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DEFAUNATION EFFECTS ON CARBON STOCK IN TROPICAL FORESTS

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Tese apresentada ao Instituto de Biociências do Câmpus de Rio Claro, Universidade Estadual Paulista, como parte dos requisitos para obtenção do título de Doutora em Ecologia e Biodiversidade

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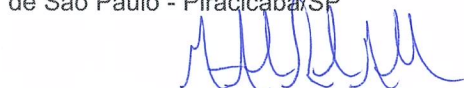
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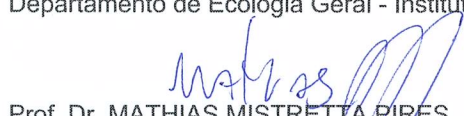
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Para Daniel Calderón.
Por ser mi soporte, el camino a casa
y la mejor cordada en esta aventura juntos en Brasil.

Ivanchis que se eleve el espíritu

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RESUMO

A extinção de animais é uma ameaça silenciosa nas florestas tropicais. As florestas tropicais estão se tornando ecossistemas defaunados, especialmente de animais de grande porte. No entanto, a defaunação vai além da perda de animais carismáticos, o que estamos perdendo são interações fundamentais que modulam a funcionalidade da floresta e, portanto, dos serviços ecossistêmicos associados. A defaunação tem efeitos sobre a dispersão de sementes, a ciclagem de nutrientes, a qualidade da água, a manipulação de matéria fecal, entre outros serviços ecossistêmicos. Nesta tese, exploramos os efeitos da defaunação de grandes animais no serviço ecossistêmico de estoque de carbono em florestas tropicais. Nós encontramos que o serviço ecossistêmico de armazenamento de carbono está sustentado pelos animais de grande porte, isso porque frugívoros grandes são os principais dispersores de árvores com sementes grandes e, as árvores com sementes grandes tendem a ser altas e com madeira densa, armazenando assim grandes quantidades de carbono. Portanto, a remoção de árvores de sementes grandes das florestas, devido à perda de dispersão induzida pela falta dos grandes frugívoros, pode reduzir o potencial do estoque de carbono da floresta. No entanto, a redução não é direta porque os frugívoros menores podem compensar parcialmente a perda dos grandes frugívoros. Além disso, a perda de grandes predadores de sementes também pode afetar o potencial estoque de carbono. Em comunidades fortemente defaunadas, pequenos roedores tendem a aumentar a sua abundância e a predação de sementes grandes, reduzindo assim o recrutamento deste tipo de árvore. Finalmente, nós exploramos o impacto da relação entre defaunação e o armazenamento potencial de carbono em programas de conservação. Nós mostramos que os projetos de restauração estão promovendo ecossistemas defaunados porque estes são dominados por árvores anemocóricas ou árvores de sementes pequenas que não irão fornecer recurso alimentar suficiente para animais grandes. Além disso, observamos que a falta de animais de grande porte pode produzir impactos econômicos nos mercados de carbono. Enfatizamos a necessidade urgente de integrar o papel dos animais em estratégias de restauração e mitigação das mudanças climáticas. O impacto econômico da defaunação no orçamento de carbono é um bom argumento para inserir os animais neste tipo de programas. Logo, devemos concentrar esforços no desenvolvimento de novas políticas nacionais e internacionais para proteger as florestas das "frentes de defaunação" assim como se tem feito com as "frentes de desmatamento."

ABSTRACT

Animal loss is a silent threat of forest ecosystem. Tropical forests are becoming defaunated ecosystems, especially defaunated of large animals. The loss of animals goes beyond than the loss of charismatic animals, what we are losing are key interactions that modulate the functionality of the forest and therefore of the associated ecosystem services. For instance, defaunation have effects over seed dispersal, nutrient cycling, water quality and dung removal among others ecosystem services. In this thesis, we explore the potential effects of defaunation of large animals in carbon stock ecosystem services of tropical forest. We found that the carbon stock ecosystem service is supported by large animals due to large frugivores are the main dispersers of large-seeded trees and, large-seeded trees tend to be tall trees with dense wood, therefore, store high quantities of carbon. Hence, the removal of large-seeded trees from the forest, because of diminished dispersal induced by the lack of large frugivores, reduce the carbon stock potential of the forest. However, the reduction is not straightforward because smaller frugivores can partially compensate for the loss of large frugivores. Moreover, strong defaunation effects in the seed predators communities can also affect the carbon stock potential of the forest. In strongly defaunated communities small rodents tend to increase their abundance and the predation pressure over large seeds, reducing their recruitment. In addition, we explore the impact of defaunation and carbon stock relation in conservation programs. We show that restoration projects are promoting defaunated ecosystems because they are dominated by abiotic trees or small-seeded trees, which will not provide enough food to large animals. Besides we observed that the lack of large animals can produce economic impacts in the carbon markets. Therefore, we argue the urgent necessity of integrating the animal role in restoration and climate mitigation strategies to. The economic impact of animal defaunation on carbon budget is a good argument to introduce animals in REED+ markets and forest restoration strategies. Within this evidence, we claim for the development of new national and international policy frames to protect forests from ‘defaunation fronts’ as well as has been done with ‘deforestation fronts’.

RESUMEN

La extinción de animales es una amenaza silenciosa en los bosques tropicales. Los bosques tropicales se están convirtiendo en ecosistemas defaunados, especialmente despoblados de grandes animales. Esta pérdida de animales va más allá de la pérdida de animales carismáticos, lo que estamos perdiendo son interacciones clave que modulan la funcionalidad del bosque y, por lo tanto, de los servicios ecosistémicos asociados. Por ejemplo, la defaunación tiene efectos sobre la dispersión de semillas, el ciclo de nutrientes, la calidad del agua, la eliminación de excrementos, entre otros servicios de los ecosistemas. A través de esta tesis, exploramos los efectos potenciales de la defaunación de animales grandes en el servicio ecosistémico de almacenamiento de carbono de los bosques tropicales. Encontramos que el almacenamiento de carbono es soportado por animales grandes debido a que los frugívoros grandes son los principales dispersores de árboles con semillas grandes y, los árboles con semillas grandes tienden a ser árboles altos con madera densa, y consequentemente, almacenan altas cantidades de carbono. En consecuencia, la eliminación de árboles de semilla grande del bosque, debido a la dispersión disminuida inducida por la falta de grandes frugívoros, puede reducir el potencial de reserva de carbono del bosque. Sin embargo, la reducción no es directa debido a que los frugívoros más pequeños pueden compensar parcialmente la pérdida de frugívoros grandes. Además, los fuertes efectos de defaunación en las comunidades de depredadores de semillas también pueden afectar el potencial de reserva de carbono del bosque debido a que, en las comunidades fuertemente defaunadas los pequeños roedores tienden a aumentar su abundancia y la presión de depredación sobre las semillas grandes, reduciendo su reclutamiento. Finalmente, exploramos el impacto de la relación entre la defaunación y el potencial de carbono de los bosques tropicales en los programas de conservación. Mostramos que los proyectos de restauración están promoviendo ecosistemas defaunados porque están dominados por árboles abióticos o árboles de semilla pequeña, que no proporcionarán suficiente alimento a los animales grandes. Además, la falta de animales grandes puede producir impactos económicos en los mercados de carbono. Por lo tanto, recalcamos la necesidad urgente de integrar el papel de los animales en las estrategias de restauración y mitigación del cambio climático. El impacto económico de la defaunación de animales en los mercados de carbono es un buen argumento para introducir los animales en los proyectos REED+ y las estrategias de restauración forestal. A partir de estas evidencias, reivindicamos la necesidad de desarrollar nuevos marcos de políticas nacionales e internacionales para proteger los bosques de los "frentes de la defaunación", así como se ha hecho con los "frentes de deforestación".

1. INTRODUCTION: DEFAUNATION EFFECTS ON CARBON STOCK IN TROPICAL FORESTS

Defaunation, known as the faunal species extinction and populations decline in natural ecosystems, is one of the most critical environmental problems of our time (Dirzo et al. 2014). The current rate of vertebrate extinctions, 100 to 1000 times higher than the background extinction rates, bring us into a new “mass extinction” event (Barnosky et al. 2011, Ceballos et al. 2015). It is estimated that we are losing two species a year with at least 322 vertebrate species extinct since 1500 (IUCN 2013, Ceballos et al. 2017). Besides, one-fifth (19%) of all tropical forest vertebrate species are under threat with their populations dropping by more than half (58%) (IUCN 2013, WWF 2016). Especially, larger vertebrates are being impacted at disproportionately high rates (Peres and Palacios 2007, Young et al. 2013).

Nevertheless, the problem harbors more than animal depletion. Large animals play important roles as herbivores, seed predators, frugivore-dispersers and predators (Malhi et al. 2016). Therefore, loss of large animals can produce cascading effects in natural ecosystems affecting other organisms and eroding key ecosystem functions and services (Markl et al. 2012, Kurten 2013). For instance, defaunation of large animals has negative effects on ecosystem services such as pollination, seed dispersal, pest control, nutrient cycling, decomposition, water quality and soil erosion (Dirzo et al. 2014). However, the relationship between defaunation and carbon stock is still poorly known.

In the tropical forest, large vertebrates modulate the trees diversity because they trample, disperse and prey upon seeds and seedlings (Nunez-Iturri and Howe 2007, Sica et al. 2014, Malhi et al. 2016, Terborgh et al. 2016a). Their loss changes the patterns of recruitment and survival of trees, generates monodominance of seedling cohorts, change the abundance of species, richness, dominance, and ultimately induce lower diversity (Cordeiro and Howe 2003, Peres and Roosmalen 2003, Nuñez-Iturri and Howe 2007, Wang et al. 2007, Terborgh et al. 2008, Kurten 2013). Therefore, if animal loss change forest composition it can also alter the carbon stock potential of the forest, especially in tropical forests where most of the terrestrial aboveground carbon is stored (Dixon et al. 1994).

Tropical forests carbon stocks play a major role in regulating the climate locally and globally (Betts et al. 2004). Trees have the ability to sequester carbon dioxide from the atmosphere and store it in their tissues. In particular, it is estimated that tropical forest store 40 % of terrestrial world carbon (Dixon et al. 1994). However, these carbon stocks are being threatened by deforestation, logging, fragmentation, and climate change, generating 17% of the global carbon emissions (Rogner et al. 2007). Moreover, tropical carbon can be especially sensitive to animal loss because up to 90% of the woody plant species have fruits and seeds that are morphologically adapted to animal-dispersal and many of those species are key contributors to carbon storage (Peres and Roosmalen 2003, Almeida-Neto et al. 2008). Therefore, we can infer that the tropical ecosystem service of carbon storage is directly or indirectly supported by distinct mutualistic interactions with animals (Brodie and Gibbs 2009).

Although some evidence had emerged in the literature supporting the link between carbon storage and animals (Terborgh et al. 2008, Brodie and Gibbs 2009, Poulsen et al. 2013), most of the studies were inconclusive (Jansen et al. 2010, Joseph Wright et al. 2010). Hence, in the present thesis, we explore in a deeper look the hypothesis that defaunation of large frugivores can affect carbon stock potential in the tropical forest due to the changes in seed dispersal and recruitment of large-seeded trees. The present introduction is structured as a summary of the 5 published chapters that compound the present thesis, with the intention of discussing it as a whole work at the light of complementary evidence that supports the effects of defaunation on the carbon stock ecosystem service. First, we present how defaunation of large frugivores is linked to carbon stock in the tropical forest through the animal and plants traits relations (Chapter 1; Bello et al. 2017. Ecology). Second, we explore how changes in forest composition induced by animal extirpation can lead to a detriment on carbon stock (Chapter 2; Bello et al. 2015. Science Advance). Third, we explore the complexity of the systems in relation to the frugivore community redundancy and antagonism compensations due to defaunation of seed predators communities (Chapter 3; Culot-Bello et al. 2017. Scientific Reports). Finally, we explore conservation implications through the economic impacts of defaunation on Carbon markets and, forest restoration (Chapter 4; Bello et al. in review. Conservation Letters and Chapter 5; Brancalion-Bello et al. 2018 Conservation Letters). In the end, we present a general discussion and implications of the main finding of the present thesis.

1.1. ANIMALS AND PLANTS RELATIONSHIPS BY WHICH DEFAUNATION OF LARGE FRUGIVORES INFLUENCES CARBON STOCK POTENTIAL IN TROPICAL FOREST

Functional traits determine the ecosystem functions and resulting ecosystem services (Hooper et al. 2005, Diaz et al. 2006, Diaz et al. 2007). The ecosystem functioning, at a given point in time, is chiefly determined by trait values of the dominant contributors in the community (Diaz 2001). Especially biogeochemical processes related to carbon, nutrient, and water cycling depends on the functional traits of the dominants species involved (Díaz et al. 2007, Diaz et al. 2009). However, the dominance and prevalence of some given traits in the community depend, to a large extent, on the relations with other organisms traits that impact their fitness via the effects on growth, reproduction, and survival (Violle et al. 2007). Hence, there must be a relationship between traits that mediated the dispersal process, in animals and plants, and traits related to carbon stock.

1.1.1. Plants and animals traits relationships

Dispersal traits, such as seed and fruit size, link different functional plants with a functional set of animals. We test the hypothesis that large-seeded trees are linked to large

animals because they are the only ones able to consume them. In Chapter 1 (Bello et al. 2017), we analyzed a large dataset of 8320 frugivore interactions among 331 vertebrate species and 788 plant species reported for the Atlantic Forest of Brazil and observed that there is a specialization between the kind of animals able to disperse large-seeded tree. Mainly large frugivores such as large birds, tapirs, large rodents, and primates are the only ones able to disperse large-seeded trees (Figure 1)(Chapter 1). Therefore, the efficient consumption and dispersal of large seeds are primarily restricted by the gaped traits and consequently, seed size is an obvious limiting trait for successful dispersal and recruitment (Galetti et al. 2013). Besides, large-bodied frugivores perform unique ecological roles such as efficient fruit removal and long-distance dispersal promoting wider gene flow and increases the probability of colonizing new habitats (Cain et al. 2000, Pérez-Méndez et al. 2015, Carvalho et al. 2016, Pérez-Méndez et al. 2016).

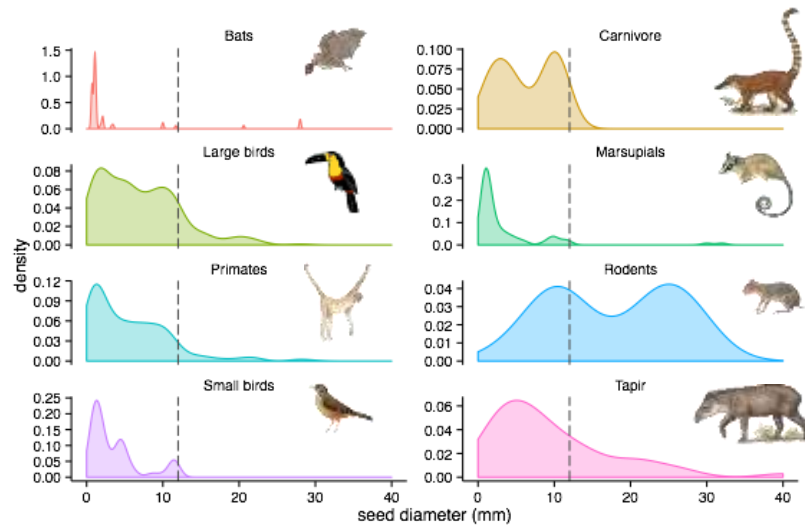


Figure 1. The distribution function of seed size diameter (mm) dispersed by the major frugivores in the Atlantic forest, Brazil. Vertical dashed line represents the 12mm seed diameter threshold. Resilient frugivores such as small birds, bats, and marsupials, which are not targeted by hunters (9), can disperse seeds up to 12.0 ± 1.1 mm in width. (Bello et al. 2017) (Chapter 1).

In contrast, small-seeded species can be dispersed by non-threatened generalist frugivores, which typically inhabit small forest fragments (Cardoso da Silva and Tabarelli 2000, Galetti et al. 2013). Some frugivorous bats (for example, *Artibeus* spp.) and terrestrial caviomorph rodents (*Dasyprocta* spp.) may occasionally eat and disperse large-seeded fruits (Melo et al. 2009), but they may not functionally replace primates and large birds (Donatti et al. 2007, Vidal et al. 2013). In fact, large rodents are mainly seed eaters (Jansen et al. 2004) and can be also locally extinct in overhunted areas (Galetti et al. 2015b).

1.1.2. Plants dispersal and carbon trait relationships

In the plant perspective, there is a supported tendency for large-seeded trees to have hardwood and big volume. Using the dataset published in Chapter 1, we observed a positive correlation between seed diameter and wood density ($r_s = 0.22$, $P < 0.001$, $N = 732$) and between seed diameter and maximum tree height ($r_s = 0.21$, $P < 0.001$, $N = 1087$), especially for animal-dispersed species (Figure 2B-C). Conversely, wind- or gravity-dispersed species did not show a significant association between seed size and wood density (Abiotic correlation $r_s = 0.11$, $p = 0.06$, $N = 246$) (Figure 2A)(Chapter 2; Bello et al. (2015)).

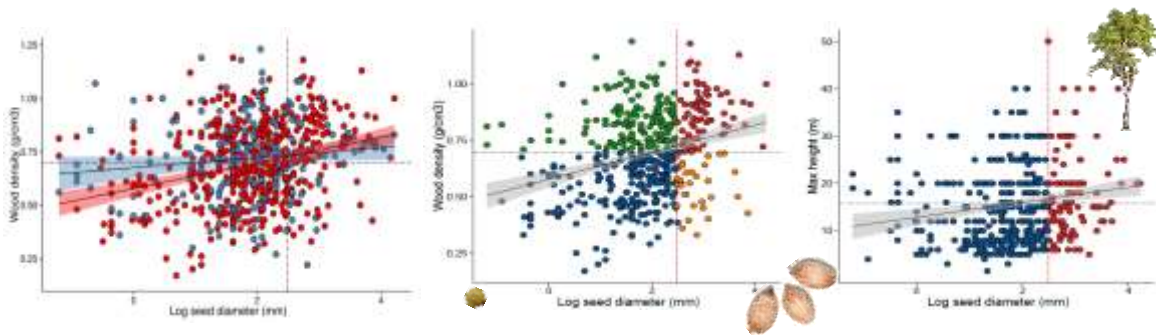


Figure 2. Relationships between seed diameter and carbon storage-related traits. (A) Wood density and seed diameter by dispersal syndrome. Animal-dispersed (red) and abiotically dispersed (blue) trees in the Brazilian Atlantic forest. (B) Wood density and seed diameter in animal-dispersed trees. Red points are endangered species with dense wood; orange points are endangered species with light wood; green points are non-endangered species with dense wood (resilient hardwood species), and blue points are non-endangered species with light wood. (C) Maximum tree height (m) and seed diameter (mm) in animal-dispersed trees. Red points are endangered species, and blue points are non-endangered species. The black solid line shows the linear regression fit for the trend and the confidence interval (gray envelopes). The red vertical line shows the seed diameter threshold of 12 mm. Black horizontal dashed line indicates the mean wood density or height of the whole dataset (Bello et al. 2015).

1.1.3. Concluding remarks

In conclusion, trees bearing larger seeds tend to have high carbon stock capacity, and large-bodied dispersers are functionally connected to forest carbon storage, given their distinct link with the dispersion of large-seeded trees.

1.2. EFFECTS OF THE RELATIONSHIPS: EXTIRPATION OF LARGE ANIMALS CAN INDUCE CHANGES IN TREE COMMUNITIES AND CARBON STORAGE IN TROPICAL FOREST.

Given that plant species differ in their ability to capture, store and release carbon, we can expect that induced changes in plant composition could change the functionality of the ecosystem and affect the carbon storage ecosystem service. As we saw in the previous section, large-seeded plants, which depend on large frugivores for dispersal, tend to be tall trees with big volume and, dense wood. Therefore, large frugivores loss may change the forest composition and indirectly threaten the ecosystem service of carbon stocks due to their relationship with trees that strongly contribute to carbon storage within local communities (Lindenmayer et al. 2012). Hence, we can hypothesize that defaunation process will lead the ecosystem to a post-depletion equilibrium condition in which the vulnerable assemblage of trees is gradually replaced by robust small seeded and trees dispersed abiotically that have a different carbon storage capacity. Let's see how evidence support or not this hypothesis (Figure 3).



Figure 3. Pathway of carbon loss in a defaunated forest. Dark blue indicates tree individuals of hardwood species with large seeds (≥ 12.0 mm) and different trunk diameters, light blue represents other tree species (Bello et al. 2015).

1.2.1. *Changes in forest composition due to defaunation*

The main process behind changes in plant composition due to the loss of animal and, their subsequent interactions, is related to what is known as the Janzen-Connell Model (Terborgh 2013). The model balances two opposing spatially explicit processes that affect the probability of recruitment: the dispersal of potentially viable seeds vs. propagule mortality drive by “enemies” (herbivores, pests, and pathogens). Both processes vary with respect to the distance of the adult tree. Seed dispersal, driven by the effects of frugivores depositions, decreases with distance. Whereas the potential for escape from enemies and competition is assumed to increase with distance (Janzen 1970, Connell 1971, Terborgh 2013)(Figure 4).

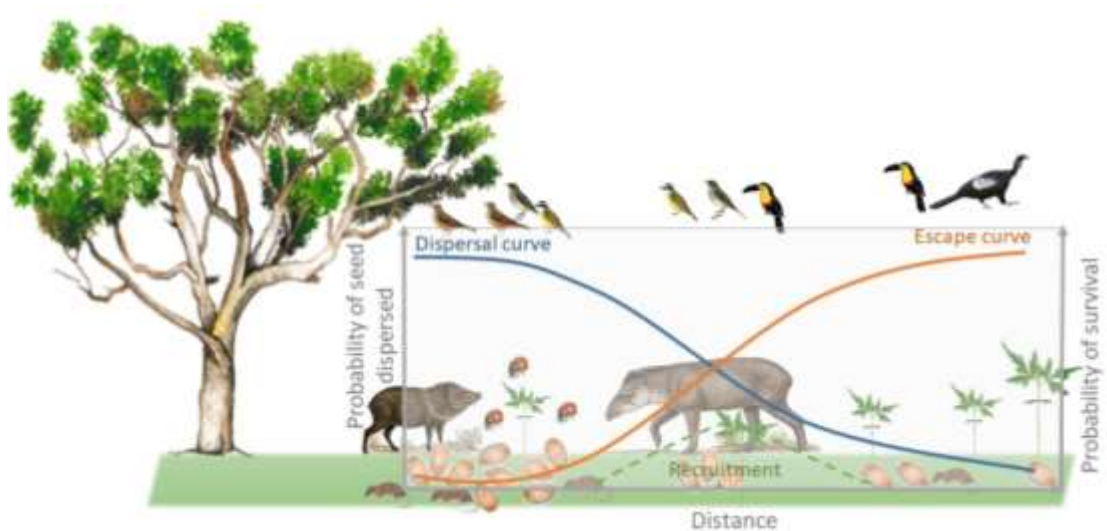


Figure 4. Representation of Janzen- Connell model. The blue line represents the probability of seed dispersal (dispersal distance curve). The orange line represents the probability of escape from seed and seedling predators (escape curve).

Therefore, changes in the seed dispersal and, seed-seedling predator communities will reshape the dispersal distance curve and the predation escape curve (Janzen 1970, Connell 1971, Terborgh 2013). In fact, plant composition changes induced by alterations in the animal communities had been demonstrated for different tropical forests, although the response is not uniform for all the ecosystems and functional groups.

Mainly, extirpation of large frugivores affects seed dispersal by reducing the visitation rate, the seed removal and dispersal distance (Markl et al. 2012). These effects produce fewer and clusters cohorts (Harrison et al. 2013, Bagchi et al. 2018), susceptible to over-predation (Janzen 1970, Connell 1971, Terborgh 2013) with phenotypic and genotypic effects (Galetti et al. 2013, Carvalho et al. 2016, Costa-Pereira et al. 2018).

In particular, it has been explored that extirpation of primates, large birds, large ungulates and even elephants reduce the recruitment success of big and hardwood trees in many neo-tropical forest (Asquith et al. 1999, Cramer et al. 2007, Nuñez-Iturri and Howe 2007, Stevenson and Aldana 2008, Terborgh et al. 2008, Lermite and Forget 2009, Anzures-Dadda et al. 2011, Stevenson 2011, Sica et al. 2014, Calle-Rendón et al. 2016, Bagchi et al. 2018), Asian tropical forest (Brodie et al. 2009, Harrison et al. 2013, Egerer et al. 2018) and Afro-tropical forest (Ganzhorn et al. 1999, Abernethy et al. 2013, Beaune et al. 2013, Effiom et al. 2013). However, in some neotropical forest no changes have been observed (Barrera Zambrano et al. 2008, Brocardo et al. 2013, Chaves et al. 2014).

Moreover, defaunation also affects seed and seedling predators communities, reshaping the escape curves of plant recruitment (Terborgh 2013). A decline in large herbivores such as

elephants and ungulates produce an increase in recruitment (Roldan and Simonetti 2001, Hanson et al. 2006, Lagendijk et al. 2011). Alternately, a decline in carnivore increases herbivores and produce rats blooms (Terborgh et al. 2001, Visser et al. 2011, Galetti et al. 2015a, Rosin and Poulsen 2016, Willoughby 2018). These increases in population densities of ungulates and rodents reduce the recruitment of seed and the survival of seedlings (Sork 1987, Hanson et al. 2006, Camargo-Sanabria et al. 2015, Culot et al. 2017). Again some forest ecosystems do not show a response in the recruitment success induced by depletion of large predators (Asquith et al. 1997, Brocardo et al. 2013), probably for a strong compensation effect (Terborgh 2013) or because of no effect over density-dependent mortality (Bagchi et al. 2018). Nevertheless, despite those contrasting effects, predators of seed and seedlings contribute to maintain beta diversity and avoid monodominance of seedling cohorts (Roldan and Simonetti 2001, Terborgh et al. 2006, Markl et al. 2012, Camargo-Sanabria et al. 2015).

In summary, changes in animal composition produce strong top- down effects on the trophic cascade that change vegetation communities altering the abundance of species, species richness, species dominance, and induce lower diversity (Cordeiro and Howe 2003; Peres and Roosmalen 2003; Wang et al., 2007; Terborgh et al., 2008; Beckman and Muller-Landau 2007, Nunez-Iturri and Howe 2007, Kurten 2013).

1.2.2. Changes in Carbon stock potential due to defaunation of large frugivores

Therefore, the disrupted plant-frugivore interactions could trigger, along with the changes in composition, a homogenization of traits in tree communities, with special effects on the ecosystem service of carbon stock potential. Indeed, In Bello et al. (2015)(Chapter 2), we test the hypothesis that the removal of large-seeded trees, induced by defaunation of large frugivores, will cause a decline in the carbon stock potential of tropical forests. To do so, we simulated the removal of large-seeded trees dispersed by large frugivores, in 31 conserved Atlantic forest communities, and its replacement with tree individuals from the remaining community. Through the simulations, we observed the changes in traits related to carbon stock potential. The results showed a significant reduction in the carbon stock potential of the forest as the removal of large-seeded trees increases (Figure 5) (Chapter 2).

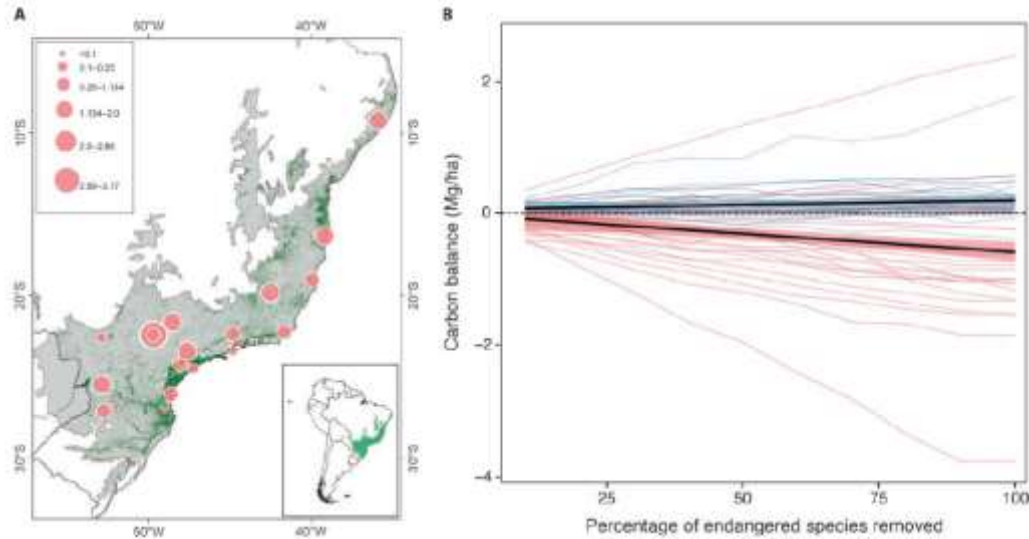


Figure 5. Carbon deficit after defaunation simulation in Atlantic forest sites. (A) Locations of the 31 communities studied. The size of the points represents the magnitude of carbon loss (Mg/ha). (B) Carbon balance after simulated changes in carbon storage capacity in the random (blue) and defaunated (red) scenarios over the 31 selected communities. Initial carbon was used as the 0 or neutral point. A negative balance represents a net carbon loss, and positive values indicate gains in carbon storage. Lines represent the simulated trajectories for each community. The black lines show the mean combined values for all communities in each scenario and their confidence interval. The width of the confidence interval for the random scenario trend was increased 2× to improve visualization.

Although we found a consistent response along the 31 forest communities. We highly that other synergic effects such as the increase of other carbon woody life forms such as lianas (Wright et al. 2007), the changes in carbon cycling and storage in leaf litter and soils (Sobral et al. 2017) or, the compensation effects in seed dispersal and seed predator species (Culot et al. 2017), can interact and exacerbate or counterattack the carbon loss. Thus, determining the exact magnitude of carbon loss induced by defaunation is still ambiguous due to the complexity of the systems.

1.2.3. Concluding remarks

Extirpation of large frugivores reshape the recruitment curves of large-seeded trees. The graduated reduction in the abundance of large-seeded trees induces a detriment in the carbon stock potential of tropical forest communities.

1.3. COMPLEXITY OF THE SYSTEM: REDUNDANCY AND COMPENSATION

Defaunation leads to significant changes in the communities of both seed dispersers and predators and, while some species respond negatively to anthropogenic activities, others can benefit because of differential functional response traits or competitive (numerical) release (Wright 2003). As we saw, plant recruitment is a complex process which depends, not only on the influence of mutualists (seed dispersers), it also depended on the activities of antagonists (seed predators, herbivores) (Harper and White 1974). Therefore, the demographic asynchrony resulting from the different defaunation process can give rise to compensatory effects (Hooper et al. 2005) that are able to mitigate, fully compensate or even invert the effects of on plant recruitment (Calviño-Cancela and Martín-Herrero 2009, McConkey and Brockelman 2011, Terborgh 2013). Hence, the relation between defaunation and carbon stock is more complex than the explorations showed above and extinctions of large frugivore will not necessary mean extinctions of the dispersed plants. In Chapter 3, we explore how functional redundancy and compensation between mutualist and antagonist species affects carbon stock potential of tropical forests along the defaunation gradient. We hypothesized that frugivores have redundant roles, so the functional role of an extinct frugivore can be compensated by the remaining community of frugivores. Besides, we test the hypothesis that defaunation in predators communities reduce the predation pressure and compensated the dispersal loss.

1.3.1. *Frugivores and predators redundancy and compensation along with a defaunation gradient*

The resilience of ecological processes to a disturbance is related to functional redundancy and capacity of compensation. These relate species that contribute equally in the provision of a given function but respond differently to disturbance and may compensate each other along disturbance gradients (Walker 1995, Elmqvist et al. 2003, Hooper et al. 2005, Nyström 2006). The diversity response concept, related with compensation, highlight that the singularities of species within functional groups promote ecological insurance, by assuring functions in the face of species extinction or environmental change (Elmqvist et al. 2003, Winfree and Kremen 2009).

In the seed dispersal process, frugivore attributes such as diet and movement are characteristics suggested to be sources of functional redundancy (Zamora 2000, Lehouck et al. 2009). Moreover, the different response on antagonism predators may also promote compensation. In Culot et al. (2017) (Chapter 3), we were able to assess the level of compensation of three functional redundant seed dispersers and antagonism seed predators in the recruitment success of a hardwood species *Cryptocarya mandioccana* (Lauraceae), along a defaunation gradient in the Atlantic Forest.

We estimate the empirical contribution the recruitment success of a hardwood species *Cryptocarya mandioccana* of the three redundant frugivores *Brachyteles arachnoids* (muriqui), *Alouatta*

guariba (howler monkey) and *Aburria jacutinga* (jacutinga) in three different Atlantic forest with different defaunation level. The contribution depends, on the probability of seed removal (P_s), the probability of germination after passing through the disperser's gut (G_s), the dispersal distance probability (D_{sm}), and the seedling survival at each dispersal distance (T_m), with s being the disperser and m the dispersal distance (Equation 1). In this system, the seed dispersers range from large (220 kg) to small (0.01 kg) in size and they respond to defaunation according to their body size (from the largest to smallest frugivore) (for more information about the methods see Chapter 3).

$$RS_{s,m} = [P_s G_s \sum_{s=1}^x \sum_{m=1}^y (D_{sm} T_m)] * 100 \quad (\text{equation 1})$$

To explore the antagonism effects of seed predators in the three areas, a total of 50 *C. mandioccana* fruits were placed in front of a camera trap for 1.5 months in each area and every event of seed predation was reported. Large rodents (e.g: agoutis, *Dasyprocta spp.*, pacas, *Cuniculus paca*), small rodents such as (*Euryoryzomys russatus*) and peccaries (white-lipped peccaries, *Tayassu pecari*, collared peccaries, *Pecari tajacu*) are the main seed predators and, they also respond to defaunation according to their body size (for more information about the methods see Chapter 3).

The results show that a partial compensation effect exists between the frugivore community in the seed dispersal process and can mitigate the effect of defaunation on the recruitment success. The compensation is observed as an increase in the overall contribution of the smallest frugivores, jacutingas and howler monkeys, as the defaunation pressure increase (Figure 8). The smallest seed disperser, Jacutingas, contributed only 0.7% towards *C. mandioccana* recruitment success where they co-occur with larger-bodied primates (muriquis and howler monkeys), while their contribution jumps to 61.4% where they are the only seed disperser in the area (Figure 6). This pattern is mostly explained by seed removal. Indeed, there is a compensatory effect in seed removal with an increasing contribution of the remaining seed dispersers, such as howler monkeys (from 41 to 47%) and jacutingas (from 1% to 16% and then to 41%), along with the defaunation gradient (Figure 6a). In addition, we observed that the model plant species still recruits without dispersers, suggesting that defaunation does not necessarily lead to the complete extinction of large-seeded species. What is not known if the seedlings without dispersal will become an adult tree.

Despite this functional compensatory effect, we observed a partial functional redundancy in the roles of the frugivores because muriquis were the only ones able to disperse seeds at long distance (Figure 6c). We observed a decreasing proportion of swallowed seeds, i.e., seeds dispersed away from the parent tree, with the loss of seed dispersers: 83% with the complete assemblage, 63% without muriquis, and 41% without muriquis and howler monkeys (Chapter 3).

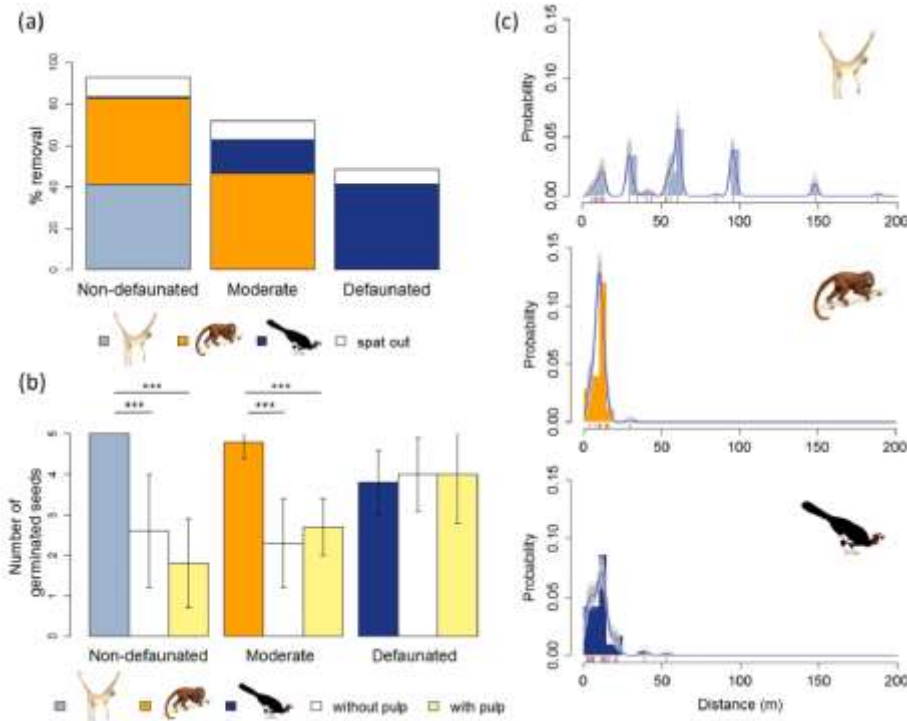


Figure 6. Components of seed dispersal effectiveness of the three main dispersers of *C. mandioccana*. (a) Percentage of seeds swallowed by muriquis, howler monkeys, and jacutingas, as well as the percentage of spat out seeds (all frugivore combined) in the three study sites characterized by different seed disperser communities: Non defaunated (muriquis, howler monkeys, and jacutingas), Moderate (howler monkeys and jacutingas), and Defaunated (jacutingas). Data are based on focal observations of *C. mandioccana* fruiting trees in 2011–2012 (Non-defaunated: N = 172 h; Moderate: N = 108 h, and Defaunated: N = 153 h). (b) Germination success of seeds defecated by muriquis, howler monkeys, and jacutingas, compared to seeds without pulp and seeds with pulp along the defaunation gradient. Bars represent the mean number of germinated seeds out of five seeds (ten replicates) and vertical lines represent the standard deviation. (c) Seed dispersal distances to *C. mandioccana* conspecifics by muriquis (N = 173), howler monkeys (N = 127), and jacutingas (N = 168). Frequency distributions of seed dispersal distances (5 m-bins) where red vertical bars represent each observed dispersal event and the blue and grey lines, a non-parametric smoothing spline fit the empirical distance distributions together with bootstrapped estimates. (Culot et al. 2017).

However, complete compensation or redundancy is achieved only when the seed dispersers are quantitatively and qualitatively similar. The quality of dispersal by howler monkeys and jacutingas was lower than muriquis in terms of seed germination success and dispersal distances, limiting their potential for compensation. The partial redundancy and compensation support the hypothesis that processes carried out by a small number of key and functionally unique species, such as the dispersal of large seeds, are most sensitive to changes

in biodiversity (Vidal et al. 2014). Besides, the pattern of recruitment success is not the only one of the possible effects of defaunation: long-distance seed dispersal is a key process for plant populations because it promotes gene flow and increases the probability of colonizing new habitats (Cain et al. 2000). Therefore, recruitment success observed in defaunated areas might hide a more pervasive effect: the strong reduction of gene flow due to the concentration of the seed rain under parent trees (Pérez-Méndez et al. 2015, Carvalho et al. 2016).

Moreover, the antagonistic role of dispersers and predators will not result in a compensatory effect that is able to mitigate or reverse the limitations in the dispersal process, as previously suggested (Hooper et al. 2005, Terborgh 2013). Counter-intuitively, the loss of large seed predators increases the net seed mortality by 7–30%, reaching similar levels as the loss of large seed dispersers. The increased mortality in defaunated ecosystems it's mainly due to a bloom in the abundance of small rodents (Culot et al. 2017). This overabundance of rodents has been reported for other defaunated ecosystems with evidence of a shift in their diets (Galetti et al. 2015a, Galetti et al. 2015b). Therefore, the loss of large seed dispersers and predators synergistically decrease the recruitment success of a hardwood tree species.

Hence, seed dispersal process is partially resilient to defaunation disturbs. The increasing contribution of smaller seed dispersers when large ones are absent indicates that smaller dispersers could benefit from the absence of large species, partially compensating their role. This has implications also for the resilience of carbon stock potential in the tropical forest. The estimation of the magnitude of the effects of defaunation on future carbon storage has been based on inferences that frugivore extinction will necessarily lead to direct effects on plant species fitness. However, in defaunated scenarios, plants can still recruit without dispersers or have multiple dispersers that can compensate the frugivore loss. A better estimation of the magnitude of carbon loss, including the compensation effect, will be used to estimate the economic value of the carbon lost, in section 4.

1.3.2. Concluding remarks

Seed dispersal process is partially resilient to defaunation due to a compensation in the frugivore communities. However, the functional role of large frugivores is just partially compensated due to a reduction in the dispersal distance (eg. Only large frugivores disperse seed at large distance). Moreover, strong disruptions in the antagonistic communities exacerbate the recruitment loss due to a competitive release effect over small rodents' populations that promote a higher abundance of rats and therefore higher rates of seed predation.

1.4. CONSERVATION CONSEQUENCES OF THE RELATIONSHIP BETWEEN DEFAUNATION AND CARBON STOCK ON RESTORATION PROJECTS AND CARBON MARKETS

Defaunation lies at the heart of the vigorous debate about the cost, effectiveness, and benefit of conservation and restoration programs. Knowing the economic consequence of defaunation is a key argument to promote conservation politics and programs. Based on the

relation of large frugivores and predators, including the compensation effects, with carbon stock, developed in the previous sections, we explore the economic loss in carbon markets induced by defaunation (Chapter 4) and the effectiveness of restoration programs in provide quality habitat for animals and their ability to restore carbon (Brancalion et al. 2018b) (Chapter 5).

1.4.1. The economic consequence of the effect of defaunation over carbon stock.

Defaunation has negative effects on ecosystem services such as pollination, seed dispersal, pest control, nutrient cycling, decomposition, water quality, soil erosion and carbon stock (Dirzo et al. 2014, Bello et al. 2015). However, the economic impacts of defaunation on ecosystem services are still poorly explored. In fact, the attempts to value the importance of animals as providers of ecosystem service are concentrated on the pollination and pest control ecosystem service through its contribution to crop production (Mburu et al. 2006, Hein 2009). Pollination, provided mostly by bees, supports between \$117 and \$200 billion dollars per year in crop production (Costanza et al. 1997, Pimentel et al. 1997, Gallai et al. 2009). In addition, local estimations on pest control reveal savings of \$USD 730 dollars per ha/ year in Cacao plantations and \$USD 9400 dollar for Coffee production in Costa Rica. However, little is known about the economic loss associated with declines in dispersion service due to frugivore defaunation.

In (Bello et al. in review) (Chapter 4), we explore the economic consequences of seed dispersal decline due to large frugivore defaunation in the carbon market. The contribution of each large frugivores to carbon storage capacity was determined by simulating the decrease of recruitment success of large-seeded-trees estimated in (Culot et al. 2017) (Chapter 3) and calculating the changes in carbon stock potential. To determine which tree species of the Atlantic forest community are dispersed by each animal we used the Atlantic-frugivore dataset from (Bello et al. 2015) (Chapter 1).

We used the Carbon emission trading market as a real market from where we can perform a direct economic valuation of the disperser contribution to carbon stock in real monetary terms. The Carbon emission trading permits the exchange of carbon emissions, calculated in tons of carbon dioxide equivalent or tCO₂e, between polluters and savers. This form of carbon emission trading is a common method used by countries or private sector in order to meet their obligations specified by the Kyoto Protocol in order to reduce (mitigate) future climate change. In this scheme forest carbon payment such as "Reducing emissions from deforestation and forest degradation (REDD+)" programs play an important role as providers of carbon stocks. Forest carbon programs can sell either carbon sequestration (deriving from the net absorption of carbon dioxide in planted trees) or by protecting carbon stocks, which would otherwise be emitted, in natural forests (Bond et al. 2009) (IPCC 2007).

Therefore, we used a direct economic valuation method known as the market price method which reflects the economic value that is bought and sold in real markets that can be attributable to a given function (e.g. in this case the role of the frugivores) (Hein 2009, Newell

et al. 2014). The economic value was calculated by multiplying the estimated contribution of each disperser, in tCO₂e, by the market transaction price for Latin America (US\$5.00/ton) (Sathaye and Shukla 2013, Kooten and Johnston 2016). (For more details see Chapter 4) (Bello et al. in review).

We found a significant decrease of potential carbon stock within almost all levels of disperser and predator loss (Figure 7). The loss of seed predator species would lead to a 2.7% reduction in future carbon storage capacity. Adding the effects of seed disperser loss would result in a total reduction of 3.5% of total carbon stock (Figure 8, red scenario).

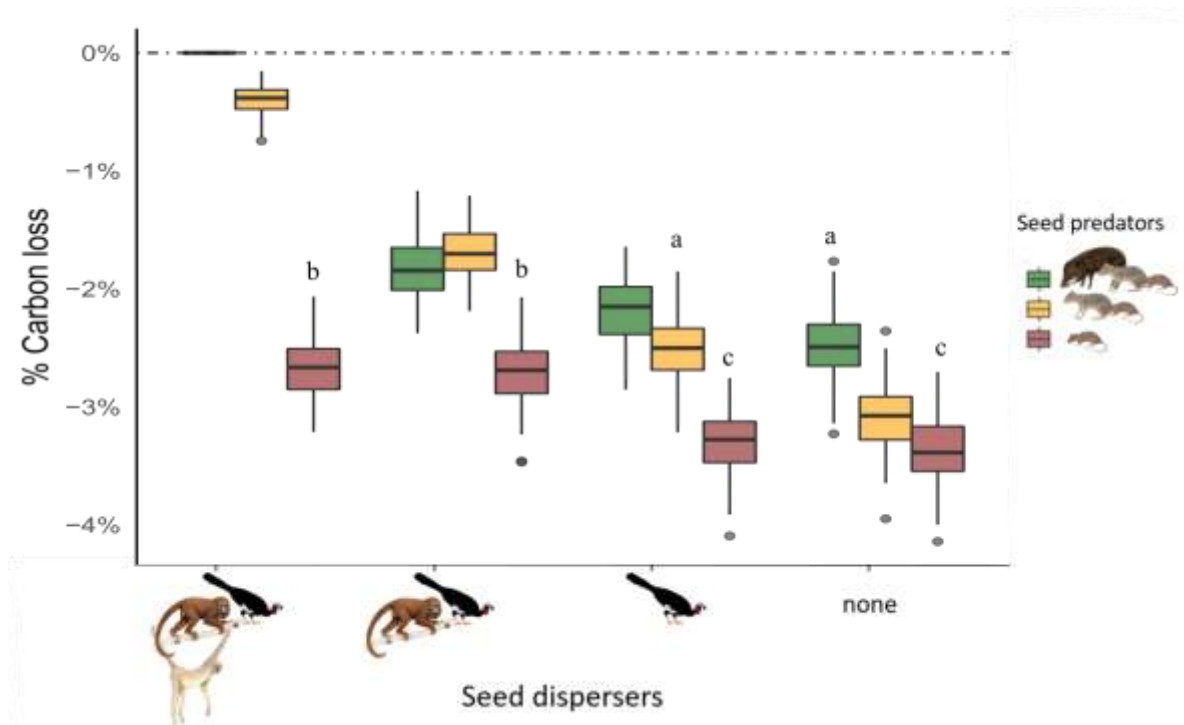


Figure 7. Simulated carbon storage potential loss according to different scenarios of seed disperser and predator communities. Results simulations from the loss of individuals of large-seeded plant species (seed diameter larger than 12 mm) consumed by muriquis, howler monkeys, and jacutingas based on the empirical data of recruitment success of the hardwood tree species, *Cryptocarya mandioccana* (Culot et al. 2017). Boxplots represent the mean (horizontal bar), lower and upper quartiles of carbon stock per hectare, whiskers represent 1.5 interquartile range and individual points, the outliers. The horizontal dotted line represents the value of carbon stock per hectare of the current adult plant community at the study site, assuming a complete set of seed dispersers and predators. All comparisons were significant at $P < 0.001$ (with the exception of the comparison between the loss of muriquis + howler monkeys and muriquis + howler monkeys + jacutingas in the yellow scenario, with $P < 0.05$) except the ones highlighted by small letters in the figure (Bello et al. in review).

Interestingly, the disruption of the seed predator community would lead to a similar loss of carbon stock as the disruption of the seed disperser community: -2.6% in a community intact in terms of seed dispersers but defaunated in seed predators versus -2.5% in a community defaunated in seed dispersers but intact in seed predators. The loss of seed dispersers in a community already defaunated of its seed predators has a lower impact on carbon stock than in a non-defaunated community (-0.9% in a defaunated community versus -2.5% and -2.7% in non-defaunated and semi-defaunated communities) (Figure 7) (Bello et al. in review).

This potential carbon storage loss will impoverish the carbon budget of areas that suffer a defaunation process. In economic terms, we found that the dispersal economic contribution of our target disperser community (M+H+J) to carbon stock rises from US\$11.1/ha to US\$ 43.4/ha depending on whether the community is defaunated or not in seed predators. Muriqui population can contribute to maintaining, in average, US\$17/ha (from US\$ 0.39/ha to US\$29.86/ha). Howler monkey population contributes to maintaining in average US\$9.51/ha (from US\$5.5 to US\$13.3). In addition, Jacutinga population maintain in average US\$5.08 /ha (from US\$ 1.9 to US\$ 9.3) (Bello et al. in review).

The economic valuation presented in (Bello et al. in review) is simple and represent just a part of the total economic value of the dispersal ecosystem service. The total value of the ecosystem service includes the value of the direct use and the value of non-use (value society is willing to pay just for the option of using it or for its existence) (Mburu et al. 2006)(Osuri et al. 2016). By now, only two studies have estimated the value of seed dispersal and both reveal different values. Hougner et al. (2006) used the replacement cost method to access a value between US\$ 2100 to US\$ 9400/ha for the seed dispersal ecosystem service performed by jays (*Garrulus glandarius*) in an oak forest in Sweden. Although the cost replacement method tends to overestimate the economic value and incorporate all the derivate benefits (e.g. (Allsopp et al. 2008), the difference in the estimated values shows the uncertainty of the current knowledge around the seed dispersal value in different ecosystems. Therefore, national and global assessments of the seed dispersal contribution to the economy are still encouraged and a lot of research has to be developed. We need a better comprehension of the seed dispersal services in both ecological and economic terms to different markets and human well-being (Daily et al. 2000, Turner et al. 2003). However, our hope is that with this economic valuation of dispersal ecosystem services we encourage the debate and contribute to the decision-making processes and policies that include the value of ecosystem services provided by animals.

1.4.2. Restoration effectiveness for counteract frugivore defaunation and restore carbon stock

Reforestation programs are a commonly used policy instrument for reversing the environmental and livelihood problems created by deforestation and climate change (Lamb et al. 2005, Chazdon 2008, Hua et al. 2016). Ecological restoration plays a crucial conservation role in fragmented mega-diverse regions (Derhe et al. 2016; Possingham et al. 2015). In the fragmented Atlantic forest, where just 12% of the forest remains (Ribeiro et al. 2009),

restoration is a key priority. In fact, the Atlantic Forest has been the stage of one of the largest tropical forest restoration programs in the world – the Atlantic Forest Restoration Pact –, a multi-stakeholder coalition with over 270 private companies, governments, NGOs, and research organizations working collaboratively to restore 15 million hectares of forests by 2050 (Melo et al. 2013).

The Atlantic Forest Restoration Pact strategy has focused on high-diversity tree plantations to recover species-rich forests in sites with low local and landscape resilience (Rodrigues et al. 2009), using innovative strategies to produce seedlings of native trees (Brancalion et al. 2012). However, the Atlantic forest is a rich carbon forest dominated by animal-dispersed tree species (Almeida-Neto et al. 2008) and the evaluation of the restoration programs to restore animal communities and carbon stock have not been done.

In Brancalion et al. (2018b) (Chapter 5), we compare the proportion of medium- and large-seeded, animal-dispersed trees that are planted to restore forests compare with nearby natural forest remnants, and its consequences for food provision for animals and potential carbon stock. We used data from 961 restoration projects distributed in private properties within 348 municipalities, comprising a total of 14,664,524 native tree seedlings of 350 tree species. Each restoration plantation accounted for an approximate area of 10 ± 8.7 hectares (mean \pm SD), totaling ca. 10,000 hectares, with a density of ca. 1,500 seedlings per hectare. The list of species and density of individuals representing each project was based on the records of seedling acquisition from 29 private forest nurseries between 2002 and 2015. We compare restoration projects against reference forest represented by 192 inventories (dbh > 4.8-5cm; > 1ha) of old-growth forest (> 80 years), distributed in southeastern Atlantic Forest (Lima et al. 2015). For carbon stocking simulations, a subset of 69 remnants located in the vicinity of restoration projects was used (nearest forest to the restoration project). We simulate the carbon stock potential of the restored forest replacing the medium- and large-seeded (scenario 1) or just large-seeded (scenario 2) tree species in remnant forests with tree species from the seedling acquisition records and evaluating the difference in carbon stock potential. We assume that the contribution of large seeds comes only from the restoration project and that fragmentation reduces the likelihood of establishment of a large-seeded tree. To access potential food provision and seed traits we used the Atlantic-Frugivore dataset from (Bello et al. 2015, Bello et al. 2017) (Chapter 1 and 2). Finally, we explore the relationship between seed size and production price and compare it against the economic carbon loss associated with the few presences of large-seeded trees in restoration projects (for more methodological details see Brancalion et al. (2018b) Chapter 5).

Large-seeded, animal-dispersed trees were significantly underrepresented among tree species used to restore Brazilian Atlantic Forest on both at species and individual level (Figure 8), with demonstrable consequences for both restoration cost and carbon storage. Small-seeded species were dominant in the seedlings acquired for restoration projects, where 25% of the species corresponded to 75% of all seedlings (Brancalion et al. 2018b) (Chapter 5).

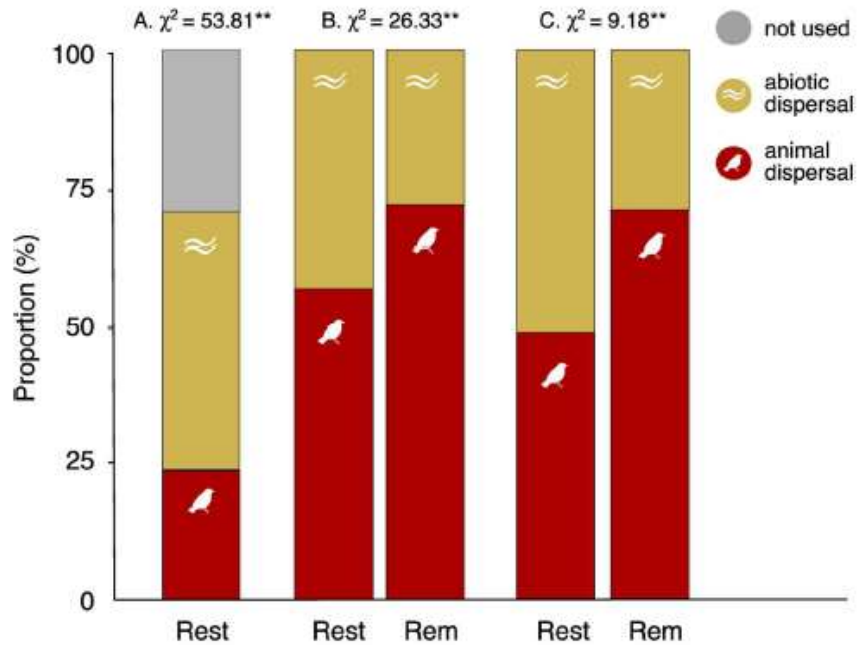


Figure 8. Proportion of abiotically-dispersed and animal-dispersed tree species used in restored forests (Rest.) and present in forest remnants (Rem.) in the Atlantic Forest of Brazil (A) proportion of species used in relation to the total species pool (B) proportion of species and (C) individuals per dispersal syndrome. In A, gray color represent other species are not accounted for restoration projects (Brancalion et al. 2018b) (Chapter 5).

Restoration plantations contained fewer medium- and large-seeded tree individuals dispersed by animals than forest remnants. In addition, fruit supply potentially offered by the species acquired in restoration plantings is lower for large and small birds, but higher for bats and not affected for other dispersal guilds (Figure 9) (Brancalion et al. 2018b).

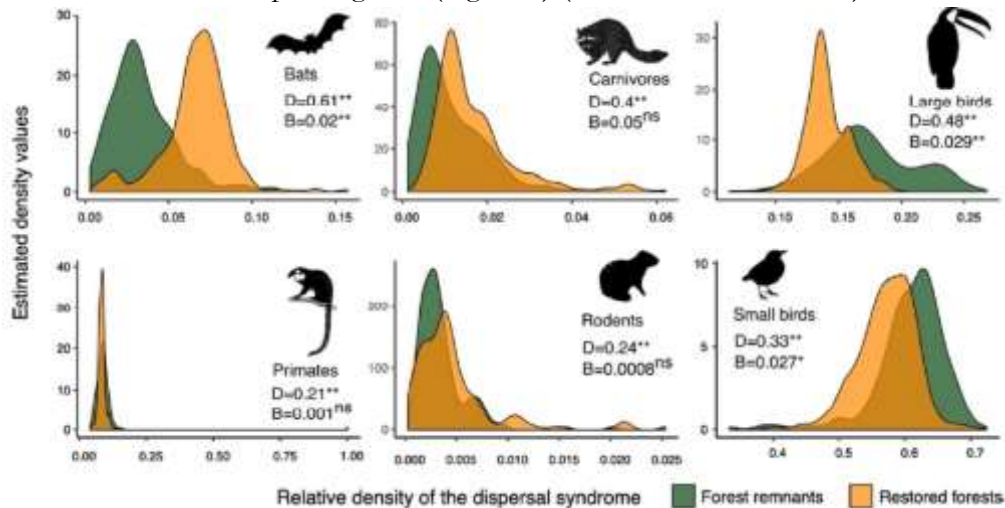


Figure 9. Frequency distributions for the relative representation (percent individual density) of tree species in forest remnants and restored forests. Panels indicate the frequencies for tree species providing food for different taxonomic groups of vertebrate frugivores. Each species may supply fruits for one or more frugivore groups, so it may have been counted more than once. Density functions were compared by the Kolmogorov-Smirnov Test (D) and mean values by a Mann-Whitney test (W) (Brancalion et al. 2018b) (Chapter 5).

This reduced abundance of medium- and large-seeded, animal-dispersed tree individuals in seedling acquisition records would lead to reductions in the relative carbon stock potential of restored forests in comparison to forest plantations (Figure 10). The reduced abundance of individuals with medium-sized seeds dispersed by animals resulted in a higher estimated impact on carbon stocking potential in restoration (decline of 10.6%) compared to the differential abundance of large-seeded species (decline of 2.8%; Figure 10). When plantations and forest remnants were grouped according to the major forest types within the Atlantic Forest region, Semideciduous Forests showed a less intense reduction of carbon stocking potential (large seeds: loss of 2.3%; medium and large seeds: 10.5%) compared to Rainforests (large seeds: loss of 3.2%; medium and large seeds: 14.2%) (Brancalion et al. 2018b).

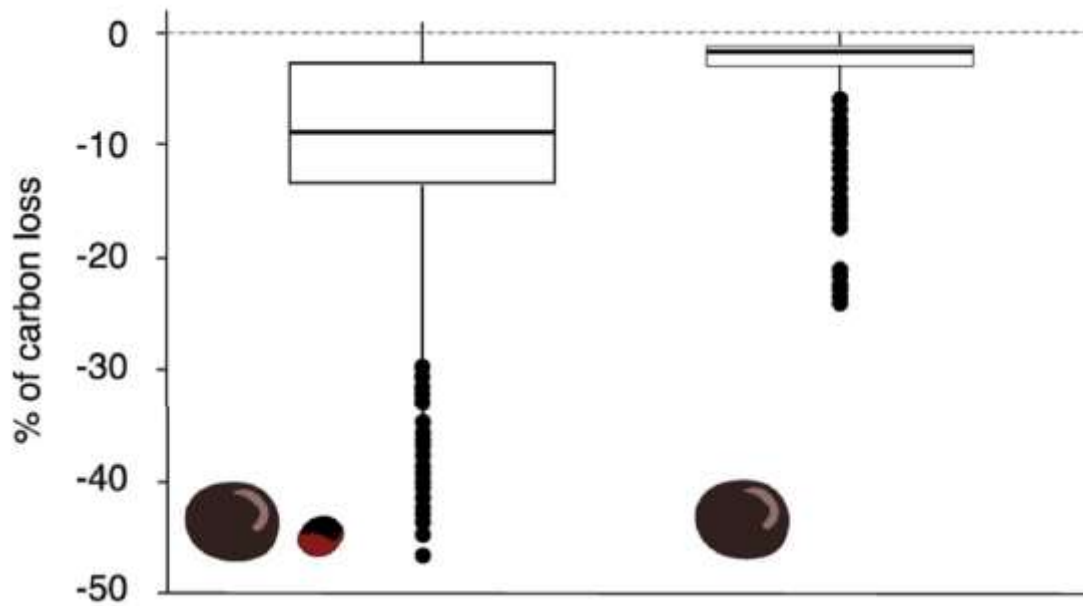


Figure 10. Potential effects on carbon stocking. The proportion of individuals with large (seed diameter > 12 mm) and medium seeds (6 mm < seed diameter < 12 mm), and only large seeds, of forest remnants, are substituted by the proportion found in restored forests in the Atlantic Forest of Brazil. No outlier was found for carbon gain.

The observed bias against large-seeded, animal-dispersed trees appears to reflect market forces operating at the seed collecting and seedling production stages. The seed market for restoration is biased towards low cost, small-seeded, abiotically-dispersed tree species. We found a significant positive correlation between seed size and production price for both abiotically-dispersed ($r = 0.91$; $t = 27.32$; $p < 0.0001$) and animal-dispersed species ($r = 0.73$; $t = 14.5$; $p < 0.0001$). Moreover, if we simulated a similar proportion of medium- and large-seeded species dispersed by animals of forest remnants, or of only large-seeded species, the production cost would be around US\$31.1 and US\$13.7 per hectare, respectively. Meanwhile, aforementioned carbon stocking potential losses, driven by the underrepresentation of large-seeded, and medium- + large-seeded tree species, would cause, in the long term, an estimated reduction of, respectively, US\$ 16.7 to US\$ 63.1 per hectare in carbon credits traded in the international market (Brancalion et al. 2018b).

Therefore, we showed that investing in a species group with high conservation value (i.e., animal-dispersed, larger-seeded trees) may promote higher carbon stocking in tropical forest restoration as well as animal recolonization. Restoration presents an opportunity to increase the range and population size of animal-dispersed, large-seeded species, which is particularly important for rare species persisting in human-modified, defaunated landscapes (Beca et al. 2017). The conservation value of forest remnants is not replaceable, but we showed science-based guidelines that may substantially contribute to increasing the value of restoration plantings for biodiversity conservation as well as carbon stocking (Shoo et al. 2016).

1.4.3. *Concluding Remarks*

Defaunation effects over carbon storage potential of tropical forests need to be incorporated in the conservation and restoration policies to achieve the complete functionality of the forests. Restoration projects need to incorporate large-seeded trees in order to restore animal communities. Besides, the economic gains achieved by carbon stock potential can easily compensate the cost of include large-seeded trees. Our hope is that with this economic valuation of dispersal ecosystem services we encourage the debate and contribute to the decision-making processes and policies that include the value of ecosystem services provided by animals.

2. GENERAL DISCUSSION

Defaunated ecosystems are emerging all over the world (Ceballos et al. 2017), being especially depleted of large animals (Dirzo et al. 2014, Ripple et al. 2016). Behind the loss of animals, depleted ecosystems are changing their functionality, due to loss of trophic interactions (Kurten 2013, Dirzo et al. 2014, Young et al. 2016). Changes in trophic interactions produce top-down forces driving ecosystem shifts towards “alternative stable states” (Estes et al. 2011). Producing far-reaching effects on processes as diverse as the dynamics of disease (Silman et al. 2003, Young et al. 2014); fire regimes (Holdo et al. 2009); carbon cycling (McSherry and Ritchie 2013, Wilmers and Schmitz 2016); invasive species (Peters 2001); and biogeochemical exchanges (Stephen et al. 2010).

In fact, evidence suggests that different top-down forces modulate carbon cycle. For example, rinderpest reduces the populations of wildebeest and buffalo in East Africa, reducing the herbivory and changing the ecosystem from a grassland to a scrubland, with consequences to fire regime and carbon stock allocation in vegetation and soils (Holdo et al. 2009). Wolf extirpation increase moose populations reducing carbon allocation in woody plants (McSherry and Ritchie 2013, Wilmers and Schmitz 2016). Changes in apex predator fishes communities induce an unbalance in the interactions between smaller planktivorous minnows, phytoplankton, and zooplankton moving lakes from net sinks, when predatory fishes are absent, to net sources of atmospheric CO₂ when fishes are present (Schindler et al. 1997). The abundance of mammal feces and vestiges organic remains produced by feeding interactions in tropical forest increase soil carbon and ultimately carbon in biomass (Sobral et al. 2017). Detriment on sea otters populations promotes sea urchin abundance, indirectly reducing carbon storage in kelp, a food source for the urchins (Wilmers et al. 2012). Whaling has reduced whales carbon movement from the deeper sea to the atmosphere (Pershing et al. 2010), directly reducing primary productivity and its influence on carbon flux and sequestration (Roman and McCarthy 2010, Stephen et al. 2010). Finally, now, we have evidence that defaunation of large frugivores have the potential of affect tropical forest carbon stock potential, affecting their important role in mitigating climate change (Poulsen et al. 2013, Bello et al. 2015, Osuri et al. 2016, Paula Mateus et al. 2018).

However, the effects of defaunation on carbon stock are sensitive to the particular animal and plant assemble and traits relationship within each community. Osuri et al. (2016) show that the relation between large-seeded trees and carbon traits vary from forest to forest. In some forest, the large seed trait is stronger related to volume traits (Diameter at breast height-DBH and height) than with wood density. In general, large-seeded animal-dispersed species have 24% greater maximum diameters on average than small-seeded trees species, but are 14% smaller, on average, than abiotically dispersed species. This relation remains for heights, being large-seeded trees 26% taller than small-seeded trees species, but 12% lower than abiotically dispersed species. Hence, at a pan-tropical scale, extirpations of large-seeded animal-dispersed species will have a different magnitude of effect over carbon stock potential. The magnitude of carbon stock detriment varies between 2.5–5.8% on average (Osuri et al. 2016). More specific cases of studies reveal that the extirpation of large ateline primates (*Lagothrix* spp. and *Ateles* spp.) and lowland tapir (*Tapirus terrestris*) throughout the Amazonian forests can induce a carbon stock detriment up to 31% (Peres et al. 2016). Summing up, carbon losses are expected in tropical forests of the Americas, Africa and South Asia where tree communities are dominated by trees families that bear animal-dispersed species (e.g. Sapotaceae, Myrtaceae, Lauraceae, Arecaceae), but not in forests of Southeast Asia and Australia where large, abiotically dispersed species are more prevalent mostly because of the dominance of Dipterocarpaceae family (Osuri et al. 2016). However, more research is needed to fulfill understand the mechanisms and conditions under which defaunation can exacerbate the carbon stock detriment.

Some clues to understanding the causes of this variability come as a reflection of the effects of defaunation effects in the Janzen –Connell model (Terborgh 2013). The induced

reorganization of the plant communities tend to generate a forest homogenization (Tabarelli et al. 2004, Nunez-Iturri et al. 2008, Terborgh et al. 2008, Lobo et al. 2011), with potential changes in carbon storage trait composition (Wright et al. 2007, Kurten 2013, Poulsen et al. 2013). Nevertheless, still, there is no consensus about the direction and magnitude of the effects. In some forest, the changes seem to be more drastic while in others they can be neutral (Bagchi et al. 2018). According to the evidence presented and compiled in the present work, we see that the variability and intensity of the effects depend on: a) the number of plant species that depend on large frugivores to disperse their seeds and how the communities are structured by fruit size. b) The intensity, ensemble and compensation probability within the antagonism community (seed and seedlings predators) in the community. c) The predominant drivers of diversity in each forest community.

Frugivory and seed dispersal are the main processes affected by defaunation in plant recruitment process, because of the important role performed by large frugivores, which are highly targeted by hunters (Peres and Palacios 2007, Galetti et al. 2018). The reduced dispersal leads more or less directly to the reduction of recruitment (Terborgh 2013). Ecosystems where frugivores have a big contribution in the tree dispersal, and where large-seeded trees highly contribute to carbon stock, will be more impaired than communities dominated by abiotic tree species (Mendes Pontes et al. 2016, Osuri et al. 2016, Paula Mateus et al. 2018). Moreover, communities in which frugivore interactions are assembled by seed size trade-offs will be more affected (Donoso et al. 2017). Future work must explore under which interactions topology carbon stock is vulnerable or resilient to defaunation of frugivores.

In addition, the structure and intensity of antagonistic interactions (seed and seedling predators) can also model the response of the ecosystem. The defaunation effects over escape curves during the recruitment process, tend to be less drastic than in the dispersal process (Terborgh 2013). Mainly the intensity of top-down forces driven by a depleted community of antagonisms can be influenced by facts such as a) predation is a uniform process in the space, so it does not change spatial configuration determined by dispersal process (Terborgh 2013). b) Density mortality is a process that operates when cohorts appear in high abundance (Terborgh et al. 1993, Hammond and Brown 1995, Swamy and Terborgh 2010), whereas tropical ecosystems are highly diverse and monodominance is uncommon (Terborgh and Wright 1994, Paine et al. 2008, Bagchi et al. 2018). c) The amount of resource produced by the tree species. Evidence suggests that large-seeded trees may produce more seeds than required for the maintenance of the reference undisturbed population as a buffer for biotic or abiotic factors (Nathan and Casagrandi 2004, Nicotra et al. 2010). d) The intensity of antagonism effect over the mortality of the seedlings (Terborgh et al. 2006): There is a big difference in the intensity of herbivory and trampling produced in ecosystems dominated by elephants or big ungulates than the intensity of the effect produced by pacas, peccaries and lonely tapirs (Young et al. 2013). e) The possibility of compensation between antagonisms agents which can substantially buffer direct effects of defaunation (Wright 1983, Asquith et al. 1997). f) Possible synergies associated with predation communities that can operate when ecosystems are highly defaunated and animal communities reach new stable conditions: In highly defaunated and transformed ecosystems rodentization is a common outcome due to predator extirpation

(Galetti et al. 2015a). In those cases, high abundance of rodents exacerbates the consumption of resources (seeds) decreasing the possible dispersal by storage observed under low abundance of rodents (Jansen et al. 2012) and by contrary can increase the seed mortality (Culot et al. 2017).

Moreover, other demographic filters that operate in juvenile or adult stages can compensate or dilute the negative effect induced by defaunation in the carbon stock (Muller-Landau 2007, Zhu et al. 2013, Neuschulz et al. 2016). However, this has not been fulfilled evaluated. Evidence of the asynchrony in different size classes of trees after 35 years of defaunation in Peruvian Amazon can infer that others filters reduce the aggregation of cohorts induced by altered dispersal process, or even that the signal of defaunation must take decades to reach the older classes (Bagchi et al. 2018)

Finally, the intrinsic characteristics that drive diversity and carbon allocation in the systems seem to be important (Doetterl et al. 2015, Terborgh et al. 2016b). In ecosystems where strong trampling determine forest diversity dominated by larger tree classes or where carbon stock is dominated by few species, defaunation can induce bigger changes than in ecosystem where diversity is presented in small tree class that can easily compensate the recruitment reduction of some species (Fauset et al. 2015, Terborgh et al. 2016b).

Thereafter, the intrinsic composition of guilds (dispersers-predators) and the topology and strength of the interactions seem to modulate the particular effects of defaunation over carbon stocks. Therefore, careful considerations must be taken with causal relations, or non-relations, observed between diversity and carbon stocks (Oscar et al. 2009, Paoli et al. 2010, Strassburg et al. 2010, Armenteras et al. 2015, Sullivan et al. 2017, Di Marco et al. 2018). Those studies are mainly developed to determine if carbon markets mechanisms as REED+ policies actually bring conservation co-benefits. However, these studies analyze biodiversity as a whole and it is clear that the ensemble of disperser and seed-seedling predators modulates carbon stock in a tropical forest.

Although variability that may exist along the different forest, the link between animals and carbon stock ecosystem services offer opportunities to introduce animal conservation into climate change and deforestation policies. Even today, foresters and carbon policies such as REED+ ignore most biotic interactions, whether positive, mutualistic or negative (Werger 2011, Putz and Romero 2012). Whether acknowledged or not, tropical forests are far more than trees. They are vertically integrated ecological communities maintained by complex webs of predation and mutualism (Terborgh and Feeley 2010), and these concepts need to be incorporated in restoration and climate mitigation strategies to guaranty future carbon stocks. The economic impact of animal defaunation on carbon budget is a good argument to introduce animals in REED+ markets (Bello et al. in review) and forest restoration strategies (Brancalion et al. 2018a). Although more case studies of economic valuations should be developed in order to have consensus estimates.

Moreover, policies to counter defaunation should go far than REED+ schemes. REED+ will not be the ‘one size fits all’ global solution to deforestation and conservations problem (Visseren-Hamakers et al. 2012). Therefore, we claim for the development of new national and international policy frames to protect forests from ‘defaunation fronts’ as well as

has been done with ‘deforestation fronts’. The proven relation of defaunation and its impacts on different ecosystem services, such as carbon stock (Dirzo et al. 2014), highly the importance of quick actions. In this context, trophic rewilding emerges as a promising strategy. Trophic rewilding is the ecological restoration strategy that uses species introductions to restore top-down trophic interactions and associated effects on the trophic cascades to promote self-regulating biodiverse ecosystems (Svenning et al. 2016). In this context, we have the fortune that most animals can present faster population recoveries than trees and overcome the changes induced in the Janzen-Conell mechanisms. Therefore, timely restoration of the animal community can prevent the progressive animal, plants and carbon loss on Planet Earth.

3. CONCLUSIONS

- Defaunation of large frugivores can affect the carbon stock potential of tropical forest. Carbon stock potential of tropical forests are supported by large frugivores because they are the main dispersers of large-seeded trees, and, large-seeded trees tend to store more carbon.
- There is a relation between the seed size and the carbon stock potential within tropical trees. Large-seeded trees tend to be taller and have denser wood than small-seeded trees or abiotic trees. Therefore, large-seeded trees stock more carbon than small-seeded trees or abiotic trees.
- The dispersal limitation of large-seeded trees, induced by the functional extirpation of large frugivores, change the tree forest composition and therefore can affect the carbon stock potential of the forest. The removal of large-seeded trees and its replacement by small-seeded trees or abiotic trees can produce a detriment in the carbon stock potential of tropical forest.
- Carbon stock potential of tropical forest is partially resilient to defaunation of large frugivores. Small, non-threaten, frugivores can partially compensate for the loss of large frugivores and continue with the dispersal of large-seeded trees. However, this is a partial compensation due to large frugivores are the only ones able to disperse seed at large distance, which constitute an advantage for the recruitment of the trees.
- Strong defaunation of the seed predator communities can also have a negative impact in the carbon stock potential of tropical forest. In defaunated seed predators communities, rats and small rodents can drastically increase their abundance, producing a higher predation pressure over large-seeded trees.

- We urgently need to incorporate the functional role of animals in forest conservation programs. The extirpation of large frugivores can produce economic impacts in the carbon budget of tropical forest. Therefore, programs such as REDD+ need to protect large animals to guaranty their carbon stock and subsequent climate change mitigation functionality in the long term.
- Forest restoration programs are promoting defaunated ecosystems. Restoration programs bias the forest composition to small-seeded trees and abiotic trees, which will not provide enough food for large animals. Beside this bias produce a detriment in carbon stock potential of the restored forest with a subsequence economic impact in the carbon budget of the restored forest.

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**CHAPTER 1. ATLANTIC FRUGIVORY. A PLANT–FRUGIVORE INTERACTION
DATA SET FOR THE ATLANTIC FOREST**

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Data Papers

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Atlantic frugivory: a plant–frugivore interaction data set for the Atlantic Forest

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Abstract. The data set provided here includes 8,320 frugivory interactions (records of pairwise interactions between plant and frugivore species) reported for the Atlantic Forest. The data set includes interactions between 331 vertebrate species (232 birds, 90 mammals, 5 fishes, 1 amphibian, and 3 reptiles) and 788 plant species. We also present information on traits directly related to the frugivory process (endozoochory), such as the size of fruits and seeds and the body mass and gape size of frugivores. Data were extracted from 166 published and unpublished sources spanning from 1961 to 2016. While this is probably the most comprehensive data set available for a tropical ecosystem, it is arguably taxonomically and geographically biased. The plant families better represented are Melastomataceae, Myrtaceae, Moraceae, Urticaceae, and Solanaceae. *Myrsine coriacea*, *Alchornea glandulosa*, *Cecropia pachystachya*, and *Trema micrantha* are the plant species with the most animal dispersers (83, 76, 76, and 74 species, respectively). Among the animal taxa, the highest number of interactions is reported for birds (3,883) followed by mammals (1,315). The woolly spider monkey or muriqui, *Brachyteles arachnoides*, and Rufous-bellied Thrush, *Turdus rufiventris*, are the frugivores with the most diverse fruit diets (137 and 121 plants species, respectively). The most important general patterns that we note are that larger seeded plant species (>12 mm) are mainly eaten by terrestrial mammals (rodents, ungulates, primates, and carnivores) and that birds are the main consumers of fruits with a high concentration of lipids. Our data set is geographically biased, with most interactions recorded for the southeast Atlantic Forest.

Key words: Atlantic Forest; frugivores; frugivory; fruit traits; mutualism; network; plant–animal interaction; seed dispersal.

The complete data sets corresponding to abstracts published in the Data Papers section in the journal are published electronically as Supporting Information in the online version of this article at <http://onlinelibrary.wiley.com/doi/10.1002/ecy.1818/supinfo>.

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ATLANTIC-FRUGIVORY: A PLANT-FRUGIVORE INTERACTION DATASET FOR THE ATLANTIC FOREST

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INTRODUCTION

Seed dispersal by animals is a crucial ecological process that has shaped the co-evolution of animals and plants for at least 80 My (Eriksson 2014). In tropical forests, plant-frugivore interactions are an ubiquitous component of biodiversity, where 70 to 94% of the woody plant species produce fleshy fruits that are both consumed and dispersed by animals (Howe and Smallwood 1982; Almeida-Neto et al. 2008; Jordano 2013). Moreover, most animals in tropical regions depend on fruits as a food source in some extent during their lifetime span (Fleming et al. 1987; Kissling et al. 2009), with intensive frugivory in many cases or during critical periods of their annual cycle (Wheelwright 1983).

Habitat loss, fragmentation, defaunation, and climate change may lead to critical changes in both frugivore and plant assemblages (Mokany et al. 2014; Morante-Filho et al. 2015; Neuschulz et al. 2016). The decline in frugivore populations affects the ecosystem functionality because it leads to a decline in seed removal rates (Pizo 1997), dispersal distances (Donatti et al. 2009), and survival probability (Rother et al. 2016). Therefore it can induce rapid evolutionary changes in seed size (Galetti et al. 2013), disrupt gene flow (Carvalho et al. 2016), and ultimately, affect key ecosystem services such as carbon storage (Bello et al. 2015; Peres et al. 2016).

These negative effects are becoming increasingly common in degraded tropical ecosystems (Arroyo-Rodríguez et al. 2015). For example, the Atlantic Forest, which is a hotspot of biodiversity (Morellato and Haddad 2000; Joly et al. 2014), has been highly threatened by forest fragmentation and overexploitation of its natural resources. Currently 80% of the Atlantic Forest fragments have less than 50 ha, and almost half of these forest remnants are composed mainly by edged and are highly defaunated areas (Ribeiro et al. 2009; Jorge et al. 2013). In this biome, frugivory plays an important role as up to 89% of the woody plants rely on animals to be dispersed (Almeida-Neto et al. 2008). Thus, the widespread defaunation and consequent changes in seed dispersal will likely affect the functionality of several ecosystem services (Banks-Leite et al. 2014; Dirzo et al. 2014).

The rapid frugivore decline creates an urgent need to understand the links that maintain seed dispersal processes and ecosystem services in the Atlantic Forest before further diversity is lost. To approach this need, we have created the ATLANTIC

dataset. This dataset is a compilation of 8320 frugivory interactions reported for the Atlantic Forest of Brazil. It includes interactions among 331 vertebrate species and 788 plant species. The records are from plant-frugivore interactions where fruit consumption and handling may end up as actual consumption of the seed and posterior seed dispersal for the plant (endozoochory). In addition, we present some functional traits important to understand frugivore process, i.e. fruit and seed size, fruit color, frugivore's body mass and gape size (Levey 1987).

METADATA

CLASS I. DATA SET DESCRIPTORS

A. Data set identity:

Title: ATLANTIC-FRUGIVORY. A plant-frugivore dataset for the Atlantic Forest

B. Data set and metadata identification codes:

Suggested Data Set Identity Codes: ATLANTIC-frugivory.csv

C. Data set description

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Abstract: The dataset provided here includes 8320 frugivory interactions (records of pairwise interactions between plant and frugivore species) reported for the Atlantic Forest. The dataset includes interactions between 331 vertebrate species (232 birds, 90 mammals, five fishes, one amphibian and three reptiles) and 788 plant species. We also present information on traits directly related to the frugivory process (endozoochory), such as the size of fruits and seeds and the body mass and gape size of frugivores. Data were extracted from 166 published and unpublished sources spanning from 1961 to 2016. While this is probably the most comprehensive dataset available for a tropical ecosystem, it is arguably taxonomically and geographically biased. The plant families better represented are Melastomataceae, Myrtaceae, Moraceae, Urticaceae and Solanaceae. *Myrsine coriacea*, *Alchornea glandulosa*, *Cecropia pachystachya*, and *Tremam micrantha* are the plant species with the most animal dispersers (83, 76, 76 and 74 species, respectively). Among the animal taxa, the highest number of interactions is reported for birds (3883), followed by mammals (1315). The woolly spider monkey or muriqui, *Brachyteles arachnoides*, and rufous-bellied thrush, *Turdus rufiventris*, are the frugivores with the most diverse fruit diets (137 and 121 plants species, respectively). The most important general patterns that we note are that larger seeded plant species (>12 mm) are mainly eaten by terrestrial mammals (rodents, ungulates, primates and carnivores) and that birds are the main consumers of fruits with a high concentration of lipids. Our dataset is geographically biased, with most interactions recorded for the southeast Atlantic Forest.

D. Key words: *Frugivory, Atlantic Forest, Plant-animal interaction, Fruit traits, Seed dispersal, Frugivores, Mutualism, Network.*

E. Description: The dataset includes 8320 plant-frugivore interactions involving 788 plant species and 331 frugivore species reported in 166 studies; however, some interactions are reported in more than one study in different locations, so in total there are 5240 unique interactions. Here, we present only the occurrence of fruit consumption events, excluding pulp consumption and seed predation interactions (Galetti 1993; Pizo et al. 1995). In addition, we do not record the strength of the interactions, so inferences about the frequency of an interaction or its actual outcome (i.e., whether the interaction resulted in successful seed dispersal and establishment) should not be made.

The dataset is restricted to the Atlantic Forest domain (Joly et al. 2014) but is mostly concentrated in the southeast of the Atlantic Forest (Figure 1). It includes 232 birds, 90 mammals, five fish, three reptiles and one amphibian interacting with 788 species of plants. The included plants are predominantly trees (68.2% of the species) and shrubs (21.5%), but palms (4%), lianas (3.1%), and epiphytes, herbs and parasites (<3%) are also present.

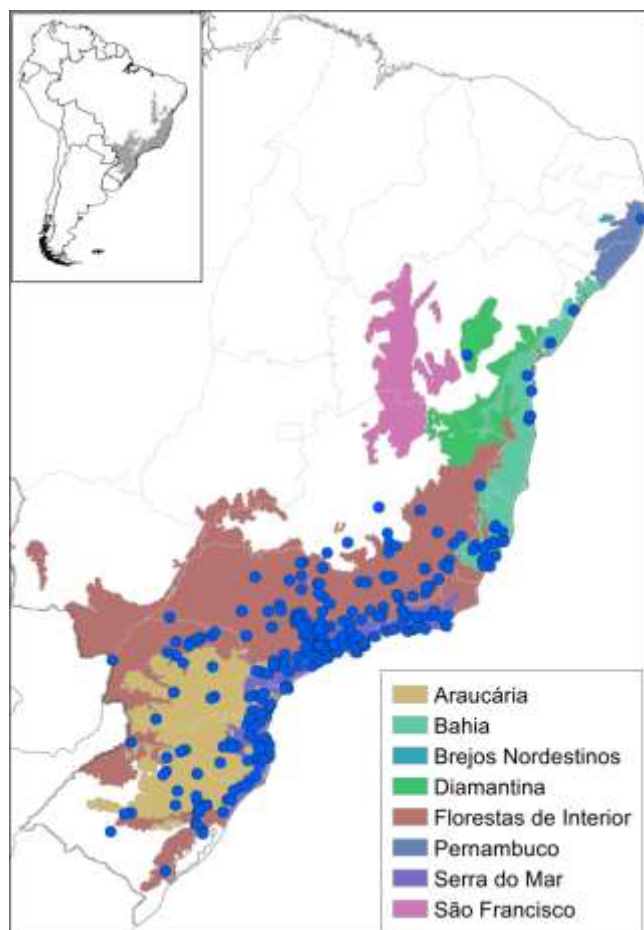


Figure 1. Distribution of the plant-frugivore interaction records according to the Bioregions of the Atlantic Forest biome. The colors show the domain of the Atlantic Forest classified to bioregions according to the map of (Olson et al. 2001). The dots show the locations of the original studies reporting plant-frugivore interactions. Light gray lines show the states of Brazil.

We found that in average each frugivore interacts with $15.8 (\pm 22.4)$ plant species, while each plant interacts with $6.6 (\pm 10.7)$ frugivore species. The plant families with most of the interactions are Melastomataceae (623 interactions), Myrtaceae (448 interactions), Moraceae (344 interactions), Urticaceae (228 interactions) and Solanaceae (214 interactions). *Myrsinecoriacea*, *Alchorneaglandulosa*, *Cecropiapachystachya*, and *Tremamicrantha* are the plant species with the greatest number of dispersers (83, 76, 76 and 74, respectively). *Euterpe edulis* is the most cited species in the frugivory studies (367 times), but it only interacts with 54 species of frugivores (Figure 2).

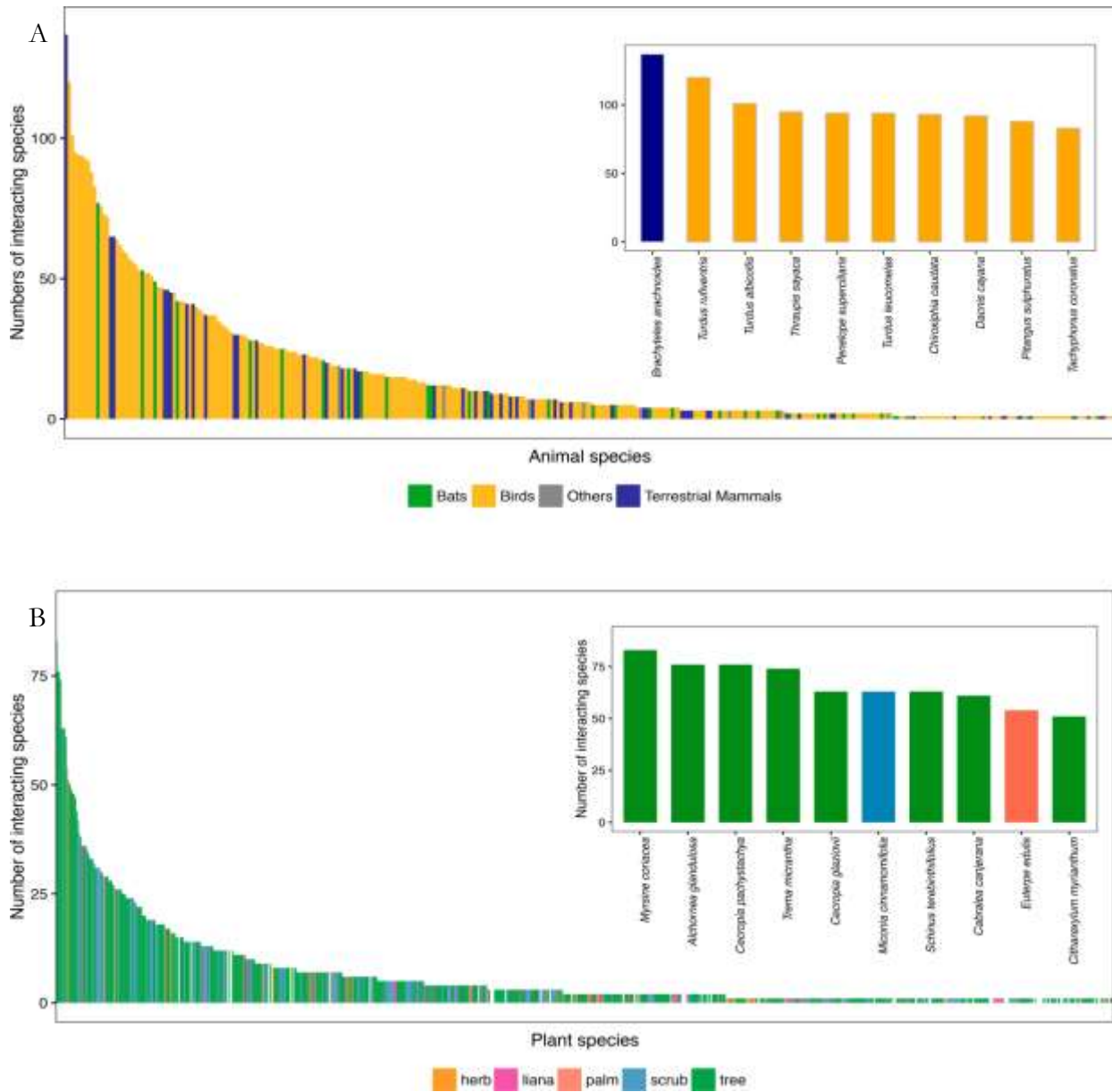


Figure 2. Rank plots of the number of interacting species for each species of animal (A) and plant (B). In the right corner, we show the top-ten species with the highest number of interactions. Animals are colored according to the main group they belong to: bats (green), birds (yellow), terrestrial mammals (primates, ungulates, rodents, carnivores, marsupials; blue), and others (gray). Plants are colored according to growth form: herbs (orange), lianas (purple), palms (pink), shrubs (blue), and trees (green).

Most of the interactions have been reported for birds (3883), followed by mammals (1315). The woolly spider monkey or muriqui, *Brachyteles arachnoides*, and the rufous-bellied thrush, *Turdus rufiventris*, are the animal species with the most diverse diets (137 and 121 plant species recorded, respectively) (Figure 2). The Atlantic Forest is a biome where all classes of vertebrates have been reported eating fruits, even amphibians.

Although several species of lizards and fish have been reported to eat fruits in the Atlantic Forest, most of these studies do not identify the plant species and, therefore, these information sources were not included here.

The dataset includes trait information for most of the animal and plants species (Table 1). Regarding those traits that are known to mediate frugivory interactions and their immediate consequences (Levey 1987; Dehling et al. 2016), we report fruit- and seed-related traits for almost half of the plant species (Table 1) and body mass and mean gape size for 98% and 58% of the animal species, respectively. The correlations between the numerical trait of animal and plant species that can be expected to limit a frugivory event through physical constraints were positive and significant but not very strong (*seed diameter*: body size $r = 0.22$, $p < 0.01$, gape size $r = 0.13$ $p < 0.01$; *fruit diameter*: body size $r = 0.34$, $p < 0.01$, gape size $r = 0.23$, $p < 0.01$).

Table 1. Summary of the trait information presented in the ATLANTIC dataset. For each trait we show the number of species for which the trait is recorded (No spp. with info), the percentage of knowledge of each trait (No of spp. with information/Number of all plants/animal species in the dataset). For each metric trait, we show the mean \pm standard deviation (minimum, maximum). For description of the traits, see the variable information section.

	Traits	No spp. with info	% of knowledge	Mean \pm standard deviation (min, max)
PLANTS	Occurrence	754	95.6%	-
	Establishment	752	95.4%	-
	Habit	739	94.0%	-
	Form	749	95.0%	-
	Fruit diameter (mm)	436	55.3%	14.66 \pm 16.2 (1, 150)
	Fruit length (mm)	417	52.9%	21.43 \pm 35.45 (0.4, 405)
	Seed diameter (mm)	361	45.8%	6.4 \pm 5.91 (0.01, 37.1)
	Seed length (mm)	304	38.6%	11.46 \pm 9.1 (0.4, 61.4)
	Fruit color	704	89.3%	-
	Lipid score	787	99.8%	-
	Presence in IUCN list	164	20.8%	-
ANIMALS	Body mass (g)	322	97.2%	1596.19 \pm 14987.15 (6, 260000)
	Mean gape size (mm)	190	57.4%	12.26 \pm 9.94 (28, 123.3)
	Frugivory score	312	94.25%	-
	Migration	171	51.6%	-

Presence in IUCN list	325	98.1%	-
Population trend	299	90.3%	-

The dataset also includes 12 exotic plant species, nine cultivated species, 24 naturalized species and 14 invasive species. In terms of conservation status, 9% of the reported animal species and 3.5% of the plant species are listed under some category of threat according to the IUCN (Table 2). Among the frugivore species, 115 are classified as having populations in decline, whereas only 29 are classified as increasing its population size.

Table 2. IUCN conservation status of animals and plants species reported in the ATLANTIC dataset.

	Animals	Plants
Critically endangered (CR)	5	3
Endangered (EN)	10	11
Vulnerable (VU)	10	11
Near Threatened (NT)	19	8
Least Concern (LC)	277	131
Data Deficient (DD)	4	3
Not evaluated (NE)	6	624

The most common fruit colors are black (32%) and red (16%), whereas other fruit colors include blue and pink. Small birds are mostly associated with red fruits, bats with green fruits whilst primates and large birds eat fruits of any color (Figure 3).

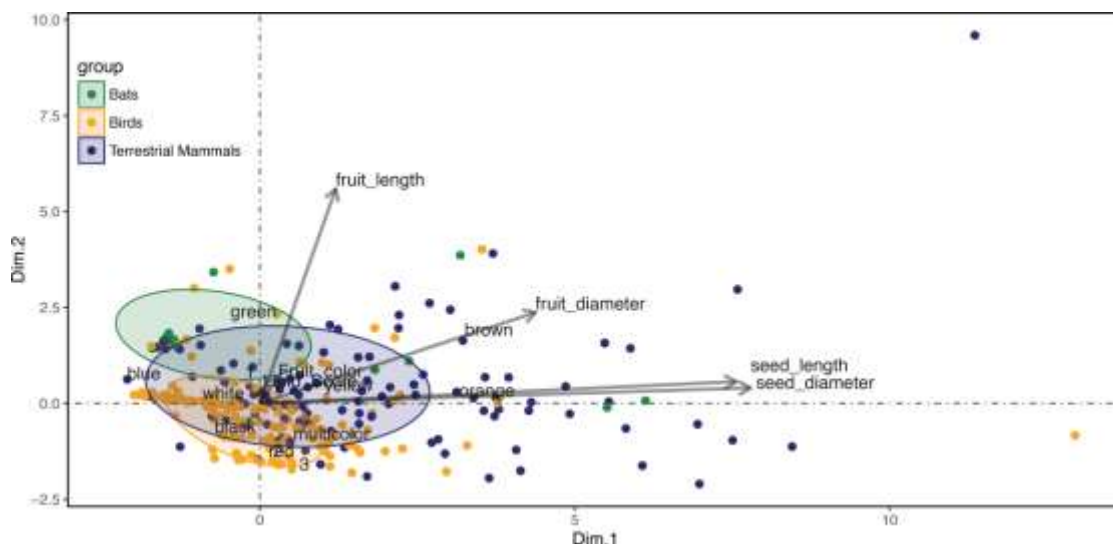


Figure 3. Factor analysis relating plant traits to animal groups. Plant traits included are seed diameter (seeddiam), seed length (seedlen), fruit diameter (fdiam), fruit length (flen), lipid concentration (Lipid_Score) and fruit color. The equiprobability ellipses include 80% of the plant species eaten by each group of animals. Arrows represent the relative magnitude of correlation of the main variables (amplified 10 times for graphical purposes) with the first two axes of the ordination. Large-seeded plant species are mostly located on the right-hand side of the plot and plants with large fruits are mostly located on the top of the plot.

We identify that ungulates, rodents, carnivores and primates are the main consumers of fruits with large seeds (Figure 3). Fruits with small seeds are more likely to be consumed by more frugivores than fruits with large seeds (Figure 4). Most of the fruits consumed by frugivores have a low lipid concentration, but birds and rodents are associated with lipid-rich fruits (Figure 5a). Frugivorous bats and rodents as well as large birds were the groups including the largest proportions of animal species with a high dependency on fruits, and they thus potentially perform a major role in seed dispersal (Figure 5b).

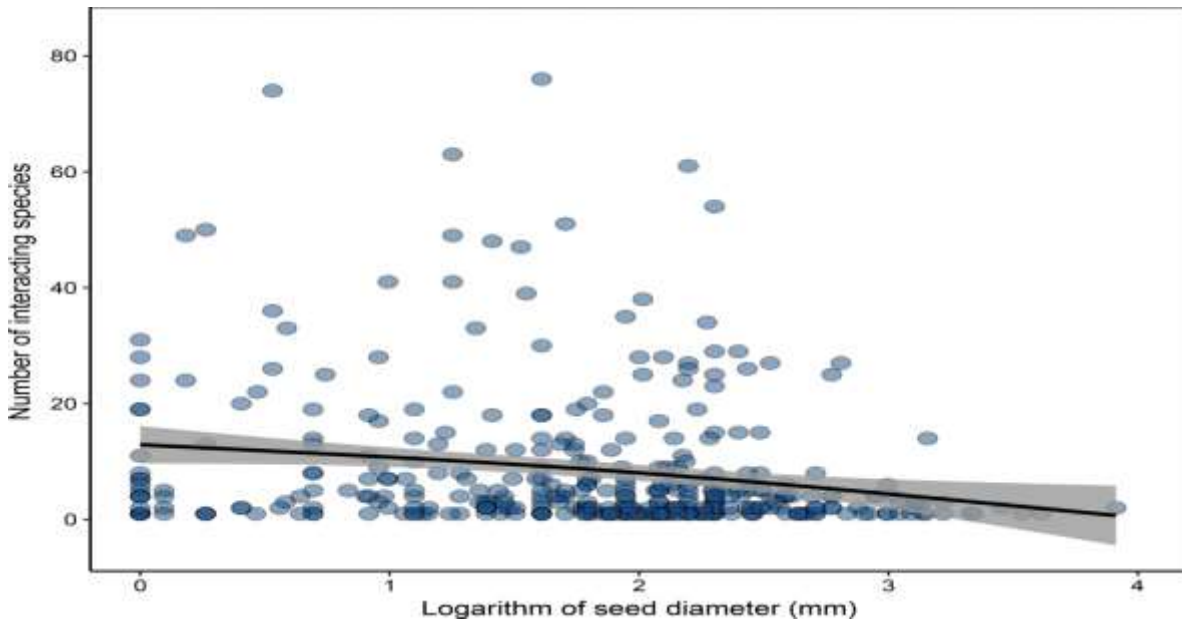


Figure 4. Relationship between seed diameter and the number of animal frugivore species recorded in interactions. Each point represents a plant species. The black line shows a non-parametric smoothing fit of the relation; the gray zone is the 95% interval of confidence.

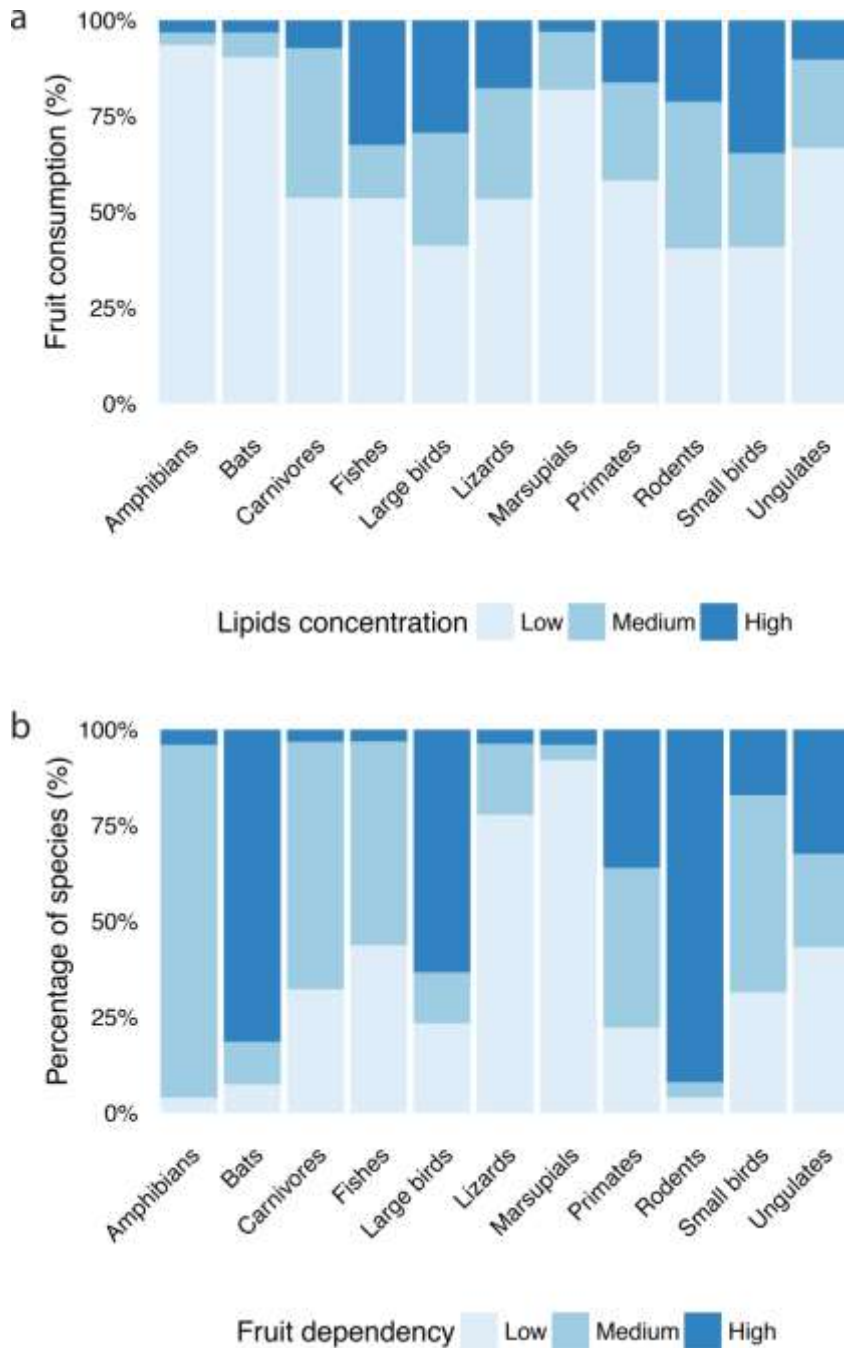


Figure 5. The lipid concentration of fruits consumed and the level of specialization to frugivory by each frugivore group. Panel a) shows the proportion of fruits consumed with low (0-10%), medium (10-20%) or high (>20%) lipid concentration for each frugivore group, where the percentages are relative to pulp dry mass. Panel b) shows the proportion of species for which the level of reliance on fruit in the diets is low (occasional consumer), medium (frequent consumer, but also consuming other kind of food) or high (strict frugivore) for each frugivore group.

The data have a geographical bias due to the variation in research effort across the Atlantic Forest bioregions (Figure 1). Geographical information is available for 62% of the

interactions reported. Most of the locations are concentrated in the southeast of the Atlantic Forest mainly in the State of São Paulo (n= 3263, 60%) and Rio de Janeiro (n= 475, 8%). Among the bioregions, the Serra do Mar domain contains the largest amount of interactions (n= 2358, 45%), followed by the seasonal-semideciduous forests of Florestas de Interior (n= 2043, 39%). The dataset includes no information for the São Francisco bioregion.

CLASS II. RESEARCH ORIGIN DESCRIPTORS

A. Overall project description

Identity: A compilation of plant-frugivore interaction records reported for the Atlantic Forest.

Period of study: Dates of source publications range from 1961–2016.

Objectives: Our objectives for compiling the data for this Data Paper were to (1) summarize information on pairwise interactions between plant and animal species for fruit consumption in the Atlantic Forest biome and provide basic information on species traits, and (2) identify major patterns in the reported interactions and identify knowledge gaps to guide future sampling efforts. Our dataset represents a first attempt to obtain a large-scale catalogue of ecological interactions with application in macro-ecological studies of diversity patterns. The dataset can also be used as a reference baseline for studies of Atlantic Forest restoration, for the assessment of global change effects (e.g., forest fragmentation) and for future documentation of the interaction component of biodiversity over large spatial scales.

Abstract: Same as above.

Sources of funding: The compilation of this dataset was supported by the São Paulo Research Foundation (FAPESP) (Grant n° 2013/50421-2, 2013/22492-2, 2014/01986-0, 2014/50434-0, 2015/23770-1, 2015/19092-8, 2015/18381-6 and 2015/15172-7). MG and MAP received a research grant from the Brazilian Research Council (DUP-SCM-MCT/CNPq). OO was supported by funding from the Academy of Finland (grant 273253 and CoE grant 284601) and the Research Council of Norway (CoE grant 223257). PJ was supported by a Junta de Andalucía Excellence Grant (RNM-5731) as well as a Severo Ochoa Excellence Award (Spanish Min. Econ. Comp., SEV-2012-0262).

B. Specific subproject description

Site description: The Atlantic Forest is an important biodiversity hotspot (Galindo-Leal and Camara 2003). It comprises tropical and subtropical forests with highly heterogeneous environmental conditions. It supports up to 8% of the world's total species richness and has one of the highest rates of endemism in the world (Morellato and Haddad 2000; Joly et al. 2014). The Atlantic Forest supports at least 15,519 plant species (3343 trees) (BFG 2015), 891 bird species (Moreira-Lima 2014), 543 amphibians (Haddad et al. 2013), 200 reptiles, 350 fishes (Ministério do Meio Ambiente 2010), and 298 mammals (Paglia et al. 2012). In addition, seed dispersal by vertebrates plays an important role in this biome, with 89% of all woody species depending on animals for their dispersal (Almeida-Neto et al. 2008).

Seventy-two percent of the Brazilian population lives in former areas of the Atlantic Forest domain (~145 million people) (IBGE 2013). Therefore, many past and present economic activities such as logging, sugarcane and coffee farming, agribusiness, industrialization and unplanned urban expansion have contributed to the deterioration of the ecosystem (Dean 1996). Currently, conservation of the Atlantic Forest is critical, with the natural remnants accounting for only 12% of the original biome and over 80% of these remnants occurring as < 50 ha fragments (Ribeiro et al. 2009). Of the remaining forest, 88% of the fragments are defaunated of large mammals (Jorge et al. 2013).

Experimental/Sampling design: The data were obtained from the published literature, including 166 papers, theses, scientific conference abstracts, technical reports, and photos on web sites (Wikiaves: <http://www.wikiaves.com.br/>), and our own unpublished observations. We searched for potential studies in the following sources: (i) online academic databases (e.g., ISI Web of Knowledge, Google Scholar, Scielo, Scopus, JStor), (ii) digital libraries of state and federal universities, (iii) references cited in “gray” literature, and (iv) email contacts with local experts. The terms used to search the online databases were “frugivorous”, “seed dispersal”, “diet”, “frugivore networks”, “focal observation” and “Atlantic Forest”, which were combined in different ways using Boolean operators. Searches were conducted in English, Portuguese and Spanish.

Research methods: We included animal-oriented and plant-oriented studies that reported the occurrence of interactions (i.e., a particular animal species feeding on fruits of a particular plant species or analyses of the diet of a particular animal species). The records in which seed damage and/or seed predation was reported were carefully removed in order to maintain only fruit consumption events with potential for legitimate seed dispersal. However, some events that did not report detailed information can be found across a broad gradient covering the range from fully antagonistic interactions (e.g., pulp consumption with seeds being dropped to the ground) to mutualistic interactions (e.g., fruit/seed handling leading to legitimate seed dispersal). Overall, the records reflect instances of pairwise interactions between plants and animals in which successful endozoochorous seed dispersal might be expected.

We also included information from interaction network studies, which recorded an entire interaction network for a specific location. From these interactions, we recorded plant and animal taxonomy and compiled for each species the traits that can affect the interaction (i.e., size of fruit, gape size, fruit color, body mass). Trait data were extracted from the literature and our own measurements using herbarium and museum specimens. In addition, we recorded basic information from each study (author, title, year, journal, volume, publisher and the link or DOI to the document) and the geographical location when provided (latitude, longitude, locality, municipality and state).

Frugivory interactions were compiled from (Carvalho 1961; Silva 1988; Bonvicino 1989; Silva et al. 1989; Brozek 1991; Motta-Jr 1991; Galetti 1992; Moraes 1992; Rodrigues et al. 1993; Chiarello 1994; Figueira et al. 1994; Galetti and Morellato 1994; Hasui 1994; de Figueiredo and Perin 1995; Masteguin and Figueiredo 1995; Ferrari et al. 1996; Galetti and Pizo 1996; Kindel 1996; Laps 1996; Pizo 1996; Zimmerman 1996; Galetti et al. 1997; Heiduck 1997; Correia 1997; Argel de Oliveira 1999; Sabino and Sazima 1999; Galetti et al.

2000;Lopes 2000;da Costa Gondim 2001;Galetti 2001;Silva and Tabarelli 2001;Valente 2001;Zimmermann 2001;Alvarenga 2002;Cazetta et al. 2002;Guerra and Marini 2002;Mikich 2002a,b;Pizo et al. 2002;Silva et al. 2002;Zimmermann et al. 2002;Aguilar et al. 2003;Castro 2003;Côrtes 2003;Guimarães 2003;Manhães 2003;Manhaes et al. 2003;Passos et al. 2003;Scheibler and Melo-Júnior 2003;Vieiralves Linhares 2003;Alves-Costa et al. 2004;Augusto and Hayashi 2004;Castro and Galetti 2004;Fadini and De Marco 2004;Gridi-Papp et al. 2004;Pimentel and Tabarelli 2004;Pizo 2004;da Rosa and Marcondes-Machado. 2005;Rocha 2005;Silva 2005;Casella and Cáceres 2006;Da Silva and De Britto-Pereira 2006;Faustino and Machado 2006;Krügel et al. 2006;Muller 2006;Pascotto 2006;Pinto and Filho 2006;Zaca et al. 2006;Amaral 2007;Castro 2007;Jesus and Monteiro-Filho 2007;Pascotto 2007;Piccoli et al. 2007;Scherer et al. 2007;Silva et al. 2007;Alves 2008;de Freitas et al. 2008;Galetti et al. 2008;Izar 2008;Keuroghlian and Eaton 2008;Lapenta et al. 2008;Marques and Oliveira 2008;Alves et al. 2009;Athiê 2009;Catenacci et al. 2009;Cortes et al. 2009;Lapate 2009;Novaes and Nobre 2009;Oprea et al. 2009;Parrini et al. 2009;Reys et al. 2009;Vasconcellos-Neto et al. 2009;Brito et al. 2010;Bueno 2010;da Silva 2010;Hilário and Ferrari 2010;Martinelli and Volpi 2010;Morim Novaes et al. 2010;Parrini and Raposo 2010;Rabello et al. 2010;Ribeiro et al. 2010;Rother 2010;Andrade et al. 2011;Cardoso et al. 2011;Caselli and Setz 2011;Colussi 2011;Parrini and Pacheco 2011a;Parrini and Pacheco 2011b;Silva 2011;Weber et al. 2011;Alves 2012;Bredt et al. 2012;Mileri et al. 2012;Pires and Galetti 2012;Sartore and Reis 2012;Vilela et al. 2012;Bueno et al. 2013;Felix et al. 2013;Galetti et al. 2013;Ikuta and de Campos Martins 2013;O'Farrill et al. 2013;Silva et al. 2013;Camargo 2014;Cid et al. 2014;Figueira et al. 2014;Parrini and Pacheco 2014;de A. Moura et al. 2015;Gonçalves and Andrade 2015;Hernández-Montero et al. 2015;Robinson 2015;Rodrigues 2015;Bufalo et al. 2016) and our own observations.

Taxonomic data: We used plant taxonomic information according to the Flora(REFLORA 2014) for the plant species and the Catalog of Life (COL) (Roskov et al. 2015) for the animal species.

Plant traits: We focused on compiling information on those plant traits that are known to affect the success of frugivorous interactions and their potential outcomes for successful seed dispersal (fruit and seed length and diameter, plant geographical distribution, seed dispersal syndrome, fruit color, lipid concentration). We compiled this information from the literature(Martius et al. 1840-1906;Mez 1963;Cowan 1967;Berg 1972;Prance 1972;Rogers and Appan 1973;Landrum 1981;Pennington et al. 1981;Kaastra 1982;Kubitzki and Renner 1982;Forero 1983;Lima and Lima 1984;Sleumer 1984;Hopkins 1986;Landrum 1986;Hekking 1988;Mori et al. 1990;Pennington 1990;Gentry 1992;Rohwer 1993;Delprete 1999;Henderson 2000;Knapp 2002)(Acevedo-Rodríguez 2003;Maas and Westra 2003;Maas et al. 2003;Madriñán 2004;Melo and Zickel 2004;Secco 2004;Mendonça-Souza 2006;de Moraes 2007;Grokovski 2007;Marquete and Vaz 2007;Prance et al. 2007;Smith and Coile 2007;Almeida-Neto et al. 2008;Silva et al. 2008;Camargo et al. 2009;Lorenzi 2009;Boeira 2010;Moreira et al. 2010;Staggemeier et al. 2010;Alves-Araujo 2012;Dutra et al. 2012;Lobão et al. 2012;Mello-Silva et al. 2012;Rodrigues 2012;Santos 2012;Fabris and

Peixoto 2013;Silva et al. 2013;CRIA 2014) and our own measurements in herbarium and private collections.

Animal traits.We compiled data on animal traits that are considered important for determining the effectiveness of frugivory, particularly mean gape size and body mass. We compiled this information from the literature (Gardner 1962;Davis 1976;Taddei and Reis 1980;Motta-Jr 1991;Hoyo et al. 1994;Argel de Oliveira 1999;Navas and Bó 2001;Dias et al. 2002;Velazco 2005;Zortéa and Tomaz 2006;Bonaccorso et al. 2007;Capusso 2007;Fonseca and Antunes 2007;Dias and Peracchi 2008;Fialho 2009;Marciente and Calouro 2009;Mottin 2011;Paglia et al. 2012;Reis et al. 2013;Louzada et al. 2015;Moratelli R 2015;Vilar et al. 2015) and our own measurements from specimens in museums (Museu de Zoologia de São Paulo-MZUSP and MuseuParaense Emilio Goeldi, Belém). Fruit dependency were obtained according to (Paglia et al. 2012) and expert knowledge.

Statistical analysis.We provide some preliminary, descriptive statistical analyses for an overview of the data. We used Pearson correlations, with the logarithmic transformation of the numerical traits, among variables that can limit the ingestion of the fruit (seed diameter, fruit diameter, body size, gape size). To explore the type of fruit eaten by each group of animals we performed a factor analysis with mixed data using the function FAMD from the package FactoMineR(Lê et al. 2008) in R. We included fruit diameter, fruit length, seed diameter, seed length, fruit color and the lipid score as analysis variables. The continuous variables were transformed and scaled to unit variance, and the categorical variables were transformed into a disjunctive data table (crisp coding) and then scaled using the specific scaling of MCA. We used the type of animal as a supplemental variable, with animal species classified into groups according to the taxonomic order level. For birds, we divided species into small (body mass < 80 g and gape size <12 mm) and large categories (body mass > 80 g and gape size >12 mm) according to (Galetti et al. 2013). We also explored the relationship between seed size (logarithmic transformation) and the number of frugivore species interacting using non-parametric smoothing. Finally, to assess the completeness of the interaction data coverage, we performed an accumulation curve analysis of the number of interactions reported as a function of the number of studies included (Jordano 2016).

C. Data limitations and potential enhancements

We recognize that documenting all frugivory interactions in a megadiverse ecosystem is a challenging task and that the present dataset is likely to include only a subset of those interactions. Therefore, caution is needed when drawing conclusions from this dataset. Biased data can lead to misidentification of ecological and evolutionary processes and the inefficient use of limited conservation resources (Hortal et al. 2015;Jordano 2016).

The first limitation of our data is its representativeness. Our dataset is arguably biased toward trees and shrubs, whereas interactions with many herbs, epiphytes and lianas are likely to be underrepresented. The dataset has a somewhat better representation of mammals known to eat fruits (e.g., primates) and birds. However, neither of these groups are comprehensively represented, as the data include 27.1% of the birds and 30.1% of the

mammals reported for the Atlantic Forest (58% if we account only for the mammalian fruit-eaters) ((Paglia et al. 2012;Moreira-Lima 2014); Table 3).

Table 3. Representativeness of our database in relation to the species known to occur in Atlantic Forest. Number of species reported for each class was obtained from literature: Aves (Moreira-Lima 2014), Amphibia, Reptilia and Actinopterygii (Ministério do Meio Ambiente 2010), Mammalia (Paglia et al. 2012). For mammals and birds, we show the total number of species that are known to eat fruits (Frugivorous species and Omnivorous species).

Class	Order	Number of species in the Atlantic Forest		Number of species in our dataset
		All Species	Frugivores and Omnivorous	
AVES		891		242
AMPHIBIA		543		1
REPTILIA		200		3
ACTINOPTERYGII		350		5
MAMMALIA		291		92
MAMMALIA	Artiodactyla	6	6	3
	Carnivora	20	8	8
	Chiroptera	113	23	36
	Didelphimorphia	22	15	12
	Perissodactyla	1	1	1
	Primates	24	24	23
	Rodentia	98	74	7
	Cingulata	7	4	0
AVES	Accipitriformes	41	0	1
	Columbiformes	17	5	8
	Coraciiformes	7	2	1
	Craciformes	9	9	6
	Cuculiformes	11	0	4
	Falconiformes	14	0	1
	Gruiformes	25	0	1
	Passeriformes	476	147	187
	Piciformes	36	17	17
	Trogoniformes	5	5	4

Some interactions are missing due to the lack of detailed studies including the taxonomic identification of the plant species eaten. For example, some species of fish, amphibians and reptilians with well-studied diets are reported to eat “vegetable matter”

(e.g., *Tropidurus*, *Mabuya*, *Brycon*) but may in fact be eating and actually dispersing seeds (Valido and Olesen 2007; Correa et al. 2015). However, as no taxonomic information is provided concerning the plant species, we did not report these interactions here. Two tortoise species that occur in the Atlantic Forest (*Chelonoidis carbonaria* and *C. denticulatus*) are known to be important seed dispersers (Strong and Fragoso 2006), but we did not find any frugivory information for the Atlantic Forest.

Our dataset lacks information on secondary seed dispersers. For example, ants are well known to be important seed dispersers in the Atlantic Forest (Pizo and Oliveira 2000; Passos and Oliveira 2002; Christianini and Oliveira 2009; Bieber et al. 2013), and other invertebrates may act as secondary seed dispersers as well (e.g., dung beetles; (Culot et al. 2013)). However, these interactions remain poorly studied and were not included in this dataset. Secondary dispersal by small mammals, raptors and parrots has been occasionally reported (Galetti and Guimaraes Jr 2004; Sazima 2008; Tella et al. 2016), but its information is poorly represented here. Only one invasive mammal species (wild boar, *Sus scrofa*) has been recorded eating fruits (F. Pedrosa et al., unpublished data).

Among the birds, we found that Passeriformes compose the majority of the interactions. The only Trogon species that is not represented in the dataset is *Trogon collaris*. Interestingly, we found some occasional interactions of species of the orders Accipitriformes, Columbiformes, Cuculiformes, Falconiformes and Gruiformes, that are not supposed to eat fruits (Table 3).

For the mammals, our dataset is positively biased towards primates. Only one of the 24 primate species reported for the Atlantic Forest has no data (*Callicebus personatus*). Other orders (e.g., Carnivora, Perissodactyla and Artiodactyla) are well represented, but the ruminants (Ruminantia suborder, Artiodactyla) have been less studied. It is important to mention that the carnivores are well represented in the dataset (Table 3). Of the eight omnivorous carnivores that frequently feed on fruits, we have information for five species (*Cerdocyon thous*, *Eira barbara*, *Lycalopex gymnocercus*, *Nasua nasua*, *Procyon cancrivorus*) but no information for *Potos flavus*, *Conepatus semistriatus*, or *Conepatus chinga*. Notwithstanding, the dataset contains information on frugivorous interactions of carnivores that are not recognized as fruit-eaters (*Leopardus tigrinus*, *Leopardus wiedii*, *Puma concolor*) or secondary seed dispersers (Sarasola et al. 2016). We also note that the role of Cingulata (*Dasypus hybridus*, *Dasypus novemcinctus*, *Dasypus septemcinctus* and *Euphractus sexcinctus*) as frugivores is completely missed in our dataset, although they have been recorded as sporadic fruit eaters elsewhere (Dalponte and Tavares-Filho 2004).

We recorded 32% of all bat species reported for the Atlantic Forest as frugivorous, including some genera well known as insectivores (e.g., *Noctilio*, *Trachops*) (Table 3), showing that, in general, bats can eat fruits more often than expected. Therefore, more efforts should be made to assess the compensatory role of bats when large frugivores are extirpated (Melo et al. 2007; Melo et al. 2009). The taxonomic bias in research imposes some limitations in the analysis of frugivory-related processes (Hortal et al. 2015). For instance, the lack of information for some groups can seriously limit our understanding of

compensation effects in the ecological process of animal-mediated dispersal under the current disturbance scenarios in the Atlantic Forest (Bueno et al. 2013).

An additional important limitation is the number of interactions reported. Although the database characterizes the main diet of frugivores, it does not contain the entire spectrum of animal diets. Our dataset reports only 2.02% (5232) of all possible interactions that can occur based on 788 plants and 331 animals. A simple interaction-accumulation analysis (with the number of studies used as a proxy for samples) shows that the dataset does not converge to an asymptotic value as would be needed to estimate of the actual number plant-frugivore interactions in the Atlantic Forest system (Figure 6). Therefore, more studies are needed for a comprehensive representation of the interaction network.

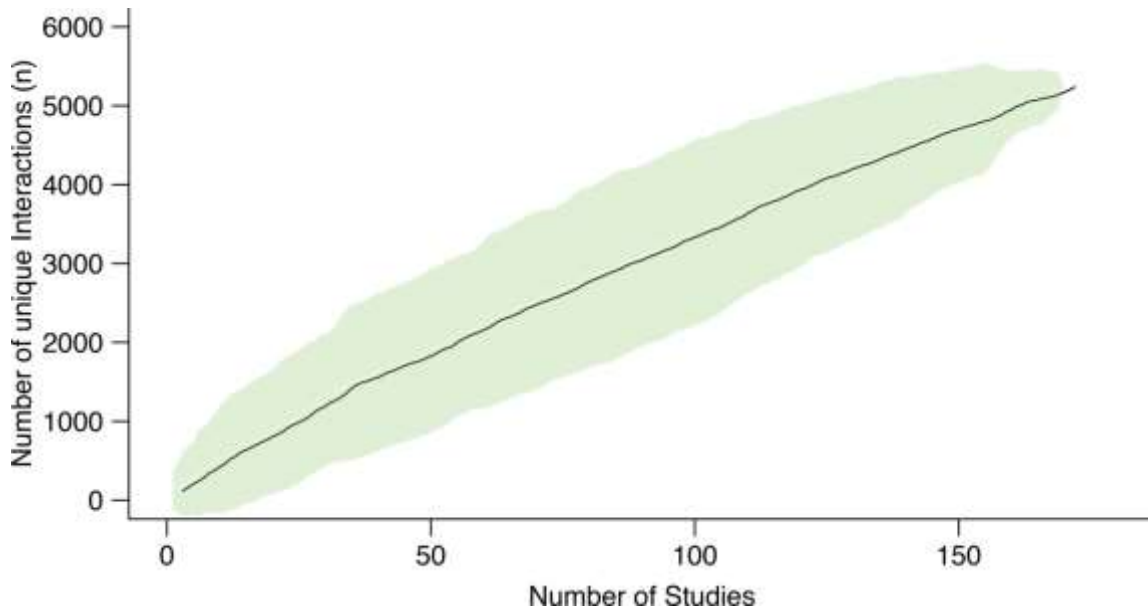


Figure 6. Number of interactions reported as a function of the number of studies included. The figure shows an accumulation analysis performed similarly as species diversity accumulation curve analysis (Jordano 2016). Here we considered each pairwise-interaction as a “species” and the different studies as sampling units. The mean expected value for 172 studies is 5151 distinct pairwise interactions; however, as the curve does not reach an asymptote, many more interactions can be expected to be found by further studies. Black line shows the mean estimate and the green shadow shows the 95% confidence interval around the estimate.

Recognizing all the above-mentioned limitations allows us to suggest guidelines for future research aimed to overcome these limitations. It is important to fill the gap in knowledge for several groups, such as bats, rodents, reptilians, fish, amphibians, cingulata and ruminants. While these groups are not strict frugivores, they may compensate for or complement the seed dispersal functions provided by large frugivores (Bueno et al. 2013). It is also important to understand the role of non-woody plants in the diets of frugivorous animals, e.g., as lianas and epiphytes can provide important fruit resources. In addition, more efforts are needed to obtain quantitative estimates of all plant-animal interactions in

the complex Atlantic Forest ecosystem. These efforts need to be focused on the local scale in order to help us to understand the effectiveness of seed dispersal processes in more detail (Vidal et al. 2014).

We hope that the compilation of the Atlantic database encourages researchers to explore of the role of frugivorous interactions that shapes the diversity of species-rich assemblages and ecosystem services. Research on the diversity and functionality of animal-plant interactions complements research focused at the species-level. It further enables the study of ecosystem processes, such as how the loss of key interactions influences food-web organization (Valiente-Banuet et al. 2015). Therefore, more research should be conducted to examine the influence of frugivory in shaping the resilience of diversity and ecosystem services in a changing world. It is time to incorporate biotic interactions in the bigger ecological picture to understand resilience to environmental changes (Araújo et al. 2011; Morales-Castilla et al. 2015). Undoubtedly, there is a demand for forecasting the dynamics and functioning of novel ecosystems emerging from differential responses of species to global change (Montoya and Raffaelli 2010; Lessard et al. 2016).

CLASS III. DATA SET STATUS AND ACCESSIBILITY

A. Status

Latest update: October 2016

Latest archive date: October 2016

Metadata status: Last update October 2016, version submitted

Data verification: Data is mostly from published sources. We searched for extreme values, corrected any transcription errors and homogenized the taxonomic information.

B. Accessibility

Contact person: Carolina Belloor Mauro Galetti, Departamento de Ecologia, Universidade Estadual Paulista, Rio Claro, São Paulo, 13506-900, Brazil E-mail: caro.bello58@gmail.com; mgaletti@rc.unesp.br

Download link: <https://github.com/pedroj/ATLANTIC>

Copyright restrictions: None.

Proprietary restrictions: Please cite this data paper when the data are used in publications. We also request that researchers and teachers inform us of how they are using the data.

Costs: None.

CLASS IV. DATA STRUCTURAL DESCRIPTORS

A. Data set file

Identity: ATLANTIC-Frugivory.csv

Size: 8320 records, 3968 KB

Format and storage mode: comma-separated values (.csv)

Header information: See column descriptions in section B.

Alphanumeric attributes: Mixed.

Data anomalies: If no information is available for a given record, this is indicated as 'NA'.

B. Variable information

1) Table 4. Interaction information. Description of the fields related with the interaction reported in the Atlantic Forest.

Type of information	Field	Description	Levels	Example
INTERACTION	Record ID number	Identifier straight pins numbered of the interaction record	1 to 8320	15
	Frugivore_Species	Scientific name of the frugivore		<i>Turdusamauroc halinus</i>
	Plant_Species	Scientific name of the plant		<i>Aegiphilaintegri folia</i>
	Type of Interaction	Describe the type of interaction included in the dataset. Mutualism refers to the act of ingesting the seed.	Mutualism	Mutualism

2) Table 5. Plant information. Description of the fields related with the plant involved in the interaction.

Type of information	Field	Description	Levels	Example
PLANT INFORMATION	Plant_family	Family taxonomic classification		Clusiaceae
	Plant_genus	Genus taxonomic classification		<i>Aegiphila</i>
	Plant_specific.epithet	Specific epithet taxonomic classification		<i>integri folia</i>
	Plant_distribution	Brazilian states in which the plants have been reported	AM; PA; MT; MG; BA; MS...	RJ; BA; MG
	Plant_origin	If the plant is native or introduced in Brazil	Native Naturalized Cultivated Invasive	Native
	fruit_diameter	Diameter in mm of the fruit		20.3
	fruit_length	Length in mm of the fruit		28.2

	seed_diameter	Diameter in mm of the seed		12.3
	seed_length	Length in mm of the seed		15
	Fruit_color	Color of the mature fruit		green
	Lipid_score		1: 0 to 10% of lipid. 2: 10 to 20% of lipid. 3: > 20% of lipid concentration in dry weight.	1
	Plants_IUCN	IUCN Classification for threatened plants	EX: Extinct EW: Extinct in the wild CR: Critically endangered EN: Endangered VU: Vulnerable NT: Near threatened LC: Least concern DD: Data deficient NE: Not evaluated	CR

3) Table 6. Animal information. Description of the fields related with the animal involved in the interaction.

Type of information	Field	Description	Levels	Example
ANIMAL INFORMATION	Frug_Class	Class taxonomic classification	Aves, Mammalia, Amphibia, Reptilia, Actinopterygii	Aves
	Frug_Order	Order taxonomic classification		Passeriformes

	Frug_Family	Family taxonomic classification		Pipridae
	Frug_Genus	Genus taxonomic classification		<i>Chiroxiphia</i>
	Frug_Group	Major type of frugivore	Amphibians, Bats, Carnivore Fish, Large Birds, Lizards, Marsupials, Primates, Rodents, Small birds, Ungulates, Tapir	Small Birds
	Frug_Body_Mass	Mean body mass of the frugivore in grams		63
	Frug_Mean_Gape_Size	Mean gape length of the frugivore in mm		12
	Frugivory_score	Grade of frugivory according to the amount of fruit in the animal diet	1: Occasional frugivore 2: Facultative frugivore 3: Strict frugivore	1
	Frug_Migration_status	Migration status	AM: Migratory R: Resident	R
	Frug_IUCN	IUCN Classification for threatened animals	EX: Extinct EW: Extinct in the wild CR: Critically endangered EN: Endangered VU: Vulnerable NT: Near threatened LC: Least concern DD: Data deficient NE: Not evaluated	EN
	Frug_Population_Trend	General population trend	Decreasing, Stable, Increasing	Stable

4) Table 7. Study information. Description of the fields related with the study that reports the interaction.

Type of information	Field	Description	Levels	Example
STUDY INFORMATION	Study reference	The study which report the interaction		Alves 2005
	Study_Method	The type of study according to the focus organisms of the study	Animal-oriented Plant-oriented Network	Animal_Oriented
	Study_Location	Specific location of the study		Carlos Botelho State Park
	Latitude	Decimal coordinates		-25.53122
	Longitude	Decimal coordinates		-47.961431
	Precision	Precision of the given coordinate	Precise Not-Precise City State Island	Precise
	DOI/Link/reference	DOI of the article, link or relevant information for accessing the study		10.4025/actascibiols.v32i3.5351

CLASS V. SUPPLEMENTAL DESCRIPTORS

A. Data acquisition

1. Data request history: None

2. Data set updates history: None

3. Data entry/verification procedures

G. History of data set usage

Bello et al. (2015) used the interactions and trait information to define which frugivores disperse large seeds in order to access how defaunation of large frugivores affects carbon

stock in tropical forest. Bufalo et al. (2016) used the primate-plant interaction data to explore the implications for the conservation of primates in the Atlantic Forest. Culot et al. (unpublished data) used the frugivore interactions to assess the diet of woolly spider monkey, howler monkey, and black-fronted piping guan and analyze the synergistic effects of seed dispersers and predators on carbon storage in tropical rainforests. Emer et al. (unpublished data) used the avian seed dispersal interactions to test how defaunation and habitat fragmentation are affecting network structure at the community level. Pizo et al. (unpublished data) used the data involving to explore the relationship between the overall diet of birds and the lipid content of the fruits they eat

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CHAPTER 2. DEFAUNATION AFFECTS CARBON STORAGE IN TROPICAL FORESTS

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Defaunation affects carbon storage in tropical forests

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Carbon storage is widely acknowledged as one of the most valuable forest ecosystem services. Deforestation, logging, fragmentation, fire, and climate change have significant effects on tropical carbon stocks; however, an elusive and yet undetected decrease in carbon storage may be due to defaunation of large seed dispersers. Many large tropical trees with sizeable contributions to carbon stock rely on large vertebrates for seed dispersal and regeneration, however many of these frugivores are threatened by hunting, illegal trade, and habitat loss. We used a large data set on tree species composition and abundance, seed, fruit, and carbon-related traits, and plant-animal interactions to estimate the loss of carbon storage capacity of tropical forests in defaunated scenarios. By simulating the local extinction of trees that depend on large frugivores in 31 Atlantic Forest communities, we found that defaunation has the potential to significantly erode carbon storage even when only a small proportion of large-seeded trees are extirpated. Although intergovernmental policies to reduce carbon emissions and reforestation programs have been mostly focused on deforestation, our results demonstrate that defaunation, and the loss of key ecological interactions, also poses a serious risk for the maintenance of tropical forest carbon storage.

INTRODUCTION

Tropical forests store ~40% of the world's terrestrial carbon (1), and their deforestation contributes to ~7 to 17% of the global carbon emissions (2, 3). However, tropical carbon has another silent threat. The disappearance of large frugivores may represent a loss in seed dispersal and natural regeneration of large-seeded hardwood plant species, which are key contributors to carbon storage. Therefore, defaunation is a largely unrecognized threat that can affect the sustainability of tropical forest carbon.

Forest degradation is related to selective logging, harvesting of natural products, fragmentation, fire events, and overhunting (4). The intensity of unsustainable hunting is a worldwide problem that has increased in the last few decades over tropical forests (5, 6). All studies on the effects of bushmeat hunting indicate unsustainable levels (7). Hunting threatens approximately 19% of all tropical forest vertebrates (8). However, it does not equally affect all animal community species, with large vertebrates being affected at disproportionately higher rates (9).

The local or functional extinction of large-bodied frugivores has profound implications to forest composition and dynamics because they perform unique ecological roles such as efficient fruit removal, long-distance dispersal, and dispersal of large-seeded plants (5, 10–13). The efficient consumption and dispersal of large seeds are primarily restricted to wide-gaped large frugivores (14); therefore, seed size is an obvious limiting trait for successful dispersal by frugivores that ingest

whole fruits or seeds (10). In contrast, small-seeded species can be dispersed by nonthreatened generalist frugivores, which typically inhabit small forest fragments (10, 15). Some frugivorous bats (for example, *Artibeus* spp.) and terrestrial caviomorph rodents (*Dasyprocta* spp.) may occasionally eat large-seeded fruits (16), but bats disperse seeds mostly in forest edges and gaps (17), a habitat not suitable for recruitment of these species (18), whereas large rodents are mainly seed eaters (19) and can be also locally extinct in overhunted areas (20).

In addition, there is a well-supported tendency for large hardwood species to have larger fruits and seeds (21–23), mainly in relatively intact forests where carbon stocks are greatest owing to the distinct contribution of large trees (24, 25). Wood density, diameter at breast height, and tree height are keys traits positively related to potential carbon storage capacity across tree species (26). Variation across communities in these traits, which are associated with changes in species composition, has been demonstrated to directly influence variation in biomass estimates by a staggering 70% (27); thus, we hypothesize that defaunation of large frugivores, which limits the recruitment of large-seeded species and induces compositional changes, can alter the community-aggregated values of wood density and height and eventually result in a markedly limited carbon storage capacity.

RESULTS

Here, we quantified the potential effect of defaunation of large-bodied seed dispersers on carbon storage on the basis of the relationship between dispersal and carbon storage traits of 2014 tree species from a tropical biodiversity hot spot, the Atlantic Forest (table S1). We then simulated how this relationship affects the carbon storage potential of 31 sites that represent the largest forest remnants (table S2) (28).

In each forest site, we simulated extinctions of large-seeded trees induced by the lack of large frugivores and compared the carbon loss between replicated scenarios of defaunation-driven extinctions and a null model with random extinctions (Fig. 1). We defined large-seeded

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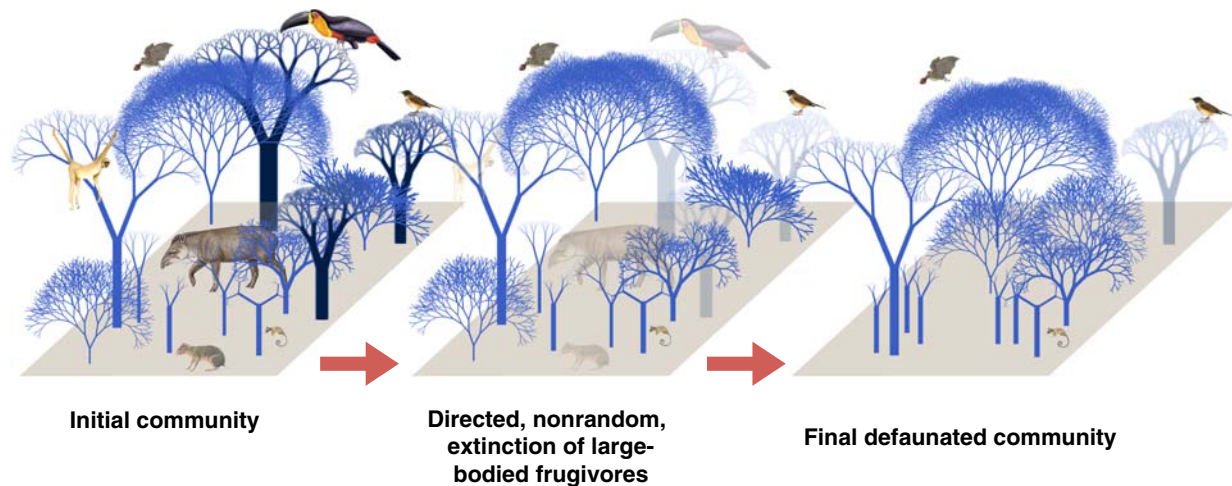


Fig. 1. Simulation pathway of frugivore defaunation on carbon storage. We generated downgraded communities with altered species composition. Each simulation had two main steps. First, we simulated directed extinctions induced by defaunation (loss of tree species with seed size ≥ 12.0 mm) or random extinction (that is, tree species removal independent of seed size). Second, we simulated a compensatory replacement of the individuals by the remaining species pool after defaunation by adding the same number of individuals and basal area removed. Dark blue indicates tree individuals of hard-wood species with large seeds (≥ 12.0 mm) and different trunk diameters, light blue represents other tree species.

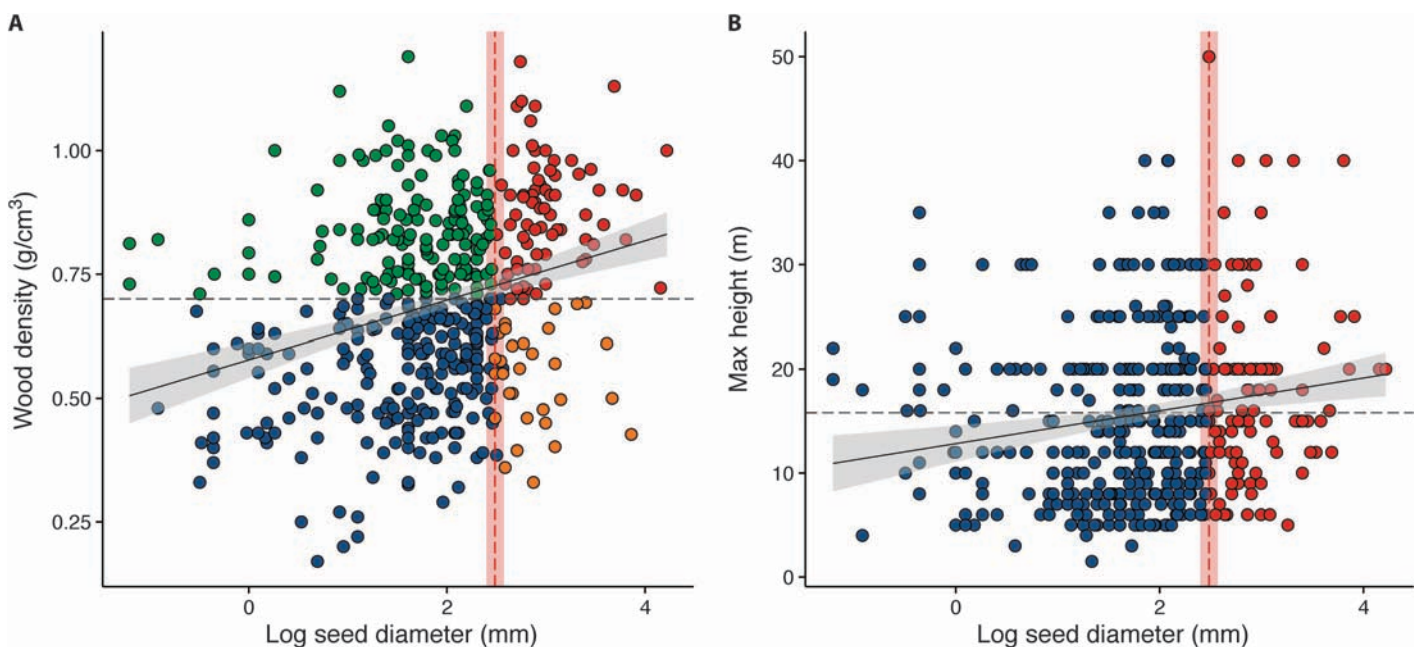


Fig. 2. Relationships between seed diameter and carbon storage-related traits in animal-dispersed trees. The black solid line shows the linear regression fit for the trend and the confidence interval (gray envelopes). The red vertical line indicates the seed diameter threshold of 12 mm. Points represent tree species. **(A)** Wood density and seed diameter ($r_s = 0.28$, $P < 0.001$, $N = 486$). The gray dashed horizontal line indicates a wood density = 0.7 g/cm^3 . Red points are endangered species with dense wood; orange points are endangered species with light wood; green points are nonendangered species with dense wood (resilient hardwood species); and blue points are nonendangered species with light wood. **(B)** Maximum tree height (m) and seed diameter (mm) ($r_s = 0.25$, $P < 0.001$, $N = 783$). Red points are endangered species, and blue points are nonendangered species.

species on the basis of the analysis of more than 5000 fruit-frugivore interactions and their seed traits for the Atlantic Forest biome (see the Supplementary Materials). We found that resilient frugivores such as small birds, bats, and marsupials, which are not targeted by hunters (9), can disperse seeds up to 12.0 ± 1.1 mm in width (fig. S1). This threshold also corresponds to a seed size limit where successful dispersal would be seriously impaired under post-defaunation scenarios in the

Atlantic Forest (10). The simulated defaunation scenarios consisted of the extinction of large-seeded species (10 to 100% of the individuals) and its replacement by any other tree species remnant in the community. The simulated scenarios are governed by a zero-sum game where communities retain the same number of individuals and the same basal area (29). We assume that the probability of extinction is proportional to seed size and the probability of recruitment is proportional to the

species abundance. We also allow any remaining large-seeded species to enter the replacement game because dispersal by bats or rodents and near-parent recruitment can occur (fig. S1).

A total of 813 species and 101,211 individuals were represented in these 31 communities, which are large forest fragments (that is, minimum area ≥ 1000 ha) spread through the whole range of Atlantic Forest types. This patch size is not prone to dispersal limitation and edge effects (30, 31). Finally, we explore how abiotic forest site (elevation, forest type, temperature, precipitation, latitude) and forest compositional characteristics (richness and abundance of abiotic and resilient species) may explain changes in carbon storage.

We observed an important contribution of large-seeded trees to carbon storage potential. Species with large animal-dispersed seeds ($\geq 12.0 \pm 1.1$ mm) represented 21% of our sample, 70% of which had high wood density (>0.7 g/cm³) and tended to be higher-stature trees (fig. S2). Fifty-four percent of these species have recalcitrant seeds that cannot tolerate drought prior to germination (table S1). In addition, we found a functional relationship between seed diameter and traits related to carbon storage. We found a positive correlation between seed diameter and wood density ($r_s = 0.22$, $P < 0.001$, $N = 732$) and between seed diameter and maximum tree height ($r_s = 0.21$, $P < 0.001$, $N = 1087$), especially for animal-dispersed species (Fig. 2 and table S3). Conversely, wind- or gravity-dispersed species did not show a significant association between seed size and wood density (fig. S3). Therefore, trees bearing seeds larger than 12 mm have high carbon stock capacity, and large-bodied dis-

persers are functionally connected to forest carbon storage, given their distinct link with large-seeded trees.

We found strong support for the hypothesis that removal of large-seeded trees will erode carbon stocks in defaunated tropical forests. We observed a greater loss of carbon as the percentage of removed large-seeded tree species increases, as a consequence of defaunation of large frugivores. This response significantly deviates from a random extinction scenario, even when few species are removed (for example, 10%) (Fig. 3B and table S4). Those changes were consistent at the landscape scale throughout the heterogeneous conditions of the different communities, being more pronounced in warmer sites (fig. S4). However, in plant communities where the dominance of hardwood resilient species (that is, small-seeded species with high wood density) exceeds ~50% of individuals (fig. S5 and tables S5 and S6), carbon loss is slowed down. Moreover, we found that the compensatory role of large frugivore substitutes that are not affected by hunting in defaunated rainforests, such as rodents and bats, remains questionable (fig. S1).

DISCUSSION

Defaunation is a human-induced process that significantly erodes key ecosystem services and functions through direct and indirect cascading effects (5, 32, 33). Defaunation has been shown to affect pollination, seed dispersal, pest control, nutrient cycling, decomposition, water quality,

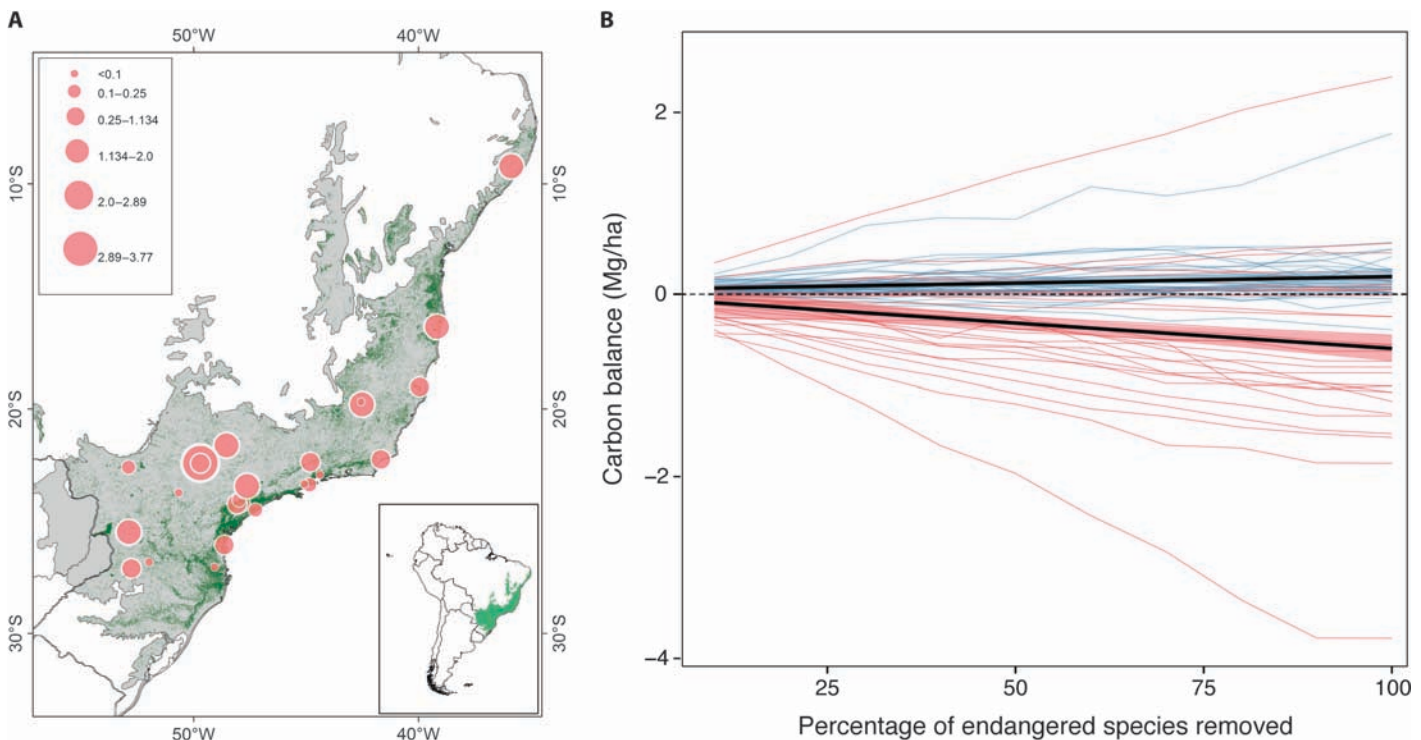


Fig. 3. Carbon deficit after defaunation simulation in Atlantic forest sites. (A) Locations of the 31 communities studied. The size of the points represents the magnitude of carbon loss (Mg/ha). **(B)** Carbon balance after simulated changes in carbon storage capacity in the random (blue) and defaunated (red) scenarios over the 31 selected communities. Initial carbon was used as the 0 or neutral point. A negative balance represents a net carbon loss, and positive values indicate gains in carbon storage. Lines represent the simulated trajectories for each community. The black lines show the mean combined values for all communities in each scenario and their confidence interval. The width of the confidence interval for the random scenario trend was increased 2x to improve visualization.

and soil erosion (34). Now, we have evidence that defaunation will, over time, result in significantly decreased carbon storage ecosystem service in tropical forests where animal-dispersed plants are abundant (35) and crucially dependent on large frugivores. Our findings may also translate into the Amazonian forests where most of the tree species that retain 50% of the carbon are also dispersed by large frugivores (36, 37), but they will be slowed down in forests that are dominated by abiotic hardwood species, such as the Dipterocarpaceae forests in Southeast Asia (32).

Our result highlights the fragility of carbon storage service in tropical forests under the current global change conditions. Processes such as fragmentation (30, 38–40), climate change, liana overabundance (41–43), and human-ignited fires (44–46) will enhance the effects of carbon loss in defaunated ecosystems.

Halting the ongoing, fast-paced defaunation of tropical forests will not only save large charismatic animals and the plants they disperse but also have effects on climate change, carbon markets, and reforestation processes. For instance, restoration and REDD+ programs should achieve a complete vision of biotic interactions and processes to guarantee carbon storage capacity and its co-benefits. Their effectiveness over climate change will be improved by ensuring the array of biotic processes that support the target ecological services addressed by these initiatives.

MATERIALS AND METHODS

Study site

The Atlantic Forest spans from 3° to 31° latitude south, from 35° to 60° longitude west, and from sea level to approximately 2800 m above sea level, which ensures a wide latitudinal and altitudinal gradient from tropical to subtropical regions (47). In this biome, about 89% of all woody species are animal-dispersed (48). We selected 31 independent large forest communities across the latitudinal and altitudinal gradients of the Atlantic Forest to simulate the effects of defaunation on carbon storage. These tree communities were obtained from a recent assessment of the existing knowledge on the Atlantic Forest that included more than 1000 tree community surveys (28). To obtain the 31 forest communities, we filtered this database by selecting only the studies (i) with a sampling area larger than or equal to 1 ha, (ii) with a cutoff criterion of stem diameter at breast height ≥ 5 cm, (iii) conducted in forest fragments ≥ 1000 ha of the whole range of Atlantic Forest types [because this is the minimum patch size at which the effect of carbon loss due to edge effect is minimized (30)], (iv) with a robust taxonomic resolution at species level recognized by REFLOA (49), and (v) with information on dispersal mode and carbon traits in more than 50% of each community species (table S2). All the communities' surveys were carried out after 1990. These large fragments represent just 0.05% of all remaining fragments of the Atlantic Forest, but concentrate 41% of the remaining area (6.6 million ha of the remnant 16 million ha of the Atlantic Forest) (50). For each community, we obtained species name, number of individuals (N), basal area [BA (m^2)], absolute density ($DA = N/\text{ha}$), and absolute dominance ($DO = BA/\text{ha}$).

Plant traits

We compiled information on tree species of the Atlantic Forest from the TreeAtlas 2.0 database (51) and TreeCo (28). We explored quantitative traits related to seed dispersal (seed and fruit diameter and length) and

to potential carbon storage (wood density and maximum height). Seed and fruit traits were obtained from previous studies (48, 52–101), our own measurements in herbaria, and private collections. Carbon traits were obtained from different literature sources (60, 102–104). For the simulation process, we used information at species level for wood density; however, when such information was not available, we used the means of the genera.

We tested the relationship between carbon and dispersal traits for 2014 species (table S1), which represent 28% of the trees and shrub species described for the Atlantic Forest (49). We used simple correlations for the whole set of species differentiated by dispersal mode. We used log transformation and Spearman correlations because not all traits satisfied a normal distribution.

Delimitation of endangered species

To determine which plant species will be threatened by the local extinction of large frugivore defaunation, we examined a plant-frugivore interaction data set combined with information on seed traits. This data set contains information on ca. 5000 fruit-frugivore interactions from the entire Atlantic Forest (105–181). This data set includes animal- and plant-oriented studies that reported the occurrence of interactions, that is, a given animal species feeding on fruits of a particular plant species. From these interactions, we recorded plant and animal taxonomy and related each plant with its carbon traits (wood density, maximum height) and dispersal traits (fruit and seed diameter and length).

We selected the maximum seed diameter dispersed by frugivores that are not threatened by hunting, such as small birds, bats, and marsupials (9), as the threshold limit for defining species endangered by defaunation of large frugivores. We also used the confidence interval of the mean seed size distribution (± 1.09 mm) around the threshold limit to allow variability in this threshold value (fig. S1). Therefore, we classified those tree species having animal-dispersed seeds and seed diameter $\geq 12 \pm 1.09$ mm as endangered because large frugivores are the only effective dispersers with gapes wide enough to effectively consume and disperse such large seeds (10, 14). We also classified as hardwood species those with a wood density > 0.7 g/cm³, according to UNE 56-540-78 (182).

Simulated scenarios

For each of the 31 large forest communities (table S2), we generated two hypothetical scenarios of downgraded communities with altered species composition: the random extinctions scenario with tree species removal independent of seed size, and the directed extinctions scenario induced by defaunation of large-bodied frugivores with removal of tree species with seed size $\geq 12.0 \pm 1.09$ mm (Fig. 1). Each simulation had two main steps. First, we simulated extinctions; and second, we simulated a compensatory replacement of the individuals by adding the numbers of individuals removed, but of species drawn from the remaining community pool, to construct a new final community.

In each scenario, we removed a crescent percentage (from 10 to 100%) of large-seeded species and did 1000 repetitions for each percentage class. These numbers ranged from 1 species (10%) to the maximum number of endangered species (100%) in each community. For the random extinctions scenarios, we randomly removed the same number of species.

In the simulations, we assumed saturated communities with zero-sum game dynamic and immigration is equal to zero (29). We made sure that the basal area and the total number of individuals remained

constant. Further, we assumed that the extinction probability of a large-seeded species is proportional to its seed size. The recruitment probability of each species is proportional to its abundance, and we allowed the remaining large-seeded species to enter in the replacement game because dispersal by bats and rodents and near-parent recruitment could occur (for detailed information, see Code file S1).

We explored the carbon balance and the magnitude of carbon loss for each percentage of endangered species removed. We assessed the carbon balance by comparing the estimated carbon of the final (downgraded) scenario community and the carbon in the initial (pristine) community for each percentage of removed species. The carbon of the initial community was used as the 0 or neutral point; therefore, carbon balance was calculated as

$$CB = C_f - C_i \quad (1)$$

where C_f is the carbon in the final community and C_i is the carbon in the initial community, both expressed in megagrams per hectare (Mg/ha).

The magnitude of carbon loss was estimated as the difference between the final carbon in the defaunated scenario and the final carbon in the random scenario at each percentage of endangered species removed. The simulations were applied independently for each community and then aggregated in the mean response for all communities. We also explored the relationship between the magnitude of carbon loss against abiotic variables (altitude, forest type, temperature, precipitation, and latitude) and species compositional variables (richness and abundance of abiotic and resilient species) using generalized linear models. We used the Gaussian family for the error distribution. We obtained the abiotic variables using the community location and climatic information from Hijmans *et al.* (183) and the forest size information from Ribeiro *et al.* (50). Compositional data were calculated from the reported abundance data of each community (table S2). The abiotic variables of the community sites were altitude, latitude, annual precipitation, mean annual temperature, and forest size. For compositional variables, we explored the percentage, quantity, and dominance of three types of species: (i) endangered species (large-seeded trees; seed diameter >12 mm), (ii) animal-dispersed resilient species (seed diameter <12 mm and dense wood), and (iii) abiotically dispersed hardwood species.

Carbon estimation

We estimated the carbon stock in each community twice: first at the initial community [initial carbon (C_i)] and then at the final community [final carbon (C_f)], in each scenario. To estimate the amount of above-ground biomass (AGB), we used a proxy for biomass that related the three main traits related to carbon storage potential: basal area (related to diameter at breast height), wood density, and maximum height (26). In particular, we used total basal area (BA) in hectares (DO) of the species. BA is widely used as a proxy for biomass and carbon stock (184, 185), and we weighted it by the effects of the wood density and tree height.

Here, we show that these estimates are linearly and closely related to AGB of Atlantic Forest communities (fig. S6), so we can have a fair estimate of the population AGB for each site based on the population BA, which is the only information available for all sites at the species level.

To inspect the relationship between this estimate, we used the data from four 10.24-ha forest plots placed at four contrasting types of forest from southeastern Brazil: rainforest, seasonal forest, white-sand (*Restinga*) forest, and savanna forest (locally known as “Cerradão”

(186). The plots vary greatly in their tree density, basal area, and species richness. Thus, they represent a good sample among the wide spectrum of possible types of Atlantic Forests. Although we have not included any savanna forest site in the main analysis (see the text), we decided to include it here to have a wider variation in total basal area estimates. Population values of BA for all four plots varied between 0.002 and 56.3 m² per 10.24 ha, whereas AGB varied between 0.003 and 444.5 Mg per 10.24 ha. These ranges cover the entire variation of BA found in the 31 sites studied here because these 10.24-ha forest plots were the sites with the largest sample sizes included in the simulations presented in the text.

For each species at each plot, we calculated the BA (m²) and AGB (Mg). Estimates of AGB were obtained using the allometric equations for moist forests provided by Chave *et al.* (26) based on individual field measurements of tree diameter at breast height and tree height. The mean values of wood specific gravity (WSG) for each species were obtained from the literature as stated above, and when this mean value was not available at the species level, we again used the generic means from the study of Chave *et al.* (26). We then used linear regression to relate the AGB for each species as a function of basal area × wood density × tree height. The variables were log-transformed prior to analysis, which was performed separately for each permanent forest plot. Thus, the analysis corresponds to a total of 601 populations of 483 tree species.

Our carbon proxy (BA × WSG × height) explained a large amount of the variation in species AGB (adjusted $R^2 \geq 93.7\%$). For all sites, our proxy explained from 93.7 to 96% of the variation in species AGB. It was more efficient in predicting AGB in seasonal forests and less efficient in rainforests (fig. S6). Although we did find a site effect on the relationship between AGB and BA × WSG, the regression performed by combining populations from the four sites had a good development (fig. S7) and still explained a large amount of AGB variation (adjusted $R^2 = 94.6\%$), resulting in the following general relationship

$$AGB = e^{-0.679 + 0.967 \ln(BA \times \text{wooden} \times \text{height})}$$

where AGB is the above-ground biomass (Mg/ha), wooden is the wood density (g/cm³), BA is the basal area (m²/ha), and height is the reported maximum height. Finally, to determine the carbon concentration in the AGB, we used the estimation of 40% of water in the AGB and 48.5% of carbon in the dry biomass (187).

SUPPLEMENTARY MATERIALS

Supplementary material for this article is available at <http://advances.sciencemag.org/cgi/content/full/1/11/e1501105/DC1>

Fig. S1. Distribution function of seed size diameter (mm) dispersed by the major frugivores in the Atlantic forest, Brazil.

Fig. S2. Maximum tree height by class of species according to its seed diameter and wood density.

Fig. S3. Relationship between wood density and seed diameter by dispersal mode.

Fig. S4. Relationships between abiotic variables and magnitude of carbon loss.

Fig. S5. Relationships between the compositional variables of each community and its magnitude of carbon loss.

Fig. S6. Linear regression of the above-ground biomass (AGB) and the proxy for basal area (BA) times the wood specific gravity (WSG) times maximum height for the different types of forest.

Fig. S7. Diagnostic plots of the regression model using basal area (BA) times the wood specific gravity (WSG) times tree maximum height (MaxHeight) as a proxy for AGB.

Table S1. Trait information of the 2014 species analyzed (available in the data repository).

Table S2. Atlantic Forest communities analyzed, their spatial localization in Brazil, and abiotic characteristics.

Table S3. Spearman correlations among dispersal traits and carbon traits.

Table S4. *T* test between carbon loss in random scenarios and defaunated scenarios at different intervals of species removed.

Table S5. Generalized linear model results showing the influence of abiotic and compositional variables on the magnitude of carbon loss of each community.

Table S6. Compositional characteristics of Atlantic Forest communities.

Supplementary code and data file available at

https://github.com/pedroj/MS_Carbon (DOI:10.5281/zenodo.31880).

Code file S1. Simulation code in R (Simulation_Code.RMD).

Code file S2. Read me (Simulation_Code.html).

Data file S1. Trait information of the 2014 species analyzed (Table S1_Trait Data. xls).

Data file S2. Community data example for the simulation code (prove_community.csv).

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CHAPTER 3. SYNERGISTIC EFFECTS OF SEED DISPERSER AND PREDATOR LOSS ON RECRUITMENT SUCCESS AND LONG-TERM CONSEQUENCES FOR CARBON STOCKS IN TROPICAL RAINFORESTS

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Synergistic effects of seed disperser and predator loss on recruitment success and long-term consequences for carbon stocks in tropical rainforests

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The extinction of large frugivores has consequences for the recruitment of large-seeded plants with potential lasting effects on carbon storage in tropical rainforests. However, previous studies relating frugivore defaunation to changes in carbon storage ignore potential compensation by redundant frugivores and the effects of seed predators on plant recruitment. Based on empirical data of the recruitment success of a large-seeded hardwood tree species (*Cryptocarya mandioccana*, Lauraceae) across a defaunation gradient of seed dispersers and predators, we show that defaunation increases both seed dispersal limitation and seed predation. Depending on the level of seed predator loss, plant recruitment is reduced by 70.7–94.9% as a result of the loss of seed dispersers. The loss of large seed predators increases the net seed mortality by 7–30% due to the increased abundance of small granivorous rodents. The loss of large seed dispersers can be buffered by the compensatory effects of smaller frugivores in seed removal, but it is not sufficient to prevent a decrease in plant recruitment. We show that the conservation of both seed predators and dispersers is necessary for the recruitment of large-seeded plants. Since these plants contribute substantially to carbon stocks, defaunation can jeopardize the maintenance of tropical forest carbon storage.

Anthropocene defaunation, known as the local or global extinction of animal populations or species, is recognized as an important driver of global environmental change¹. Indeed, defaunation extends well beyond species loss; it concerns a shift in species composition and its impact on ecological and evolutionary processes and on ecosystem services^{2–5}. Previous studies highlight the impact of defaunation on ecological services such as pollination, seed dispersal, nutrient cycling and decomposition, water quality, and dung removal^{1,6,7} and, more recently, on carbon storage^{8–10}. Despite the evidence suggesting that the decline or loss of frugivores affects plant recruitment success and leads to changes in plant communities¹¹, the estimation of the magnitude of the effects of defaunation on future carbon storage has been based on inferences that frugivore extinction will necessarily lead to direct effects on plant species fitness^{8–10}. However, in defaunated scenarios, a decrease in seed predation pressure may buffer the effects of seed disperser loss¹² and many plant species can still recruit without or with few dispersers¹³ or have multiple dispersers that could buffer plant extinction^{14,15}.

Therefore, the effects of frugivores on carbon storage have been based on simple models that do not consider the potential consequences of the altered seed predator community. It is well known that plant recruitment depends on the activities of both mutualists (seed dispersers) and antagonists (seed predators, herbivores)¹⁶. Vertebrate defaunation leads to significant changes in the communities of both seed dispersers and predators

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Functional group	Species	Common names	Mass (kg)	CB - High (Non-def)	IC (Mod def)	CB - Low (Def)
Seed dispersers	<i>Tapirus terrestris</i>	Tapir	220	com	ex	fe
	<i>Brachyteles arachnoides</i>	Muriqui	12	com		fe
	<i>Alouatta guariba</i>	Howler monkey	8	com	com	fe
	<i>Aburria jacutinga</i>	Jacutinga	1.2	com	com	com
Seed predators	<i>Tayassu pecari</i>	White-lipped peccary	35	fe	com	low
	<i>Pecari tajacu</i>	Collared peccary	15	com	com	com
	<i>Cuniculus paca</i>	Spotted Paca	5	com	com	com
	<i>Dasyprocta leporina</i>	Red-rumped Agouti	3	low	com	com
	<i>Trinomys iheringi</i>	Ihering's Spiny Rat	0.4	com	com	com
	<i>Euryoryzomys russatus</i>	Russet Rice Rat	0.2	com	com	com
	<i>Juliomys pictipes</i>	Lesser Wilfred's Mouse	0.02	com		com
	<i>Sooretamys angouya</i>	Paraguayan rice rat	0.02	com		com
	<i>Thaptomys nigrita</i>	Blackish Grass Mouse	0.01	com		com
	<i>Oligoryzomys nigripes</i>	Black-footed Pygmy Rice Rat	0.01	com	com	com
	<i>Akodon montensis</i>	Montane Grass Mouse	0.01	com		com

Table 1. Seed disperser and predator assemblages in the intact (Carlos Botelho, highlands – CB-High), moderately defaunated (Ilha do Cardoso – IC), and defaunated areas (Carlos Botelho, lowlands – CB-Low). ‘com’ indicates that the species is common in the area, ‘low’ that it occurs in low density, ‘fe’ that the species is functionally extinct, and ‘ex’ that the species is extinct.

and, while some species respond negatively to anthropogenic activities, others can benefit because of differential functional response traits or competitive (numerical) release¹². This demographic asynchrony can give rise to compensatory effects¹⁷ that are able to mitigate, fully compensate or even invert the effects of defaunation on the seed dispersal process¹⁸. Compensatory effects are possible if a certain degree of redundancy exists in seed dispersal and predation services^{14,19}. Therefore, functional redundancy among mutualist and antagonist species and possible compensatory effects still need to be investigated in a defaunation context.

While the traditional determination of changes in seedling communities highlights important defaunation effects on the future plant composition of tropical forests^{20,21}, they do not enable the identification of the underlying processes leading to this result. The detailed study of one plant species likely to be affected by defaunation enables to understand and disentangle the effects of mutualistic and antagonistic interactions, identify the causes of recruitment failure, and highlight the mechanisms underlying possible compensatory effects of the resilient frugivore community²². Here, we address the effects of defaunation, of both seed dispersers and predators, on the recruitment success of a large-seeded hardwood tree. We investigated the contributions of the seed dispersers (southern muriquis – *Brachyteles arachnoides*, southern brown howler monkeys – *Alouatta guariba*, and black-fronted piping guans, hereafter called jacutingas – *Aburria jacutinga*) of a large-seeded hardwood tree species, *Cryptocarya mandioccana* (Lauraceae), in three areas across a defaunation gradient of seed dispersers and predators to assess the magnitude of possible compensatory effects. The seed dispersers and the seed predators (peccaries – *Pecari tajacu* and *Tayassu pecari*, agoutis – *Dasyprocta* sp., and small rodents) range from large (220 kg) to small (0.01 kg) in size (Table 1), and they respond to defaunation according to their body size (from the largest to smallest frugivore). By comparing seed dispersal effectiveness among the seed dispersers, we predicted the relative impacts of their local extinction on plant recruitment, taking into account possible compensatory effects and changes in the seed predator community.

Results

Contribution of seed dispersers to recruitment success. We estimated recruitment success, and the contribution of each seed disperser to the recruitment success, of *C. mandioccana* in three areas of Atlantic Forest differing in their seed disperser and predator communities (Table 1; see Fig. S1 in Supplementary Information). The lowest recruitment success was in the intact forest (9%), while it was highest in the moderately defaunated forest (15.51%). The most defaunated forest presented an intermediate value (12.77%) (see Table S2). The quantity and quality components of seed dispersal effectiveness (Fig. 1) as well as of seed predation (see Table S2 and Fig. S3) explain these results. The overall contribution of jacutingas and howler monkeys increased along the seed disperser defaunation gradient (see Table S2). Jacutingas contributed only 0.7% towards *C. mandioccana* recruitment success where they occur together with larger-bodied primates (muriquis and howler monkeys), while their contribution reached 61.4% where they are the only seed disperser (see Table S2). This pattern is mostly explained by seed removal (Fig. 1a). Indeed, there is a partial compensatory effect in seed removal with an increasing contribution of the remaining seed dispersers, such as howler monkeys (from 41 to 47%) and jacutingas (from 1% to 16% and then to 41%), along the defaunation gradient (Fig. 1a, see Table S2). Despite this functional compensatory effect, we observed a decreasing proportion of swallowed seeds, i.e., seeds dispersed away from the parent tree, with the loss of seed dispersers: 83% with the complete assemblage, 63% without muriquis, and 41% without muriquis and howler monkeys (Fig. 1a).

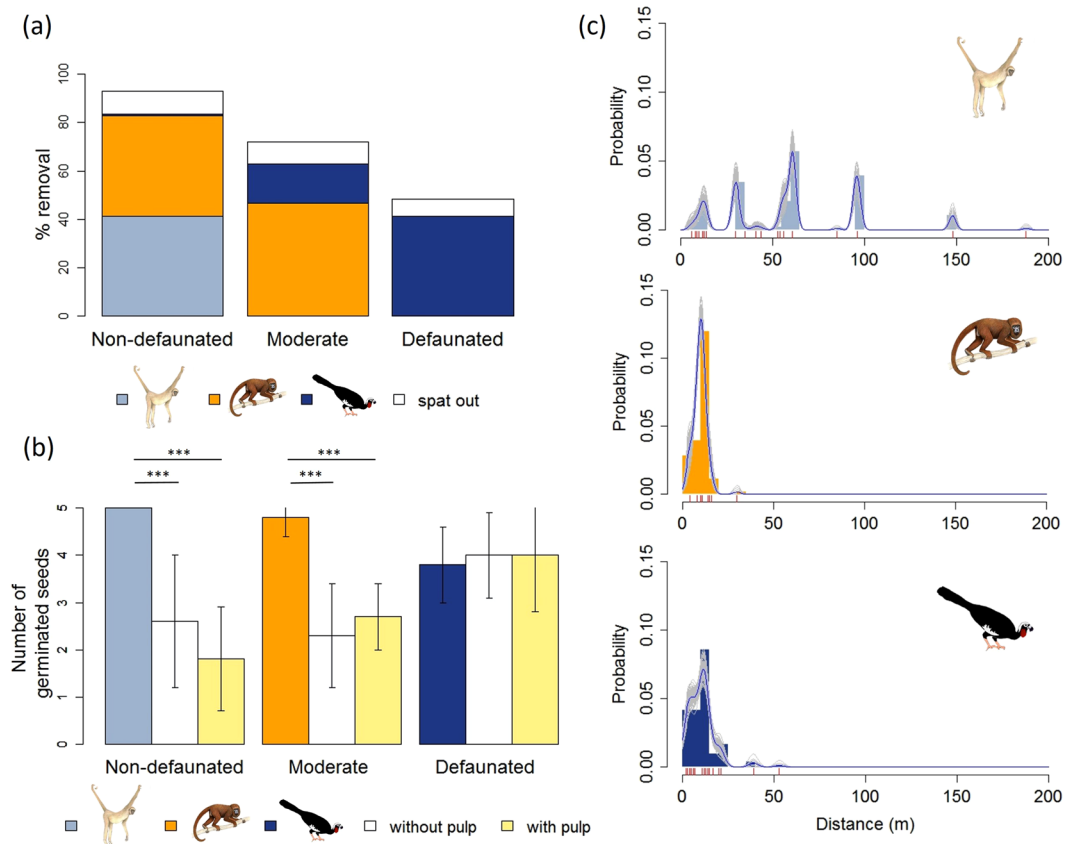


Figure 1. Components of seed dispersal effectiveness of the three main dispersers of *C. mandioccana*. (a) Percentage of seeds swallowed by muriquis, howler monkeys, and jacutingas, as well as the percentage of spat out seeds (all frugivore combined) in the three study sites characterized by different seed disperser communities: Non defaunated (muriquis, howler monkeys, and jacutingas), Moderate (howler monkeys and jacutingas), and Defaunated (jacutingas). Data are based on focal observations of *C. mandioccana* fruiting trees in 2011–2012 (Non-defaunated: N = 172 h; Moderate: N = 108 h, and Defaunated: N = 153 h). (b) Germination success of seeds defecated by muriquis, howler monkeys, and jacutingas, compared to seeds without pulp and seeds with pulp along the defaunation gradient. Bars represent the mean number of germinated seeds out of five seeds (ten replicates) and vertical lines represent standard deviation. (c) Seed dispersal distances to *C. mandioccana* conspecifics by muriquis (N = 173), howler monkeys (N = 127), and jacutingas (N = 168). Frequency distributions of seed dispersal distances (5 m-bins) where red vertical bars represent each observed dispersal event and the blue and grey lines, a non-parametric smoothing spline fit to the empirical distance distributions together with bootstrapped estimates. (Illustrations of: muriqui and howler monkey - Copyright Stephen D. Nash; jacutinga - Copyright Fabio Martins Labecca, authorized by the authors).

The germination success of seeds defecated by muriquis and howler monkeys was significantly higher than that of non-defecated seeds with or without pulp (muriquis: N = 10, F = 24.1, $P < 0.0001$; howler monkeys: N = 10, F = 30.8, $P < 0.001$; Fig. 1b). Conversely, the germination success of seeds defecated by jacutingas did not significantly differ from that of non-defecated seeds with or without pulp (N = 9, F = 0.1, $P = 0.9$) (Fig. 1b; see Supplementary Method S4). Muriquis, a large-bodied frugivore, dispersed seeds about six times farther than smaller-bodied howler monkeys and jacutingas (N = 468, F = 271.26, $P < 0.05$; post hoc test: $P < 0.0001$), with a mean of 59.7 ± 35.7 m from the nearest conspecific compared to 9.7 ± 3.4 m and 10.5 ± 7.3 m for howler monkeys and jacutingas, respectively (Fig. 1c). However, while muriquis largely contributed, quantitatively, to recruitment success through high seed removal (Fig. 1a), their contribution was qualitatively low due to extremely high seed mortality at all distances at the site where they occur (see Table S2 and Fig. S3). Survival tended to increase with distance but this effect was only significant in the moderately defaunated site in 2011 (N = 240, Z = 2.01, $P < 0.05$) and in the defaunated site in 2012 (N = 240, Z = 2.17, $P < 0.05$) (see Fig. S3), with both sites harboring a more complete assemblage of seed predators.

Compensatory effect and expected recruitment success. We simulated a sequence of seed disperser loss (from the largest to smallest frugivore) in the intact area to explore how seed disperser and predator extinctions could affect *C. mandioccana* recruitment. We took into account three scenarios based on the seed predator community and compensatory effects of the disperser community. In all scenarios of seed disperser loss, recruitment success decreased with the decline in the richness of seed predators (Fig. 2), possibly because of increased

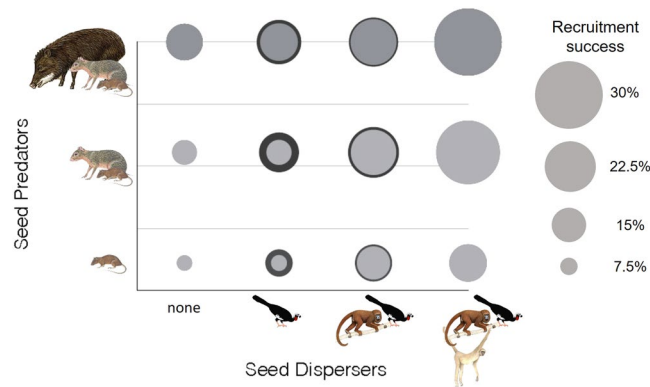


Figure 2. Expected recruitment success of *C. mandioccana* with and without compensation effect of the disperser community. The loss of seed dispersers was simulated in the area where the complete assemblage of seed dispersers is currently present (Carlos Botelho State Park, highlands) and the recruitment success of *C. mandioccana* estimated in three scenarios of seed predator (x axis) and seed predator (y axis) communities considering (dark grey circles) or not (light grey circles) compensation effects of the disperser community. The contribution of the disperser community in the compensation scenario is based on the data collected in Cardoso Island (community without muriquis) and in the lowland part of Carlos Botelho State Park (community without muriquis and howler monkeys). (Illustrations of: muriqui and howler monkey - Copyright Stephen D. Nash; peccary, agouti, and rodent - Copyright Fiona A. Reid; jacutinga - Copyright Fabio Martins Labacca, authorized by the authors).

predation pressure by small rodents as evidenced by the higher frequency of visits by small rodents to *C. mandioccana* fruits in the seed predator-defaunated site (see Table S5). Taking the recruitment success of the scenario with the most intact seed predator community as reference, the loss of all seed dispersers would decrease the recruitment success of *C. mandioccana* individuals by 70.7% if the complete set of seed predators is maintained, by 86.7% if coupled with the extinction of peccaries, and by 94.9% if coupled with the extinction of both peccaries and agoutis (Fig. 2).

Taking the recruitment success of each seed predation scenario as a reference, the inclusion of a frugivore compensatory effect reduces the loss of recruitment resulting from the loss of muriquis to -47.2% instead of -54.0% in the scenario with all seed predators, to -36.2% instead of -49.5% in the scenario without peccaries and to -1.9% instead of -23.2% in the scenario without peccaries and agoutis (Fig. 2). Likewise, the inclusion of a compensatory effect reduces the cumulative loss of recruitment resulting from the loss of both muriquis and howler monkeys to -56.7% instead of -69.2% in the scenario with all seed predators, to -60.8% instead of -84.1% in the scenario without peccaries and to -46.7% instead of -82.4% in the scenario without peccaries and agoutis (Fig. 2). The loss of the largest-bodied seed disperser, the muriqui, had the highest impact on *C. mandioccana* recruitment success when the seed predator community remained intact. In contrast, the loss of howler monkeys and jacutingas - with the latter only in the compensation scenario - had the highest impact in the most defaunated area in terms of seed predators compared to more intact areas (Fig. 2).

Discussion

We showed that the loss of large seed dispersers and predators synergistically decrease the recruitment success of a hardwood tree species. In defaunated scenarios, the antagonistic role of dispersers and predators will not result in a compensatory effect that is able to mitigate or reverse the limitations in the dispersal process, as previously suggested^{17,18}. In contrast, the combined effects of defaunation on large disperser and predator assemblages can exacerbate dispersal limitation and decrease recruitment success. However, the partial compensatory effect in the seed dispersal process mitigates the decrease in recruitment success. In addition, our model species still recruits without dispersers, suggesting that defaunation does not necessarily lead to the complete extinction of large-seeded species. A complete seed predator community and compensatory effects in the seed dispersal process buffer the negative effect of defaunation of large seed dispersers but are not sufficient to prevent a decrease in plant recruitment.

Partial compensation supports the hypothesis that processes carried out by a small number of key and functionally unique species, such as the dispersal of large seeds, are most sensitive to changes in biodiversity^{17,23}. The increasing contribution of howler monkeys and jacutingas to *C. mandioccana* seed dispersal when muriquis are absent indicates that smaller dispersers could benefit from the absence of large species, partially compensating for their role. Complete compensation or redundancy is achieved only when the seed dispersers are quantitatively and qualitatively similar^{14,19}, which is not what we found in our study system. The quantity component was never totally compensated. The quality of dispersal by howler monkeys and jacutingas was lower than that by muriquis in terms of seed germination success and dispersal distances, limiting their potential for compensation. When no clear distance effect is observed on seed/seedling survival, the functional attributes of the resilient seed disperser community compensate better (but not totally) the absence of muriquis because of the lack of long-distance seed

dispersal benefits. However, the pattern of recruitment success is only one of the possible effects of defaunation: long-distance seed dispersal is a key process for plant populations, because it promotes gene flow and increases the probability of colonizing new habitats²⁴. Therefore, high recruitment success observed in defaunated areas might hide a more pervasive effect: the strong reduction of gene flow due to the concentration of the seed rain under parent trees^{25,26}. It is thus urgent to combine field data of plant recruitment dynamics to plant population genetics in order to determine the possible evolutionary trajectories of these populations in the future²⁷.

The contribution of each seed disperser is a context-dependent process, which is highlighted by the differential impacts of disperser extinction according to the seed predator community. This suggests that mechanisms other than compensation can influence the resilience of an ecosystem in response to a perturbation¹⁷. For example, we observed that the benefits of long distance seed dispersal provided by muriquis are almost eliminated when the seed predator community is disrupted. This effect mainly occurs because of the unexpected increase in seed predation at all distances, possibly due to the dominance of small rodents where large seed predators are absent. Indeed, our camera trap results show an up to 14-fold increase in the frequency of visits by small rodents in the seed predator-defaunated area compared to the area with an intact seed predator community. This is in line with recent evidence of a positive effect of defaunation on seed predation in Atlantic Forest explained by an increase in the population of small rodents due to the absence of large mammals (competitive release) and by a shift of some rodent species to a more peccary-like diet²⁸. Therefore, the increase in seed predation and the absence of a distance effect in our seed predator-defaunated area might be due to the lack of satiation in the rodent population^{29,30}, inverting the expected plant recruitment trajectory based on the dispersal curves and confirming what has been observed for other plant species having peccaries and small rodents as their main seed predators³¹.

Our study shows the complexity of the cascading effects of defaunation on plant recruitment of one large-seeded species, highlighting compensatory effects and synergistic feedbacks, two ecological processes that are fundamental in exploring the effects of defaunation on the carbon stock ecosystem service. Indeed, a lack of information regarding these processes in future carbon stock modelling is likely to bias the estimate. Taking into account these complex cascading effects at the community level is challenging because of the difficulty to extrapolate the results of one plant species to the entire community since the response of each plant species depends on its traits and on the frugivore community with which it interacts. However, if enough knowledge is available, it is possible to predict defaunation effects from the study of the Janzen-Connell curves – dispersal and escape curves – as suggested by Terborgh¹⁸. The occurrence and magnitude of the effects of dispersal failure and compensation are directly linked to plant species traits. Seed size is likely to be related to the degree of redundancy in seed dispersal and predation networks³² while the capacity of plant species to germinate with pulp and recruit under parent trees could reduce the effects of dispersal failure¹³. Species like *C. mandioccana* that has the ability to germinate with pulp and rely on several seed dispersers might be more robust to changes in frugivore community. Therefore, defaunation effects on their recruitment dynamics should be mainly driven by establishment limitation. Defaunation effects on plant species with no redundancy of seed dispersers and unable to germinate with pulp or under parent trees³³ should be driven by dispersal limitation since the seeds would not be able to establish even in absence of predation.

Future studies should thus attempt to identify patterns in the responses to defaunation across plant species traits to enable the inclusion of the magnitude of this variation when modelling the effects of seed disperser and predator loss. The inclusion of both mutualistic and antagonistic interactions is a necessary step to make more realistic predictions about the consequences of defaunation on ecosystem services. While it is clear that the extinction of large-seeded, animal-dispersed species results in a carbon stock loss that cannot be totally compensated for small-seeded or abiotically dispersed species^{8–10}, the magnitude of the carbon loss may have been overestimated. There is a need to take into account the feedback induced by redundant frugivore and predator communities and the fact that many plant species can suffer from a decrease in recruitment rather than extinction⁹. It is also urgent to better understand the possible effect of density-dependent mortality after plant recruitment³⁴. In our study, we identified the reduced recruitment success of undispersed seeds after one year. This higher density-dependent mortality is likely to affect later stages (e.g., the at least three-year recruitment stage in *Cryptocarya crassifolia* in Madagascar)¹⁵, and including this effect in future models would certainly improve our evaluation of carbon stocks.

Present-day seed dispersal, predation and post-dispersal events such as trampling and herbivory, have direct consequences on the future carbon stocks of tropical forests in a similar way to how past plant-animal interactions determined current carbon stocks. The ecological knowledge of the contribution of specific frugivore communities to plant recruitment allows to add value to their ecological services³⁵. If an area is given a higher monetary value because it harbors a complete frugivore community, assuring the long-term maintenance of carbon stocks, policy makers and land owners should be encouraged to preserve both wildlife and forests, or even facilitate the restoration of extinct plant-animal interactions³⁶. Estimates of the monetary value of ecosystem services are relatively common for pollination services but still extremely rare for seed dispersal³⁷. Although one can argue that we cannot “value the priceless”, it should be noted that the objective is rather to increase the awareness of the general public and policy makers³⁷ whose daily decisions are driven by the price that we explicitly or implicitly give to an ecosystem³⁸. Consequently, bad decisions can be made because we have a better idea of the value of a plantation than the value of a forest³⁸. To be able to do that, we need to better know the contribution of the frugivore community to forest regeneration. Actions to prevent charismatic animal extinction will contribute to ensuring the economic value of possible REDD+ programs (Reducing Emissions from Deforestation and forest Degradation). Based on the results of our studied species, a complete assemblage of seed dispersers and predators must be protected to guarantee REDD+ economic values but more studies are necessary to confirm this result for plant species with different seed traits. Since biomes with high carbon storage also harbor high biodiversity, the application of carbon-based conservation is likely to benefit many areas³⁹. However, we must keep in mind that other conservation strategies must also be taken into account since carbon-poor regions with high biodiversity

exist and might be jeopardized by the large-scale implementation of REDD+³⁹. Although challenging and somewhat controversial, the attribution of monetary values to the ecological services provided by wildlife might be an important strategy to encourage their conservation.

Methods

Study site and model species. We studied the recruitment of a long-lived tree species, *Cryptocarya mandioccana* (Lauraceae), that relies on large mammals and birds to disperse its seeds⁴⁰. *C. mandioccana* is a hardwood tree (0.72 g/cm³) that can reach up to 35 m in height and has yellow fleshy fruits containing one seed; the seeds are 1.34–3.00 cm in length and 1.16–1.92 cm in width^{40,41}. Their seeds are dispersed by two primate species (the southern miqui, *Brachyteles arachnoides*, and the southern brown howler monkey, *Alouatta guariba*) and one large cracid bird (jacutinga, *Aburria jacutinga*)^{40,42}. Tapirs (*Tapirus terrestris*) are also thought to disperse *C. mandioccana* seeds but are likely not a reliable disperser for this species since our study did not identify seed dispersal events despite a quite large sampling effort (see Methods S4 in Supporting Information). Rodents (e.g., agoutis, *Dasyprocta* spp., pacas, *Cuniculus paca*, and small rodents such as *Euryoryzomys russatus*) and peccaries (white-lipped peccaries, *Tayassu pecari*, and collared peccaries, *Pecari tajacu*) are the main seed predators. Effective secondary seed dispersal by agoutis or other small rodents is quite unlikely since they rarely cache seeds smaller than 5 g⁴³ (*C. mandioccana* seed mass = 2.4 g)⁴⁴.

We worked in non-fragmented Brazilian Atlantic Forest to avoid any potential bias due to edge and fragmentation effects⁴⁵. We studied the assemblage of seed dispersers and predators of *C. mandioccana* in three protected areas with distinct community compositions in 2011 and 2012 (Table 1; see Fig. S1 in Supporting Information). These protected areas used to contain all native seed dispersers and predators of *C. mandioccana*⁴⁶, but illegal hunting led to the severe population decline of large-bodied species, particularly miquis, tapirs and white-lipped peccaries. The first site, located in the highlands of Carlos Botelho State Park (São Miguel Nucleus), harbors the complete set of seed dispersers (tapirs, miquis, brown howler monkeys, and jacutingas) but lacks large seed predators (white-lipped peccaries)⁴⁷; we classified it as “intact”. The second site, Ilha do Cardoso State Park, lacks tapirs and miquis but harbors all seed predators (small rodents, agoutis, white-lipped and collared peccaries)⁴⁸; we classified it as “moderately defaunated”. The third site, classified as “defaunated”, is located in the lowland forests of Carlos Botelho State Park (Sete Barras Nucleus) and harbors only jacutingas as seed dispersers, and small rodents and agoutis as seed predators⁴⁷ (Table 1). All experiments were approved by the “Ministério do Meio Ambiente - MMA” and “Instituto Chico Mendes de Conservação da Biodiversidade” of Brazil through the authorization number 26261 and by the “Secretaria do Meio Ambiente” of São Paulo State through the authorization number 260108-000.577/2011. The study complies with current Brazilian laws.

Data collection. We defined the recruitment success ($RS_{s,m}$) of *C. mandioccana* at our three study sites as the percentage of seeds produced by a tree in one year that will result in seedlings surviving for one year⁴⁹. We evaluated the $RS_{s,m}$ by estimating the contribution of each disperser to dispersal, germination, and seedling establishment. The contribution of seed dispersers depends on the probability of seed removal (P_s), the probability of germination after passing through the disperser’s gut (G_s), the dispersal distance probability (D_{sm}), and the seedling survival at each dispersal distance (T_m), with s being the disperser and m the dispersal distance, modified from ref. 49.

$$RS_{s,m} = \left[P_s G_s \sum_{s=1}^x \sum_{m=1}^y (D_{sm} T_m) \right] * 100 \quad (1)$$

We determined seed removal by arboreal frugivores through 108 to 172 h of focal observations of fruiting *C. mandioccana* trees in each area and by terrestrial frugivores through 270 to 463 days of camera trapping (see Supplementary Method S4 and Table S5). Seed germination success was assessed through *in situ* germination experiments of defecated seeds, seeds with pulp and seeds without pulp (see Supplementary Method S4). We determined the seed dispersal distances from conspecific trees by following habituated and semi-habituated groups of miquis and howler monkeys, respectively, and by searching for tapir and jacutinga feces (see Supplementary Method S4). Finally, we assessed seedling survival through seed predation experiments at four distances from *C. mandioccana* trees (5, 15, 30, and 50 m) (see Supplementary Method S4).

Data analyses. *Contribution of seed disperser to recruitment success.* We estimated the recruitment success and the contribution of each disperser using equation 1. The overall recruitment success corresponds to the activity of the current frugivore assemblage at each site, in 2011–2012, with data from the two years pooled together. We used a one-way ANOVA for a randomized block design to test the effect of seed treatment on germination success in each area. We used a generalized linear mixed model to test the effect of distance to the parent tree (fixed effect) on the one-year survival of dispersed seeds (response variable) using the “lme4” package⁵⁰. As random effects, we included an intercept for trees as well as by-tree random slopes. The error structure of the response variable fits a Poisson distribution, and thus we used the logarithmic link function, and a χ^2 test for significant effects of the explanatory variables in the model.

Compensatory effect and expected recruitment success. We simulated a sequence of seed disperser loss (from the largest to smallest frugivore) in the intact area to explore how seed disperser and predator extinctions affect *C. mandioccana* recruitment. We considered three scenarios based on the seed predator community and compensatory effects of the disperser community. The loss of seed dispersers without compensation consists of removing the contribution of the extinct disperser in the calculation of recruitment success (by zeroing out its seed removal probability and correcting the value of spat out and undispersed seeds in Table S2) without changing the values

of the remaining dispersers. When a compensatory effect was added, the values of seed removal of the remaining dispersers as well as of spat out and undispersed seeds were changed according to field observations, i.e., data from the other communities. The effect of seed predators was calculated by applying the escape curves (survival according to distance) of the three study areas to the intact site.

Data availability. The datasets generated during and/or analyzed during the current study are included in this published article (and its Supplementary Information files) or are available from the corresponding author on reasonable request.

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Author Contributions

L.C. and M.G. conceived the ideas and designed the methodology; L.C. collected the data; L.C., C.B., and M.G. analyzed the data; L.C., C.B. and M.G. wrote the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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**CHAPTER 4.PUTTING A PRICE TAG ON FRUGIVORE SEED DISPERSAL
SERVICE TO CARBON STOCK MARKETS**

This chapter is under review in Conservation Letters. Authors: Bello, C., L. Culot, C. Ruiz, J. L. F. Batista, H. T. Z. d. Couto, and M. Galetti

Putting a price tag on frugivore seed dispersal service to carbon stock markets

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Keywords:	Economic valuation, frugivores, seed dispersal, ecosystem service, carbon stock, <i>Brachyteles arachnoides</i> , <i>Alouatta guariba</i> , <i>Aburria jacutinga</i>
Abstract:	Defaunation, extinction and decline of animal populations, erodes ecosystem services with negative effects for human wellbeing. However, economic impacts of defaunation are poorly known. Defaunation of large frugivores alter the recruitment of hardwood trees, reducing the carbon stock services. We are presenting the first economic evaluation of the frugivores seed dispersal service to tropical carbon markets. Based on the dispersal contribution of three endangered large frugivores to tree species with high carbon storage capacity, we quantify their economic contribution to carbon markets. The loss of seed dispersers would reduce the carbon stock in 2.5%. Adding the loss of seed predators the reduction would rise to 3.5%. The economic contribution of our target dispersers rises from US\$11.1/ha to US\$ 43.4/ha. We highlight the importance of animal role to guarantee long-term viability of carbon markets. We are convinced that the knowledge of the economic consequences of defaunation can encourage animal conservation.

Putting a price tag on frugivore seed dispersal service to carbon stock markets

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Abstract

Defaunation, extinction and decline of animal populations, erodes ecosystem services with negative effects for human wellbeing. However, economic impacts of defaunation are poorly known. Defaunation of large frugivores alter the recruitment of hardwood trees, reducing the carbon stock services. We are presenting the first economic evaluation of the frugivores seed dispersal service to tropical carbon markets. Based on the dispersal contribution of three endangered large frugivores to tree species with high carbon storage capacity, we quantify their economic contribution to carbon markets. The loss of seed dispersers would reduce the carbon stock in 2.5%. Adding the loss of seed predators the reduction would rise to 3.5%. The economic contribution of our target dispersers rises from US\$11.1/ha to US\$ 43.4/ha. We highlight the importance of animal role to guarantee long-term viability of carbon markets. We are convinced that the knowledge of the economic consequences of defaunation can encourage animal conservation.

Introduction

Defaunation, the local or global animal extinction or population decline (Dirzo et al. 2014), leads to cascading effects in natural ecosystems affecting other organisms and eroding key ecosystem services and functions (Kurten, 2013; Markl et al., 2012; Poulsen, Clark, & Palmer, 2013). Defaunation has negative effects on ecosystem services such as pollination, seed dispersal, pest control, nutrient cycling, decomposition, water quality, soil erosion and carbon stock (Bello et al., 2015; Dirzo et al., 2014). However, economic impacts of defaunation on ecosystem services are still poorly explored.

In fact, the attempts to value the importance of animals as provider of ecosystem service are concentrated on the pollination ecosystem service through its contribution to crop production (Hein, 2009; Mburu, Collette, Gemmill, & Hein, 2006). Pollination, provided mostly by bees, supports agriculture economy and food safety. Around 75% of global primary food crops require animal pollination (Klein et al., 2007). It is estimated that the worldwide pollinator decline produces an economical loss in crop production between \$117 and \$200 billion dollars per year (Costanza et al., 1997; Nicola Gallai, Salles, Settele, & Vaissière, 2009; Pimentel et al., 1997). These monetary values have motivated the national governments to establish political organisms to counter pollinator declines (N. Gallai & Vaissière, 2009).

However, efforts to assess the economic value of animals' contribution to seed dispersal service are lacking. In particular, the loss of large frugivores affects seed dispersal and natural regeneration of large seeded trees. Large seeded trees tend to grow taller and have dense wood compared to small seeded trees, and consequently they are able to store more carbon (Bello et al., 2015). Defaunation is particularly important in tropical forests

where frugivores disperse 70 to 94% of the woody plant species (Almeida-Neto, Campassi, Galetti, Jordano, & Oliveira-Filho, 2008; Dixon et al., 1994; Howe & Smallwood, 1982; Jordano, 2013) and where ~59% of the world's forest carbon is stored (Dixon et al., 1994).

Therefore, as the stock of tropical carbon is threatened by the decline of large frugivores ((Bello et al., 2015; Peres, Emilio, Schiatti, Desmoulière, & Levi, 2016; Rumeu et al., 2017), we can assess in monetary terms the contribution of frugivores to the seed dispersal ecosystem services through carbon markets. Here, we are presenting the first attempt to value the economic impacts of animal loss through their contribution to carbon markets in tropical forest. Using empirical data of the dispersal contribution of endangered large frugivore to tree species with high carbon storage capacity, within a defaunation gradient in a tropical forest (Culot, Bello, Ferreira Batista, Zarate do Couto, & Galetti, 2017), we were able to determine the economic contribution of three large frugivores to carbon markets.

Methods

Frugivore contribution to recruitment success.

We used the frugivore contributions to the recruitment success of a typical hardwood tree species, *Cryptocarya mandioccana* (Lauraceae), in the Atlantic Forest estimated by (Culot et al., 2017). The authors investigated the contributions of three seed dispersers to a large-seeded hardwood tree species: muriquis (M) (*Brachyteles arachnoides*), howler monkeys (H) (*Alouatta guariba*) and Jacutingas (J) (*Aburria jacutinga*); in three areas across a defaunation gradient of seed dispersers and predators.

Culot et al. (2017) define the recruitment success as a result of the contribution of each frugivore to dispersal, germination, and seedling establishment. The contribution of

seed dispersers depends on the probability of seed removal (P_s), the probability of germination after passing through the disperser's gut (G_s), the dispersal distance probability (D_{sm}), and the seedling survival at each dispersal distance (T_m), with s being the disperser and m the dispersal distance (Culot et al., 2017).

$$RS_{s,m} = [P_s G_s \sum_{s=1}^x \sum_{m=1}^y (D_{sm} T_m)] * 100 \quad (\text{equation 1})$$

The overall contribution of the three frugivores to the recruitment success varies according to the level of defaunation in seed dispersers and predators. The loss of large frugivores induces a partial compensation effect, which means that the loss of the largest frugivore (muriqui), is partially compensated by the activity of the smaller ones (Howler monkeys and Jacutinga) (Culot et al., 2017). Remarkably, the authors also found that, as the level of defaunation in seed predators increases, the predation pressure increases due to an over-bloom of small rodents (Galetti et al. 2015, Culot et al. 2017). This means that the cumulative loss of the frugivores along the defaunation gradient will have different impacts according to the predation pressure (Culot et al. 2017). Hence, Jacutingas and howler monkeys are responsible for the recruitment success of 2 to 6% of the seeds, while miquis are responsible for 1 to 13% according to the level of defaunation in seed predator. The loss of muriqui will reduce the recruitment success from 47 to 69%. The additive effect of the loss of howler monkeys will decrease the recruitment success by 56% to 83%. A community without any of the three frugivores will decrease the recruitment success by 71 to 95%. Finally, in a community intact in seed dispersers, the loss of seed predators reduces the recruitment success of large seeded trees by 10 to 69%. (Table 1).

Carbon storage calculation

We estimated the aboveground biomass based on the non-defaunated forest where Culot et al. (2017) collected the empirical data of frugivore contribution to recruitment success (Carlos Botelho State Park). We decided to use Carlos Botelho State Park as a baseline for carbon stock because it represents a pristine Atlantic Forest where current carbon stock results from the activity of the complete set of seed dispersers and predators. In this forest, we surveyed all tree individuals with a diameter at breast height (DBH) bigger than 5 cm in a 11.52 ha plot. For each tree individual, we measured the DBH and identified the species. We used mean wood density values (ρ) for each species obtained from Chave et al (2005). Whenever this mean value of wood density was not available at species level, we used generic means instead. The aboveground biomass was accessed using the Chave et al (2014) equation:

$$AGB = \exp(-1.803 - 0.976 E + 0.976 \ln(\rho) + 2.673 \ln(DBH) - 0.0299(\ln(DBH))^2)$$

(Equation 2)

Where AGB is the aboveground biomass, DBH is the diameter at breast height, ρ is the wood density, and $E = 0.19112$ is a measure of environmental stress for the study area obtained from Chave et al (2014). Finally, to determine the carbon concentration in the AGB, we used the estimation of 40% of water in the AGB and 48.5% of carbon in the dry biomass (Higuchi & Carvalho, 1994).

Simulations of future carbon storage decrease due to the loss of frugivores

We determined the contribution of large frugivores to carbon storage capacity by simulating the decrease of recruitment success of large-seeded-species dispersed by each frugivore and calculating the changes in carbon stock potential. To determine which tree species of the plot community are dispersed by each animal, we used the Atlantic-frugivore dataset which has information of approximately 5,000 fruit-frugivore interactions from the entire Atlantic Forest (Bello et al., 2015). The dataset includes animal- and plant-oriented studies that reported the occurrence of interactions, i.e. a given animal species feeding on fruits of a distinct plant species.

Each simulation consisted in two steps: first, we removed a given percentage of large seeded individuals according to the reduction of recruitment success estimated for disperser and predators' scenario (e.g: in the absence of muriquis, we removed a percentage of the tree species dispersed by muriquis). Second, we made a compensatory replacement of the individuals by adding the same numbers of individuals removed but of species drawn from the remaining community pool, in order to construct a new final community. We allowed that remaining large seeded species dispersed by others animals can enter in the replacement game. In the simulations, we assumed saturated communities with zero-sum game dynamic and immigration rate equals to zero (Hubbell, 2001). We made sure that the basal area and the total number of individuals remained constant. Finally, we evaluated the initial and the final carbon stock using the equation mentioned above. We made 1000 repetitions of each simulation for each dispersal and predation scenario, and we tested the significance of the carbon change with a two-way ANOVA and a post-hoc comparison with a Turkey test. All the tests were performed with a percentage of error of 0.05.

Valuing the seed dispersal services

We used a modification of the production value approaches. This is a widely used approach to value pollination ecosystem service by accessing the crop production attributable to pollination (Allsopp, de Lange, & Veldtman, 2008; Losey & Vaughan, 2006; Morse & Calderone, 2000; Olschewski, Tschardtke, Benítez, Schwarze, & Klein, 2006). This method assumes that the production, or yield, will be reduced when pollinators decline. The reduction in yield is approximated using studies of the dependency of fruit set for insect pollinators (Klein et al., 2007). The expected fractional yield loss in the absence of pollinators is then multiplied by the market value of production. In an analogous way, we valued the dispersion ecosystem service as the contribution of each disperser to the carbon stock “yield” of the forest. We also assume that the carbon stored in the forest will decline with the loss of seed dispersers (Bello et al., 2015; Osuri et al., 2016). Later, we multiplied this contribution by the market value of production.

To calculate the contribution of each seed disperser we estimated the difference of the mean carbon stock per hectare between the three scenarios of disperser loss (loss of M, loss of M+H, loss of M+H+J) at the three seed predation levels. For carbon credits calculations, we multiplied the molecular weight of equivalent carbon dioxide by a modest average transaction price of carbon for Latin America (US\$5.00/ton) (Kooten & Johnston, 2016; Sathaye & Shukla, 2013):

$$Dv_i = Cc_i * Ca * Cp \quad (\text{Equation 3})$$

Where: Dv is the dispersion value, Cc_i is the carbon contribution of the animal i , Ca is the carbon stock in the area, and Cp is the carbon price in the market (Hamrick & Goldstein, 2016).

Results

We evaluated the aboveground biomass of the adult tree community (all species) currently present at the non-defaunated forest as 314.1 tons/ ha (88.35 tons of carbon/ ha). Taking into account the area of the park we estimated a total potential carbon stock of 3,325,847 tons with a value of US\$ 16,629,237 (at average market prices). We assumed that the current potential carbon stock in a pristine Atlantic Forest (the Carlos Botelho State Park) results from a recruitment success corresponding to the activity of the complete set of seed dispersers and predators.

We observed a significant decrease of potential carbon stock within almost all levels of disperser and predator loss (Fig. 1). The loss of seed predator species would lead to a 2.7% reduction in future carbon storage capacity. Adding the effects of seed disperser loss would result in a total reduction of 3.5% of total carbon stock (Fig. 1, red scenario). Interestingly, the disruption of the seed predator community would lead to a similar loss of carbon stock as the disruption of the seed disperser community: -2.6% in a community intact in terms of seed dispersers but defaunated in seed predators versus -2.5% in a community defaunated in seed dispersers but intact in seed predators. The loss of seed dispersers in a community already defaunated of its seed predators has lower impact on carbon stock than in a non-defaunated community (-0.9% in defaunated community versus -2.5% and -2.7% in non-defaunated and semi-defaunated communities) (Fig. 1).

This potential carbon storage loss will impoverish the carbon budget of areas that suffer a defaunation process. In economic terms, we found that the dispersal economic contribution of our target disperser community (M+H+J) to carbon stock rises from US\$11.1/ha to US\$ 43.4/ha depending on whether the community is defaunated or not in seed predators. Muriqui population can contribute to maintain, in average, US\$17/ha (from US\$ 0.39/ha to US\$29.86/ha). Howler monkey population contributes to maintain in average US\$9.51/ha (from US\$5.5 to US\$13.3). In addition, Jacutinga population maintains in average US\$5.08/ha (from US\$ 1.9 to US\$ 9.3). The contribution of the dispersal ecosystem service of the muriqui population to the carbon budget is greater for the Muriqui populations is ~6 times greater than the contribution of Howler and Jacutinga populations, as long as the seed predators' community remains undisturbed. However, when the seed predator community is disrupted the dispersal contribution to carbon stock of the Howler and Jacutinga populations becomes 25 times more important. Finally, we estimate that the contribution of seed dispersal ecosystem service of these three animal species for the carbon budget of the Carlos Botelho State Park is US\$1,515,318 (at average market prices).

Discussion

Estimates of the monetary value of ecosystem services are relatively common for pollination services but still extremely rare for seed dispersal. Our study is the first, to our knowledge, to value the animal dispersal ecosystem services in a tropical forest through the potential economic impacts of the loss of dispersers in carbon markets. We estimate the direct economic value of the dispersal service performed by these three large frugivores to 43 US\$/ha, being the largest species (muriqui) of higher value than the smaller species (howlers and jacutingas) due to their higher contribution to recruitment success.

The economic value presented here should be considered as a conservative assessment of the gross value of the frugivore dispersal services. The estimated value corresponds to the potential carbon stock production that can be directly attributed to the seed dispersal performed by those three large frugivores, which are the main contributors to the recruitment of hardwood species. However, the small seed dispersers also contribute to carbon stock. Besides, positive externalities of the seed dispersal services may exist. For instance, seed dispersal contributes to provide a variety of benefits including food and fiber, plant-derived medicines, pest control, restoration, ornamentals and other aesthetics, genetic diversity, and overall ecosystem resilience (Millennium Ecosystem Assessment, 2005), for which the economic values are not incorporated in this study.

We are aware that the economic valuation method implemented here is simple and that we are valuing just a part of the total economic value of the dispersal ecosystem service. The total value of the ecosystem service includes the value of direct use and the value of non-use (value society is willing to pay just for the option of using it or for its existence) (Mburu et al., 2006). Our valuation corresponds to the direct value of use estimated through the contribution of seed dispersal in the direct market price of carbon market production, in a similar sense done for pollination ecosystem service (Brading, El-Gabbas, Zalat, & Gilbert, 2009; Losey & Vaughan, 2006; Morse & Calderone, 2000) (Barfield, Bergstrom, & Ferreira, 2012; N. Gallai & Vaissière, 2009). The market price method reflects the economic value that is bought and sold in markets (Hein, 2009; Newell, Pizer, & Raimi, 2014). In the case of carbon stock, we used the largest ecosystem service market in the EU Emissions Trading Scheme (ETS) designed to reduce carbon emission (Boehnert, 2016). Herein, the market prices paid by transaction reflect the value of a product produced by the dispersal service. However, many improvements and research have to be done to properly estimate the particular changes to consumer and producer

surplus. According to neo-classical welfare economics, the welfare generated by an ecosystem service is determined by the aggregated utility (surplus) gained by all individuals because of the provision of the ecosystem service (Hein, 2009).

Hence, our estimated value is a local-low-bound value, extrapolation to other systems needs to be considered carefully. The value corresponds to a pristine Atlantic Forest where large frugivores still have a lot of contribution to tree regeneration (Bueno et al., 2013; Culot et al., 2017). However, in depauperate forest or in a forest dominated by non-animal disperser tree species, the contribution of dispersers to carbon stock is likely to be reduced (Osuri et al., 2016). By now, the two studies that have tried to value dispersal service (including the present study) reveal different values. Hougner, Colding, and Söderqvist (2006) used the replacement cost method to assess a value between US\$ 2100 to US\$ 9400/ha for the seed dispersal ecosystem service performed by jays (*Garrulus glandarius*) in an oak forest in Sweden. Although the cost replacement method tends to overestimate the economic value and incorporate all the derivative benefits (e.g. (Allsopp et al., 2008)), the difference in the estimated values shows the uncertainty of the current knowledge around the seed dispersal value. Therefore, national and global assessments of the seed dispersal contribution to economy are still encouraged and a lot of research has to be developed. We need a better comprehension of the seed dispersal services in both ecological and economical terms to different markets and human wellbeing (Daily et al., 2000; Turner et al., 2003). Our hope is that economic valuation of dispersal ecosystem services will provide information on the economic consequences of defaunation and contribute to the decision-making processes regarding selection of alternative mitigation strategies.

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CHAPTER 5. MAXIMIZING BIODIVERSITY CONSERVATION AND CARBON STOCKING IN RESTORED TROPICAL FORESTS

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Maximizing biodiversity conservation and carbon stocking in restored tropical forests

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Abstract

Assessing the conservation value of restoration plantings is critical to support the global forest landscape restoration movement. We assessed the implications of tree species selection in the restoration of Brazil's Atlantic Forest regarding carbon stocking and species conservation. This assessment was based on a comprehensive dataset of seedling acquisition records from 961 restoration projects, more than 14 million seedlings, 192 forest remnants, and functional data from 1,223 tree species. We found that animal-dispersed trees with larger seeds tend to have higher seed prices, yet are underrepresented in the seedlings acquired for restoration plantations. Compared to forest remnants, fruit supply potentially offered by the species acquired for restoration plantings is lower for birds, but higher for bats. Reduced abundance of medium- and/or large-seeded, animal-dispersed trees lead to declines of 2.8–10.6% in simulated potential carbon stocking. Given the uncertainty in these estimates, policy interventions may be needed to encourage greater representation of large-seeded, animal-dispersed tree species in Atlantic Forest restorations. These findings provide critical guidance for recovering tree functional diversity, plant-frugivore mutualistic interactions, and carbon stocking in multi-species tropical forest restoration plantings.

KEYWORDS

forest nurseries, keystone species, mutualistic interactions, restoration monitoring, restoration plantations, seed dispersal, seed size, seedling production, species reintroduction

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1 | INTRODUCTION

Ecological restoration plays a crucial conservation role in fragmented mega-diverse regions, particularly for endangered species with low dispersal rates (Derhe, Murphy, Monteith, & Menendez, 2016; Possingham, Bode, & Klein, 2015). Frameworks for assessing the conservation value of restoration plantings are not yet developed, but they are urgently needed to support the emerging movement of global forest and landscape restoration (Chazdon et al., 2017; Holl, 2017). Biodiversity recovery is assumed to be a co-benefit of tree cover gains (Banks-Leite et al., 2014; Mukul, Herbohn, & Firn, 2016), yet full recovery was not achieved in forest restoration projects that have been investigated so far (Crouzeilles et al., 2016; Moreno-Mateos et al., 2017). Species with impoverished populations, limited dispersal capacity, and important functions as food resources for animals should be prioritized for active reintroduction in order to increase the conservation value of restored forests (Cole, Holl, Keene, & Zahawi, 2011). However, seedlings from these species are often hard to find or too costly to include in many restoration projects.

In tropical forests, large-seeded, animal-dispersed trees are commonly targeted for reintroduction as a consequence of their limited recolonization of regenerating forests and high ecological importance (Cole et al., 2011). These species have low seed availability in human-dominated landscapes due to naturally low species abundance, overexploitation for timber production (Oliveira, Santos, & Tabarelli, 2008), higher sensitivity to edge effects (Osuri & Sankaran, 2016), and lack of large-bodied seed dispersers (Galetti et al., 2013; Harrison et al., 2013). These species make up a substantial proportion of late-successional tropical tree species, have mutualisms with threatened vertebrates (Howe & Smallwood, 1982), and often have a higher potential to store carbon than other tree species due to their larger size, denser wood, and greater longevity (Bello et al., 2015; Peres, Emilio, Schietti, Desmouliere, & Levi, 2016).

The Atlantic Forest of Brazil exemplifies the need for assisted recolonization of large-seeded, animal-dispersed trees in tropical forest restoration. Currently, only 12% of the Atlantic Forest biome remains forested (Ribeiro, Metzger, Martensen, Ponzoni, & Hirota, 2009), and most forest remnants are defaunated of large mammals capable of dispersing large seeds (Jorge, Galetti, Ribeiro, & Ferraz, 2013). Yet animal-dispersed trees can compose up to 89% of tree species in a single community (Almeida-Neto, Campassi, Galetti, Jordano, & Oliveira, 2008). Forest restoration projects in this region have been promoted—and in some cases obligated by the Forest Code and other legal instruments (Brancalion et al., 2016)—to mitigating an enormous species extinction debt (Banks-Leite et al., 2014) and safeguarding water supplies and energy to a large and growing population (nearly

60% of the Brazil's population lives in this biome and 62% of Brazil's electricity is produced by reservoirs in this biome; Joly, Metzger, & Tabarelli, 2014).

From 2009 onward, Atlantic Forest restoration projects received a major push from the establishment of The Atlantic Forest Restoration Pact (AFRP)—a multi-stakeholder coalition with over 270 private companies, governments, NGOs, and research organizations working collaboratively to restore 15 million hectares of forests by 2050 (Melo et al., 2013). AFRP projects have employed high-diversity (>80 species) tree plantations to recover species-rich forests in sites with low ecological resilience (Rodrigues, Lima, Gandolfi, & Nave, 2009). However, less attention has been paid to the particular functional groups that compose these high-diversity plantings (Brancalion & Holl, 2016), which could strongly influence carbon sequestration and biodiversity conservation in restored forests (Bello et al., 2015).

Here, we used seedling acquisition records in the Atlantic Forest biome to assess the potential conservation value of restoration plantings in terms of functional diversity, potential for supporting plant-frugivore mutualistic interactions, and carbon stocking potential. Three overarching research questions and associated hypotheses guided our investigation: (i) What is the representation of animal-dispersed trees acquired for restoration projects in terms of their taxonomic and functional diversity? We expected animal-dispersed trees, especially those bearing large seeds, to be underrepresented in restoration projects compared to natural forest remnants. (ii) How does the proportion of medium- and large-seeded, animal-dispersed trees that are planted to restore forests compare with nearby natural forest remnants, and how will this difference affect potential carbon stocking? We expected that the relative abundance of medium- and large-seeded, animal-dispersed trees would be lower in restored forests compared to remnant forests, leading to lower potential carbon stocking. (iii) How is seed price influenced by seed size, dispersal syndrome, and frequency of species use in restored forests? We expected that large-seeded, animal-dispersed tree species would be more expensive and less frequently used in forest restoration compared to smaller-seeded, abiotically dispersed tree species.

2 | METHODS

2.1 | Restored and reference forests

The study was performed in the south and southeastern parts of the Atlantic Forest of Brazil (Figure 1), where landscapes are dominated by intensive agriculture and farmers have been

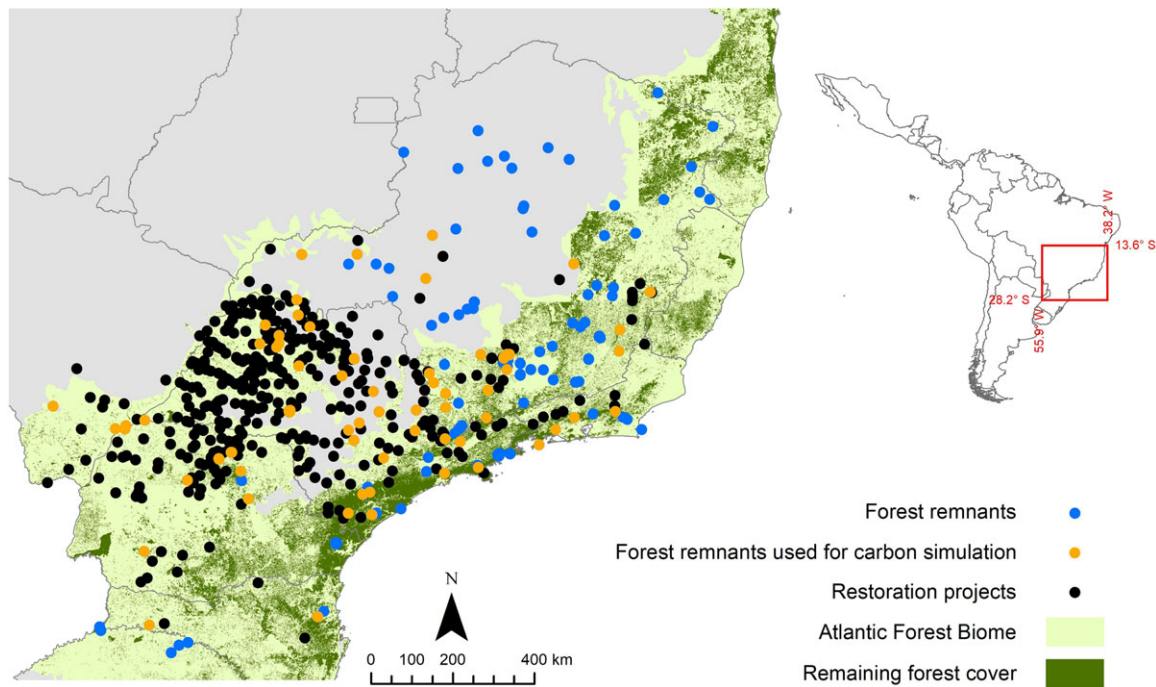


FIGURE 1 Restored forests and natural forest remnants in the Atlantic Forest. Forest remnants also occur in areas of Seasonal Semideciduous Forest outside of the official, coarse-scale map of the biome, where some restoration projects were also established. Restoration projects were distributed across six Brazilian states (Santa Catarina, Paraná, São Paulo, Mato Grosso do Sul, Minas Gerais e Rio de Janeiro), which borders are represented by black lines in the map

obliged to restore native vegetation to comply with environmental legislation (for more information, see Brancalion et al., 2016; Joly et al., 2014; Rodrigues et al., 2011). We used data on abundance and composition of tree seedlings acquired for 961 restoration projects distributed in private properties within 348 municipalities and six states, comprising a total of 14,664,524 native tree seedlings (Figure 1). Each restoration project accounted for an approximate area of 10 ± 8.7 hectares (mean \pm SD), totaling ca. 10,000 hectares, with density of ca. 1,500 seedlings per hectare. Seedling species abundances for each project were based on seedling acquisition records from 29 private forest nurseries between 2002 and 2015. The conservation NGO SOS Mata Atlântica purchased the seedlings, donated them to restoration projects, and field checked if the donated seedlings had been outplanted by the land manager; seedlings that were purchased but never planted were excluded from this analysis. Thus, we did not work with forest inventory data; rather, we evaluated species composition based on seedlings purchased for and planted in restoration projects. Survival of planted seedlings is usually high ($>70\%$) in the study region, so most of the initial composition of forests undergoing restoration are determined by the species pool initially used in tree plantings. The functional composition of tree species acquired for restoration projects was compared to that of 192 forest remnants older than 80 years distributed in southeastern and south Brazil (Figure 1). Species composition and structure of these remnants were

obtained from peer-reviewed and grey literature describing forest inventory assessments (dbh > 4.8 – 5 cm; remnants > 1 ha) deposited in the TreeCo database (Lima et al., 2015). A subset of 69 remnants located in the vicinity of restoration projects (Figure 1) was further used for aboveground carbon stocking simulations.

2.2 | Seed dispersal syndrome, size, and price

A total of 2,588 and 416 tree species were found, respectively, in 192 forest remnants and in the seedling acquisition records for 961 restoration projects. Of these, 1,223 remnant forest species (48%) and 350 restoration project species (84%) had functional trait information available and were used for subsequent analyses. Seed trait information was obtained through literature survey and measurements using herbarium and museum specimens (Bello et al., 2017). Our trait sample was biased toward more common species, since the abundance of species with trait information was higher than that of species without information (t -test = 3.45, $df = 117.62$, $p = 0.0007$). However, since ecosystem functioning is mostly driven by the more abundant species (Díaz, 2001), our sample may well represent the impacts of species selection on mutualistic interactions with frugivores and carbon stocking. Each species in this subset was categorized according to its seed dispersal syndrome (abiotic- or animal-dispersed), preferential group of vertebrate dispersers (animal-dispersed

species only), and seed diameter (animal-dispersed species only). Seed diameters were generalized into three size classes: small (diameter < 6 mm); medium (6 mm < diameter < 12 mm); and large (diameter > 12 mm), based on the assumption that seeds larger than 12 mm in diameter are predominantly ingested by large-gaped frugivorous birds and mammals (Bello et al., 2015, 2017; Galetti et al., 2013). The mean price per seed was calculated based on the price per kilogram of seeds supplied by six private seed nurseries trading native seeds, for a total of 376 species (186 of which were animal-dispersed), combined with the number of seeds per kilogram for each species, obtained from the literature (Lorenzi, 2002; Souza-Júnior & Brancalion, 2016). When a species was sold by different nurseries, we used the mean price.

2.3 | Data analysis

Question 1: We employed Chi-square statistics to assess the level of floristic representation of the Atlantic Forest species pool per dispersal syndrome in the seedling acquisition records of restoration projects, as well as to compare the proportion of abiotic- and animal-dispersed species and individuals between restoration and remnants. A Kolmogorov–Smirnov test was used to compare the distributions of tree individuals preferentially consumed by bats, carnivores, rodents, primates, small birds (body mass < 80 g and gape size < 12 mm), and large birds (body mass > 80 g and gape size > 12 mm; Galetti et al., 2013) between seedling records and remnants. We identified which plants are eaten by each vertebrate group using the data from Bello et al. (2017).

Question 2: We used simulations to test whether potential carbon stocks in the forests to be restored with the tree assemblages described in seedling acquisition records would be different from forest fragments as a consequence of the differential representation of animal-dispersed species of different seed sizes. Simulations were performed following the methodology developed by Bello et al. (2015); its application for our dataset is described in detail in supplementary material 1. In the simulations, medium- and large-seeded (scenario 1) or just large-seeded (scenario 2) tree species in remnant forests were replaced with tree species from seedling acquisition records, and the difference in potential carbon stocking was estimated. We further estimated the potential economic impacts of carbon stocking losses, considering the market price of carbon credits as US\$5.00 per ton (Hamrick & Goldstein, 2016), and we compared the results with the additional cost of increasing the abundance of species with medium and large seeds to similar levels as in remnant forests (Table S1). We analyzed the Atlantic Forest as a whole and its two major for-

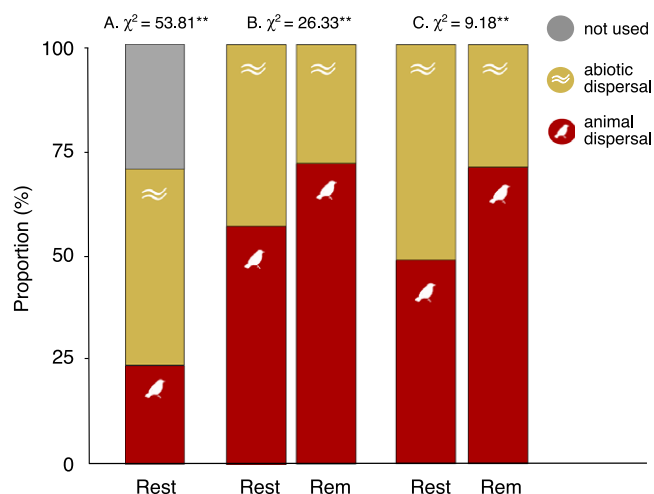


FIGURE 2 Proportion of abiotically dispersed and animal-dispersed tree species, compared by Chi-square tests, used in restored forests (Rest.) and present in forest remnants (Rem.) in the Atlantic Forest of Brazil according to: (A) proportion of species used in relation to the total species pool, (B) proportion of species, and (C) individuals per dispersal syndrome

est types (Seasonal Semideciduous Forests and Rainforests) separately.

Question 3: Species acquired for restoration projects were classified according to their frequency of use, based on the quantiles of the distribution of the number of seedlings per species in tree plantations (Figure S1). A two-step regression model between seed diameter and price was performed for the 186 animal-dispersed species, and between seed mass and price for the 148 abiotic-dispersed species with prices available. These models were used to assign a price for the species used in our dataset that did not have prices available. Kruskal–Wallis tests were used to compare seed price according to species' frequency of use, inclusion in restoration projects, dispersal syndrome, and seed size of animal-dispersed species.

3 | RESULTS

3.1 | Taxonomic and functional diversity of restoration projects

The floristic representation of animal-dispersed species in restoration projects was half of that of abiotic-dispersed species (Figure 2A). Compared to forest remnants, seedling acquisition records showed a lower proportion of animal-dispersed tree species (Figure 2B) and individuals (Figure 2C). Compared to forest remnants, fruit supply potentially offered by the species acquired for restoration plantings is lower for large and small birds, but higher for bats and not affected for other dispersal guilds

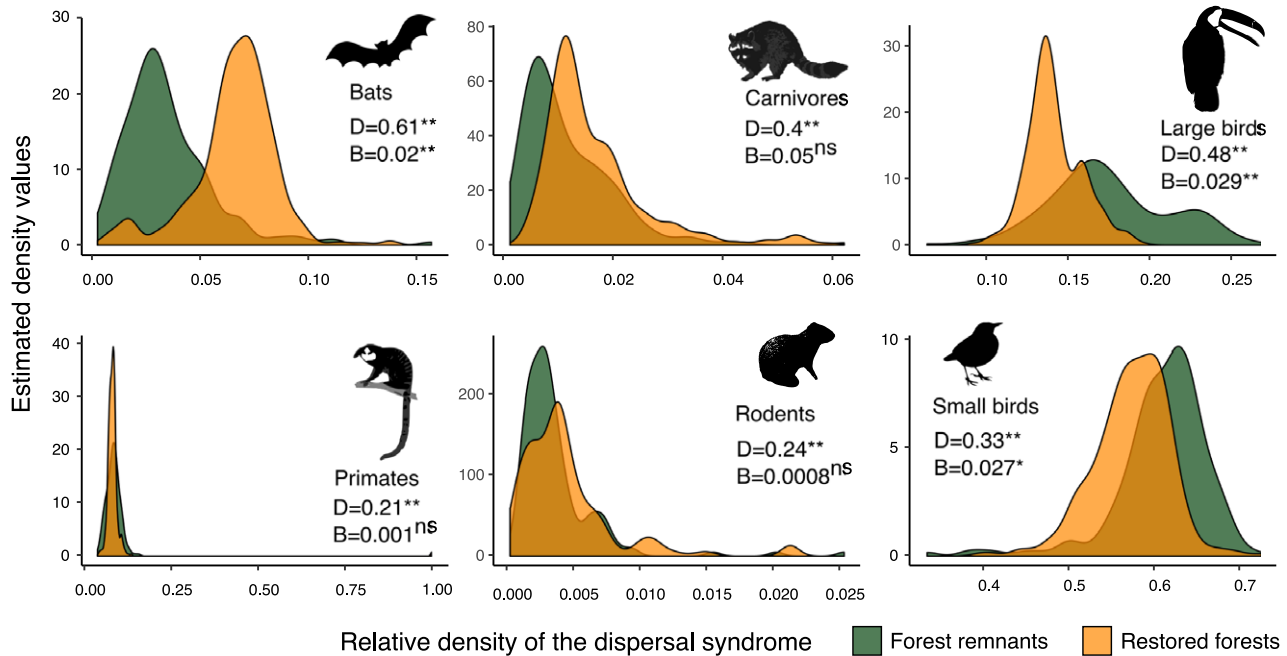


FIGURE 3 Frequency distributions for the relative representation (percent individual density) of tree species in forest remnants and restored forests. Panels indicate the frequencies for tree species providing food for different taxonomic groups of vertebrate frugivores. Each species may supply fruits for one or more frugivore groups, so some may have been counted more than once. Density functions were compared by the Kolmogorov-Smirnov test (D) and means values by Mann-Whitney tests (W)

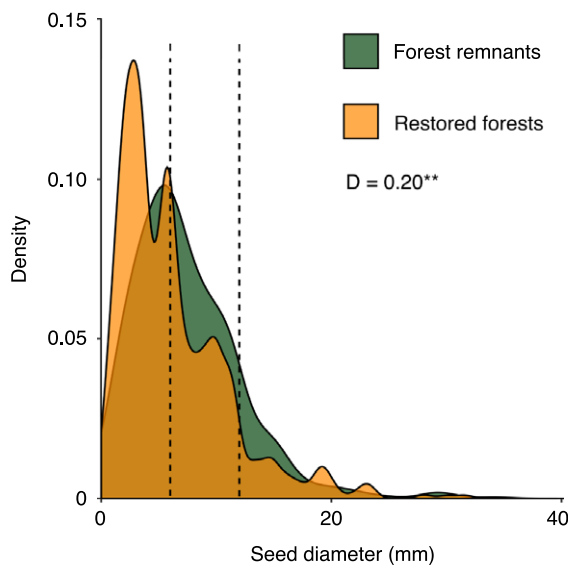


FIGURE 4 Probability density distributions for tree species according to seed diameter (mm) computed for the proportion of individuals of animal-dispersed trees when grouped by seed size in restored forests and forest remnants across the Atlantic Forest of Brazil. Density functions were compared by the Kolmogorov-Smirnov Test (D). Dashed, vertical lines indicate seed diameter threshold values of 6 and 12 mm

(Figure 3). Significantly lower abundances of medium- and large-seeded tree individuals dispersed by animals were found in seedling acquisition records compared to remnants (Figure 4).

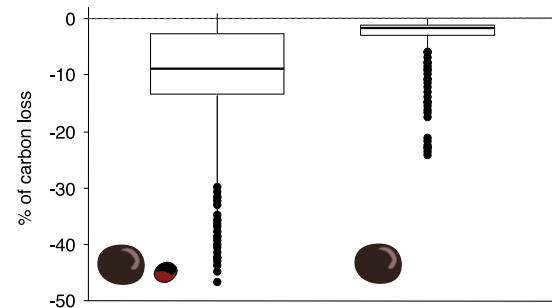


FIGURE 5 Potential effects on carbon stocking if the proportion of individuals with large (seed diameter > 12 mm) and medium seeds (6 mm < seed diameter < 12 mm), and only large seeds, of forest remnants are substituted by the proportion found in restored forests in the Atlantic Forest of Brazil. No outlier was found for carbon gain. In the box plots, the central bar represents the median, boxes represent the interquartile range (IQR), whiskers extend to observations within ± 1.5 times the IQR and dots represent outliers

3.2 | Impacts of species selection on the potential of carbon stocking in restored forests

The reduced abundance of medium- and large-seeded, animal-dispersed tree individuals in seedling acquisition records would lead to reductions in the relative carbon stock potential of restored forests in comparison to forest remnants (Figure 5). The reduced abundance of individuals with medium-sized seeds dispersed by animals resulted in a higher estimated impact on carbon stocking potential in restoration

(decline of 10.6%) compared to the differential abundance of large-seeded species (decline of 2.8%; Figure 5). When projects and remnants were grouped according to the major forest types within the Atlantic Forest region, Semideciduous Forests showed a less intense reduction of carbon stocking potential (large seeds: loss of 2.3%; medium and large seeds: 10.5%; Figure S2) compared to Rainforests (large seeds: loss of 3.2%; medium and large seeds: 14.2%; Figure S2). These aforementioned carbon stocking potential losses, driven by underrepresentation of large-seeded, and medium- plus large-seeded tree species, would cause, in the long term, an estimated reduction of, respectively, US\$ 16.7 to US\$ 63.1 per hectare in carbon credits traded in the international market (Table S1).

3.3 | Seed price and species representation

Small-seeded species were dominant in the set of seedlings acquired for restoration projects, where 25% of the species corresponded to 75% of all seedlings (Figure S1). Overall, species not used in restoration, species with reduced frequency of use, species dispersed by animals, and species with larger seeds had higher seed prices (Figure 6). We found a significant positive correlation between seed size and price for both abiotically dispersed ($r = 0.91$; $t = 27.32$; $p < 0.0001$) and animal-dispersed species ($r = 0.73$; $t = 14.5$; $p < 0.0001$) (Figure S3). The price model based on seed size explained 87% of the variance for abiotic-dispersed species and 68% for animal-dispersed species. Achieving a similar proportion of medium- and large-seeded species dispersed by animals of forest remnants, or of only large-seeded species, would cost US\$31.1 and US\$13.7 per hectare, respectively (Table S1).

4 | DISCUSSION

Large-seeded, animal-dispersed trees were significantly underrepresented among tree species used to restore Brazilian Atlantic Forest on both at species and individual level, with demonstrable consequences for both restoration cost and carbon storage. This shortcoming came despite a well-organized, regional restoration strategy with an emphasis on high-diversity plantings (Melo et al., 2013; Rodrigues et al., 2009). Although species deficits at the planting stage may be compensated through natural recolonization for some guilds at some sites, large-seeded, animal-dispersed species are particularly dispersal limited (Reid, Holl, & Zahawi, 2015; Silva & Tabarelli, 2000), and the highly deforested, defaunated, and fragmented remnants of the Atlantic Forest provide little functional connectivity in many restoration areas (Ribeiro et al., 2009). Collectively, this situation represents an important challenge for conserving and restoring the biodiversity of the Atlantic Forest hotspot; a lack of

large-seeded, animal-dispersed trees not only compromises contemporary biodiversity and ecosystem services within restoration sites, it also precludes the possibility for restoration to promote landscape-scale gene flow for fragmented populations of threatened tree species that are already facing strong selective pressures (Galetti et al., 2013; Zucchi et al., 2017).

Bias against large-seeded, animal-dispersed trees appears to reflect market forces operating at the seed collecting and seedling production stages. The seed market for restoration is biased towards low cost, small-seeded, abiotically dispersed tree species. Seed prices reflect access to trees and fruit, seed cleaning, pre-germination treatments, seed storage, and nursery production (Brancalion, Viani, Aronson, Rodrigues, & Nave, 2012). Large-seeded, animal-dispersed species may be particularly expensive to collect as they often distribute fruit production over long periods (reducing the amount that can be collected during a single visit); produce relatively few fruits per tree and few seeds per fruit (Greene & Johnson, 1994); are competed for by other fauna (sometimes including humans, e.g., Brazil nuts [*Bertholletia excelsa*] in the Amazon); are often tall trees far from edges in more remote forests (increasing collection costs) (Benchimol & Peres, 2015), and occupy more volume in seed storage facilities. These market forces are directly affecting the conservation value of restored forests by biasing the types of seeds and seedlings used in in situ restoration programs. Since the large-seeded, animal-dispersed trees with available seed prices that were used to generate the seed price model tend to be more common than rarer species lacking seed price data, the true cost of some large-seeded species may be higher than that estimated by our analysis, potentially increasing the overall cost of achieving greater species representation of large-seeded, animal-dispersed trees in restored forests.

The negative impacts of species selection bias on potential carbon stocking (−2.8 to −10.6%) were within the range found for other tropical forest regions globally (Osuri et al., 2016). This reduction was stronger for Rainforests, which had a higher proportion of animal-dispersed species, than for Seasonal Semideciduous Forests (Almeida-Neto et al., 2008). Whereas carbon benefits are often viewed as disconnected from biodiversity conservation in practice, in spite of the scientific evidences of this connection (Lindenmayer et al., 2012; Mukul et al., 2016; Strassburg et al., 2010), we showed that investing in a species group with high conservation value (i.e., animal-dispersed, larger-seeded trees) may promote higher carbon stocking in tropical forest restoration. However, the relationship between large-seeded, animal-dispersed trees and carbon stocking is subject to some uncertainty due to the relatively small predictive power of the correlation between wood density and seed size (Bello et al., 2015). Moreover, the degree to which planted trees will store carbon is contingent on their persistence (Korner, 2017;

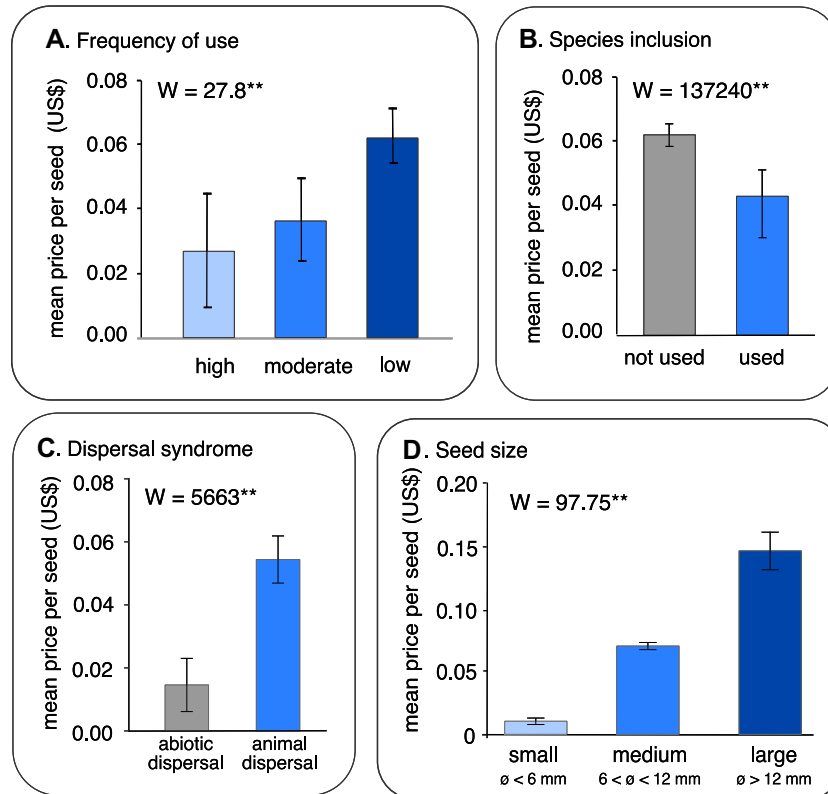


FIGURE 6 Mean seed price of tree species used in restoration projects across the Atlantic Forest of Brazil according to: (A) frequency of use (high: >122,905 seedlings/species; medium: 52,084 < seedlings/species < 122,905; low: < 52,084 seedlings/species); (B) species inclusion in restoration projects; (C) dispersal syndrome, and (D) seed size of animal-dispersed species (small: seed diameter < 6 mm; medium: 6 mm < seed diameter < 12 mm; large: seed diameter > 12 mm). Vertical lines in each bar represent the confidence interval, and mean values were compared with a Kruskal–Wallis test

Reid et al., 2017), which is highly uncertain given variable survival and growth rates in early stages of stand development. Lack of confidence in the potential of carbon markets to offset the additional cost of planting more large-seeded, animal-dispersed species could further complicate the uptake of this new information by practitioners (Fletcher, Dressler, Büscher, & Anderson, 2016). Collectively, these limitations suggest that economic incentives may need to be supplemented by policy interventions in order to increase the representation of large-seeded, animal-dispersed tree species in restoration.

So far, offset policies have not considered the level of conservation value of species used in tropical forest restoration, or matching the conservation value of trees lost to the conservation value of trees restored (Maron et al., 2012). This problem could be solved retroactively through enrichment planting in existing offset projects, since many large-seeded, animal-dispersed trees are shade tolerant (Cole et al., 2011); however, rebuilding viable tree populations may also require reintroduction of seed dispersers in some cases (Galetti, Pires, Brancalion, & Fernandez, 2017). Looking forward, countries could incentivize additional stocking of large-seeded, animal-dispersed species by subsidizing their production

costs and creating programs to encourage their use, potentially in partnership with conservation organizations, such as the Ecological Restoration Alliance of Botanical Gardens (<http://www.erabg.org/>), whose mission is well aligned with this problem, but which is itself underrepresented among Brazilian botanical gardens.

Market-driven species selection biases may manifest in restoration programs in other regions with potentially different—and greater—consequences for biodiversity conservation and ecosystem services. Although the comprehensive datasets used in our study are rare in the tropics, data from nurseries and forest fragment inventories could be used to evaluate the conservation potential of any restoration planting. Compared to most, Atlantic Forest restoration plantings may have relatively high conservation value given the history of scientific, technological, and regulatory development of high-diversity plantings in this biome (Rodrigues et al., 2009).

Restoration presents an opportunity to increase the range and population size of animal-dispersed, large-seeded species, which is particularly important for rare species persisting in human-modified, defaunated landscapes (Beca et al., 2017). We highlight the economic limitations and regulation opportunities to better incorporate these high conservation

value trees in restoration. Tree species with higher dispersal limitation may not be favored by simple increases in tree cover in degraded landscapes, as targeted by most international forest and landscape restoration programs. The active encouragement of the recolonization of restored forests by these species has to be especially considered in order to better obtain more robust conservation benefits (McAlpine et al., 2016). The conservation value of forest remnants is not replaceable, but science-based guidelines and appropriate policies may substantially contribute to increase the value of restoration plantings for biodiversity conservation as well as carbon stocking (Shoo, Freebody, Kanowski, & Catterall, 2016). However, this effort will probably require long-term interventions, monitoring and adaptive management beyond the typical 3–5 year window of active management (Holl, 2017).

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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