

The cost of restoring carbon stocks in Brazil’s Atlantic Forest

Pedro H. S. Brancalion¹, Joannès Guillemot², Ricardo César³, Henrique Andrade³, Alex Mendes³, Taísi Sorrini³, Marisa Piccolo⁴, Marina Peluci⁵, Vanessa Moreno^{3,6}, Gabriel Colletta³, and RL Chazdon⁷

¹University of São Paulo Luiz de Queiroz College of Agriculture

²CIRAD

³USP ESALQ

⁴Universidade de São Paulo

⁵Universidade de São Paulo Centro de Energia Nuclear na Agricultura

⁶University of São Paulo

⁷University of Connecticut

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Abstract

Knowing which restoration approach provides the best returns on investment for accumulating carbon is essential to foster restoration planning, financing, and implementation. We assessed the recovery of carbon stocks, implementation and land opportunity costs of forests established by natural regeneration and high-diversity native tree plantations. Our study was based on chronosequences (10-60 yr) of 12 naturally regenerating forests, 13 restoration plantations, and 5 reference forests located in Brazil’s Atlantic Forest. Restoration plantations accumulated approximately 50% more above-ground carbon than regenerating forests throughout the chronosequence. When controlling for soil clay content, soil carbon stocks were higher in reference than in restored forests, but they were comparable between plantations and regenerating forests. After 60 years of stand development, recovery of total carbon stocks in both restoration management types reached only half of the average stocks of reference forests. Total cost-effectiveness for carbon accumulation, including both implementation and land opportunity costs, was on average 60% higher for regenerating forests than for plantations (15.1 kgC.US\$-1 and 9.4 kgC.US\$-1, respectively). Both restoration management types had cost-effectiveness for carbon accumulation markedly lower than the price of carbon credits considered, so some voluntary forest carbon markets are not adequately priced to support restoration derived offsets. Although tree plantations initially had higher rates of carbon storage than regenerating forests, their higher implementation and land opportunity costs make them less cost-effective for carbon farming. Our results further suggest that carbon markets alone have a limited potential to up-scale restoration efforts in Brazil’s Atlantic Forest.

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Pedro H. S. Brancalion^{1*}, Joannès Guillemot^{1,2,3}, Ricardo Gomes César¹, Henrique Sverzut Andrade¹, Alex Mendes¹, Taísi Bech Sorrini¹, Marisa de Cássia Piccolo⁴, Marina Conte Peluci⁴, Vanessa de Souza Moreno¹, Gabriel Colletta⁵, Robin L. Chazdon^{1,6,7,8}

¹Department of Forest Sciences, “Luiz de Queiroz” College of Agriculture, University of São Paulo, Piracicaba, SP, 13418-900, Brazil.

²CIRAD, UMR Eco&Sols, 34060 Montpellier, France

³Eco&Sols, University of Montpellier, CIRAD, INRA, IRD, Montpellier SupAgro, 34060 Montpellier, France

⁴Nuclear Energy Center for Agriculture, University of São Paulo, Piracicaba, SP, 13400-970, Brazil.

⁵Postgraduate Program in Plant Biology, Institute of Biology, State University of Campinas, Campinas, SP, 13083-862, Brazil.

⁶Department of Ecology & Evolutionary Biology, University of Connecticut, Storrs, CT, 06269-3043, USA

⁷Tropical Forests and People Research Centre, University of the Sunshine Coast, Maroochydore, Queensland 4558, Australia

⁸Global Restoration Initiative, World Resources Institute, Washington, DC, 20002, USA

*Correspondence to: *Pedro H. S. Brancalion* Email: pedrob@usp.br

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Keywords: carbon sequestration; passive restoration; natural regeneration; restoration plantations; soil carbon; tree planting

Introduction

Tropical forest restoration is a central strategy in the global efforts to mitigate climate change (Bernal, Murray, & Pearson, 2018; Griscom et al., 2017; Houghton, Unruh, & Lefebvre, 1993; Pugh et al., 2019; Silver, Ostertag, & Lugo, 2000). Regenerating forests in the lowland tropics have high rates of carbon accumulation in aboveground biomass. On average, regenerating forests recover over 100 Mg of biomass per hectare within 20 years (L. Poorter et al., 2008) and reach biomass stocks comparable to old-growth forests within 66 to 80 years (Martin, Newton, & Bullock, 2013). Protecting young regenerating forests in Neotropics over the next 40 years could accumulate an amount of carbon sufficient to offset emissions from fossil fuel burning and industrial processes across all Latin American and Caribbean countries over the 1993-2014 period (Robin L. Chazdon et al., 2016).

The Bonn challenge, launched in 2011, is a global commitment of countries, NGOs, and private companies that aims to restore 350 M ha of degraded forests by 2030 (R. L. Chazdon et al., 2017; Grassi et al., 2017; K. D. Holl, 2017). The success of large-scale restoration programs will rely crucially on their economic viability over both short- and long- time scales, as well as the benefits they may provide to human wellbeing in relation to alternative land uses (Pedro H. S. Brancalion et al., 2019). Restoring large areas of tropical forests requires knowledge about which restoration approach provides the best returns on investment for accumulating carbon and other expected benefits, such as reducing extinction risk, improving water supplies, and increasing food security (Pedro H.S. Brancalion et al., 2018; Crouzeilles et al., 2017; Luke P. Shoo et al., 2017).

Natural regeneration is widely recognized as a core restoration strategy to mitigate climate change due to its potential to accumulate biomass at large spatial scales and at lower costs compared to tree plantations (R. L. Chazdon & Guariguata, 2016; Evans et al., 2015; Gilroy et al., 2014; Lewis, Wheeler, Mitchard, & Koch, 2019). This potential is already well demonstrated worldwide through several examples of forest transitions, where the abandonment of marginal agricultural lands led to the widespread expansion of forest cover through natural regeneration (Aide et al., 2013; Nanni et al., 2019; Rudel et al., 2005). As a spontaneous, uncontrolled reassembling process, natural regeneration trajectories can vary remarkably even among stands with similar local biophysical conditions and disturbance regime (Arroyo-Rodríguez et al., 2016; Mesquita, Massoca, Jakovac, Bentos, & Williamson, 2015; Norden et al., 2015). This variation has to be accounted for in restoration planning (Pedro H. S. Brancalion, Schweizer, et al., 2016; Uriarte & Chazdon, 2016).

In contrast with natural regeneration, tree plantings permit tighter control on the characteristics of the restored forest stand. Tree planting has often been established by restoration practitioners when ecosystem resilience is expected to be insufficient to support effective natural regeneration (K. D. Holl & Aide, 2011), or where rapid recovery of forest structure is required for legal compliance (Pedro H. S. Brancalion, Schweizer, et al., 2016; Chaves, Durigan, Brancalion, & Aronson, 2015; Rodrigues et al., 2011). Intensive management practices, such as planting trees at regular spacing, fertilizing soil, and controlling weeds and leaf-cutter ants, can promote rapid accumulation of above-ground biomass in tree stands (Rubilar et al., 2018; Wheeler et al., 2016). However, plantation management is costly, and restoration projects do not provide sufficient revenues to offset high implementation and maintenance costs (P.H.S.; Brancalion et al., 2019). In addition, most low-resilience sites where tree planting is required to support restoration have been historically used for intensive agricultural production and therefore have high land opportunity costs (Laurance, Sayer, & Cassman, 2014) and altered biophysical conditions that reduce the potential for natural regeneration (R.L. Chazdon, 2014).

Comparing restored forests established by tree planting and natural regeneration (i.e. second-growth forests) within the same geographic region is key to guide the selection of appropriate restoration approaches for different socioecological contexts and expected benefits (Luke P. Shoo et al., 2017). As stated above, tree planting and natural regeneration are usually found in contrasting biophysical conditions within landscapes. Consequently, *in situ* comparisons cannot be used to develop general guidelines about the relative costs and benefits of restoration practice (Reid, Fagan, & Zahawi, 2018), to provide a basis for guiding decisions regarding *how* to restore a given piece of land. Rather, such comparisons have the potential to highlight the actual efficiencies of “real-world” restoration practices, as they are determined by environmental, social and economic constraints. Such comparisons can help to guide decisions regarding how to invest limited resources for implementing forest restoration approaches across a range of socio-ecological conditions.

At the global scale, natural regeneration was shown to be more effective (Crouzeilles et al., 2017) or present similar outcomes (Meli et al., 2017) than tree plantations for recovering forest biodiversity and structure. At the local scale, however, L. P. Shoo, Freebody, Kanowski, and Catterall (2016) found that restoration plantations 1-25 yr old in the Australian wet tropics had a faster recovery of wood volume than natural regeneration sites, and César et al. (2017) found similar results in the Atlantic Forest of Brazil for 7-15 yr old forests undergoing restoration. These previous works focused mainly on above-ground carbon, with no assessment of the cost-effectiveness of restoration approaches. Cost-effectiveness assessments, rather than the evaluation of costs and effectiveness independently, are essential for guiding decision-making in restoration (Birch et al., 2010; Molin, Chazdon, Ferraz, & Brancalion, 2018; Strassburg et al., 2019). Moreover, the relative effect of tree planting and natural regeneration for soil carbon sequestration remain unknown.

Here, we assessed the carbon accumulation (above-ground and soil), implementation and land opportunity costs of forests established by natural regeneration (i.e, passive restoration) and high-diversity native tree plantations (i.e, active restoration). Our study was based on chronosequences (10-60 yr) in human-modified landscapes of Brazil’s Atlantic Forest. Brazil’s Atlantic Forest is a highly degraded biodiversity hotspot with low remnant native forest cover (only 12-28% of the original Atlantic Forest remains today, depending on remote sensing resolution; Rezende et al., 2018; Ribeiro, Metzger, Martensen, Ponzoni, & Hirota, 2009).

Deforestation and fragmentation resulted mainly from the expansion of profitable agricultural and forestry commodities such as sugarcane, cattle ranching, and eucalypt plantations (Joly, Metzger, & Tabarelli, 2014), making cost-effectiveness a fundamental topic for the upscaling of restoration in this biome (Pedro Henrique Santin Brancalion, Viani, Strassburg, & Rodrigues, 2012). This work aimed to compare current management practices in order to guide the ambitious restoration programs recently established for the Atlantic Forest (Molin et al., 2018; Soares et al., 2014; Strassburg et al., 2019). Restoration practitioners and organizations worldwide have to make hard decisions on where and how to invest in restoration to enhance carbon accumulation while promoting biodiversity and other ecosystem services (Luke P. Shoo et al., 2017). The solutions identified for carbon farming through restoration with native trees in the Atlantic Forest of Brazil may be readily transferrable to other tropical forest regions with comparable economic and environmental contexts, and hopefully will contribute to more effective use of the limited resources currently available for forest restoration.

Methods

Study sites

We studied 12 second-growth forests established for 11-47 years on former pasturelands, 13 restoration plantations of 10-61 years of age established on pasturelands and croplands, and five old-growth, reference forests (Fig. S1; Table S1). Second-growth forests were sampled in the Corumbataí watershed, southeastern Brazil (Fig. S1). Pastureland is the principal land use in this watershed (43.7% of area), followed by sugarcane fields (29.4%), and remaining native forest cover (12.4%; Silvio F. B. Ferraz et al., 2014). Previous land use and the age of regenerating forests were determined based on panchromatic aerial photographs and annual LANDSAT 5 and 8 images. Further information about this watershed and forest patch sampling can be found in César et al. (2017). Second-growth forests of the Corumbataí watershed are found regenerating almost exclusively in marginal lands, such as steep slopes and/or sandy or rocky soil, where mechanized agriculture is not possible. Extensive cattle ranching or eucalypt woodlots have been established in these marginal agricultural lands, and their less intensive historical soil management, at least compared to sugarcane or other crop production, have led to the regeneration of secondary forests when land is abandoned (César et al., 2017). All second-growth forests were found away from riparian areas and were expansions of existing forest remnants.

Restoration plantations were mostly identified in the same region (< 100 km) of second-growth forests, but some additional plantations (three out of the four plantations older than 25 years old) were sampled (< 300 km) to include older sites in our dataset (Fig. S1). These plantations were established with a high diversity of native tree species (20-100 species) and had comparable levels of tree richness than the studied second-growth and reference forests (Fig. S2). Plantation management consisted of planting nursery-grown seedlings in regular spacing (usually 3×2 m), fertilizing the soil before (base fertilization) and after planting (broadcast fertilization), and weeding ruderal plants with glyphosate spraying or mowing (see details in P.H.S.; Brancalion et al., 2019). Land use prior to plantation establishment was determined by interviewing restoration project managers. Only three sites were established on pasturelands, and the rest were established on former sugarcane fields. Twelve sites were found in riparian buffers and were established to comply with the Forest Code (Pedro H. S. Brancalion, Garcia, et al., 2016). Nine of the 12 sites were isolated from native forest remnants, and three sites were established within the neighborhood of existing degraded remnants. Consequently, our analysis did not allow for a controlled comparison of properties between tree plantations and natural regeneration because these restoration approaches were established in quite different biophysical conditions in the studied landscapes. Although not appropriate for objectively comparing these restoration approaches *per se* and isolating uncontrolled factors (Reid et al., 2018), our study design depicts the cost-effectiveness of restoration approaches currently being implemented in agricultural landscapes of Brazil's Atlantic Forest (see Pedro H. S. Brancalion, Schweizer, et al., 2016).

We complemented our sampling with five reference forests, represented by old-growth remnants distributed around the Corumbataí watershed. These remnants were selected for being the best conserved forests of the study region, with a well-developed forest structure and some large (> 50 cm diameter at breast height)

late-successional remnant trees (Fig. S1). These forests do not represent the pre-disturbance carbon stocks of the original forests of this region, since these remnants are small (<200 hectares) and are embedded within a patchy agricultural matrix. However, they represent an appropriate benchmark for restoration in this region, given that restored forests will likely persist as small patches surrounded by agriculture.

The forests sampled were selected according to different criteria. The second-growth forests were selected systematically based on available information on second-growth forest age and previous land use, aiming at a representation of approximately five forests per age class x previous land use (S. F. B. Ferraz et al., 2014). Restoration plantations and old-growth forests were selected based on the availability of these forest typologies with different ages within and closer to the Corumbataí watershed, the focus area of the study. We sampled all restoration plantation >15 years old and old-growth forests we knew in the region due to the scarcity of these kinds of forest, and seven restoration plantations <15 years old based on their location (forests found within the watershed or closer to it was prioritized) and access.

Forest inventories

We established one 20 × 45 m plot in each of the aforementioned forest stands, totaling 30 plots. For second-growth forests and restoration plantations, which usually had a small and elongated area, we allocated the inventory plots as centralized as possible in the forest stand in order to avoid edge effects. In old-growth forest stands, which were larger than the aforementioned forest typologies, we took the main trail that crossed these forests and established the inventory plot when distant at least 50 m from the forest edge. For all plots, we avoided forest gaps or patches affected by human disturbances (e.g. fire or logging).

We measured the diameter at breast height (DBH) of all trees and shrubs (DBH [?] 5 cm) within each plot and identified them to species level, without distinguishing between planted or spontaneously regenerated trees, and used these data to calculate above-ground biomass based on the equations developed by Chave et al. (2014), with wood density values mostly compiled from Chave et al. (2009) and Cesar et al. (2017). Above-ground carbon stocks were calculated by multiplying above-ground biomass by 0.46, the average carbon content of dry woody biomass of Atlantic Forest trees (Ferez, Campoe, Mendes, & Stape, 2015).

Soil characteristics

One composite soil sample (18 sub-samples systematically distributed per plot) was made within each plot at both 0-10 cm and 10-20 cm depth and analyzed for sum of bases (cations were determined by spectrophotometry and P by colorimetry), cation exchange capacity, and texture, which was analyzed using the hydrometer method. Soil samples were additionally collected with a cylindrical auger of known volume at 0-10 cm and 10-20 cm depth, in three sampling points distributed systematically within each plot (one at the center of the plot and one 10 m apart from each of its lateral edges), to measure soil texture and total soil carbon. The soil bulk density of each plot ($n = 3$) and depth was determined by the core method on a core of 0.5 cm diameter and 5.0 cm deep for the 0-10 and 10-20 cm depth (samples oven-dried at 105degC until constant weight), using the methodology described by Donagema, Campos, Calderano, Teixeira, and Viana (2011). Soil samples were air-dried and sieved in 2 mm open mesh to obtain air-dried fine soil, and then a portion of the sample was ground to pass through 100 mesh sieve to measure the C content. Soil texture was measured according to (EMBRAPA, 1997). Total C content was quantified by dry combustion method (1000degC) using a LECO elemental analyzer (TruSpec CHNS, LECO). Due to logistical problems, texture data were missing for one of the reference forest. Soil carbon stock (SCS, Mg.ha⁻¹) of a soil layer i was then calculated as follows:

$$SCS_i = t_i \times TCC_i \times BD_i \quad (Eq. 1)$$

where t is layer thickness (cm), TCC is total carbon content (gC.g⁻¹), and BD is soil bulk density (g.cm⁻³). We considered a soil layer thickness of 10 cm, allowing in this case the estimate of SCS in the 0-10 and 10-20 cm horizons, which was subsequently summed to obtain SCS in the 0-20 cm horizon.

Restoration costs

Restoration implementation costs were obtained from Molin et al. (2018), which indicated that restoration plantations established on croplands and pasturelands in the region cost US\$2,500.ha⁻¹ and US\$3,750.ha⁻¹, respectively (more expensive in pasturelands due to fencing costs); these estimates include all costs associated with tree planting and maintenance for up to three years (Molin et al., 2018). Unassisted natural regeneration in croplands had no implementation cost and in pasturelands it was US\$1,250.ha⁻¹ due to fencing costs (Molin et al., 2018). Annual land opportunity cost was estimated based on land rental prices for sugarcane and cattle ranching in the Piracicaba region (where the Corumbataí watershed is located), based on official survey of the Institute of Agriculture Economics of São Paulo (São Paulo, 2017), and was estimated as US\$106.66.ha⁻¹.year⁻¹ for cattle ranching and US\$389.23.ha⁻¹.year⁻¹ for sugarcane (Molin et al., 2018). We calculated the accumulated land opportunity cost by multiplying these aforementioned annual costs by the age of the restored forests. Total restoration cost was calculated by summing implementation and accumulated land opportunity costs (e.g., total cost for 10-year old restoration plantation on cropland = US\$2,500.ha⁻¹ + US\$389.23.ha⁻¹.year⁻¹ × 10 years = US\$6392.3). No discount rate was applied because we aimed to compare tree planting and natural regeneration on the present value.

Data Analysis

The cost-effectiveness of restoration was calculated by dividing above-ground carbon by the cost of restoration. Cost-effectiveness was calculated based on above-ground carbon only (e.g. Birch et al., 2010; Strassburg et al., 2019), because no information on the net soil carbon changes attributable to forest restoration was available in this study, and soil carbon dynamics following restoration in the Atlantic Forest remains poorly known (Mendes et al., 2019). The explored model was as follows:

$$Y \sim MT \times stem_{density} + MT \times clay + MT \times age$$

where Y is above-ground carbon accumulation, soil carbon accumulation or cost-effectiveness for above-ground carbon accumulation - models were adjusted separately for each dependent variables. MT is management type (categorical variable). $stem_{density}$, clay and age are density of stems per hectare (#stem/ha), clay content (%) and stand age (years), respectively (covariates).

For each dependent variable, two models were adjusted, where MT factor was used to test for differences between reference and restored forests, and between plantations and naturally regenerated forests. When comparing reference and restored forests, stand age was not included in the models. The models were simplified using F-tests. Data from different sites were considered as independent observations. Log-log transformation was used when necessary to linearize relationships among variables and/or correct for residual heteroscedasticity. When log-log transformation was applied, model fit was presented with its natural power form in the figures. We did not report critical autocorrelation of the explanatory variables in our dataset (VIF<4). The compliance to linear model assumptions was checked using standard procedures (Zuur, Ieno, Walker, Saveliev, & Smith, 2009).

We further explored the drivers of above-ground biomass and soil carbon accumulation by conducting a model selection procedure (Burnham & Anderson 2002). For each variable, competing models including all possible combinations of explanatory variables were adjusted and ranked using $[\Delta]AICc$. $[\Delta]AICc$ is the difference between the Akaike Information Criteria corrected for small samples (AICc) of a given model and the AICc of the best-fitting model (minimum AICc). To assess the contribution of explanatory variables, we retained for each forest carbon stock components a subset of best-fitting models ($[\Delta]AICc < 2$). The averaged coefficient, standard error and relative importance of explanatory variables (the weighted proportion of the models $[\Delta]AICc \leq 2$ that contain the driver) were calculated from the final model subsets. The soil characteristics considered in this analysis included sum of bases, cation exchange capacity, and texture. Soil carbon content was analyzed separately at depths 0-10 cm and 10-20 cm. All analyses were carried out in the R 3.0 environment (R Development Core Team, 2013), using the package “MuMIn” (Barton, 2016).

Results

Carbon accumulation outcomes in restored forests

Restoration management significantly affected biomass accumulation ($F_{1,21} = 7.9$, $P < 0.001$): tree plantations accumulated approximately 50% more above-ground carbon than second-growth forests throughout the chronosequence (Fig. 1A). Soil carbon stocks at 0-20 cm depth were not affected by forest age for any of the restoration management type ($F_{1,11} = 0.25$, $P = 0.62$ and $F_{1,10} = 1.6$, $P = 0.22$ for plantations and second-growth forests, respectively; Fig. 1B). Similar results were observed when soil layers 0-10 and 10-20 cm were analyzed separately (Fig. S2). Soil carbon stocks were strongly correlated with clay content (Fig. 2), which positively influenced soil carbon stocks in restored forests ($F_{1,11} = 26.2$, $P < 0.001$ and $F_{1,10} = 22.6$, $P < 0.001$ for plantations and second-growth forests, respectively; Fig. 2). When controlling for the effect of clay content, soil carbon stocks were higher for reference than for restored forests ($F_{1,27} = 23.9$, $P < 0.001$), but were similar between plantations and second-growth forests ($F_{1,22} = 2.18$, $P = 0.15$). Stem density had no significant effect on any of the explored dependent variables.

Drivers of above-ground and soil carbon accumulation in restored forests

The best-fitting models (ΔAIC [?] 2) explaining above-ground carbon accumulation in restored forests included restoration type and/or forest age, whereas the best-fitting models explaining soil carbon stocks included exclusively soil attributes, except for the inclusion of above-ground carbon stocks as explanatory variable of 10-20 cm soil carbon (Table 1). Clay content was included in all soil carbon models, whereas soil sum of bases and soil density were included in two models (one for 0-10 cm and one for 10-20 cm; Table 1). Restoration through natural regeneration accumulated less above-ground carbon than native tree plantations (Fig. 3; Fig. S3). Soil carbon stocks were positively correlated with higher sum of bases, clay content (Fig. S3), and soil density at both 0-10 and 10-20 cm, with the relative importance of each variable changing for the different soil depths (Fig. 3).

Cost-effectiveness of restoration approaches for above-ground and soil carbon accumulation

The amount of carbon accumulated per invested US\$ in restored forests increased with time when only implementation costs were considered ($F_{1,22} = 12.8$, $P = 0.001$), because of the gradual increase of carbon stocks and the absence of additional costs after the first years of implementation (Fig. 4A). However, the increase of land opportunity costs was higher than the increase of carbon accumulation, which resulted in a decrease of the opportunity cost-effectiveness for carbon accumulation along the chronosequence ($F_{1,22} = 10.5$, $P = 0.003$; Fig. 4B). These opposing trajectories of implementation and accumulated land opportunity cost-effectiveness along the chronosequence nullified changes in total cost-effectiveness with age in restored forests ($F_{1,22} = 2.8$, $P = 0.1$; Fig. 4C). Implementation cost-effectiveness was significantly higher for second-growth forests than for plantations throughout the chronosequence ($F_{1,22} = 9.4$, $P = 0.005$; Fig. 4A). Opportunity cost-effectiveness showed a similar trend but the average difference between plantations and second-growth forests was not significant ($F_{1,22} = 2.7$, $P = 0.1$; Fig. 4B). Total cost-effectiveness, i.e. the amount of accumulated carbon standardized by the total cost of restoration (implementation + opportunity costs), was significantly higher for second-growth forests ($F_{1,22} = 9.2$, $P = 0.006$; Fig. 4C). On average, second-growth forests displayed a total cost-effectiveness that was 60% higher than plantations (15.1 kgC.US\$⁻¹ and 9.4 kgC.US\$⁻¹, respectively). Average differences between second-growth forests and plantations were higher for total cost-effectiveness than for its components (i.e. implementation and accumulated land opportunity cost-effectiveness). This indicates that differences in both implementation and opportunity costs contributed to the resulting differences in total cost-effectiveness between restoration practices. We note that one tree planting site was significantly older (61 years old) than the rest of the restoration dataset. Removing this site from the analyses did not change any results or conclusions of this work.

Discussion

Native tree plantations were shown to be more effective in accumulating above-ground and soil carbon stocks than natural regeneration during the first 50 years, but their higher implementation (tree plantations: US\$2,788 *versus* natural regeneration: US\$1,250) and land opportunity (tree plantations: US\$324 per year *versus* natural regeneration: US\$106 per year; Molin et al. 2018) costs make them less cost-effective for carbon farming. It is important to note that our work assessed high-diversity plantations of native tree

species rather than monoculture tree plantations, to which natural regeneration has often been compared (Lewis et al., 2019). Several independent factors have contributed to this outcome. Exploring them is key to understanding how the cost-effectiveness of different restoration approaches may vary within human-modified tropical landscapes.

Most of the plantations included in the present study were found in riparian buffers - a privileged environmental condition for biomass accumulation due to the reduced water deficit and higher soil fertility - and in landholdings dominated by intensive agriculture, where soils usually display high nutrient and clay content. The studied tree plantations may therefore have benefited from higher nutrient and water availability than second-growth forests, which usually regenerate on slopes and sandy soils distant from watercourses. Water deficit and low soil fertility are known to limit tropical forest successional development (Jakovac, Pena-Claros, Kuyper, & Bongers, 2015; Martins, Marques, dos Santos, & Marques, 2015; Lourens Poorter et al., 2016; Zermeno-Hernandez, Mendez-Toribio, Siebe, Benitez-Malvido, & Martinez-Ramos, 2015), and may have reduced the biomass accumulation rates of second-growth forests in our study. Water limitation, in particular, may have played a critical role for the differential performance of restoration approaches, since the study region has a seasonal climate with annual water deficits of 20 mm or more depending on geographical features (Alvares, Stape, Sentelhas, Gonçalves, & Sparovek, 2013). In addition, tree plantations were fertilized, weeded, and planted at a regular spacing, which allow an efficient occupation of the deforested area by trees and enhance their growth, resulting in a higher accumulation of biomass per area (P.H.S.; Brancalion et al., 2019; Ferez et al., 2015). Our observation that tree plantations initially accumulate more carbon than second-growth forest corroborates previous results obtained in southern Costa Rica (Karen D. Holl & Zahawi, 2014) and Queensland, Australia (L. P. Shoo et al., 2016), but contradict the findings of Lewis et al. (2019) based on commercial forestry plantations.

The predominance of soil properties over land use effects on soil carbon stocks in the tropics has been reported by Powers, Corre, Twine, and Veldkamp (2011) and is confirmed in our study landscape. Greater biomass productivity and carbon inputs are expected to increase soil carbon stocks (Jandl et al., 2007; Karlen & Cambardella, 1996), even though changes in soil microbial communities may affect this causal dependency (Fontaine, Bardoux, Abbadie, & Mariotti, 2004). As a result, intensive forest management, afforestation, and reforestation are commonly associated with increased soil carbon stocks (Don, Schumacher, & Freibauer, 2011; Guo & Gifford, 2002). We do not report such an association between above-ground biomass and soil carbon stocks, as plantations displayed soil C stocks comparable to naturally regenerated forests, and the temporal accumulation of above-ground biomass in restored forests was not accompanied by a similar increase in soil carbon stocks (Fig. 1 and 2). Variations in soil properties among study plots may have obscured the relationship between soil carbon stocks and restored forest age at landscape level, as also reported by Mora et al. (2018) and Martin et al. (2013). Strikingly, none of the restoration management types recovered soil carbon stocks comparable to reference forests. Our results thus corroborate a global meta-analysis in tropical regions that found that second-growth forests stored 9% less soil carbon than primary forests (Don et al., 2011). The differences between forest types was in our case remarkably higher, with reference forests having approximately 50% higher soil carbon stocks at similar soil clay content. Taken as a whole, our results show that both above-ground biomass and soil carbon were enhanced in plantations compared to second growth forests, but that 60 years of stand development was not sufficient for the restored areas to recover stocks comparable to reference forests.

The inclusion of restoration costs in the analysis reversed the priority order of restoration approaches for carbon farming, and natural regeneration emerged as the most cost-effective solution. In other words, the cost reduction allowed by natural regeneration compared to planting more than compensated for the slower rate of accumulation of biomass, even in the unfavorable environmental conditions for tree growth in which second-growth forests regenerated in the study region. It is also important to note that we included in our analysis the direct financial costs of passive restoration (i.e., natural regeneration; Zahawi, Reid, & Holl, 2014) and considered both implementation and land opportunity costs. Natural regeneration may show even higher cost-effectiveness in regions where these costs are reduced, such as in landscapes not dominated by agriculture, where land rental prices are usually low. In addition, natural regeneration can be assisted (Shono,

Cadaweng, & Durst, 2007), potentially at much lower costs than tree planting over the whole area. Assisted regeneration has the potential to enhance the growth performance of spontaneously regenerating trees, thus enhancing the biomass accumulation potential with lower implementation costs. We note that our results may be affected by a site selection bias, possibly resulting in an over-estimation of natural regeneration success. As was highlighted recently (Reid et al., 2018), natural regeneration is commonly conducted at sites closed to secondary forests remnants, which could bias conclusions of restoration practice comparisons. Additional studies would be needed to adequately represent the Atlantic Forest, a 1.3 million km² ecosystem with several biogeographical zones and socioeconomic conditions that would affect the comparisons made in this study.

Carbon market currently values a carbon credit approximately 5 US\$ (Hamrick & Goldstein, 2016) for 1 ton of CO₂ (273 kgC), i.e. 54.6 kgC.US\$⁻¹. Here, we report average total cost-effectiveness values for above-ground carbon of 9.1 kgC.US\$⁻¹ and 15.1 kgC.US\$⁻¹, for plantations and naturally regenerated forests, respectively. The market price of 5 US\$ thus underestimates by more than a factor of 3 the actual price of carbon accumulation in restored forests. This clearly demonstrates that the revenues potentially obtained by trading carbon credits do not adequately cover the basic costs of both active and passive restoration. Overall, our results suggest that carbon markets as they are today offer a very low potential to up-scale restoration efforts in the Atlantic Forest. Other complementary revenue sources like those resulting from timber and non-timber forest products' exploitation and payments for watershed services have been proposed to make tropical forest restoration financially viable (P.H.S.; Brancalion et al., 2017), which could be bundled with carbon farming for more favorable financial results. Notwithstanding, carbon farming will continue to be one of the major demands of environmental organizations, private companies, and governments supporting forest restoration in tropical regions, and finding the most cost-effective restoration approaches for this objective remains as a critical research challenge.

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Authors' contributions

PHSB, RGC and RLC conceived the ideas and designed methodology; AM, RGC, HSA, TBS, MCP, and VSM collected the data; MCP led soil carbon analysis; JG analyzed the data; PHSB and JG led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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Tables

Table 1. Best models (ΔAIC [?] 2) describing above-ground carbon and soil carbon accumulation in cronosequences of tree plantations and second-growth forests established in agricultural landscapes of the Atlantic Forest of Brazil.

Response variable	Soil data depth	Model	Intercept	Forest age	Clay content	Sum of bases	Species
Above-ground C	0-20 cm	1	54.98	1.30	NS	NS	NS
		2	47.06	1.06	NS	NS	NS
Soil C	0-10 cm	1	-24.45	NS	0.33	0.05	NA
		2	-15.63	NS	0.34	NS	NA
	10-20 cm	1	7.92	NS	0.24	NS	NA
		2	7.11	NS	0.24	0.02	NA
		3	6.67	NS	0.24	NS	NA
		4	0.85	NS	0.26	NS	NA

Figure legends

Figure 1. Above-ground carbon (A) and soil carbon accumulation (B) in chronosequences of tree plantations and second-growth forests, and reference forest values, in agricultural landscapes of Brazil's Atlantic Forest. Solid and dashed lines represent, respectively, significant and non-significant power regressions. ANCOVA on log-log transformed data indicated a significant difference ($P < 0.05$) of estimated intercepts between plantations and second-growth forests for above-ground carbon biomass (A) and soil carbon stocks (B).

Figure 2. Soil carbon association with clay content in tree plantations, second-growth forests, and reference forests within agricultural landscapes of Brazil's Atlantic Forest. Solid lines represent significant power regressions. Soil carbon stocks *versus* clay content relationship: ANCOVA on log-log transformed data

indicated a significant difference ($P < 0.05$) of estimated intercepts between restored and reference forests, and between plantations and naturally regenerated forests.

Figure 3. Graphical representation of the influence of different drivers of above-ground carbon and soil carbon stocks in chronosequences of tree plantations and second-growth forests established in agricultural landscapes of Brazil's Atlantic Forest. Results reflect the average model developed by merging all models [?] AIC_c [?] 2. Arrow color represent the sign of the average coefficient, and relative importance express the weighted proportion of the models [?] AIC_c [?] 2 that contain the driver.

Figure 4. Temporal variation of restoration implementation costs (A), accumulated land opportunity costs (B), and total (C) costs for accumulating above-ground carbon stocks (i.e., cost-effectiveness) in chronosequences of tree plantations and second-growth forests established in agricultural landscapes of Brazil's Atlantic Forest. Solid and dashed lines represent, respectively, significant and non-significant power regressions. ANCOVA on log-log transformed data indicated a significant difference ($P < 0.05$) of estimated intercepts between plantations and second-growth forests for implementation cost-effectiveness (A) and total cost-effectiveness (C).







