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REVIEW

Green deserts, but not always: A global synthesis of native woody species regeneration under tropical tree monocultures

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Abstract

Tree monocultures constitute an increasing fraction of the global tree cover and are the dominant tree-growing strategy of forest landscape restoration commitments. Their advantages to produce timber are well known, but their value for biodiversity is highly controversial and context dependent. Therefore, understanding whether, and in which conditions, they can harbor native species regeneration is crucial. Here, we conducted meta-analyses based on a global survey of the literature and on a database created with local, unpublished studies throughout Brazil to evaluate the regeneration potential of native species under tree monocultures and the way management influences this regeneration. Native woody species regeneration under tree monocultures harbors a substantial fraction of the diversity (on average 40% and 68% in the global and Brazilian surveys, respectively) and abundance (on average 25% and 60% in the global and Brazilian surveys, respectively) of regeneration observed in natural forests. Plantations with longer rotation lengths, composed of native tree species, and located adjacent to forest remnants harbor more species. Pine plantations harbor more native individuals than eucalypt plantations, and the abundance of regenerating trees is higher in sites with higher mean temperatures. Species–area curves revealed that the number of woody species under pine and eucalypt plantations in Brazil is 606 and 598 species, respectively, over an aggregated sampled area of ca. 12 ha. We highlight that the understory of tree monocultures can harbor a considerable diversity of regenerating native species at the landscape and regional scales, but this diversity strongly depends on management. Long-rotation length and favorable location are key factors for woody regeneration success under tropical tree monocultures. Therefore, tree monocultures can play a role in forest landscape restoration and conservation, but only if they are planned and managed for achieving this purpose.

KEYWORDS
forest landscape restoration, forest restoration, forestry, natural regeneration, plantations, planted forests, understory, woody species diversity

1 | INTRODUCTION

Ambitious forest and landscape restoration initiatives have been promoted globally to recover biodiversity and ecosystem services across millions of hectares of degraded and deforested landscapes (Brancalion, Niamir, et al., 2019; Fagan et al., 2020). At the same time, a wide range of interventions have been employed to increase tree cover in different socio-ecological contexts, based on a complex combination of tree-growing approaches (e.g., natural regeneration, agroforestry, restoration plantations, monoculture tree plantations) and expected benefits (e.g., timber production, carbon sequestration, biodiversity recovery) (Chazdon et al., 2021; Di Sacco et al., 2021; Gann et al., 2019). Tree monocultures represent the most controversial approach. They aim at maximizing the wood production of fast-growing exotic tree species with well-structured markets and supply chains through the use of industrial plantations. (FAO, 2020).

Tree monocultures supply almost half of the global industrial roundwood demand and play an important role in many countries (Jürgensen et al., 2014; Payn et al., 2015), providing financial benefits to millions of farmers and forest managers (Lamb et al., 2005; Nambiar, 2021). For instance, the forest sector represents 3% of Sweden's GDP (Freer-Smith et al., 2019) and 1.2% of Brazil's GDP (Ibá, 2022). In spite of their economic importance, tree monocultures are often referred to as “green deserts” (Acosta, 2011), due to the establishment of homogeneous tree stands often devoid of biodiversity, and without natural regeneration of seedlings in the understory. In fact, tree monocultures have reduced levels of biodiversity and ecosystem services provisioning compared to other tree cover types (Freer-Smith et al., 2022; Hua et al., 2022).

Tree monocultures have been long criticized for their potential damage to biodiversity and ecosystem services, causing degradation instead of restoration (Bremer & Farley, 2010; Brockerhoff et al., 2008). In South America, Oceania, and Eastern and Southern Africa, tree monocultures are predominantly established with exotic species (Payn et al., 2015), many of them invasive (Becerra et al., 2017), and with reported allelopathic effects, especially eucalypts (Cannell, 1999; Fang et al., 2009; Wang et al., 2011; Zhang & Fu, 2009). Moreover, studies have shown contrasting results regarding the ability of tropical tree monocultures to support native forest recovery through the establishment of diverse communities of plants and birds in the understory (Cesar et al., 2018; Cuong et al., 2013; Lopes et al., 2015). Freer-Smith et al. (2022) observed that tree plantations generally have lower impact on land use than agricultural systems on the same site due to longer rotations, lower use of biocides and fertilizers, and lower frequency of interventions. In spite of the concerns mentioned about tree crops, studies suggest that commercial exotic trees can be used as nurse trees for forest restoration (Feyera et al., 2002; Lugo, 1997) or that they can be mixed with native trees to offset restoration costs through their harvesting a few years after planting (Brancalion, Amazonas, et al., 2019).

The discrepancies among these findings likely arise from the fact that the potential of tree monocultures to support biodiversity recovery results from the complex interactions among plantation management (e.g., rotation length, species, spacing, fertilization, understory clearing, harvesting), local site conditions (e.g., soil fertility, slope, previous land use), and landscape features (e.g., native forest cover, disturbance regimes, climate; Brockerhoff et al., 2008; Carnus et al., 2006; Wang et al., 2011). Whereas fast-growing, short-rotation tree monocultures in limiting conditions for natural regeneration may offer limited opportunities for native species recolonization in the understory (Brockerhoff et al., 2008), long-rotation tree monocultures located in wet climates and close to native forest remnants have frequently presented a dense and diverse community of native woody species in the understory (Longworth & Williamson, 2018; Ostertag et al., 2008).

As commercial tree monocultures comprise nearly half of the forest landscape restoration pledges under the Bonn Challenge (Lewis et al., 2019), and most of these pledges have been made for tropical and subtropical regions (Brancalion, Niamir, et al., 2019), where most of global biodiversity is located, it is critical to understand whether and in which conditions monocultures can contribute to native species recovery. Here, we synthesized the literature on the abundance and diversity of native woody species (i.e., trees and shrubs) regenerating under tree monocultures across the tropics and subtropics. To better understand the potential regeneration of woody species in tree monoculture understories, we (1) systematically reviewed papers reporting natural regeneration under tree monocultures, (2) conducted a meta-analysis on the characteristics driving native species regeneration under tree monocultures compared to the species regeneration observed in natural forests, and (3) evaluated the regeneration of native woody species specifically in monocultures of *Pinus* spp. (hereafter pines), *Eucalyptus* spp., and *Corymbia* spp. (hereafter eucalypts) in Brazil, based on a new database created with local studies, previously unpublished in international scientific journals. We expected that native species regeneration under tropical and subtropical tree monocultures could be modulated by management practices and plantation locations favoring or inhibiting seed dispersal from neighboring remnants. We hypothesized that short-rotation monocultures (less than 10 years), regardless of the identity of the planted species and distance from native forest remnants, would explain the low abundance and diversity of native woody species communities in intensively managed commercial tree monocultures.

2 | SURVEY METHOD

2.1 | Systematic review

We systematically reviewed papers on native species regeneration under tropical tree monocultures in the Web of Science. For an article to be selected, it had to contain at least one keyword from each of the following groups: (a) ‘plantation forestry’, ‘tree monoculture’, ‘tree plantation’, ‘exotic monoculture’, ‘plantation forest’, ‘eucalypt’, ‘eucalyptus’, ‘pine’, ‘pinus’, ‘acacia’; (b) ‘regeneration’, ‘native tree species’, ‘richness’; and (c) ‘tropical’, ‘subtropical’, 'dry forest'. We included 'Eucalyptus', 'eucalypt', 'pine', 'Pinus', and 'acacia' as search terms because these are the most planted genera in the world (Carle & Holmgren, 2008; Messier et al., 2021; Paquette & Messier, 2010), and we expected that the other less common planted genera would be covered by the broader keywords. We read the abstract of the articles found in the search described above. Both primary studies (i.e., articles with original data) and secondary studies (i.e., reviews, meta-analysis, opinion articles, and others that did not involve direct data collection) were selected in the first round of review. Secondary studies were selected only to consult their references. In a second step, we reviewed the references to these articles. If the title of the reference was in line with the topic, we searched the article and reviewed the abstract. All pre-selected articles were entirely read. The study had to present at least the monoculture genus and native woody species richness or abundance to meet the inclusion criteria. Our survey included only English-language peer-reviewed literature (see Supplementary Material S1 for more information). Because studies on native species regeneration in tree monocultures are expected to be performed at sites exhibiting some level of understory regeneration, our survey has a potential bias toward sites harboring substantial species regeneration. Therefore, rather than quantifying the regeneration of native species in tree monocultures at large scale, our survey assesses the potential of species regeneration under monocultures.

The final selection resulted in 75 articles (Supplementary Material S2). We retrieved information about the location, plantation characteristics, and native woody regeneration metrics (species richness and individual abundance) directly from tables, main text, and supplementary material for both tree monocultures and a nearby reference natural forest when available (see Supplementary Material S3).

When data were not available in the text, we used WebPlotDigitizer (Rohatgi, 2020) to extract data from figures, or we contacted authors. When available, we extracted data for each independent observation (hereafter records) from the studies, that is, individual plots or different species within the same study; therefore, one study could generate more than one record. In order to standardize as much as possible among the different studies, we used regeneration measurements from the entire plot and did not use subplot data. In addition, using the coordinates provided in each study, we extracted the corresponding soil and climate variables available in global databases (Fick & Hijmans, 2017; Wieder et al., 2014). Furthermore, we consulted both scientific (e.g., Web of Science, Google Scholar) and non-scientific (e.g., Google) search engines for information about the nitrogen-fixing ability of the monoculture tree species of the selected studies. If no report was found, we assumed that the species was not nitrogen-fixing. We focused on woody (i.e., tree and shrub species) regeneration; therefore, articles that aggregated woody and non-woody vegetation data were discarded.

This review included studies carried out in four tropical and subtropical biomes, 41 ecoregions (according to Dinerstein et al., 2017), 26 countries, and six continents (Figure 1a). The country with the largest number of studies was China (10), followed by India (7) and Brazil (6). The studies included 42 different monoculture genera, and 66% of the plantations were not native to the site they were planted. The most common genera in the studies were *Eucalyptus* (29), *Pinus* (26), *Acacia* (10), and *Cupressus* (10). Plantation age ranged from 1 to 80 years (see Supplementary Material S4 for more information on plantation characteristics).

The reviewed studies measured plants at different stages to evaluate regeneration. Twenty studies included only larger individuals (hereafter "trees"; DBH ≥5 cm or stem height ≥5 m), two studies measured only saplings (1 cm ≤ DBH < 5 cm or 1 m ≤ height < 5 m), five studies included seedlings only (DBH <1 cm or h <1 m), and one study included shrubs only. A third of the studies (n = 25) included both saplings and trees; four studies included both seedlings and saplings; and 18 included seedlings, saplings, and trees.

2.2 | Global meta-analysis

We used the studies from the systematic review to conduct a meta-analysis including specifically the studies that contained a reference forest (n = 42 studies/243 records) (Supplementary Material S2) with the same vegetation inclusion criteria for regeneration assessment as the monocultures. We calculated the log-response ratio (RR) for both richness and abundance as follows:

$$RR = \log\left(\frac{\text{monoculture}}{\text{reference}}\right)$$

A positive RR indicates that tree monocultures present higher richness or abundance than the reference area, while a negative RR represents a lower value than the reference sites, and an RR close to zero has little or no effect. We calculated a grand mean response ratio across all studies to test the overall effect of monoculture on regenerating woody species richness and abundance, and we back-transformed it to percentage. This RR was considered significant if its 95% confidence interval did not include zero (Koricheva et al., 2013). We used linear mixed effects models to test the effects of each factor on RR, named as species origin (native, exotic), previous land use (forest, agriculture), monoculture capacity to fix nitrogen, most common planted species (pine, eucalypt), monoculture plant group (gymnosperm, angiosperm), stand basal area, stand age, time since abandonment (time since the management practices were interrupted), distance from native forest, cation exchange capacity (CEC), annual precipitation, and annual mean temperature. The identity of the study was included as a random effect to account for correlations among effect sizes calculated from the same study. As no estimates of within-study variance were reported for most of the studies, we used the total sampling area surveyed in each study as a metric of sampling size to weigh individual effect size in the model (Gurevitch et al., 2018).

Thirty-eight studies (225 records) were used to perform a meta-analysis on abundance data. The abundance reported in different

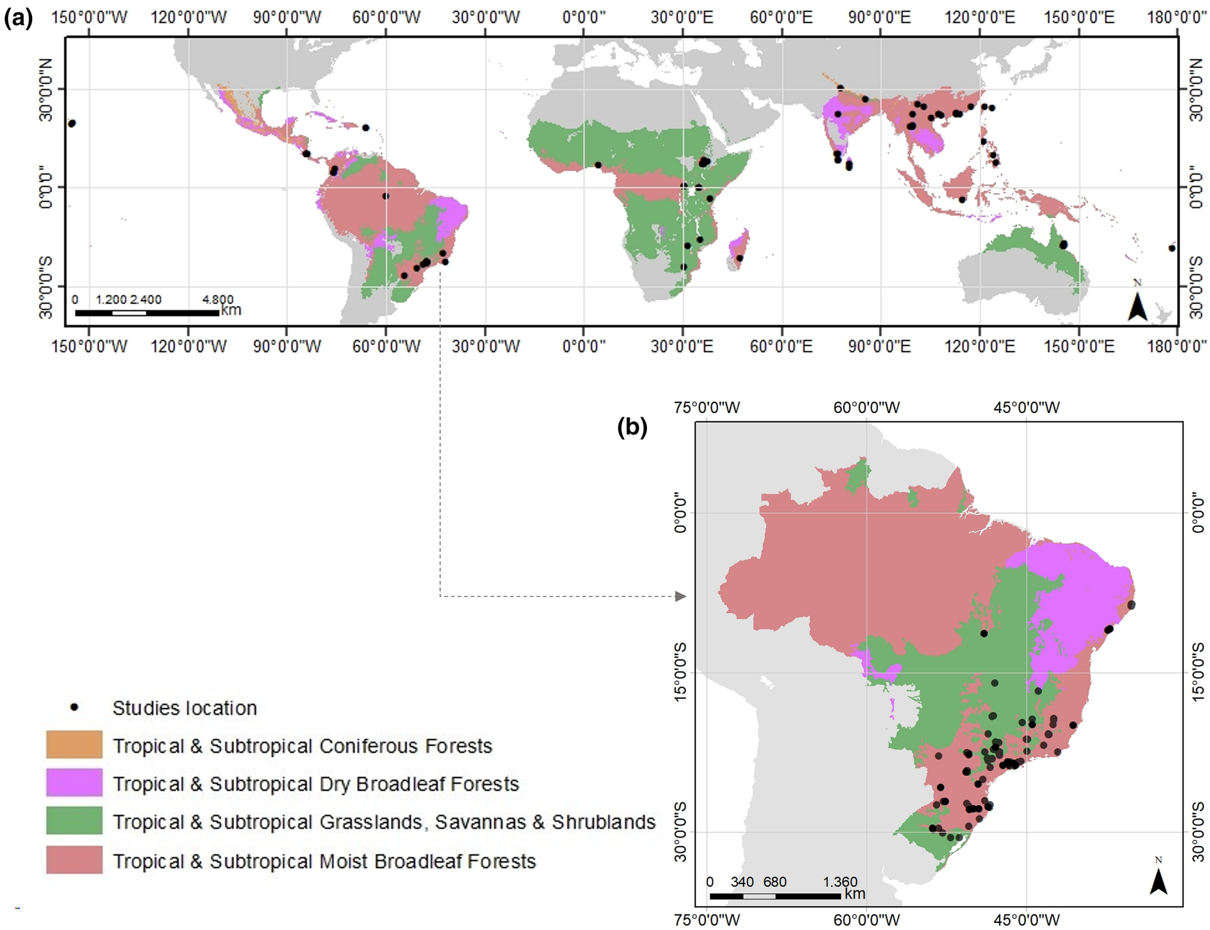

FIGURE 1 Location of the reviewed studies on natural regeneration in tree monoculture plantations in the tropics (a), and location of the surveyed plots with data used for the study case in Brazil (b). Map lines delineate study areas and do not necessarily depict accepted national boundaries.

studies was converted into stems per hectare. To perform a meta-analysis on richness data, we selected studies where the sampling area for richness under the monoculture and reference forest had the same size ($n=32$ studies/218 records). All the analyses were performed in R v4.1.1 (R Core Team, 2021).

2.3 | Case study: Tree monocultures in Brazil

We created a database of regenerating woody species surveyed in eucalypt and pine tree plantations in Brazil, specifically in the Atlantic Forest and Cerrado ecoregions, separately from the global database. We included only these genera because they represent over 95% of the commercial tree plantations in Brazil (Ibá, 2022). The search was carried out on Google Scholar and the Brazil Ministry of Education scientific journal collection (in Portuguese, *Portal de Periódicos da CAPES/MEC*), using "understory of Eucalyptus" and "understory of Pinus" as keywords, and the corresponding terms in Portuguese ("*sub-bosque de eucalipto*" and "*sub-bosque de Pinus*"). We chose the word "pinus" to refer to pines in our search because it is also the popular name of this genus in Portuguese. This review assessed 106 studies, including scientific articles, dissertations, monographs, conference abstracts, theses, book chapters, and undergraduate theses, carried out in 11 Brazilian states and 69 municipalities (Figure 1b). São Paulo state concentrated most of the studies (42%), followed by Minas Gerais (17%) and Santa Catarina (13%). Seventy-four percent of the studies assessed the understory regeneration of eucalypt plantations, while 33% included the regeneration under pine plantations.

As primary studies of the Brazilian dataset did not include reference forests, we used the TreeCo database (Lima et al., 2015, 2020) to obtain this data and calculate RR. We selected forest references that were located in the same municipality as the tree monoculture and that had the same inclusion criteria for sampling woody plants (e.g., tree, sapling, seeding). The areas sampled in the TreeCo database plots differed from the areas sampled in the tree monoculture primary studies. Therefore, we used the Shannon index as a diversity measure for this meta-analysis, because it standardizes diversity metrics using the total number of observed trees in each plot. Thirty-five studies (53 records) and 42 studies (69 records) were included for the woody species diversity and individual abundance meta-analysis, respectively.

In addition, we built species–area curves of the cumulative number of woody species surveyed in eucalypt and pine tree plantations. Species–area curves are suitable to assess large-scale biogeographical patterns comprising explicitly heterogenous areas (Colwell & Coddington, 1994).

3 | RESULTS

The global review showed the expected positive trend between regenerating species richness and sampling area, although with a high variability among studies even when considering those with the same sampling area and monoculture genera (Supplementary Material S4, Figure S4-1). A similar trend was observed for the Brazilian case study (Supplementary Material S6, Figure S6-1).

The mean response ratio across all studies for richness was −0.91 (Figure 2a), which means that the understory of tree monocultures hosted on average 40% of the native species richness compared to the understory of reference forests. Stand basal area, nitrogen-fixation ability of the planted species, taxonomic group of the planted species (angiosperm vs. gymnosperm), and previous land use had no significant effect on species richness (Figure 3b). Plantations established for longer time periods (increase of 0.008 on RR per year), with native species, pine trees (as compared to eucalypt), adjacent to native forests (zero meters away from native forests vs. more than zero meters away), and unmanaged for a longer time (at least 10 years vs. more than 10 years) harbored significantly more species (Figure 2b). The distribution of the RR richness values for each of the considered variables can be consulted in the Supplementary Material S5 (Figures S5-1 and S5-2).

The monocultures had nearly a quarter of the reference forest woody species abundance (RR = −1.37, Figure 3a). Pine tree plantations had more native individuals than eucalypt plantations, and higher mean temperatures resulted in more woody plants (Figure 3b). The distribution of the RR abundance values for each of the considered variables can be seen in the Supplementary Material S5 (Figures S5-3 and S5-4).

When plantations abandoned for 10 years or more were considered, no difference was found between eucalypt and pine for both species richness and individual abundance; native monocultures continued to have more native species regenerating in the understory than exotic monocultures, but no difference was found regarding the number of regenerating individuals.

When considering the Brazilian case study, we found a total of e (798 dispersed by animals) from 368 genera and 85 families regenerating under eucalypt and pine plantations (Supplementary Material S6, Figures S6-2 and S6-3). This species–area curve (Figure 4) showed a total of 606 and 598 native woody species

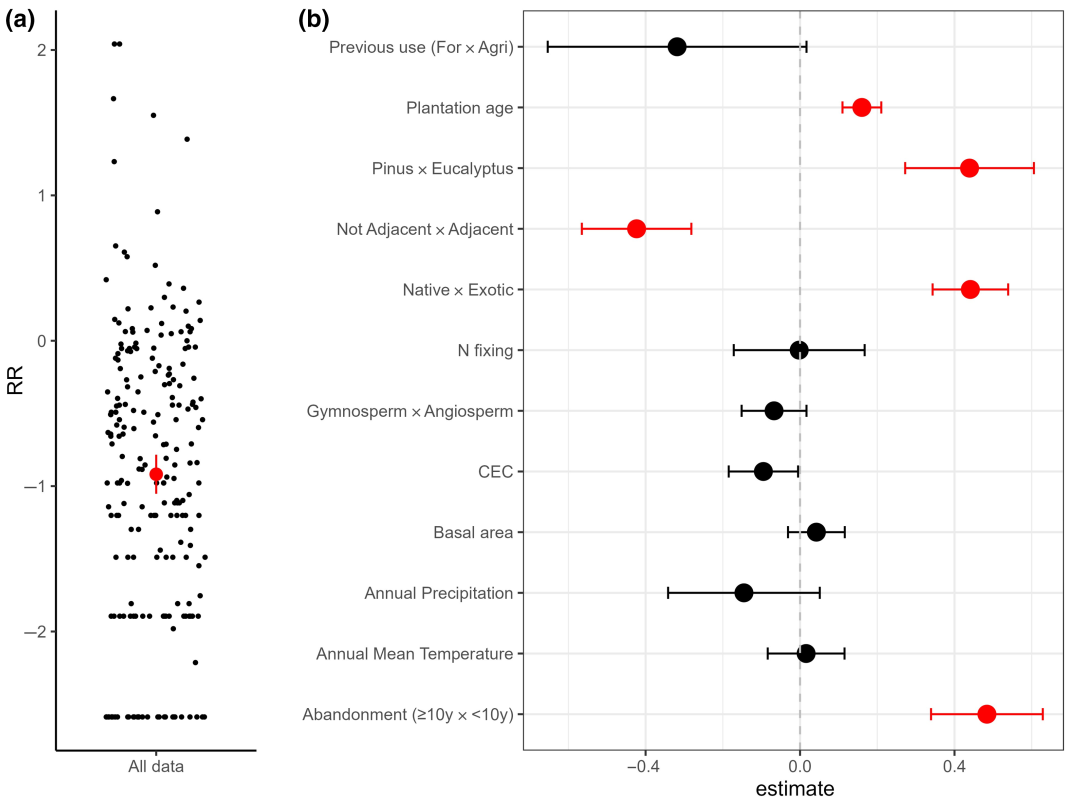

FIGURE 2 Comparison of the woody species richness regenerating in tree monocultures and in reference forests: overall comparison (a) and effects of monoculture and environmental characteristics (b). RR is the log-response ratio. RR is greater than 0 when monocultures exhibit higher species richness than reference forests, lower than 0 otherwise, and the error bar represents the standard deviation. Red means a significant response at a 95% confidence interval.

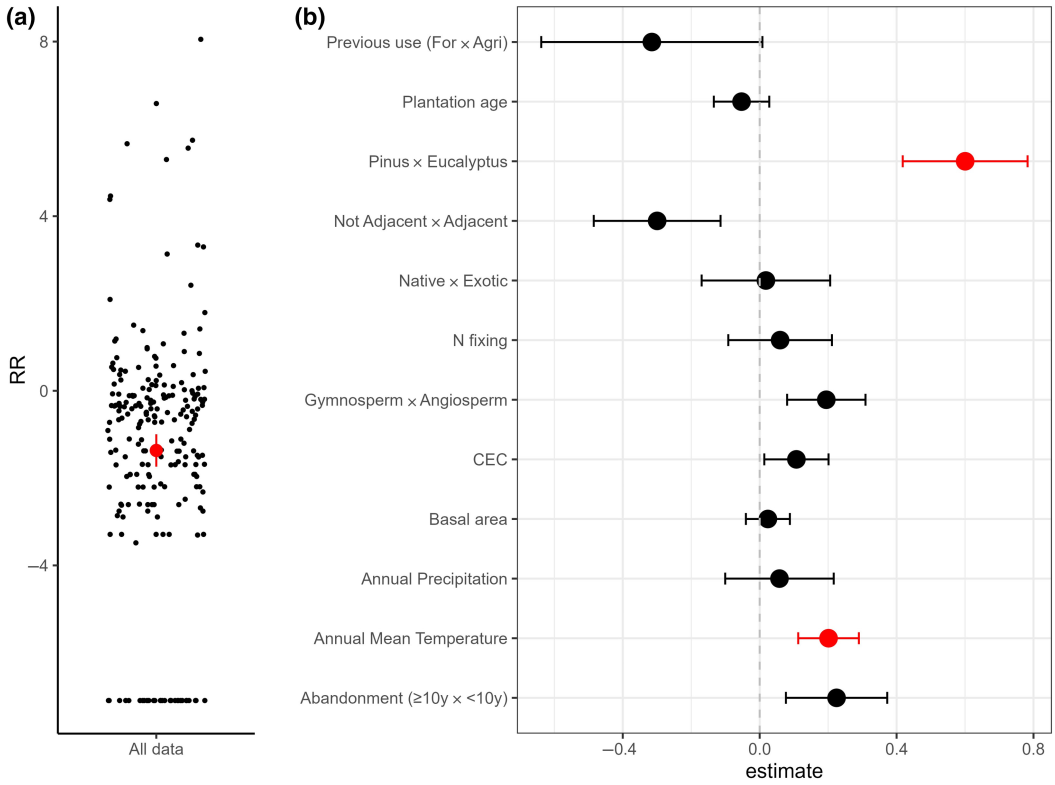

FIGURE 3 Comparison of the abundance of woody species regenerating in monoculture and in reference forests: overall comparison (a) and effects of monoculture and environmental characteristics (b). RR is the log-response ratio. RR is greater than 0 when monocultures exhibit a higher abundance than reference forests, lower than 0 otherwise, and the error bar represents the standard deviation. Red means a significant response at a 95% confidence interval.

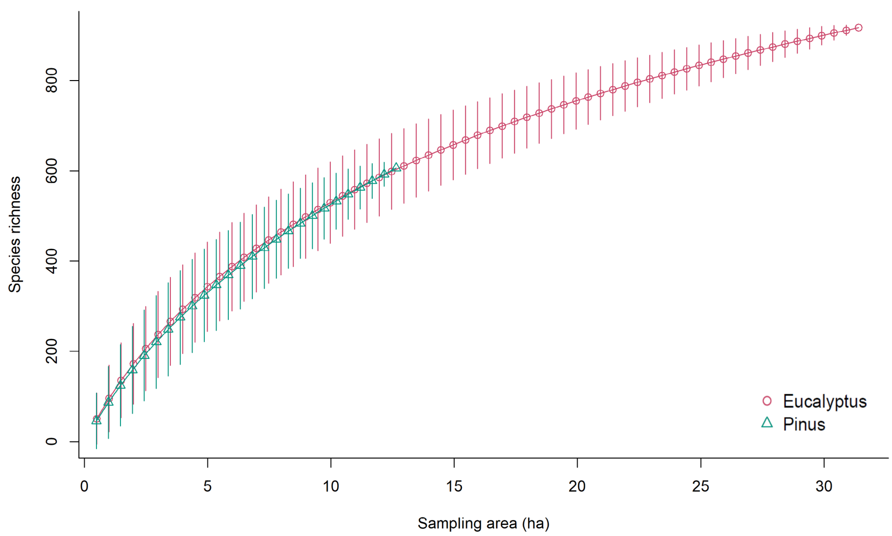

FIGURE 4 Species–area curve of native woody species regenerating under eucalypt and pine tree plantations in Brazil.

regenerated in approximately 12 ha (the total sampling area for pine tree plantations) under eucalypt and pine tree monocultures. This analysis considers all sampling plots assessed in our survey in the Atlantic Forest and Cerrado ecoregions, covering an extensive environmental gradient. In eucalypt plantations, with a sampled area of approximately 31 ha, 917 species were recorded. None of the curves are saturating, which indicates that the total pool of species regenerating under eucalypt and pine tree monocultures across the studied region is likely greater. The trend was similar for eucalypt and pine tree monocultures.

The mean response ratio for the Brazilian case study meta-analysis for diversity, using the Shannon index, was −0.38 (Figure 5a), and for woody species individual abundance, it was −0.5 (Figure 5b), which means that the understory of tree monocultures hosted on

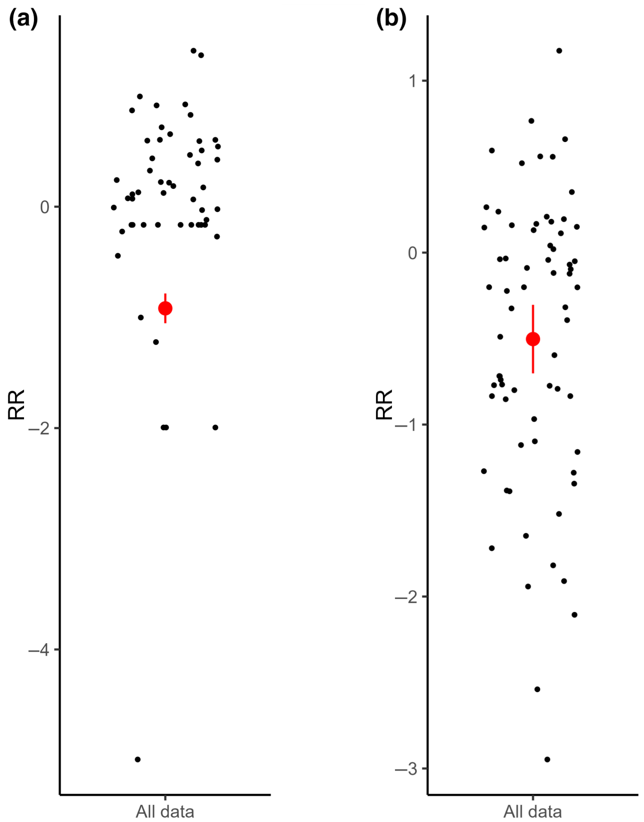

FIGURE 5 Overall comparison of the Shannon diversity index (a) and abundance (b) of woody species regenerating in monoculture and in reference forests. RR is the log-response ratio. RR is greater than 0 when monocultures exhibit higher species richness than reference forests, lower than 0 otherwise, and the error bar represents the standard deviation. Red means a significant response at a 95% confidence interval.

average 68% of the native species Shannon diversity and 60% of the individual abundance of reference forests.

4 | DISCUSSION

4.1 | Monoculture tree plantations can harbor substantial native woody species diversity

The view that tree monocultures are necessarily detrimental to the environment can be partially based on their direct comparison with native forests, as the conversion of forest remnants to tree monocultures has been an important driver of biodiversity loss across the tropics (Barlow et al., 2007; Iezzi et al., 2018; Seifert et al., 2022). However, when tree monoculture plantations are compared with other anthropogenic land uses, such as pasturelands and croplands, they may have considerably higher native species diversity, as plantations may attract more seed dispersers and their understory may have much better microsite conditions for woody seedling regeneration than open, intensively managed agricultural systems (Feyera et al., 2002; Schlaepfer et al., 2011). Our results suggest that tree monocultures are not always "green deserts" and can harbor diverse woody species regeneration in particular circumstances, such as longer rotation and near forest fragments. The regeneration of hundreds of native woody species in monoculture plantations widely distributed across the tropical and subtropical regions indicates that commercial tree monocultures, even those established with exotic species, do not always create major impediments for the regeneration of tree species of varying families, genera, and functional groups. Our results are in contrast with the broadly disseminated assumption that some of the most commonly used exotic trees in commercial monocultures, like eucalypts, prevent understory regeneration through allelopathy and/or soil acidification. Rather, they suggest that other management practices, especially the rotation length, are responsible for the poor regenerating diversity often found in tree monocultures across the tropical region.

Species–area curves in eucalypt and pine plantations in the Brazilian Atlantic Forest and Cerrado showed a marked potential of tree monocultures to harbor diversity at the landscape and regional scales. This result is important for forest management in the country, considering the relevance of this sector for the national economy and its huge biodiversity. The planted forest industry in Brazil generated an income of R$ 244.6 billion (approximately US$ 48.6 billion) and represents a total planted area of 9.93 million ha (Ibá, 2022). Eucalypt and pine tree species are the most commonly used in commercial plantations, totaling 75.8% and 19.4% of the total planted area in the country, respectively (Ibá, 2022). The negative social perception that these plantations are "green deserts"—which is true for most industrial plantations—can be attributed to their intense management and short rotation, rather than to a particular effect of the tree species planted, since monocultures of both species have the potential to shelter abundant understory regeneration, with more than 67% of the regenerating species being dispersed by animals. This negative perception is therefore supported by our results, as most of the eucalypt and pine plantation areas in Brazil are short rotation and intensively managed, two factors undermining native species regeneration in monocultures' understory. In line with previous studies (Hua et al., 2022; Phillips et al., 2017), our results suggest that woody species richness and woody individual abundance are significantly lower than in reference forests.

Therefore, our results support the first golden rule for reforestation by Di Sacco et al. (2021) and Cook-Patton et al. (2021): before planning reforestation initiatives, it is important to protect existing forests because of their irreplaceable conservation value (Barlow et al., 2007; Watson et al., 2018). Poorter et al. (2021) found that secondary tropical forests recovered 78% of old-growth forest species richness in 20 years; however, the recovery of composition is slower and can take more than 120 years. Even after more than 20 years of not managing or lightly managing the stands, plantations still do not host plant abundance and diversity comparable to native forests (Fimbel & Fimbel, 1996; Longworth & Williamson, 2018; Ostertag et al., 2008). However, two-thirds of the plantations included in the meta-analysis were former agricultural lands. Establishing plantations in this situation, rather than replacing native ecosystems, can be beneficial to overcome the ecological barriers that can hamper the colonization of native species in abandoned agricultural areas, such as unfavorable microclimate conditions, herbivory by leafcutter ants, a lack of seed dispersal, and competition with ruderal grasses (Brockerhoff et al., 2008; Schlaepfer et al., 2011). Due to these potential benefits for forest recovery, some exotic commercial trees have been tested as "nurse trees" for kickstarting forest recovery. For instance, Ashton et al. (1998) also had positive results testing *Pinus caribaea* as a "nurse tree" for shade-tolerant species in Sri Lanka, and Norisada et al. (2005) observed that *Acacia mangium* was a promising "nurse tree" candidate for planted native species on degraded sandy soils in the Malay Peninsula as it had a positive impact on microclimate for seedling establishment.

Indeed, in some circumstances, the diversity and structure of native species stands regenerating in tree monocultures can be comparable to old-growth forests (George et al., 1993; Nerlekar et al., 2019) or similar to secondary forests (Santos et al., 2019), which indicates that the potential of regeneration varies in different locations and landscape contexts. Actually, many native woody species are highly sensitive to competition with C4 invasive grasses. Therefore, fast-growing tree monocultures may, in some instances, foster native seedling establishment in the understory by hastening canopy closure (Brancalion, Campoe, et al., 2019; Lugo, 1997).

We compiled stand ages, ranging from 1 to 80 years old, with different time periods since abandonment. These different ages have influenced the results, mainly if we consider that older stands presented significantly more woody species richness than younger stands. Conversely, we expect that the native forests used as our reference were not necessarily old-growth, which are rare in the human-modified tropical and subtropical landscapes where commercial tree monocultures are usually established. Despite our efforts to always select the most conserved forests available in the studies as a reference, some of them were second-growth forests. Then, the conservation value of tree monocultures would be relatively lower if compared with more diverse forests and would never replace the unique value of native forests for biodiversity conservation. However, better managed tree monocultures may create habitat and increase landscape connectivity, thus contributing to biodiversity and complementing the conservation role of native forest remnants and other strategies to restore tree cover.

Nonetheless, native trees regenerating in long-rotation tree monocultures might not reach the reproductive stage due to resource and growing time limitations. Therefore, the long-term contributions of these plantations for conservation, which were not assessed in this research, will only be substantial if long-rotation monoculture plantations are a transitional step toward forest restoration (Brancalion, Amazonas, et al., 2019). These plantations could also act as a source of seedlings for restoration projects, mostly for species that are not usually produced in nurseries (Brancalion et al., 2012).

4.2 | Plant native species, adjacent to forest remnants, and delay harvesting: Fostering the conservation value of tree monocultures

While many studies found that the identity of the tree species managed in plantations crucially influences the natural regeneration growing in the understory (Fimbel & Fimbel, 1996; Firn et al., 2007; Otsamo, 2000; Parrotta, 1995; Powers et al., 1997; Thijs et al., 2014), others found that other factors, such as environmental conditions and landscape structure, were more important drivers (Brancalion, Amazonas, et al., 2019; Duan et al., 2010; Geldenhuys, 1997). We posit that the greater species richness found in pine trees than in eucalypt monocultures are a potential consequence of management: the stand rotation of pine trees, which is mostly used in the tropics to produce saw wood (15–20 years), is usually longer than the rotation of eucalypt stands, which are mostly used to produce pulp and charcoal (5–7 years) (Otuba & Johansson, 2016), and longer rotation may increase the likelihood of seedling establishment over time. Our results support this idea since we found a significant relationship between species richness and both stand age and time since abandonment. When we considered only pine and eucalypt plantations unmanaged for 10 years or more, no significant difference was observed, which emphasizes how rotation length is an important driver of regeneration.

Native species seem to harbor more species diversity than exotic stands. This outcome agrees with the results of Bremer and Farley (2010), who compared tree plantations and secondary forests and observed a higher richness in native plantations than in secondary forests, while exotic plantations usually had lower richness. Native tree species have a better potential to shelter native plants and animals, and they can provide an environment with structural and understory conditions more similar to natural forests (Brockerhoff et al., 2013; Stephens & Wagner, 2007). Commonly planted exotic species, such as eucalypts and pine trees, produce low-quality litter characterized by a low concentration of nutrients and high mass (Lugo et al., 1990). The decomposition of such low-quality litter occurs at slow rates, resulting in litter accumulation that negatively affects seedling establishment and species richness (Zhang et al., 2022). Furthermore, the native plantations are usually less intensively managed because they are planted to meet other purposes than timber production, such as social and ecological benefits, and have longer rotations due to their slow growth (Lamb, 1998).

Previous studies found that the richness of native plants is greatest in older stands because they provide a better environment for natural regeneration by ameliorating microclimate and soil conditions and reducing grass cover (Brockerhoff et al., 2008; Geldenhuys, 1997; Hua et al., 2022). All plantations go through a thicket stage, which is the stage where the tree stand is dense and there is canopy closure. Short-length rotation plantations keep the plantation in this stage, which is not suitable for regeneration because of low light availability in the understory and high litter layer accumulation rates. In older stands, the canopy closure decreases, and the light and humus conditions tend to improve. A simpler and complementary explanation is that if regeneration is a stochastic process with a given rate of occurrence, the longer the period considered, the higher the regeneration.

Our study suggests that previous land use does not affect the natural regeneration potential of the stands, which was a surprising finding. We expected that previously forested areas would present higher natural regeneration than areas formerly occupied by agriculture, consistent with Bremer and Farley (2010) and Feyera et al. (2002). Ritter et al. (2018) found that land use history had a minor effect on plant abundance and species richness but had a clear effect on the species composition in loblolly pine plantations in the Atlantic Forest of Argentina. Nevertheless, plantations adjacent to native forests present a significant, positive effect on natural regeneration, which implies that the landscape matrix may be more important than land use history. Since many tropical species are dispersed by fauna (Kakishima et al., 2015), a fact that was also corroborated in our case study, the area legacy may be less important than the proximity to the fragments. As distance to native forests decreases, species richness tends to rise (Longworth & Williamson, 2018; Ostertag et al., 2008) because forests nearby act as seed resources (Duan et al., 2010).

4.3 | Implications for management

Stakeholders generally have conflicting attitudes toward tree monocultures: farmers and companies promote them to maximize timber production of commercially valuable species, whereas environmentalists try to reduce their expansion as they may harbor low biodiversity levels when compared to native forests. Conversely, in a context of rapid climate change, plantations' resilience may increasingly rely on higher levels of diversity (Messier et al., 2021). Here, we demonstrated that, under appropriate biophysical and management conditions, tree monocultures represent a viable "middle way" between financial and conservation interests, which can be integrated into a mix of landscape forest restoration strategies. However, if wood production is not a priority, other restorative practices are more suitable to promote biodiversity and environmental benefits (Gann et al., 2019; Hua et al., 2022). We highlight a potential trade-off between timber production and conservation potential in plantations, as intensively managed plantations will offer lower opportunities for native tree species recruitment and development, whereas unmanaged or abandoned plantations (e.g., due to changes in market conditions, land ownership, legal demands) may foster a more effective forest recovery.

Other "middle way" approaches have been proposed to achieve this aim, like intercropping exotic eucalypts with native trees to offset restoration implementation and maintenance costs and kickstarting regeneration processes (Brancalion, Amazonas, et al., 2019). In Brazil, for example, the Native Vegetation Protection Law issued in 2012 allows the planting of exotic tree species (in maximum 50% of the area) in mixture with native species to restore Legal Reserves (20%–80% of the farm area, depending on the biome) (Brancalion et al., 2016), which emphasizes the relevance of our findings for validating or suggesting public policies for tropical and subtropical countries in a way to make forest restoration financially viable and tree monocultures a more sustainable land use.

We report that rotation length is a crucial determinant of the conservation value of tree monocultures in the tropical and subtropical regions. As younger plantations have a higher leaf area index and then lower light availability in the understory (Le Maire et al., 2019) and are managed more intensively (e.g., herbicide spraying in the understory, higher mechanization), delaying timber harvesting can be an effective measure to increase the conservation value of plantations at the landscape scale. In some cases, the financial setback of extending harvesting cycles, caused by the decline in stand growth rates with time, could be compensated by carbon credits generation through the Improved Forest Management mechanism (Daigneault et al., 2022; Griscom et al., 2017). Our findings highlight that this mechanism could also be used to improve the contributions of plantations to biodiversity, and not only to increasing carbon stocks in the long run.

Finally, we reiterate that not all tree monocultures are the same. Commercial tree monocultures can harbor, in favorable circumstances such as longer rotation length and proximity to forest fragments, a considerable diversity of native woody species at the landscape and regional scales. Although not ideal for biodiversity recovery, as more sensitive species may never recolonize monoculture plantations and rarely, if ever, reach maturity, the conservation value of tree monocultures can be maximized by favorable management conditions. In addition to conserving existing native forests and promoting mixed and native species plantations in forest landscape restoration initiatives, improving the management of existing and new tree monocultures can help maximize the benefits of plantations for achieving restoration benefits at the landscape scale.

AUTHOR CONTRIBUTIONS

Laura H. P. Simões: Conceptualization; data curation; formal analysis; investigation; methodology; project administration; writing – original draft. **Joannès Guillemot:** Conceptualization; formal analysis; methodology; supervision; writing – review and editing. **Carlos C. Ronquim:** Conceptualization; data curation; resources; writing – review and editing. **Emanuela W. A. Weidlich:** Formal analysis; methodology; visualization; writing – review and editing. **Bart Muys:** Data curation; resources; writing – review and editing. **Matheus S. Fuza:** Data curation; visualization. **Renato A. F. Lima:** Data curation; resources. **Pedro H.S. Brancalion:** Conceptualization; funding acquisition; methodology; supervision; writing – review and editing.

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CONFLICT OF INTEREST STATEMENT

PHS Brancalion is a partner at Re.green, a restoration company; he has received research funding from different forestry and agriculture companies, aiming at developing cost-effective restoration approaches.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in figshare at http://doi.org/10.6084/m9.figshare.23968044.

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SUPPORTING INFORMATION

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

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