

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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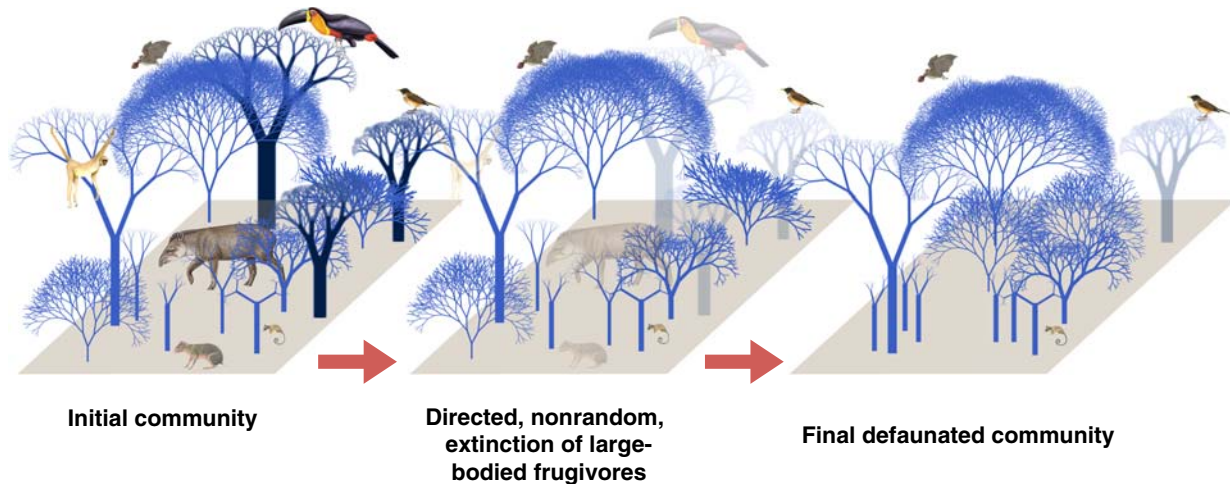


Fig. 1. Simulation pathway of frugivore defaunation on carbon storage. We generated downgraded communities with altered species composition. Each simulation had two main steps. First, we simulated directed extinctions induced by defaunation (loss of tree species with seed size ≥ 12.0 mm) or random extinction (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.

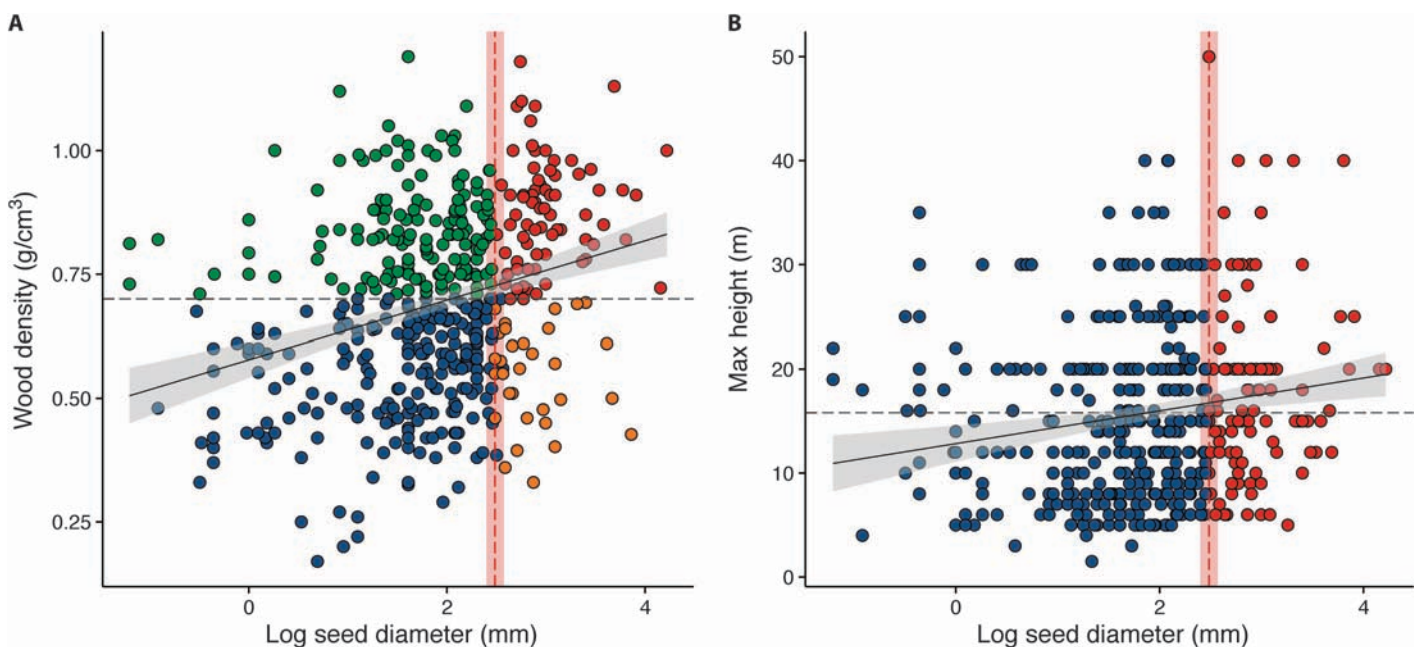


Fig. 2. Relationships between seed diameter and carbon storage-related traits in animal-dispersed trees. The black solid line shows the linear regression fit for the trend and the confidence interval (gray envelopes). The red vertical line indicates the seed diameter threshold of 12 mm. Points represent 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 = $0.7 \text{ g}/\text{cm}^3$. 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,

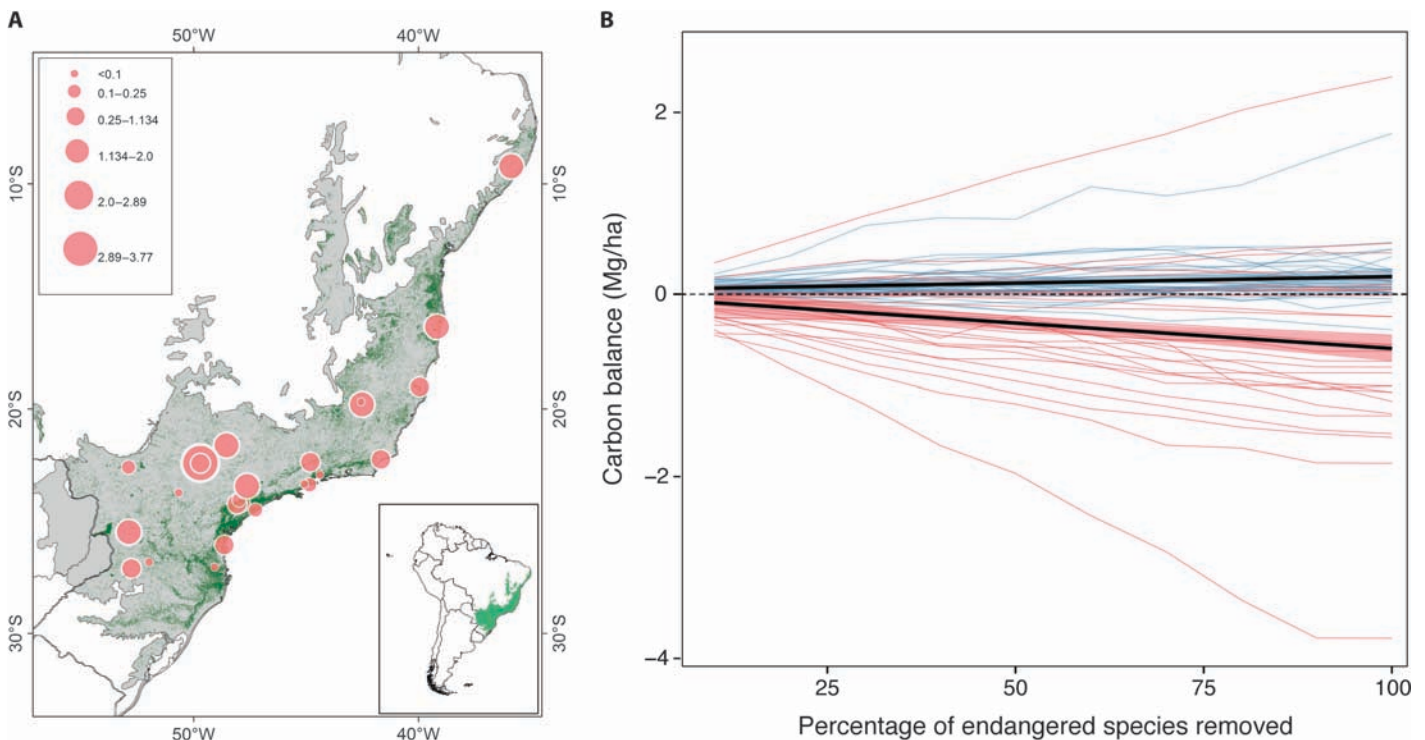


Fig. 3. Carbon deficit after defaunation simulation in Atlantic forest sites. (A) Locations of the 31 communities studied. The size of the points represents the magnitude of carbon loss (Mg/ha). **(B)** Carbon balance after simulated changes in carbon storage capacity in the random (blue) and defaunated (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 TreeAtlan 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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Defaunation affects carbon storage in tropical forests

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