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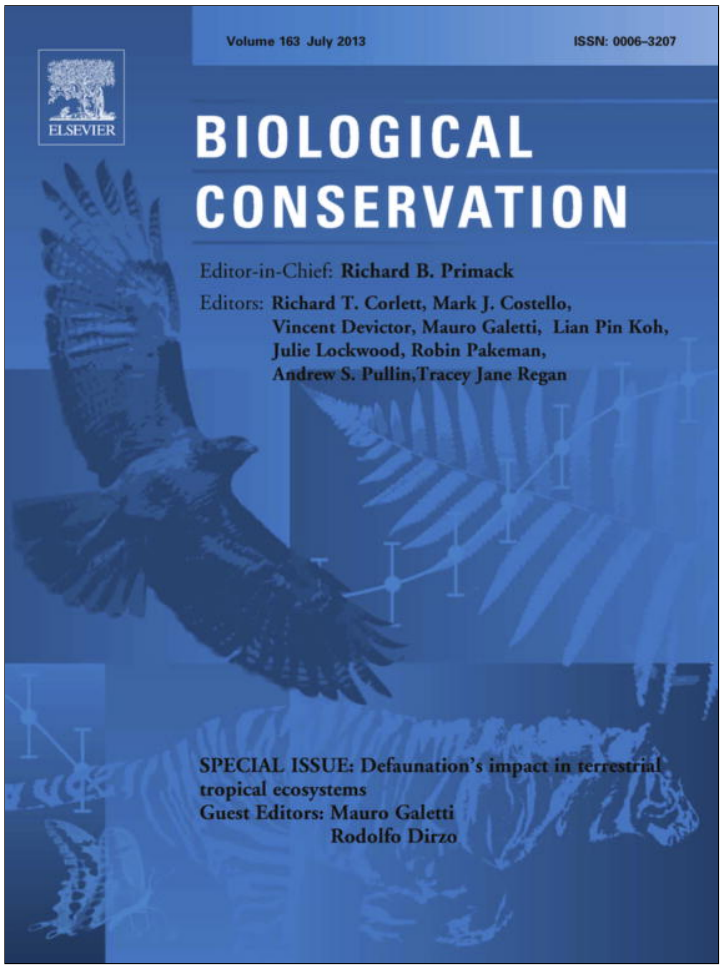

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Special Issue: Defaunation's impact in tropical terrestrial ecosystems

Large vertebrates as the missing components of seed-dispersal networks

Mariana M. Vidal [1], Mathias M. Pires [1], Paulo R. Guimarães Jr. *

Departamento de Ecologia, Instituto de Biociências, CP 11294, Universidade de São Paulo, São Paulo 05422-970, Brazil

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ABSTRACT

Large-bodied frugivores may play a key role in the networks of plants and their seed dispersers. These species, however, are often threatened by human impacts that lead to defaunation. In this paper, we discuss the potential implications of the loss of large frugivores for seed-dispersal networks. First, we review the role of large vertebrates as seed dispersers in different tropical ecosystems to show that these species are likely to be important components of seed-dispersal networks. Second, we showed that, despite their importance, large vertebrates are absent from most of the seed-dispersal networks described in the available literature. We identified three main reasons for this absence: (1) large vertebrates have already died out in the studied areas; (2) studies focus on particular taxonomic groups that consist mostly of small birds; and (3) it is inherently difficult to describe the interactions of naturally rare and secretive species such as large vertebrates. We argue that a proper evaluation of the importance of large frugivores within seed-dispersal networks would benefit from considering aspects other than the frequency of interactions. We suggest weighting pairwise interactions by their ecological consequences to quantify the contribution of large frugivores to outcomes of seed dispersal, such as landscape connectivity.

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1. Introduction

In tropical rainforests, fruits are an important food resource for vertebrates, with approximately 70–94% of all woody species relying on fruit-eating birds and mammals for seed dispersal (Howe and Smallwood, 1982; Jordano, 2000). Because seed dispersal affects seed survival, it greatly influences the fitness of individual plants. Moreover, frugivores determine how seeds are distributed in space, setting the template for the distribution of the adults of many plant species (Howe, 1989; Nathan and Muller-Landau, 2000). Thus, plant-frugivore interactions have ecological and evolutionary consequences at the individual, population and community levels (Jordano et al., 2007).

The seed-dispersal service provided by different species depends on characteristics of the seed disperser, such as diet, fruit handling, digestive physiology and movement patterns, all of which affect the qualitative and quantitative components of seed dispersal (Schupp et al., 2010). Diet breadth and movement patterns are often associated with body size. Large-bodied seed dispersers, such as ungulates, large primates and large birds such as toucans and hornbills differ in their roles as seed dispersers compared to small-bodied seed dispersers such as terrestrial small mammals, small monkeys and passerine birds. Large-bodied frugivores, having larger gape widths and mouth sizes, are able to feed on fruits of a wider range of sizes (Levey, 1987) and are therefore likely to interact with many different plant species. They are especially important for large-seeded plants that cannot be dispersed by other animals (Peres and van Roosmalen, 2002; Wheelwright, 1985). Some palm species, for instance, have seeds that are too large to be processed by small vertebrates, such as passerine birds and small mammals, and they are only dispersed by large ungulates such as the tapir (Galetti et al., 2001). Moreover, large frugivores can move long distances, thereby providing long-distance seed dispersal (Fragoso et al., 2003; Holbrook and Loiselle, 2009).

Large vertebrates are also threatened by hunting, habitat destruction and fragmentation, and they have already died out or occur at low densities in many tropical ecosystems (Markl et al., 2012; Peres and Palacios, 2007). Because large vertebrates occur naturally at low densities, it is hard to evaluate their role as seed dispersers, even in pristine environments. Indeed, large vertebrates have rarely been included in community-level studies on plant-frugivore interactions (but see Donatti et al., 2011; Gautier-Hion et al., 1985).

Assemblages of interacting species can be seen as networks of ecological interactions (Bascompte and Jordano, 2007). In this paper, we use the network approach to discuss the role of large vertebrates in interacting assemblages of plants and frugivores. We start by reviewing the literature on the importance of large vertebrates as seed dispersers in different tropical ecosystems. Next, we discuss how defaunation may already have altered communities, emphasizing the potential consequences of extinctions of large frugivores for the structure and dynamics of mutualistic networks.

* Corresponding author. Tel.: +55 11 3091 7597.
E-mail address: prguima@usp.br (P.R. Guimarães Jr.).
[1] These authors contributed equally.

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We then discuss possible reasons for the general absence of large seed dispersers from descriptions of seed-dispersal networks in the available literature. Finally, we highlight limitations of the network approach for interactions between plants and large frugivores and suggest ways to circumvent these limitations.

2. The importance of large-bodied vertebrates as seed dispersers

Defining a cut-off to differentiate between large- and small-bodied seed dispersers requires relative criteria. We consider large terrestrial mammals to include not only extremely large species such as elephants but also large- and medium-sized ungulates such as tapirs, bovids and cervids. Large-bodied fruit-eating primates include species weighing >5 kg, such as Atelidae monkeys and apes. Among birds, toucans, hornbills, cracid birds and ratites are the largest seed-dispersing species. We thus distinguish between large- and small-bodied species within each major group of dispersers (e.g., atelidae monkeys versus marmosets and toucans versus passerine birds).

Because large vertebrates often occur at lower densities than do small-bodied species, it can be argued that they have negligible effects on seed dispersal. Although studies showing how the loss of large-bodied dispersers affects the plant community are scant, several studies from tropical regions suggest that seed dispersal by large vertebrates is nonetheless important. In Asian tropical forests, multiple plant species seem to be largely dependent on large birds, primates, civets and terrestrial herbivores for seed dispersal, all of which have now reduced ranges and densities due to hunting pressure (Corlett, 1998; Kitamura et al., 2002). Large-bodied frugivores have a broad diet that includes both small- and large-seeded fruits and the small-gaped birds that survive are unable to disperse most of the large-seeded plant species and thus are unlikely to compensate for the loss of larger frugivores (Kitamura et al., 2002). If large-bodied frugivores are extirpated, small-seeded, small-fruited and fast-growing plants are expected to increase in density (Corlett, 1998). For instance, hunting of primates and ungulates reduced seed dispersal of the canopy tree *Choerospondias axillaris,* and intensified poaching is expected to cause further reductions in the population (Brodie et al., 2009). Similarly, Asian elephants provide long-distance seed dispersal for a wide variety of fruiting plants, and other large mammals such as the Asian tapir may not compensate for their absence (Campos-Arceiz et al., 2008, 2012).

In Africa, elephants are important seed dispersers in all habitats in which they occur and are unlikely to be replaced by other frugivores when populations decline (Campos-Arceiz and Blake, 2011). Primates and large birds such as hornbills are also important frugivores in Africa (Poulsen et al., 2002; Tutin, 1999). Studies on hornbills and primates in western African rainforests have shown that they have distinct diets (Poulsen et al., 2002) and are therefore unlikely to compensate for each other. The extirpation of either group will thus most likely result in declines in populations of the plants they disperse (Poulsen et al., 2002). Indeed, in Central Africa, sites where large mammals such as primates had been extirpated by hunting, seedling diversity dropped significantly (Vanthomme et al., 2010).

In the rainforests of Australia, the cassowary (*Casuarius casuarius*) is one of the only remaining large-bodied seed dispersers. Cassowaries consume fruits from more than 200 plant species and provide effective long-distance dispersal for several plants (Westcott et al., 2005). Declines in cassowary populations are expected to result in selection for changes in fruit size and to affect the population dynamics of large-seeded plant species (Westcott et al., 2005). In the Neotropics, large-seeded plants rely heavily on large birds such as cotingas, toucans and guans (Brooks and Strahl, 2000; Galetti and Aleixo, 1998), large scatter-hoarding rodents such as the agouti (Jansen et al., 2012), and large-bodied mammals such as primates (Chapman and Onderdonk, 1998) and ungulates for seed dispersal. For instance, the largest extant frugivore in the Neotropics is the lowland tapir (Olmos, 1997); while it can also act as a seed predator, the tapir provides long-distance dispersal for large-seeded plants that cannot be dispersed by other frugivores (Fragoso et al., 2003; Galetti et al., 2001). Studies in the Neotropics also show that defaunation significantly impairs seed dispersal. Among the frugivores that feed on the fruits of *Virola flexuosa* in Ecuador, large primates and large birds such as toucans were the most important seed dispersers, and seed removal was reduced in sites where such species had declined due to hunting (Holbrook and Loiselle, 2009). In fact, comparisons between protected and hunted sites in Panama have shown that small-seeded plants dispersed by abiotic means or by small-bodied dispersers were overrepresented at sites where large dispersers had been hunted to low densities (Wright et al., 2007). Similarly, hunting of large fruit-eating primates significantly reduced plant species richness and the density of primate-dispersed plants in the Peruvian Amazon (Nuñez-Iturri and Howe, 2007). In defaunated sites in the Neotropics, large-seeded species often rely on dispersal by scatter-hoarding species, such as the agouti (*Dasyprocta* spp.), which caches seeds in the soil (Jansen et al., 2012); however, when defaunation intensifies and even agoutis are locally driven to extinction, smaller rodents do not compensate for their absence (Donatti et al., 2009).

There is thus substantial evidence suggesting that while large-bodied frugivores often occur at lower densities than do small-bodied vertebrates, they are relevant as seed dispersers in the Tropics, especially for large-seeded plant species. Moreover, defaunation has consequences for entire plant communities through indirect effects. In this sense, large-bodied seed dispersers might be similar to top predators, which, despite their lower densities, play central roles in ecosystem structure and function (Estes et al., 2011).

3. Are large-bodied vertebrates hubs in seed-dispersal networks?

Assemblages of interacting species form networks of interactions (Bascompte and Jordano, 2007). Because of the general relationship between body mass and dietary breadth, the role of species within networks generally differs for species that greatly differ in size (Woodward et al., 2005). Large-bodied frugivores tend to have wider gapes and are able to feed on fruits of a wide range of sizes (Jordano, 2000; Wheelwright, 1985). These patterns also hold at the community level. In a seed-dispersal network in the Pantanal, Brazil, the number of interactions of frugivorous mammals was positively related to body mass, with the largest frugivores having more interactions (Donatti et al., 2011). In mutualistic networks, species with few interactions often interact with highly connected species, which also interact with species that have many partners (Bascompte et al., 2003). For instance, in the few semi-deciduous forest fragments of southeastern Brazil where tapirs still occur, the tapirs consume fruits from plant species that are used by many small mammals and birds, such as the palm *Euterpe edulis*, but they are also among the few species that disperse the large-seeded palm *Syagrus oleracea* (Galetti et al., 2001).

In network theory, nodes connected to multiple nodes in the network are referred to as hubs (Strogatz, 2001). Because they directly or indirectly participate in most of the node connections, network hubs are pivotal in system functioning (Strogatz, 2001). Similarly, species with many interactions within an ecological network will directly or indirectly affect most of the interactions in the community and are thus likely to be central to ecosystem functioning (Jordán et al., 2006, Jordano et al., 2003). Indeed, studies

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simulating species loss in ecological networks show that the number of secondary extinctions is much greater when species with many interactions die out (Memmott et al., 2004; Silva et al., 2007; Solé and Montoya, 2001). As highly connected species are removed, some species may lose all their partners and become extinct as a consequence. If the highly connected species are resilient, the networks are extremely robust to species loss. However, in seed-dispersal networks, an insidious combination may make these networks vulnerable to the current extinction process: large vertebrates may be both the most connected species and the most sensitive to anthropogenic pressures such as hunting, habitat loss and fragmentation (Canale et al., 2012; Markl et al., 2012; Peres and Palacios, 2007; Wright, 2007).

Although large-bodied seed dispersers are likely to be important in the seed-dispersal network, they are unlikely to be equally important for all of the plant species with which they interact. Because large-bodied species often occur at low densities compared to smaller-bodied seed dispersers, the strength of their interactions is likely to be relatively low for small-seeded plants, which have alternative dispersers. Accounting for the strength of interactions (Bascompte et al., 2006), large-bodied species may lose their relevance as seed dispersers for many small-seeded plants; however, they would still be topologically important, especially because indirect effects may reach species that are seemingly disconnected. As a consequence, the loss of these species might disrupt species-rich seed-dispersal networks (Donatti et al., 2011). Moreover, if large frugivores contribute to the topology of seed-dispersal networks with multiple weak interactions, current theory predicts that these weak interactions favor coexistence in species-rich mutualisms (Bascompte et al., 2006).

Highly connected species within ecological networks are also likely to be evolutionarily important. A combination of evolutionary models and network analysis suggests that species with many interactions may drive evolutionary dynamics (Guimarães et al., 2011). In seed-dispersal systems, some large vertebrates may occur at such low densities that they are unlikely to be the main drivers of evolutionary dynamics in the community. In this case, the selective pressures they impose would be restricted to large-seeded plants. On the other hand, several large vertebrates such as monkeys and elephants are highly frugivorous, which could compensate for their relative low abundances. Furthermore, large vertebrates may facilitate gene flow among distant plant populations, potentially affecting the evolutionary dynamics of interacting plants. One of the most obvious traits potentially under selection by frugivores is fruit size (Jordano, 1995; Mack, 1993). As defaunation proceeds and smaller species increase in relative importance as seed dispersers, larger fruits and seeds may be selected against (Lord, 2004; Mack, 1993), affecting the demographics of plant populations (Moles and Westoby, 2004).

4. General absence of large frugivores from the literature on seed-dispersal networks

Despite the empirical and theoretical evidence for the importance of large vertebrates for seed-dispersal systems, these animals are often absent from studies on seed-dispersal networks. In a dataset compiled from the literature of 25 seed-dispersal networks from different parts of the world, we found that the vast majority of represented seed dispersers weigh less than 0.1 kg (Fig. 1A). In almost 60% of the networks, the body mass of the largest disperser was less than 1 kg (Fig. 1B). The low frequency of large vertebrates is partly a consequence of the true predominance of small-bodied frugivores in ecological communities. Nonetheless, at least a few large-bodied dispersers do occur or used to occur in most environments, and their general absence from seed-dispersal networks may have three main causes.

First, the data used to construct many seed-dispersal networks often originate from areas where most large-vertebrate populations have been significantly reduced by hunting and/or habitat loss and fragmentation. Ecosystems across the globe lost large-bodied vertebrates with potential importance as seed dispersers in the megafaunal extinction at the end of the Pleistocene (Donatti et al., 2007; Guimarães et al., 2008). However, defaunation is ongoing in most tropical forest remnants (Canale et al., 2012) and is likely to deplete seed-dispersal networks (Kitamura et al., 2002). For instance, in the seed-dispersal network of the Santa Genebra forest fragment in southeastern Brazil, all large frugivorous birds but one toucan and one guan species are locally extinct (Galetti and Pizo, 1996). Large mammalian frugivores are also absent, with the exception of the brocket deer (*Mazama gouazoubira*) and the howler monkey (*Alouatta guariba*).

Second, research on seed-dispersal networks often focuses on particular taxonomic groups of frugivores (often birds). Gathering data on seed dispersal requires intensive fieldwork that includes direct observation of foraging behavior, focal observation of fruiting plants and sampling of frugivore feces (Donatti et al., 2011; Silva et al., 2007). These techniques provide high-quality data, but it is unfeasible to include distinct taxonomic groups in similar ways in the sampling process. Moreover, many studies on seed-dispersal networks are based on data collected in previous studies, which were designed and conducted for purposes other than network analysis. Thus, many studies of seed-dispersal networks are restricted to particular taxonomic assemblages, depending on the aims of each data source.

Third, in areas where large vertebrates still remain, it is hard to assess their roles as seed dispersers because many of them occur in low abundance (either naturally or because of hunting) and exhibit secretive behavior (Borges, 1999; Norris et al., 2008). These traits hamper their inclusion in research on seed-dispersal networks, as their interactions with fruiting plants are difficult to detect and quantify. For example, a simulation study on the vulnerability of a seed-dispersal network from a pristine Atlantic forest reserve (Silva et al., 2007) showed that the extinction of endangered species—most of them large vertebrates, such as monkeys, guans, and tapirs—would have minor impacts on seed-dispersal services (Silva et al., 2007). However, this result might be in part a consequence of the difficulties of describing the interactions of rare and secretive large vertebrates. Even years of hard and careful fieldwork, as in this case, might not have been sufficient to characterize the interactions of some large species. For instance, in the aforementioned network, only four plant species were recorded as being dispersed by tapirs; however, there is evidence that tapirs in several locations have a very diverse frugivorous diet (O'Farrill et al., in press). Accordingly, we found that the number of interactions predicted by body mass (Donatti et al., 2011) greatly surpasses the observed number of interactions of mammals in this network (Fig. 2). If the consequences of interacting with seed dispersers were simply a function of the abundances of these animals in the environment, the underestimation of the interaction patterns of large frugivores would most likely have only minor implications. However, in the next section, we discuss the potential implications of seed dispersal by large vertebrates that advance the argument beyond the quantity of seeds dispersed.

5. Seed-dispersal networks: beyond the frequency of interactions

The number of seeds dispersed by a frugivore is an important component of seed-dispersal services (Schupp et al., 2010);

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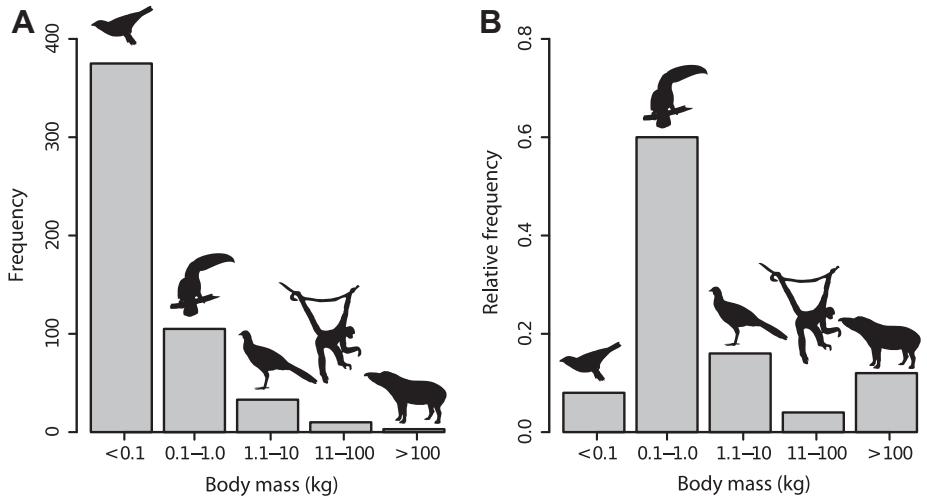

Fig. 1. (A) Frequency of frugivores within each body-mass category in seed-dispersal networks published in the literature ($n = 25$ networks). (B) Relative frequency of seed-dispersal networks ($n = 25$ networks) in which the largest seed disperser falls within each category. Datasets compiled from the Interaction Web Database (2012), Donatti et al. (2011) and Rezende et al. (2007). Body-mass classes are represented by species of the Atlantic rainforest: a tanager (Thraupidae), a toucan (Ramphastidae), a guan (Cracidae), a muriqui (*Brachyteles arachnoides*) and a tapir (*Tapirus terrestris*).

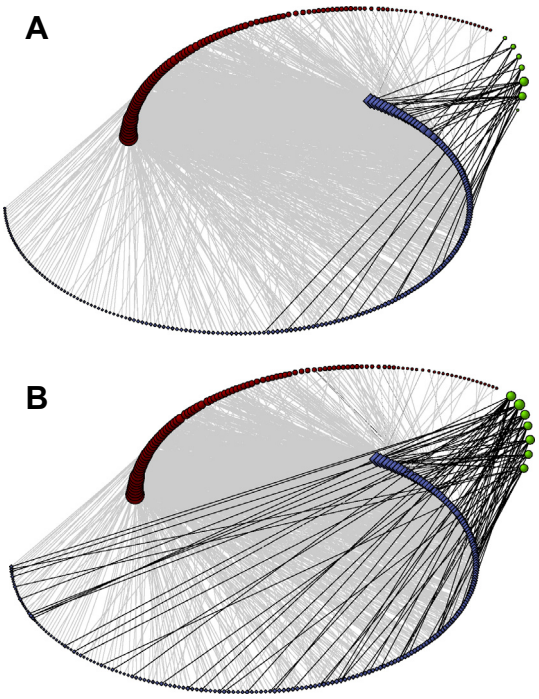

Fig. 2. Networks representing seed-dispersal interactions at Parque Estadual Intervales, a well-preserved Atlantic Forest site in southeastern Brazil (Silva et al., 2007). Circles represent animals, and diamonds represent fleshy-fruit plants. Lines connecting circles and diamonds represent interactions between animal and plant species. Black lines represent interactions involving large mammals. The green circles represent mammals weighing >1 kg (top to bottom: *Mazama* sp., *Tapirus terrestris*, *Brachyteles arachnoides*, *Alouatta guariba*, *Cerdocyon thous*, *Sapajus nigritus*, *Eira barbara*), whereas the red circles represent different animals, including birds and small mammals. The size of the circles and diamonds is proportional to the number of associated interactions. A. Original seed-dispersal network, in which large mammals show few interactions. In B, we used the relationship between the number of interactions and the species body mass from a well-sampled seed-dispersal network (Donatti et al., 2011) to estimate the number of interactions mammal species should have based on their body masses. For each mammal (>1 kg), we then computed the difference between the estimated and the actual number of interactions and randomly assigned the missing interactions. Note that the relative number of interactions of mammals predicted from body mass is considerably greater than the number of interactions recorded in the field. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

however, seed dispersal is a crucial process that goes beyond the quantity of seeds dispersed (Carlo and Yang, 2011; Schupp et al., 2010). Seed dispersal is relevant to a number of processes involving plant populations, from how frugivores shape seed distributions (Schupp et al., 2010) to the ways they link plant populations across fragmented landscapes (Fortuna and Bascompte, 2006; Jordano et al., 2007). Research on seed-dispersal networks often includes quantitative aspects, such as the number of fruits from a given plant species that are consumed by a frugivore species; however, it remains challenging to infer the implications of seed-dispersal networks for other aspects of seed dispersal (Carlo and Yang, 2011).

Addressing aspects other than the frequency of interactions in seed-dispersal networks may provide new insights on their effects on system dynamics and functioning (Carlo and Yang, 2011). Much of the importance of large vertebrate frugivores as seed dispersers may derive from their unique features, such as handling behaviors, gut-passage effects on germination, deposition patterns and movement patterns. Here, we used the approach introduced by Carlo and Yang (2011) to illustrate the effect of large frugivores on the ecological outcomes of seed dispersal. In short, the idea is to build networks by weighting the frequency, or presence, of pairwise interactions by a measure of the contribution of seed dispersal to a given ecological process, which is defined according to specific study questions. We illustrate the approach with a theoretical example of how to evaluate the role of different frugivores in promoting landscape connectivity for plant populations (Fig. 3).

Holding everything else constant, the larger representatives of a given taxonomic group are more likely to act as long-distance seed dispersers (Wotton and Kelly, 2012), because of their large home ranges, higher travel speed, larger gut capacity and longer seed-retention time (Nathan et al., 2008). Long-distance dispersal, in turn, allows metapopulation dynamics to emerge in fragmented landscapes (Trakhtenbrot et al., 2005). Thus, by facilitating long-distance dispersal (Paradis et al., 1998), large vertebrates are likely to connect otherwise isolated plant populations in fragmented landscapes, promoting landscape connectivity and, as a consequence, long-term species persistence (Trakhtenbrot et al., 2005). It is, however, important to recognize that movement across the landscape depends not only on the organism under consideration but also on matrix quality (Fahrig, 2001). For simplification, in our example, we do not consider the effects of the inter-patch matrix on movement across the landscape.

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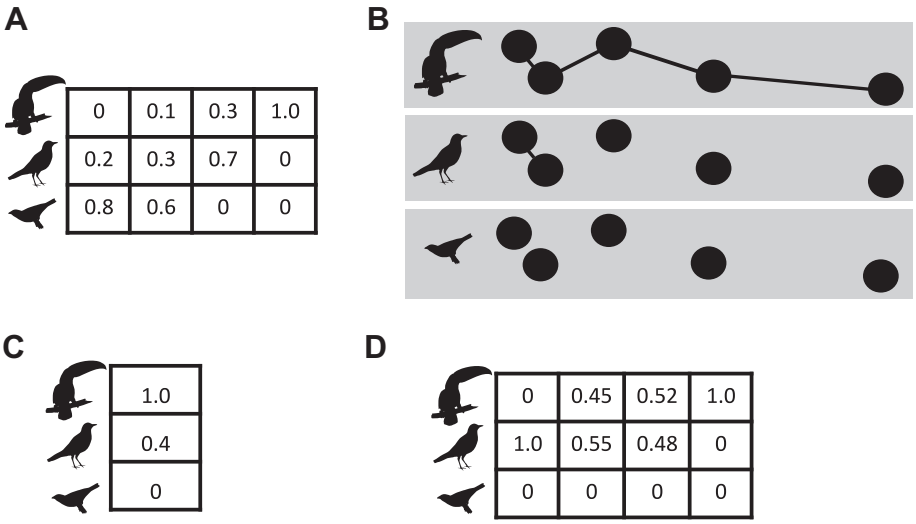

Fig. 3. An approach to explore the effects of large frugivores on landscape connectivity. (A) Hypothetic matrix **W** describing the relative frequency of interactions of each plant (column) and frugivore (rows). (B) A set of fragments (circles) and lines indicate that the frugivore is able to connect plant populations across fragments. (C) A vector describing the proportion of fragments connected by seed dispersal by frugivores. (D) Matrix **M,** in which the relative frequency of interactions is weighted by the capacity of the frugivore to connect fragments. The element m_{ij} is the contribution of animal species i to the landscape connectivity for plant species j, as follows: $m_{ij} = d_i w_{ij} / \sum_{k=1}^{A} d_k w_{kj}$, in which k are animal species, A is the animal species richness, and d_i (d_k) are the proportions of sites an animal i (k) can connect. More sophisticated measures of landscape connectivity can use the same approach.

Let us assume that we are able to estimate the frequencies of interaction among species and define a matrix **W** (Fig. 3A), in which w_{ij} is the frequency of seed-dispersal events of plant species j by the animal i. The second step would be to estimate how each frugivore disperses the seeds of each plant species among the fragments, i.e., the frugivore contribution to the landscape connectivity of plants. Even for small seed-dispersal networks, estimating these multiple frequencies is not feasible. Therefore, we simplify and aggregate these frequencies. Let us assume that the probability an animal i disperses a seed of species j depends not on the identity of j, but on how individuals of i move across the landscape. Then, the contribution of seed disperser i to landscape connectivity for j depends on the landscape connectivity of i. Because estimating landscape connectivity for a given species is challenging (Bélisle, 2005), we might opt for even simpler approaches. The simplest approach would be to use the distance an animal is able to move across fragments and to calculate which fragments this frugivore would connect (Fig. 3B). Although more complex characterizations of landscape connectivity are possible (Dale and Fortin, 2010), a first step would be to estimate the proportion of fragments that could be connected due to seed dispersal by a given frugivore in the landscape (Fig. 3C). We can then define a new matrix **M**, in which the number of fragments the species can connect weights the frequency of interactions (Fig. 3D). This matrix defines a network that describes not the frequency of interactions among species, but the potential contribution of each seed disperser to landscape connectivity for a given plant. Because large animals are likely to move long distances (Bowman et al., 2002), we would expect the role of these species to be much more prominent in the network defined by **M** than in the network defined by **W**. This approach could be easily adapted to explore the role of large seed dispersers in other aspects of landscape connectivity or plant and animal population dynamics, such as the probability of seed dispersal to different habitats (Carlo and Yang, 2011). The weighted matrices generated by this approach could be used as templates for simulations of species extinctions, for example, providing insights on how the loss of large-bodied vertebrates may impact ecological processes.

6. Future directions

The absence of large frugivores from most of the published literature on seed-dispersal networks may have important consequences for our understanding of their ecological dynamics. In addition to the approach suggested here, other procedures might help us better understand the relevance of large vertebrates to seed-dispersal networks. Combining different types of data, including observational data and also information gathered by examining seed content in frugivores' feces (analyses of scat and seed morphology, as well as molecular approaches), can provide more precise evaluations of the importance of each seed disperser. There is great need in the field for procedures that account for the variation in the detectability of different frugivore species. As discussed previously, large vertebrates usually occur at lower densities or exhibit secretive behavior, which makes their interactions harder to record when obtaining data for an interaction network. One way to circumvent this problem is to use accumulation curves to establish whether enough interactions were sampled (e.g., Donatti et al., 2011); however, because large frugivores represent a small component of the species richness in seed-dispersal networks, large numbers of the best-sampled species may mask insufficient sampling of large frugivores. Thus, accumulation curves should be performed at the species level. Other approaches, such as sampling methods that account for per-capita sampling effort or rarefaction analyses that evaluate how uneven sampling affects network patterns, might help in obtaining less biased data.

In places where large vertebrates are already extinct or occur at such low densities that they are functionally extinct, we need to develop approaches to estimate the impact of these extinctions. A promising avenue for future research is to assess the differences between defaunated and non-defaunated areas (Dirzo and Miranda, 1991) in terms of the structures of seed-dispersal networks at different sites. Various hypotheses could be explored, e.g., whether there is an increase in the modularity of seed-dispersal networks as large vertebrates are lost, given that they might connect species groups. We also need to understand whether the loss of large-bodied species is compensated for in network topology by smaller

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species that become new hubs. If the frequency of interactions or other quantitative proxies are considered and weighted networks are built, such comparisons may yield better insights on how the reorganization of seed-dispersal networks translates into changes in plant populations in fragmented landscapes.

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