



Forest restoration of Amazonian mine lands: Identifying factors driving tree recruitment

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Abstract

Increasing deforestation in the Amazon and its potential impacts on ecosystem services make restoration necessary for the survival of this important Neotropical biome. Although mining accounts for only 9% of Amazonian deforestation, the damage it causes to the ecosystem is one of the most intensive. However, few studies focus on forest restoration on mined sites and most of them study sites less than 10 years old. Furthermore, one of the major challenges to ensure the long-term success of forest restoration is to re-establish forest dynamics (including tree recruitment). This thesis focuses on closing the knowledge gap about tree recruitment by assessing its ecological and management drivers in a 27-year-old chrono-sequence of surface mining sites in the Brazilian Amazon undergoing restoration. To achieve this, 86 monitoring plots were assessed in 6 mines in Southern Amazon, Rondônia state, Brazil, during the dry season of 2019. Linear mixed models were developed in R to analyse the effects of different management and ecological factors on recruit species richness, species composition and density. Ecological factors included successional age, canopy closure, litter depth, soil properties and amount of surrounding forest area. Management factors comprised mine zones and planted species richness, species composition and density. The results show that seed availability from planted trees and surrounding forests influenced recruit species richness, species composition and density. Light availability influenced recruit species richness and density, but it had no effect on species composition probably because all dominant species have similar light requirements. Mine zones and their associated soil properties influenced recruit species richness, species composition and density. This study evidences the complex processes involved in tree recruitment after tree planting, which is crucial for the long-term success of forest restoration efforts. It also provides suggestions about the importance of acknowledging seed availability. Finally, it expands the understanding of the roles of light and soil in establishment to inform management decisions in order to increase recruit species richness and density and avoid arrested succession pathways.

1. Introduction

The Amazon is the largest rainforest in the world. It holds a high biodiversity and provides ecosystem services (e.g., water supply, carbon sequestration and climate regulation) not only at a local but also at a worldwide scale. Unfortunately, this forest and its biodiversity are threatened by the combined effects of climate change and deforestation (Brockerhoff et al., 2017; Gomes et al., 2019). A reversal in protection policy has contributed to increased deforestation rates and provoked fires in Brazil (which possesses around 60% of the Amazon) since 2012 (Amaral et al., 2019; Carvalho et al., 2019; Pereira et al., 2019). This may not only risk taking this crucial biome to a point of no return, but could also disrupt its rainfall generation potential, alter the hydrological cycle of most of South America and intensify the effects of climate change worldwide (Amaral et al., 2019; Lovejoy & Nobre, 2019; Staal et al., 2020). Unfortunately, many industries in Brazil, such as agroindustry and mining, require forest clearance, which promotes the continuation of these deforestation practices.

Although mining only accounts for 9% of Amazonian deforestation, it has one of the most intensive land-uses in the area (Sonter et al., 2017; Tyukavina et al., 2017). Due to Brazilian environmental legislation, restoration measures are required to offset environmental impacts after mining operations (Cappellari, 2018; Gastauer et al., 2019). Surface mining, a type of mining that involves the removal of soil and rock, is the most widespread class of mining in forested areas. This type of mining poses several challenges for restoration that can be summarized in the recovery of the adequate conditions for vegetation establishment and succession (Macdonald et al., 2015). However, research on forest restoration in mined sites is scarce worldwide, with only 10% of restoration studies focusing on these areas (Guerra et al., 2020; Martins et al., 2020).

One of the major challenges to ensure the long-term success of forest restoration, and the associated recovery of species richness, composition, and tree density, is to re-establish forest dynamics (e.g., plant growth, survival and tree recruitment). However, most research on forest restoration on mined sites aim to evaluate current

ecosystem functioning and structure in restoration sites under 10 years old (Martins et al., 2020). Considering this, the following thesis is focused on closing the knowledge gap about tree recruitment by assessing its ecological and management drivers in a 27-year-old chrono-sequence of surface mining sites in the Brazilian Amazon undergoing restoration.

Tree recruitment depends on seed availability and the presence of sites with the adequate conditions for the germination and establishment of the seeds available (Clark et al., 1999; Muller-Landau et al., 2002). For this research, I will assess the recruitment of planted species and colonizing species from surrounding forests in reforested areas. Taking this into account, recruitment success can be summarised as the consequence of drivers and processes that allow seeds from planted trees and surrounding forests to establish as saplings (Figure 1).

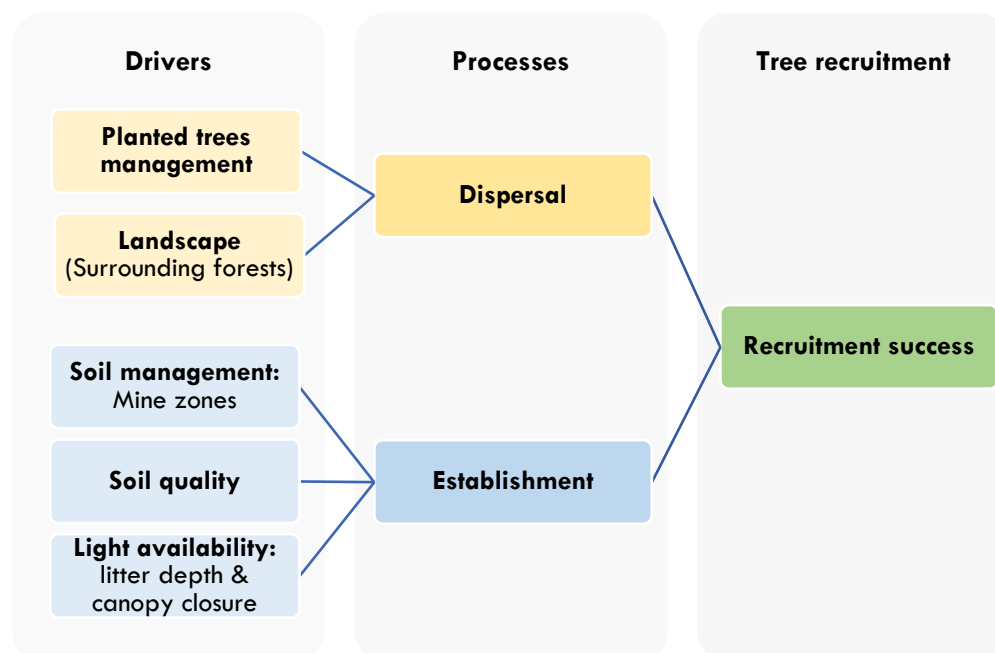


Figure 1. Drivers and processes determining tree recruitment in restoration projects.

Note: Drivers of establishment were simplified to focus on resources assessed by this thesis.

Seed availability depends on their production by mature trees and dispersal to available sites. The amount of seeds produced by tree communities in both planted trees and neighbour forests influenced their availability. However, the amount of seed at available sites depend on their dispersal strategies and the distance from the source trees (Clark et al., 1999; Dalling et al., 2002; Muller-Landau et al., 2002).

Once seeds have been successfully dispersed to an available site, recruitment success will depend on having adequate conditions to establish (Muller-Landau et al., 2002). This study is focused on environmental factors that influence establishment. Considering that all the plots were assessed on the same national park, similar precipitation and water availability conditions can be expected across the plots. Therefore, this study assessed resources with known variability in the area: soil properties and light availability.

Previous research has shown that soil properties such as texture and physicochemical properties favour different species compositions. Soils with higher clay concentration benefit species adapted to fertile and moist conditions, while sandy soils benefit species adapted to drier and more unfertile conditions. Additionally, the land reclamation techniques employed in different mine zones and their effect on the terrain and soil properties interacted with the planted species composition to affect recruited species composition (König, 2018).

Planted species appear to affect performance by influencing two factors related with light availability: canopy shading and leaf litter cover (Dupuy & Chazdon, 2008; Peña-Claros, 2003). The effect of canopy shading varies largely across the stages of succession. Its absence promotes pioneer species that require high light conditions at the beginning of this process, while its later increase starts a process in which shade-tolerant species are progressively favoured (Peña-Claros, 2003). The effect of leaf litter cover was shown in an experiment performed in bauxite tailing substrates in Amazonian flood-prone forests, promoting seedling establishment, especially for nitrogen fixing species, which thrive in this nutrient-poor environment (Dias et al., 2012). Furthermore, another study in lowland forest succession in Costa Rica reported that leaf litter cover and canopy cover benefit the recruitment of shade-tolerant species, while the opposite conditions foster light-demanding saplings (Dupuy & Chazdon, 2008).

The present study seeks to close the knowledge gap of the effect of management and ecological factors on recruitment success during forest restoration. This is crucial to guarantee the long-term success of restoration efforts in tropical rainforests. To investigate this, the following research questions and hypotheses are proposed:

- 1) How do management and ecological factors interact to determine recruit species richness?
I expect recruit species richness to be positively influenced by the amount of surrounding forest, light availability in the understory and soil quality.
- 2) How do management and ecological factors interact to determine recruit species composition?
I expect that planted tree density, light availability and soil quality will promote different species compositions.
- 3) How do management and ecological factors interact to determine recruit density?
I expect recruit density to be positively influenced by planted tree density and negatively influenced by canopy cover and litter depth.

Conceptual models per hypothesis are included in Appendix 1. These models explain the expected relations between the variables considered in this study.

2. Materials and methods

2.1 Study site conditions

This study was performed in the Jamari National Forest in the municipality of Itapuã do Oeste, Rondônia state, Brazil. This national forest covers 215 000 hectares within the Amazon rainforest and allows economic activities like mining and logging. Data was obtained from 86 plots in 6 deactivated cassiterite mines, a mineral used for tin production (Figure 2 and Table 1). The mine land, which comprises those deactivated mines and a remaining operating mine, constitutes 10% of the forest reserve area. The other 90% is covered by open tropical forest with small patches of tropical rainforest. The tropical wet and dry climate (Aw on the Köppen scale) is separated into a dry season from July to August, and a wet season from December to March. The annual mean temperature is 22°C. The annual rainfall ranges from 1750 to 2750mm. Oxisols (soils rich in iron and aluminium oxides), ultisols (red clay soils), and hydromorphic soil types dominate the Jamari National Forest (Ribeiro et al., 2016).

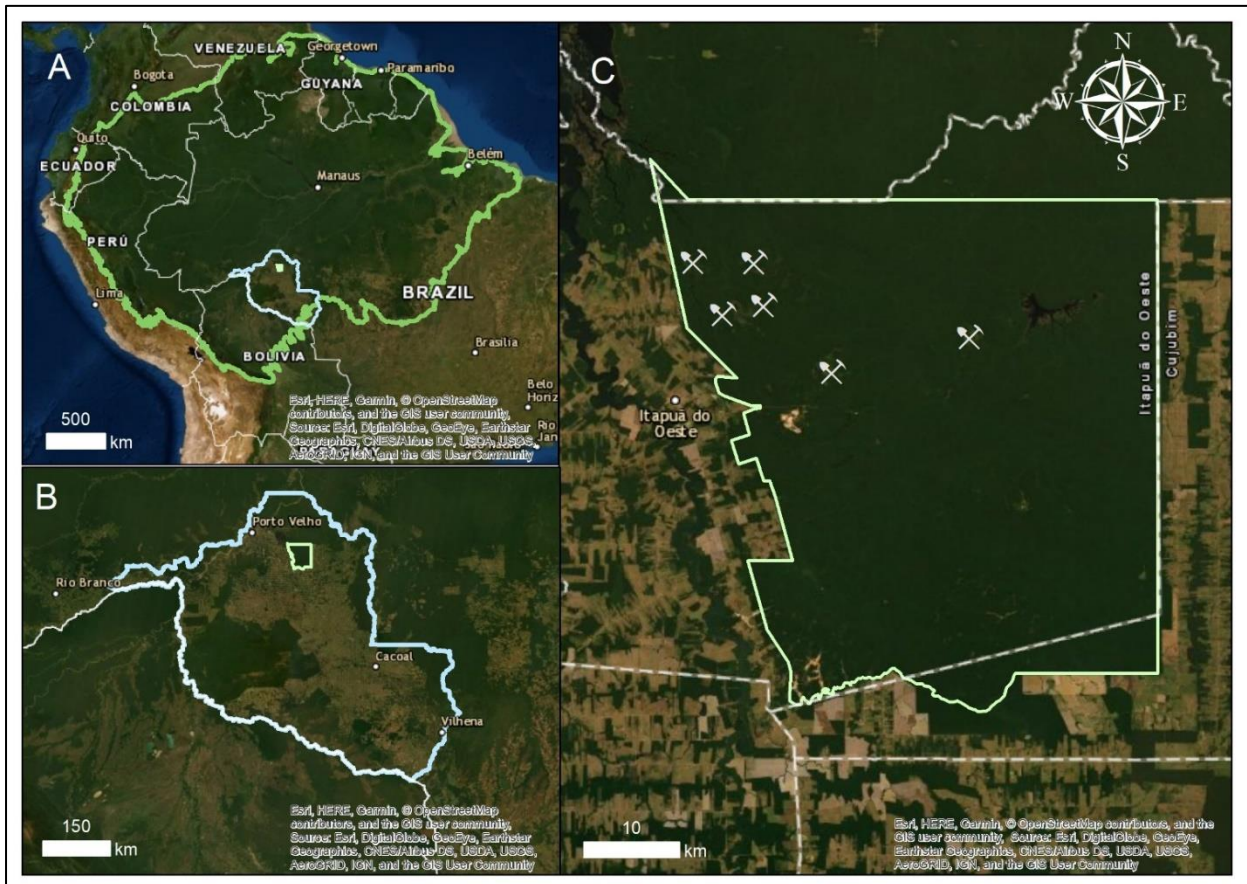


Figure 2. A. Location of the mines and the state of Rondonia within the Amazonian rainforest. B. Location of the mines within the state of Rondonia. C. Deactivated cassiterite mines included in this study.

Initial site conditions

Mining in the lowlands is performed through two different techniques: pit mining and washing plant, both applied in the area. The restoration areas were separated into 5 zones according to their location within mines and the use these areas had during the mining process in the past. Pit mining areas were distributed in 4 restoration zones: mining floor and dry, wet and capped tailings. The washing plant technique area was converted into a washing plant tailings zone. A description of each of these mine areas is presented in the following subsections (Table 1).

Mining floor

Areas surrounding the mining pits where heavy machinery was used. These areas have a high soil compaction.

Mine tailings

Tailing dams containing sterile soils from filling and removals obtained from the mining operation. They are exposed to slope to allow water drainage. The slope and long-term weather exposure create a soil gradient with a higher sand content at the top and clay content at the bottom. Consequently, this slope can be divided among two different mine zones: dry and wet.

Dry tailings

Upper dam zones are called dry tailings, as they present high sand content and a low water retention capacity and a loose soil structure.

Wet tailings

Lower dam zones are called wet tailings, as they become waterlogged due to high clay content and its lower position.

Capped tailings

Some of the wet tailings and fewer dry tailings were covered with topsoil after the mines' closure and therefore classified as capped tailings. This topsoil was obtained from recent forest clearing elsewhere, and contained organic matter, soil biota, and seeds.

Washing plant

This zone originated from washing plant mining technique. The soil excavation, mineral extraction and soil restitution was done by a single machine in one step, where the thin layer of mined soil was returned to the same site and no mining pit or tailings were formed. In contrast with the other zones, the conditions of the mined soil are closer to the original soil structure and properties, as there was no separation of soil particles.

Table 1. Overview of mines regarding the number of areas and plots per mine zone

Mines	Number of areas	Number of plots per mine zone					Total plots
		Mining floor	Capped tailings	Dry tailings	Wet tailings	Washing plant	
Mine 1	11	6	12	4	2		24
Mine 2	1					5	5
Mine 3	7			11			11
Mine 4	6	3	2	2			7
Mine 5	3					12	12
Mine 6	9	6	8	5	8		27
Total	37	15	22	22	10	17	86

2.2 Restoration measures

This section includes the restoration measures undertaken on these mining sites. This process was performed in two steps: restoring the soil fertility required for an adequate plant growth and reforestation activities to ensure tree cover recovery.

Soil fertilization

The soil was limed and fertilized with green manure (leguminous species) and cow manure during three years before tree planting. After this treatment, soil analyses were performed, and 9 restoration areas were selected for top-soil transplantation. Each tree was chemically fertilized when planted and then annually during the next 5 years.

Reforestation

After soil fertility restoration, saplings obtained from seed trees, inside and outside the national forest, were planted in all restoration areas. The reforestation process started in 1991 has been continuously maintained until present day. An average of 1700 individuals (selected out of a pool of 91 tree species) have been planted per hectare.

The most abundantly planted tree species were *Syzigium cumini*, an exotic species from India, and *Inga thibaudiana*, a native legume tree. Both species were prioritized at the beginning of the reforestation process because of their drought resistance and ability to fix nitrogen. Nevertheless, *S.cumini* trees have been recently ring-barked because of the government's policy of avoiding exotic species on reforestation.

2.3 Data collection

Data collection was performed on 86 plots during the dry season (June to October) of 2019. These plots are part of the reforestation monitoring performed annually since 2009. This survey spans 67 reforestation areas located in 8 deactivated mines. I selected 86 plots within 37 of these areas in 6 of those mines (Table 1). The plot sizes were 50 x 50 meters, containing 6 subplots for measuring different tree sizes (Table 2). Data on tree density and species richness and composition was registered by trained personnel. Trees were included in subplots if they met the corresponding inclusion criteria (Table 2). All trees were identified to the genus or species level by para-taxonomists. The origin of each tree was established to distinguish between trees originating from natural regeneration or from plantings.

Table 2. Subplot design including the size and subplot inclusion criteria (DBH and tree height)

Subplot	Size (m)	DBH (cm)	Height (m)	Measured variables
1	2x10	< 10	0.3 to 1.3	species, height
2	5x10	< 10	1.3 to 3.0	species, height
3	10x10	< 10	> 3.0	species, height
4	10x50	10 to 30		species, DBH, estimated height
5	20x50	30 to 50		species, DBH, estimated height
6	50x50	> 50		species, DBH, estimated height

Response variables (Recruitment success)

Recruits were defined as woody plants with a DBH under 10 cm and height between 30 and 300 cm. Recruit density, species richness and species composition were registered in subplots 1 and 2 (Table 2) for the 86 plots included in Table 1.

Explanatory management variables

Mine zones, related to the initial site conditions and the land reclamation techniques, were associated to all plots as a categorical variable including “mining floor”, “dry tailings”, “wet tailings”, “capped tailings” and “washing plant”. A detailed overview of the areas and their mine zones, size, age, and number of plots is provided in Appendix 2.

Additionally, the variables planted species richness, planted species composition and planted tree density in each reforested area includes only mature planted trees with a DBH above 10 cm (subplots 4, 5 and 6), because this previous observations in the area suggested that trees of this size are frequently reproductive, making them potential seed sources for the recruits.

Explanatory ecological variables

Successional age

The successional age was considered as the number of years since the first trees were planted in each plot until 2019.

Canopy closure

To assess canopy closure, a spherical densitometer was employed. Measurements were taken every 2m along the central line of subplot 1 (Figure 3). The final canopy closure value for each plot was based on the average of measurements (Jakovac et al., 2015).

Litter depth

Litter depth was measured from the top of the litter layer until the top of the soil layer using a ruler. A measurement was registered every meter along a transect at the middle of each subplot 1, following its length (10 m), totalizing 11 measurements in each subplot (Figure 3).

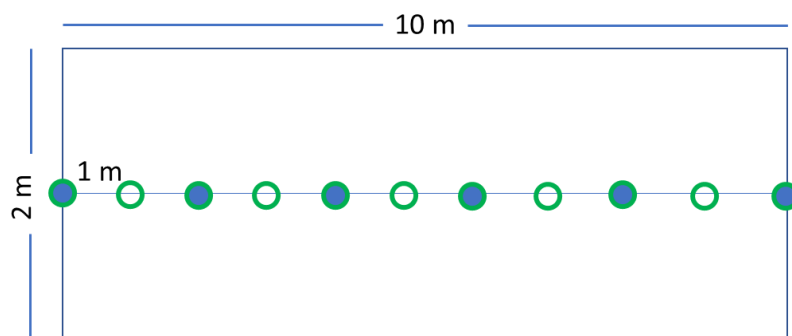


Figure 3. Canopy closure and litter depth measurement points along the centre of subplot 1. Note: Blue dots: canopy closure measurements. Green circles: litter depth measurements.

Soil properties

Data on soil properties included soil texture (soil particle fractions of sand and clay content) and soil chemical properties, which were comprised by organic matter, pH, aluminium and macro-nutrients: calcium, magnesium, potassium, phosphorus and sulphate. Data collected in 2011 was used because other evaluations missed some of the areas.

Surrounding forest area

The amount of area of surrounding forests within a radius of 500 m of each reforestation plot was measured using high resolution satellite images and detailed land use maps in ArcGIS. The radius of 500 m was chosen as it was assessed to be the most representative for this zone (König, 2018). This data was separated into two different variables for the analysis: area of secondary forests (SF) within 500 m and area of old-growth forests (OGF) within 500 m.

Additional data from a previous survey performed on surrounding secondary and old-growth forest on 2018 was used as a reference, but not included in the statistical analysis.

2.4 Statistical analysis

Tree density data (for recruits and planted trees) acquired in the subplots was standardized to one hectare. Species composition was based on the extrapolated data and was ordinated using a principal coordinates analysis (PCoA, Bray-Curtis ordination) in Canoco 5. The resulting scores from axis 1 and 2 were used as explanatory variables in further analysis.

Soil properties were ordinated using principal component analysis (PCA) in Canoco 5. The first two components were used as explanatory soil variables in further analyses. Sand and clay content are given in percentages, so an arcsine transformation was performed before including them in the PCA.

Before performing the analyses, all continuous variables were transformed to ensure normality and standardized to make their scales comparable. The direction and effect size of the explanatory variables was assessed through a series of linear mixed effects models (LMM) for each response variable. The study design's nestedness was accounted for by defining mines as random factors. Variables included in each of the models are listed in Table 3. Models were selected through the backward stepwise removal of the least significant explanatory factors. The resulting models were fitted using the restricted maximum likelihood method (REML) (Zuur et al., 2009). LMMs were performed in R 3.6.1 (R Core Team, 2019) using package nlme. Additionally, the conditional and marginal coefficients of explanation of the models was obtained using package MuMIn and graphs were elaborated using package ggplot2 in R.

Table 3. Input variables for each linear mixed-effects model (LMM)

Variable	Type	Factor	Recruit species richness	Recruit species composition	Recruit density
Mines	Categorical	Random	X	X	X
Mine zones (land reclamation techniques)	Categorical	Fixed	X	X	X
Planted tree density	Continuous	Fixed	X	X	X
Planted species richness	Continuous	Fixed	X		
Planted species composition	Continuous	Fixed	X	X	
Successional age	Continuous	Fixed	X	X	X
Canopy closure	Continuous	Fixed	X	X	X
Litter depth	Continuous	Fixed	X	X	X
Soil properties	Continuous	Fixed	X	X	X
Surrounding forest area within 500m	Continuous	Fixed	X	X	

3. Results

3.1 Soil characteristics

The first axis of the PCA performed on soil properties (soil 1) has a high positive correlation with cations (Mg^{2+} and Ca^{2+}) and sand content, therefore it will be referred as “cation and sand content” axis (Figure 4). This axis also had a high negative correlation with clay, sulphur and aluminium. The second axis (soil 2) showed a high positive correlation with pH values and clay content, while a high negative relation with phosphorus content. This axis will be referred as “pH and clay content” axis. It is relevant to mention that although this axis was influenced by higher pH values, all the soil values registered in this study were below 7. Values of soil properties are summarized in boxplots in Appendix 4.

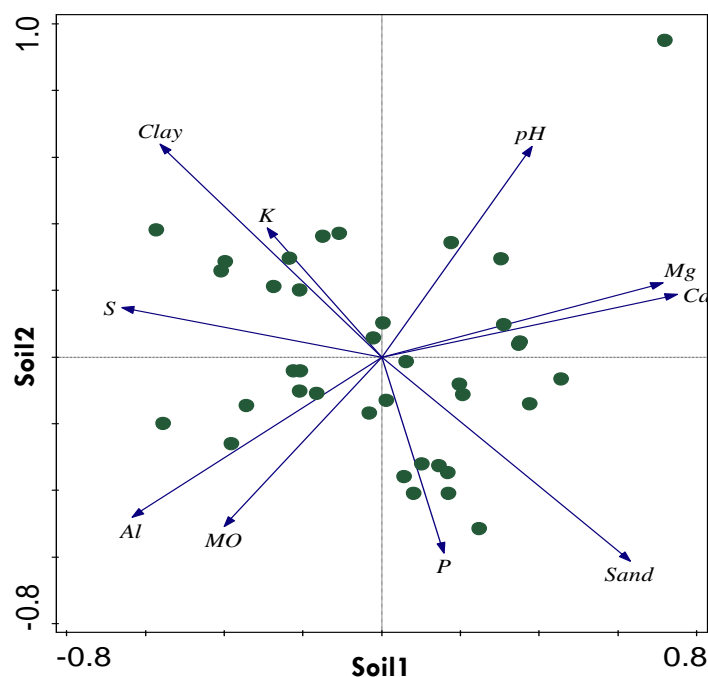


Figure 4. PCA-biplot of samples (dark green dots) and soil variables (blue arrows). Variation explained by the first two axis: Soil 1 (30,5%), Soil 2 (22,8%).

3.2 Planted and recruit species composition

The first axis of the PCoA performed on planted trees' species density data (planted PCoA 1) was positively correlated to planted tree communities dominated by *Syzigium cumini* (exotic species) (Figure 5). The second axis (planted PCoA 2) was explained by planted tree communities dominated by both *Inga laurina* (native species) and *S. cumini*.

Higher values on the first axis of the PCoA performed on recruit species density data (recruit PCoA 1) were related to increasing dominance by *Psidium guianensis* and decreasing dominance by *Myrcia splendens*. Neither species were found in the surrounding forests, but both were planted during reforestation. For the second axis (recruit PCoA 2), higher values were correlated to increasing dominance of *Siparuna guianensis* and *Vismia guianensis* in recruit communities (both species were found in surrounding forests) and decreasing dominance by *Toulicia guianensis* (not found in surrounding forests but was planted during restoration).

Table 4. Descriptive statistics of response and explanatory variables (n=86). Mean, standard deviation (SD), minimum (Min) and maximum (Max) values are shown. Boxplots on response variables are provided in Appendix 5 and on explanatory variables in Appendix 6.

	Mean	SD	Min	Max
Response variables				
Recruit species richness	12,28	8,67	1	36
Recruit PCoA1	0,00	1,01	-1,95	2,09
Recruit PCoA2	0,00	1,01	-1,49	2,76
Recruit density (recruits/ha)	15484	14779	500	69600
Explanatory variables (Ecological)				
Successional age (years)	16,14	5,45	7	27
Canopy closure (%)	79,54	10,54	7,61	93,59
Litter depth (cm)	3,16	0,84	1,36	6,20
Soil 1 (PCA axis 1 of soil properties)	-0,10	0,97	-1,95	2,45
Soil 2 (PCA axis 2 of soil properties)	0,21	0,86	-1,76	3,24
Area of secondary forest within 500m radius (%) ¹	27,59	11,15	7,75	52,28
	35,14	14,19	9,86	66,57
Area of old-growth forest within 500m radius (%) ¹	12,46	12,38	0,00	44,03
	15,86	15,76	0,00	56,06
Explanatory variables (Management)				
Planted trees' species richness	6,97	3,42	1	15
Planted PCoA1	0,00	0,24	-0,49	0,42
Planted PCoA2	0,00	0,21	-0,34	0,43
Planted trees' density (trees/ha)	361,20	175,18	40	950
Mine zones	cat. ²			

Notes: (1) Percentages estimated out of the total area of a 500 m radius (78,54 ha) 500m from each reforestation plot.

(2) Categorical variable with 5 mine zone categories.

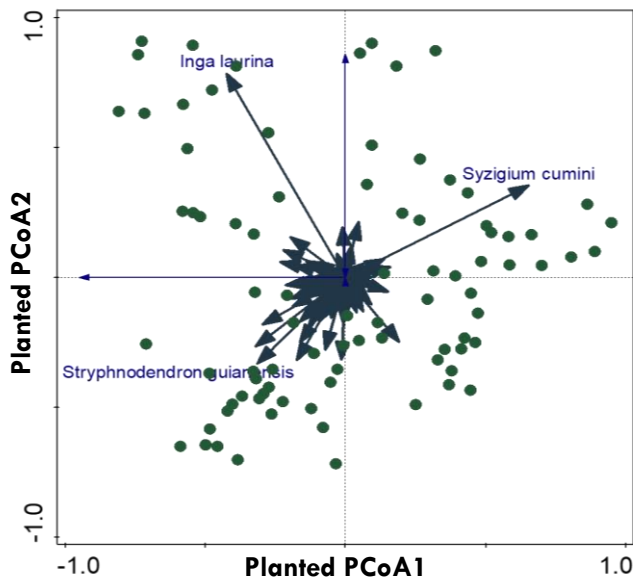


Figure 5. PCoA-biplot of planted trees: plots (dark green dots) and species (blue arrows). Variation explained by the first axis (14,7%) and second axis (12,1%).

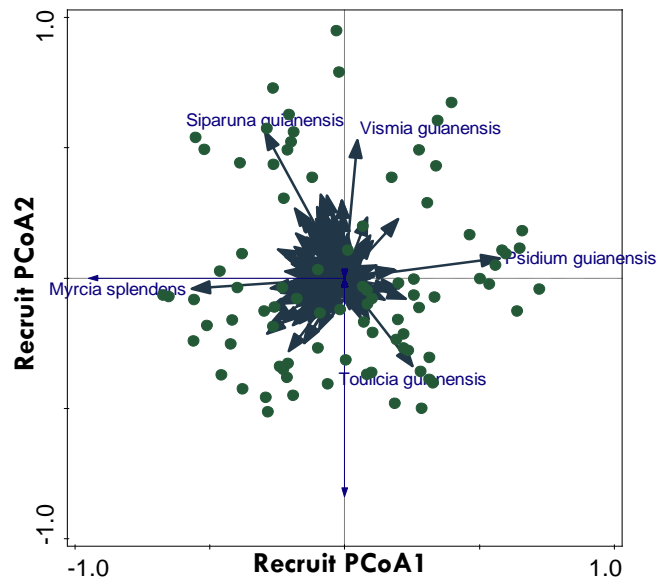


Figure 6. PCoA biplot of recruited species: plots (dark green dots) and species (blue arrows). Variation explained by the first axis (9,7%) and second axis (7,6%).

3.3 Drivers of recruit species richness

The species richness of recruits was positively influenced by successional age ($t=2,77$; $p<0,01$) and canopy closure ($t=3,77$; $p<0,01$). The interaction of Planted PCoA2 with canopy closure showed a positive effect under higher values of in communities of planted trees dominated by *Inga laurina* and *Syzigium cumini* ($t=3,66$; $p<0,01$). Planted PCoA2 also interacted with mine zones, with a significant negative effect for its interaction with dry tailings ($t=-3,63$; $p<0,01$). OGF area interacted with mine zones, with positive significant effects for its interactions with washing plant ($t=2,37$; $p=0,02$) and dry tailings ($t=2,16$; $p=0,03$). Finally, planted tree richness had a positive interaction with soil2 (pH and clay content axis) ($t=4,01$; $p<0,01$).

Both marginal and conditional r^2 were 0,503 which implies that the fixed factors explained half of the data's variance, while the random factor (mines) had no influence on this model. Full model and the interactions' plots can be found in Appendices 7 and 8, respectively.

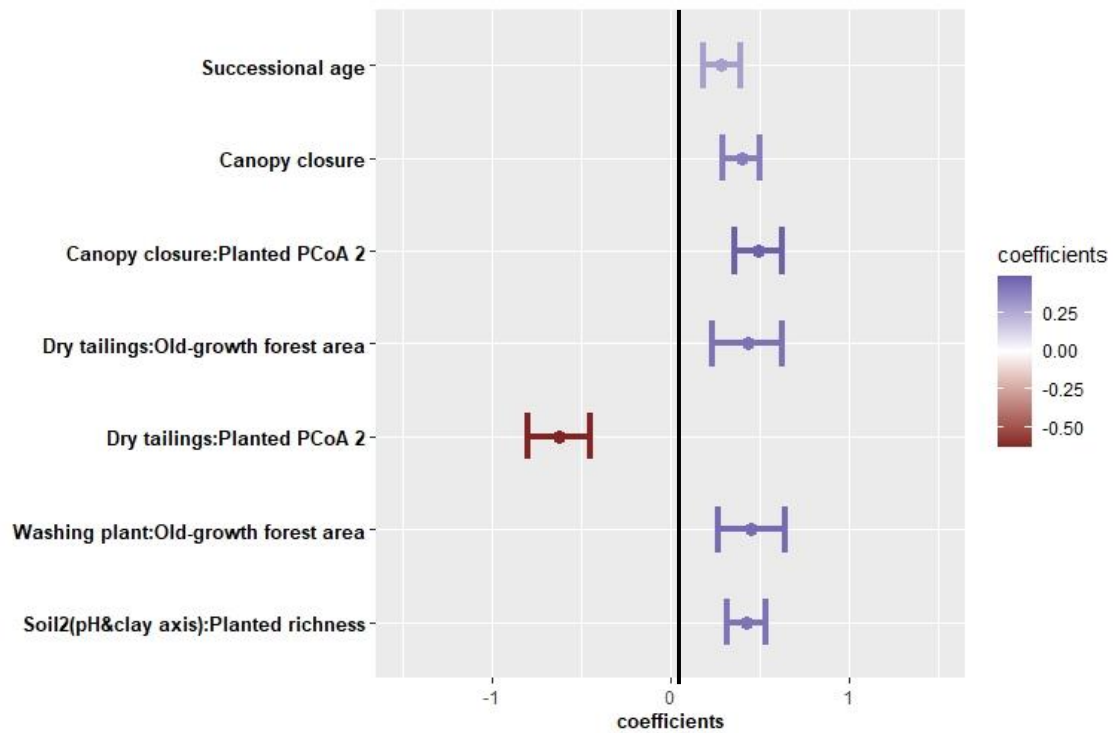


Figure 7. Significant results of linear mixed model of recruit species richness.

3.4 Drivers of recruit species composition

Two variables had a positive effect on recruit PCoA 1, implying they promoted *Psidium guianensis* dominated recruit communities: wet tailings ($t=2,27$; $p=0,03$) and soil 1 (cation and sand content axis) ($t=6,74$; $p<0,01$). Additionally, several variables had a negative effect on recruits PCoA 1, promoting recruit communities dominated by *Myrcia splendens*. These variables were successional age ($t=-2,62$; $p=0,01$), planted trees' density ($t=-3,11$; $p<0,01$), mining floor ($t=-3,84$; $p<0,01$), SF area ($t=-3,41$; $p<0,01$), old-growth forest area ($t=-3,93$; $p<0,01$) and the interaction of planted trees' density and soil2 (pH and clay content axis) ($t=-2,24$; $p=0,03$), and mining floor and planted PCoA2 (planted trees communities dominated by *Inga laurina* and *Syzigium cumini*) ($t=-3,04$; $p<0,01$). Full model and the interactions' plots can be found in Appendices 7 and 8, respectively.

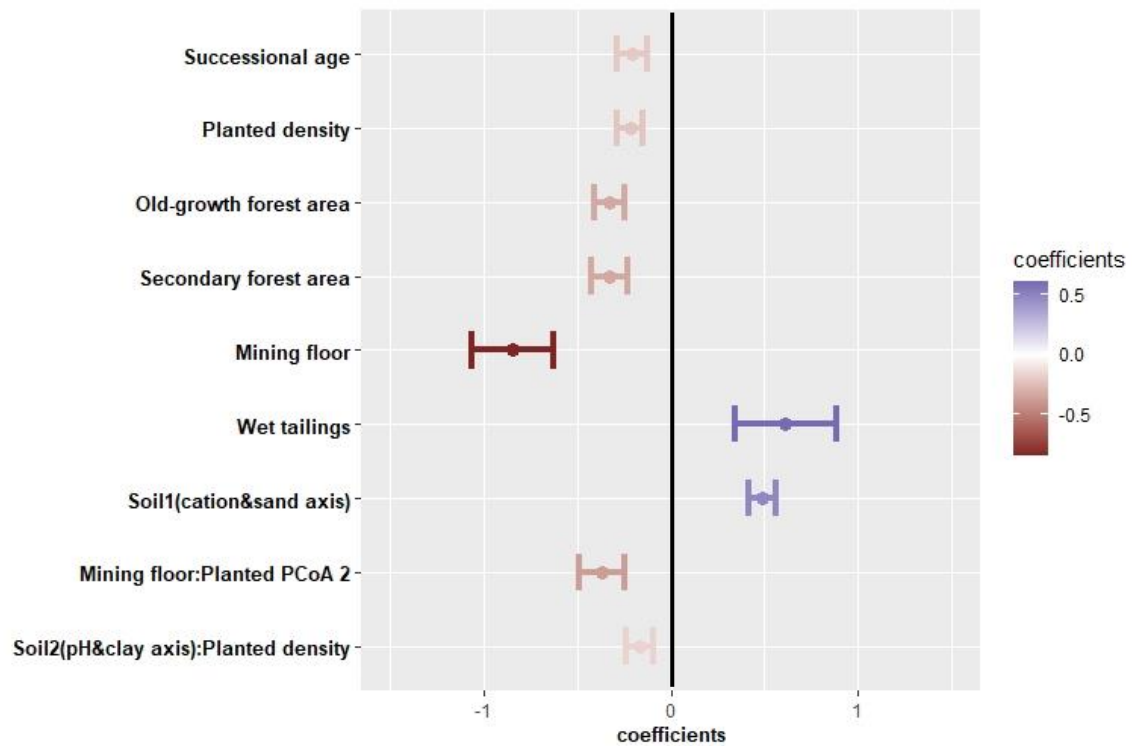


Figure 8. Significant results of linear mixed model of recruit PCoA 1. Positive effects promote recruit communities dominated by *Psidium guianensis*, while negative effects promote *Myrcia splendens* dominated recruit communities. Marginal $r^2=0.756$ and conditional $r^2=0.776$.

Soil 1 (cation and sand content) ($t=-2.27$; $p=0.03$) and SF area ($t=-1.99$; $p=0.05$) had negative effects on recruits PCoA 2, which implies they promoted recruit communities dominated by *Toulicia guianensis* (which has not been found in surrounding forests but was included among planted species). However, their interaction ($t=2.17$; $p=0.03$) had a positive effect on recruits PCoA 2, promoting the dominance of *Siparuna guianensis* and *Vismia guianensis* (both secondary forest species that were not among the pool of planted species) among recruits. This suggests that in places with higher amounts of surrounding secondary forests, *S.guianensis* and *V.guianensis* outcompete *T.guianensis*. Full model and the interaction plot can be found in Appendices 7 and 8, respectively.

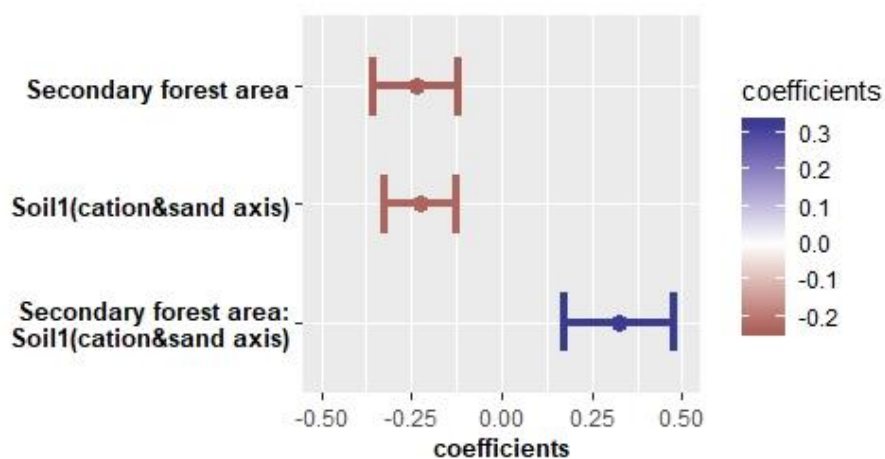


Figure 9. Significant results of linear mixed model of recruit PCoA 2 (*Siparuna guianensis* and *Vismia guianensis* dominated recruit communities).

3.5 Drivers of recruit density

Several variables had significant effects on recruit density. Regarding soil properties and management, cation and sand content in soil had a negative effect on recruit density ($t=-3.53$; $p<0.01$) and wet tailings also had a negative effect on this response variable ($t=-2.99$; $p<0.01$). Successional age had a positive effect on recruit density ($t=2.32$; $p=0.02$). Additionally, planted tree density and light availability influenced recruit density through two very contrasting interactions. The interaction of planted tree density and canopy cover had a positive effect on recruit density ($t=2.48$; $p=0.02$), while the interaction of planted tree density and litter depth had a negative effect on it ($t=-3.11$; $p<0.01$).

Marginal r^2 was 0.41 and conditional r^2 was 0.44 which implies that the fixed factors explained most of the variance explained by this model, while the random factor had almost no influence. Full model and the interactions' plots can be found in Appendices 7 and 8, respectively.

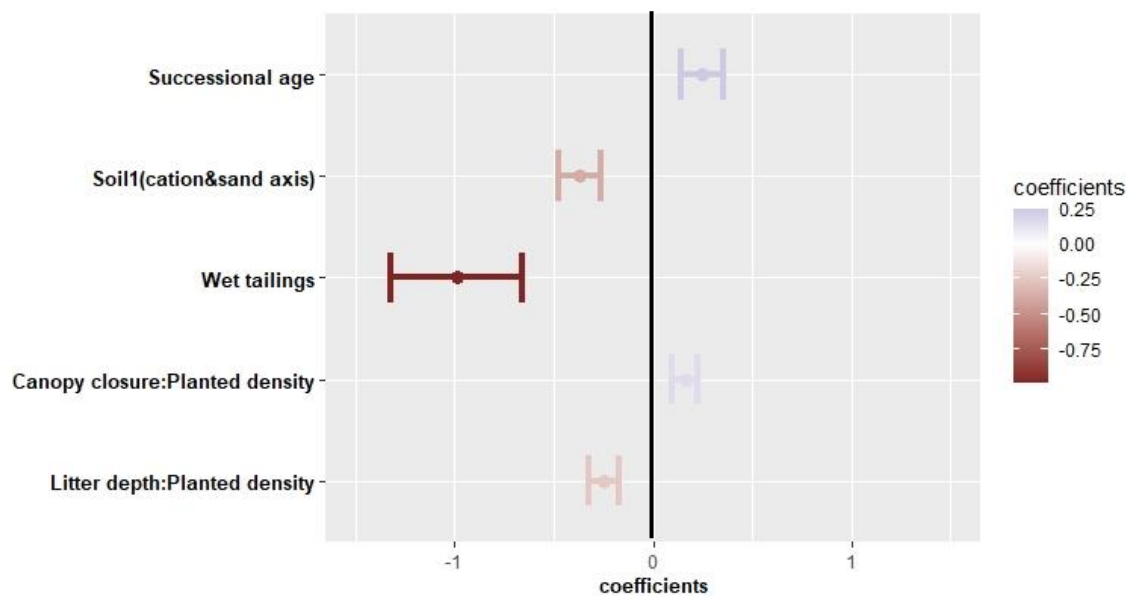


Figure 10. Significant results of linear mixed model of LMM of recruit density.

4. Discussion

Tree recruitment success is the consequence of two processes: seed dispersal and recruit establishment. Planted trees and surrounding forests influenced seed dispersal and consequently seed availability on the assessed restoration areas. This influence was evidenced by its effect on recruit species composition. However, it did not have a significant effect on recruit richness or density, except when it interacted with other variables. Mine zones, soil properties and light availability (canopy closure and litter depth) were considered as drivers of recruit establishment. All of them were significant factors for determining recruit species richness. Mine zones and soil properties influenced recruit species composition, but light availability did not have a significant effect on it, probably because the dominant recruit species had similar light demands. Soil properties and mine zones had a significant effect on recruit density. However, light availability only influenced recruit availability through its interaction with planted tree density, a main source of seeds.

4.1 Methodological considerations

Considering this study on a landscape level, its location in the Amazon can give us a clue of how the studied variables could influence similar restoration projects in this biome. At a more local scale, assessing areas undergoing restoration efforts within the same national park provided homogenous conditions regarding climatological variables such as temperature and rainfall, allowing their exclusion from the study. The scale of

the national forest and the mined sites provided a large set of restoration plots (86 sites) for this study. Additionally, the presence of different mine zones allowed comparisons between different soil management strategies.

The cross-sectional design of this research, which implies focusing data collection on a specific moment in time (in this case 2019 dry season), limited the possibility to assess the influence of factors driving establishment on recruitment success on the long-term (Ruxton & Colegrave, 2011). Due to the increasing pressure of climate change on water availability in the Amazon and its consequent effect on tree dynamics, I consider a long-term study will also be necessary to understand the changing patterns of recruitment in the future (Esquivel-Muelbert et al., 2019). Another temporal factor that should be further assessed is the different responses of the studied factors along the different life stages that are involved in the process of tree recruitment (e.g., germination, seedling establishment, sapling survival) (Marchand et al., 2020; Pillay et al., 2018).

Regarding management, it is important to acknowledge that seedling planting was the only restoration strategy applied in this area. Therefore, it was not possible to compare the efficiency of this strategy with others such as seed planting or natural regeneration. However, several studies have confirmed this strategy has significantly higher recruit species richness and density than other restoration strategies as it allows selecting species that are better adapted to each areas' conditions (Cruz et al., 2020; Martins et al., 2020; Palma & Laurance, 2015). Additionally, the lack of detailed information on management practices might have limited the analyses. A detailed, quantitative database of management practices could be a useful tool for assessing the impact of management decisions on tree recruitment. Finally, I suggest considering competition and herbivory in future studies, as these factors might affect also recruit establishment on sites undergoing restoration.

4.2 What drives recruit species richness?

According to my results, recruit species richness was not influenced by any variable related to seed dispersal, except when they interacted with abiotic conditions. Instead, lower light availability in the understory, caused by higher canopy closure values, promoted higher recruit species richness. This contradicts my hypothesis that light availability would promote a higher species richness. However, the interaction of higher values of canopy closure with the planted tree communities dominated by *Syzygium cumini* and *Inga laurina* suggests that this effect might be due to the negative effect of lower light availability on dominant pioneer species and its consequent promotion of species with a higher shade tolerance. This result contradicts other studies which have suggested that higher light availability in the understory might promote a higher species richness (Nicotra et al., 1999). However, it is supported by several studies that have found that understory light availability promotes the survival of different species according to their shade tolerance (or light demand). Furthermore, canopy closure in the area is consistently above 60% (Appendix 6), which coincides with a probability of survival higher than 90% for shade tolerant seedlings according to a study performed by Lin et al. (2014) in temperate forests in China. Additionally, the same study presented a survival rate as low as 55% for seedlings of light demanding species under a canopy closure of 75% (Lin et al., 2014; Tsvuura & Lawes, 2016; Uriarte et al., 2018).

My results also evidenced that in soils with higher pH and clay content, and lower phosphorus concentration, planted tree richness promoted a higher recruit species richness. This supports the hypothesis that soil quality can be a significant promoter of species richness. Most plots had a soil pH ranging between 3,6 and 4,4. This implies higher soil pH values promoted higher species richness because they were closer to the optimum pH of 5,1 for Amazonian plant species as estimated by Crespo-Mendes et al. 2019. Phosphorus has been found to be a limiting factor for tree productivity (van der Sande et al., 2018). Although this could seem to contradict my results, other studies in the neotropics have evidenced the negative effect of high soil phosphorus content on the species richness of naturally regenerated tree communities (Freitas et al., 2019). A possible reason for this might be that most plant species have a preference for soils with either high or low phosphorus contents, with their tolerance ranges overlapping at intermediate concentrations (Condit et al., 2013; Record et al., 2016). In addition, my results also align with previous studies that found that soils with high clay content in Central Amazonia have higher species richness (De Oliveira & Mori, 1999).

Dry tailings had one of the lowest recruit species richness, possibly because of the negative effect of the high concentration of sand in its soils (see Appendices 4 and 5). Despite this, higher amounts of surrounding old-growth forest were able to increase the seed rain enough to overcome the adverse effect of these sandy soils. This led to a significant increase of recruit richness within this mine zone. Additionally, when interacting with communities dominated by *Syzygium cumini* and *Inga laurina*, this mine zone evidenced a reduction in species richness. This apparent contradiction might imply that those two species have a higher fitness than the other species in sandy, well-drained soils. This coincides with the dominance of highly specialized tree species and its consequent lower species richness found in Amazonian white-sand soils (Ter Steege et al., 2013).

4.3 What drives recruit species composition?

As I hypothesized, abiotic factors (e.g., soil properties and light availability) and management practices influence species composition.

Recruit PCoA1 consisted of a gradient of recruit communities dominated by either *Psidium guianensis* or *Myrcia splendens*. Soils with higher cation content promoted the dominance of *Psidium guianensis* in recruit communities, which coincides with a previous study in the same area that found a higher density of this species' seedlings in sandy soils (König, 2018). Additionally, this community pattern is promoted by wet tailings. Considering this mine zone undergoes periodical flooding, I believe a plausible explanation for this could be the high survival rate of *Psidium* species under very wet and even submerged conditions, which might increase their fitness in these areas (Arroyo et al., 2020; Myster, 2007; Parolin, 2002). However, the influence of flooding and dry conditions as a possible driver of species composition in different mine zones should be further assessed to confirm this.

The dominance of *Myrcia splendens* in recruit communities was promoted by factors related to seed availability such as planted tree density and larger amounts of surrounding forests (both secondary and old growth). This suggests that although this species was not found in surrounding forests' plots, it might exist in these areas as well as in the planted tree species pool. This recruit community composition was additionally favoured by the interaction of planted tree density with soils higher in pH and clay content, which coincides with previous assessments of this area (König, 2018).

Soil properties and soil management factors related to seedling establishment also influenced the dominance of *M. splendens*. Mining floor promoted these recruit communities, which might indicate a higher tolerance of this recruit community to soil compaction. This effect was increased by the interaction of this mine zone planted tree communities dominated by *Syzygium cumini* and *Inga laurina*. This could imply that these tree communities might be generating favourable environmental conditions for *M. splendens* and other species related to this recruit community. This could be related to the nitrogen fixation by *Inga laurina* and planted legume trees (de Faria et al., 2020).

Recruit PCoA2 consisted of a gradient of recruit communities dominated by either *Toulicia guianensis* or *Siparuna guianensis* and *Vismia guianensis*. The promotion of *Toulicia guianensis*-dominated recruit communities by higher cation and sand contents in soil suggested that these soil conditions benefited this species. Considering that *Toulicia guianensis* was not found in surrounding forests, the encouragement of this recruit community pattern by bigger secondary forest areas seems contradictory. However, data suggests this might be due to the influence of a higher density of other species related to negative values in the recruit PCoA2 axis. The interaction of higher cation and sand content, and bigger secondary forest area promoted recruit communities dominated by *Siparuna guianensis* and *Vismia guianensis* (both found in the surrounding secondary forest). This suggests that under a larger seed rain of these two species, they can outcompete *Toulicia guianensis*' dominance. It also implies that these species are better adapted to higher cation and sand content than other secondary forest species, over-competing them in plots with these soil conditions.

I did not find a significant effect of light availability (canopy cover and litter depth) on recruit species composition on either PCoA axis. This contradicts previous studies that evidenced the importance of light availability in the

understory as a driver of species composition (Lin et al., 2014; Nicotra et al., 1999; Tsvuura & Lawes, 2016; Uriarte et al., 2018) However, this might be related to the fact that the different recruit communities had similar light requirements as they were mainly dominated by light-demanding species.

4.4 What drives recruit density?

Recruit density was not influenced by any variable related to seed dispersal, except when they interacted with factors related to light availability (litter depth and canopy closure). These interactions evidenced opposite effects of light availability. Therefore, my hypothesis regarding a positive significant effect of planted tree density and light availability was not met. However, my results reveal a more complex story with different effects being related to the different stages of recruitment.

The interaction of deeper litter layers with planted tree density reduced recruit density. This contradicts other studies that found that litter increased both seedling growth and density. However, as these studies also suggest, litter effect on recruitment might be linked to both light availability and seed size. As they observed, litter reduced the survival and growth rates of seedlings with small seeds, which correspond mainly to pioneer species, because it constrains their light availability during germination. In this sense, the reduction of recruit density by litter depth could imply that current conditions favour the recruitment of species that are less light-demanding than the dominant *I. laurina* and *S. cumini* (Dias et al., 2012; Dupuy & Chazdon, 2008). This can also be associated to the effect I observed for the interaction of canopy closure with planted tree density. This interaction promoted higher recruit density under a denser canopy (less light availability). This suggests that reduced light availability is increasing shade tolerant species recruit density, which would align with the observed results for recruit species richness and previous studies (Lin et al., 2014; Nicotra et al., 1999; Tsvuura & Lawes, 2016; Uriarte et al., 2018). Overall, both interactions imply an increasing shade tolerance in the assessed recruits' communities. However, these recruits do not seem to have big enough seeds to escape the negative effect of litter on them.

Regarding the effect of establishment-related factors, I found that higher cation and sand content reduced recruit density. This could be due to an overall preference of species in the area for soils with higher clay content, as seen in the recruit species richness results. This finding also coincides with the observed importance of this variable in shaping species composition, as it promoted the dominance of certain species, possibly lowering the chances of survival of the non-dominant species.

Finally, wet tailings reduced recruit density. The low sand and high clay content of this mine zone's soils suggests that this effect is probably unrelated to soil conditions. However, it could be related to periodical flooding in these areas because of their lower position in the terrain. It has been suggested that the reduced nutrients reserve in small seeded species could reduce their probability of survival in flooded areas, which would align with my finding regarding litter depth (Parolin, 2002).

4.5 Implications for restoration

Climate change and policy trends, that have led to an increase in fires and deforestation in the past years in the Brazilian Amazon, make forest restoration essential for preserving this biome (Amigo, 2020). However, restoration is an expensive activity, usually with limited funding (Brancalion et al., 2019). Understanding how different ecological variables and management practices promote natural regeneration can reduce its costs, while increasing biodiversity and ecosystem services (Chazdon, 2008).

Seed availability promoted by planted trees and surrounding forests had a significant effect on recruit species composition. Knowing how different factors promote distinct successional pathways can be important to ensure a more diverse restoration and promote forest communities that are more similar to the original. Among these pathways, succession arrest by *Vismia* dominated secondary forests, which has been observed in previous studies in neotropical rainforests, must be taken into account to ensure a successful restoration process. Adding topsoil to reduce areas with sandy soils might decrease *Vismia guianensis* and *Siparuna guianensis* dominance on recruits communities (Jakovac et al., 2014; Mesquita et al., 2015).

With adequate soil conditions, planted richness and the amount of surrounding forests significantly influenced recruit richness. Surrounding forest must be taken into account in restoration planning. Higher number of planted tree species should be considered to increase the set of species available in places where the chance of dispersal of non-planted species is low.

Establishment related factors such as light availability and soil quality also have several implications for restoration. The promotion of recruit species richness and density by canopy closure implies that restoration projects should avoid creating gaps as this might limit the colonization of shade-tolerant species. Soil and terrain management in washing plant zones should be further assessed for its potential to increase recruit species richness under adequate seed dispersal conditions from surrounding forests. Furthermore, the decrease in recruit richness caused by the interaction of dry tailings with communities of planted trees dominated by *I.laurina* and *S.cumini* suggests that progressively reducing the density of these highly competitive planted tree species should be considered, especially for this mine zone. The role of *I.laurina* and *S.cumini* dominated planted tree communities in moderating the increase of recruit species richness promoted by canopy closure implies that the influence of canopy cover must be reassessed if the systematic reduction of these species is applied. Finally, the influence of flooding on the lower densities found in wet tailings should be further assessed. Potential solutions for this could be building a drainage system or planting flood-resistant species in this mine zone.

5. Conclusions

Recruitment during forest restoration is a complex process that involves several factors related to seed availability, germination and seedling establishment. In this study, recruit density and species richness were affected by seed availability, light availability, and soil properties. Higher canopy closure might affect the dominance of pioneer species, increasing species richness. Higher pH and clay content, and lower phosphorus concentration also promote a higher species richness. Light availability was not found to influence species composition, because all dominant species were light demanding. Seed availability, mine zones and soil properties influence recruit species composition and density. The interactions that influenced recruit density suggested that seed size could be an important factor for this response variable which should be further assessed.

This study provides cues into how management strategies can be focused to improve recruitment patterns in tropical rainforest restoration projects, especially on abandoned mine sites. Species availability in the surrounding forests should be accounted when deciding the number of planted species to include. Understanding how abiotic conditions influence successional pathways is also relevant to avoid arrested successional pathways. The successional stage of restoration areas should be taken into account to understand the effects of light availability. Washing plant mining technique should be further assessed as a potentially less harmful mining method than pit mining, as its resulting mine zone had higher recruit richness. Finally, strategies such as adding topsoil, improving drainage or introducing species adapted to soil conditions could be applied to mine zones with low values of recruit richness or density such as dry and wet tailings.

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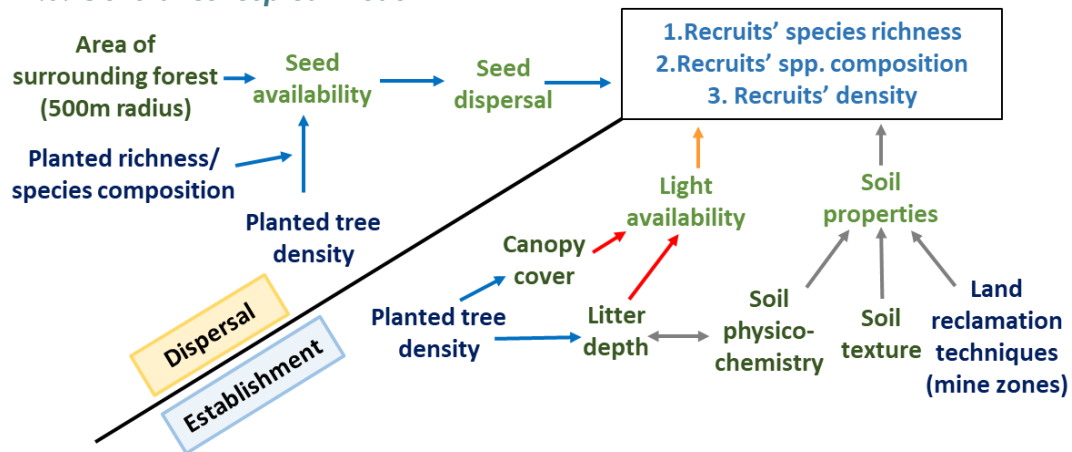
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Appendices

Appendix 1: Conceptual models

Appendix 1.0: General conceptual model

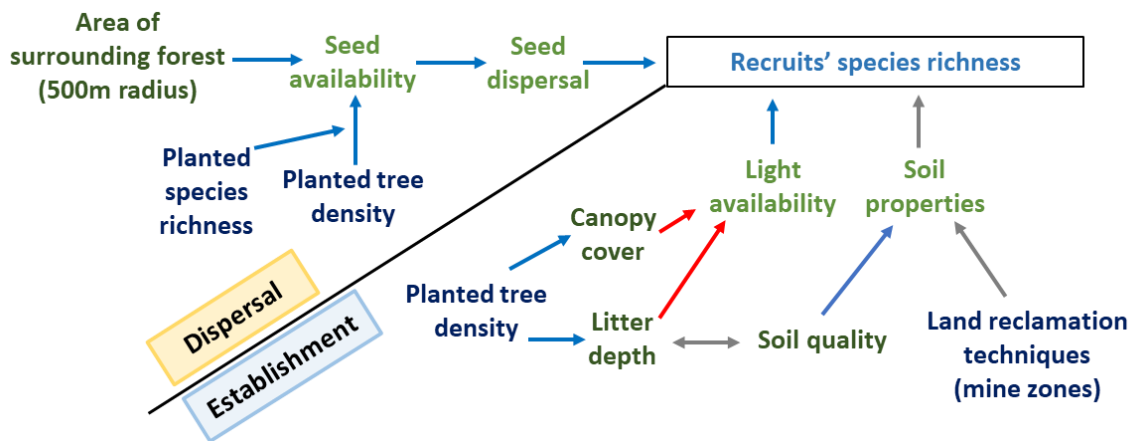


Legend:

- Dark blue text: Management factors directly included in model
- Dark green text: Ecological factors directly included in model
- Light green text: Ecological factors not directly included in model

- Red arrow: Negative relation expected
- Blue arrow: Positive relation expected
- Orange arrow: Promotion of light-demanding species composition/ Positive relation towards richness and density
- Grey arrow: Relation expected to vary across species and mine zones

Appendix 1.1: Specific conceptual model for hypothesis 1

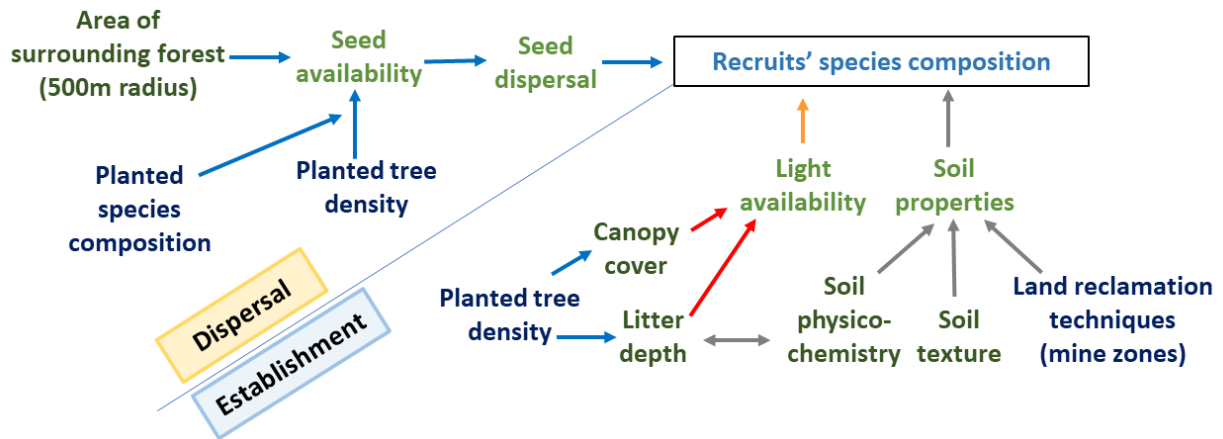


Legend:

- Dark blue text: Management factors directly included in model
- Dark green text: Ecological factors directly included in model

- Light green text: Ecological factors not directly included in model
- Red arrow: Negative relation expected
- Blue arrow: Positive relation expected
- Grey arrow: Relation expected to vary across species and mine zones

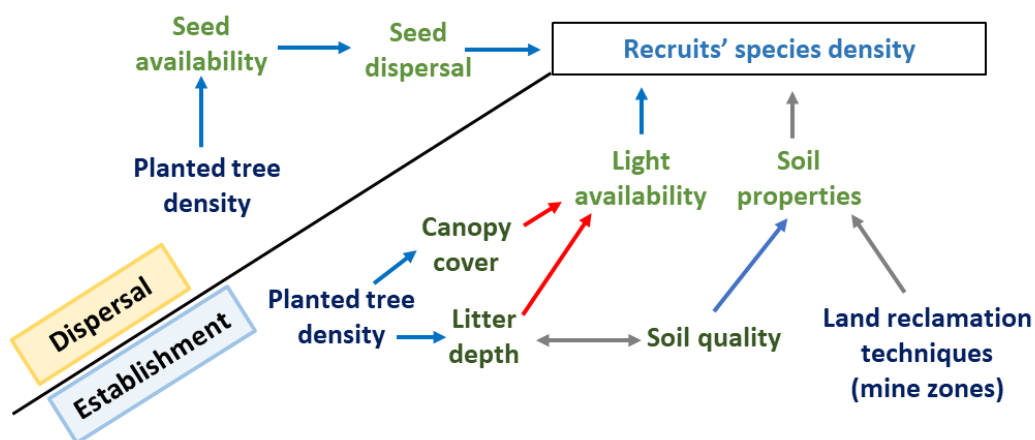
Appendix 1.2: Specific conceptual model for hypothesis 2



Legend:

- Dark blue text: Management factors directly included in model
- Dark green text: Ecological factors directly included in model
- Light green text: Ecological factors not directly included in model
- Red arrow: Negative relation expected
- Blue arrow: Positive relation expected
- Orange arrow: Promotion of light-demanding species
- Grey arrow: Relation expected to vary across species and mine zones

Appendix 1.3: Specific conceptual model for hypothesis 3



Legend:

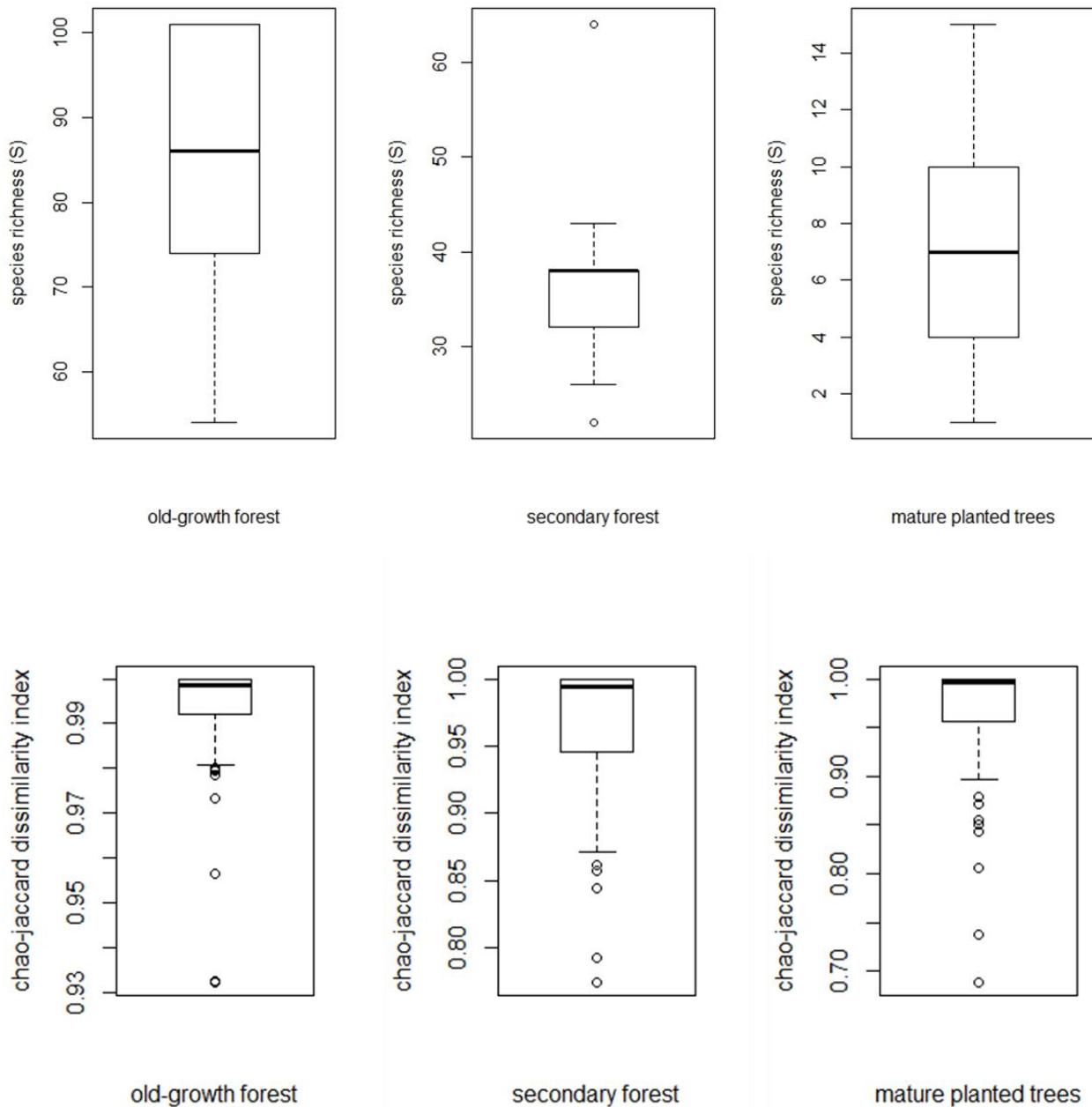
- Dark blue text: Management factors directly included in model
- Dark green text: Ecological factors directly included in model
- Light green text: Ecological factors not directly included in model
- Red arrow: Negative relation expected
- Blue arrow: Positive relation expected
- Grey arrow: Relation expected to vary across species and mine zones

Appendix 2: Overview of mines, areas and plots

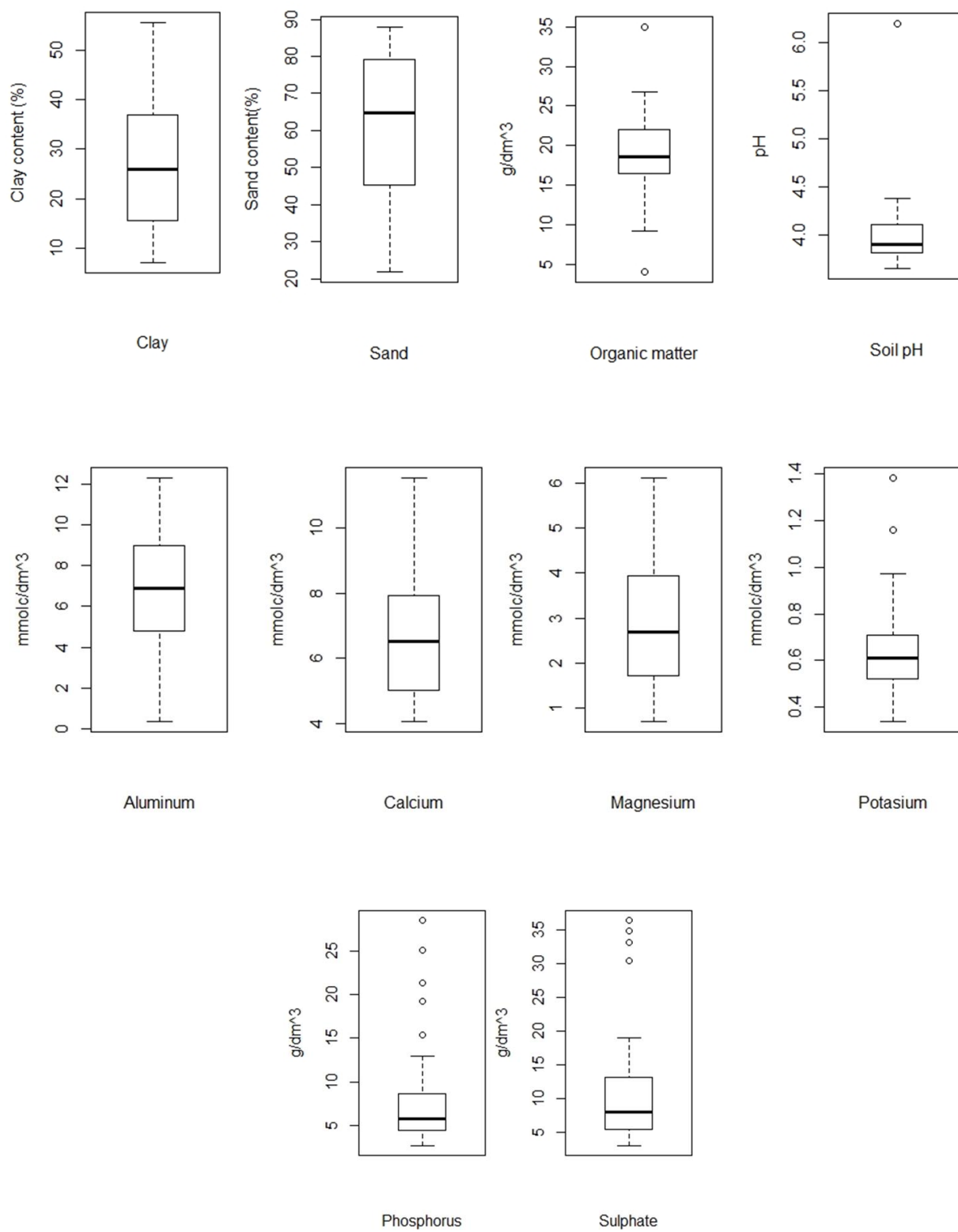
Mine	Area	Mine zone	Successional age (on 2019)	Plots	Area size (ha)	Assessment area (ha)
Mine1	1	Capped tailings	16	2	9.82	0.50
	1a	Capped tailings	14	7	4.54	1.75
	2	Capped tailings	22	1	3.63	0.25
	2a	Capped tailings	14	1	9.40	0.25
	2b	Mining floor	7	2	15.29	0.50
	3	Capped tailings	15	1	5.21	0.25
	4	Mining floor	14	4	26.66	1.00
	7	Dry tailings	16	2	5.61	0.50
	7a	Dry tailings	16	1	0.75	0.25
	11	Wet tailings	14	2	33.14	0.50
	12	Dry tailings	11	1	1.00	0.25
Mine2	1	Washing plant	27	5	38.20	1.25
Mine3	1	Dry tailings	13	3	9.84	0.75
	2	Dry tailings	26	2	2.60	0.50
	3	Dry tailings	7	2	5.90	0.50
	4	Dry tailings	13	1	9.71	0.25
	5	Dry tailings	11	1	0.58	0.25
	6	Dry tailings	10	1	2.20	0.25
	7	Dry tailings	10	1	0.78	0.25
Mine4	1	Capped tailings	15	1	2.71	0.25
	4	Dry tailings	14	1	1.83	0.25
	7	Capped tailings	14	1	2.32	0.25
	9	Dry tailings	14	1	4.50	0.25
	15	Mining floor	22	1	5.32	0.25
	16	Mining floor	22	2	6.08	0.50
Mine5	1	Washing plant	26	8	53.80	2.00
	2	Washing plant	13	3	4.20	0.75
	3	Washing plant	12	1	1.80	0.25
Mine6	2	Mining floor	17	1	2.30	0.25
	3	Mining floor	16	1	2.69	0.25
	4	Dry tailings	13	4	25.65	1.00
	5	Dry tailings	13	1	0.99	0.25
	6	Capped tailings	13	8	16.89	2.00
	7	Mining floor	13	1	0.38	0.25
	8	Mining floor	19	2	6.60	0.50
	9	Wet tailings	14	8	135.61	2.00
	11	Mining floor	19	1	3.87	0.25
Total				86	462.40	21.50

Appendix 3: Reference plots

The following boxplots seek to compare the species richness and species composition of mature trees in reforested plots, secondary forest and old-growth forest. Species composition was based on its comparison with recruit species composition in was represented as the value of the Chao-Jaccard dissimilarity index (values from 0 to 1), which is higher when the species composition of recruit in each plot and a reference plot of mature trees are more distinct.

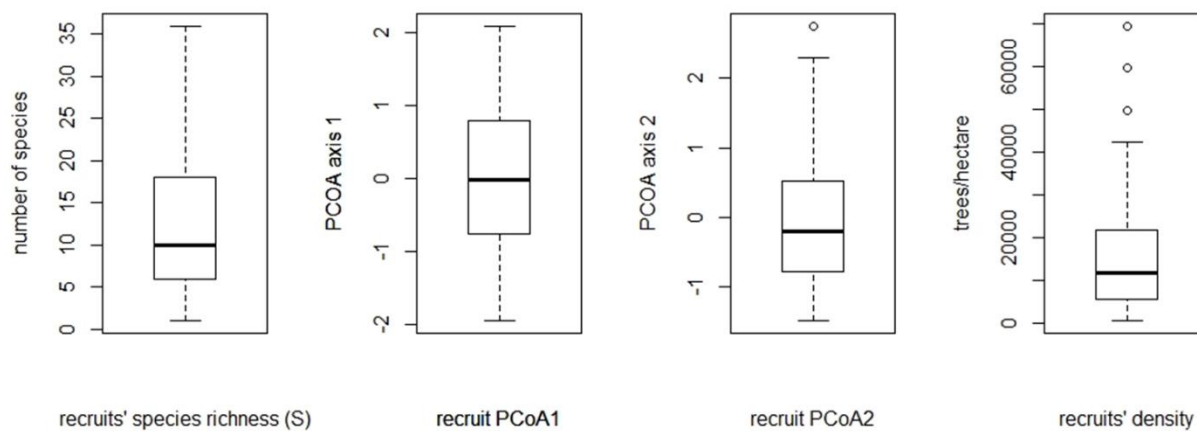


Appendix 4: Soil analysis boxplots

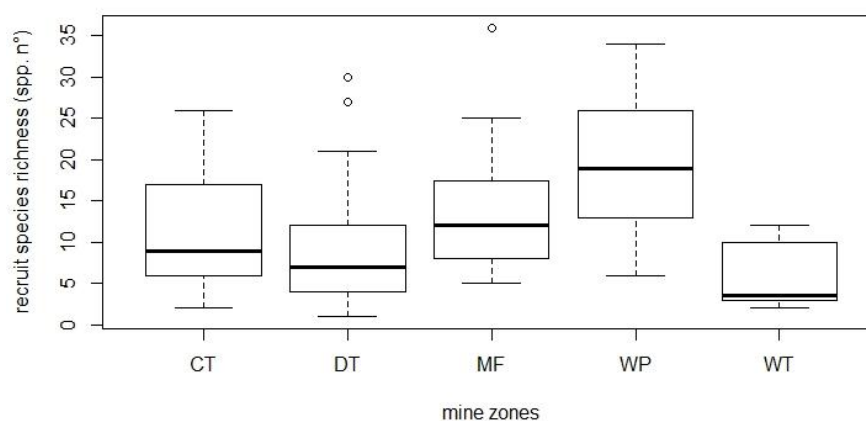


Appendix 5: Response variables boxplots

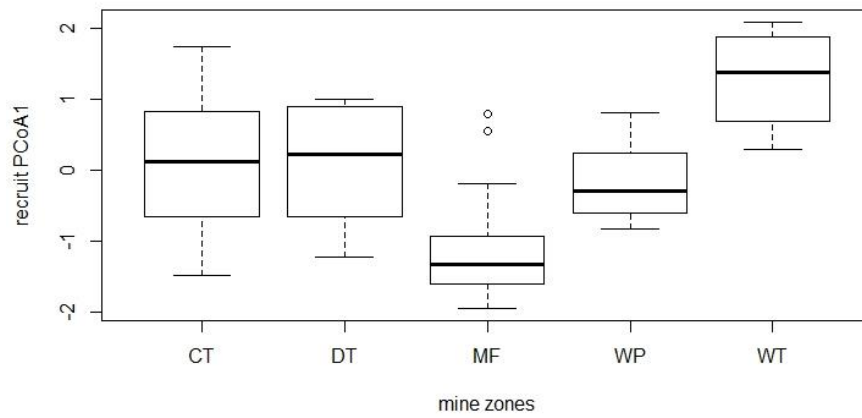
Response variables boxplots for all plots



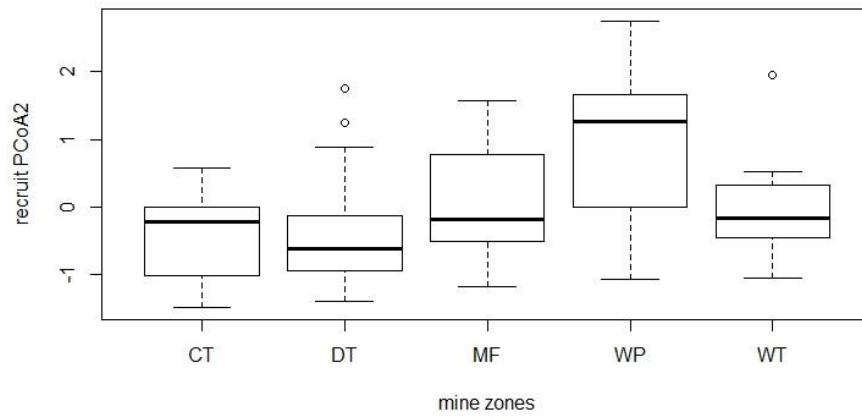
Response variables boxplots per mine zone



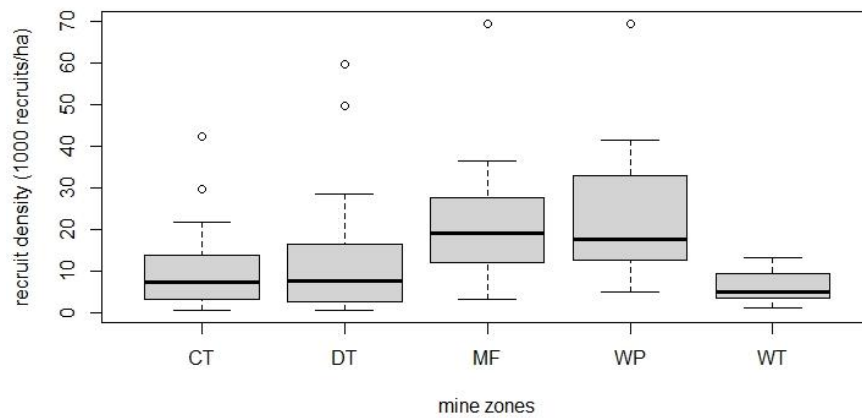
Note: CT= capped tailings, DT= dry tailings, MF= mining floor, WP= washing plant, WT= wet tailings



Note: CT= capped tailings, DT= dry tailings, MF= mining floor, WP= washing plant, WT= wet tailings



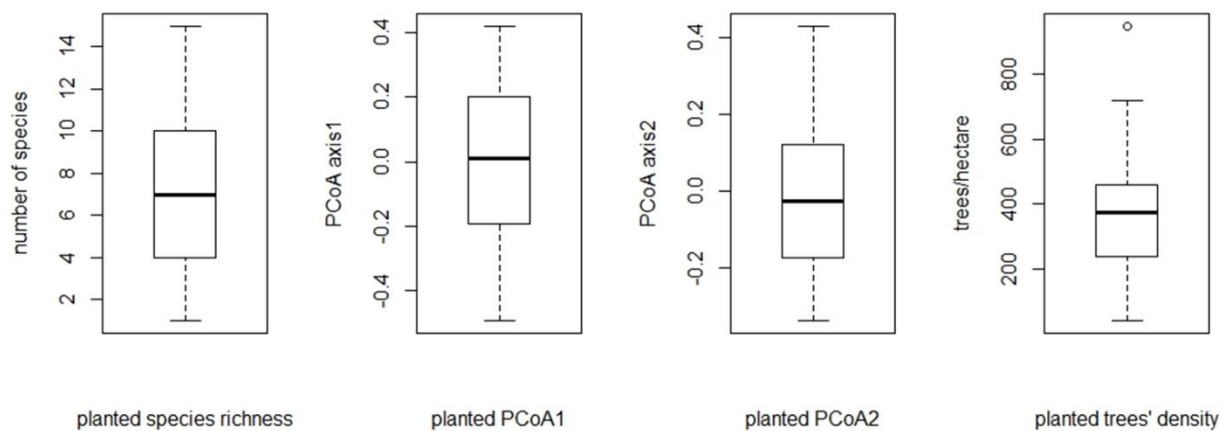
Note: CT= capped tailings, DT= dry tailings, MF= mining floor, WP= washing plant, WT= wet tailings



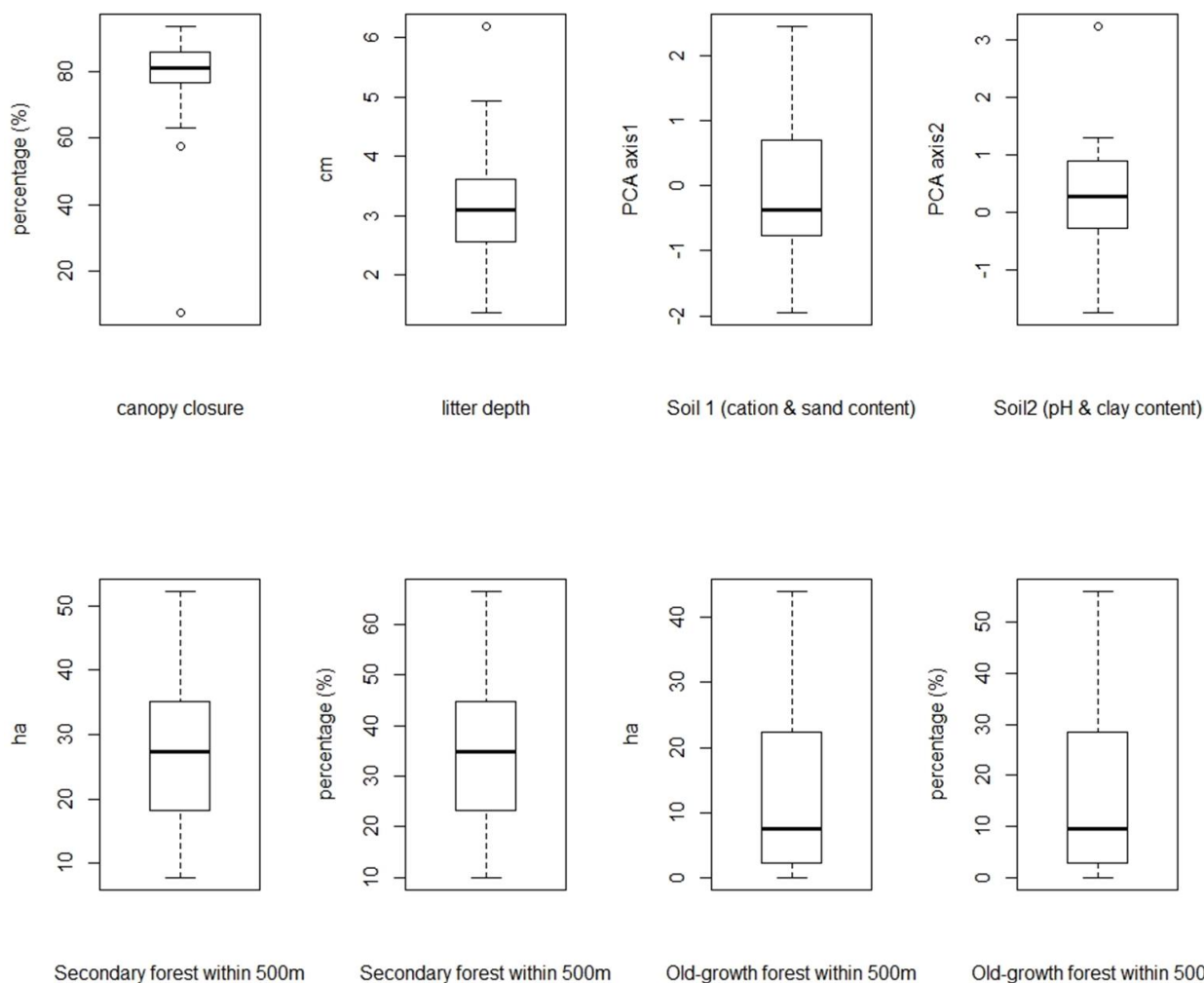
Note: CT= capped tailings, DT= dry tailings, MF= mining floor, WP= washing plant, WT= wet tailings

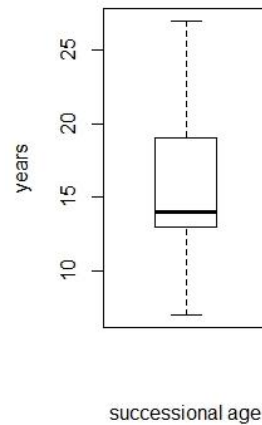
Appendix 6: Explanatory variables boxplots

Explanatory management variables boxplots



Explanatory ecological variables boxplots





Appendix 7: Test statistics of linear models:

Full linear mixed model

Response variable \sim age + planted tree density*soil1 + planted tree species*soil1 + old-growth forest area*soil1 + secondary forest area*soil1 + planted tree density*soil2 + planted tree species*soil2 + old-growth forest area*soil2 + secondary forest area*soil2 + planted tree density*mine zones + planted tree species*mine zones + old-growth forest area*mine zones + secondary forest area*mine zones + planted tree density*litter + planted tree species*litter + old-growth forest area*litter + secondary forest area*litter + planted tree density*canopy + planted tree species*canopy + old-growth forest area*canopy cover + secondary forest area*canopy cover, random=1/mines

Note: Planted tree species: planted tree richness (on recruit species richness model) or planted species composition axes (on recruit species richness and composition models). This variable was not included in recruit density model.

Simplified linear mixed model

Response variable \sim successional age + recruitment-promoting variable: environmental variable, random=1/mines

Linear mixed model results for recruit species richness

Variables	Value	Std.Error	DF	t-value	p-value
(Intercept)	0.014	0.108	66	0.130	0.897
Successional age	0.285	0.103	66	2.771	0.007
Canopy closure	0.396	0.105	66	3.769	0.000
Canopy closure: Planted PCoA2	0.488	0.133	66	3.661	0.001
Planted tree richness: soil2	0.426	0.106	66	4.015	0.000
Planted PCoA2: Capped tailings	-0.071	0.177	66	-0.399	0.691
Planted PCoA2: Dry tailings	-0.626	0.173	66	-3.625	0.001
Planted PCoA2: Mining floor	-0.294	0.173	66	-1.700	0.094
Planted PCoA2: Washing plant	0.290	0.264	66	1.098	0.276
Planted PCoA2: Wet tailings	-0.473	0.369	66	-1.281	0.205
Old-growth forest area: Capped tailings	-0.208	0.208	66	-0.999	0.322
Old-growth forest area: Dry tailings	0.430	0.199	66	2.162	0.034
Old-growth forest area: Mining floor	-0.241	0.209	66	-1.151	0.254
Old-growth forest area: Washing plant	0.454	0.191	66	2.374	0.021
Old-growth forest area: Wet tailings	-0.023	0.472	66	-0.049	0.961

Linear mixed model results for recruit species composition (Recruit PCoA 1)

Variables	Value	Std.Error	DF	t-value	p-value
(Intercept)	0.01	0.17	64.00	0.07	0.95
Dry tailings	-0.10	0.18	64.00	-0.55	0.58
Mining floor	-0.84	0.22	64.00	-3.84	0.00
Planted PCoA2: Capped tailings	-0.08	0.12	64.00	-0.64	0.52
Planted PCoA2: Dry tailings	0.11	0.11	64.00	1.01	0.32
Planted PCoA2: Washing plant	0.14	0.20	64.00	0.74	0.46
Planted PCoA2: Wet tailings	0.28	0.23	64.00	1.22	0.23
Planted PCoA2: Mining floor	-0.37	0.12	64.00	-3.04	0.00
Old-growth forest area	-0.33	0.08	64.00	-3.93	0.00
Planted tree density	-0.21	0.07	64.00	-3.11	0.00
Planted tree density: Soil2	-0.16	0.07	64.00	-2.24	0.03
Secondary forest area	-0.33	0.10	64.00	-3.41	0.00
Soil1	0.49	0.07	64.00	6.74	0.00
Successional age	-0.21	0.08	64.00	-2.62	0.01
Washing plant	0.39	0.31	4.00	1.27	0.27
Wet tailings	0.61	0.27	64.00	2.27	0.03

Linear mixed model results for recruit species composition (Recruit PCoA 2)

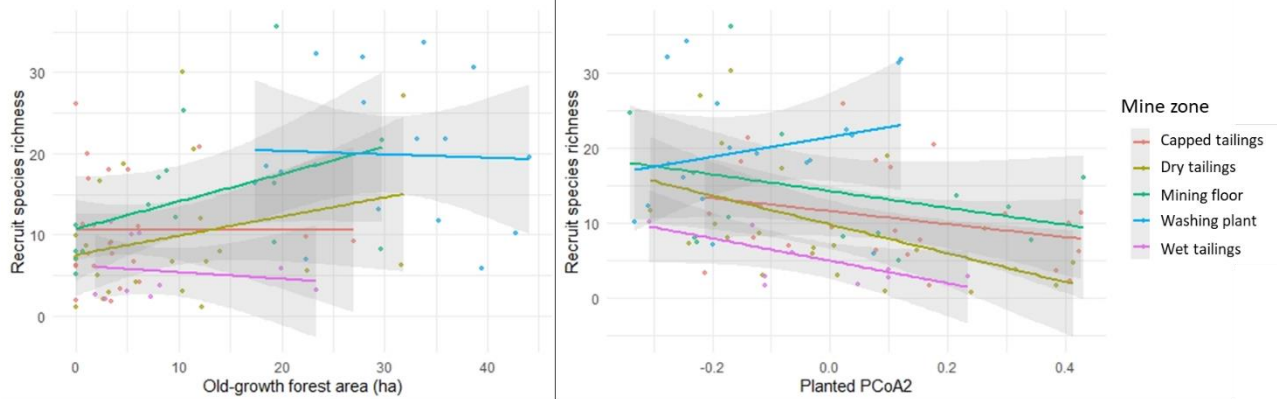
Variables	Value	Std.Error	DF	t-value	p-value
(Intercept)	-0.080	0.143	73.000	-0.559	0.578
Secondary forest area	-0.238	0.119	73.000	-1.992	0.050
Soil1	-0.227	0.100	73.000	-2.266	0.026
Secondary forest area: soil1	0.325	0.150	73.000	2.168	0.033

Linear mixed model results for recruit density

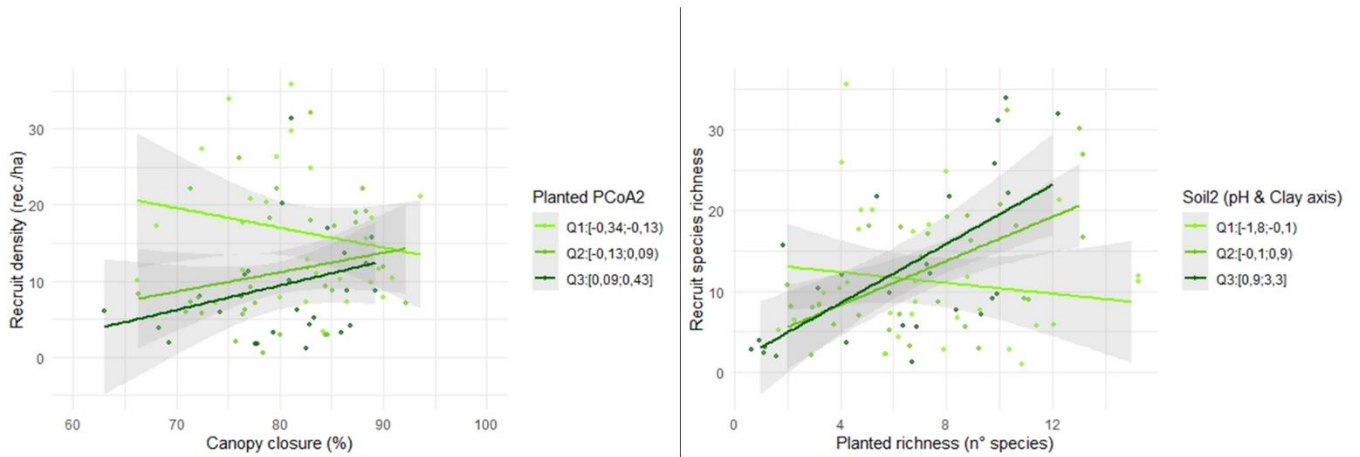
Variables	Value	Std.Error	DF	t-value	p-value
(Intercept)	-0.114	0.206	73	-0.554	0.581
Successional age	0.250	0.107	73	2.325	0.023
Planted tree density: canopy closure	0.162	0.065	73	2.479	0.015
Planted tree density: litter depth	-0.247	0.079	73	-3.114	0.003
Dry tailings	0.216	0.254	73	0.851	0.397
Mining floor	0.224	0.301	73	0.744	0.459
Washing plant	0.453	0.349	4	1.296	0.265
Wet tailings	-0.989	0.331	73	-2.993	0.004
Soil1	-0.370	0.105	73	-3.534	0.001

Appendix 8: Interactions' plots

Interactions in linear mixed model for recruit species richness

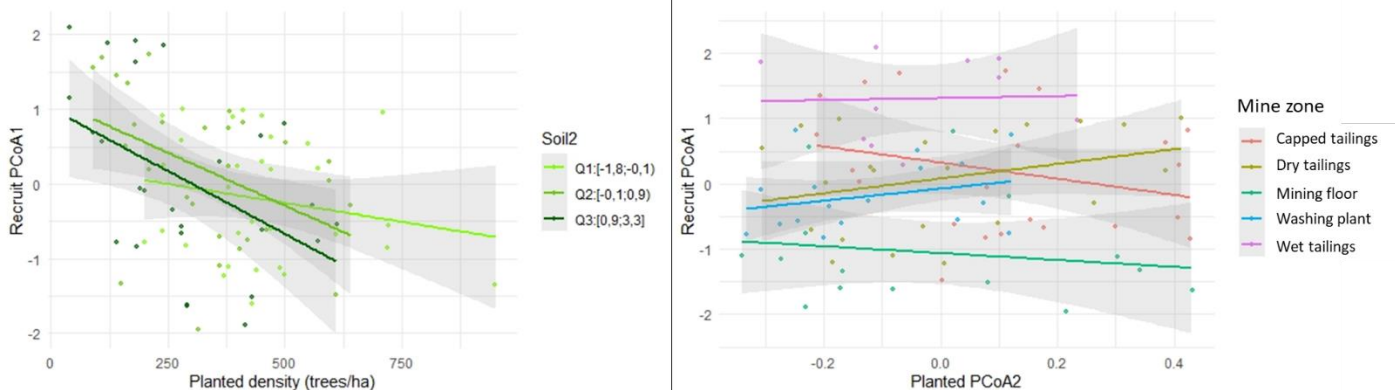


Mine zones interactions with old-growth forest (left) and planted PCoA2 (right).



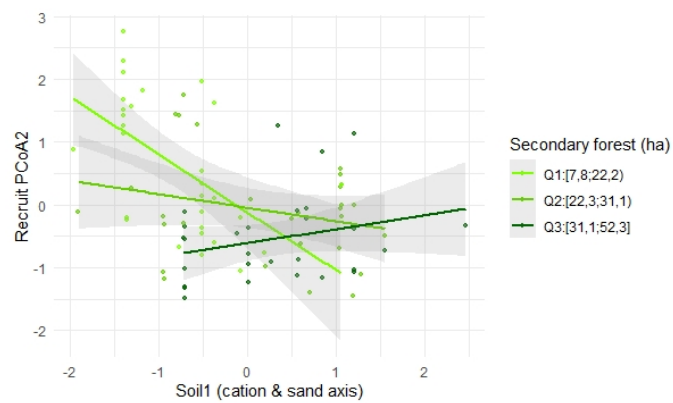
Left: Planted PCoA2 interaction with canopy closure. Right: Soil 2 (pH & clay axis) interaction with planted species richness. Planted PCoA2 (which is positively related to communities of planted trees dominated by *Inga laurina* and *Syzygium cumini*) and soil 2 values were split into three quantiles.

Interactions in linear mixed model for recruit PCoA1



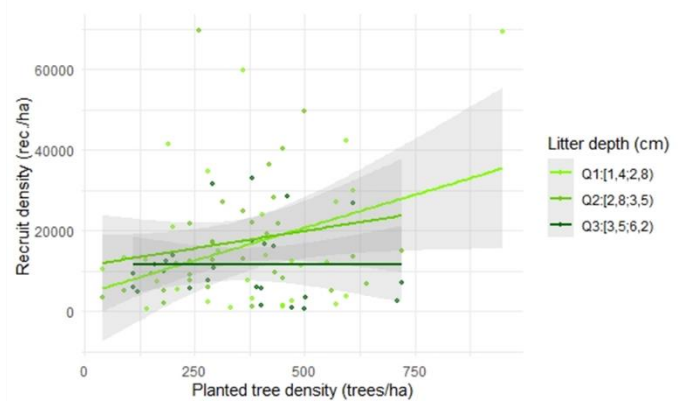
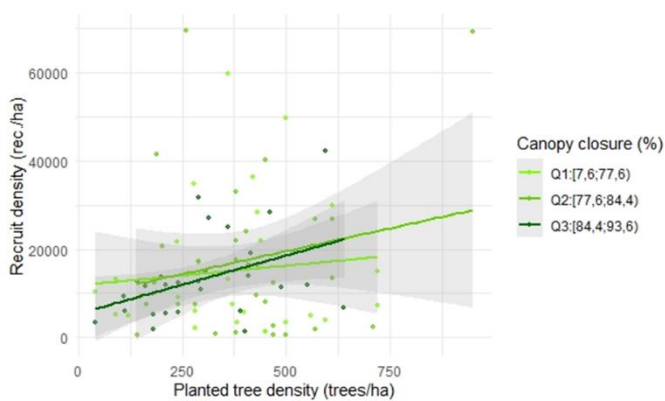
Left: Soil2 (pH & clay axis) interaction with planted tree density (trees /ha). Right: mine zones interaction with planted PCoA2 (which is positively related to communities of planted trees dominated by *Inga laurina* and *Syzygium cumini*).

Interactions in linear mixed model for recruit PCoA2



Interaction of secondary forest area (ha) and soil 1 (cation & sand axis).

Interactions in linear mixed model for recruit density



Interaction of canopy closure (%) (left) and litter depth (right) with planted tree density (trees/ha).