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LETTER

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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 than14 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

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

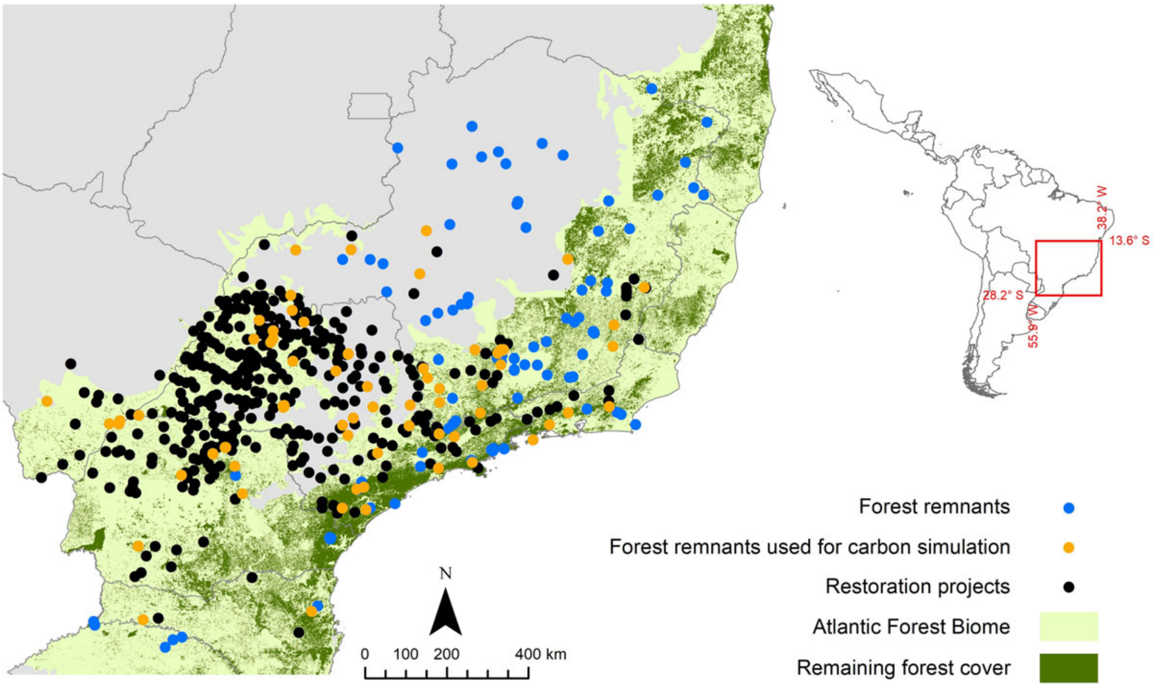

FIGURE 1 Restored forests and natural forest remnants in the Atlantic Forest. Forest remnants also occur in areas of Seasonal Semideciduous Forest outside of the official, coarse-scale map of the biome, where some restoration projects were also established. Restoration projects were distributed across 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 ± 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 forest types (Seasonal Semideciduous Forests and Rainforests) separately.

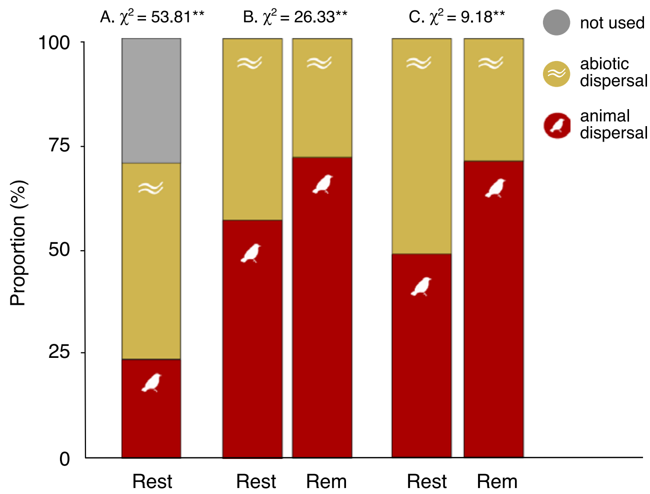

FIGURE 2 Proportion of abiotically dispersed and animal-dispersed tree species, compared by Chi-square tests, used in restored forests (Rest.) and present in forest remnants (Rem.) in the Atlantic Forest of Brazil according to: (A) proportion of species used in relation to the total species pool, (B)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

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

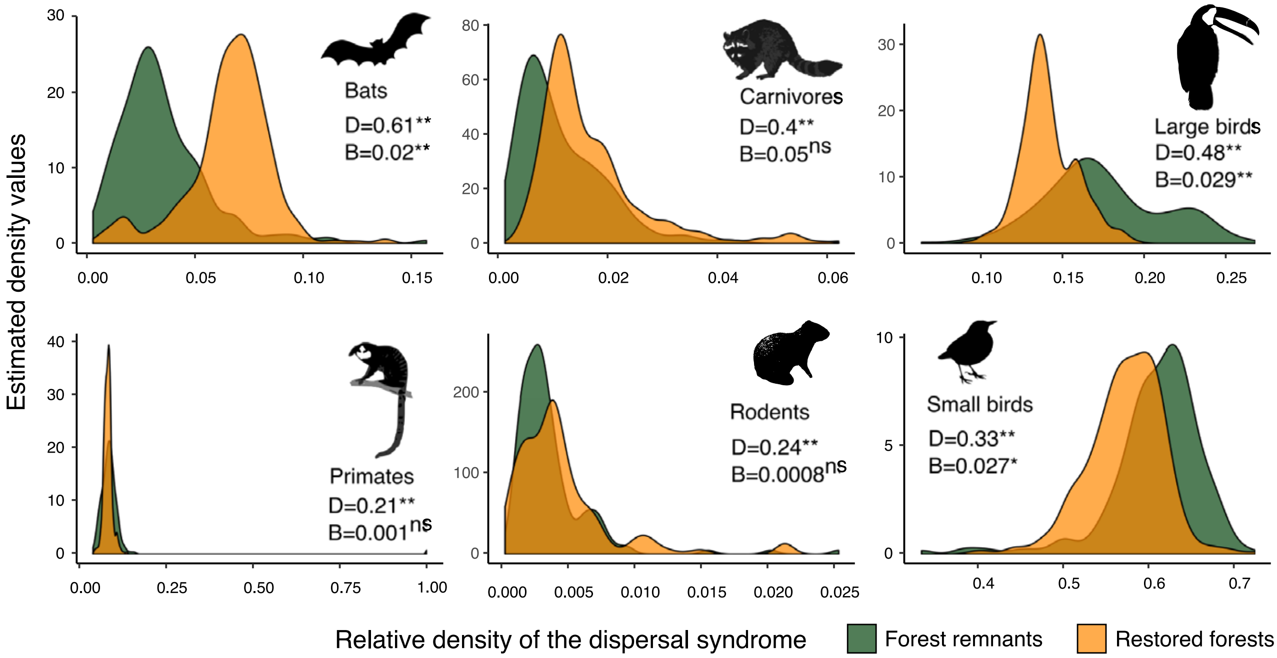

FIGURE 3 Frequency distributions for the relative representation (percent individual density) of tree species in forest remnants and restored forests. Panels indicate the frequencies for tree species providing food for different taxonomic groups of vertebrate frugivores. Each species may supply fruits 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)

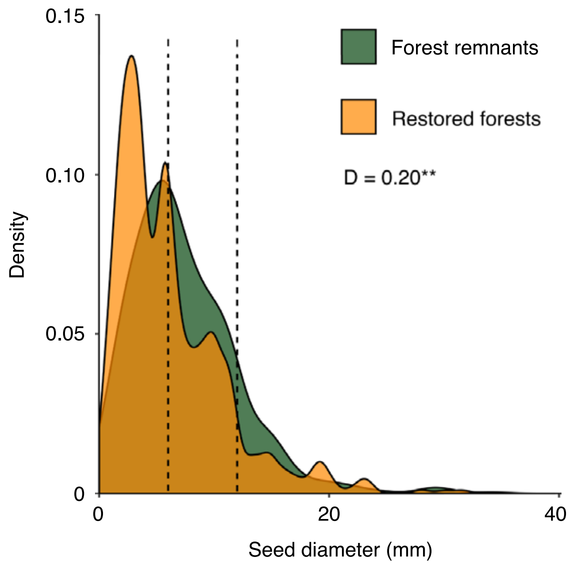

FIGURE 4 Probability density distributions for tree species according to seed diameter (mm) computed for the proportion of individuals of animal-dispersed trees when grouped by seed size in restored forests and forest remnants across the Atlantic Forest of Brazil. Density functions were compared by the 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).

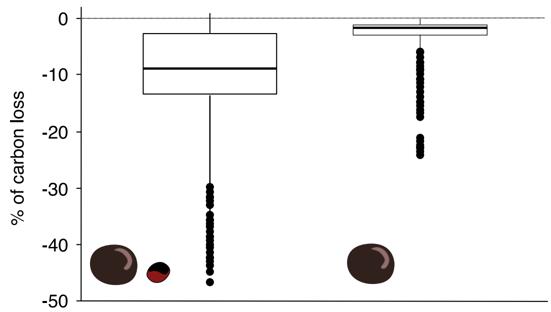

FIGURE 5 Potential effects on carbon stocking if the proportion of individuals with large (seed diameter > 12 mm) and medium seeds (6 mm < seed diameter > 12 mm), and only large seeds, of forest remnants are substituted by the proportion found in restored forests in the Atlantic Forest of Brazil. No 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;

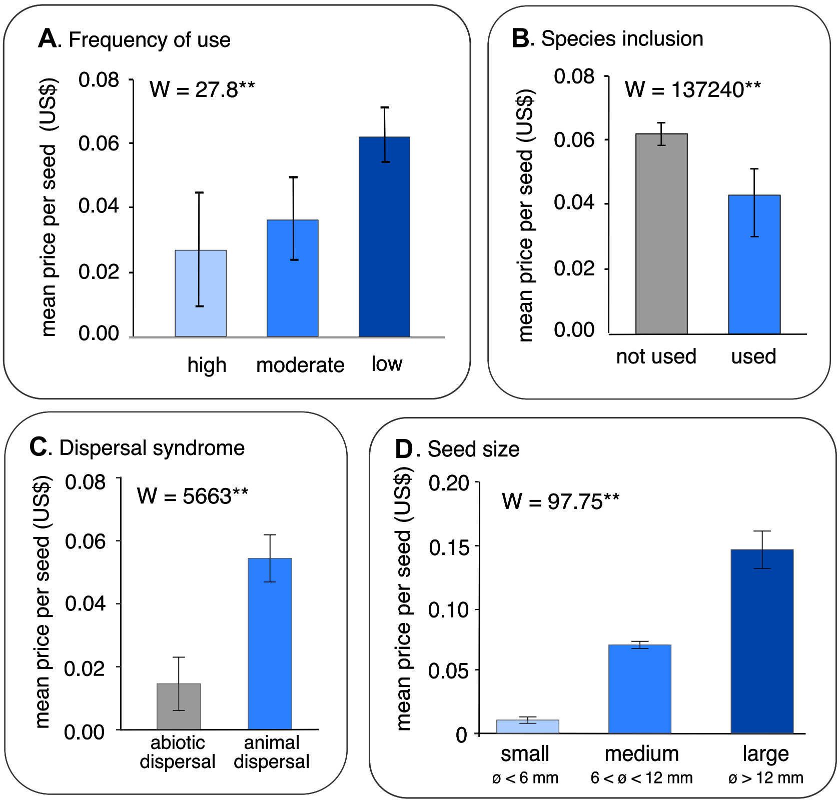

FIGURE 6 Mean seed price of tree species used in restoration projects across the Atlantic Forest of Brazil according to: (A) frequency of use (high: >122,905 seedlings/species; medium: 52,084 < seedlings/species < 122,905; low: < 52,084 seedlings/species); (B) species inclusion in restoration projects; (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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