



# Seed Dispersal by Primates and Implications for the Conservation of a Biodiversity Hotspot, the Atlantic Forest of South America

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**Abstract** Primates play a fundamental role as seed dispersers, particularly in tropical rainforests. Because defaunation and fragmentation are leading several primate species to local extinction, it is fundamental to understand the role of primates as effective seed dispersers. Here we present a systematic review of studies of seed dispersal by primates in a biodiversity hotspot, the Atlantic Forest of South America, to 1) highlight gaps in our knowledge, 2) determine species richness and proportion of seed species dispersed, and 3) test the relationship between primate body size and the size of dispersed species. Our review found 79 studies of the diet of six ecospecies (*Callithrix*, *Leontopithecus*, *Callicebus*, *Sapajus*, *Alouatta*, *Brachyteles*) but only 20 of these report information on seed dispersal, and none of these are on *Callithrix* or *Callicebus*. We found a strong bias in the distribution of species and regions, with most of the studies concentrated in southeastern Brazil. All ecospecies dispersed a large proportion of the seed species they handled (72.1–93.6%). *Brachyteles* dispersed the highest diversity of plants ( $N = 73$ ), followed by *Sapajus* ( $N = 66$ ), *Leontopithecus* ( $N = 49$ ), and *Alouatta* ( $N = 26$ ). Although we found no significant relationship between primate body size and the size of seeds dispersed, *Brachyteles* disperse a higher diversity of large-seeded species than smaller-bodied primates. These results suggest that the local extinction of large primate species may lead to dramatic changes in the plant community, as many large-seeded plants are inaccessible to smaller arboreal frugivores. We propose guidelines for future

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research on primate seed dispersal to enable the evaluation of seed dispersal effectiveness and to improve our understanding of the fundamental role of primates in this key ecosystem process.

**Keywords** Defaunation · Ecosystem services · Primate conservation · Seed dispersal effectiveness · Seed dispersal network

## Introduction

Seed dispersal is a critical step in the biological cycle of plants and a key process for the maintenance of tropical forest biodiversity (Wang and Smith 2002), enabling a reduction in density and distance-dependent mortality, the colonization of new areas, and the promotion of gene flow (Janzen 1970; Schupp *et al.* 2010; Wenny 2001). Both primates and birds represent a large proportion of the seed-dispersing community. Primates are important because they travel long distances daily and can swallow bigger seeds than most rainforest-dwelling birds (Chapman and Onderdonk 1998; Terborgh 1986; Yumoto *et al.* 1999). More than 380 primate species eat fruits, and disperse or depredate, i.e., destroy, seeds worldwide (Gómez and Verdú 2012). In tropical forests, primates represent from 25% to 40% of the frugivore biomass (Chapman 1995; Terborgh 1992), and they are able to disperse the seeds of many plant species, mostly by defecating large numbers of seeds (Bueno *et al.* 2013; Julliot 1997; Lambert 1999, 2010; Stevenson 2007).

Primate frugivory in the Neotropical region is relatively well studied when compared to other biogeographic regions (Hawes *et al.* 2013). All Neotropical primates consume fruits (Gómez and Verdú 2012), but large-bodied species feed on a greater diversity of fruits (Hawes and Peres 2014). The wide variety of body sizes among Neotropical primates (Ford and Davis 1992; Rylands *et al.* 1996) enables tests of the relationship between body size and the size of seeds handled. The morphological characteristics of fruits such as fruit and seed sizes, fruit color, and pulp-to-seed ratio are important factors in fruit selection by frugivores (Lomáscolo *et al.* 2008). Whereas seed dispersal by birds is highly dependent on gape width (Galetti *et al.* 2013; Tabarelli and Peres 2002), primates use strategies such as fruit/seed handling and tool use. It is unknown how these strategies modify the relationship between the frugivore body size and seed size (Corlett and Lucas 1990; King 1986).

As primates are among the largest arboreal frugivores and some of the last mega-faunal seed dispersers (Bueno *et al.* 2013; Haugaasen and Peres 2005), their local decline or extinction is likely to affect the ecosystem functioning (McConkey *et al.* 2012; Nunez-Iturri *et al.* 2008; Peres and van Roosmalen 2002; Stevenson and Aldana 2008). Primates are particularly sensitive to habitat loss and hunting (Estrada and Coates-Estrada 1996; Rylands *et al.* 2008). To make predictions about the potential of tropical forests to regenerate in the absence of primates, we need to understand the relationships between primates and plant species in terms of seed dispersal effectiveness (Schupp *et al.* 2010). The Atlantic Forest holds a high diversity of primates (24 species, of which 18 are endemic) (Paglia *et al.* 2012) but only 12% of its original extension remains (Ribeiro *et al.* 2009). Most of the remaining fragments are highly defaunated (Jorge *et al.* 2013), and are too small to maintain viable primate populations (Brito and Grelle 2006). This makes the Atlantic Forest an ideal model of a human-

altered landscape where a better understanding of the functional role of primates in dispersing seeds is necessary to predict the possible consequences of their extinctions in forest regeneration.

Here, we aimed to 1) determine the potential of primates in dispersing seeds in terms of seed species richness and the proportion of fruit species consumed of which seeds are dispersed, 2) test the link between primate body size and the size of dispersed species, and 3) highlight gaps in our knowledge of primate seed dispersal in the Atlantic Forest. We also provide guidelines for future studies of primate seed dispersal to include the parameters needed to determine the effectiveness of seed dispersal.

## Methods

### Data Compilation

To obtain data on seed dispersal by primates in Atlantic Forest, we reviewed an extensive list including both published and unpublished sources (including dissertations and theses) from Google Scholar and Web of Science. We used the following key words and combinations of them to search for sourced material published before 2013: “frugivory,” “seed dispersal,” “seed predation,” “diet,” “primates,” and “Atlantic Forest.” We also included all genera and species, taking into account changes of nomenclature; e.g., we searched for both *Cebus* and *Sapajus*. We found studies from 1983 to 2013; the oldest seed dispersal study was from 1989. We considered a study to be a “seed dispersal study” when it reported both fruit consumption and seed swallowing, and/or when it listed the presence of intact seeds in primate feces. Throughout the article, “seed dispersal” or “dispersed seeds” refer to the endozoochorous mode of seed dispersal through defecation. We acknowledge the importance of other seed dispersal modes by primates such as seed spitting or wadging (Corlett and Lucas 1990; Gross-Camp and Kaplin 2011; Kaplin and Moermond 1998) for plant regeneration. However, whereas these seed dispersal modes are widespread in Old World primates and relatively widely described and quantified (Albert *et al.* 2013; Gross-Camp and Kaplin 2011), this is not the case for New World primates (*cf.* Barnett *et al.* 2012). The seed dispersal studies included document seed dispersal events by a single or multiple primate species at a defined study site during a defined time period.

Owing to the lack of available data for all 24 primate species found in the Atlantic Forest, we followed Hawes and Peres (2014) and grouped them into six ecospecies corresponding, in our case, to primate genera (*Alouatta*, *Brachyteles*, *Sapajus/Cebus*, *Callicebus*, *Leontopithecus*, and *Callithrix*). We assumed that the distribution, feeding habits, body size, daily locomotion, and group sizes among species of the same genus were sufficiently similar to consider them as members of the same functional groups (Peres and Janson 1999).

From each study included in the dataset, we recorded 1) the primate species studied; 2) study site; 3) study duration in months; 4) sampling effort, i.e., hours of observation; 5) the plant species recorded in the study; 6) fruit and seed traits (fruit and seed lengths and diameters); and 7) the seed fate (dispersed, depredated, and not dispersed, when seeds were recorded in studies as dropped or spat out during field observations) (Electronic Supplementary Material [ESM] Tables SI and SII). We recorded the

sampling effort to calculate a rarefied richness of seed species dispersed (see Measures of Seed Dispersal), as the number of species registered in studies is related to the sampling effort. We standardized sampling effort across different sampling methods in terms of the total number of hours following the method used by Hawes and Peres (2014): For studies that only mentioned the number of encounters with the study group, we assumed a 10-min opportunistic observation bout for each encounter (3 of 20 studies recorded) based on the average of observation periods recorded in studies in Amazonia (Hawes *et al.* 2013). For studies that mentioned only the number of fecal samples collected in the field, we assumed 3 h for each fecal sample (4 of 20 studies). For studies that mentioned the total of complete days spent following the primates, we calculated the standard number of hours of activity per day for the species (1 of 20 studies) (Hawes and Peres 2014). When authors did not present data on fruit and seed traits, we searched for this information in the available literature, visited botanical collections, and used the dataset for the Atlantic Forest (Bello *et al.* 2015). We reviewed and updated plant species names according to the APG III system (APG III 2009) and condensed synonyms using available sources.

### Measures of Seed Dispersal

As the number of plant species dispersed is likely to be biased by the total sampling effort dedicated to each frugivore ecospecies, we produced sample-based rarefaction curves using the BiodiversityR package in R (Kindt and Coe 2005) to compare the rarefied number of plant species between ecospecies (Hawes and Peres 2014). This allowed us to compare the number of plant species dispersed as if each ecospecies had been studied 1191.4 h, which corresponded to the smallest sampling effort recorded. We rescaled the  $x$ -axis of plots to show that samples represent individual studies, expressing effort in terms of number of observation hours.

To compare the different ecospecies in terms of their seed dispersal potential, we implemented a dispersal index following the formula

$$\text{SD Index} = \frac{\text{dispersed}}{\text{dispersed} + \text{depredated} + \text{not dispersed}}$$

Dispersed seeds are seeds reported as found intact in primate feces; depredated seeds are seeds that were reported to be systematically destroyed by the ecospecies, and thus inviable after handling; seeds not dispersed are the fruit species that were reported to be consumed by the ecospecies but the seeds were never found in feces. Values of the SD Index close to 0 indicate that the primate ecospecies depredates, spits out, or throws away most of the seed species it handles. Values close to 1 indicate that the primate ecospecies disperses most of the seed species it handles. We tested the relationship between the ecospecies body mass and seed size (length and width) with Spearman correlations.

### Seed Dispersal Network

We grouped the seeds into three size classes: small (<3 mm), medium (3–12 mm), and large (>12 mm) based on previous studies (Galetti *et al.* 2013; Lapenta 2002). Owing to

the lack of available data on seed diameters for some plant species, we analyzed seed sizes for only 200 of the 234 plant species recorded as dispersed (64 from 73 for *Brachyteles*; 58 from 64 for *Alouatta*; 93 from 98 for *Sapajus*; and 71 from 88 for *Leontopithecus*).

Using the bipartite package in R (Dormann *et al.* 2008), we built a weighted mutualistic network to characterize seed-dispersal interactions between primates and plants, connecting the primate ecospecies to the plant families it dispersed. In this network, each link represents the number of plant species dispersed of each family by each primate ecospecies (Bascompte *et al.* 2003). We built another weighted network connecting the primate ecospecies to the three classes of seed size dispersed. In this network, each link represents the number of plant species dispersed of each class of seed size by each primate ecospecies based on the rarefied species richness. We calculated the rarefied species richness using the method described in the preceding text. We calculated the degree of nestedness for each network using the weighted NODF (Nestedness metric based on Overlap and Decreasing fill) (Almeida-Neto and Ulrich 2011) in the “oecosimu” function of the “vegan” package (Oksanen *et al.* 2011). We used our network matrix to test whether interactions (weighted by rarefied species richness) between plants (classified by seed size classes or by family) and smaller ecospecies are a subset of the interactions between plants and larger ecospecies ( $N$  columns statistic; Almeida-Neto and Ulrich 2011). In the same way, we tested whether the interactions between primate ecospecies and large-seeded plants are a subset of the interactions between primate ecospecies and medium or small-seeded plants ( $N$  rows statistic; Almeida-Neto and Ulrich 2011). In other words, we tested whether smaller primate ecospecies disperse small-seeded species that larger ecospecies do not disperse ( $N$  columns statistic) and whether primate ecospecies dispersing large-seeded plants also disperse the medium and small-seeded plants ( $N$  rows statistic). The combination of these two statistics is given as the NODF statistic. We also calculated measures of the dependence of primate ecospecies on plant species and seed size classes on the one hand, and of plant species and seed size classes on primate ecospecies on the other hand, for both networks. This analysis highlights the proportions of the total number of interactions of each vertex for both networks represented by specific interactions (Bascompte *et al.* 2006; Dormann *et al.* 2009). We did not calculate other network metrics because they are not very informative for such small networks.

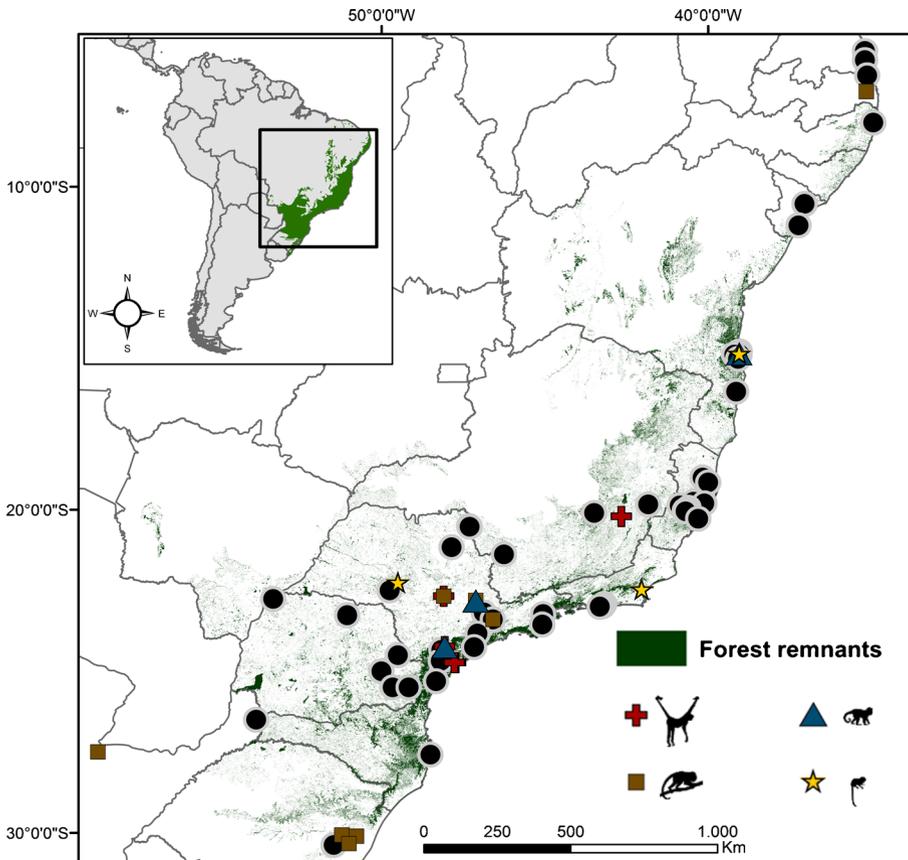
## Results

### Primate Seed Dispersal Studies in Atlantic Forest

We found 95 references to 79 different studies describing the consumption of fruits by primates in the Atlantic Forest. Only 20 of those were related to seed dispersal. Only four studies were conducted in northeastern Brazil (one in Paraíba and three in Bahia). We found no seed dispersal studies for Espírito Santo, Santa Catarina, and Paraná states in the southern and southeastern regions of Atlantic Forest. Southeast Brazil was the best studied region, with studies concentrated in São Paulo (8), Rio de Janeiro (2), and Minas Gerais (1) states. We found three seed dispersal studies in the Southern region of Atlantic Forest, in Rio Grande do Sul state. We also found two seed dispersal studies in

Argentina. We found no studies of seed dispersal for 14 of the 24 primate species in the Atlantic Forest. Consequently, we found no information on seed dispersal for two of the six primate ecospecies: *Callithrix* and *Callicebus*. Furthermore, most of the primate species present in the Atlantic Forest have been the subject of only one study on seed dispersal: *Sapajus nigritus*, *Sapajus xanthosternos*, *Leontopithecus chrysopygus*, *Brachyteles hypoxanthus*, and *Alouatta belzebul* (Fig. 1, ESM Table SII).

The most studied primate species in terms of sampling effort is *Alouatta caraya*, with 1743.2 h, while the species with the smallest sampling effort is *Sapajus nigritus*, with 61.2 h. *Brachyteles hypoxanthus* is also poorly sampled, with only 62.8 h. *Alouatta guariba* was the most studied primate, with six studies relating to seed dispersal. The best-sampled ecospecies is *Alouatta*, with a total of 3330.2 h and 9 studies. *Leontopithecus* are the second best-sampled ecospecies, with a total of 2963.1 h and 5 studies, followed by *Sapajus* with a total of 1835.2 h and 3 studies, and *Brachyteles* with a total of 1191.4 h and 5 studies (Fig. 2, ESM Table SIII).



**Fig. 1** Geographical distribution of studies of primate diet and seed dispersal for four ecospecies of primate in the Atlantic Forest from 1989 to 2013. Black circles indicate dietary studies while other marks indicate seed dispersal studies: red crosses for *Brachyteles*, brown squares for *Alouatta*, blue triangles for *Sapajus*, and yellow stars for *Leontopithecus*.

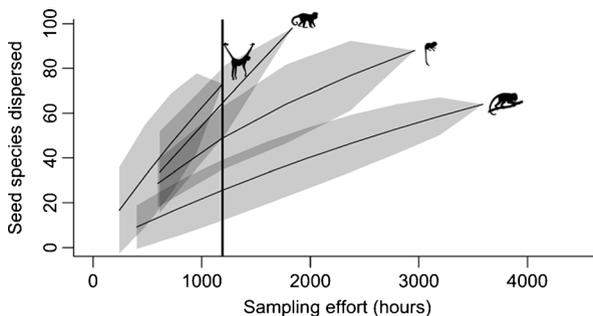
## Measures of Seed Dispersal

We recorded 647 plant species eaten by primates in the Atlantic Forest but data on the likelihood with which they are dispersed by primates was available for only 276 of these. Primates of the Atlantic Forest dispersed 234 of these 276 plant species, belonging to 133 plant genera from 64 families. We recorded 97 plant species from 41 families dispersed by *Sapajus*, 94 species from 26 families for *Leontopithecus*, 74 plant species from 33 families for *Alouatta*, and 75 plant species from 43 families for *Brachyteles* (ESM Table SI). However, this pattern changes when we standardize sampling effort (1191.4 hours), with *Brachyteles* presenting the highest number of plant species dispersed (73), followed by *Sapajus* with 66, *Leontopithecus* with 49, and *Alouatta* with 26 species (Fig. 2).

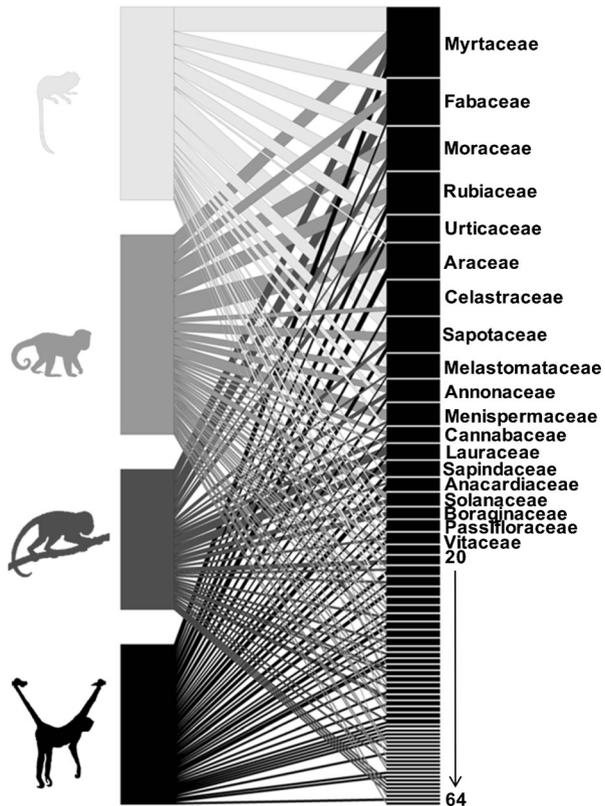
All four ecospecies dispersed a large proportion of the seed species they handled. *Brachyteles* dispersed 93.6% of the plant species it handled, followed by *Alouatta* (92.7%), *Sapajus* (79.7%), and *Leontopithecus* (72.1%). We found no significant relationship between ecospecies body mass and seed size (seed length:  $N = 230$ ,  $R = 0.01$ ,  $P = 0.9$ ; seed width:  $N = 279$ ,  $R = 0.03$ ,  $P = 0.6$ ).

## Seed Dispersal Network

Myrtaceae was the family with the greatest number of species dispersed (24), followed by Fabaceae (16) and Moraceae (14) (Fig. 3). Together, Myrtaceae, Fabaceae, Moraceae, Rubiaceae, Urticaceae, and Araceae represent more than 30% of the interactions of each ecospecies (30.1% for *Brachyteles*, 35.9% for *Alouatta*, 41.8% for *Sapajus*, and 42.0% for *Leontopithecus*). We found that 75.0% of Celastraceae plant species and 66.7% of Apocynaceae are dispersed by *Leontopithecus*. Most Myristicaceae plant species are dispersed by *Brachyteles* (66.7%) and *Sapajus* disperse 66.7% of Olacaceae. Moreover, 24 of the 64 plant families interact with only one ecospecies (Chrysobalanaceae, Achariaceae, Amaranthaceae, Araliaceae, Canellaceae, Humiriaceae, Phyllanthaceae, Phytolaccaceae, Symplocaceae and Zingiberaceae dispersed only by *Brachyteles*; Meliaceae, Erythroxylaceae, Lecythidaceae, Primulaceae, Rosaceae, Rutaceae, and Salicaceae by *Alouatta*; Combretaceae, Cucurbitaceae,



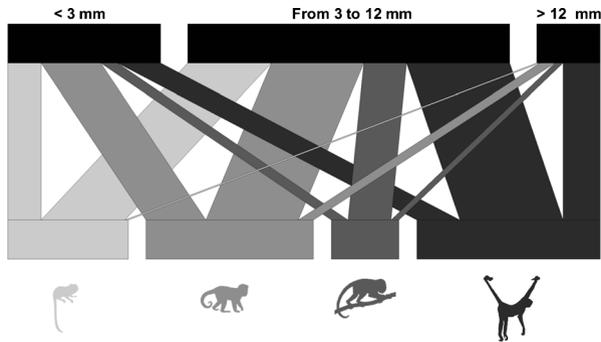
**Fig. 2** Sample-based rarefaction curves for plant species (seeds) dispersed by four primate ecospecies in the Atlantic Forest (from left to right: *Brachyteles*, *Sapajus*, *Leontopithecus*, and *Alouatta*). We rescaled the x-axis to show the cumulative observation hours across studies. Gray shading represents 95% confidence intervals. Thick vertical black line indicates the cumulative number of hours for the least studied ecospecies (1191.4 h: *Brachyteles*).



**Fig. 3** Weighted network indicating interactions between primate ecospecies (*Leontopithecus*, *Sapajus*, *Alouatta*, and *Brachyteles*) and plant families dispersed in the Atlantic Forest. Link width represents the number of plant species dispersed in each plant family. We ordered plant families according to the number of interactions per family. Numbers 20 to 64 correspond, respectively, to Acanthaceae, Arecaceae, Clusiaceae, Malpighiaceae, Marcgraviaceae, Apocynaceae, Burseraceae, Cactaceae, Myristicaceae, Olacaceae, Polygalaceae, Bromeliaceae, Caricaceae, Chrysobalanaceae, Ebenaceae, Euphorbiaceae, Flacourtiaceae, Lamiaceae, Loganiaceae, Meliaceae, Musaceae, Rhamnaceae, Siparunaceae, Verbenaceae, Achariaceae, Amaranthaceae, Araliaceae, Canellaceae, Combretaceae, Cucurbitaceae, Erythroxylaceae, Humiriaceae, Hypericaceae, Lecythidaceae, Malvaceae, Nyctaginaceae, Phyllanthaceae, Phytolaccaceae, Primulaceae, Rosaceae, Rutaceae, Salicaceae, Schlegeliaceae, Symplocaceae, and Zingiberaceae.

Malvaceae, Nyctaginaceae, and Schlegeliaceae by *Sapajus*; Flacourtiaceae and Hypericaceae dispersed only by *Leontopithecus*).

The plant genera most often recorded are *Ficus*, *Inga*, and *Miconia*, with eight plant species being dispersed in each genus. The species recorded most frequently were *Pourouma guianensis* (3–12 mm), *Inga subnuda* (3–12 mm), *Helicostylis tomentosa* (3–12 mm), and *Cecropia pachystachya* (<3 mm), each reported in six different studies. All ecospecies dispersed *Ficus gomelleira* (<3 mm) while three ecospecies dispersed *Cecropia pachystachya*, *Pourouma guianensis*, and *Inga subnuda*. *Sapajus* and *Leontopithecus* dispersed *Helicostylis tomentosa*. The plant–primate interaction network was not significantly nested (NODF = 29.3,  $P = 1$ ). The interactions (in terms of rarefied species richness of dispersed seeds) between plant families and small primate ecospecies are not a subset of the interactions with larger primate ecospecies ( $N$  rows = 11.8,  $P = 1$ ).



**Fig. 4** Weighted seed dispersal network, showing interactions between primate ecospecies (bottom boxes from left to right: *Leontopithecus*, *Sapajus*, *Alouatta*, and *Brachyteles*) and seed size classes (upper black boxes) in the Atlantic Forest. Each link represents the rarefied species richness of each size class dispersed by each primate ecospecies.

The network of primate ecospecies and seed size classes was not significantly nested ( $N$  columns = 0,  $N$  rows = 0, NODF = 0;  $P = 1$ ), indicating that the distribution of the interactions of smaller ecospecies with plants is not a subset of the interactions between larger ecospecies and plants, and that interactions between large-seeded species and primate ecospecies are not a subset of the interactions between small or medium-seeded species and primates (in terms of rarefied plant species richness dispersed). *Brachyteles*, but not *Alouatta*, disperse a greater number of large-seeded species than small-bodied primates (Fig. 4). Based on rarefied species richness, *Brachyteles* dispersed 13 large-, 36 medium-, and 15 small-seeded plant species. *Alouatta* dispersed 3 large-, 15 medium-, and 6 small-seeded species. *Sapajus*, although smaller than *Alouatta*, dispersed a larger rarefied species richness of large-seeded species (5). *Sapajus* also dispersed high numbers of medium- and small-sized seeds (32 and 21, respectively). *Leontopithecus* dispersed more plant species with medium-sized seeds (29) than large and small-seeded species (1 and 11, respectively). Atelines showed the greatest proportion of links with large seeds (20.3% for *Brachyteles* and 11.8% for *Alouatta*) while *Leontopithecus* presented the lowest proportion (2%). Proportionally, medium-sized seed species represented >50% of the interactions of each ecospecies (56.2% for *Brachyteles*, 63.3% for *Alouatta*, 55.2% for *Sapajus*, and 69.6% for *Leontopithecus*). *Sapajus* dispersed the highest proportion of small-seeded species (35.8%), followed by *Leontopithecus* (27.6%), while *Alouatta* and *Brachyteles* showed the lowest proportions (24.9% and 23.4% respectively).

*Brachyteles* disperse a high proportion of seeds of all size classes: 58.5% of large seeds, 32% of medium seeds, and 28.1% of small seeds. *Sapajus* disperse most small seeded-species (39.1%) and a high proportion of medium-seeded species (28.6%). *Alouatta* disperse the lowest proportions of medium and small seeds (13.2% and 11%). *Leontopithecus* disperse the lowest proportion of large seeds (5.2%).

## Discussion

Seed dispersal studies focusing on primates are relatively scarce, and unevenly distributed across the range of the Atlantic Forest, with most concentrated in southeastern

Brazil. Despite this bias, some interesting patterns emerge. All ecospecies studied for whom data are available disperse species of all size classes. However, *Brachyteles* disperse more plant species and usually disperse more large-seeded species than smaller-bodied primates.

Of the 10 primate species considered, only *Alouatta guariba*, *Brachyteles arachnoides*, and *Sapajus nigritus* have been sampled at more than one study site (six, three, and two studies, respectively). Furthermore, seed dispersal remains unstudied for 58% of the primate species of Atlantic Forest, and four of the studied species have been studied at only one site (*Alouatta belzebul*, *Brachyteles hypoxanthus*, *Leontopithecus chrysopygus*, and *Sapajus xanthosternos*). This pattern is also observed for diet studies in the Neotropics, where most sampling effort is skewed to a small number of sites (Hawes *et al.* 2013). Insufficient sampling effort is a problem when discussing seed dispersal over such a wide area, particularly for primate species occurring over extensive ranges, e.g., *Alouatta guariba*: from Bahia to Rio Grande do Sul and northern Argentina (Mendes *et al.* 2008) with different floristic characteristics (Oliveira-Filho and Fontes 2000).

The lack of studies for two of the primate genera of Atlantic Forest (*Callicebus* spp. and *Callithrix* spp.) deserves attention, as *Callicebus* spp. are recorded to eat 140 fruit species and *Callithrix* spp. are recorded to eat 101 species (ESM Table SI). Moreover, 14.3% of the species recorded for *Callicebus* spp. and 19.8% for *Callithrix* spp. are small seeded, which increases the chances of dispersing intact seeds. *Callicebus* spp. may arouse little interest for seed dispersal studies because of the high level of seed predation presented by Pitheciine species (Barnett and Brandon-Jones 1997; Barnett *et al.* 2005; Kinzey 1992). However, recent studies (not included in our sample) have highlighted the role of *Callicebus coimbrai* as an important seed disperser for some plant species in a forest fragment of Sergipe state (Baião *et al.* 2015). The lack of seed dispersal studies for marmosets (*Callithrix* spp.) may be due to their reliance on exudates and insect prey (Hawes and Peres 2014). However, they are also likely to disperse seeds and their role as seed dispersers in the ecosystem deserves more attention.

In addition to a relatively small sampling effort, many primate seed dispersal studies give few or no details about the traits of fruits and seeds consumed or dispersed. The available literature presents few data about the species handled vs. the species dispersed and almost no information on the seeds depredated. Comparing the size of the seeds found in feces with the size of the seeds found in fruits can highlight seed size selection within a plant species, which cannot be inferred from seed size reported in the literature. These limitations may bias our results for the seed size classes dispersed by primates of different sizes by overestimating the size of seeds swallowed. While Neotropical primate species also disperse seeds by spitting them out, this is rarely mentioned and/or quantified (*cf.* Barnett *et al.* 2012). Studies of Old World primates show a higher establishment rate for spit seeds than for defecated seeds (Balcomb and Chapman 2003; Gross-Camp and Kaplin 2011). Although Neotropical primates lack the cheek pouches present in cercopithecoid monkeys, which enable them to transport and subsequently spit seeds out at a distance from the parent trees, they may still spit seeds out under the parent trees; this deserves investigation. In addition, few studies present detailed information on the spatial patterns of seed dispersal such as dispersal distances or seed shadow. This is of paramount importance to understand the selective pressures acting

on seed dispersal process (Bueno *et al.* 2013; Culot *et al.* 2010; Stevenson *et al.* 2005). Primary seed dispersal is followed by secondary dispersal, predation, and seedling establishment (Wang and Smith 2002). These postdispersal events determine the overall effectiveness of seed dispersal and modify the initial template produced by primate seed dispersal, and should also be included in primate seed dispersal studies.

The dispersal index shows that we can expect that primates of the Atlantic Forest disperse 84.5% (mean of the dispersal index of all ecospecies) of the fruit species consumed, which would correspond to 547 of the 647 plant species recorded in diet studies. However, we found only 234 plant species in the seed dispersal studies, corresponding to 36.2% of the total number of fruit species consumed. This finding demonstrates the lack of studies of seed dispersal by primates in the Atlantic Forest where 75.4 % ( $N = 1728$ ) of plant species are animal dispersed (Almeida-Neto *et al.* 2008).

Primates seem to play a disproportionately important role as dispersers for some plant families compared to other plant families. Fifty percent of the plant species dispersed by primates belong to only 10 plant families. The dependency of some plant families on one or few primate ecospecies deserves attention. Even if primates are not the only dispersers of these plant families, primates may act as key agents in the reproduction of some families (Chapman and Onderdonk 1998). These findings must be interpreted with caution because they may also result from an insufficient sampling. In addition, unlike typical mutualistic networks (Bascompte *et al.* 2003), our plant families–primate ecospecies network was not nested. This may be due to the low complexity of our network (Bascompte *et al.* 2003) and to the way we weighted the interactions (rarefied species richness instead of number of interactions). However, this pattern suggests that smaller primate ecospecies of the Atlantic Forest do not disperse a subset of the plant families dispersed by larger ones, highlighting their importance in increasing the diversity of plants dispersed.

The seed dispersal network indicates that all primate ecospecies interact with all seed size classes. Although there is a weak but significant relationship between primate body size and the size of seeds dispersed in Amazonia (Peres and van Roosmalen 2002), we found no such relationships in the Atlantic Forest. This can be explained by two factors: 1) we used seed size reported in the literature due to the absence of measurements of dispersed seeds in most primate seed dispersal studies, so we may have overestimated the size of the seeds that are effectively swallowed; and 2) our data do not take into account the quantity of seeds dispersed in each class, giving the same importance to an ecospecies that occasionally disperses a large-seeded species (which can also be smaller than the average size reported in the literature) and an ecospecies that frequently disperses a large-seeded species. Nonetheless, our study shows that large-sized primates are more likely to swallow and consequently disperse intact seeds than small-sized primates. Moreover, by dispersing most of the seeds they handle, *Brachyteles* and *Alouatta* play a key role in forest regeneration, reinforcing the need to ensure their protection (Chapman and Russo 2006). Unexpectedly, we found no relationship between the number of seed species dispersed and primate size. This can be explained by an antagonistic relationship between the degree of frugivory of these ecospecies and their body size. The largest primate ecospecies (*Brachyteles*) presented the highest rarefied species richness of dispersed seeds, followed by *Sapajus*, *Leontopithecus*, and finally, *Alouatta*. *Leontopithecus* and *Sapajus* are the most frugivorous primates of the

ecospecies considered in this study with 76.1% and 48.5% of fruits in their diet, respectively (Hawes and Peres 2014), while *Brachyteles* and *Alouatta* are less frugivorous (42.6% and 35.1% respectively). Owing to their large size, *Brachyteles* and *Alouatta* can disperse most of the seeds they handle while *Leontopithecus*, and to a lesser extent, *Sapajus*, are limited by their size and have lower dispersal indices than their larger counterparts.

Despite their small size, *Leontopithecus* disperse large-seeded species, although these represent only 2% of the species they disperse. This ecospecies disperses seeds with diameters >20 mm, corroborating findings for its Amazonian ecological equivalent, *Saguinus* (Knogge and Heymann 2003). It has been suggested that large seed swallowing by callitrichid primates is associated with the removal of gut parasites or, more likely, with a foraging strategy consisting of ingesting a maximum of fruits in a minimum of time while exposed in the canopy (Garber and Kitron 1997; Heymann 2013). Large seed dispersal by *Leontopithecus* and *Sapajus* highlights their importance in the maintenance of ecosystem functions because they require relatively small fragments owing to their small body sizes and diversified diets (Chiarello 2003). However, they probably do not compensate, quantitatively, for the role of larger-bodied primates in dispersing large-seeded species.

Most of the ecospecies studied are Endangered or Critically Endangered, indicating possible local loss of ecological functions due to reduced population size (McConkey and O'Farrill 2015). According to IUCN Red List for Threatened Species (2015), *Brachyteles* (Critically Endangered for *B. hypoxanthus* and Endangered for *B. arachnoides*) and *Leontopithecus* (*L. rosalia*, *L. chysomelas*, and *L. chrysopygus* Endangered and *L. caissara* Critically Endangered) are the most threatened ecospecies. *Sapajus* also requires attention, as two species are considered Critically Endangered (*S. flavius* and *S. xanthosternos*). *S. robustus* is considered Endangered and *S. libidinosus* and *S. nigritus* are categorized as Least Concern. Along with *Brachyteles*, *Alouatta* are the ecospecies that dispersed the highest proportion of large-seeded species. Nonetheless, their Least Concern conservation status (only *A. belzebul* is categorized as Vulnerable; Mendes *et al.* 2008), their wide distribution across the Atlantic Forest (Chiarello and Galetti 1994), and high dispersal index underline the importance of this ecospecies as the most resilient primate seed disperser of the biome.

Primates disperse a large number of plant species of which a large proportion have large seeds that are inaccessible to smaller arboreal frugivores, making primate conservation critical to ensure effective seed dispersal and forest regeneration (Chapman and Onderdonk 1998; Cramer *et al.* 2007; Peres and van Roosmalen 2002). Large seed size is a trait associated with shade-tolerant, mature phase forest species (Leishman *et al.* 2000). Large-seeded trees also tend to be slow growing and have harder wood than small-seeded zoochoric or abiotic species, which also indicates higher carbon storage capacity (Bello *et al.* 2015; Brodie and Gibbs 2009; Wright *et al.* 2007). As a consequence, we can hypothesize that the loss of primate ecospecies that disperse large-seeded plants would lead to changes in plant community (Chapman and Onderdonk 1998; Nunez-Iturri *et al.* 2008), with drastic changes in carbon storage capacity and possible consequences for the global climate (Bello *et al.* 2015; Peres *et al.* 2016).

Based on the importance of primates for rainforest regeneration, and the fast pace of fragmentation and defaunation around the globe (Dirzo *et al.* 2014), we highlight the importance of studies of primate diet that provide clear information on the qualitative

and quantitative components of seed dispersal effectiveness (Schupp *et al.* 2010). The following simple guidelines will provide fundamental information for our understanding of the role of primates in forest regeneration:

- 1) Primatologists must make an effort to identify seeds to species level and deposit the specimens in botanical collections. We lack information on the seed dispersal role of many primate species that have been studied for long periods, e.g., *Brachyteles hypoxanthus*, *Leontopithecus chrysopygus*.
- 2) Clearly report and quantify if seeds are destroyed or dispersed and how they are dispersed (spit or defecated seeds)
- 3) Provide data on gut transit times (see Lambert 1998 for a discussion of the parameters affecting gut transit time) so the role of primates as long-distance dispersers can be estimated
- 4) Provide information on seed and plant morphological traits, such as seed size and tree size (Bello *et al.* 2015; Benítez-Malvido *et al.* 2014)
- 5) Perform germination tests comparing seeds from feces (with and without fecal matter) with seeds from which pulp has been removed manually and seeds with pulp (Samuels and Levey 2005) to disentangle the effect of pulp removal from the effect of gut passage and feces presence
- 6) Report the dispersal distances, spatial distributions, defecation patterns, and seed shadow (Bialozyt *et al.* 2014; Bueno *et al.* 2013)
- 7) Determine postdispersal seed fate including secondary seed dispersal, predation, seedling establishment, and survival (Andresen and Levey 2004; Culot *et al.* 2009, 2011)
- 8) Study the role of *Callithrix* and *Callicebus* as seed dispersers because these species are able to thrive in small forest fragments (Bernardo and Galetti 2004) and thus play a role in forest regeneration

By following these guidelines and extending their research to underrepresented species and areas, primatologists will be able to obtain the information necessary to understand the importance of the ecosystem services provided by primates as seed dispersers.

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