality, quantity, and distribution of available datasets. Here, our aim was to perform a review to characterize the state of the art, to detect potential biases affecting current understanding of tropical seed dispersal networks, and to identify emerging patterns related to the identity and functional traits of the keystone dispersers and plants and discuss their implications for conservation, something not previously tackled by previous revisions. For these purposes, we searched for articles published up to 2016 on seed dispersal networks in the tropics using the following search terms in *Web of Science* and *Scopus*: “seed dispersal network” OR “frugivor\* dispersal network” OR “plant-frugivor\* network” OR (“mutualistic interaction network” AND dispersal) in the title, keywords or abstract. This search resulted in 58 articles. An additional search was performed in *Google Scholar* with the same keywords for papers published in 2015–2016 to detect articles accepted for publication but still not available in *Web of Science*. Additional studies were compiled from two specialized databases: *Interaction Web Data Base* (<https://www.nceas.ucsb.edu/interactionweb>) and *Web of Life* (<http://www.web-of-life.es/2.0/index.php>). After processing all publications, we selected 43 studies that provided information on seed dispersal or frugivory networks at the community level within tropical latitudes (23.5°N and S). From each study, we compiled the following information: location (latitude and longitude, country and biogeographic region), main habitat type, and level of disturbance (Table 7.1). Regarding the taxonomic groups, we recorded the number of animal taxa included in each network, and the class of each animal (e.g., bird, mammal, reptile); for mammals, we further classified them according to the order to which they belong (e.g., ungulate, rodent, primate). Moreover, we obtained (1) the total number of plant species in the network and the number of links, (2) whether the network was qualitative (binary) or quantitative (weighted), (3) the sampling method implemented (e.g., visitation census or fecal analyses), and (4) whether extinction simulations were performed (Table 7.1). When the studies highlighted the role of particular species owing to their contribution to network structure, this information was also extracted and the main traits of these species were compiled.

Table 7.1 Information of the networks included in this review

Country, Region	Lat	Long	Habitat	Sampling method	P	A	Guilds	Authors	Year
Trinidad, N	10.7	61.3	DF*	V, W	50	14	B	Snow and Snow	1971
Australia, Au	-17.8	-146	RF	V, B	72	7	B	Crome	1975
Mexico, N	18.5	89.4	EDF	V, B	5	27	B	Kantak	1979
New Guinea, Oc	-7.3	-146.7	MF	VF, W	31	9	B	Bechler	1983
Costa Rica, N	10.3	84.4	MF	VF, B	169	40	B	Wheelwright et al.	1984
Malaysia, Or	3.7	102.2	RF	V, B	24	61	B	Lambert	1989
Brazil, N	-22.8	-47.1	DF*	NA, W	7	18	NA	Galetti and Pizzo	1996
Brazil, N	-22.8	-47.1	DF*	V, W	35	29	B	Galetti and Pizzo	1996
Papua, N. Guinea, Oc	-6.7	-145.1	RF	V, B	29	32	B	Marck and Wheelwright	1996
C. Phillipine, Or	10.7	123.2	MF*	F, B	36	19	B, Ba, M	Hamman and Curio	1999
Gabon, A	0.16	11.6	EDF	F, B	16	8	M	Tutin et al.	1997
Panama, N	9.1	79.6	DF	F, W	67	32	B	Poulin et al.	1999
Brazil, N	-24.3	48.4	AF*	VF, B	207	110	NA	Silva et al.	2002
Puerto Rico, N	18.3	66.8	EDF	V, W	25	16	B	Carlo et al.	2003
Puerto Rico, N	18.3	66.5	EDF*	V, W	34	20	B	Carlo et al.	2003
Puerto Rico, N	18.2	66.6	EDF	V, W	25	13	B	Carlo et al.	2003
Puerto Rico, N	18.3	66.6	EDF*	V, W	21	15	B	Carlo et al.	2003
Brazil, N	-24.2	-48.2	AF*	VF, B	207	110	B, Ba, M	Silva et al.	2007
Brazil, N	-19.3	-56.1	DF	VF, B	46	46	B, R, F, M	Donatti et al.	2011
Regional, N	NA	NA	NA	NA, B	85	18	B, Ba	Mello et al.	2011a
Regional, N	NA	NA	NA	F, W	NA	NA	B	Mello et al.	2011b
Thailand, Or	14.3	101.2	RF	VF, B	17	41	B	Sankamethawee et al.	2011
Kenya, A	0.1	34.5	RF*	V, W	33	88	B, M	Schleuning et al.	2011
Mexico, N	21.5	99.2	EDF*	F, B	16	7	Ba	Garcia-Morales et al.	2012
Kenya, A	0.1	34.5	RF*	V, W	8	54	BM	Menke et al.	2012

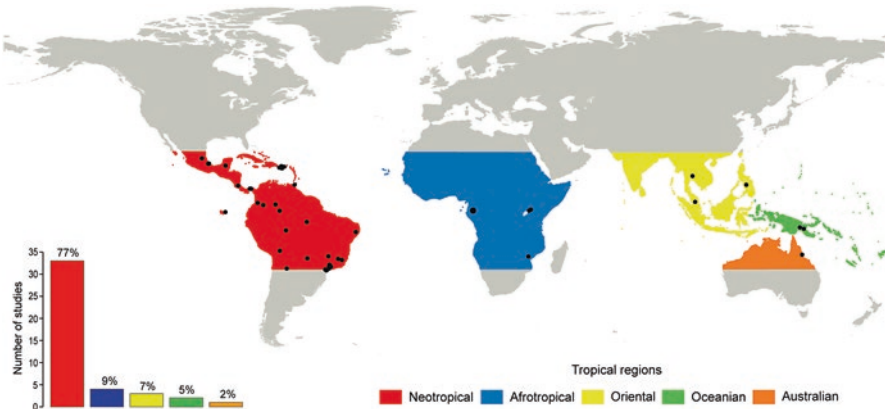
Ecuador, N	-0.4	-89.6	DF	F, W	58	18	B, R,	Heleneo et al.	2013
Bolivia, N	-16.2	-67.3	MF*	V, W	40	47	B	Saavedra et al.	2014
Brazil, N	-8.6	-36.3	AF*	F, B	56	20	B, Ba	Sarmiento et al.	2014
Brazil, N	-23.5	-47.2	RF	V, B	88	59	B	Vidal et al.	2014
Regional, N	-4.5	-56.3	FPF*	F, NA	234	69	NA	Correa et al.	2015
Mexico, N	19.3	96.6	MF	F, W	30	16	Ba	Hernández-Montero et al.	2015
Regional, N	NA	NA	NA	VF, B	NA	NA	B, Ba	Mello et al.	2015
Ecuador, N	-0.4	-89.6	EDF	F, B	34	28	B, R, M	Nogales et al.	2016
Brazil, N	-22	-47	AF*	NA, NA	51	39	B	da Silva et al.	2015
Colombia, N	2.4	74.1	RF	V, W	73	68	B, M	Stevenson et al.	2015
Brazil, N	-20	-42	AF	NA, B	234	4	M	Buñalo et al.	2016
Mozambique, A	-18.6	-34.2	DF*	F, W	43	17	M	Correia et al.	2016
Brazil, N	-19.6	-43.6	AF	F, W	34	9	M	Genrich et al.	2016
Colombia, N	3.3	76.4	MF*	V, B	75	60	B	Palacio et al.	2016
Mexico, N	19.4	96.2	DF*	VF, W	42	44	B	Ramos-Robles et al.	2016
Argentina, N	-23.5	-64.5	MF	VF, W	69	52	B	Ruggera et al.	2016
Brazil, N	-18.5	-47.5	DF	V, W	12	66	B	Silva et al.	2016
Panama, N	9.1	-79.1	DF	F, W	12	66	B	Silva et al.	2016

*N* neotropical, *A* afro-tropical, *Or* oriental, *Oc* Oceanian, *Au* Australian. Animals: *B* birds, *M* mammals, *Ba* bats, *R* reptiles, *F* fish. Habitat types: *RF* rain forest, *MF* montane forest, *AF* Atlantic forest, *EDF* evergreen dry forest, *DF* deciduous forest, *FPF* flood plain forest. Anthropogenic disturbed habitats are denoted with a star (\*). *V* visitation censuses, *F* fecal analyses, *W* weighted; or *B* binary. A full list of the references is available at CSIC-Repository-Pending code assignment

## 7.2 Temporal and Spatial Distribution of Tropical Seed Dispersal Networks

The gathered studies range from 1971 to 2016, although 56% of them were performed in the last 5 years, denoting the growing interest in the subject. More recent networks tend to include more animal guilds and to quantify interactions based on the identification of dispersed seeds (Table 7.1). The vast majority of tropical seed dispersal networks have been collected in the Neotropics (77%,  $n = 33$ ), particularly in Brazil (36%  $n = 12$ ), Mexico (12%  $n = 4$ ), and Puerto Rico (12%  $n = 4$ ) (see Fig. 7.1). This bias had already been detected by Corlett (1998) who pointed out the lack of studies in certain areas, such as tropical Asia, despite the great proportion of tree species adapted to seed dispersal by frugivores. Given the low proportion of studies outside the Neotropics (23%), our analyses will only distinguish between studies from the Neotropics and the Paletropics, including Oceania.

The 43 selected studies encompassed five main habitat types: deciduous and evergreen forests, rain forests, montane forests, and Atlantic forest, all being evenly represented in the dataset (Table 7.1). Similarly, these studies included both habitats with low anthropogenic disturbance ( $n = 22$ ) and highly humanized habitats ( $n = 18$ ), these last ones including secondary forests (44%,  $n = 8$ ), fragmented habitats (33%,  $n = 6$ ), and shade plantations of coffee and cocoa (22%,  $n = 4$ ).



**Fig. 7.1** World map representing the tropical regions on different colors. Black dots represent the locations of the studies included in this review. The barplot on the lower left handside indicates the number and percentage of studies in each tropical region. Differences on the number of studies between regions were significant ( $\chi^2 = 87.12$ ,  $df = 4$ ,  $P < 0.001$ )

### 7.3 Basic Network Descriptors and Methodological Bias

On average, seed dispersal networks in the tropics involved 60 plant species and 37 animal species. The average number of plants was greater for the Neotropics than the Paleotropics, the former ranging from 5 to 234 plant species and the latter from 8 to 72 plant species (Table 7.2). Animal richness, in contrast, did not follow this trend and no differences were found between the two regions. The overall species richness was greater for the Neotropics than for Paleotropics (Table 7.2) and, accordingly, Neotropical networks were less connected than Paleotropical ones (Table 7.2). Web asymmetry was consistently negative in the two regions, in agreement with the greater abundance of plants compared to animals (Table 7.2). Network robustness to species extinction ( $R$ ) is defined as the network resistance to species loss (Bascompte and Jordano 2007) and can be quantified by the area below the extinction curve generated by secondary extinctions (Dormann et al. 2009). Only 14% ( $n = 6$ ) of the studies evaluated network robustness by means of extinction simulation analyses. Such studies showed robustness values ranging from 0.50 to 0.87 with the lowest values found in fragmented rainforests (Menke et al. 2012; Stevenson et al. 2015; Palacio et al. 2016). Overall, thus, seed dispersal networks seem to be quite robust to random extinctions (Stevenson et al. 2015; Palacio et al. 2016). However, when keystone species (species with high linkage level and betweenness) are removed first, rapid secondary extinctions occur and the network collapses much sooner (Stevenson et al. 2015; Palacio et al. 2016).

### 7.4 Methodological Bias

Forty six percent of the networks in our dataset were binary whereas 54% were weighted (Table 7.1). Methods based on visitation census or on fecal content analyses were evenly used (43 vs. 33%), whereas the combination of both was less frequent (23%).

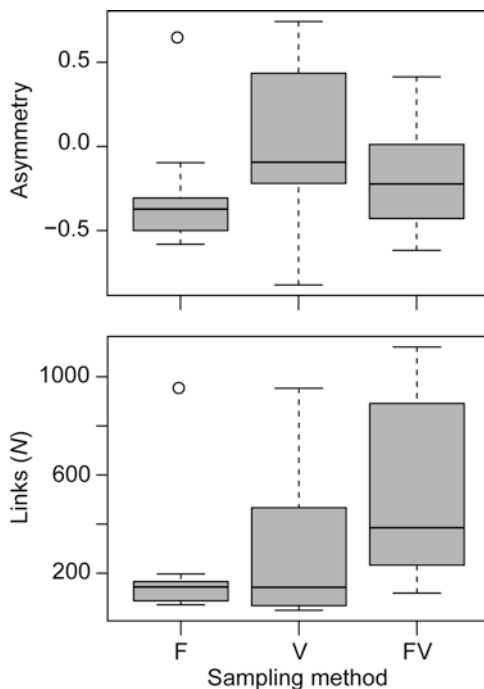
**Table 7.2** Number of plants, animals and overall species, links, connectance, and web asymmetry (mean  $\pm$  SE) for the Neotropics and Paleotropics

	Neotropics	Paleotropics	Test statistic ( $t/\chi^2$ )	df	$P$ -value	$N$
Plants	69 $\pm$ 11.6	31 $\pm$ 5.4	2.06	25	0.049	31, 10
Animals	38.1 $\pm$ 4.8	33.6 $\pm$ 8.6	0.58	14	0.567	31, 10
Species	107.13 $\pm$ 15.1	64.5 $\pm$ 8.3	3.94	13	0.003	31, 10
Links	356 $\pm$ 72.5	182 $\pm$ 48.4	1.12	21	0.275	24, 8
Connectance	0.19 $\pm$ 0.03	0.31 $\pm$ 0.1	2.27	14	0.039	24, 8
Web asymmetry	-0.18 $\pm$ 0.07	-0.035 $\pm$ 0.2	0.33	1	0.564	31, 10

Number of studies used for each variable are shown in the last column for Neo and Paleotropics, respectively. Mean differences were evaluated with a  $t$ -test in all cases except for Web asymmetry, which was compared with a Kruskal-Wallis test as it violated the assumptions of normality

It has been previously shown that the method used to collect plant–animal interaction data can influence the number of plants, animals, or links detected in a network (Bosch et al. 2009; Gibson et al. 2011). We thus evaluated whether the methodology used in each study influenced web asymmetry and the number of links detected. We found that networks sampled through visitation census tended to be more symmetrical than those sampled via seed recovery from feces; however, these results were not statistically significant ( $F_{2,34} = 2.51$   $P = 0.095$ ; see Fig. 7.2). The number of links, by contrast, was affected by the type of sampling method ( $F_{2,27} = 2.67$ ,  $P = 0.05$ ), with those networks based on a combination of the two methods encompassing on average more links than those based either on only visits or only feces (Fig. 7.2). This pattern has been previously found for pollination networks (Bosch et al. 2009) and may be explained by the underestimation of interactions with rare plants or with those outside the boundaries of the study area when methods are only based on visits. By recovering the seeds that frugivores consumed, such interactions are more likely to be detected. In addition, seed recovery also offers the possibility of obtaining information on seed dispersal quality, such as seed viability after dispersal, germination capacity, or microhabitat suitability (Schupp et al. 2010). As previously mentioned, such information allows moving forward towards seed dispersal effectiveness networks, providing data on recruitment dynamics and effective ecosystem service (Schleuning et al. 2015). Accordingly, the inclusion of methods based on seed recovery is strongly recommended.

**Fig. 7.2** Effects of interaction sampling method on Web asymmetry and Links number. The method did not affect web asymmetry ( $F_{2,34} = 2.51$   $P = 0.095$ ) whereas a higher number of links was detected in the networks based on a combined method of visit census ( $V$ ) and fecal analyses ( $F$ ), ( $F_{2,27} = 2.67$ ,  $P = 0.05$ )





## 7.5 Taxonomical and Functional Composition of Seed Dispersal Networks

### 7.5.1 *Dispersers' Guilds*

Among the 43 studies, most (74%,  $n = 32$ ) have focused on a single disperser guild, 13% ( $n = 6$ ) and 9% ( $n = 4$ ) of studies included two and three animal guilds, respectively, and only 2% ( $n = 1$ ) of the studies have considered all relevant disperser guilds (Table 7.1). A strong bias was detected on the frequency of animal taxa studied in seed dispersal networks ( $\chi^2 = 60.45$ ,  $df = 4$ ,  $N = 57$ ,  $P < 0.001$ ) with birds being the most frequently studied seed dispersers. Seventy nine percent of the studies ( $n = 34$ ) included birds while terrestrial mammals, the second group most frequently studied, appeared in 25% of the studies ( $n = 11$ ) followed by bats (12%,  $n = 7$ ); reptiles and fish were accounted for in only 5% ( $n = 3$ ) and 3.5% ( $n = 1$ ) of the studies, respectively. Within the group of terrestrial mammals, primates were the most frequently studied followed by ungulates and rodents.

### 7.5.2 *Keystone Species in Tropical Seed Dispersal Networks*

Only 11 (25%) of the 43 revised studies identified the most important species based on their contribution to network structure, yet using different methods for such purpose. Some works used the contribution to network modularity (Olesen et al. 2007), namely the within-module degree ( $z$ ) and among module connectivity ( $c$ ) values (e.g., Donatti et al. 2011; Nogales et al. 2016); da Silva et al. 2015). Other studies used the topological position of species within the network, i.e., centrality, with the indexes betweenness centrality ( $BC$ ), closeness centrality ( $CC$ ), and degree centrality or standardized degree ( $k_s$ ) among others (González et al. 2010; Mello et al. 2015; Genrich et al. 2016). The third most frequently used method was the ad hoc categorization of species as being part of the core or the periphery of the network (Palacio et al. 2016; Ramos-Robles et al. 2016). Still, other studies followed an integrated approach combining several methods (Sarmiento et al. 2014; Vidal et al. 2014; Ruggera et al. 2016). According to all those metrics, 70 species played disproportionately important roles in these tropical seed dispersal networks. Of those 70 species, 26 were plants and 44 animals with one bird species (*Catharus ustulatus*) appearing in two studies performed in Argentina and Panama as a “relevant species.” Hereafter, all these species performing a relevant role (i.e., being network or module hubs or connectors, belonging to the central core, or with high standardized degrees) will be referred to as “keystone species” regardless of the metric used to determine such role. Nonetheless, the coherence and matching of keystone species according to different methodologies is poorly understood and warrants further research (Jordán et al. 2009; Stevenson et al. 2015).

### 7.5.3 *Keystone Dispersers*

Animal keystone species belonged to 19 families, with uneven representations ( $\chi^2 = 34.8$ ,  $df = 18$ ,  $N = 45$ ,  $P = 0.01$ ). The Paleotropical families Pycnonotidae and Lybiidae (bulbuls and barbets) and the Neotropical Pipridae and Thraupidae (manakins and tanagers) were expected to be more relevant than other families for seed dispersal given their higher number of interactions, both at the network level and also as connectors of different modules (Schleuning et al. 2014). The most frequent families in the networks were Thraupidae (15%) and Turdidae (15%) followed by Pipridae (11%), Cotingidae, Cracidae, Ramphastidae, and Tyrannidae (6% each), with all other families represented by a single species, except the bat family Phyllostomidae with two species (4%). These findings add to previous evidence supporting the relevant role of Neotropical manakins and tanagers, both typical understory species (Fleming et al. 1987). Neither bulbuls nor barbets were identified as keystone families, probably due to the scarcity of data from the Paleotropics (Schleuning et al. 2014). Interestingly, our results revealed other groups of keystone dispersers including megafauna, monkeys, canopy specialist birds such as chachalacas, guans (Cracidae), and toucanets (Ramphastidae), temperate migrants (e.g., thrushes; Turdidae), and also phyllostomid bats.

### 7.5.4 *Keystone Plants*

A total of 34 plant species belonging to 16 families were identified as keystone in their networks. The most frequently represented families were Melastomataceae and Myrtaceae, which together represented 32% of all plants in the dataset. Moraceae and Urticaceae represented 24% of the species (12% each) followed by Rubiaceae (8%) and Solanaceae (6%), being the rest of the families represented only by one species. However, these differences were not significant probably owing to the scarcity of data ( $\chi^2 = 20.58$ ,  $df = 15$ ,  $N = 34$ ,  $P = 0.15$ ). All these plant families have been previously highlighted as relevant for frugivores (Snow 1981; Wheelwright et al. 1984). Other important plant families for tropical frugivores, such as Lauraceae and Palmae (Crome 1975; Snow 1981; Wheelwright et al. 1984) are, however, missing from the dataset analysed here. These families typically bear large fleshy fruits, having a mastozoochory dispersal syndrome (Snow 1981; Kuhlmann and Ribeiro 2016); thus, a possible explanation for the absence of these families on the identified keystone species group may be the difficulty of detecting the large animals that typically disperse large fruits and seeds. In contrast, the plant species identified as keystone tend to bear small fruits usually preferred by small birds. This is the case of *Miconia* (Melastomataceae), the most frequently detected genus among the keystone plants, as well as many Rubiaceae species. The typical fruits of these species are small juicy berries containing many tiny seeds. Plants with these fruit types on the mentioned families are typical of early successional stages with high colonization ability, thereby frequently appearing in cleared areas and edges (Snow 1981; Saavedra et al. 2015; Silva et al. 2016).

Some studies found ecological conditions such as species abundance, and its spatiotemporal variation, and morphological constraints as key drivers of network roles (Vázquez et al. 2009b; Silva et al. 2016). Our results reveal a strong phylogenetic component on the identity of keystone species, which does not only result of ecological contingency but is also determined by inherited characteristics shaped by evolutionary history (Vázquez et al. 2009b). The identification of keystone species and their effects on community stability are strongly relevant to understand evolutionary patterns and ecosystem services delivery (Sakai et al. 2016). Therefore, the interplay between drivers of keystone species, such as species abundance, functional traits, and phylogeny needs to be further explored (Vázquez et al. 2009b).

## 7.6 Functional Traits of Keystone Species of Tropical Seed Dispersal Networks

Previous attempts to explain why some species play a more relevant role in seed dispersal networks have evaluated several morphological and behavioral traits, of which the most common are dietary specialization, body size, and migratory behavior (Donatti et al. 2011; Sarmento et al. 2014; Schleuning et al. 2014; Vidal et al. 2014; Mello et al. 2015; Palacio et al. 2016). In the case of plants, most frequently studied traits were fruit size, seed burden, fruit type, and life form (Donatti et al. 2011; Vidal et al. 2014; Palacio et al. 2016; Ruggera et al. 2016). Accordingly, we compiled this information for the 70 species recorded as keystone in our database, as well as their IUCN conservation status ([www.iucnredlist.org](http://www.iucnredlist.org)). When trait information was not available in source articles, in addition to scientific literature, specialized databases were used ([www.hbw.com](http://www.hbw.com), [animaldiversity.org](http://animaldiversity.org), [www.tropicos.org](http://www.tropicos.org)). The categories assigned owing to dietary specialization were obligate, partial, or opportunistic frugivores. A species was considered an obligate or partial frugivore when fruit constitutes the majority (>50%) or a relevant (20–30%) component of its diet, respectively, whereas frugivores that consume fruits only occasionally were classified as opportunistic (Mello et al. 2015; Palacio et al. 2016). Animals up to 74 g of weight were classified as small sized, those in the range 75 to 250 g as medium, whereas large animals were those over 250 g and up to 40 kg (Dirzo et al. 2014; Silva et al. 2016; Mello et al. 2015). Over such weight, species were considered as megafrugivores (Dirzo et al. 2014). According to fruit diameter, plant species were classified as small (<5 mm), medium (5–10 mm), large (11–50 mm), or mega (>51 mm) and in multi- or single-seeded species according to seed number (Wheelwright et al. 1984; Saavedra et al. 2015).

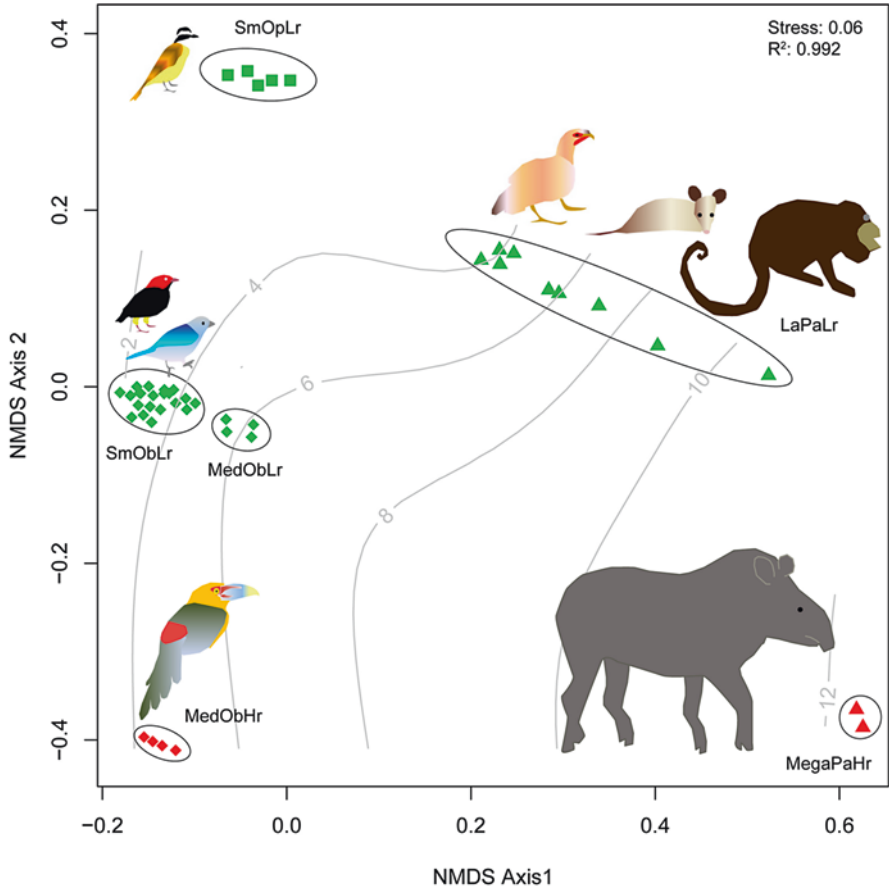
## 7.7 Keystone Dispersers' Functional Traits

We found that most animal species identified as keystone were either obligate (62.2%) or partial frugivores (24.4%), with less than 15% being opportunistic frugivores ( $\chi^2 = 17.733$ ,  $df = 2$ ,  $P > 0.001$ ). Interestingly, two thirds of the keystone species

(64%) were small frugivores, around 30% were either medium or large sized and only 6% were megafrugivores ( $\chi^2 = 38.11$ ,  $df = 3$ ,  $P > 0.001$ ). Only 14% of the keystone species were classified with higher risk of extinction (i.e., Near threatened, Vulnerable) relative to 86% that were classified as Least Concern ( $\chi^2 = 24.2$ ,  $df = 1$ ,  $P > 0.001$ ). We detected that the categories of these three variables were not randomly distributed; for instance, most obligate frugivores were small sized whereas mega and large keystone species were most frequently partial frugivores ( $\chi^2 = 19.48$ ,  $df = 6$ ,  $P > 0.005$ ). Also, larger species tended to be in higher extinction risk ( $\chi^2 = 16.04$ ,  $df = 3$ ,  $P = 0.001$ ). In contrast, dietary specialization and extinction risk were not correlated ( $\chi^2 = 1.17$ ,  $df = 2$ ,  $P = 0.57$ ). To classify frugivores according to the four variables studied (dietary specialization, body size, conservation status, and migratory behavior) a Non-metric Multidimensional scaling analysis (NMDS) was performed using the packages (*vegan* and *FD* in the R platform 3.2 (Dixon 2003; Laliberté and Legendre 2010)). We found an ordination of keystone species on several groups coherent with previous analyses on trait distribution frequency. The group gathering most species was that of small obligate frugivores; several species of tanagers, manakins, and phyllostomid bats were the most frequently represented (Fig. 7.3). Another group was that of medium to large partial frugivores of low conservation concern including several species of tucanets, chachalacas, guans, and terrestrial and arboreal mammals such as opossums and howler monkeys. Most keystone species were not threatened; however, we detected two specific groups of keystone dispersers that face an higher extinction risk, namely: some small and medium-sized obligate frugivores such as tucanets and cotingas on one side, and two mega dispersers, the Galapagos giant tortoise (*Chelonoidis nigra*) and the lowland tapir (*Tapirus terrestris*) (Fig. 7.3).

## 7.8 Keystone Plants Functional Traits

Keystone plants differed much in fruit size ( $\chi^2 = 9.6$ ,  $df = 3$ ,  $N = 27$ ,  $P = 0.022$ ). Most frequent keystone species (78%) bore medium (5–10 mm) and small fruits (>5 mm) while plants with larger fruits played more rarely such a role (Large: 11–50 mm, 18% and Mega: >51 mm, 4%). Most keystone plants produced berries (52%) followed by drupes (18%) and achenes (11%). Keystone species were typically multi-seeded, with only 20% being single-seeded ( $\chi^2 = 9.14$ ,  $df = 1$ ,  $N = 28$ ,  $P = 0.002$ ). Trees (55%) and shrubs (38%) were the most frequent life forms, whereas herbs (3.5%) and lianas (3.5%) were scarcely represented ( $X^2 = 23.27$ ,  $df = 3$ ,  $N = 29$ ,  $P < 0.001$ ). In contrast to animal functional traits, there was not interdependency of different plant traits and thus no further analyses were performed. The threatened category is not shown as most species were classified as non-evaluated.



**Fig. 7.3** Keystone species Non-metric Multidimensional scaling (NMDS). Representation of keystone dispersers based on log transformed body size (shown in the isolines), dietary specialization (diamonds: obligate frugivores, triangles: partial frugivores; squares: opportunistic frugivores), and conservation status (Red: species at higher risk of extinction, green: low risk of extinction). Ellipses denote dispersers with similar traits: *SmOpLr* Small, Opportunistic frugivores at Low risk of extinction (tyranid), *SmObLr* Small, Obligate frugivores at Low risk (manakin and tanager), *SmObHr* Small, Obligate frugivores at High risk (tucanet), *MedObLr*, *MeObHr* Medium Obligate frugivores at Lower and Higher risk of extinction, respectively (tucanets), *LaPaLr* Large, Partial frugivores at Low risk (cracid, opossum, howler monkey), *MegaPaHr* Megafauna, Partial frugivores at High risk (tapir). Species inside brackets are representative of each group

### 7.9 Trait-Based Niche Complementarity Among Network Keystone Species

There is rather low consistency among previous studies on the role of animal species traits to determine their relevance in seed dispersal networks. Some works did not find a relationship between body size and species importance in network structure

(Schleuning et al. 2014, Vidal et al. 2014, Mello et al. 2015) while others suggested that large animals tend to be the most relevant in the network (Donatti et al. 2011). Dietary specialization has been pointed out as a pivotal trait with obligate and partial frugivores playing the role of keystone species (Sarmiento et al. 2014; Schleuning et al. 2014; Mello et al. 2015; Pigot et al. 2016) other studies find that the only relevant characteristic determining animal species contribution to dispersal network was the threatened category, being keystone species those that are at higher risk of extinction (Vidal et al. 2014).

Our approach based on multivariate analyses allowed the determination of keystone frugivores integrating all relevant traits. Dietary specialization and body size seem thus the pivotal variables determining the role of keystone species in tropical seed dispersal networks (see also Pigot et al. 2016). Small-sized species of obligate frugivores were the most frequent keystone group though with the condition of being obligate frugivores (Schleuning et al. 2014; Mello et al. 2015). However, medium- to large- and mega-sized frugivores functioned as keystone species, even when they have more generalized diets. These groups of keystone species seem to provide functional complementarity to tropical dispersal networks. Namely, (1) small specialized frugivores forming the core of the keystone species and likely responsible for a large quantity of local seed dispersal of small- to medium-sized seed species; and (2) large and mega-sized animals with a more generalized diet, that may consume an array of fruits and seed types mobilized over long distances (Jordano et al. 2007; Donatti et al. 2011; Escribano-Avila et al. 2014). This pattern resembles a trait-based niche complementarity according to which closely related species (in our case tanagers, manakins and thrushes) tend to share functional traits (small-sized, obligate frugivores) and to disperse similar plants (Dehling et al. 2016; Pigot et al. 2016). Conversely, unrelated species (cracids, toucanets, opossums, howler monkeys, giant tortoises, and mega herbivores) exhibit obvious heterogeneous functional traits on size, behavior, and diet that may lead to wider arrays of dispersed species likely related to plants and animals trait matching (Dehling et al. 2016; Pigot et al. 2016).

## 7.10 Conservation Implications

There is a growing concern that seed dispersal services might be compromised in the future due to the decline and eventual extinction of frugivores populations (Galetti et al. 2013). Large animals, which tend to play a preponderant role as dispersers of many fleshy-fruited plant species (Muñoz et al. 2016; Pigot et al. 2016) are particularly threatened in many ecosystems due to hunting and poaching (Dirzo et al. 2014), further threatening seed dispersal services (Galetti et al. 2013; Vidal et al. 2013). Owing to a strong non-random matching in the morphologies of dispersers and fruits (Dehling et al. 2016), large-fruited and seeded plants are dispersed by the larger frugivores in the community (Hamann and Curio 1999). Thus, larger-fruited plants exhibit a scarcer coterie of frugivore partners than smaller-fruited

species (Crome 1975; Wheelwright et al. 1984; Donatti et al. 2011; Vidal et al. 2014; Muñoz et al. 2016; Palacio et al. 2016) and are more vulnerable to the loss of their seed dispersers, eventually truncating their reproductive capacity (Wotton and Kelly 2011). Large fruited and seeded plants are typically late-successional species that play a unique role in ecosystems (Bello et al. 2015). Therefore, further attention should be paid to the conservation status and the regeneration capacity of these species in a world depauperated of large frugivores.

## 7.11 Conclusions

The last decades have seen substantial advances in our understanding of the structure and function of seed dispersal interactions and how they might shape tropical ecosystems. Here, we identify two main functional groups of seed dispersers: one homogeneous group of small, specialized, and abundant dispersers moving many small seeds at the local scale, and another more heterogeneous group formed by larger dispersers with lower abundances and dispersing both small- and large-seeded fruits at larger regional scales. The recent advent of highly resolved, comprehensive, and quantitative seed dispersal networks encompassing whole communities will surely pave the road to further advances in the near future. Such new studies are vital to clarify global patterns on seed dispersal networks, characterize the role of large herbivores and megafauna (including extinct species) in seed dispersal, and further advance ecological network theory by incorporating temporal, spatial, and evolutionary changes into this key ecosystem service.

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