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ORIGINAL ARTICLE

It is not just about time: Agricultural practices and surrounding forest cover affect secondary forest recovery in agricultural landscapes

Ricardo G. César[1] | Vanessa de S. Moreno[1] | Gabriel D. Coletta[2] | Daniella Schweizer[1] | Robin L. Chazdon[1,3] | Jos Barlow[4] | Silvio F. B. Ferraz[1] | Renato Crouzeilles[5,6,7] | Pedro H. S. Brancalion[1]

[1]Department of Forest Sciences, "Luiz de Queiroz" College of Agriculture, University of São Paulo, Piracicaba, Brazil

[2]Plant Biology Graduate Program, Biology Institute, University of Campinas, Campinas, Brazil

[3]Department of Ecology and Evolutionary Biology, University of Connecticut, Storrs, CT, USA

[4]Lancaster Environment Centre, Lancaster University, Lancaster, UK

[5]International Institute for Sustainability, Rio de Janeiro, Brazil

[6]International Institute for Sustainability Australia, Canberra, ACT, Australia

[7]Mestrado Profissional em Ciências do Meio Ambiente, Universidade Veiga de Almeida, Rio de Janeiro, Brazil

Correspondence
Ricardo G. César, Department of Forest Sciences, "Luiz de Queiroz" College of Agriculture, University of São Paulo, Pádua Dias Av. 11, Piracicaba, SP 13400-970, Brazil.
Email: ricardogoce@yahoo.com.br

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Abstract

Natural regeneration of forests has significantly led to increased native forest cover in some regions. Several studies have explored the spatial drivers of forest cover increase, yet little is known about their effects on forest structure and species richness and diversity. We quantified the effects of local (forest age, remnant *Eucalyptus* basal area, slope, soil fertility, and clay content) and landscape drivers (surrounding land use, distance from streams, and surrounding forest cover and its change over time) on the aboveground biomass, species density, and phylogenetic diversity of native trees in second-growth forests. We sampled 44 naturally regenerating forests established on former pastures and abandoned *Eucalyptus* plantations for 11–46 years in agricultural landscapes of the southeastern Atlantic Forest, Brazil. We used generalized linear mixed effect models to quantify the effect drivers on forest attributes. While only *Eucalyptus* basal area and proximity to sugarcane plantations had a consistent negative effect on forest biomass, other drivers were among the best models to explain forest attributes, but their effect was variable. Age increased tree biomass but the effect was not consistent. Similarly, species richness and phylogenetic diversity were mainly affected by landscape drivers such as surrounding forest cover. In tropical agricultural landscapes, effective forest recovery requires more than just time, as forest age can be less important in determining forest attributes than human land uses and surrounding native forest cover. Crucially, forest recovery can be improved

through interventions and policies that promote less impactful human activities and enhance existing forest cover.

Abstract in Portuguese is available with online material.

KEYWORDS
Atlantic Forest, carbon sequestration, ecological restoration, forest landscape restoration, forest succession, landscape ecology, natural regeneration

1 | INTRODUCTION

Currently, second-growth forests represent more than half of global forest cover (FAO, 2015), and this proportion is expected to increase as primary forest continues to be lost and second-growth forest expands in some regions (Nanni et al., 2019). There is growing evidence that fostering natural regeneration is a valuable and cost-efficient way to support biodiversity conservation and ecosystem services provisioning in human-modified tropical landscapes and mitigate climate change (Chazdon, 2014; Chazdon et al., 2020; Crouzeilles et al., 2017). However, to harness the power of natural regeneration to achieve global targets, we must better understand the drivers of forest structural and functional attributes.

Land abandonment may not always lead to the establishment of well-developed second-growth forests (Molin et al., 2017), as native species recolonization may be insufficient and human disturbances or invasive species may arrest successional forest development (Arroyo-Rodriguez et al., 2015). Even positive assessments of second-growth recovery show that forests take several decades to recover plant richness or aboveground biomass values similar to old-growth forests, and centuries for full recovery of species composition (Chazdon et al., 2016; Crouzeilles et al., 2016; Oliveira et al., 2018; Rozendaal et al., 2019).

These new forests will have greatest conservation and climate change-mitigation benefits if they accumulate biomass and provide effective habitat for native species. Understanding the drivers that either promote or inhibit the recovery of second-growth forests is therefore critical for the planning and implementation of successful restoration initiatives. Forest age has largely been the main studied driver of forest change, and time is needed for all successional processes (e.g., Martin, Newton, & Bullock, 2013; Norden, Chazdon, Chao, Jiang, & Vílchez-Alvarado, 2009). Yet, many studies also show that recovery depends on several context-dependent drivers beyond age (Arroyo-Rodriguez et al., 2015; Norden et al., 2015). For example, soil structure can alter water retention, and soil fertility can alter tree growth and survival, and thus structure and diversity of second-growth forests (Martins et al., 2015; Toledo et al., 2018). Additionally, landscape factors, such as the amount of surrounding forest cover (Jakovac et al., 2015) and distance from other forest patches, affect the abundance and composition of seed arrival, as well as the likelihood and quality of natural regeneration (Chua et al., 2016; Crouzeilles et al., 2020; Molin et al., 2017). Finally, human disturbances—such as logging and fire—can severely alter forest structure (reducing abundance and biomass) and species composition (Arroyo-Rodriguez et al., 2015; Jakovac et al., 2015). While previous research assessed these multiple drivers of succession separately in forested landscapes (Arroyo-Rodriguez et al., 2015; Crouzeilles et al., 2016; Goosem et al., 2016; Holl et al., 2017; Jakovac et al., 2015; Lennox et al., 2018), understanding their relative roles in deforested agricultural landscapes—where forest restoration is most urgently needed—could help practitioners to plan more effective forest restoration interventions.

We sampled 44 s-growth forests across a range of local and landscape contexts in highly deforested agricultural landscapes in the south-east portion of the Atlantic Forest biodiversity conservation hot spot in Brazil. We estimated the relative effect of biophysical local and landscape drivers on three key forest attributes that can be used as indicators of forest recovery: (a) aboveground biomass: It is directly related to forest carbon stocks and also indicates forest structure and nutrient cycling processes such as litter decomposition (Lohbeck & Martínez-Ramos, 2015); (b) species density: the number of species found in each sample plot, used to infer species taxonomic richness in the different forests studied, and (c) phylogenetic diversity of native trees: which differentiates from species density by including species evolutionary distance, also a proxy for functional diversity (Pellens & Grandcolas, 2016), hereafter mentioned collectively as "attributes"). By assessing the drivers' relative importance, we investigate if age is the dominant driver of changes in forest attributes in these landscapes (Letcher & Chazdon, 2009). Given overall low surrounding forest cover and intensive agricultural use in the landscapes sampled, we hypothesize that forest recovery would also be significantly influenced by surrounding forest cover (Zermeño-Hernández et al., 2015), intensity of former and surrounding land use, and soil nutrient content (Jakovac et al., 2015; Martins et al., 2015; Zermeño-Hernández et al., 2015).

2 | METHODS

2.1 | Study region

Our study was carried out in the 1,700 km^2 Corumbataí river basin in south-east Brazil, which had 12.4% forest cover remaining in 2016. The Köeppen-Geiger classification of the region's climate

is Cwa, with dry winters and wet summers (Alvares et al., 2013). Mean annual precipitation is 1,367 mm, most of it (80%) falling in the rainy season from October to March. Mean monthly temperature is 20.5°C (minimum and maximum monthly averages of 15.6°C and 29.5°C, respectively). The main soil types are Acrisols (44%) and Ferralsols (22%). Our study site is an ecotone between the Atlantic Forest and the Cerrado biomes. Forest sampling included only seasonal semi-deciduous forests and did not include parts of the basin once covered by native grasslands, savannas, or savanna woodlands.

Most large-scale deforestation occurred in the early 19th century and declined in the early 20th century. It was initially driven by coffee production and subsequently replaced by cattle ranching and sugarcane plantations (Dean, 1997). Industrial development in the 1970s led to rural–urban migration and favored the consolidation of sugarcane plantations in flat areas, while marginal agricultural lands either became extensive pastures, *Eucalyptus* (*Eucalyptus* spp.) plantations, or were abandoned, some of them regenerating back to native forests (César et al., 2018). As hypothesized by the forest transition theory, severe deforestation of the past is being followed by a significant increase in native forest cover, which doubled between 1962 and 2008 (Ferraz et al., 2014; Mather, 1992). In 2014, pastures and sugarcane fields occupied 43.7% and 29.4% of the Corumbataí river basin, respectively, while native forest patches, *Eucalyptus* plantations, and other land uses (buildings, water bodies, roads, etc.) occupied 12.4%, 7.3%, and 7.2% of the area. The remaining forests are affected by cattle grazing, wildfires, and herbicide drift from sugarcane fields. However, wildfires are now much less prevalent as sugarcane burning, used to ease manual harvesting, have declined over the last 10 years, and were prohibited in 2016.

2.2 | Experimental design

In order to define the location and size of the landscapes where second-growth forests (hereafter SGF) would be sampled, we used the diversity variability analysis approach proposed by Pasher et al. (2013) to (a) divide the study region in square grids of five different scales: 1, 2, 3, 4, and 5 km square grid cells, (b) calculate the Shannon landscape diversity index for each grid size based on a 30-m resolution land map from 2002, and (c) plot mean landscape diversity of each grid size against the cell size. Thus, we selected the 4 km (16 km^2) square grid size as the smallest sample size that represents the study region (i.e., Shannon landscape diversity index of the 16-km^2 landscape had no variation when compared to the index of larger sample sizes). Please refer to Ferraz et al. (2014) for more details. We used visual interpretation and field inspection to classify land cover using panchromatic images for the years 1962, 1978, and 1995 (1:25,000 scale) and a panchromatic image from a High-Resolution Panchromatic Camera (HRC) of CBERS (2.7 m of spatial resolution) from 2008. Land use was classified as sugarcane plantations, pasture, old-growth native forest, young-regenerating native forest, orange plantations, *Eucalyptus* plantations, urban areas, and other types (Ferraz et al., 2014).

We estimated age and previous land use of existing native forest cover by overlaying land-use classification maps of different ages (i.e., 1962, 1978, 1995, 2000, and 2008). We further refined forest age estimates by visually interpreting topographic maps from 1969, 1975, and 1979. We used LANDSAT 5 images from 1984 to 2012 and LANDSAT 8 images from the years 2013 to 2015. When the exact age of SGF establishment was not clear, we considered the average of the possible dates of establishment to calculate forest age. Sampled SGF age estimates ranged from 11 to 46.5 years old. Landscapes' maps can be found on Appendix 1.

2.3 | Forest inventories

In these landscapes, forest age ranged from 11 to 46 years and the most common previous land uses where SGF regenerated were abandoned *Eucalyptus* plantations and pastures (Figure 1, Appendix 1). We discriminated forests based on previous land use and age (Figure 1) and installed a total of 44 plots of 900 m^2 (20 × 45 m) to sample SGF tree communities. Within each plot, we measured the diameter at breast height (DBH) and identified to the species level whenever possible all the living rooted trees and shrubs DBH ≥ 5 cm (hereafter "trees") by comparing with materials in the Superior School of Agriculture (ESA in Portuguese) herbarium at the University of São Paulo and virtual herbariums such as speciesLink (http://splink.cria.org.br/). All sampled trees were classified according to species origin (native or non-native to the study region), and we considered only native species for calculating the forest attributes, as the non-native *Eucalyptus* (the main non-native species in the study site) could inflate carbon stock and taxonomic and phylogenetic richness of sampled forests.

2.4 | Potential drivers of second-growth forest recovery

2.4.1 | Local drivers

We selected forest age, basal area of remnant *Eucalyptus* trees, slope and soil sum of bases, and clay content as potential local drivers of SGF development. We obtained information on forest age as described above, and the other drivers were evaluated as described below:

Basal area of Eucalyptus: We used the basal area of remnant *Eucalyptus* stems as a direct measure of the continued influence of this previous land use on forest regeneration. Tree basal area is directly related to its canopy and root system, functioning as a proxy for competition. On the other hand, its fast growth could also shade competitive grasses and quickly develop a canopy structure. Thus, we aimed to infer the legacy effect of non-native species cultivated before SGF establishment. Forests with no remnant *Eucalyptus* established in abandoned pastures.

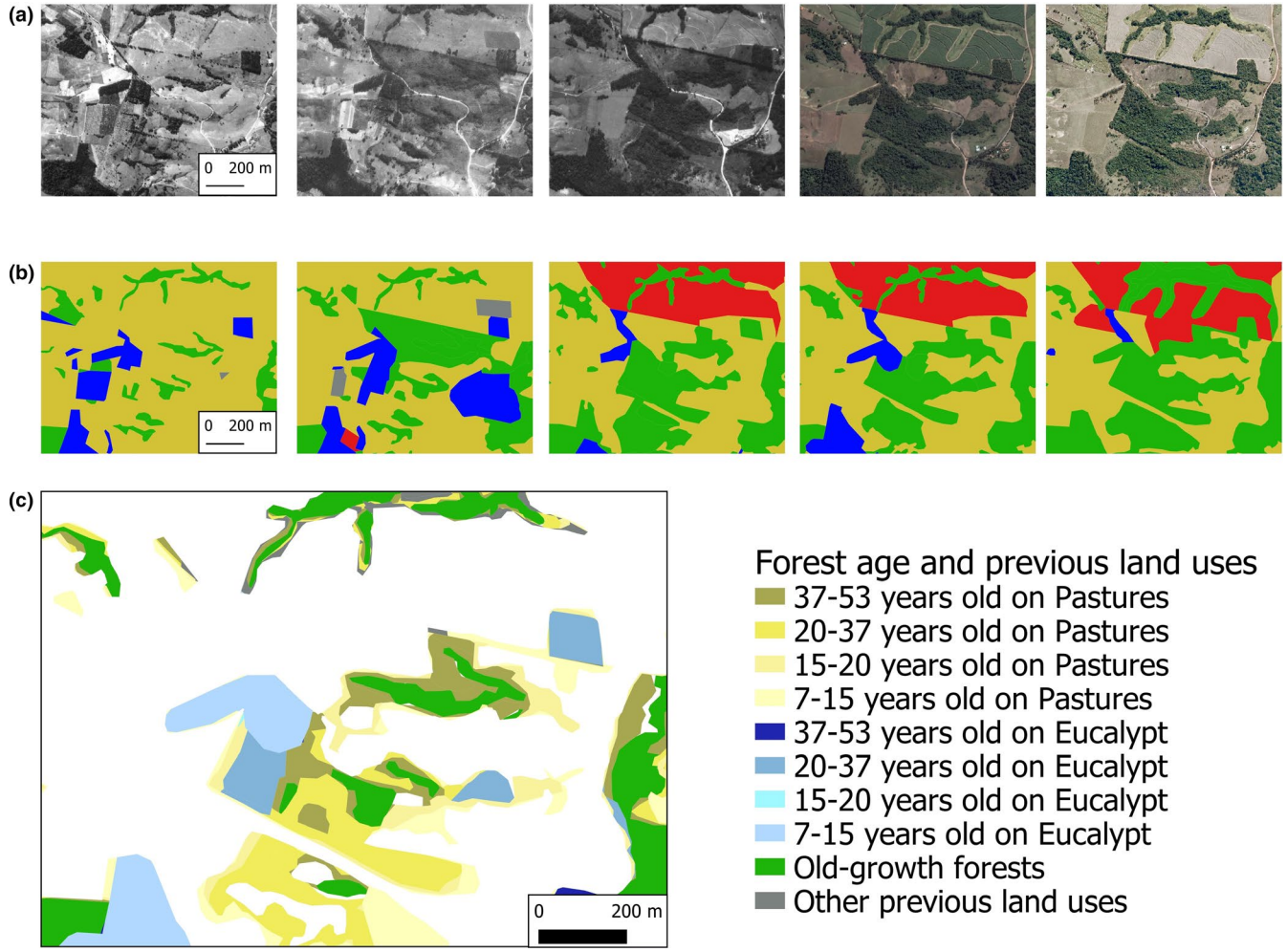

FIGURE 1 An example of our forest classification protocol used to define time since abandonment and previous land use. (a) High-resolution images for the studied landscapes for the years 1962, 1978, 1995, 2000, and 2008. (b) Classification of land use based on the images (sugarcane plantations in red). (c) Overlaying the images of different dates obtained in b, we classified existing forests in a mosaic based on age and land use before forest establishment. Appendix 1 details the landscapes where SGF were sampled

Slope: Bedrock tends to be closer to the surface, and water retention is reduced in steep slopes, and thus, this driver may affect growth and composition of SGF (Becknell et al., 2018; Lavorel et al., 2011). Steeper areas are also more prone to natural regeneration in the region, due to their marginal use in agriculture (Molin et al., 2017). This driver was estimated based on the Digital Elevation Model (DEM) of the region (30 meters of resolution) obtained by 1:50.000 contour line vectorization and interpolated by *Topo to Raster* function in ArcGIS 10 (Environmental Systems Research Institute (ESRI) 2012). The DEM was processed to calculate the slope raster dataset, in degrees. We then extracted the slope value from raster pixel at the center of each SGF sampling plot.

Soil attributes. Soil fertility is related to plant growth, while soil structure is related to water retention, which may affect both SGF growth and species composition (Toledo et al., 2018). *i) sum of bases:* We obtained three composite soil samples, each composed of three sub-samples at depth 0–20 cm per plot. We determined soil pH and H + Al by potentiometry (described in pages 181–188 and 200–212 of Raij et al. (2001)), organic matter by colorimetry (Raij et al., 2001, pages 173–180); and P, K, Ca, Na, and Mg using an ion exchange resin (Raij et al., 2001, pages 189–199). We then conducted a principal component analysis for soil sum of bases (calculated as sum of Ca + Mg +K content), all macronutrients (P, Ca, Mg, and K) and other soil attributes (pH, organic matter content, cation exchange capacity, and base saturation; see Appendix 2). As soil sum of bases was closely aligned to most other drivers, we conduced our analysis using this as the sole indicator of soil fertility. ii) *Soil clay content:* We used the Hydrometer Bouyoucos method, considering soil fractions < 0.002 mm as clay (Bouyoucos, 1962).

2.4.2 | Landscape drivers

To describe the landscape context, we quantified surrounding land use, distance from streams (most of them < 4 m wide), average surrounding native forest cover, and relative change of surrounding native forest cover over time.

Surrounding land use: Human land use next to forests is a proxy for human disturbances that encroach into the forest itself, potentially affecting forest structure and conservation value (Barlow et al., 2016; Martinez-Ramos et al., 2016). Pasture or sugarcane was the dominant land uses near sampled forests in the last 15 years before data gathering (Appendix 3). Both land uses represent a historical source of degradation of forest remnants, as most remnants are not fenced and cattle grazing in the understory can compromise natural regeneration processes, and sugarcane has been burnt before harvesting and favored forest fires as well (Martinelli & Filoso, 2008). We calculated the Euclidean distance from the plot centroid to identify the closest land use for the years 2000, 2008, and 2015.

Distance from streams: In the study region, SGF are more likely to naturally establish near streams (Molin et al., 2017). This increased likelihood is partly in response to the mandatory law of recovery of riparian areas (Soares-Filho et al., 2014) and the greater survival of seedlings near streams (Brown & Archer, 1990). We calculated the Euclidean distance from the centroid of each SGF plot to the nearest stream.

Surrounding native forest cover: Related to SGF connectivity and, therefore, chance of seedling arrival, establishment, and thus species richness of these forests (Crouzeilles et al., 2019; Toledo et al., 2018). Based on the high-resolution land-use images from 1962, 1978, 1995, 2000, 2008, and 2015, we estimated average surrounding native forest cover in a 1-km buffer around each plot (as a proportion of total buffer area) and estimated two drivers: i) average surrounding forest cover since SGF establishment, and ii) change in surrounding forest cover since SGF establishment, calculated as the surrounding forest cover at the time of data gathering minus forest cover at the time of forest establishment. Details and justification of the processes employed to select this driver are in Appendix 4. Patch size and surrounding native forest cover for each plot are in Appendix 5.

2.5 | Attributes of second-growth forests

We used three forest attributes as response variables: (a) aboveground biomass of native trees (AGB) calculated using equation (7) developed by Chave et al. (2014), with wood density data mainly from Chave et al. (2009) and Zanne et al. (2009) (Dataset S2). We calculated biomass for native species and included unidentified morphospecies to calculate AGB, given that the relatively few non-native trees are easily identifiable in the field, we considered unidentified morphospecies as native species. Wood density estimates for species not included in these databases were estimated as follows: (i) average of the species of the same genus in this study, or (ii) average of species of the same genus in Zanne et al. (2009), or (iii) average of species of the same family on the study site. Wood density of families identified only to the genus or family level was estimated as the average values of the taxon level for the study site (more details in César et al. (2018)). (b) Native tree species density (number of species per plot). (c) Phylogenetic diversity of native trees. We used the program Phylocom (Webb, Ackerly, & Kembel, 2008) to estimate phylogenetic diversity, which increases with the number of distantly related relatives in the sample. Phylogenetic diversity complements measures of species diversity, since given trait conservatism it is a proxy for functional diversity (Liu et al., 2016; Tucker et al., 2017). We employed the *bladj* algorithm implemented in the Phylocom software and evolutionary ages published by Wikstrom, Savolainen, and Chase, (2001) to estimate the ages of the interior nodes of the evolutionary tree and evenly space the nodes between them. Phylogenetic diversity was estimated as the Net Relatedness Index (Webb, Naturalist, & Aug, 2000) for each of the sampled forests compared with a null value. Details of the phylogenetic analyses procedures are shown in Appendix 6. The complete dataset of this work can be found in "Dataset S1."

2.6 | Data analyses

To compare the relative contribution of local and landscape drivers on forest attributes, we used generalized mixed linear models considering the 16-km^2 landscape where the SGF were located as the random factor (Moscatelli, Mezzetti, & Lacquaniti, 2012) and our selected local and landscape potential drivers as predictor variables. For each SGF attribute, we considered all combinations of models using the drivers above plus a null model (512 models). We did not develop models using interaction among drivers since this may disrupt model averaging (Cade, 2015). For each candidate model, we calculated the Akaike information criteria corrected for small samples (AICc), and the marginal (R^2m) and conditional (R^2c) sum of squares, which represent the sum of squares without and with the random factor, respectively. We ranked models according to the $\Delta AICc_i$ ($AICc_i$ – minimum AICc).

Since our goal was to find the relative importance of local and landscape drivers on these attributes, we used model averaging to assess the importance of each driver for each forest attribute. We generated average models to estimate the average coefficient and 95% confidence interval of the drivers among models $\Delta AICc_i \leq 2$ and function *model.avg* from R Package MuMIn (Barton, 2016). Model averaging generates estimates of parameter for a group of models, considering model selection uncertainty (Johnson & Omland, 2004), being a valuable tool to capture the effect of different parameters when none of the best models is predominantly better than the others (i.e., best model weight < 0.9). As variable importance from model averaging has been disputed (Cade, 2015), we also present both the averaged coefficient estimates and 95% confidence interval. When the null model was within the models $\Delta_i \leq 2$ for a given SGF attribute, we considered that all drivers are uninformative to explain that attribute. Values are shown as mean ± 95% confidence interval. All analyses were carried out in the R 3.0 environment (R Core Team, 2018), using the packages "*MuMIn*" (Barton, 2016) and *glmer* in R 3.0 (R Core Team, 2018). We checked for collinearity among drivers using the Variable Inflation Factor method from the VIF function from "*car*" package (Fox & Weisberg, 2019).

3 | RESULTS

We sampled 4,661 trees, composed of 213 identified species, belonging to 137 genera and 60 families. A total of 29 morphospecies were identified at the genus level. The most abundant tree species sampled were *Casearia sylvestris* Sw. (6.3% of all trees sampled), *Eucalyptus* spp. (4.4%), *Luehea candicans* Mart. & Zucc. (3.9%), and *Piptadenia gonoacantha* (Mart.) J.F.Macb (3.4%).

Remnant *Eucalyptus* basal area and proximity to sugarcane plantations consistently reduced AGB (Figure 2), while other drivers were important to estimate SGF attributes, their effect were not as consistent (i.e., the 95% confidence interval overlapped zero). We will address these cases throughout this section.

Surrounding native forest cover showed a mostly positive relationship with species density, phylogenetic diversity, and AGB (Tables 1 and 2). The basal area of remnant *Eucalyptus* reduced species density in SGF (Figure 3), while SGF near sugarcane plantations showed lower phylogenetic diversity. Forest age was among the best models for AGB only (Table 1 and 2, Figure 2). Overall, models using a single factor were poor estimates of forest attributes (Table 2). The complete list of models generated can be found in Dataset S3 and graphical representations of the main drivers in Appendix 7.

Overall, native species AGB was negatively impacted by increasing slope, soil clay content (Appendix 7). On the other hand, AGB tended to increase with age and surrounding forest cover in the landscape (Table 1, Figure 2). When *Eucalyptus* biomass was included, forest AGB was approximately twice as high in forests with remnant *Eucalyptus* compared with other SGF (Appendix 6, Figure 3).

Historical gains in native forest cover and higher native forest cover in the landscape tended to increase species density. The presence of nearby sugarcane plantations had a context-dependent effect on this attribute (Figure 2). Resprouted *Eucalyptus* stems composed 48 ± 10% of the basal area of SGF established in abandoned plantations of this species. But SGF showed similar species richness in areas with and without *Eucalyptus* after abundance-based rarefaction (Figure 4). The complete list of species sampled can be found in Dataset S4.

Phylogenetic diversity estimates were negatively related to the presence of sugarcane plantations near SGF, and positively associated with surrounding native forest cover. Change in surrounding native forest cover was included in most of the best models for phylogenetic diversity (importance: 0.65), but its coefficient was highly variable (Figure 2).

4 | DISCUSSION

Continental-scale models to predict the carbon sequestration potential of SGF rely primarily on forest age (Chazdon et al., 2016), a driver that is generally a robust predictor of AGB accumulation in chronosequence-based studies (Letcher & Chazdon, 2009). Although our results show that AGB tends to increase with forest age, nearby sugarcane plantations and remnant *Eucalyptus* biomass were more consistent as negative drivers of native biomass. The best models for species richness and phylogenetic diversity of SGF, on the other hand, contained mainly surrounding forest cover and nearby sugarcane plantations as drivers. Thus, land use within heavily deforested agricultural landscapes, more than forest age, plays a key role in the recovery of tropical restored forests in this region.

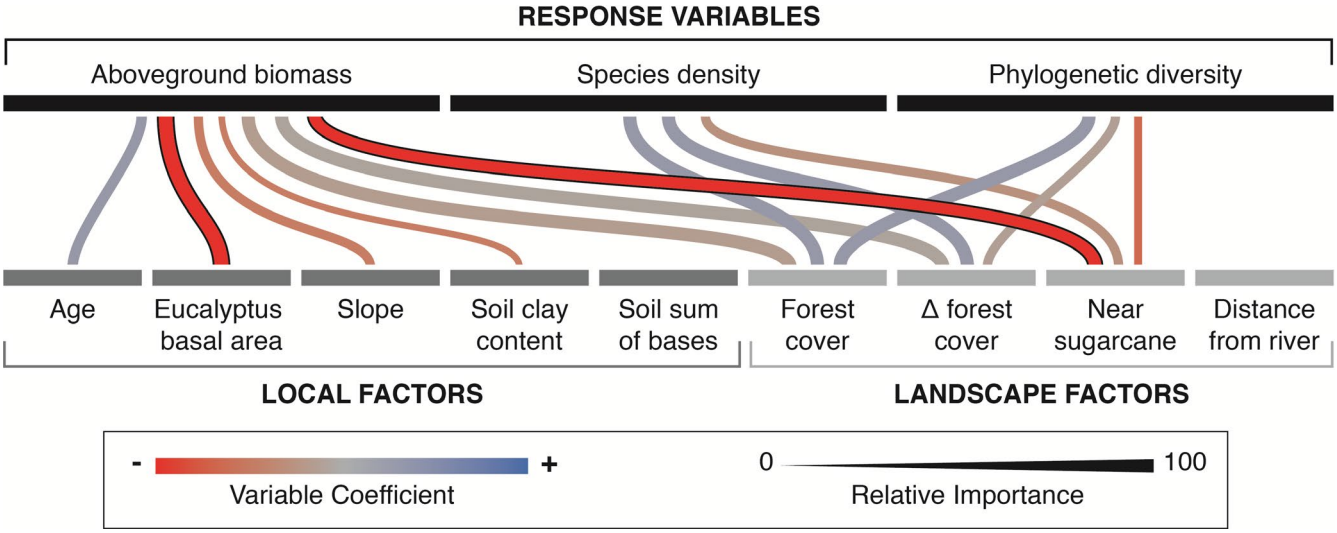

FIGURE 2 Graphical representation of local and landscape drivers influencing tropical second-growth forest (SGF) in agricultural landscapes of the Atlantic Forest of South-east Brazil. We considered only the drivers in model averages (i.e., drivers in models ΔAIC ≤ 2). Blue-red gradient represents the percentage of the 95% confidence interval of the average model that is positive or negative for that factor, respectively. Lines with black frame indicate drivers which the range of coefficient ± 95% coefficient interval was fully within negative values (i.e., drivers with a clear negative effect on the SGF attribute). Gray lines are drivers that did not fit the requisites mentioned before (i.e., driver effect is variable and/or context-dependent). Results reflect the average model developed by merging all models ΔAICc ≤ 2. Graphical representation of individual drivers can be found in Appendix 7 and values in Appendix 8

TABLE 1 Best linear mixed models (ΔAIC < 2) to estimate biomass, species density, and phylogenetic diversity in second-growth forests in tropical agricultural landscapes of South-east Atlantic Forest, Brazil. AGE: forest age (years); CLAY: soil clay content (%); EUC: basal area of *Eucalyptus* (m^2/ha); FC: average proportion of native forest cover in a 1-km radius since forest establishment (%); ΔFC: current proportion of native forest cover in a 1-km radius minus forest cover at the time of SGF establishment (%); NU: nearby sugarcane plantation; SL: slope (%); marginal and conditional R^2 refer to coefficient of determination for fixed effects and fixed + random effects, respectively. Weight refers to the relative likelihood of a model being supported by the data, when compared to the other models. ∑weight estimates weight of that group of models in explaining the data, relative to all the other models

Model	Drivers	ΔAIC	R^2 Marg.	R^2 Cond.	Weight	∑weight
Biomass of native species						
1	AGE + EUC + SL + NU + FC + ΔFC	0.00	0.42	0.57	0.17	0.17
2	EUC + SL + NU + FC + ΔFC	0.52	0.39	0.54	0.13	0.30
3	AGE + EUC + NU + FC + ΔFC	1.06	0.41	0.52	0.10	0.40
4	EUC + CLAY + SL + NU + FC + ΔFC	1.20	0.40	0.52	0.09	0.49
5	AGE + EUC + CLAY + SL + NU + FC + ΔFC	1.29	0.43	0.54	0.09	0.58
6	AGE + EUC + CLAY + NU + FC + ΔFC	1.67	0.42	0.50	0.07	0.65
7	EUC + CLAY + NU + FC + ΔFC	1.81	0.38	0.47	0.07	0.72
8	EUC + NU + FC + ΔFC	1.87	0.37	0.47	0.07	0.78
492	*NULL*	*42.83*	*0.00*	*0.09*	8×10^{-11}	*1.00*
Native species density						
1	NU + FC + ΔFC	0	0.07	0.07	0.32	0.32
2	FC + ΔFC	1.31	0.06	0.07	0.17	0.49
77	*NULL*	*13.54*	*0.00*	*0.02*	*0.003*	*0.99*
Phylogenetic dispersion						
1	NU + FC + ΔFC	0.00	0.09	0.18	0.25	0.25
2	FC + ΔFC	0.15	0.04	0.14	0.23	0.49
3	NU + FC	1.14	0.10	0.17	0.14	0.63
4	FC	1.58	0.03	0.13	0.11	0.75
7	*NULL*	*4.33*	*0.00*	*0.10*	*0.03*	*0.90*

4.1 | Divergence of forest succession by local and landscape drivers

The negative impact of *Eucalyptus* is likely to be a simple consequence of their displacement of native species due to the space occupied by the resprouting stumps. When considering the biomass of *Eucalyptus*, SGF biomass doubled, on average, compared with SGF without remnant *Eucalyptus*: This finding demonstrates the potential of resprouting remnant *Eucalyptus* trees to rapidly sequester carbon, but we cannot evaluate if resprouting native stems would have performed similarly to *Eucalyptus* after clear felling.

Although inconsistent, the negative effect of soil clay content on forest biomass was unexpected (Appendix 7). Soil clay content was expected to favor AGB accumulation because this driver is usually associated with higher nutrient and water availability to plants, and thus favors tree growth (Toledo et al., 2018). However, it may also be indirectly associated with a more intense previous land use, as farmers prefer soils with higher clay content for crop cultivation, in such a way that clay content could be a surrogate of previous land-use intensification in the study region. Additionally, clay soils are more prone to compaction after agricultural activities, another characteristic that may reduce AGB of the studied forests. The direct and indirect effects of soil clay content in forest regeneration thus merit further attention.

The lack of a relationship between SGF age and diversity-related attributes contrasts with many other studies on secondary forest (Ferreira et al., 2018; Gilroy et al., 2014; Lennox et al., 2018; Magnago et al., 2015) and may be explained by several methodological and context-dependent drivers. First, forest age was estimated between >5 years of intervals of high-resolution aerial photographs and low-resolution satellite images, and therefore, forest age estimates are not exact, particularly for SGF that may have been regenerating in abandoned *Eucalyptus* plantations before 1984 (year of the first Landsat images). Second, diversity-related attributes may take longer to recover and respond to local context, disturbance regime, and stochastic drivers that are amplified in human-modified landscapes (van Breugel et al., 2013). Third, SGF sampled are all >10 years and were subjected for many years to unique disturbance regimes and landscape dynamics. These initial conditions and the accumulated impacts of these drivers along time may have driven SGF to somewhat unique successional trajectories that can be better estimated by disturbance-related drivers rather than by forest age alone (Arroyo-Rodriguez et al., 2015; Martinez-Ramos, Ortiz-Rodriguez, Pinero, Dirzo, & Sarukhan, 2016). Our results do not

TABLE 2 Coefficients and 95% confidence interval, marginal, and conditional R^2 values and ΔAICc for the model containing only one factor for each forest attribute. The complete list of models can be found in Dataset S3

	Biomass of native species				Species density				Phylogenetic diversity			
	Coeff ± 95%CI	R^2 Marg.	R^2 Cond.	ΔAICc	Coeff ± 95%CI	R^2 Marg.	R^2 Cond.	ΔAICc	Coeff ± 95%CI	R^2 Marg.	R^2 Cond.	ΔAICc
Forest age	1.80 ± 1.20	0.16	0.21	36.50	0.14 ± 0.17	0.07	0.16	16.36	−0.005 ± 0.026	0.00	0.11	13.40
Eucalypt basal area	−2.55 ± 1.36	0.23	0.29	32.06	−0.14 ± 0.18	0.05	0.09	16.55	−0.009 ± 0.031	0.01	0.10	12.88
Soil sum of bases	0.23 ± 0.33	0.04	0.07	45.40	−0.01 ± 0.04	0.00	0.02	21.73	−0.001 ± 0.008	0.00	0.10	16.05
Soil clay content	−0.19 ± 1.32	0.00	0.11	44.04	−0.08 ± 0.16	0.02	0.07	18.19	0.006 ± 0.027	0.00	0.09	13.29
Slope	0.06 ± 3.35	0.00	0.09	42.31	−0.01 ± 0.41	0.00	0.02	17.29	−0.033 ± 0.066	0.02	0.14	10.78
Nearby use	−64.92 ± 36.60	0.23	0.32	26.84	−0.34 ± 4.54	0.00	0.03	12.37	−0.617 ± 0.774	0.06	0.15	4.44
Distance from river	−0.05 ± 0.21	0.01	0.08	47.71	−0.02 ± 0.02	0.05	0.09	20.65	−0.002 ± 0.004	0.02	0.13	16.18
Surrounding forest cover	−114.63 ± 245.12	0.02	0.09	32.94	16.68 ± 28.24	0.03	0.05	7.45	3.013 ± 4.687	0.03	0.13	1.58
Δ Surrounding forest cover	−7.22 ± 283.07	0.00	0.11	33.58	13.92 ± 29.69	0.02	0.03	7.84	−1.601 ± 5.221	0.01	0.11	2.58
Null Model	111.40 ± 19.25	0.00	0.09	42.83	24.18 ± 2.68	0.00	0.02	13.54	−1.212 ± 0.551	0.00	0.10	4.33

suggest that forest age should be ignored in successional studies of historically disturbed forests; rather, they suggest that successional studies should consider a myriad of drivers (including forest age) in highly dynamic human-modified landscapes, as these may interact with each other to influence regeneration potential.

4.2 | Surrounding agricultural practices can hamper forest recovery

The lower estimates of AGB and phylogenetic diversity in SGF surrounded by sugarcane plantations (Appendix 7) are likely due to crop-specific agricultural practices. Until c. 10 years before data collection, sugarcane plantations were burned in the dry season to facilitate manual harvesting, which, as fires usually went out of control, resulted in recurrent fires in native forests. Currently, herbicides are sprayed by airplanes to enhance sugarcane maturation (i.e., induction of plant senescence to increase the concentration of sugar on stems), which increases the chance of herbicide drift into neighboring SGF. Chronic disturbances caused by these surrounding agricultural practices could gradually collapse SGF structure; however, the impacts of some of these disturbances, such as herbicide drift, are poorly understood, and require further study to understand how they influence forest structure and species. Also, since most of SGF are located at riparian areas, they are exposed to sediment deposition from agricultural lands (Guidotti et al., 2020).

Sugarcane plantations near SGF could reduce AGB of these forests to values similar of forests decades younger (i.e., SGF are expected to have a biomass reduction of 50.71 ± 44.05 Mg/ha when nearby sugarcane [Figure 3 and Appendix 8]). Overall, humid tropical forest species are poorly adapted to fire, with even low-intensity understory wildfires resulting in a collapse of forest structure and biomass (Barlow & Peres, 2008). Although we did not directly measure causality, our results corroborate that disturbances from more intense agricultural practices, such as sugarcane, reduced the phylogenetic diversity of native species in nearby SGF (Dinnage, 2009). While the recent ban on burning sugarcane plantations may benefit AGB and phylogenetic diversity of nearby SGF, more research is needed to assess the effects of airplane herbicide spraying on native forests embedded in agricultural landscapes, as herbicide drift may counterbalance the benefits of fire exclusion. Thus, besides incorporating effects of fragmentation, surrounding disturbances should be considered to promote forest recovery and conservation of forest remnants in agricultural landscapes.

4.3 | Forest cover and conservation potential of SGF

Whereas the overall positive effects of surrounding native forest cover on the estimates of species density and phylogenetic diversity in SGF were expected, based on previous studies (Martínez-Ramos et al., 2016; Matos et al., 2016), very few studies have shown the

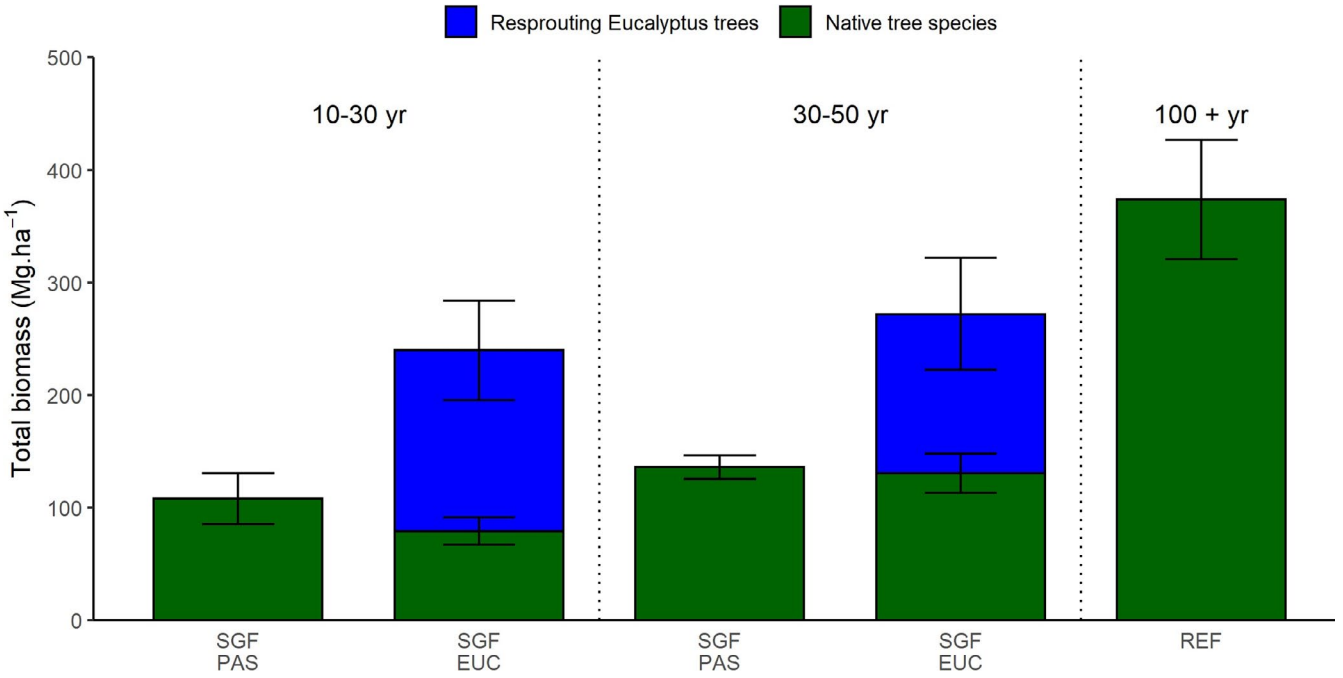

FIGURE 3 Aboveground biomass accumulation for second-growth forests (SGF) established in abandoned pastures (PAS) and abandoned eucalypt plantations (EUC). No significant differences in native tree AGB were observed among the different areas. Error bars represent 95% confidence intervals

combined effects of forest cover along with other drivers, such as forest age (Liu & Ferry Slik, 2014). In contrast, Letcher and Chazdon (2009), and Holl et al. (2016) observed that previous land use, and not surrounding forest cover, was a significant predictor of biodiversity and biomass recovery of naturally regenerating forests and native tree plantings, respectively, in Costa Rica. Lennox et al. (2018) also found that forest cover was relatively unimportant for estimating the occurrence of forest species. However, these studies were carried out in landscapes with higher ranges of forest cover (11%–90%, in contrast to 9%–31% in our study area), in which the influence of neighboring forest cover may be lower as a consequence of the maintenance of high levels of connectivity across the whole landscape.

The amount of surrounding forest cover around regenerating forests increases the species pool and the probability of dispersal (Charles et al., 2016; Fahrig, 2003). Using a global meta-analysis, Crouzeilles et al. (2019) found that low levels of forest cover in a 5-km radius decreased the likelihood of biodiversity recovery during forest regeneration. Besides safeguarding surrounding forest cover, other strategies such as enrichment planting, restoration of degraded forest remnants, and the establishment of ecological corridors may be needed to safeguard the biological potential of forests undergoing restoration to persist over time even in highly fragmented landscapes (Brancalion et al., 2013). The maintenance of mobile link species, such as larger-bodied frugivorous birds and mammals, could also provide vital connectivity across the landscape (Lundberg & Moberg, 2003), especially as secondary forests in more favorable landscapes can be dominated by smaller seeded species with low wood density (Hawes et al., 2020). Conserving and restoring seed-dispersing fauna will require tighter, not looser, environmental regulation related to hunting, since the fauna in the study region is sensitive to hunting pressure (Galetti et al., 2009). Nevertheless, there are currently two bills under discussion in the Brazilian parliament that could increase poaching in the seasonal forests of the study region, a key forest type for mammal conservation in the Atlantic Forest (Abessa et al., 2019).

4.4 | Identifying drivers of recovery of second-growth forest attributes

Several studies attest that successful natural regeneration is encouraged by a mix of economic drivers (e.g., steeper slopes have lower opportunity costs for agriculture) and biophysical drivers (e.g., unassisted regeneration is more likely if the previous land use was less intensive and the site is close to forest remnants [Chazdon et al., 2020; Martinez-Ramos et al., 2016; Molin et al., 2017; Rezende et al., 2015]). While these drivers refer to the likelihood (presence/absence) of natural regeneration, they do not address the attributes of these forests once established. For example, we observed that slope, a driver that favors the chance of natural regeneration, tended to have a negative relationship with AGB. Such contrasting influence of slope may be related to the different effects this driver has on regeneration; for example, lower opportunity costs increase the chance of land abandonment for natural regeneration (Molin et al., 2017) on one hand, but also soils tend to be closer to the bedrock which compromises tree growth. The present study shows

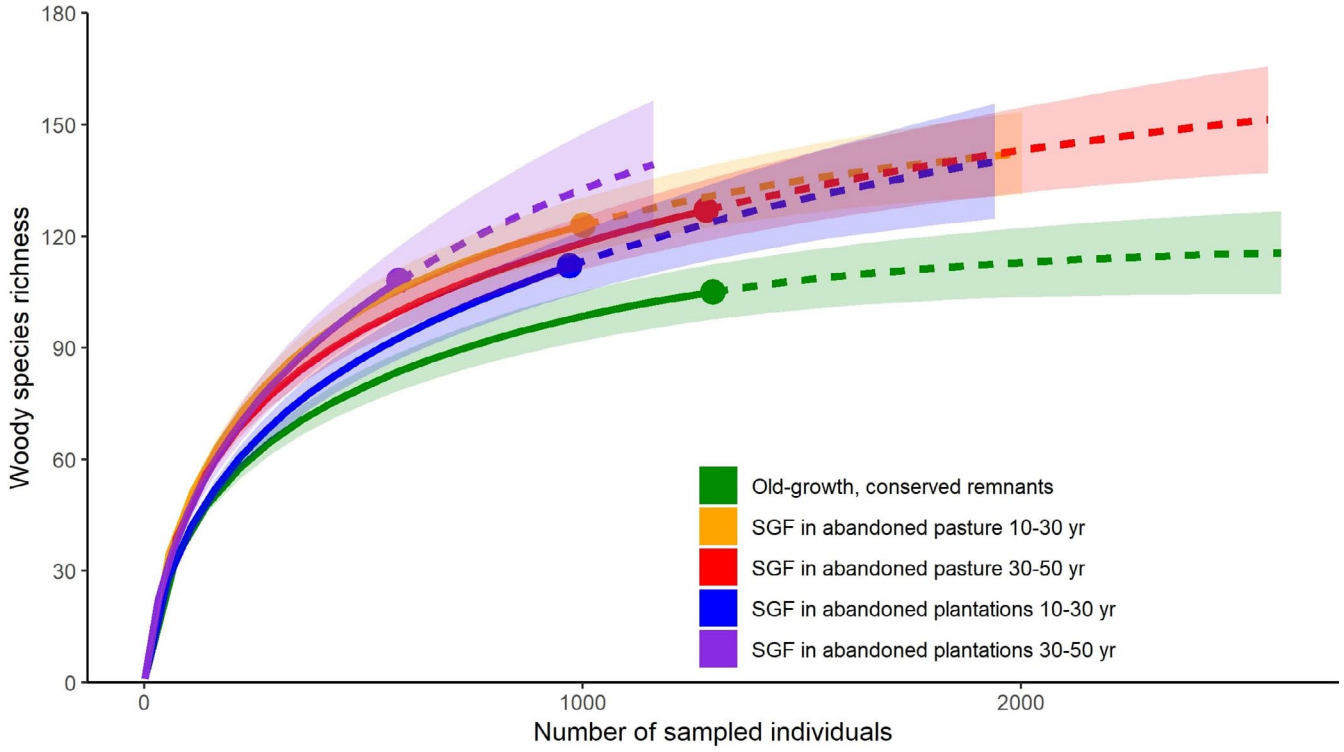

FIGURE 4 Rarefied native woody species richness of second-growth forests (SGF) established in abandoned pastures and abandoned eucalypt plantations (DBH ≥ 5 cm). Shading represents 95% confidence intervals

how landscape models developed to define priority areas for restoration based on where forest cover is more likely to increase can be complemented with information about where forest succession may have more biomass and diversity, such as investigated by Crouzeilles et al. (2019).

4.5 | Implications for conservation

Understanding the impact of past and current anthropogenic activities on the structure and composition of SGF provides more accurate estimates of the long-term potential of these forests to mitigate climate change and conserve biodiversity. Most policies and programs on climate change mitigation and biodiversity conservation focus on the forest areas per se, and not on their surrounding land uses. However, we found that the land use surrounding regenerating forests can significantly affect their structure and attributes. Thus, in some cases we could facilitate the recovery of SGF and improve their ecosystem service provisioning by modifying the surrounding land uses only, without requiring direct intervention within the remnant. This work calls for public policies regulating land use in agricultural landscapes of the Atlantic Forest to (a) promote biodiversity-friendly agricultural practices to reduce the degradation of forest fragments; (b) enhance and conserve existing forest patches; and (c) increase native forest cover through active and passive restoration in agricultural landscapes. Thus, preserving forest remnants that share the landscape with intensive agriculture is more complex than just considering land-use restriction by buffer strips around streams and the proportion of properties to be occupied by native vegetation, as enforced by the Brazilian Native Vegetation Law (Soares-Filho et al., 2014). In addition, we point to the need for more research on the impacts of current land management practices on forest recovery, such as the impact of herbicides, the longer-term role of non-native species such as *Eucalyptus* (Brancalion et al., 2020), and the effect of soil properties in forest AGB. Finally, these changes are all occurring under a warming planet, and the potential interactions between surrounding land cover and climate change on forest recovery could be important in guiding restoration practices (see also Elias et al., 2020). As we begin the UN Decade of Ecosystem Restoration, there is still a lot we need to learn about how to restore forests that provide multiple ecological and climate change benefits.

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CONFLICT OF INTEREST

The corresponding author confirms on behalf of all authors that there have been no involvements that might raise the question of bias in the work reported or in the conclusions, implications, or opinions stated.

AUTHOR CONTRIBUTIONS

RGC conceptualized the study, involved in formal analysis, investigated, contributed to methodology and software, visualized the study, and wrote the original draft and review. VSM curated the data curation, investigated, and validated the study. GDC curated the data and validated the study. DS curated the data, involved in formal analysis, contributed to methodology and software, and involved in writing review. RLC conceptualized the study, contributed to methodology, supervised the study, and wrote the original draft and review. JB curated the data, contributed to methodology supervision, and involved in writing review. SFBF contributed to methodology writing—review. RC involved in formal analysis, contributed to methodology, supervised the study, and wrote—review. PHSB conceptualized the study, contributed to funding acquisition, project administration, resources, supervision, writing original draft, and writing review.

DATA AVAILABILITY STATEMENT

The data that support the results in this study are available upon request only. Since we carried out forest inventories in remnants in private properties in São Paulo State, Brazil. Such data can only be used for academic purposes, maintaining the anonymity of landowners, and plot location.

ORCID

Ricardo G. César https://orcid.org/0000-0002-3392-8089
Vanessa de S. Moreno https://orcid.org/0000-0002-6714-2578
Pedro H. S. Brancalion https://orcid.org/0000-0001-8245-4062

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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