

# Active Restoration Initiates High Quality Forest Succession In A Deforested Landscape In Amazonia

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## Research

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# Abstract

**Background:** Amazonia is well known for its high natural regeneration capacity; for this reason, passive restoration is normally recommended for the recovery of its degraded forests. However, highly deforested landscapes in southern Amazonia require active restoration. Since restoration methods can shape the quality and speed of early forest recovery, this study aimed to verify how active restoration pushes non-resilient sites towards forest recovery.

**Methods:** We evaluated early forest succession at active restoration sites, i.e. soil plowing, direct seeding of pioneer species and seedling stock planting at low density. We analyzed forest structure, diversity and species composition in two age classes, 0.5 – 3.5 and 4.5 – 7.5 years old. As reference, we evaluated natural regeneration as performed on more resilient sites in the same region. We sampled 36 active restoration and 31 natural regeneration sites along the Madeira river, southern Amazonia.

**Results:** Active restoration triggered succession to similar or higher levels of forest structure than sites where natural regeneration was taking place. The most dominant species did not overlap between active restoration and natural regeneration sites. The overall composition of species was different between the two restoration methods. Dominant species and size class distribution indicate that active restoration is performing successfully.

**Conclusions:** Soil preparation combined with a high availability of seeds of pioneer trees resulted in a high stem density and basal area of facilitative pioneer trees. Planted seedlings added species diversity and increased density of large trees. Interventions to increase the odds of natural regeneration can be effective for non-resilient sites located in resilient landscapes.

## Introduction

Natural regeneration can be the most cost-effective method for tropical forest restoration (Chazdon and Uriarte 2016). Throughout the world, tropical forests are recovering after being deforested and replaced for pasture and agriculture (Chazdon and Guariguata 2016). In fact, when natural regeneration capacity is high, active restoration can hinder or alter the successional trajectory already taking place (Holl and Aide 2011). However, even in the highly resilient Amazon forests (Poorter et al. 2016), succession may be arrested depending on the intensity and length of previous land use (Rezende and Vieira 2019; Jakovac et al. 2016; Mesquita et al. 2015). In such cases, assisted natural regeneration or active restoration are recommended (Freitas et al. 2019; Rezende and Vieira 2019; Chazdon and Guariguata 2016).

In southern Amazonia, intensive agriculture and pastures, which involves annual soil revolving and application of herbicides, have dominated the landscape (VanWey et al. 2013). Through the reduction of forest cover and the elimination of local sources of regeneration (e.g., soil seed and sprouts bank) these landscapes have lost, or suffered severe reductions of, their potential for natural regeneration (Freitas et al. 2019; Rezende and Vieira 2019). In these cases, where natural regeneration does not initiate within a few years, active restoration is suggested (Corbin and Holl 2012; Holl and Aide 2011).

Even if two or more methods are successful in restoring a site, each one leaves its own footprints on the recovery trajectory (Freitas et al. 2019; Rodrigues et al. 2019; Corbin and Holl 2012). For example, although seedling planting restoration accelerates canopy closure and facilitates natural regeneration it also promotes a homogeneous dense canopy (Corbin and Holl 2012) that can hinder recruitment of early successional species (Sansevero et al. 2011). In contrast, unassisted natural regeneration leads to a heterogeneous forest structure because of the heterogeneity of soil types, varying densities of invasive species, and random timing of species colonization. However, also in sites with high potential for natural regeneration, a monodominant canopy can be formed by native aggressive species (Chazdon and Uriarte 2016; Mesquita et al. 2015). In direct seeding of native species at high densities, another active restoration method, the canopy closes rapidly by the proximity of the stems (Freitas et al. 2019), but the initial species composition is biased towards species adequate for seed and seedling production (Rodrigues et al. 2019). Natural regeneration and active restoration will often result in succession communities with different species composition because of the restrictions imposed by seed availability, germination efficiency and survival in active plantings (Rodrigues et al. 2019; César et al. 2018), which might potentially conduce to divergent successional trajectories.

In this study we aim to understand how active restoration can put exotic grasses dominated and non-resilient sites on the path to recovery. We compared early successional trajectory of active restoration sites with naturally regenerating sites, as reference. In this study area, active restoration is applied to sites without natural regeneration, and natural regeneration is applied to sites where natural regeneration is occurring. Active restoration consists of a mix of interventions: soil preparation, control of invasive grasses, seedling planting and direct seeding of native species. We hypothesized that vegetation structure is higher for active restoration than natural regeneration, because it (i) eliminates grasses, a major tropical forest recovery obstacle (Weidlich et al. 2020); (ii) improves seedling emergence of pioneer tree seeds from the seed bank and seed rain by providing full sun and uncompact soils (Freitas et al. 2019; Camargo et al. 2002); and (iii) adds individuals and species from the onset of the restoration, by directly seeding and seedling planting (César et al. 2018). We also hypothesized that species composition differs between the restoration methods, because natural regeneration sites start with an assemble of recruiting species and have not been subject to any intervention, while active restoration sites start without natural regeneration and have been submitted to interventions that stimulate the establishment of a larger pool of species. Active restoration would be more predictable than natural regeneration, because non-regenerating sites are more homogeneous, and the interventions are standardized.

## Methods

### *Study area*

The study sites are located south of the Jirau Hydroelectric Reservoir, in the Rondônia State, Brazil, and are included in the buffer zone of 30 to 100 m of riparian forest along ca. 100km of the Madeira River, designed to protect the margins of the reservoir. The most common vegetation type in the study area is terra-firme forests, which occupies well-drained, nutrient-poor soils (Cochrane and Cochrane 2010). The

forests were cleared in the 1970s for livestock pastures, resulting in sites dominated by the productive African grass *Urochloa brizantha* (see Rocha et al. 2016 for more details). Pastures in the region are generally intensively managed with the use of herbicides, mowing, and fire for pasture renovation and elimination of non-pasture plants regeneration. Less intensified pastures are left to fallow for a few years and then renewed, a process that can be repeated multiple times. Old-growth and secondary forests cover 37% of the landscape in the study area (Rocha et al. 2016).

The restoration project uses an adaptive restoration plan, where the choice for the restoration method depends on a diagnosis of the potential for natural regeneration of each site. This is a practice to reduce costs and increase restoration success (Kishy et al. 2020). The presence of abundant natural regeneration, mostly dominated by *Vismia* spp., previous to any management indicated the potential for using natural regeneration as the restoration method. Natural regeneration (NR) data was extracted from a study conducted in the same riparian buffer. In 2013, Rocha et al. (2016) studied abandoned pastures 0–15 years of forest succession (fallow age provided from Landsat imagery classification). We selected 31 of those sites to ensure the same age range of active restoration sites.

In Jun-Ago 2019, we sampled 36 sites subject to active restoration between 2012 and 2018. Active restoration (AR) was carried out on sites covered by African pasture grasses and with low or no natural regeneration of forest species. Active restoration was improved with experience, by adding direct seeding and reduced seedling stock density after 2015. Thus, we considered it as two different treatments: before 2015, active restoration with seedling planting (Active SP), and after 2015, active restoration with seedling planting and direct seeding (Active SP + DS).

In all sites, the soil was harrowed at 20–30 cm depth with a tractor-driven disc harrow to remove exotic grasses. In Active SP (4.5–7.5 y-old sites), seedling spacing varied among sites. In sites with very low or without natural regeneration ( $< 400$  tree recruits $\cdot$ ha $^{-1}$ ), seedlings were planted at a 3m $\times$ 2m spacing; in sites with 400–1000 tree recruits $\cdot$ ha $^{-1}$ , the spacing was 5m $\times$ 5m or 5m $\times$ 4m. We compared the structural attributes between narrow and wide spacing, grouping the sites with age between 4.5 and 7.5 years, and found no statistical difference for all vegetation attributes but absolute richness, where higher seedling density resulted in 41 species, while wide spacing sites had 35 species on average (t-test<sub>(n=12)</sub>; Basal Area:  $t = 2.06$ ;  $p = 0.091$ ; Canopy Height:  $t = 1.91$ ;  $p = 0.080$ ; Density of trees:  $t = -0.24$ ;  $p = 0.812$ ; Density of seedlings:  $t = 0.40$ ;  $p = 0.694$ ; Richness:  $t = 2.35$ ;  $p = 0.038$ ; Rarefied richness:  $t = 1.51$ ;  $p = 0.156$ ). Therefore, all Active SP sites were considered homogeneous.

Active SP + DS sites (0.5-3 y-old sites) had seedling planting at 5 $\times$ 5 m spacing and additionally were directly seeded with pioneer species. The four pioneer tree species *Trema micrantha*, *Senna alata*, *Solanum quaesitum*, *Solanum crinitum* and *Bixa orellana* were directly seeded by manual broadcasting over the entire site. Seed densities and species composition varied slightly among sites (Appendix S1: Table S1).

In all active restoration sites, along the first two years after planting, herbicide (glyphosate) was applied one to four times to control *Urochloa* grasses that emerged from the seed bank until the tree canopy could shade out the grasses. Herbicide application was also subject to a learning process, where the oldest (7.5-y old) sites had extensive application of herbicides, avoiding the planted seedlings, while the younger sites had application targeted to the grass tussocks.

Active restoration and natural regeneration sites were evenly distributed along the riparian buffer (Fig. 1).

### *Sampling and species classification*

In NR sites, one circular plot with a 10 m radius was established on each site, totaling 31 plots (for a more detailed description, see Rocha et al. 2016). In each plot, all stems of tree species with height > 30 cm were identified and measured. Diameter of stems was measured with a digital caliper to ground level. From the available data, we separated trees (height > 2 m) from seedling (0.3 m < height < 2 m) to perform comparative analyses. To estimate DBH, we transformed the diameter at the base using the equation for secondary forest plants provided by Gehring et al. (2008), which transforms D30cm to DBH.

We sampled 36 restoration sites, ranging from 0.9 to 39.7 ha. Five 25 x 10 m plots were randomly allocated in each site, where trees (height > 2 m) were measured. Seedlings (0.3 m < height < 2 m) were measured within five 25 x 4 m subplots nested along the longitudinal centerline of the plot. We identified seedlings and trees, and measured height (H) and diameter at breast height (DBH) of trees. Species were collected and identified with assistance of botanists of the herbarium of Embrapa Genetic Resources and Biotechnology (CEN).

Species and stems were classified as “planted seedling”, “direct seeded or natural regeneration” and as “natural regeneration”. Stems were identified as “planted seedlings” in the field by their systematic location and species pool. It was not possible to distinguish between direct seeded- and natural regeneration-stems because direct seeded species were from the regional pool and normally colonize restoration sites. They were seeded to enhance and assure dense populations. We used the list of seeded species for each site, and when a species was seeded it was classified for that site as “direct seeding or natural regeneration”. The non-planted species in each site were assigned to “natural regeneration”.

### *Data analysis*

We calculated basal area ( $m^2/ha$ ), density of trees and seedlings (ind/ha) and canopy height (m). The basal area was calculated including all tree stems (height > 2m). The canopy height was defined as the upper decile of the height of trees sampled in each site. We calculated the rarefied species richness per 25 individuals, which was the lowest number of individuals of all plots, to allow direct comparisons between active restoration and natural regeneration. The comparisons between active restoration and natural regeneration were made separately for younger and older sites in order to consider the two different methods of active restoration: NR × Active SP (for 4.5–7.5 y-old sites) and NR × Active SP + DS (for 0.5–3.5 y-old sites). We performed ANCOVAs to assess difference in vegetation attributes between the two

restoration methods, considering age as a co-variable. Density of trees and seedlings were square-root and log-transformed, respectively, to meet model assumptions.

To test if species composition differs between AR and NR sites and if AR is more predictable (homogeneous), we applied a distance-based redundancy analysis (db-RDA; Legendre and Anderson 1999). We included age (as continuous variable), and method (active and passive) as predictors of the species composition. Then, we used ANOVA to test the significance of the overall model and constraint variables. The distance index between pairs of sites used was the Chao-Jaccard on the abundance matrix. We found no spatial autocorrelation of species composition when applying a Mantel's test.

We described AR and NR sites in relation to the 10 most dominant species, separately for younger and older sites in order to consider the two different methods of active restoration.

To evaluate how restoration unfolds in active restoration sites, we estimated the relative contribution of “planted seedlings”, “seeded seeds or natural regeneration” and “natural regeneration” on the tree community over time. Directly seeded seedlings were not distinguishable from natural regeneration, as the direct seeded species also regenerate naturally.

All analyses were conducted in R version 3.6.2 (R Core Team 2019), using *vegan* and *stats* packages.

## Results

At the NR sites, we recorded 2,063 trees (in 0.85 ha) and 1,125 seedlings (in 0.97 ha), from 45 families (with 2 non-identified stems) and 183 species. At the AR sites, there were 8,794 trees (in 4.37 ha) and 6,280 seedlings (in 1.8 ha), from 36 families and 155 species (with 15 non-identified stems; Appendix S1: Table S2).

Active restoration triggered a structural forest succession to the same or higher levels of sites where natural regeneration was occurring (Fig. 2). In average, basal area was 3.49 m<sup>2</sup>/ha for AR and 3.27 m<sup>2</sup>/ha for NR at younger sites, and 8.86 m<sup>2</sup>/ha and 9.35 m<sup>2</sup>/ha at older sites. Canopy height was 4.69 m for AR and 4.36 m for NR at younger sites, and 7.20 m and 7.35 m at older sites. Tree density was not different between AR and NR in both age classes. Seedling density was almost twice higher in AR SP + DS sites (mean of 2003 ind/ha) than in NR sites (mean of 1134 ind/ha), and six times higher at older ages (AR SP = 5927 ind/ha; NR = 978 ind/ha). Rarefied richness was higher in younger AR PS + SD (9.88 species per 25 stems) than in younger NR (6.66 species), as well as absolute richness, which was 27.5 in AR PS + SD and 9.66 species in NR in average. At older ages rarefied and absolute richness was not significantly different between AR and NR, as AR did not increase, and NR increased relative to younger sites.

Active restoration had higher size-structure heterogeneity than natural regeneration, increasing the density of recruits (< 2 m high trees; Fig. 2), reducing intermediary size-classes and increasing density of large stems (> 25.1 cm DBH; Appendix S1: Fig. S1).

The most dominant species were highly different between AR and NR (Fig. 3). NR showed strong dominance and little dynamics; sites were strongly dominated by *Vismia* spp that was responsible for 58% of the total basal area in younger sites and 45% in older sites (Fig. 3). AR younger sites were dominated by a larger pool of species with the ten most abundant species responsible for 62% of the total basal area. The species were fast growth and short life-span species *S. alata*, *T. michrantha* (direct seeded), *Solanum* spp., *M. calabura*, *C. purpurascens* and *P. guajava* (not seeded). In older AR sites, the basal was evenly distributed with 55% composed by the ten most abundant species, which were mostly non-planted.

The db-RDA explained 28.6% ( $R^2$ ) of the variation in species composition and the model was significant (overall model:  $F_{2,64} = 8.01$ ;  $p = 0.001$ . Figure 4). First axis (CAP1) explained 24.1% and was mainly driven by the restoration method (AR or NR). The second axis (CAP2) explained an additional 4.5%, being age the most important variable. The effects of method and age on species composition were significantly different from random. The restoration method explained 23% of the variation in species composition ( $F_{1,64} = 2.79$ ;  $p = 0.006$ ) and age explained only 3% ( $F_{1,64} = 13.22$ ;  $p = 0.002$ ).

In active restoration sites, planted seedlings had little contribution to basal area and stem density, reaching less than 30% of the basal area and 14% of the total stems in both AR SP + DS (younger) and AR SP sites (older; Fig. 5a, b). Planted seedlings accounted for 42% of species richness in AR SP + DS, and for 25% in AR SP sites (Fig. 5c). Natural regeneration dominated basal area, stem density and species richness in active restoration sites (Fig. 5). Direct seeding was applied only to 0.5 to 3.5 y-old sites. Seeded species, which could also be natural regeneration, contributed to 29% of the basal area, 24% of the stem density, and 9% of the species richness in AR PS + SD sites, where it was applied (Fig. 5).

## Discussion

Our results showed that active restoration triggered a healthy succession on sites formerly dominated by African grasses, with weak or no natural regeneration. Forest structure in active restoration sites developed in a similar rate as sites naturally regenerating, therefore subject to passive restoration. Stem density and rarefied richness were higher in active restoration sites, due to seed and seedling addition and, especially, to the stimulus of new stems and species recruitment. Species composition in active restoration sites included a shared dominance of short life-span, pioneer trees, typical of less disturbed natural regeneration sites, in opposition to the *Vismia*-dominated natural regeneration sites (Mesquita et al. 2015).

### *Active restoration is a matter of eliminating regeneration filters*

The success of the active restoration was explained by preparing a loose soil, free from exotic grasses, with small furrows and mounds, associated with a high availability of seeds of pioneer trees. That resulted in high stem density and basal area of pioneer trees, as seen in the older sites with no direct seeding intervention. Planted species (direct seeding and seedlings) contributed to 50 and 25% of the

species richness in younger sites and older, respectively, and only 48% and 28% of the basal area. In an experiment designed for decoupling the effects of soil preparation and seed and seedling addition, stem density was similar in plots with only soil preparation and those with soil preparation and seeding or seedling planting (Rezende and Vieira 2019). These results show that the barrier to natural regeneration in this landscape is not seed availability, but the conditions to germinate and establish.

For the restoration project studied here, direct seeding is a safety strategy for sites that do not have enough seed density from seed rain or seed bank. However, in landscapes with even lower forest cover and lower abundance of pioneer trees in the agricultural matrix, direct seeding might be necessary. Direct seeding of highly abundant pioneer trees is a relatively cheap strategy (Rezende and Vieira 2019), but one cannot decide on doing it after seeing the early results of the restoration. It needs to be applied during the first months after soil harrowing, which is the window of opportunity for germination and establishment.

Forest landscape cover affects the effect size of the active restoration. Active restoration is more necessary to guarantee restoration success in landscapes with low forest cover (Crouzeilles and Curran 2016). An effective active forest restoration method should introduce pioneer trees that contribute to fast structuring a canopy, and introduce late successional species, that will guarantee a long-term forest (Rodrigues et al. 2009). However, in the studied landscape planted species promoted higher species richness in the restored sites only in the first few years. Species colonization was happening in natural regeneration sites to a point of no difference in species richness. We suggest that with the forest cover in the studied landscape of Amazonia (37%; Rocha et al. 2016), restoration intervention should focus in structure a tree canopy in order to facilitate natural colonization. In the southern border of Amazonia, in a landscape with 18% of forest cover on average, non-planted species colonize sites in an average rate of 0.4 species/year along 10 years after direct-seeding restoration (considering a plot size of 500m<sup>2</sup> for adults, 100m<sup>2</sup> for saplings and 25m<sup>2</sup> for seedlings; Freitas et al. 2019). Thus, even within highly deforested landscapes, active interventions will be more efficient if designed for triggering natural regeneration, than planting an assembled forest.

Differently from the southern Amazonia, other restored tropical forests are sustained by the planted seedlings (Rodrigues et al. 2019; César et al. 2018; Shoo et al. 2015; Sansevero et al. 2011). In the Atlantic forest, 97% of the above ground biomass in 7–20 year-old active restoration sites were from planted trees (César et al. 2018), evidencing that natural regeneration was scarce. Yet, in older (up to 53 years) active restoration sites in Atlantic forest, there is an increase of species- and life-form diversity, becoming similar in structure and species composition to old growth forests (Suganuma and Durigan 2015).

#### *Active restoration × naturally regenerating forests in Amazonia*

In our study, pastures were mechanized and used for cattle ranching during 9.3 years on average (Rocha et al. 2016). Forest structure and richness in these pastures before active restoration were lower than the heavy-use pastures (> 7 years used as pasture, 1–2 fires and mechanized for grass seeding) described by Uhl et al. (1988). Before active restoration interventions, those sites were dominated by a healthy *U. brizantha* pasture, cultivated through intense soil management, and removal of trees resprouting and

recruitment by harrowing and herbicide application (Rezende and Vieira 2019). Probably as a result of intensive pasture management all seed bank and sprouts were eliminated, which may explain why not even the most important tree-weed in Amazonian pastures, *Vismia* spp. could vigorously resprout.

The active restoration sites of up to 7.5 years old were dominated by different species when compared with the, formerly more resilient, natural regeneration sites. Natural regeneration sites were dominated by *Vismia* species responsible for 58 and 45% of basal area in younger and older sites. After active restoration, sites with a stable *U. brizantha* cover, were dominated by *Senna alata*, *Cecropia* spp., *Solanum* spp, *Muntingia calabura* and *Trema michranta* in the first three years and then by *Cecropia purpurascens*. The dominance of *Cecropia* spp. makes actively restored sites more similar to highly resilient sites of Amazon forests than to the *Vismia*-dominated sites. In other parts of Amazonia, sites that have low resilience because they were subject to decades of exotic grasses cultivation and frequent fires to prevent forest recovery, tend to be dominated by *Vismia* spp. Sites that were subjected to milder use and thus have higher resilience tend to be dominated by *Cecropia* and to be more biodiverse (Jakovac et al. 2016; Mesquita et al. 2015).

The cause for the impoverished regenerating community at *Vismia* dominated sites is attributed to the degradation of soil quality, loss of sprouting ability of most species, and non-facilitative life-history traits of *Vismia* spp. (Jakovac et al. 2016; Williamson et al. 2012). In this project (see also Rezende and Vieira 2019), we were able to verify that preparing soil and eliminating *U. brizantha* cover triggered an early community dominated by *Cecropia*. Thus, our study adds that the exotic grass cover is a strong filter that affects compositional trajectory. Removing the grass cover is a low-cost intervention that allows for a healthier succession. However, further studies are needed to assess if the early community facilitated by the intervention advances in a similar way to the highly resilient *Cecropia*-dominated sites in Central Amazonia.

Active restoration sites were remarkably different from natural regeneration sites in respect to species composition. Natural regeneration sites were dominated by *Vismia* spp., species that maintain dense stem populations in heavily used pastures by resprouting (Mesquita et al. 2015). Self-thinning in *Vismia*-dominated secondary forests is slower than in more resilient forests, because *Vismia* species have a long life-cycle and because they maintain the recruitment of new individuals by sprouting (Norden et al. 2011). This resulted in less emergent trees and less species recruitment, compared to active restoration sites.

In active restoration sites, initial recruitment originated from seed rain of short life-cycle trees, such as *Solanum* spp. and *T. michranta*, and from the directly seeded *S. alata*. In high stem density sites, these species died after ca. 3 years, opening space for new recruitment. *Solanum* spp. is a genus of shrubs and small trees that colonize active pastures (Uhl et al. 1988) and, in our study, it colonized sites with prepared soil. *Solanum* spp. attract high densities of bats that bring *Cecropia* seeds to the site (Silveira et al. 2011). Consequently, *Cecropia* spp. emerged. This extremely fast compositional change promoted higher size-structure heterogeneity, increasing density of recruits and reducing intermediary size-classes. In addition, planted seedlings developed large trees (> 25.1 cm DBH) in active restoration sites.

## *Active restoration or Natural regeneration?*

This study contributes to the understanding of how restoration methods can shape early trajectories of forest recovery. Our study does not allow to recommend which one is more cost-effective, since active restoration was applied only at less-resilient sites and natural regeneration was applied at more-resilient sites. Given the low levels of funding for restoration, a simple recommendation would be to use natural regeneration where the natural regeneration potential is high enough to trigger and maintain a successional trajectory (Chazdon and Uriarte 2016; Holl and Aide 2011). However, different compositional trajectories (Jakovac et al. 2016; Mesquita et al. 2015; Uhl et al. 1988) and even more contrasting rates of structural development have been observed in natural regeneration (Heinrich et al. 2021), depending on the land use history. Variations are also observed in actively restored sites, due to different intervention methods (Gardon et al. 2020; Giudice Badari et al. 2020; Freitas et al. 2019; Shoo et al. 2015). Thus, a relevant question is if we can significantly improve secondary forests quality, for biodiversity and carbon increment, with cost-effective interventions. We suggest that simple and cheap interventions directed at improving the odds of natural regeneration can be effective for non-resilient sites located in resilient landscapes.

Passive restoration might not be an option in some regions in southern Amazonia. In the very state of Rondônia, there are municipalities with 15% of forest cover, and landscapes with less than 5% of forest cover if we consider landscape sizes of 25 km<sup>2</sup> (analyzed from Project MapBiomias Collection [4.1] [www.mapbiomas.org.br](http://www.mapbiomas.org.br)), which is landscape size in which forest cover affects restoration success worldwide (Crouzeilles and Curran 2016). Southern Amazonia has the largest area demanding for restoration in order to comply with Brazilian environmental laws (Rajão et al. 2020); sites will probably need active restoration or assisted natural regeneration.

## **Declarations**

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### **Ethics approval and consent to participate**

Not applicable

### **Consent for publication**

Not applicable

### **Availability of data and materials**

The datasets generated and/or analysed during the current study are available in the ForestPlot repository, <https://www.forestplots.net>

### **Competing interests**

The authors declare that they have no competing interests.

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### **Authors' contributions**

DLMV conceptualized the research. GPER, GR and AB collected the data. SBR, DLMV and CCJ analyzed the data, interpreted the results and contributed to writing. All authors read and approved the final manuscript.

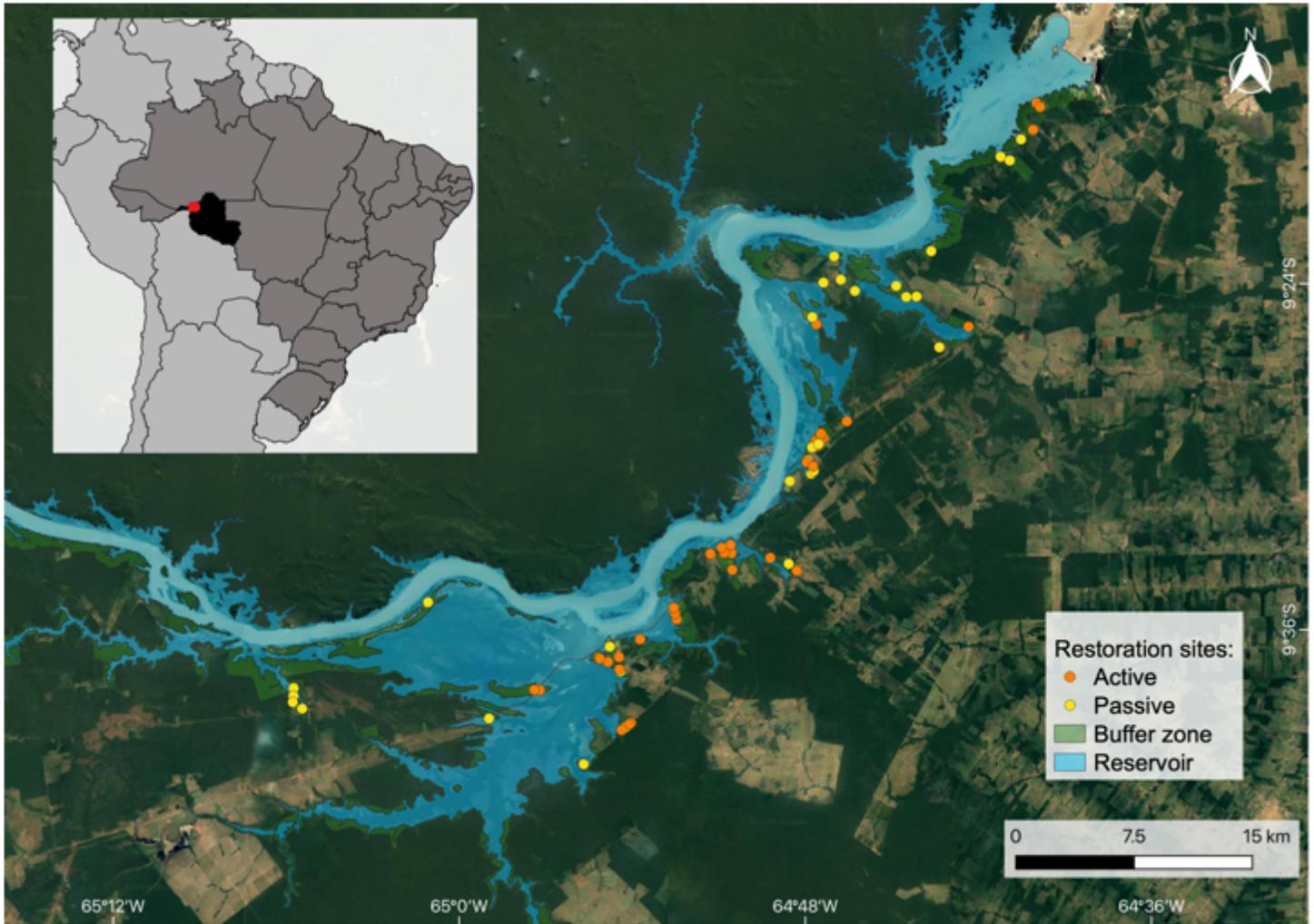
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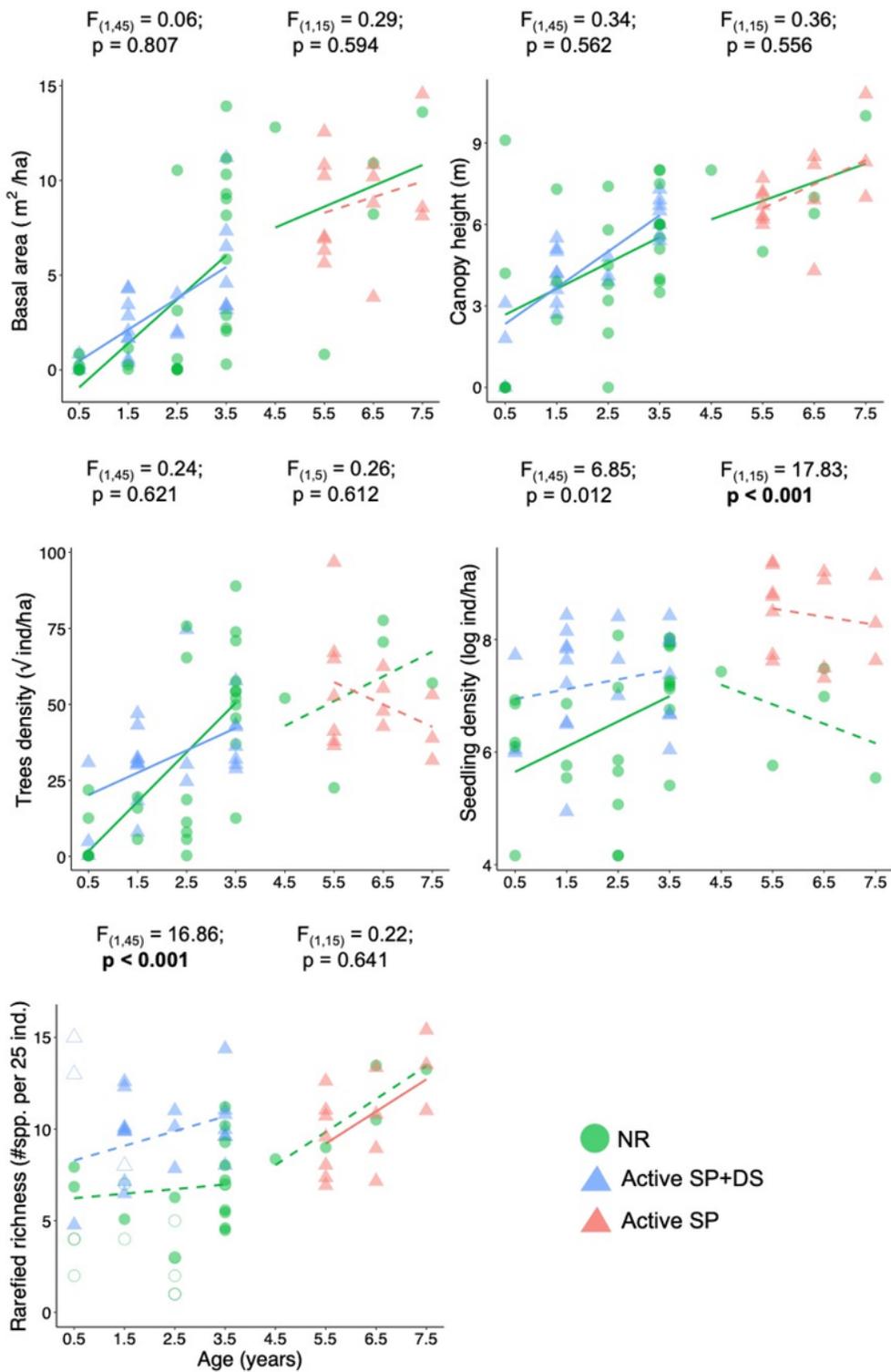
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## Figures



**Figure 1**

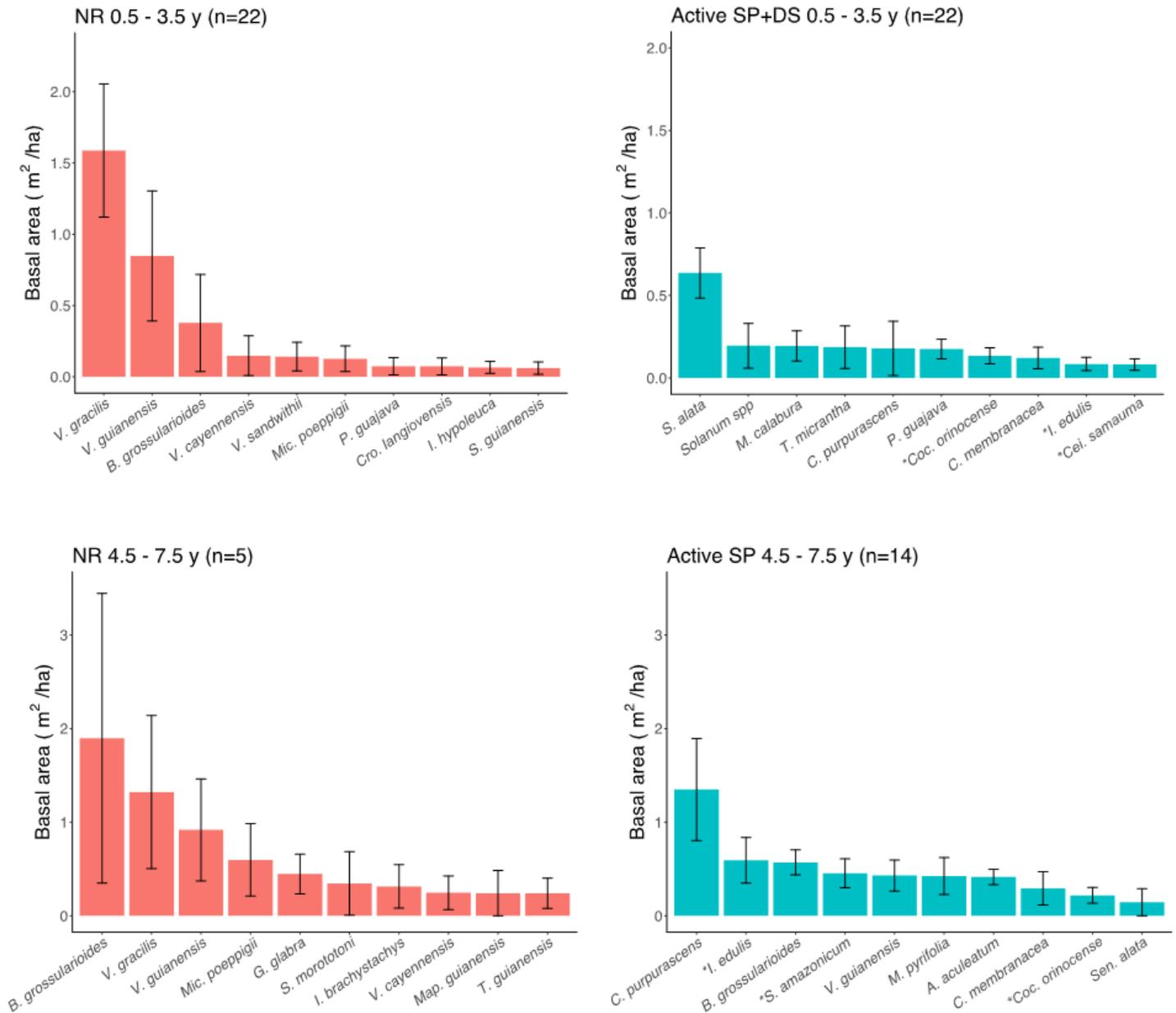
Active restoration and natural regeneration sites sampled in the buffer zone of the Jirau hydroelectric reservoir along the upper Madeira river, Rondônia State (Brazil). Note: The designations employed and the presentation of the material on this map do not imply the expression of any opinion whatsoever on the part of Research Square concerning the legal status of any country, territory, city or area or of its authorities, or concerning the delimitation of its frontiers or boundaries. This map has been provided by the authors.



**Figure 2**

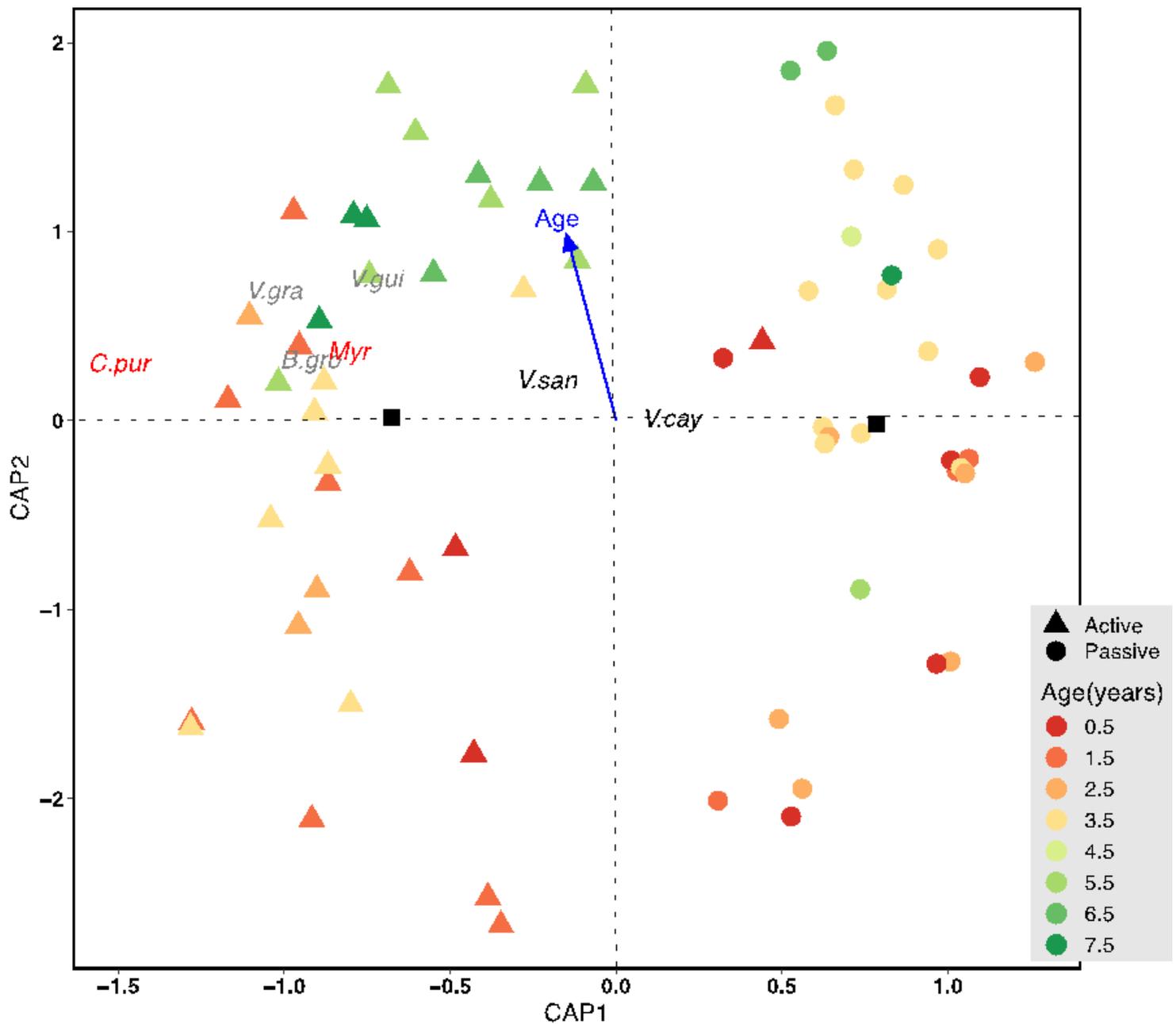
Forest structure attributes of vegetation community in active restoration and natural regeneration sites, located south of Jirau Hydroelectric Reservoir, along the upper Madeira River. Dots and triangles represent sampled sites. Regression lines describe the trajectories of the attribute over time divided in two blocks: 0.5 to 3.5 y-old sites, where Active Restoration included seedling planting and direct seeding of pioneer species (AR SP+DS) and 4.5 to 7.5 y-old sites, where it included only seedling plantings (Active SP). In the

rarefied richness plot, non-filled shapes represent sites with less than 25 individuals sampled and absolute richness values were used in the plot, but not considered for the regression fit.



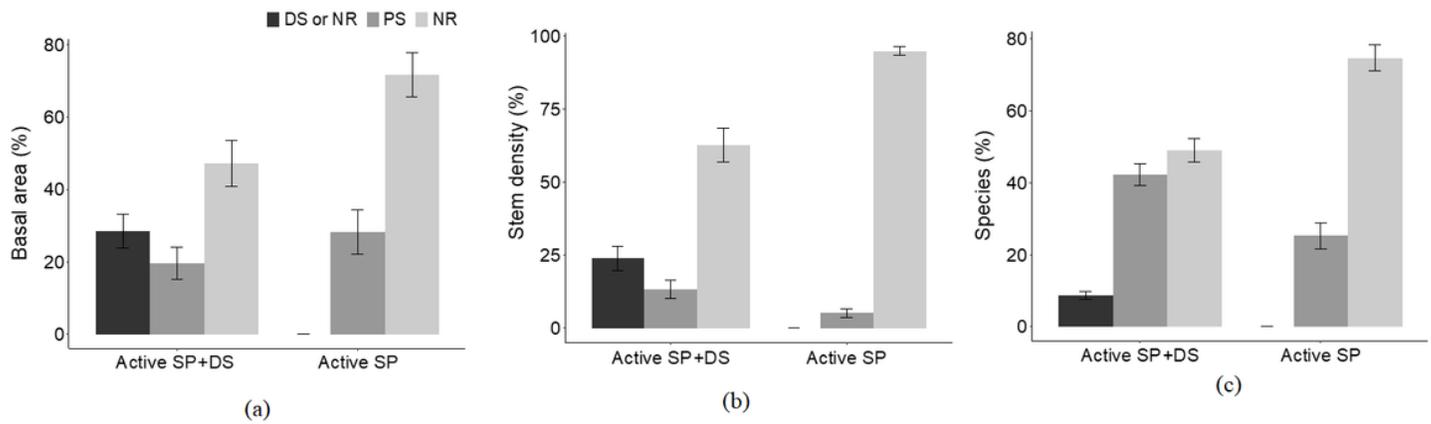
**Figure 3**

Basal area (mean  $\pm$  standard error) of the ten most dominant species sampled in sites of natural regeneration (31) and active restoration (36) located in the south of Jirau Hydroelectric Reservoir, along the upper Madeira River. For 0.5 to 3.5 y-old sites, Active Restoration included seedling planting and direct seeding of pioneer species (AR SP+DS) and for 4.5 to 7.5 y-old sites, it included only seedling plantings (Active SP). Species with the asterisk (\*) were planted as seedlings in active restoration sites.



**Figure 4**

Biplot of the db-RDA of the species composition in 36 active restoration sites (triangle) and 31 natural regeneration sites (circles) located south of Jirau Hydroelectric Reservoir along the upper Madeira River. Black squares represent the centroids of the restoration methods. Abbreviations are the names of the most abundant species sampled in active sites (in red), passive sites (in black), and both methods sites (three grey names), B.gro: *Bellucia grossularioides*; C.pur: *Cecropia purpurascens*; Myr: *Myrcia* sp.; V.cay: *Vismia cayennensis*; V.gra: *Vismia gracilis*; V.gui: *Vismia guianensis*; V.san: *Vismia sandwithii*.



**Figure 5**

Contribution (mean percentage  $\pm$  standard error) of planted seedlings (PS), direct seeding or natural regeneration (DS or NR), and natural regeneration (NR) to the (a) basal area, (b) stem density, and (c) species richness of active restoration sites. For 0.5 to 3.5 y-old sites, Active Restoration included seedling planting and direct seeding of pioneer species (AR SP+DS) and for 4.5 to 7.5 y-old sites, it included only seedling plantings (Active SP). A total of 36 active restoration sites were sampled in the south of Jirau Hydroelectric Reservoir along the upper Madeira River.

## Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- [AppendixA.docx](#)