





RESEARCH ARTICLE

Exotic eucalypts: From demonized trees to allies of tropical forest restoration?

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Abstract

1. International forest landscape restoration commitments have promoted the restoration of millions of hectares of degraded and deforested lands globally, but few forest restoration approaches provide both ecologically-sound and financially-viable solutions for achieving the spatial scale proposed. One potential revenue source for restoration is selective harvesting of timber, a product for which there is a clear global market and increasing demand. The use of commercially valuable exotic trees may attract farmers to restoration, but can be a major concern for ecologists.
2. Here, we present results collected over 7 years from experimental studies at three sites across the Brazilian Atlantic Forest to assess the impacts of incorporating exotic eucalypts as a transitional stage in tropical forest restoration on above-ground biomass accumulation, native woody species regeneration and financial viability.
3. Biomass accumulation was nine times greater in mixed eucalypt-native species plantations than native only plantings due to fast eucalypt growth. Nonetheless, the growth of native non-pioneer trees was not affected or only slightly reduced by eucalypts prior to logging.
4. Eucalypts did not negatively affect the natural regeneration of native woody species before or after eucalypt logging. Canopy cover regrew quickly but was slightly lower a year following logging in mixed eucalypt-native species plantations. Natural regeneration richness and planted non-pioneer growth were similar across treatments in the post-logging period. We found higher variation of biomass accumulation and native species regeneration among sites than between plantation types within sites.
5. The income from eucalypt wood production offset 44%–75% of restoration implementation costs.
6. *Synthesis and applications.* Many of the negative effects attributed to eucalypts on the growth and natural regeneration of native trees depend on features of the production system, landscape structure, soil, and climate in which they are grown, rather than the effects of eucalypts per se. In Brazil's Atlantic Forest region, exotic eucalypts can become important allies of tropical forest restoration, and their use

and investment opportunities should be considered within the portfolio of options supported by public and private funding and policies.

KEYWORDS

Atlantic forest, ecological restoration, *Eucalyptus*, forest and landscape restoration, large-scale restoration, natural regeneration, restoration costs, restoration economy

1 | INTRODUCTION

Tropical forest restoration has emerged as a promising intervention to mitigate climate change, biodiversity loss, and improve human well-being in regions of the planet where high endemic species richness coincides with widespread deforestation and forest fragmentation (Holl, 2017). Ambitious restoration targets have been set for tens to hundreds of millions of hectares in tropical forest regions at the national, regional, and international scales (e.g. Bonn Challenge, Initiative 20 × 20 in Latin America, Atlantic Forest Restoration Pact in Brazil; Chazdon et al., 2017). But the high costs of forest landscape restoration present a major obstacle for widescale adoption. For example, the implementation phase alone can cost upwards of US\$3,700 per hectare in Brazil (Molin, Chazdon, Ferraz, & Brancalion, 2018), and international financing for such efforts is limited compared to the large area proposed for restoration (12 M ha in Brazil alone). Restoring tropical forests requires more than just compensating landowners for the use of the land. It demands substantial investments in the implementation, maintenance, and long-term protection and monitoring of recovering forests (Brancalion et al., 2017; Reid, Fagan, Lucas, Slaughter, & Zahawi, 2018). Hence, tropical countries need to develop innovative, financially-viable approaches to forest restoration that are not heavily dependent on external aid that can stimulate large-scale application to reach scale (Ding et al., 2017).

One potential revenue source for restoration is selective harvesting of timber, a product for which there is a clear global market and increasing demand (Putz et al., 2012). From a narrow ecological perspective, forest restoration projects should only use native tree species. However, fast-growing, exotic species comprise a potential alternative, if they can help offset planting costs, do not inhibit the recolonization and growth of native species, and speed up the recovery of forest functions (Ashton, Gamage, Gunatilleke, & Gunatilleke, 1997; Catterall, 2016; Lamb, Erskine, & Parrotta, 2005). Extensive production knowledge and established timber markets for certain exotic tree species may transform restoration plantings into a profitable activity and create investment opportunities (Brancalion, Viani, Strassburg, & Rodrigues, 2012; Grossman, 2015; Payn et al., 2015). Several studies have found abundant and diverse regeneration of native woody species in the understory of commercial tree plantations across the global tropics (e.g. Brockerhoff, Jactel, Parrotta, & Ferraz, 2013; Pryde, Holland, Watson, Turton, & Nimmo, 2015; Wu et al., 2015), and highlight the potential of timber plantations to promote large-scale

forest restoration (Lugo, 1997; Parrotta, Turnbull, & Jones, 1997). However, we are not aware of any controlled or replicated experiments that rigorously assess the ecological and economic outcomes of interplanting commercial exotic species with a diverse suite of native species to facilitate regeneration of a diversity of tropical forest species and offset restoration implementation costs by harvesting exotic planted trees.

Exotic eucalypts, planted for wood pulp and timber, are ubiquitous in tropical regions, and currently cover over 20 million hectares globally. Only nine out of >700 *Eucalyptus* and *Corymbia* species (hereafter referred to as “eucalypts”) comprise >90% of the global planted area (Stanturf, Vance, Fox, & Kirst, 2013). The prominent environmental concerns associated with the large plantation area and ecological characteristics of exotic eucalypts have motivated several studies to assess their biodiversity value, allelopathic effects, water consumption, and potential for invading unplanted areas (Becerra et al., 2017; Bremer & Farley, 2010; Stanturf et al., 2013). The effects of eucalypts vary, however, with regional climate, previous land use, and plantation management practices (Brockerhoff et al., 2013).

Eucalypts are grown in Brazil mostly for pulp, but also for round logs, sawn lumber, firewood, charcoal, fencing poles, and oil (IBA, 2018). Such flexible uses and high productivity (Brazil's average: 35 m³ ha⁻¹ year⁻¹, but reaching >60 m³ ha⁻¹ year⁻¹ in some regions) make eucalypts popular commercial trees for farmers (Goncalves et al., 2013); hence, eucalypts comprise 71% of tree plantation area in Brazil (5.7 Mha, IBA, 2018) and are widely used in plantations throughout Latin America (Geary, 2001; Salas et al., 2016). Most of these plantations have been intensively managed in short rotations (~5–7 years) and as extensive monocultures, which prevent the natural regeneration of native woody species and resulted in so-called “green deserts” (Bremer & Farley, 2010). However, less intensively managed and abandoned eucalypt plantations in many regions host a high diversity of plants and birds (César et al., 2017; Lopes, Gussoni, Demarchi, Almeida, & Pizo, 2015; Marsden, Whiffin, & Galetti, 2001; Silva-Junior, Scarano, & Cardel, 1995).

Forest restoration projects in the Atlantic forest region of Brazil mostly plant a high diversity of native tree species (Brancalion et al., 2018; Rodrigues et al., 2011), but the Native Vegetation Protection Law of 2012, allows for intercropping exotic, commercially-valuable tree species with native species in restoration projects to meet restoration requirements. The justification for this legislative change from the earlier 1965 Forest Code was the need to transform restoration into a financially-viable

land use (Brancalion et al., 2012), which compensates farmers for the opportunity costs of foregone agricultural land use. Here, we draw on results from experimental studies at three sites across the Brazilian Atlantic Forest to assess rigorously the impacts of incorporating exotic eucalypts as a transitional stage in tropical forest restoration on above-ground biomass accumulation, native woody species regeneration, and costs. This information is important to evaluate the ecological and financial viability of this novel legal norm and its potential for dissemination to other global regions to leverage tropical forest restoration.

2 | MATERIALS AND METHODS

2.1 | Experimental plantings

2.1.1 | Experiment setup

We established experimental plantings in three municipalities distributed across the eastern portion of the Atlantic Forest (Site 1: Aracruz-Espírito Santo, Site 2: Mucuri-Bahia, and Site 3: Igrapiúna-Bahia; Table S1; Figure 1). The experiments were established as a

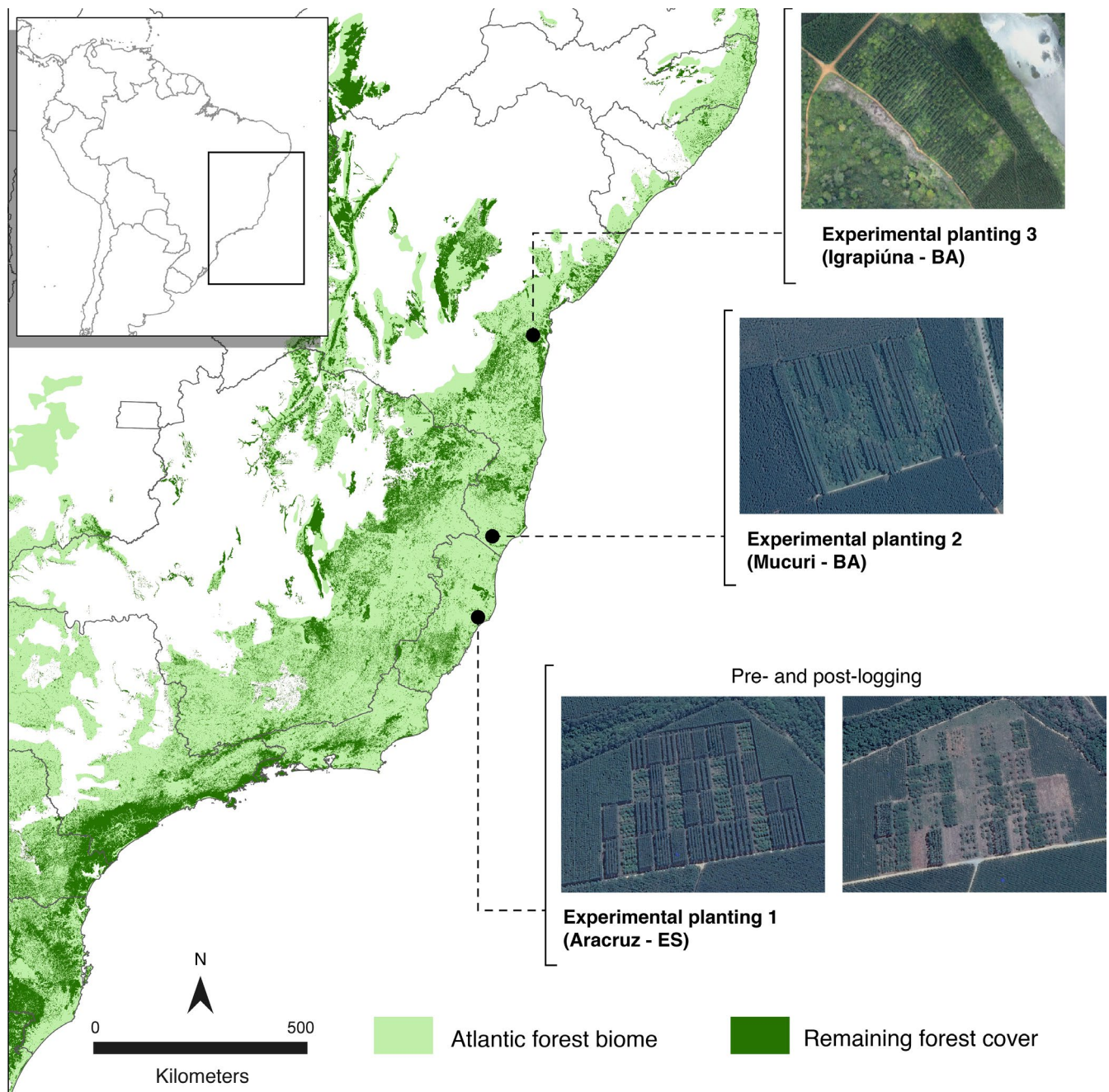


FIGURE 1 Study sites within the Atlantic Forest of Brazil. Black lines in Atlantic Forest map indicate state boundaries. See Table S1 for biophysical and experimental site details. Other treatments were tested in these sites and can be seen in the images (e.g. eucalypt monocultures, intercropping eucalypts and native species in single lines), but these treatments are not discussed in this paper

joint effort of the Atlantic Forest Restoration Pact with two eucalypt pulp companies and one conservation NGO to develop new forest restoration models with the objective of offsetting implementation costs and providing income to farmers. We initially established two experimental treatments at each site:

- (i) *“native” treatment*: native tree species planting composed of 23–30 non-pioneer species intercropped with 9–10 pioneer species (Figure 2a; Table S1);
- (ii) *“mixed” treatment*: mixed plantings of native species (the same 23–30 non-pioneer species used in the native treatment) and one eucalypt species, which replaced the 9–10 pioneer species used in the native treatment (Figure 2b; Table S1).

Native non-pioneer trees included three threatened species and were mostly composed of valuable timber species, which could potentially be harvested by farmers in long rotation cycles to further contribute to the financial viability of restoration.

We employed a randomized block design with five (site 1), four (site 2) and six (site 3) blocks containing one plot per treatment

(native and mixed plantings; a third treatment – logged mixed plantings – was added at site 3, as described below), thus totaling ten (site 1), eight (site 2) and 18 (site 3) plots per site (Table S1). Plot size was 30×72 m ($2,160$ m²) in sites 1 (two outer rows as borders) and 2 (two outer rows as borders), and 24×45 m ($1,080$ m²) in site 3 (one outer row as border; Table S1). In sites 1 and 2, we left a 6-m width corridor without tree planting around each plot to reduce the influence of one treatment on another. Sites 1 and 2 were planted at 3×3 m spacing ($1,111$ trees/ha), and site 3 at 3×2 m spacing ($1,666$ trees/ha); we alternated two planting lines of each species group (native pioneers, native non-pioneers, or eucalypt) in all treatments. The differences in experimental layout at each site reflected space constraints and desires of our land management partners.

2.1.2 | Eucalypt logging

We logged eucalypt trees in all mixed plantation plots at site 1 with a harvester and forwarder after 57 months, and logged all eucalypt trees in half of these plots (six harvested and six unharvested) in site

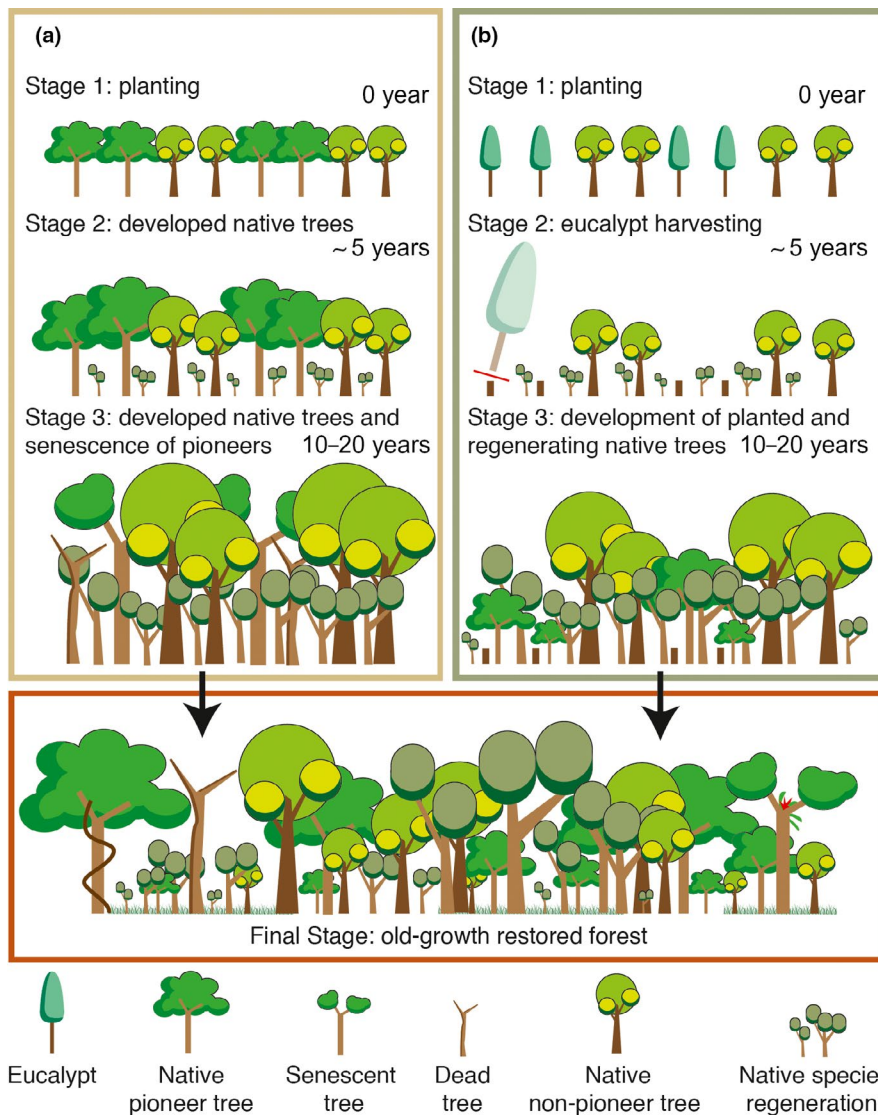


FIGURE 2 Schematic representation of the restoration plantings using pioneer and non-pioneer native species (a) and replacing the native pioneer species with one eucalypt species (b), as well as the anticipated future development of these planting schemes

3 with chainsaw and animal traction after 45 months; mixed plantations have not yet been harvested at site 2 because it is being managed for a longer rotation cycle. We left unharvested plots at site 3 to compare the longer-term impacts of maintaining versus logging eucalypts on the further development of planted native trees and natural regeneration. We employed a reduced impact logging approach in order to minimize logging impacts on planted native trees and natural regeneration. This consisted of: (a) pre-harvest planning of trails for machinery movement and dragging logs to minimize damage to soil and native vegetation in logged plots, (b) directional felling of eucalypts to concentrate the impacts of falling trees and dragging logs on the space in between each pair of planting lines of eucalypts in order to minimize their impacts on the neighbouring native tree planting lines. Eucalypts sprouts were controlled few weeks after harvesting by glyphosate spraying, in order to prevent the persistence of eucalypts in restoration.

2.2 | Data collection

2.2.1 | Above-ground biomass accumulation and growth of planted non-pioneer trees

We measured the DBH and height of all planted native trees and eucalypts in the effective area of experimental plots in site 1 (pre-logging: 38, 51 and 57 months; post-logging: 83 months), site 2 (pre-logging: 48 months) and site 3 (pre-logging: 31 and 43 months; post-logging: 53, 60, and 84 months; Figure S1; see Table S1 for details on the experimental design). We estimated native tree above-ground biomass (AGB) 4–5 years after planting using an equation developed for 5-year old restoration plantings in the Atlantic Forest (Ferez, Campoe, Mendes, & Stape, 2015), and calculated eucalypt AGB with an equation developed specifically for eucalypt stands in the study region (Rocha, 2014). Wood density values of most native tree species were obtained from a five years old restoration planting established with 120 tree species in the Atlantic Forest of São Paulo state, southeastern Brazil, based on wood discs collected from three individuals per species (data not shown). For few species, we used the average of the species of the same genus sampled in this other experiment. In the native plantations, we calculated the AGB of pioneer and non-pioneer trees separately in order to assess the differential impact of eucalypts and native pioneers on the growth of native non-pioneer trees.

2.2.2 | Regeneration environment and woody species regeneration

We assessed the light environment and invasive grass cover in the plantation understory right before (Site 1:57 months; Site 3:43 months) eucalypt logging, and the light environment immediately following and 7 (Site 1) to 12 (Site 3) months after eucalypt logging (Figure S1). We did not take natural regeneration measurements in site 2 because the company in charge of maintaining the site inadvertently sprayed glyphosate in the plantation understory

to control grasses, a standard practice in eucalypt plantations, which also killed native regenerating trees; moreover, since the site is being managed on a longer-term rotation, we could not take post-harvest natural regeneration data.

We estimated light availability using two methods due to different weather conditions at the sites. In site 1, where open sky days predominated during the data collection period, we measured photosynthetically active radiation from 11 to 13 hr in the plantation understory and outside the plantation with a ceptometer AccuPAR LP-80 (Decagon Devices Inc., 1999) and calculated the leaf area index (LAI). In site 3, where cloudy days predominated during the data collection period, we measured the red:far red ratio in plantation understory with a Skye SKR 110 sensor (Skye Instruments), which captures radiation between 660 and 730 nm wavelengths and does not require measurements in open areas; lower red:far red ratio indicates reduced diffuse transmittance through a more closed canopy (Capers & Chazdon, 2004). We regularly distributed ten (Site 1) and six (Site 3) 2 × 2 m quadrat subplots in each experimental plot and visually estimated invasive grass cover (mostly *Urochloa decumbens* (Stapf) R.D. Webster) according to five classes (0, 25, 50, 75, and 100% approximate cover). We then identified and quantified all spontaneously regenerating tree species individuals (height ≥50 cm) growing within the subplots used for grass cover measurements, prior to logging (Site 1:57 months; Site 3:43 months) and 3–4 years after post logging.

2.2.3 | Logging impacts on planted non-pioneer trees

We evaluated the immediate damages of eucalypt logging on planted non-pioneer species in Sites 1 and 3 based on a methodology adapted from Sist and Nguyen-Thé (2002), through which trees were classified as with or without the trunk broken, and with or without damages (damages on tree crown, trunk/bark, and/or bole inclination). We assessed if broken or damaged trees survived seven months after logging, based on the presence of living leaves of new sprouts.

2.3 | Data analysis

2.3.1 | Above-ground biomass accumulation and growth of planted non-pioneer trees

We compared the total AGB and the AGB of non-pioneer species between mixed and native plantations at the pre-harvesting stage 4–5 years after planting at all three sites. AGB stocks were compared by independent *t* tests as data showed normality and homoscedasticity. To compare the growth of planted non-pioneer trees with and without eucalypts, and before and after eucalypt logging, we used linear mixed-models following a model-building approach in order to detect and prevent heteroscedasticity and dependency (Zuur, Ieno, Walker, Saveliev, & Smith, 2009). Models were fitted in R using *lme* function in the *nlme* package (Pinheiro, Bates, DebRoy, & Sarkar,

2018), using *varPower* and *corAR1* model options when necessary. We used basal area of non-pioneer trees as the response variable, time and treatment as fixed factors and time factor and individual identity as random variables in our mixed models. Then, we analysed how non-pioneer trees responded after eucalypt logging at two sites by comparing plots where eucalypts were logged and areas where non-pioneer trees were growing with native pioneer trees. We compared the basal area increment (difference between the basal area of the pre- and post-logging inventories) between treatments with Welch *t* test, since data showed normal distribution but unequal variances.

2.3.2 | Regeneration environment and woody species regeneration

The leaf area index (Site 1) and red:far red ratio (Site 3) data were compared between treatments and along time by mixed model approach and paired *t* tests. As consequence of the frequent number of subplots with 0 values of grass cover, we employed a Zero-Inflated Mixed Model approach (Zuur et al., 2009) with the function *zeroinfl* (Zeileis, Kleiber, & Jackman, 2008) of *pscl* package (Jackman, 2010), using the treatments and the light environment variable as fixed factors in the models. We compared the rarefied species richness and species composition similarity of saplings regenerating in the understories of native and mixed plantations, prior to and after eucalypt logging (Figure S1). In site 3, we also included unlogged plots of mixed plantations, which allowed us to infer the persistence impacts of eucalypts on native species regeneration.

We compared native species richness through rarefaction curves based on sample-sizes with 95% confidence intervals using the R package *iNEXT* (Hsieh, Ma, & Chao, 2016), and composition similarity according to the Chao-Jaccard similarity index. We compared the abundance of regenerating native species through Poisson Generalized Linear Mixed Model, following a model construction approach (Zuur et al., 2009), using *glmer* function from *lme4* package (Bates, Mächler, Bolker, & Walker, 2015) and post hoc test with *lsmeans* package (Lenth, 2016), where time and treatment were fixed factors and plot ID as random factor.

2.3.3 | Financial calculations

We quantified plantation implementation (site preparation, seedling acquisition, fencing, tree planting) and maintenance (weeding, control of leaf-cutter ants, and sequential fertilization) costs based on the prices of services and materials supplied by professional restoration companies near Site 1. We assumed the costs of Site 1 Aracruz region to be the same as for the other sites, an assumption justified by a large-scale study showing similar costs of restoration management practices across in Brazil. We quantified the differential seedling costs of the two treatments; but we did not quantify the labour and inputs costs of mixed and native plantations separately, although mixed plantings should have lower weeding costs due to faster canopy cover.

We applied a timber price of harvested trees (US\$ 28.41 m⁻³) and discounted logging and transport costs (US\$ 6.35 m⁻³), for the Site 1 region (Brazilian-Tree-Industry, 2015; Silva, 2012), to calculate total revenue. Timber production was evaluated based on direct harvesting of eucalypts in two sites (Site 1:100.38 m³/ha, Site 3:174.08 m³/ha) and estimated in Site 2 based on the relationship between basal area and wood harvested obtained in Site 1 and applied to the forest inventory of Site 2 (93.72 m³/ha). The revenue obtained from eucalypt logging in experimental plantings was calculated based on the Net Present Value, assuming the financial parameters of: (a) R\$1.00 = US\$0.3131; (b) inflation of 1.06 (2011–2014) and 1.11 (2015), based on the Broad National Consumer Price Index - IPCA (www.bcb.gov.br/pec/Indeco/Ingl/indecoi.asp); and (c) basic interest rate of 11% for 2014 (www.bcb.gov.br/Pec/Copom/Port/taxaSelic.asp).

3 | RESULTS

3.1 | Above-ground biomass accumulation and growth of planted trees

Above-ground biomass of mixed plantations was approximately nine times greater than native plantations, mostly as consequence of the rapid growth of eucalypts (Figure 3). These results were accompanied by a slight, but significant, reduction in the AGB of non-native pioneer trees in two experimental sites (Figure 3).

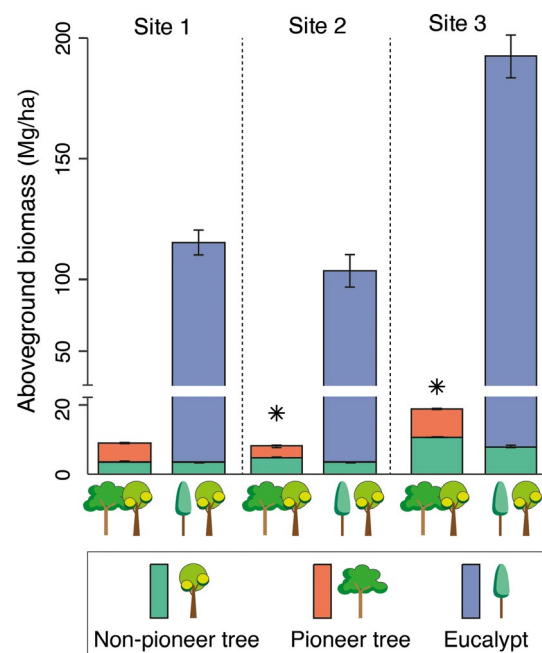


FIGURE 3 Above-ground biomass (AGB) accumulation in experimental restoration native and mixed plantings. Total AGB was higher in mixed plantations with eucalypts in all sites, and asterisks indicate that AGB of non-pioneer trees was significantly higher without eucalypts (*t* tests, $p < .05$) in two sites. Error bars represent 95% confidence intervals

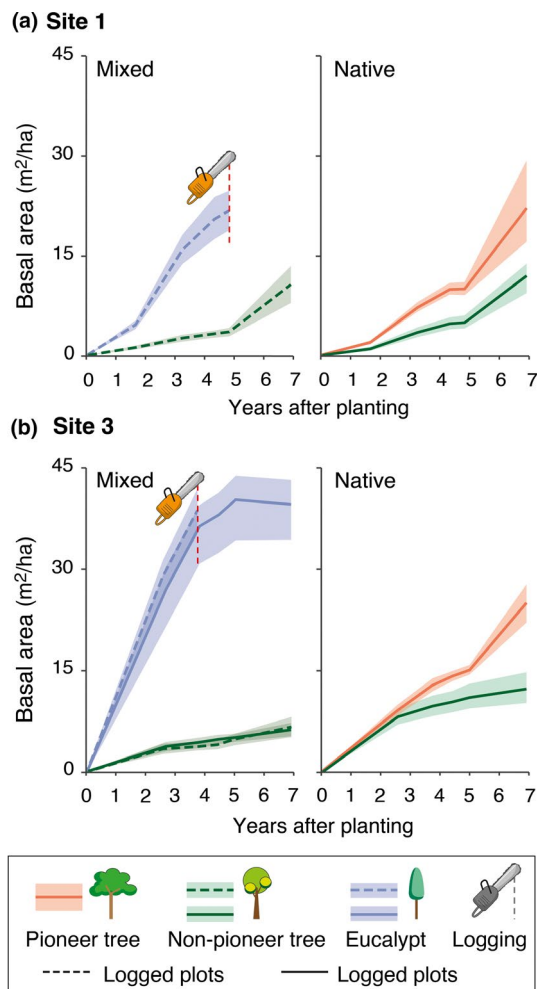


FIGURE 4 Temporal variation in basal area of species groups in experimental restoration mixed (left) and native plantings (right), submitted or not to logging. Shading represents 1 SE

In Site 1, the basal area of non-pioneer species showed similar increases across treatments over time ($F_{1,58} = 3.33$, $p = .07$; treatment \times time interaction $F_{1,58} = 5.31$, $p = .02$) so basal area in both native and mixed plantations was similar for the last inventory ($t_{11} = 0.672$, $p = .98$; Figure 4a; Table S2). In Site 3, the basal area of non-pioneer species increased faster in native plantations during the experiment (slope estimate \pm SE: native = 0.102 ± 0.03 ; mixed logged = 0.042 ± 0.02 , and mixed unlogged = 0.044 ± 0.02 ; treatment \times time interaction $F_{1,46} = 8.94$, $p < .005$; Figure 4b), which resulted in a 94% higher basal area seven years after planting in the native compared to mixed plantation ($t_6 = 4.318$, $p < .005$). Eucalypt

logging did not affect basal area increment in mixed plantations ($t_{10} = 0.868$, $p = .406$).

3.2 | Logging impacts on planted non-pioneer trees

Logging impacts were higher in site 3 (45.4% of non-pioneer trees), where eucalypt was logged with chainsaw, than in site 1 (13.2%), where logging was done using a harvester machine (Table 1). Nonetheless, mortality was very low in both sites after seven months (Table 1), since most broken and damaged trees resprouted following logging damage.

3.3 | Regeneration environment

The leaf area index of native and mixed plantations was similar in site 1 prior to logging ($t_{7,1} = 1.03$; $p = .38$; Figure 5a). Eucalypt logging reduced LAI by nearly a third in mixed plantations ($t_9 = 11.95$; $p < .001$; Figure 5a), but the growth of the remaining planted and regenerating native trees more than tripled the LAI of logged plots and reached 84% of pre-logging values 7 months after logging (Figure 5a). In site 3, red:far red ratio was lower (i.e. canopy cover was higher) in native plantations prior to logging ($F_{2,429} = 132.88$; $p < .001$; Figure 5b; Figure S2). Eucalypt logging showed a similar trend in site 3 (~30% increase in red:far red ratio values; $t_{143} = 25.97$; $p < .001$; Figure 5b). One year post logging, the growth of the remaining planted trees and spontaneously regenerating trees increased canopy cover and light interception in logged plots (logged plots reached 85% of red:far red ratio values of unlogged mixed plots and 68% of native plantations values), yet logged mixed plots had the highest red:far red ratio values at this time ($F_{2,429} = 426.5$; $p < .0001$; Figure 5b). Invasive grass cover was low in both sites (Site 1: ~10%; Site 3: ~7%) and did not differ between treatments prior to logging (Site 1: $|Z| < 1.44$; Site 3: $|Z| < 0.53$; $p > .05$).

3.4 | Regeneration of native woody species

Rarefied species richness and composition of native woody species that colonized the understory of native and mixed plantations were similar in the pre-logging period (Site 1: Chao-Jaccard similarity: 0.75; Figure 6a; Site 3: Chao-Jaccard similarity: 0.95; Figure 6b) with twice as many species at site 3 compared to site 1. Rarefied species richness doubled and tripled in sites 1 and 3, respectively, in the post-logging period, but did not differ among plantation types within each site (Figure 6). We did not observe a single regenerating eucalypt

TABLE 1 Impacts of eucalypt logging (Site 1: harvester; Site 3: chainsaw) on planted non-pioneer trees in mixed plantations, and mortality of impacted trees seven months after harvesting

Study Site	Broken trees (%)	Broken trees mortality (%) ^a	Damaged trees (%)	Damaged trees mortality (%) ^a
1	0.0 \pm 0.0	0.0 \pm 0.0	13.2 \pm 1.8	0.0 \pm 0.0
3	16.9 \pm 3.4	2.6 \pm 0.5	45.4 \pm 4.8	0.7 \pm 0.5

^aPercentage of dead trees in relation to the total number of alive trees before logging.

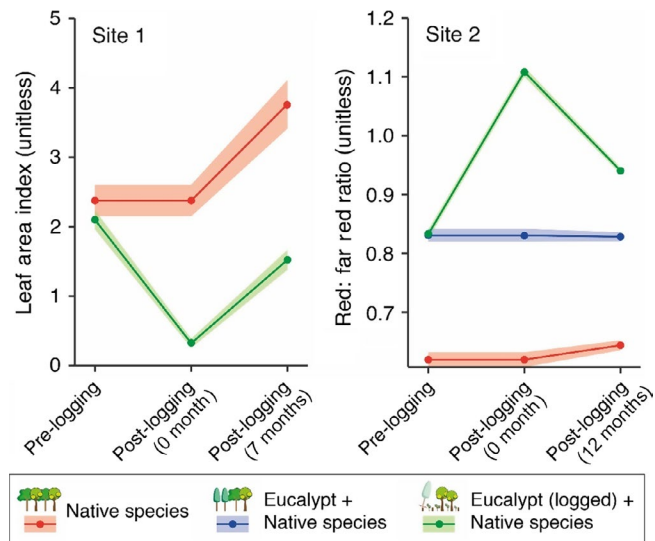


FIGURE 5 Temporal variation of light environment in the understory of experimental restoration plantings of native and mixed plantations, submitted or not to logging. Shading represents 1 SE

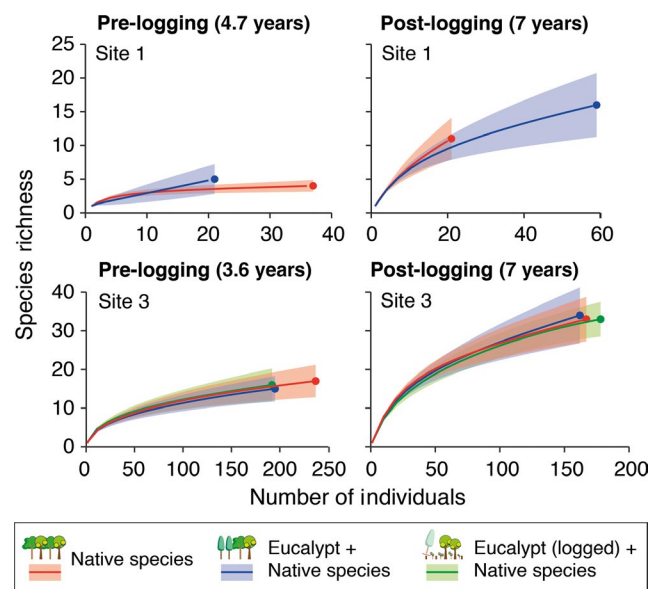


FIGURE 6 Rarefied species richness of naturally regenerating native woody species in native and mixed restoration plantings with or without eucalypt logging. Shading represents 95% confidence intervals

seedling in either site pre- or post-logging. In site 1, the abundance of regenerating native species was higher in native plantations in the pre-logging period, but was similar at the post-logging period (Table 2), as consequence of a slight abundance decrease in native plantations and increase in mixed plantations between periods (slope estimate \pm SE: Site 1: native = -0.28 ± 0.25 ; mixed = 1.55 ± 0.24 ; treatment \times time interaction $|Z| = 5.33$, $p < .001$; Table 2). In site 3, the abundance of regenerating native species was similar in treatments in the pre-logging period, but was higher in native plantations

TABLE 2 Abundance of regenerating native wood species per plot (seedlings/m²; mean and minimum – maximum confidence limits by nonparametric bootstrap, 95% confidence interval and 1,000 bootstrap resamples)

Site	Treatment	Before logging (50 months)	After logging (83 months)
Site 1	Native	9.3 (7.0 – 11.8)	7.0 (4.8 – 9.8)
	Mixed logged	2.3 (1.6 – 3.1)	11.0 (5.3 – 17.7)
Site 3	Native	7.3 (4.6 – 10.6)	8.2 (6.1 – 10.4)
	Mixed logged	5.7 (4.1 – 7.4)	3.9 (3.0 – 4.9)
	Mixed unlogged	6.3 (4.5 – 8.2)	4.7 (3.9 – 5.6)

in the post-logging period, when logged and unlogged plots did not differ (Table 2). We observed a slight increase in the abundance of regenerating species in native plantations and a decrease in mixed plantations (native = 0.06 ± 0.09 ; mixed logged = -0.35 ± 0.11 , and mixed unlogged = -0.29 ± 0.11 ; treatment \times time interaction $|Z|_{\text{logged}} = 2.79$, $p = .005$, and $|Z|_{\text{unlogged}} = 2.42$, $p = .02$; Table 2).

3.5 | Financial assessment of eucalypt logging

Wood production in mixed plantations with eucalypts helped to offset the high implementation and maintenance costs ($\$3,360 \text{ ha}^{-1}$). Eucalypt harvesting in 4–5 year old experimental plantings yielded 100 (Site 1), 94 (Site 2), and $174 \text{ m}^3/\text{ha}$ (Site 3) of roundwood for pulp, firewood or fencing poles (DBH 15–25 cm), compensating for 46.6 (Site 1), 44.00 (Site 2), and 75.3% (site 3) of total restoration implementation costs 4–5 years after planting (Table S4).

4 | DISCUSSION

Our results show that mixing plantations of eucalypts and native trees is a promising restoration strategy to help offset restoration implementation costs without undermining the ecological outcomes. The growth of native non-pioneer trees was not affected (1 site) or slightly reduced (2 sites) by eucalypts prior to logging despite the greatly enhanced biomass production of mixed plantations. Moreover, the richness of regenerating native woody species was not reduced by eucalypts either before or after eucalypt logging, yet the abundance of regenerating native species was higher in native plantations in sites 1 (pre-logging) and 3 (post-logging).

The most evident difference between native and mixed plantations was the short-term difference in AGB accumulation. With nearly nine times higher AGB stocks prior to logging, mixed plantations clearly demonstrated the value of integrating eucalypts as a transitional phase in restoration if wood production is one of the expected outcomes (Amazonas, Forrester, Oliveira, & Brancalion, 2017; Lamb, 2018). The fact that the impressive biomass accumulation of eucalypts did not strongly reduce the growth of planted native non-pioneer trees may be due to the naturally slow growth of this group of species (Chazdon, 2014) and their adaptation to

tolerate low to medium light conditions (Loik & Holl, 1999). We lack plantations of exclusively non-pioneer trees to disentangle competition in these systems.

We had anticipated that the fast growth of eucalypts would result in higher canopy cover and consequently less grass cover than native plantations. In contrast, we found the opposite result for canopy cover in one site and no difference in another, and no impact on grass cover in either site. These unexpected results can be explained by the contrasting architecture of the tree crowns of eucalypts and native species. The eucalypt species used in the experimental plantations have monopodial branching, which concentrate leaves at the top of plantation canopy and result in a leafless midstory (Almeida et al., 2019). On the other hand, native plantations usually have branches and leaves throughout all the forest vertical strata to maximize light absorption by species with different ecophysiological behaviours and niche requirements (Sapijanskas, Paquette, Potvin, Kunert, & Loreau, 2014). The shade levels in both plantations types appeared to be sufficiently high to prevent grass regrowth in the understory, a major barrier for restoration success in the Atlantic Forest region.

A valid concern about interplanting eucalypts with native species is that falling trees and dragging logs could damage the native non-pioneer trees interplanted with eucalypts and the abundant natural regeneration of the understory. In fact, the visual impression right after logging was that all regenerating individuals were destroyed in eucalypt planting lines, where logging impacts were concentrated (Figure S3). In site 3, nearly half of planted non-pioneer trees were damaged by logging; but most broken trees resprouted and damaged trees survived seven months after logging, resulting in negligible mortality levels. Logging eucalypts with a harvester (Site 1) resulted in lower impacts on planted non-pioneer trees than chainsaws (Site 3; Table 1). However, we cannot recommend a harvesting approach based on our assessments, because site 3 is more sloped, which limits the control of the direction of falling trees and, thus, the damaged to neighbouring native trees. Moreover, the harvester is sophisticated, expensive equipment that is only used by large pulp companies and not available to individual farmers. Regardless, our results suggest that both harvesting methods could be used successfully for eucalypt logging in mixed plantations.

The species richness of regenerating woody plants was similar between logged mixed plantations and native plantations a few years after logging, but the abundance of regenerating individuals was reduced in both logged and unlogged mixed plantations in site 3 compared to native plantations. We had expected planted native non-pioneer trees would grow faster in the post-logging period, given that seedling growth is commonly light limited in plantations (Paquette, Bouchard, & Cogliastro, 2006) and tropical secondary forest (Chazdon, Pearcy, Lee, & Fetcher, 1996), but growth post-logging growth rates were similar in logged and unlogged treatments. In site 3, the potential benefits of greater light availability may have been counterbalanced by the higher levels of physical damage of logging to planted native non-pioneer trees. A key factor for the ecological

viability of mixed restoration plantings with eucalypts is then the adoption of reduced impact logging to minimize the damages on planted native trees and regenerating woody species.

The lack of differentiation of regenerating communities both in terms of species richness and composition, may reflect the spatial proximity of the plots. Although we used large experimental plots (2,160 and 1,080 m²), compared to those traditionally used in restoration experiments (Shoo & Catterall, 2013), seed dispersers may have been attracted to the heterogeneous forest structure and abundant animal-dispersed trees of the experimental site in general (Reid, Harris, & Zahawi, 2012). This local enhancement of seed dispersal could mask the differential potential of native trees, especially of pioneers, to attract seed dispersers. In addition, the buffer area between plots may have been insufficient to prevent the effect of one planting treatment on another. As with all restoration experimental manipulations, the next step is to work with land managers to scale up the treatments to an area typical for restoration projects and monitor the outcome (Bakker, Delvin, & Dunwiddie, 2018).

On the other hand, the floristic similarity between regenerating communities of native and mixed plantings suggest that they may provide similar habitat value to local fauna. Although we do not present data on faunal communities here, several previous studies report moderate to high diversity of birds (Jacoboski, Mendonça-Lima, & Hartz, 2016; Lopes et al., 2015; Marsden et al., 2001), mammals (Martin, Gheler-Costa, Lopes, Rosalino, & Verdade, 2012; Stallings, 1990; Timo, Lyra-Jorge, Gheler-Costa, & Verdade, 2015), and leaf litter organisms (da Rocha et al., 2013) in the understory of eucalypt plantations in the Atlantic Forest region. Certainly, the conservation value of native, mixed, or eucalypt plantations is highly influenced by landscape context and ongoing management regime (Fonseca et al., 2009; Millan, Develey, & Verdade, 2015).

Differences in both above-ground biomass accumulation and natural regeneration were much more strongly affected by site factors than by planting treatment. The nearly three-fold higher tree growth rates at site 3 likely reflect more favorable soil and climate conditions (site 3 vs. site 1: soil sum of bases: 23.81 vs. 1.93 mmol_c/dm³; clay content: 71.4% vs. 20.9%; annual rainfall: 2,191 vs. 1,412 mm; Table S1) and less intensive prior land use (extensive pasture in site 3 vs. intensive eucalypt plantation in site 1). The greater species richness of recruits in site 3 may be explained by those factors, as well as higher landscape forest cover (20.8% vs. 6.3%) than site 1. All three factors have been demonstrated to affect the rate of tropical forest recovery in prior studies (reviewed in Chazdon, 2014; Holl, 2007).

Eucalypt allelopathic effects (Becerra et al., 2017), cases of invasion (Tereraí, Gaertner, Jacobs, & Richardson, 2013), reduction in soil moisture (Robinson, Harper, & Smettem, 2006) and problems with wildfires (Moreira & Pe'er, 2018), have been reported predominantly in drier climates. These do not seem to be problematic issues in wetter tropical regions, as suggested by our results

and several previous studies in tropical regions that found diverse and abundant regeneration of native species in the understory of eucalypt plantations (e.g. Bremer & Farley, 2010; Pryde et al., 2015; Silva-Junior et al., 1995). We did not find any evidence of natural recruitment of eucalypts in our plots. Data from a related study at our sites (Amazonas et al., 2017) showed minimal differences in soil volumetric water content in shallow soil layers (up to 1.3 m depth) of ~4.5-year native, mixed, and eucalypt monoculture plantations. This lack of difference in soil water availability may be due to the fact that most native pioneer species also require large amounts of water to sustain their fast growth (Filoso, Bezerra, Weiss, & Palmer, 2017). We recommend the implementation of similar experiments in drier areas, where competition for water could eventually limit the growth of planted and regenerating native trees and, thus, compromise the viability of the use of eucalypts in mixed restoration plantings.

As expected, eucalypt logging resulted in a valuable contribution to offset ~45%–75% of restoration implementation and maintenance costs. Harvesting eucalypts or other commercially valuable native or exotic trees in restoration could partially overcome the financial barrier for adopting active restoration approaches, which can cost up to ten times more than natural regeneration (Shoo et al., 2017), but are needed in many cases due to low site resilience (Rodrigues et al., 2011; Shoo, Freebody, Kanowski, & Catterall, 2016). Exotic eucalypts can thus become important allies of tropical forest restoration, and their use should be considered within the portfolio of options supported by public and private funding and policies (Catterall, 2016). Together, our results suggest eucalypt use as a transitional stage in restoration has a neutral effect on natural regeneration and can help offset restoration costs along with complementary strategies that aim to transform restoration into a competitive land use, like payments for ecosystem services and harvesting valuable native timber species in long rotations (Brancalion et al., 2017). Like any novel restoration strategy, this approach must be considered in the context of the ecosystem type and evaluated for localized positive and negative effects prior to large-scale implementation. For example, this novel restoration approach should be limited to closed-canopy forest ecosystems, as eucalypts and other commercial trees could suppress the development of the shade intolerant species typical of open ecosystems.

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AUTHORS' CONTRIBUTIONS

P.H.S.B. conceived the idea, designed the study, and led the writing. K.D.H. co-led the writing. P.H.S.B. and K.D.H. decided on statistical analysis and J.v.M. conducted them. N.T.A., C.C.S., T.B.S., P.H.S.B., and R.R.R. planned the experiment and collected data. R.L.C. helped to structure and review the manuscript.

DATA AVAILABILITY STATEMENT

Data available via Zenodo Repository <https://doi.org/10.5281/zenodo.2583906> (Brancalion et al., 2019).

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REFERENCES

- Almeida, D. R. A., Stark, S. C., Chazdon, R., Nelson, B. W., Cesar, R. G., Meli, P., ... Brancalion, P. H. S. (2019). The effectiveness of lidar remote sensing for monitoring forest cover attributes and landscape restoration. *Forest Ecology and Management*, 438, 34–43. <https://doi.org/10.1016/j.foreco.2019.02.002>
- Amazonas, N. T., Forrester, D. I., Oliveira, R. S., & Brancalion, P. H. S. (2017). Combining *Eucalyptus* wood production with the recovery of native tree diversity in mixed plantings: Implications for water use and availability. *Forest Ecology and Management*, 418, 34–40. <https://doi.org/10.1016/j.foreco.2017.12.006>
- Ashton, P. M. S., Gamage, S., Gunatilleke, I. A. U. N., & Gunatilleke, C. V. S. (1997). Restoration of Sri Lankan rainforest: Using Caribbean pine *Pinus caribaea* as a nurse for establishing late-successional tree species. *Journal of Applied Ecology*, 34, 915–925.
- Bakker, J. D., Delvin, E. G., & Dunwiddie, P. W. (2018). Staged-scale restoration: Refining adaptive management to improve restoration effectiveness. *Journal of Applied Ecology*, 55, 1126–1132. <https://doi.org/10.1111/1365-2664.13050>
- Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, 67, 1–48.
- Becerra, P. I., Catford, J. A., Inderjit, McLeod, M. L., Andonian, K., Aschehoug, E. T., ... Callaway, R. M. (2017). Inhibitory effects of *Eucalyptus globulus* on understorey plant growth and species richness are greater in non-native regions. *Global Ecology and Biogeography*, 27, 1–7. <https://doi.org/10.1111/geb.12676>
- Brancalion, P. H. S., Amazonas, N. T., Chazdon, R. L., van Melis, J., Rodrigues, R. R., Silva, C. C., ... Holl, K. D. (2019). Data from: Exotic eucalypts: From demonized trees to allies of tropical forest restoration? Zenodo Repository, <https://doi.org/10.5281/zenodo.2583906>
- Brancalion, P. H. S., Bello, C., Chazdon, R. L., Galetti, M., Jordano, P., Lima, R. A. F., ... Reid, J. L. (2018). Maximizing biodiversity conservation and carbon stocking in restored tropical forests. *Conservation Letters*, 11(4), e12454. <https://doi.org/10.1111/conl.12454>
- Brancalion, P. H. S., Lamb, D., Ceccon, E., Boucher, D., Herbohn, J., Strassburg, B., & Edwards, D. P. (2017). Using markets to leverage

- investment in forest and landscape restoration in the tropics. *Forest Policy and Economics*, 85, 103–113. <https://doi.org/10.1016/j.forpol.2017.08.009>
- Brancalion, P. H. S., Viani, R. A. G., Strassburg, B. B. N., & Rodrigues, R. R. (2012). Finding the money for tropical forest restoration. *Unasylva*, 63, 25–34.
- Brazilian-Tree-Industry. (2015). *Relatório Iba 2015* (77 pp). Brasília: IBÁ.
- Bremer, L. L., & Farley, K. A. (2010). Does plantation forestry restore biodiversity or create green deserts? A synthesis of the effects of land-use transitions on plant species richness. *Biodiversity and Conservation*, 19, 3893–3915. <https://doi.org/10.1007/s10531-010-9936-4>
- Brockerhoff, E. G., Jactel, H., Parrotta, J. A., & Ferraz, S. F. B. (2013). Role of eucalypt and other planted forests in biodiversity conservation and the provision of biodiversity-related ecosystem services. *Forest Ecology and Management*, 301, 43–50. <https://doi.org/10.1016/j.foreco.2012.09.018>
- Capers, R. S., & Chazdon, R. L. (2004). Rapid assessment of understory light availability in a wet tropical forest. *Agricultural and Forest Meteorology*, 123, 177–185. <https://doi.org/10.1016/j.agrfor.2003.12.009>
- Catterall, C. P. (2016). Roles of non-native species in large-scale regeneration of moist tropical forests on anthropogenic grassland. *Biotropica*, 48, 809–824. <https://doi.org/10.1111/btp.12384>
- César, R. G., Moreno, V. S., Coletta, G. D., Chazdon, R. L., Ferraz, S. F. B., Almeida, D. R. A., & Brancalion, P. H. S. (2017). Early ecological outcomes of natural regeneration and tree plantations for restoring agricultural landscapes. *Ecological Applications*, 28(2), 373–384. <https://doi.org/10.1002/eap.1653>
- Chazdon, R. L. (2014). *Second-growth: The promise of tropical forest regeneration in an age of deforestation*. Chicago, IL: Chicago University Press.
- Chazdon, R. L., Brancalion, P. H. S., Lamb, D., Laestadius, L., Calmon, M., & Kumar, C. (2017). A policy-driven knowledge agenda for global forest and landscape restoration. *Conservation Letters*, 10, 125–132. <https://doi.org/10.1111/conl.12220>
- Chazdon, R. L., Pearcy, R. W., Lee, D. W., & Fetcher, N. (1996). Photosynthetic responses of tropical forest plants to contrasting light environments. In S. S. Mulkey, R. L. Chazdon, & A. P. Smith (Eds.), *Tropical forest plant ecophysiology* (pp. 5–55). New York: Chapman and Hall.
- da Rocha, P. L. B., Viana, B. F., Cardoso, M. Z., de Melo, A. M. C., Costa, M. G. C., de Vasconcelos, R. N., & Dantas, T. B. (2013). What is the value of eucalyptus monocultures for the biodiversity of the Atlantic forest? A multitaxa study in southern Bahia, Brazil. *Journal of Forestry Research*, 24, 263–272. <https://doi.org/10.1007/s11676-012-0311-z>
- Ding, H., Altamirano, J. C., Anchondo, A., Faruqi, S., Verdone, M., Wu, A., ... Vergara, W. (2017). *Roots of prosperity: The economics and finance of restoring land* (p. 80). Washington, DC: World Resources Institute.
- Ferez, A. P. C., Campoe, O. C., Mendes, J. C. T., & Stape, J. L. (2015). Silvicultural opportunities for increasing carbon stock in restoration of Atlantic forests in Brazil. *Forest Ecology and Management*, 350, 40–45. <https://doi.org/10.1016/j.foreco.2015.04.015>
- Filoso, S., Bezerra, M. O., Weiss, K. C. B., & Palmer, M. A. (2017). Impacts of forest restoration on water yield: A systematic review. *PLoS ONE*, 12(8), e0183210. <https://doi.org/10.1371/journal.pone.0183210>
- Fonseca, C. R., Ganade, G., Baldissera, R., Becker, C. G., Boelter, C. R., Brescovit, A. D., ... Vieira, E. M. (2009). Towards an ecologically-sustainable forestry in the Atlantic Forest. *Biological Conservation*, 142, 1209–1219. <https://doi.org/10.1016/j.biocon.2009.02.017>
- Geary, T. F. (2001). Afforestation in Uruguay: Study of a changing landscape. *Journal of Forestry*, 99, 35–39.
- Gonçalves, J. L. D. M., Alvares, C. A., Higa, A. R., Silva, L. D., Alfenas, A. C., Stahl, J., ... Epron, D. (2013). Integrating genetic and silvicultural strategies to minimize abiotic and biotic constraints in Brazilian eucalypt plantations. *Forest Ecology and Management*, 301, 6–27. <https://doi.org/10.1016/j.foreco.2012.12.030>
- Grossman, J. J. (2015). Eucalypts in agroforestry, reforestation, and smallholders' conceptions of "nativeness": A multiple case study of plantation owners in eastern Paraguay. *Small-Scale Forestry*, 14, 39–57. <https://doi.org/10.1007/s11842-014-9272-8>
- Holl, K. D. (2007). Oldfield vegetation succession in the Neotropics. In R. J. Hobbs & V. A. Cramer (Eds.), *Old fields* (pp. 93–117). Washington, DC: Island Press.
- Holl, K. D. (2017). Restoring tropical forests from the bottom up. *Science*, 355, 455–456. <https://doi.org/10.1126/science.aam5432>
- Hsieh, T. C., Ma, K. H., & Chao, A. (2016). iNEXT: An R package for rarefaction and extrapolation of species diversity (Hill numbers). *Methods in Ecology and Evolution*, 7, 1451–1456. <https://doi.org/10.1111/2041-210X.12613>
- IBA, B.T.I. (2018). Report 2017 (77 pp).
- Jackman, S. (2010). pscl: Classes and methods for R. Developed in the Political Science Computational Laboratory, Stanford University. Department of Political Science, Stanford University, Stanford, CA. R package version 1.03.5. Retrieved from <http://www.pscl.stanford.edu/>
- Jacoboski, L. I., Mendonça-Lima, A. D., & Hartz, S. M. (2016). Structure of bird communities in eucalyptus plantations: Nestedness as a pattern of species distribution. *Brazilian Journal of Biology*, 76, 583–591. <https://doi.org/10.1590/1519-6984.18614>
- Lamb, D. (2018). Undertaking large-scale forest restoration to generate ecosystem services. *Restoration Ecology*, 26, 657–666. <https://doi.org/10.1111/rec.12706>
- Lamb, D., Erskine, P. D., & Parrotta, J. D. (2005). Restoration of degraded tropical forest landscapes. *Science*, 310, 1628–1632. <https://doi.org/10.1126/science.1111773>
- Lenth, R. V. (2016). Least-squares means: The R package lsmeans. *Journal of Statistical Software*, 69, 1–33.
- Loik, M. E., & Holl, K. D. (1999). Photosynthetic responses to light for rainforest seedlings planted in abandoned pasture, Costa Rica. *Restoration Ecology*, 7, 382–391. <https://doi.org/10.1046/j.1526-100X.1999.72033.x>
- Lopes, I. T., Gussoni, C. O. A., Demarchi, L. O., De Almeida, A., & Pizo, M. A. (2015). Diversity of understory birds in old stands of native and Eucalyptus plantations. *Restoration Ecology*, 23, 662–669.
- Lugo, A. E. (1997). The apparent paradox of reestablishing species richness on degraded lands with tree monocultures. *Forest Ecology and Management*, 99, 9–19. [https://doi.org/10.1016/S0378-1127\(97\)00191-6](https://doi.org/10.1016/S0378-1127(97)00191-6)
- Marsden, S. J., Whiffin, M., & Galetti, M. (2001). Bird diversity and abundance in forest fragments and Eucalyptus plantations around an Atlantic forest reserve, Brazil. *Biodiversity & Conservation*, 10, 737–751.
- Martin, P. S., Gheler-Costa, C., Lopes, P. C., Rosalino, L. M., & Verdade, L. M. (2012). Terrestrial non-volant small mammals in agro-silvicultural landscapes of Southeastern Brazil. *Forest Ecology and Management*, 282, 185–195. <https://doi.org/10.1016/j.foreco.2012.07.002>
- Millan, C. H., Develey, P. F., & Verdade, L. M. (2015). Stand-level management practices increase occupancy by birds in exotic Eucalyptus plantations. *Forest Ecology and Management*, 336, 174–182. <https://doi.org/10.1016/j.foreco.2014.10.005>
- Molin, P. G., Chazdon, R., Ferraz, S. F. B., & Brancalion, P. H. S. (2018). A landscape approach for cost-effective large-scale forest restoration. *Journal of Applied Ecology*, 55(6), 2767–2778. <https://doi.org/10.1111/1365-2664.13263>
- Moreira, F., & Pe'er, G. (2018). Agricultural policy can reduce wildfires. *Science*, 359, 1001–1001.
- Paquette, A., Bouchard, A., & Cogliastro, A. (2006). Survival and growth of under-planted trees: A meta-analysis across four biomes. *Ecological*

- Applications, 16, 1575–1589. [https://doi.org/10.1890/1051-0761\(2006\)016\[1575:SAGOUT\]2.0.CO;2](https://doi.org/10.1890/1051-0761(2006)016[1575:SAGOUT]2.0.CO;2)
- Parrotta, J. A., Turnbull, J. W., & Jones, N. (1997). Catalyzing native forest regeneration on degraded tropical lands. *Forest Ecology and Management*, 99, 1–7. [https://doi.org/10.1016/S0378-1127\(97\)00190-4](https://doi.org/10.1016/S0378-1127(97)00190-4)
- Payn, T., Carnus, J. M., Freer-Smith, P., Kimberley, M., Kollert, W., Liu, S. R., ... Wingfield, M. J. (2015). Changes in planted forests and future global implications. *Forest Ecology and Management*, 352, 57–67. <https://doi.org/10.1016/j.foreco.2015.06.021>
- Pinheiro, J., Bates, D., DebRoy, S., & Sarkar, D. (2018). nlme: linear and nonlinear mixed effects models. R package version 3.1-137.
- Pryde, E. C., Holland, G. J., Watson, S. J., Turton, S. M., & Nimmo, D. G. (2015). Conservation of tropical forest tree species in a native timber plantation landscape. *Forest Ecology and Management*, 339, 96–104. <https://doi.org/10.1016/j.foreco.2014.11.028>
- Putz, F. E., Zuidema, P. A., Synnott, T., Pena-Claros, M., Pinard, M. A., Sheil, D., ... Zagt, R. (2012). Sustaining conservation values in selectively logged tropical forests: The attained and the attainable. *Conservation Letters*, 5, 296–303. <https://doi.org/10.1111/j.1755-263X.2012.00242.x>
- Reid, J. L., Fagan, M. E., Lucas, J., Slaughter, J., & Zahawi, R. A. (2018). The ephemerality of secondary forests in southern Costa Rica. *Conservation Letters*, e12607.
- Reid, J. L., Harris, J. B. C., & Zahawi, R. A. (2012). Avian habitat preference in tropical forest restoration in southern Costa Rica. *Biotropica*, 44, 350–359. <https://doi.org/10.1111/j.1744-7429.2011.00814.x>
- Robinson, N., Harper, R. J., & Smettem, K. R. J. (2006). Soil water depletion by *Eucalyptus* spp. integrated into dryland agricultural systems. *Plant and Soil*, 286, 141–151. <https://doi.org/10.1007/s11104-006-9032-4>
- Rocha, J. H. T. (2014). Reflexos do manejo de resíduos florestais na produtividade, nutrição e fertilidade do solo em plantações de *Eucalyptus grandis*. MSc, University of São Paulo.
- Rodrigues, R. R., Gandolfi, S., Nave, A. G., Aronson, J., Barreto, T. E., Vidal, C. Y., & Brancalion, P. H. S. (2011). Large-scale ecological restoration of high-diversity tropical forests in SE Brazil. *Forest Ecology and Management*, 261, 1605–1613. <https://doi.org/10.1016/j.foreco.2010.07.005>
- Salas, C., Donoso, P. J., Vargas, R., Arriagada, C. A., Pedraza, R., & Soto, D. P. (2016). The forest sector in Chile: An overview and current challenges. *Journal of Forestry*, 114, 562–571. <https://doi.org/10.5849/jof.14-062>
- Sapijanskas, J., Paquette, A., Potvin, C., Kunert, N., & Loreau, M. (2014). Tropical tree diversity enhances light capture through crown plasticity and spatial and temporal niche differences. *Ecology*, 95, 2479–2492. <https://doi.org/10.1890/13-1366.1>
- Shoo, L. P., & Catterall, C. P. (2013). Stimulating natural regeneration of tropical forest on degraded land: Approaches, outcomes, and information gaps. *Restoration Ecology*, 21, 670–677. <https://doi.org/10.1111/rec.12048>
- Shoo, L. P., Catterall, C. P., Nicol, S., Christian, R., Rhodes, J., Atkinson, P., ... Wilson, K. A. (2017). Navigating complex decisions in restoration investment. *Conservation Letters*, 10, 748–756. <https://doi.org/10.1111/conl.12327>
- Shoo, L. P., Freebody, K., Kanowski, J., & Catterall, C. P. (2016). Slow recovery of tropical old-field rainforest regrowth and the value and limitations of active restoration. *Conservation Biology*, 30, 121–132. <https://doi.org/10.1111/cobi.12606>
- Silva, A. L. P. (2012). Custo de produção, colheita e transporte de madeira de eucalipto proveniente do programa produtor florestal no sul do Espírito Santo. PhD, Universidade Federal do Espírito Santo.
- Silva-Junior, M. C., Scarano, F. R., & Cardel, F. S. (1995). Regeneration of an Atlantic Forest formation in the understorey of a *Eucalyptus grandis* plantation in South-Eastern Brazil. *Journal of Tropical Ecology*, 11, 147–152.
- Sist, P., & Nguyen-Thé, N. (2002). Logging damage and the subsequent dynamics of a dipterocarp forest in East Kalimantan (1990–1996). *Forest Ecology and Management*, 165, 85–103. [https://doi.org/10.1016/S0378-1127\(01\)00649-1](https://doi.org/10.1016/S0378-1127(01)00649-1)
- Stallings, J. R. (1990). The importance of understorey on wildlife in a Brazilian eucalypt plantation. *Revista Brasileira De Zoologia*, 7, 267–276. <https://doi.org/10.1590/S0101-81751990000300008>
- Stanturf, J. A., Vance, E. D., Fox, T. R., & Kirst, M. (2013). *Eucalyptus* beyond its native range: Environmental issues in exotic bioenergy plantations. *International Journal of Forestry Research*, 2013, 1–5. <https://doi.org/10.1155/2013/463030>
- Terera, F., Gaertner, M., Jacobs, S. M., & Richardson, D. M. (2013). *Eucalyptus* invasions in riparian forests: Effects on native vegetation community diversity, stand structure and composition. *Forest Ecology and Management*, 297, 84–93. <https://doi.org/10.1016/j.foreco.2013.02.016>
- Timo, T., Lyra-Jorge, M., Gheler-Costa, C., & Verdade, L. (2015). Effect of the plantation age on the use of *Eucalyptus* stands by medium to large-sized wild mammals in south-eastern Brazil. *iForest – Biogeosciences and Forestry*, 8, 108–113. <https://doi.org/10.3832/ifer1237-008>
- Wu, J. P., Fan, H. B., Liu, W. F., Huang, G. M., Tang, J. F., Zeng, R. J., ... Liu, Z. F. (2015). Should exotic *eucalyptus* be planted in subtropical China: Insights from understory plant diversity in two contrasting *eucalyptus* chronosequences. *Environmental Management*, 56, 1244–1251. <https://doi.org/10.1007/s00267-015-0578-x>
- Zeileis, A., Kleiber, C., & Jackman, S. (2008). Regression models for count data in R. *Journal of Statistical Software*, 27, 1–25.
- Zuur, A., Ieno, E., Walker, N., Saveliev, A., & Smith, G. R. (2009). *Mixed effects models and extensions in ecology with*.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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