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PERFORMANCE OF TREE SPECIES AND EVALUATION OF A RESTORATION PLANTATION

TESE DE DOUTORADO

BRUNA ELISA TRENTIN

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PERFORMANCE OF TREE SPECIES AND EVALUATION OF A RESTORATION PLANTATION

Tese apresentada à Universidade Estadual do Centro-Oeste, como parte das exigências do Programa de Pós-Graduação em Ciências Florestais, área de concentração em Manejo Sustentável de Recursos Florestais, para a obtenção do título de Doutora.

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Dedico, à minha família que sempre esteve comigo em todos os momentos, fáceis ou difíceis, obrigada por tudo Dionisio, Neusa, Vanessa, Paulo, Juline, Guilherme e Dixie

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EPÍGRAFE

“When we have a fact-based worldview, we can see that the world is not as bad as it seems - and we can see what we have to do to keep making it better” (ROSLING, 2018, p. 255)

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GENERAL ABSTRACT

A rally for actions to restore ecosystems is urgent and Brazil has committed to much needed global restoration goals to mitigate climate change, however restoration of forests faces many challenges, starting with the lack of silvicultural knowledge in further regions of this continental country. Among 70 native species from Subtropical Atlantic Forest, we aimed to assess: 1) how much carbon a high-diversity restoration plantation stores; 2) compare carbon sequestration among 70 tree native species; 3) the role of species ecological groups in carbon sequestration, 4) highlight the best regional species for carbon-focused restoration projects, 5) which species performed better for survival, growth, and canopy closure? 6) were the ecological group's classification, as - “filling” and “diversity” -, consistent with the field results? 7) which species were more sensitive to frost? 8) how do growth strategies vary among species groups and within groups? 9) how was the evolution of canopy closure in a high diversity plantation? and 10) which successional stage has the stand reached after 8.5 years? Filling species stored more carbon when compared to diversity ones at all ages, and after 8.5 years this high-diversity plantation stored 46.04 tC ha^{-1}, that could increase to 121.49 tC ha^{-1} if we select the top-performing species for carbon. Up to four years after planting, filling species dominated the top ten rank of growing in height, dbh and crown area; however, after 8.5 y diversity species were half of the top ten rank for the same variables. Some species did not grow as expected, and a distinct growth group emerged, where four filling species were growing faster than the rest from ages one up to four years, being less distinct after 8.5 years. Higher mortality rates were found up to two years after planting and frost negatively affected species survival in general. We developed a rank of species performance to address tree species selection for restoration plantations. We also found differences in growth strategies among and within groups, however, most filling species invested more in crown area and height while

most diversity species invested more in height than dbh. The high diversity plantation reached a closed canopy four years after plantation. After 8.5 years, the stand reached an early successional stage. Restoration practices should focus on the use of native species with better performance in order to reach restoration goals faster and efficiently.

RESUMO GERAL

Há uma urgência de ações para restaurar ecossistemas e o Brasil se comprometeu com metas globais de restauração, metas muito necessárias para mitigar as mudanças climáticas, porém a restauração das florestas enfrenta muitos desafios, a começar pela falta de conhecimento silvicultural de espécies nativas. Entre 70 espécies nativas da Mata Atlântica Subtropical, buscamos avaliar: 1) quanto carbono um plantio de restauração de alta diversidade armazena; 2) comparar o sequestro de carbono entre 70 espécies nativas; 3) o papel dos grupos ecológicos das espécies no sequestro de carbono, 4) destacar as melhores espécies regionais para projetos de restauração com foco em carbono, 5) quais espécies tiveram melhor desempenho para sobrevivência, crescimento e fechamento do dossel 6) a classificação dos grupos ecológicos de - “preenchimento” e “diversidade” -, foi consistente com os resultados de campo? 7) quais espécies foram mais sensíveis à geada? 8) como as estratégias de crescimento variam entre grupos de espécies e dentro de grupos? 9) como foi a evolução do fechamento do dossel em um plantio de alta diversidade? e 10) qual estágio sucessional o plantio atingiu após 8,5 anos? As espécies de preenchimento estocaram mais carbono quando comparadas às de diversidade em todas as idades, e após 8,5 anos o plantio de alta diversidade armazenou 46,04 tC ha^{-1}, que poderia aumentar para 121,49 tC ha^{-1} se selecionarmos as espécies de melhor desempenho em relação ao carbono. Até quatro anos após o plantio, as espécies de preenchimento dominaram as dez primeiras posições no ranking de crescimento em altura, DAP e área de copa; no entanto, após 8,5 anos as espécies de diversidade eram metade das dez melhores posicionadas no ranking. Algumas espécies não cresceram como esperado, e um grupo de crescimento distinto emergiu, onde quatro espécies de preenchimento cresceram mais rápido que as demais, no período de um a quatro anos de idade, sendo menos distintas após 8,5 anos. Maiores taxas de mortalidade foram encontradas até dois anos após o plantio e as geadas afetaram negativamente a sobrevivência das espécies em geral. Desenvolvemos um ranking de desempenho de espécies

para auxiliar na seleção de espécies nativas para plantios de restauração. Também encontramos diferenças nas estratégias de crescimento entre e dentro dos grupos, no entanto, a maioria das espécies de preenchimento investiu mais em área de copa e altura, enquanto a maioria das espécies de diversidade investiu mais em altura do que em DAP. O plantio de alta diversidade atingiu um dossel fechado quatro anos após o plantio. Após 8,5 anos, o povoamento atingiu um estágio sucessional inicial. As práticas de restauração devem focar no uso de espécies nativas com melhor desempenho para atingir os objetivos de restauração de forma mais rápida e eficiente.

GENERAL INTRODUCTION

The 2020s began marked by a climate emergency warning, through a paper signed by more than 11,000 scientists from 153 countries, reiterating that conservation efforts are needed to lessen the climate crisis (Ripple et al. 2019). The main activities causing climate change include population and livestock increase, meat production, loss of tree cover,
consumption of fossil fuels, and CO2 emissions (Ripple et al. 2019; Rudel et al. 2020). Carbon dioxide (CO2) is a greenhouse gas released by human activities such as deforestation and the burning of fossil fuels, as well as other natural processes, and over the last 170 years, human activities have increased the concentration of CO2 by 47% compared to levels found in 1850, being this increase higher than the natural increase that happened over a period of 20,000 years (NASA 2022).

The net loss of forest cover has been decreasing worldwide over the past decade, but the deforestation and degradation of areas still have alarming rates, resulting in a significant loss of biodiversity (Seymour and Harris 2019; FAO 2020). About 40% of deforestation in both tropical and subtropical regions is caused by large-scale agriculture, led by cattle raising and followed by soy plantations; however, subsistence agriculture also plays an important role in deforestation, accounting for about 33% (FAO 2020), which means that approximately 73% of deforestation is related to agricultural production, whether small or large landowners are to blame.

At a regional level, the situation of the Atlantic Forest biome is extremely worrying. According to SOS Mata Atlântica, this biome has approximately 12.4% of remaining vegetation nowadays (SOSMA 2020), classifying it as a global hotspot: one of the most biodiverse and threatened biomes in the world (Conservation International 2023). Public or private policies to accelerate the transition from degraded to forested areas can lessen the effects of climate change, reduce biodiversity losses, and also prevent future degradation of natural resources, and this occurs due to the gain in forest areas and the increase in carbon sequestration by these forests (Lambin and Meyfroidt 2010; Rudel et al. 2020).

Increasing forest cover brings multiple benefits, from the protection of biodiversity, and protection of water resources to job creation (Lewis et al. 2019). When talking about increasing forest cover a misconception can be created, that any species can be used and will provide the same benefits, including monocultures such as commercial plantations, however, according to (Lewis et al. 2019) the use of commercial plantations is much less effective to store carbon when compared to natural forests without anthropic disturbances, and this occurs, because when these forests are harvested, the CO2 once sequestered is released back into the atmosphere, while natural forests continue to sequester carbon for decades. When we think about restoration multiple benefits, it includes everything from climate change mitigation, biodiversity conservation, ecosystem services, local livelihoods, economic gains, and food security to the population's well-being, but this requires attention to the restoration processes, thinking only about increasing tree coverage in a short period of time can become something negative in the long term (Chazdon and Brancalion 2019).

In this scenario, several goals were created globally for restoration, including the Paris agreement, the 20x20 initiative in Latin America (WRI 2014), and the Bonn Challenge (IUCN 2016), reaching a target of 350 million hectares to be restored by 2030 worldwide, added to national initiatives such as the National Plan for Recovery of Native Vegetation aiming to restore 12 million hectares by 2030 (MMA 2017) and the Pact for the Restoration of the Atlantic Forest, which aims to restore 15 million hectares by 2050. A scenario suggested by the Intergovernmental Panel on Climate Change estimates that just to sequester all the carbon needed to limit climate change to current levels, it would be necessary to plant around 24 million hectares of forest annually from 2019 to 2030 (IPCC 2018; Lewis et al. 2019).

Restoration ecology has grown in recent decades and it has become very important for the conservation of degraded ecosystems (Hobbs et al. 2011; Guerra et al. 2020). The need for large-scale restoration has been growing in recent years, and planting seedlings is still the most used restoration technique in the Atlantic Forest (Guerra et al. 2020). Hobbs et al. (2011) use the term intervention when referring to restoration, which implies people's role in this process, from choosing the method to species selection, becoming really important that those responsible for restoration projects are able to rely on studies that help them to choose more efficient species.

Pacts and agreements in the restoration decade end up encouraging the planting of native species in Brazil, aiming forest re-composition as one of the main alternatives to slow down climate change consequences, however, few studies have focused on the growth of native species. Studying the growth potential of native species for restoration directly impacts the reduction of implantation and maintenance costs of forest re-composition (Leles et al. 2011). Furthermore, the use of a higher number of native species in restoration projects can provide a more favorable environment for the development of other species, triggering the facilitation process (Petit and Montagnini 2004). Therefore, knowledge about native species' growth, such as their shading capacity, for example, is very important for forest restoration, and the use of species that are not efficient in these aspects can result in economic losses for a failed project. The use of species that have greater shading capacity for example is directly linked to the ability to control invasive species, one of the biggest problems in areas undergoing restoration, making it more difficult and more expensive to return the ecosystem to its original state (Vitousek 1997).

In addition, the use of restoration methodologies that are effective, which includes the use of more efficient species, is a major current challenge. In this way, this work arises to fill the knowledge gap about the performance of native species, especially in the southwestern subtropical region of Brazil, regarding the efficiency of these species for use in restoration areas, aiming to recommend species with better silvicultural performance for more efficient restoration projects.

OBJECTIVES

General objective

The general aim of this study is to evaluate the performance of seventy native tree species in the Southwestern Atlantic Forest of Brazil, for restoration purposes.

Specific objectives

- Look at differences in carbon stock between filling and diversity ecological groups and among species
- Assess aboveground carbon stock for all species in early years
- Predict carbon sequestration scenarios with selected high-performance species
- Verify if the group's classification of filling and diversity is consistent with observed species development
- Evaluate species performance in survival, growth, canopy closure and resistance to frost
- Evaluate species growth strategies variations between groups and within the group
- Assess canopy cover through age
- Estimate the successional stage that a high-diversity plantation stand achieved at 8.5 years

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CHAPTER 1 - Assessing carbon sequestration in a high-diversity restoration plantation in the Atlantic forest of southwestern Brazil

Abstract

A rally for actions to restore ecosystems is urgent to promote CO_2 sequestration. We aimed to assess: 1) how much aboveground carbon a high-diversity restoration plantation stores in early years; 2) compare carbon sequestration among 70 tree native species; 3) the role of species ecological groups in carbon sequestration, and 4) highlight the best regional species for carbon-focused restoration projects. Species planted in filling (fast-growing and early-shade) and diversity (slow-growing) lines were monitored from six months after planting to 8.5 y. Our high-diversity plantation stored 46.04 tC ha^{-1} at 8.5 years, however, if we select the top-performing species, the carbon stored at the same age could be more than double (121.49 tC ha^{-1}). Filling species stored more carbon when compared to diversity ones at all ages. Seven filling species and nine diversity species were the top-performing species for each group. Restoration practices should focus on the use of native species with higher carbon sequestration rates to more efficiently respond to the climatic emergency. Balancing selected fast-growth species combined with slow-growth species seems to be the best option to reach these goals in the short and long term; however, these selected lower diversity species combinations should be tested in the field.

1. Introduction

The United Nations decade on Ecosystem Restoration has just begun, and a rally for actions of protection and recovery of ecosystems worldwide is taking place, aiming to restore ecosystems to enhance people's livelihood, prevent future climate change impacts, and help to conserve biodiversity (UN Decade on Restoration, 2021). The decade extends from 2021 to 2030, which is an important timeline seen as the last chance to mitigate catastrophic events due to climate change (Dinerstein et al. 2019). More than 11,000 scientists representing 153 nations declared a climatic emergency in 2019 (Ripple et al. 2019)**.** Even though alarming trends have been exposed for more than 40 years in order to cease climate change, not much action has taken place (Gills and Morgan 2020). Recently, many climate-related disasters have occurred worldwide including flooding, wildfires, and hurricanes (Ripple et al. 2021). In the past two years, the world has seen extreme values for atmospheric concentrations of CO_2 and other greenhouse gasses, the highest levels of CO_2 emissions were recorded in 2017-2018 and now the planet has the highest CO_2 concentration in the atmosphere at a level we have not seen in human history (Ripple et al. 2019, 2021). We are near to reaching an important threshold of 450 ppm (417 ppm in Dec. 2021, according to (NASA 2022)) of carbon concentration (a critical level to keep the global temperature from rising more than 1.5 °C), we need climate action on a massive scale and tropical forest restoration is a viable tool to accumulate and store carbon (Solomon et al. 2009; Ripple et al. 2021) while we reduce emissions.

Climate change could impact the capacity of forests to work as carbon sinks, and forests could sequester less carbon in years when the temperature is high and precipitation is low (Liu et al. 2017; Mitchard 2018). Tropical forests are responsible for approximately a third of carbon sink in the planet (Beer et al. 2010; Mitchard 2018), however, this storage is spatially variable. Deforestation, primarily in the tropics, is a huge source of carbon emission (Baccini et al.

2012), and Brazil's Atlantic Forest has a long legacy of logging and land conversion, with about 13%~28% of its original vegetation cover remaining (Rezende et al. 2018) making it a prime location for restoration efforts.

In order to lessen climate change impacts, restoration plantations offer an alternative to address this problem, aiming not only for land cover and ecosystem services re-establishment such as carbon sequestration but also biodiversity recovery. A major restoration challenge is to find convergence points between carbon stocks, biodiversity, and costs, to create multiple ecosystem benefits from these forests as quickly as possible (Gilroy et al. 2014; Bechara et al. 2021). In Brazil, public policies such as the National Policy for the Recovery of Native Vegetation which aims to promote the forest restoration of at least 12 million hectares by 2030 (Brazil 2017), especially in the Atlantic forest region have arisen from The Bonn Challenge (IUCN, 2016), which aims to restore 350 million hectares by 2030 globally.

Restoration plantations are the most usual forest recovery method in the Brazilian Atlantic Forest, but most of these plantations used fewer than ten tree species (Guerra et al. 2020). According to the "insurance hypothesis", ecosystem productivity would be maintained close to its maximum value as long as species richness is sufficiently high for the ecosystem to reach redundancy: that happens when the ecosystem processes reach a plateau for a given number of species and adding more species will not enhance these processes (Yachi and Loreau 1999). This begs the question: how many species are enough? The occurrence of different species in a given forest is strongly related to multiple services, which suggests that the use of monocultures will lead to the reduced production of these services (Gamfeldt et al. 2013) however, there is little evidence that higher diversity plantations will promote higher diversity in the long term (Guerin et al. 2021). Species selection is important to optimize carbon management in degraded areas (Böttcher and Lindner 2010) and studies have shown how relevant it is to use a high tree diversity to restore ecosystems, using species with different functional traits, which may increase productivity in the long-term (Bongers et al. 2021; Guerrero-Ramírez 2021). High-diversity restoration plantations can produce more aboveground biomass when compared to native species monocultures (Montagnini and Piotto 2011). While species selection will influence early restoration success through the use of high-survival species and thereby reducing costs of restoration (Bechara et al. 2021), species selection based on functional diversity can demonstrate restoration success through biodiversity effects (Guerrero-Ramírez 2021).

Selecting species from a combination of ecological groups with higher carbon sequestration rates and long-term storage potential would be the best option to address climate change through forest restoration. The filling tree species ecological group (early-canopy development and fast-growth) will likely achieve higher carbon stocks earlier when compared to the diversity species group (slow-growth, long-lived species), even though the diversity species may have higher carbon stocks as the plantation develops in the future because of their longevity (Böttcher and Lindner 2010; Needham et al. 2022). In this scenario, we should prioritize plantations that are multifunctional and provide multiple ecosystem services such as carbon sequestration and storage, conservation of biodiversity, water and soil protection (Messier et al. 2021); however, few studies have selected native species that could also ensure high rates of carbon sequestration. We investigated how much aboveground carbon a high-diversity plantation stores in early years. We aimed to compare carbon sequestration among 70 species, as well as to investigate if the species ecological groups (filling and diversity) have a role in the amount of carbon sequestered in early years. Finally, we highlight candidate species for carbon-focused restoration projects in the Brazilian Atlantic forest of southwestern Brazil. We expect that this work could provide a starting point in studying and recommending specific species combinations for restoration also in other Atlantic forest regions of Brazil, and allowing restoration projects to address both biodiversity and carbon goals.

2. Material and Methods

2.1 Study site

The research was conducted at the Federal University of Technology – Paraná, Dois Vizinhos, Brazil (25º41'44" - 25º41'49" S; 53º06'23" - 53º06'07" W) in an experimental site established in October 2010 (Figure 1).

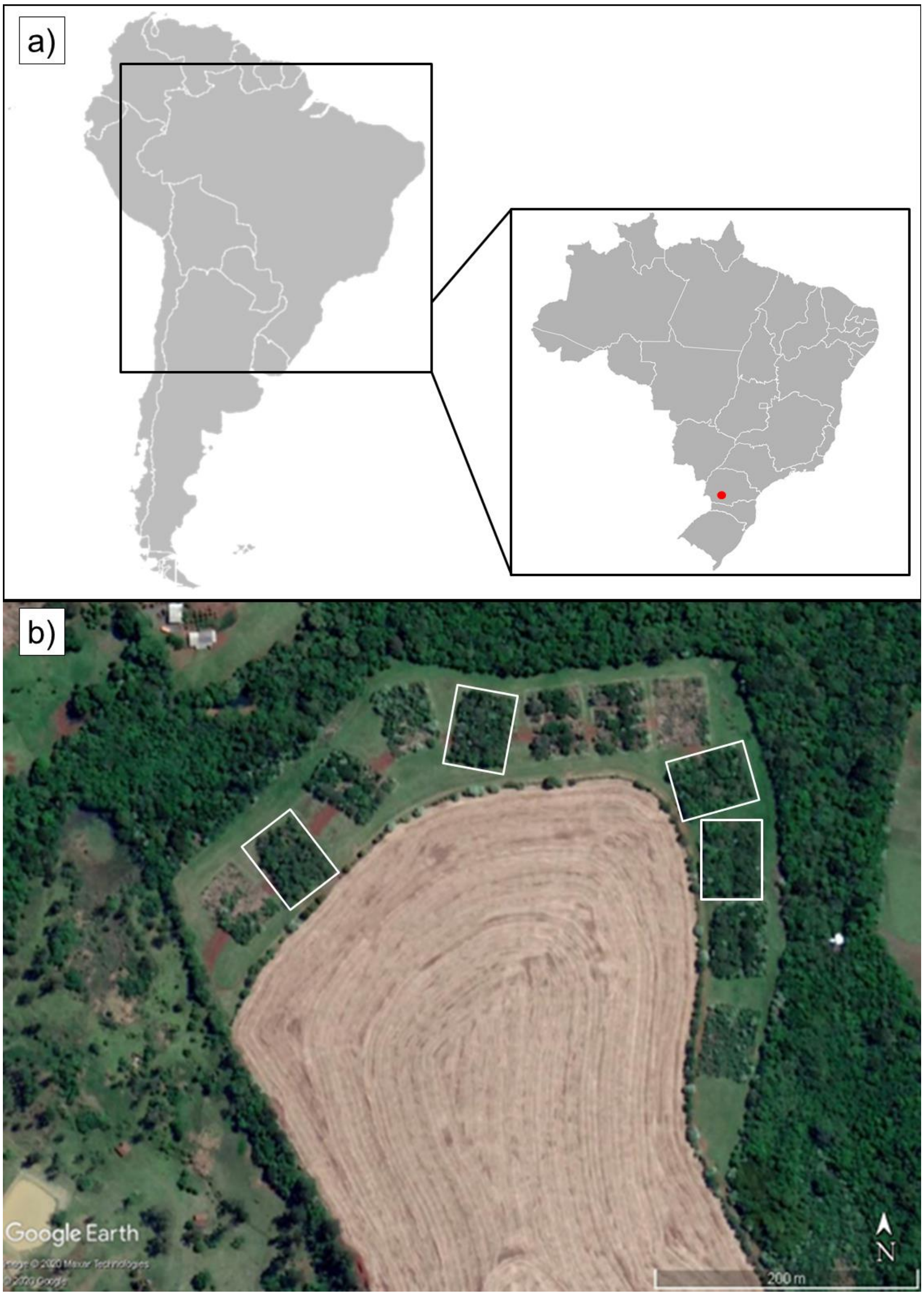

Figure 1: a) Study site location in Brazil where the red dot shows our site. b) Plots used in this study are indicated in white rectangles, size of each plot is 40x54 m. Image year: 2019.

The climate is humid subtropical, with an average annual precipitation of 2,044 mm (without water deficit) and the soil is a Dystroferric Red Nitisol (Santos et al. 2011). The average annual temperature is 19.2°C with approximately one frost every two years. Elevation ranges from 495 to 504 m and the vegetation is an Atlantic Forest ecotone between *Araucaria*

Forest and semideciduous seasonal forest (IBGE 2004; Bechara et al. 2021). The planting started with mowing and herbicide sprayed to the total area, followed by soil preparation including planting lines. Saplings were fertilized with 360 g of NPK 5-20-10, irrigated with 3 L of hydrated gel in the pits, mulching cardboards, and systematic control of cutting ants, and it also included intensive management - semiannual invasive plants control and annual fertilization - during the first three years.

2.2 Planting design

The restoration planting was established using two ecological species groups (based on (Rodrigues et al. 2009): 1) filling species with early shading and fast-growth; and 2) diversity, slow-growth species; the species selection and classification on each group was based on the literature and field experts considering also regional development of each species. The planting included 10 filling and 60 diversity species, selected to compare performance among species and groups (see Appendix I). Our regional species have a wide distribution in the Brazilian Atlantic Forest (BFG 2021).

Initial sapling age was not controlled in the analysis, since the seedlings came from different regional nurseries; however, all of them came from similar size tree tubes. We are taking the planting time as a reference time for the saplings' age. The planting spacing was 3 m between rows and 2 m within the row (a total of 1,667 plants per hectare) and the two ecological species groups were intercalated within rows. The species composition design was systematic, where each species was planted at the exact relative location in each plot, with a total of four plots of 40 m by 54 m, distant 31±19 m apart (Figure 2).

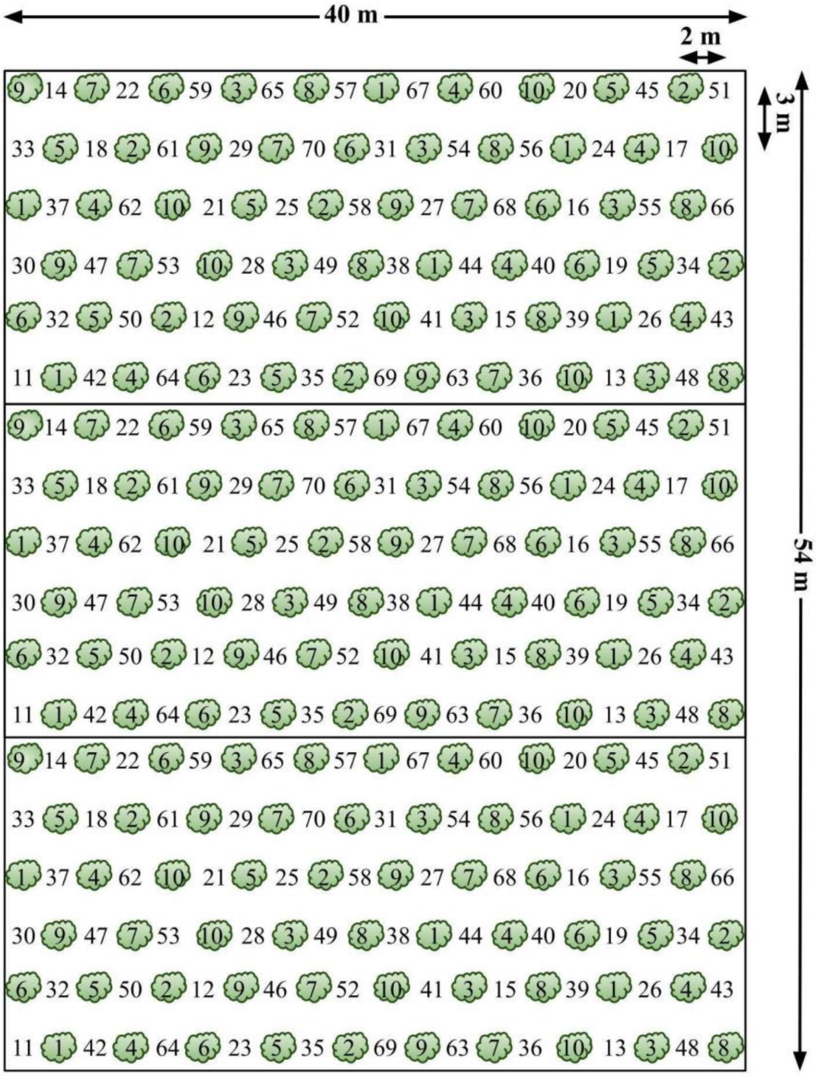

Figure 2: Planting method using filling and diversity species groups. Filling species are indicated by green crowns. Each number corresponds to a species (see Appendix I). Horizontal lines indicate the three subplots.

Inside each plot, there were three repetitions for the species design (subplots). We planted 360 saplings in each plot (180 saplings of filling and 180 of diversity species), bringing to a total of 1,440 individuals. In total, filling species had 72 sapling repetitions, and diversity species had 12 repetitions.

2.3 Tree sampling

Saplings monitoring started in Jun 2011 (six months after planting), followed by November 2011, June 2012, November 2012, May 2013, November 2013, June 2014, December 2014, and finally August 2019 (ages of 0.5 to 8.5 y, respectively). Every individual was measured considering: i) diameter at breast height (dbh; if > 5 cm dbh) and ii) total height. Dead individuals received the value 0 for dbh and height to include them in the species average. Replanting occurred three times, from age of 0.5 y to 2 y (March 2011, September 2011, December 2011, and November 2012) when about 15% of filling individuals and 9% of diversity were replanted.

2.4 Carbon equation

To quantify the carbon stock of aboveground biomass for each tree, we used a total carbon estimate equation developed for *Araucaria* forests (Ratuchne 2010), as native species-specific carbon equations were not available. The model was developed based on a set of species common to those planted in this study, with trees ranging from 5 cm dbh up to 105 cm, and included 91 individuals from 38 species ($R^2 = 0.975$, $F = 1550.46$):

$$C = 1.343 + 0.088 * dbh^2 + 0.005 * (dbh^2 * h) \quad \text{(Eq. 1)}$$

Where C is the carbon stock in kg, *dbh* is the tree diameter at breast height in cm, and h is the total height of the individual in meters. In the carbon analysis, we included only individuals and species that had already reached > 5 cm of dbh resulting in the exclusion of 13 diversity species that never reached that threshold (see Appendix I).

We also compared a commonly used equation of aboveground biomass (AGB) developed for tropical forests (Chave et al. 2014) which includes wood density (C = 48% of AGB) in contrast to the local equation. We found similar results when comparing Chave et al. (2014) equation to the local equation, although Chave et al. seemed to overestimate carbon stocks for big trees for our data. The top carbon sequestration species were majorly the same, and when comparing the top 20 species, we had 8 filling species and 12 diversity species with both equations. The top three species were in the exact same relative position in both estimations. We then opted to use the local equation for being more site-specific.

2.5 Data analysis

Total carbon was estimated using the equation described above for each individual in each year (kg/ind), and then we estimated carbon stock in tons per hectare for comparison purposes, considering the plantation spacing for each tree (6 m^2/ind). Dead individuals, or individuals that did not reach minimum dbh were accounted as carbon stock equal to 0 (and accounted for average), thus we had a factual estimative of the situation in the field. However, we only considered measurements after 2012/2 since, before that timeline, no species had reached 5 cm dbh. For the comparison of carbon between filling and diversity ecological groups, we used a t-test and considered $p \leq 0.05$ as significant. For the comparison among species, we used the Kruskal-Wallis test followed by Dunn’s test and considered the adjusted p-value using Bonferroni adjustment ($\alpha = 0.05$). All analyses were performed using R™ software 4.1.1 (R Core Team 2020), and the packages *data.table* (Dowle and Srinivasan 2021), *tidyverse* (Wickham et al. 2019), *ggpubr* (Kassambara 2020), *FSA* (Ogle et al. 2021), *rcompanion* (Mangiafico 2021) and *plotrix* (Lemon 2006).

2.6 Carbon sequestration simulations

We selected the species that sequestered the most carbon in both filling and diversity groups to test potential carbon storage in restoration models with different combinations of species, which included scenarios with different proportions of filling and diversity species. For our simulation, we assumed that all species would have similar performance regardless of influences of different neighboring species in the rows, but acknowledged that not all species may behave the same in alternative planting arrangements. Considering a usual restoration plantation (1,667 individuals per hectare) the following composition designs were simulated: the first scenario included only filling species, and 7 spp were selected; the second scenario included only diversity species, and 9 spp were selected; the third scenario included 5 filling and 5 diversity species, in different proportions (86% and 14%, respectively); and the fourth predicted scenario included 7 filling and 9 diversity species, also in different proportions (82% and 18%, respectively). The 16 species were selected based on higher carbon sequestration rates for each group. The age and carbon relationship was best fitted by a polynomial model for all scenarios, selected using the AIC criterion. We fitted a model for each scenario, based on the 12 individuals measured for each diversity species and the 72 for each filling species. We decided not to extrapolate beyond 10 y since we only collected data up to 8.5 years.

3. Results

3.1 Differences in carbon stock between ecological groups

We tested differences in carbon storage between groups from age 2 y (which was the first year that minimum dbh was recorded) to the last age monitored (8.5 y). At all ages, we found strong evidence that the amount of carbon stored was higher in the filling group than in the diversity group species (Figure 3, p<0.05).

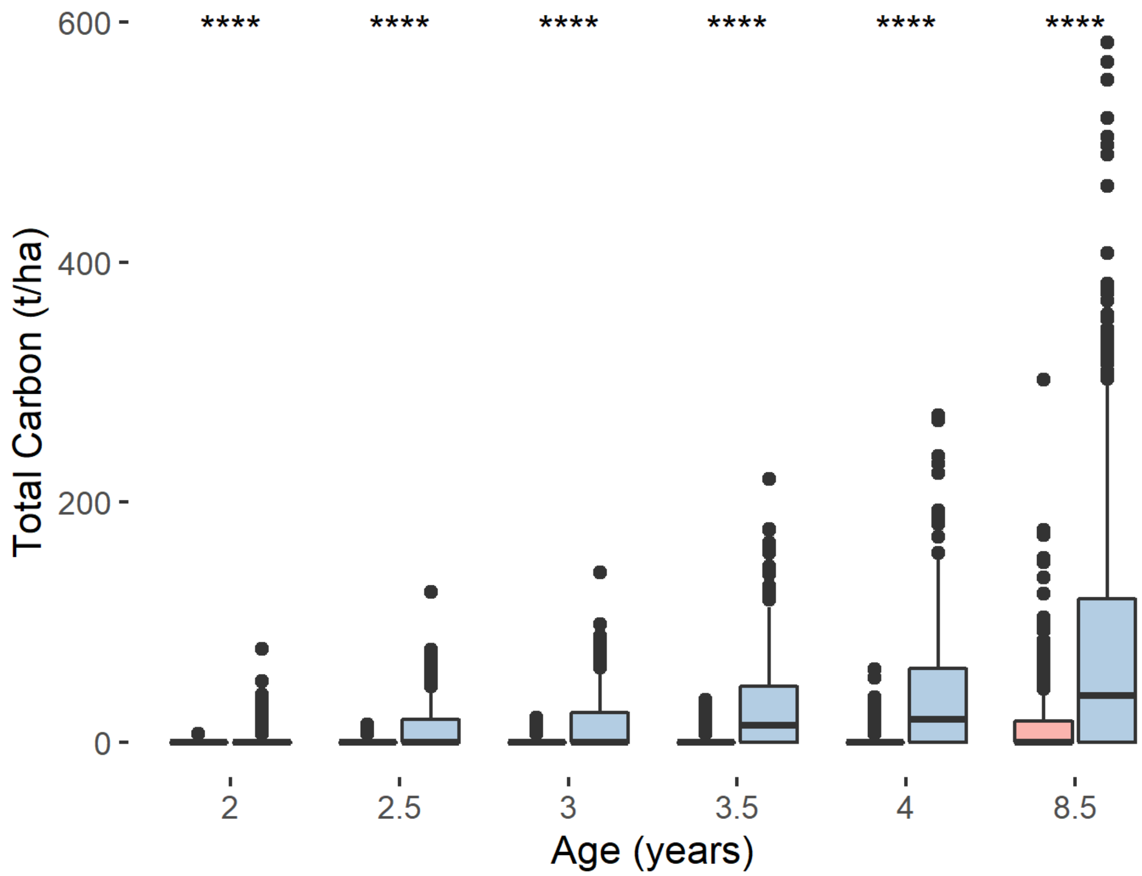

Figure 3: Total carbon stock (t ha^{-1}) comparison between filling and diversity species groups in each age. Black dots indicate the outliers individual trees. Blue boxes (right) represent the filling species group and red boxes (left) represent the diversity species group. **** indicates a significant difference between groups' total carbon stock in each year (p<=0.05).

We expected filling species to store more carbon than diversity species in the first few years. We found that after 8.5 y, filling species stored on average about six times more carbon (79.33 t ha^{-1}) when compared to diversity species (12.75 t ha^{-1}), which means that planting more filling species could improve carbon sequestration up to six times in the early years of restoration. The filling species are obviously important early carbon sinks in restoration plantations; however, there was substantial variation within species in each group (Figure 3).

Species previously classified in the same ecological group behave differently over time, and some diversity species could store more carbon in early years than some filling species (see Appendix I) which is why we suggest it is important to look not only to the species group but also the species level.

3.2 Variation among species in carbon stock

We found considerable variation among species carbon stock potential within the ecological groups. Within the filling group, there was substantial variation among species and through time. From the ten planted species, *Trema micrantha* is already losing more aboveground carbon than sequestering at the year 8.5 (Figure 4) decreasing carbon stored compared to 4 y, due to mortality.

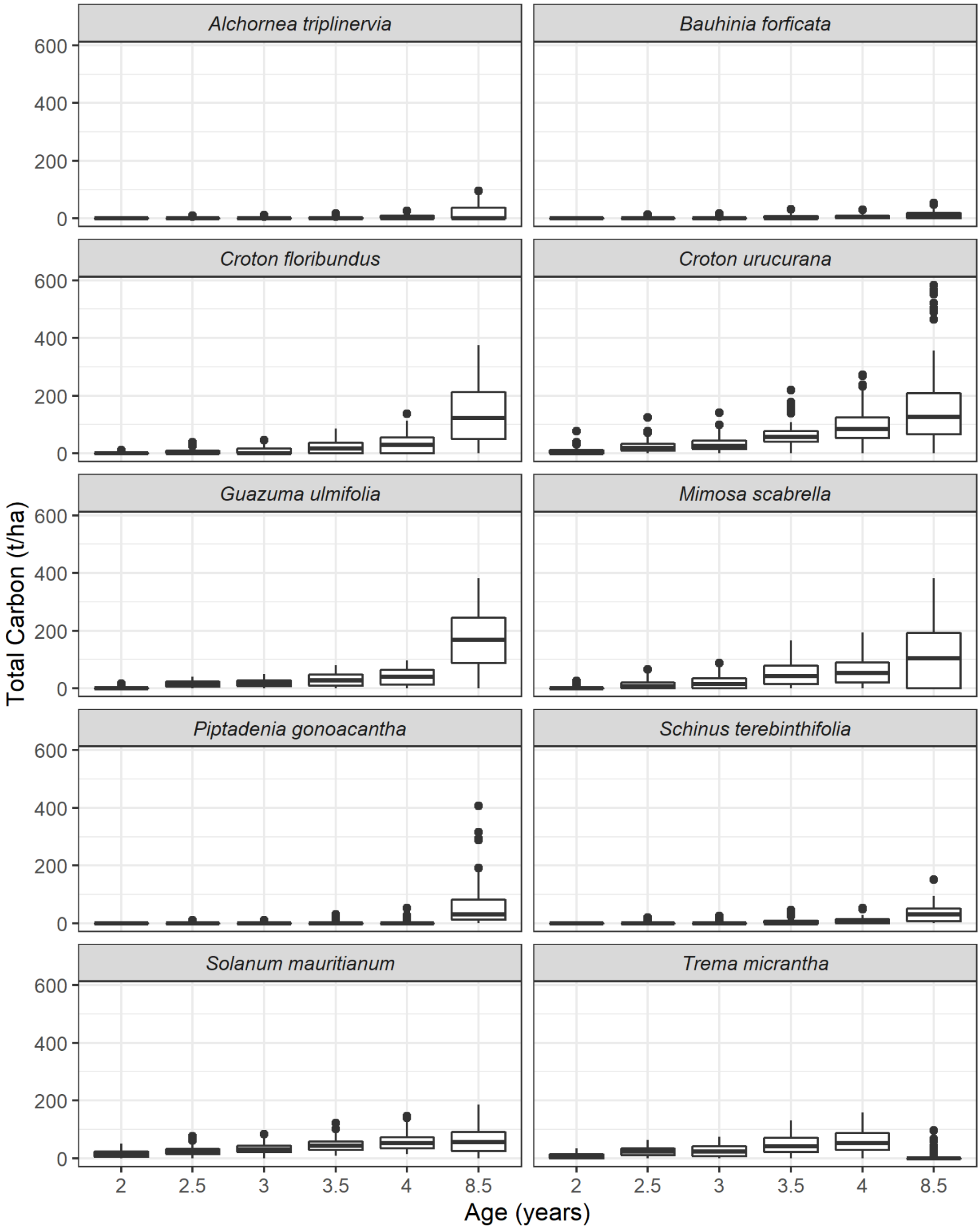

Figure 4: Total carbon stock (t ha^{-1}) for each filling species from ages 2 to 8.5 (2012 to 2019).

Examining the carbon stored in 2019 (Figure 5), three species can be highlighted for having the largest amount of stored carbon: *Guazuma ulmifolia*, *Croton urucurana*, and *Croton* *floribundus*. *Mimosa scabrella* also had large carbon stocks even though it already had many dead individuals in 2019 (about 35%). The filling species with lowest carbon stocks were *T. micrantha*, *Bauhinia forficata* and *Alchornea triplinervia*, while *Solanum mauritianum*, *Piptadenia gonoacantha*, and *Schinus terebinthifolia* had intermediate values of carbon stored.

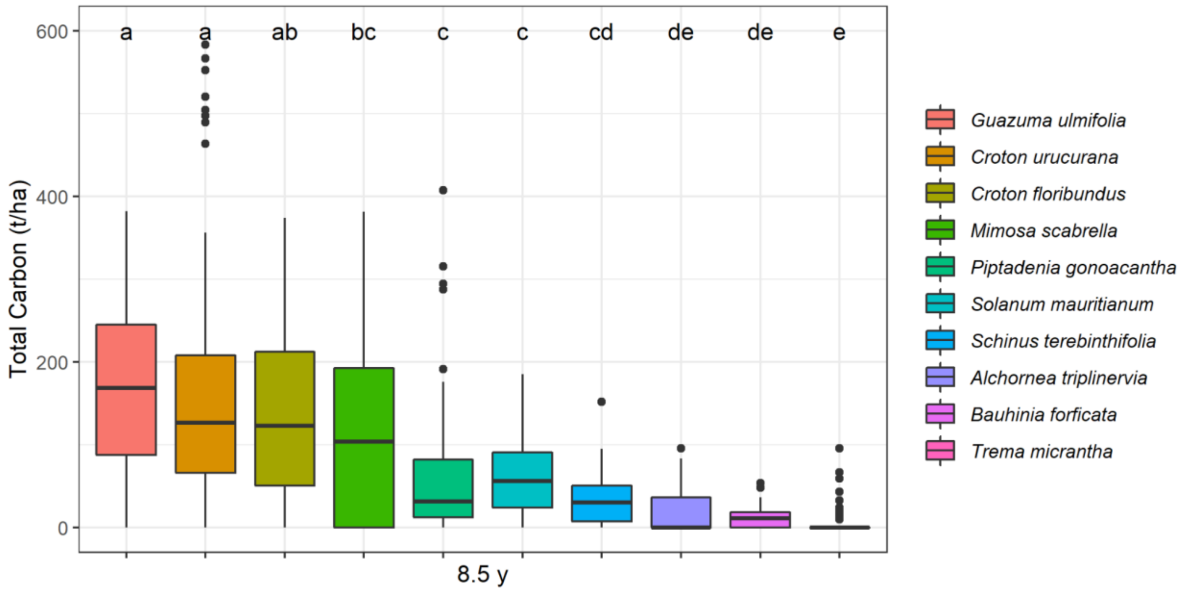

Figure 5: Total Carbon stock (t ha^{-1}) for each filling species at 8.5 years (2019). Different letters indicate significant difference on total carbon average based on Bonferroni adjustment ($p < 0.05$).

For the diversity group, we also found variations among species, which was expected because of the larger number of species. We selected the top ten species with the highest carbon stored at age 8.5 y to evaluate their performance. In the diversity group, only *Zanthoxylum rhoifolium* started having carbon stored after 2 y, which is related to the age its individuals reached dbh, while the others reached the minimum diameter threshold after 2.5 y or later (Figure 6).

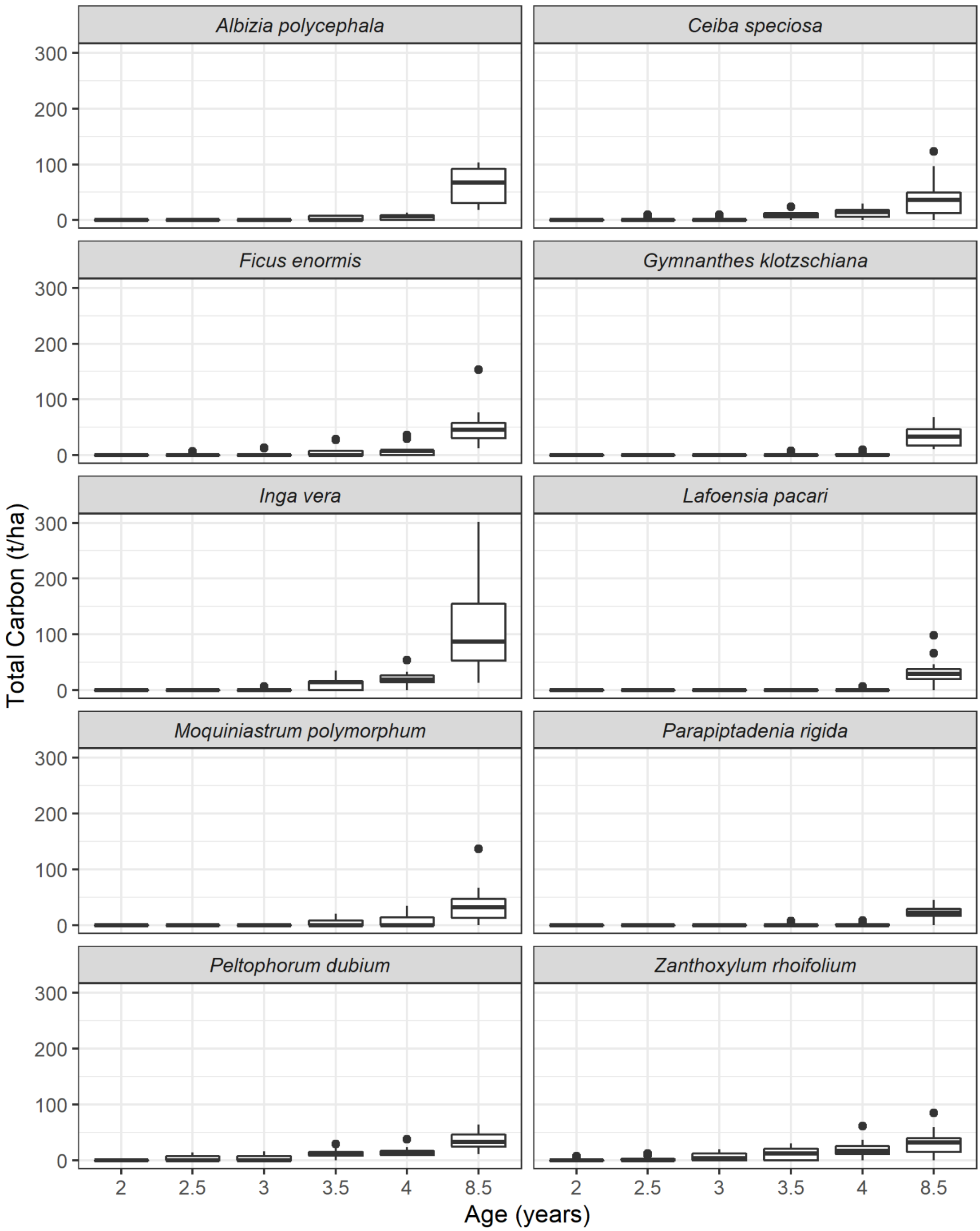

Figure 6: Total Carbon stock (t/ha) for each diversity species from ages 2 to 8.5 (2012 to 2019).

When examining the total carbon stored at 8.5 y, *Inga vera* had the highest carbon amount stored while the other species had similar values, except *Parapiptadenia rigida* which had the lowest value (Figure 7).

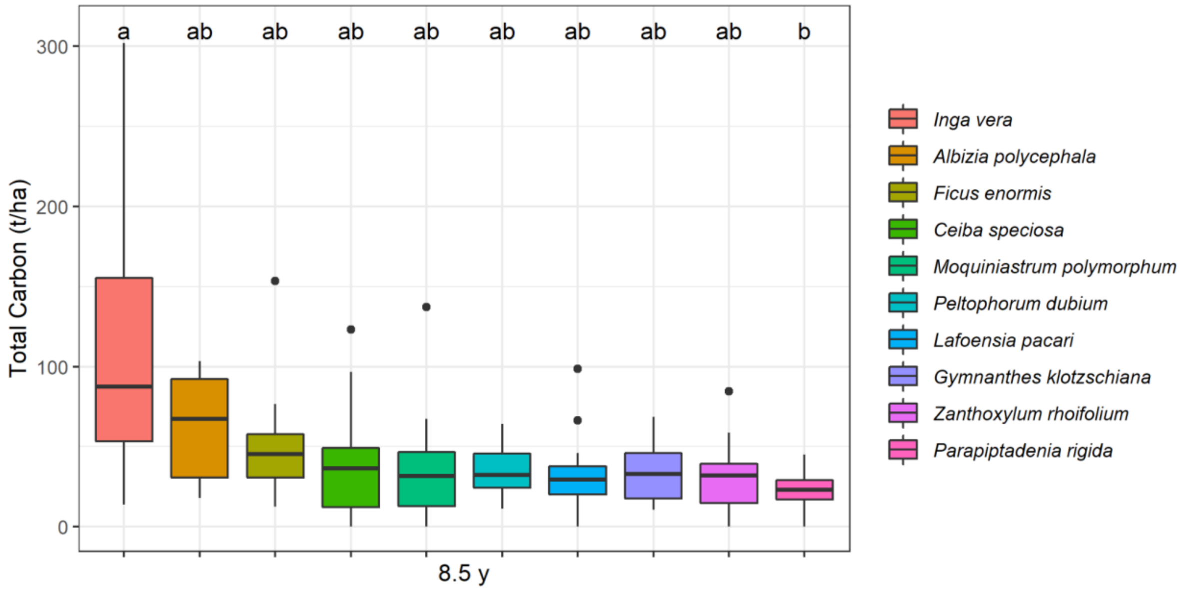

Figure 7: Total Carbon stock (t/ha) for 10 diversity species at 8.5 years (2019) with higher carbon stock values. Different letters indicate significant differences in the total carbon average based on Bonferroni adjustment ($p < 0.05$).

3.3 High-diversity plantation carbon stock

Total carbon stored by the whole high-diversity plantation reached an average of 46.04 tC ha^{-1} of carbon at age 8.5 y (2019) (Figure 8).

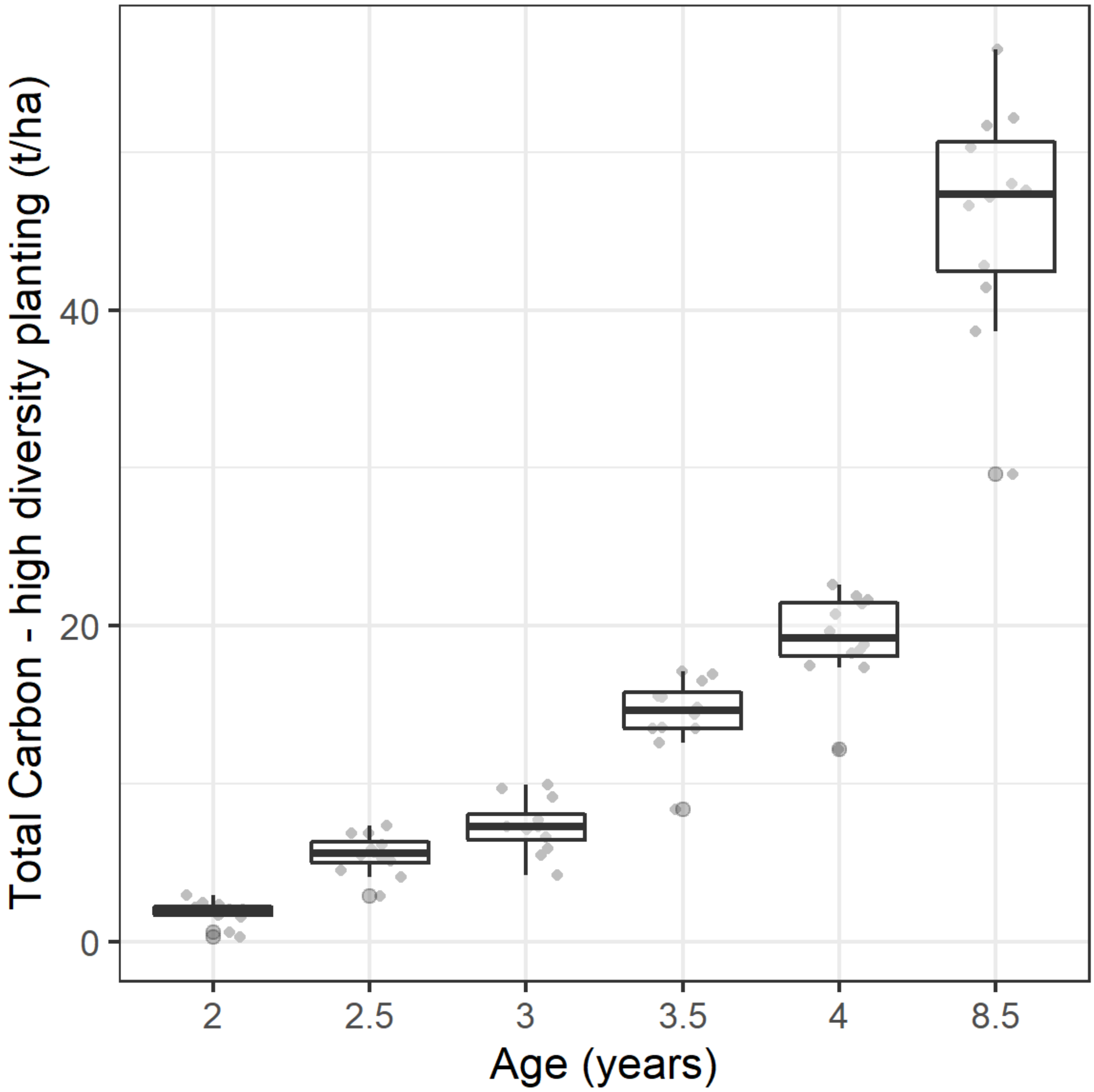

Figure 8: Carbon stock (t ha^{-1}) for high diversity planting at each age. Gray dots indicate subplots average, larger gray dots indicate the outliers.

There was a variable increase in the average of carbon stored from one year to the next, from an annual increase of 5.5 t ha^{-1} in the early years, up to 11.9 t ha^{-1} increasing annually at 4.5 y (Table 1). In the early years, variation was lower among subplots; however, this variation increased over the years and reached the greatest variation in 2019.

Table 1: High-diversity plantation carbon stock. Average considering all individuals.

Total Carbon mean (t ha^{-1})	SE	Year/Semester	Age (years)
1.797	0.162	2012.2	2
5.496	0.333	2013.1	2.5
7.301	0.425	2013.2	3
14.358	0.731	2014.1	3.5
19.200	0.941	2014.2	4
46.041	2.152	2019.1	8.5

3.4 Carbon sequestration predictions on selected species

From the filling group, we selected seven species that had the highest carbon stock in the first 8.5 y, excluding the three species with the lowest values (letter *e* on Figure 5), and for the diversity group, we selected 9 species, based on a comparison among species, excluding the lowest among the top ten (letter *b* on Figure 7).

A polynomial regression model was built for each scenario, considering the 16 species with the highest carbon stock. The scenario models (Table 2) were used to predict carbon stock over the first 10 years.

Table 2: Polynomial regression models for the four prediction scenarios of carbon estimation (y) based on age (x).

Scenario	Model	R^2	p value
Filling (7spp) - (100% Filling)	Carbon = -41.2994 + 22.7686 * x - 0.6124 * x^2	0.306	< 2.2e-16
Diversity (9spp) - (100% diversity)	Carbon = -6.8873 + 1.8655 * x + 0.5439 * x^2	0.438	< 2.2e-16
Filling (5spp) + diversity (5spp) - (86% filling + 14% diversity)	Carbon = -39.3938 + 19.9885 * x -0.1249 * x^2	0.352	< 2.2e-16

Filling (7spp) + diversity (9spp) - (82% filling + 18% diversity)	Carbon = -35.2267 + 19.0799 * x -0.4084 * x^2	0.288	< 2.2e-16

Considering the plantation at age 8.5 y, using the top 5 filling species + 5 diversity species resulted in the highest carbon stock estimation (121.49 tC ha^{-1}) followed by using only the selected top 7 filling species (107.99 tC ha^{-1}) and the top 16 species (7 filling + 9 diversity) (97.45 tC ha^{-1}). The lowest stock was when we used only the top 9 diversity species (48.27 tC ha^{-1}). Most predictions yielded greater carbon storage than the field whole planting, which included 10 filling species and 60 diversity species and stored 46.04 tC/ha at 8.5 years (Figure 9).

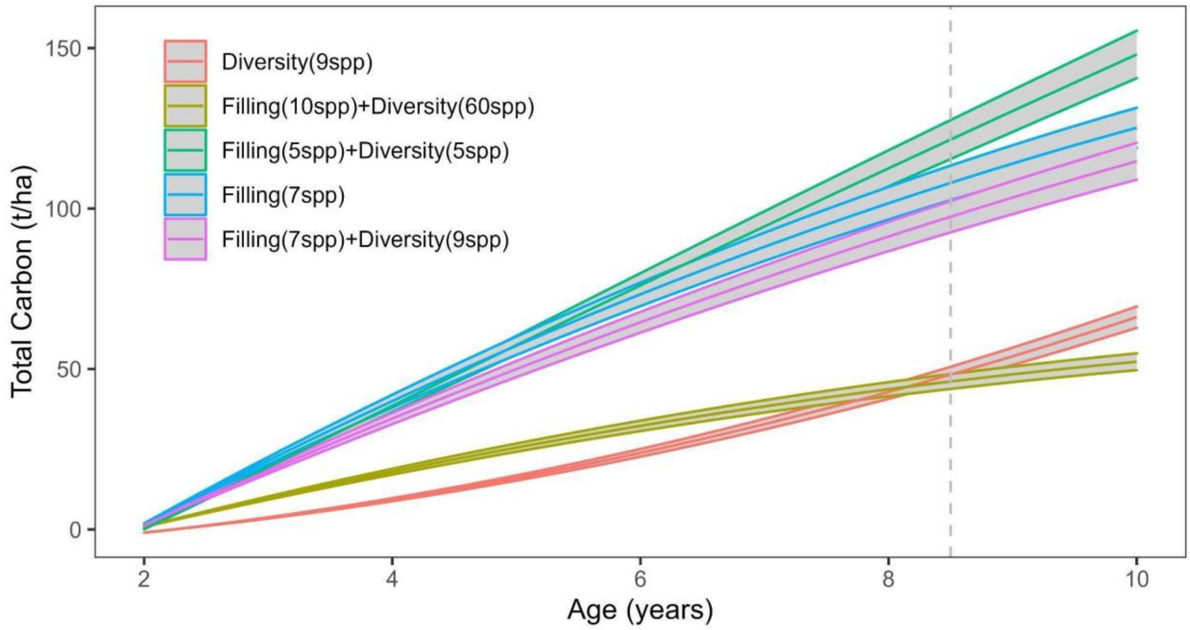

Figure 9: Total carbon (t ha^{-1}) predictions in simulated restoration composition/density designs, using a specific selection of species and different proportions of filling and diversity species. Dashed vertical line represents where predictions start. Species included in each scenario are highlighted on Appendix I.

4. Discussion

We found that a high-diversity plantation stored an average of 46.04 tC ha^{-1} after 8.5 years. However, when we modeled carbon storage balancing a subset of ten species in equal proportions by ecological group, we estimated we could more than double the carbon stored at the same age (121.49 tC ha^{-1}). As expected, we found differences in the amount of carbon stored when comparing, isolated, filling and diversity species groups, where filling species stored more carbon when compared to diversity species at all ages. We also observed substantial variation within the groups and concluded that from the ten filling species tested, seven could be best recommended for carbon-focused restoration projects, and nine diversity species were selected as more suitable for the same purpose.

4.1 How much carbon does a high-diversity plantation store?

Carbon stocks in old-growth tropical forests can vary following species richness and biomass gradients, with an average of 140 t ha^{-1} in South America (Sullivan et al. 2017). In Parana state, the average for forests' aboveground carbon stocks is 55 t ha^{-1} (SFB, 2018). However, when evaluating restoration methods, many variables could affect biomass production, including species richness, plantation density, and management intensity, besides edaphoclimatic conditions (Ferez et al. 2015; Pontes et al. 2019; Zanini et al. 2021). In our high-diversity plantation, a carbon stock of 46.04 tC ha^{-1} was estimated after 8.5 years, in a density of 1,667 trees ha^{-1}, and 70 species. A similar value (43.8 tC ha^{-1}) was found in a 9-y Atlantic Forest restoration site with 22 species planted in a semi-deciduous seasonal forest (Melo and Durigan 2006). Intensive management resulted in higher carbon stocks after 6 y, resulting in an increase of 32% (Ferez et al. 2015). Similarly, Campoe et al. (2010) found that intensive management increased biomass in the first three years of the restoration plantation. However, according to Pontes et al. (2019), the species richness can also affect carbon stocks over time when comparing different restoration methods after 19 years, where sites with higher species richness planted will produce more biomass in the future when including regenerated individuals and slow-growing long-lived species. Intervention intensity, which is related to human interference applied in order to restore, can affect carbon stocks at early ages when comparing active and passive restoration methods (Zanini et al. 2021). Carbon stocks can be highly variable under different restoration methods, which indicates that besides environmental conditions, changes in species composition could make a difference in carbon storage (Bunker et al. 2005; Kirby and Potvin 2007). Our plantations are relatively young and the rate of carbon stocks of filling and diversity species is non-static because diversity species tend to store more carbon than filling spp in the long term. On the other hand, filling species are natural colonizers, and this group's C stock will probably be more related to its regenerated and spread population in the long term. We also found that not only do species richness and ecological groups seem to have a role in the potential sequestration of carbon, but also individual species growth, which is influenced by management intensity.

4.2 Do ecological groups (filling and diversity) have a role in the amount of carbon sequestered in early restoration?

We observed that filling species stored on average more carbon than diversity species from ages 2 up to 8.5 (Figure 3), however, there was substantial variation within the ecological groups. Basically, filling and diversity groups composition will determine whether we have more carbon stored in the early years or in the future. Campoe et al. (2010) showed that using higher proportions of fast-growth species (67% vs. 50%; 20 species) in a semi-deciduous seasonal forest did not result in contrasting biomass accumulation in the first three years, while Shimamoto et al. (2014) studying six fast-growth and four slow-growth species in Atlantic Forest, predicted that fast-growing species stored more carbon in plantations up to 38 years, while slow-growing and long-lived species will store more carbon after this age.

4.3 Which species are better candidates for carbon-focused restoration projects?

Positive relations between species richness and biomass production have been previously described when compared to single-species plantations (Montagnini and Piotto 2011; Huang et al. 2018; Bongers et al. 2021; Guerrero-Ramírez 2021), but there is no exact number of species to define how many are enough, therefore, the question remains: is there a threshold of how many species it takes to make a highly diverse and productive plantation? It is probably not about species richness *per se*, but species facilitation traits that are matched to the site. Nitrogen-fixing species, for example, could increase the growth of all species planted in nutrient-poor locations (Forrester and Bauhus 2016). After eight years, high-diversity plantations more than doubled the amount of carbon sequestered when compared to monocultures in a subtropical forest in China (Huang et al. 2018). However, when considering the Yachi and Loreau (1999)`s insurance hypothesis, species richness in which the ecosystem productivity reaches its maximum will vary in relation to each species' response to ecosystem variation and not only based on the number of species used. In other words, the identity traits of the species used can play a major role in the functioning of the plantation which is why we explore different combinations of species.

Even though the species group has a strong influence on the amount of carbon stored, we found that some, previously classified by us, diversity species stored more carbon than filling species in our conditions, which means that not only the species group is important in defining carbon sinking goals but it is necessary to look at the species level. Based on average carbon stocks and ecological groups, we selected the 16 species with higher values of carbon stored in the early stage. We highlight these top-performing species as candidate species for carbon-focused restoration projects in our region (see Appendix I). Planting an intercalated combination of filling and diversity selected species will potentially increase carbon storage on restoration projects, besides making them more biodiverse. We recommend that more studies should be performed testing the use of fewer species and choosing species more carbon-efficient, as we highlight here, to evaluate if decreasing species richness would impact carbon stocks in the future.

4.4 How can we design a more carbon-efficient restoration composition?

Simulations of different combinations of fast (short-lived) and slow-growing (long-lived) species revealed that the best option when considering both short and long-term carbon storage would be to use an equal number of filling and diversity species (Shimamoto et al. 2014). However, while some studies show that fast-growth species could experience increasing mortality from 10 to 20 years (Parrotta and Knowles 1999), shortening the initial higher rates of carbon sequestration to early years and a shift towards a higher number of fast-growth species could lead to a decrease of 34% in carbon storage (Bunker et al. 2005). In Atlantic forests, plantations with only filling species could have more carbon stored when compared to mixed ones for up to 38 years (Shimamoto et al. 2014), which is a long time span for climate change mitigation purposes. Ten years seems to be a short scenario in nature when thinking about the future succession, however, the next ten years are the most important to humanity to prevent climate change to reach a threshold from where we cannot mitigate catastrophic events anymore, which means that restoration efforts should focus on enhancing carbon sequestration as much as possible in these next years while also conserving biodiversity.

Using the carbon sequestration models to predict carbon in different restoration composition designs is a helpful tool to understand how to promote higher carbon stocks. The best option, thinking in both short-term and long-term recovery, could be balancing the same number of filling and diversity species, *e.g.* focusing on our 10 top species (5 filling + 5 diversity). However, these predictions are based on the performance of these species in this specific high-diversity (70 spp.) design, where we are assuming that all species would perform the same even in different levels of diversity and species neighborhood, which should be further tested in the field. However, even if our findings result from simulations, they can have high applicability in subtropical silviculture, especially in selecting regional species for restoration projects in the southwestern Paraná state, Brazil.

We are aware that putting all the best performer species together in one planted forest may not necessarily provide the highest carbon stock because they may suffer from low complementary in terms of resource usage, however, in a restoration context, the goal is to create conditions that allow for natural regeneration and the establishment of a more diverse range of species over time (Bechara et al. 2016). As these species grow and mature, they will begin to use resources in different ways, leading to greater complementarity and more efficient resource use, which will eventually lead to higher overall productivity and carbon storage in the ecosystem.

5. Conclusions

Taking into account the climatic emergency that we are facing, restoration practices should focus on the use of mixed species with higher carbon sequestration rates. Our results could help improve species selection for restoration regional projects to reach carbon goals and inspire others to attempt to enhance biodiversity and carbon sequestration simultaneously. Finally, we recommend practitioners to test in the field our top-performance species, combining the fast and slow-growth tree species that could allow restoration projects to become more carbon-efficient.

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CHAPTER 2 - Performance of native tree species in a high diversity reforestation plantation in the subtropics of Brazil

Abstract

Brazil has committed to much needed global restoration goals to mitigate climate changes, however restoration of forests faces many challenges, starting with the lack of silvicultural knowledge in further regions of this continental country. We evaluated seventy native tree species in southwest Brazil. We examine important forest silvicultural variables including crown area, height, dbh, survival, species group classification, and frost resistance aiming to answer which species performed better for survival and frost resistance, growth, and canopy closure. We investigate if the species´ ecological group classification in “filling” (large-crowned pioneers) and “diversity” (non-pioneers) were consistent with field results in our region. Finally, predictions of climate change suggest climate variability will become greater so we wanted to examine which species were more sensitive to freezing temperatures.

We found that mortality rates varied among species, but overall higher mortality rates were found up to two years after planting. Eleven species had 100% survival, and all of them were from the “diversity” group. Up to four years after planting, filling species dominated the top ten rank of growing in height, dbh and crown area; however, after 8.5 years diversity species were half of the top ten rank for height, a similar pattern was found for dbh and also for canopy area. Some species did not grow as expected, and a distinct growth group emerged, where four “filling” species were growing faster than the rest from ages one up to four years, being less distinct after 8.5 years. Frost negatively affected survival in general, however some species were severely affected. We developed a rank of species performance to address tree species selection for restoration plantations in our still not well researched region.

1. Introduction

People depend on ecosystem services, while deforestation and degradation negatively affect the provision of these services, and forest restoration becomes important to contribute to the re-establishment of sustainable goals (Jong et al. 2021). Countries all over the world have started to take action for increasing restoration of forests, mostly as an effort to slow down climate change impacts (Campoe et al. 2010; Ripple et al. 2019, 2021; Aronson et al. 2020; Dubey et al. 2021). Brazil has created its own restoration goals, aiming to restore 12 to 15 million ha by 2030-2050 (MMA 2017). The lack of knowledge about native species performance in forest restoration efforts is one of the major challenges that Brazil faces to reach these goals (Morais Junior et al. 2020), especially in further regions of this continental and highly ecosystems diverse country.

Restoration methods have changed over the decades and more recently have shifted from single-species forests to more diverse and complex forests, because of the benefits of high biodiversity to restore ecosystem services (Jong et al. 2021). Since the same species may perform differently in distinct bioclimatic regions, choosing the right species for restoration goals is a difficult task, besides most local native species are still not tested in the field (Rorato et al. 2017). Showing evidence in the field to select native species that will thrive in not well researched restoration regions is also crucial to guide the production in forest nurseries.

One example of high-diversity restoration plantation methodology comprises the classification of species in ecological (successional) or silvicultural groups. However, any categorization of species requires assumptions, but these groupings can be useful when approaching a problem. In mature tropical forests, the pioneer and non-pioneer ecological groups strategy indicates growth rate and species survival, but the question remains if these categorizations could consistently predict success in restoration plantations (Martínez-Garza et al. 2013).

Seedlings survival planted in the field is very important since it directly affects restoration costs (Bechara et al. 2021). Seedling mortality can be high in the initial phases of restoration (usually 1-3 years) because they are more susceptible to environmental factors and transplanting shock (Grossnickle 2012; Charles et al. 2018). There is a lack of species survival information for mixed species plots with high levels of diversity (Charles et al. 2018). We still need to understand which local factors and how they affect species survival in the field, which will allow us to have more effective and efficient restoration projects.

Canopy cover is considered one of the most important indicators of the success of restoration plantations since its main idea is to quickly eliminate exotic grasses invasion and catalyze understory diversity colonization (Bechara et al. 2016). The coverage of the ground by the tree canopy needs to occur in the shortest possible time to reduce restoration costs and reduce reentry into the plantation for corrective measures (PACTO 2013). Species selection based on the ability to establish a closed canopy facilitates the restoration process.

Distinguishing ecological groups can be a good basis for species selection, but sometimes species can be too susceptible to local environmental factors such as freezing temperatures (Rorato et al. 2017). Frost occurrence can be a limiting factor for species performance in subtropical regions in high-elevation areas (Gatti et al. 2008) and forest restoration practices should be enhanced by focusing on nurse species that demonstrate frost resistance or resilience (Marcuzzo et al. 2014). Climate change and extreme events could impact restoration efforts, as distribution and frequency of frosts will likely change, ultimately changing species distribution (Inouye 2001). Here, we evaluate the species response to freezing temperatures to provide some insights into species selection for frost resistance.

In this scenario, our main goal was to evaluate species performance in a high-diversity plantation which includes detecting performance differences in growth strategies and mortality rates. We also aimed to test if there were differences in the ecological group classification among species over time. The following questions are addressed: 1) which species performed better for survival, growth, and canopy closure? 2) were the ecological group's classification - “filling” and “diversity” - consistent with the field results? 3) which species were more sensitive to frost?

2. Methods

2.1 Study site

This study was conducted at the Federal University of Technology in Parana, Dois Vizinhos, Brazil, in an experimental field (25º41’44” - 25º41’49” S; 53º06’23” - 53º06’07” W) established in October 2010 (Figure 10). The annual temperature average is 19.2 °C and frosts occur approximately once every two years. Annual precipitation is about 2,044 mm and the elevation ranges from 495 to 504 m. The vegetation is an Atlantic Forest ecotone between *Araucaria* Forest and Seasonal Semideciduous Forest (Bechara et al., 2021; IBGE, 2004).

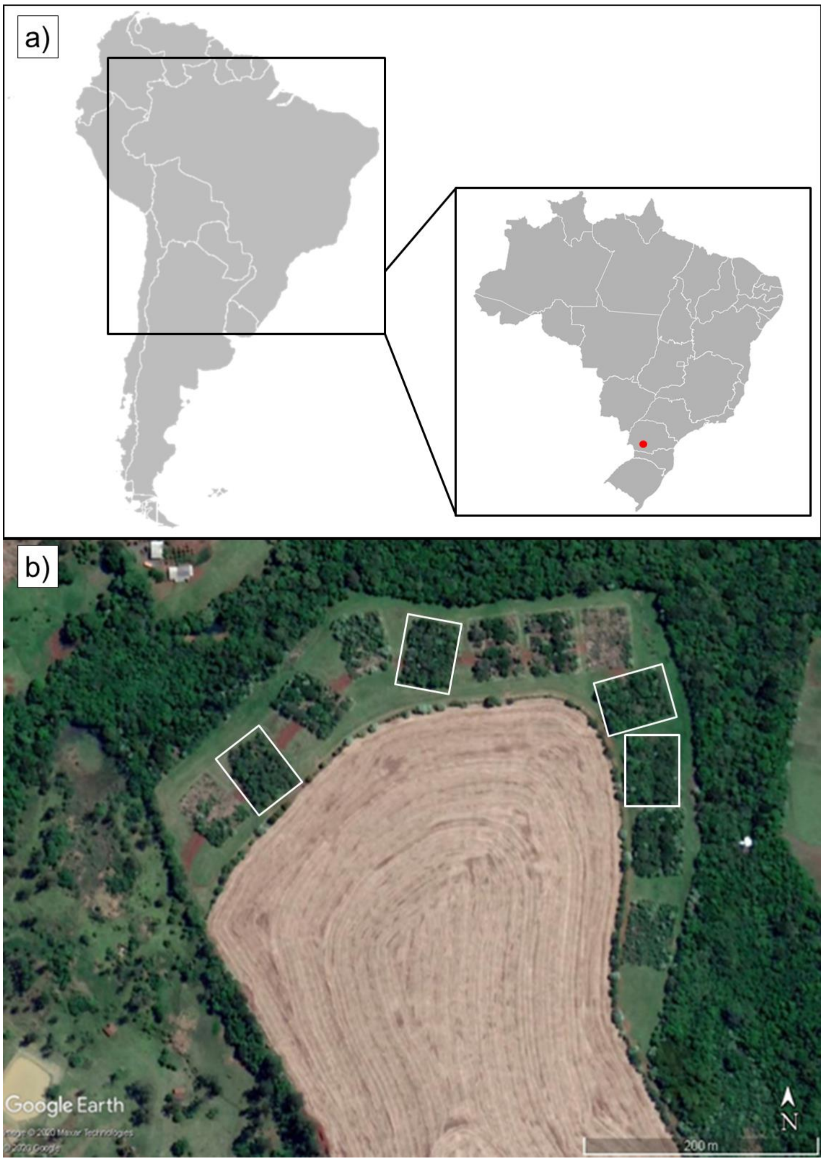

Figure 10: a) Study site relative location in Brazil where the red dot shows the study site in Paraná state, Brazil. b) Plots used in this experimental area (Bechara et al, 2021) are indicated in white rectangles.

2.2 Experimental design

Plantation was settled by preparing the soil by tractor furrowing planting lines, mowing and applying herbicide in total area. Native tree seedlings were planted receiving fertilization on the pits (NPK 5-2-10) and hydrated gel (3L). We also used cardboard mulching and insecticide traps for ants. We planted species by considering two different ecological groups (based on Rodrigues et al., 2009): 1) “filling species” - fast-growth and early shady canopy development ; and 2) diversity - slow-growth species; the species selection and classification on each group was based on the literature and field experts considering also regional development of each species. We selected 10 species from the filling group and 60 species from the diversity group to test species performance in a mixed culture (see Appendix I). The plantation maintenance included intensive management (fertilization, replantings, invasive plants and ants control) during the first three years. We selected the planting age as a reference time for saplings because we could not control its biological age since they came from several regional nurseries, however, all came from similar size tubes.

Seedlings were planted using the spacing of 2 m within the row and 3 m between rows, including a total of 1,440 individuals planted, 360 in each plot, 180 from filling species, and 180 from diversity species. Each filling species had 72 repetitions and each diversity species had 12 repetitions. The two ecological groups were intercalated between rows and within the row. Every species was planted with the same species neighbors, in a systematic way, in each of a total of four plots (40 x 54 m each, Figure 11). Each species neighbors design had 3 repetitions inside each plot.

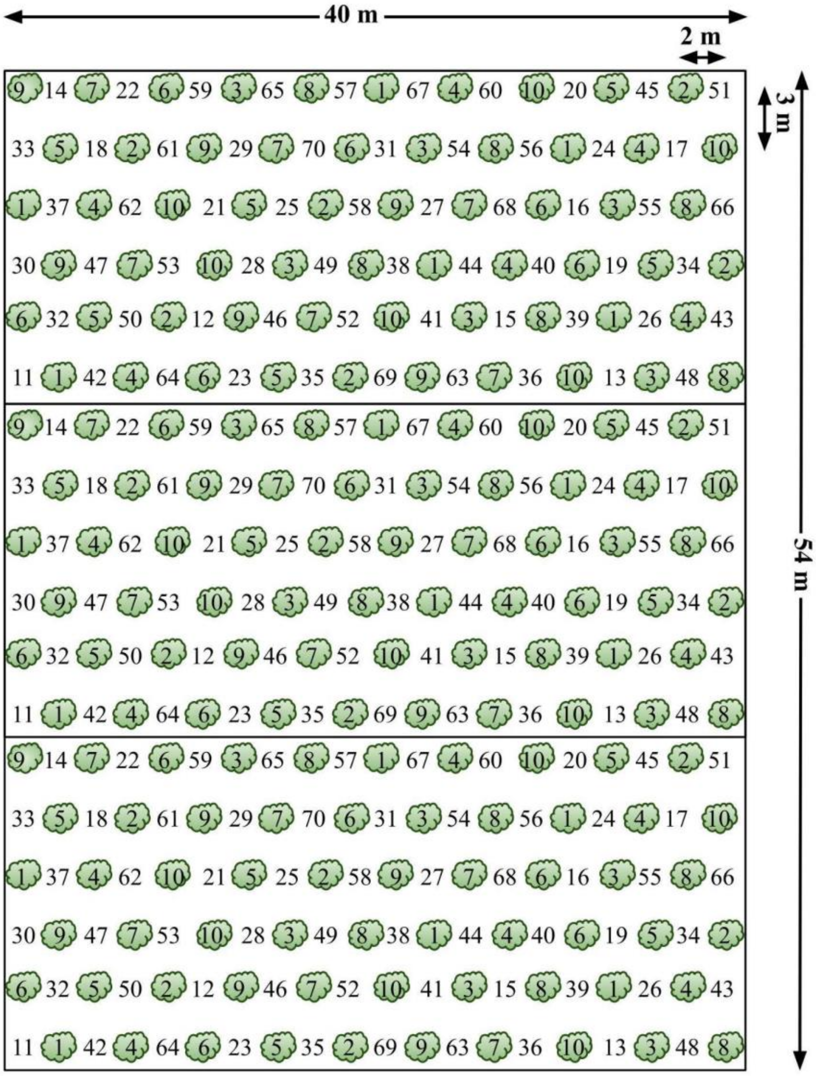

Figure 11: Ecological groups planting method in filling (green crowns) and diversity species. Each number corresponds to a species (see Appendix I).

2.3 Tree sampling

Seedlings were monitored starting in June 2011 (six months after planting), followed by Nov 2011, Jun 2012, Nov 2012, May 2013, Nov 2013, Jun 2014, Dec 2014, and finally Aug 2019 (ages of 0.5 to 8.5 y, respectively). Every individual was measured considering: i) diameter at breast height (dbh; if > 5 cm dbh) or root collar diameter (rcd; if dbh < 5cm); ii) total height (m); and iii) crown area (m^2), using two perpendicular measurements for each tree. Dead individuals received the value 0 for all variables. Replantings occurred three times, from age of 0.5 y to 2 y (Mar 2011, Sep 2011, Dec 2011, and Nov 2012), when dead individuals were tracked and replaced.

2.4 Data analysis

All analyses were performed using R software 4.1.1 (R Core Team, 2020), and we used the packages *data.table* (Dowle and Srinivasan, 2021), *tidyverse* (Wickham et al., 2019), *ggpubr* (Kassambara, 2020), *fuzzySim* (Barbosa, 2015), *FactoMineR* (Lê et al., 2008), *factoextra* (Kassambara and Mundt, 2020) and *ggplot2* (Wickham, 2016). We first fitted regression models to estimate rcd based on dbh using data for species where we measured both dbh and rcd because some diversity group species never reached dbh even after 8.5 years. For diversity species, we tested three different regression models using all species data together, the first model was a linear model considering rcd as a response variable of dbh; in the second model we fitted a linear mixed-effects model, adding species as a random effect for slope; in the third model we fitted a linear mixed-effects model, adding species as a random effect for slope and dbh as a random effect for intercept; the best model for diversity species (selected using AIC) was the linear mixed-effects model allowing each species to have a random intercept and slope. For the filling species, since more data was available, we fitted a linear model for each species. Using these models, we estimated RCD values for all species at all ages.

2.4.1 Principal component analysis and cluster analysis

We used a principal component analysis followed by cluster analysis to test if there was a difference between the groups' classification and the growth rate of the species in the field by selecting two points in time to test it. First, we considered the ages 0.5 to 4 y (Jun 2011 to Dec 2014), where we calculated the annual growth rate for RCD, total height, crown area, and crown height; then we calculated the average for each species using all rates and also age 4-y values for all variables. Second, we considered the ages 4 to 8.5 y (Dec 2014 to Aug 2019) and calculated the same variables as described above; however, *Butia capitata* was excluded from the last years because rcd values were too high, since it's a palm that can reach 1 m of rcd. We then scaled all variables (RCD, RCD annual rate, total height, total height annual rate, crown area, crown area annual rate, crown height and crown height annual rate for each age, 4 y and 8.5 y), and ran a PCA followed by k-means analysis. We ran a silhouette analysis (Rousseeuw 1987) to decide the ideal number of clusters, although it indicated that the most parsimonious number of clusters was two, three was almost as good, we decided to test three clusters because based on expert knowledge from the field, we expected a small number of filling species to have faster growth when compared to other filling and diversity species.

2.4.2 Performance analysis

To evaluate the performance of each species on survival, we calculate the annual mortality rate for each census interval. Survival was calculated based on the 12 individuals planted at first for the diversity species and the 72 individuals planted for the filling species. The annual mortality rate was calculated based on dead individuals through time between measurements and replantings (total of 13 points in time, 9 measurements, and 4 replantings) (Eq. 1), a commonly used equation for tropical regions where λ is the annual mortality rate, n_0

is the number of individuals at the beggining of the measurement interval, n_t is the number of individuals at the end of the measurement interval, and t is the time between measurements.

$\lambda = \ln(n_0) - \ln(n_t) / t$ *(Eq. 1)* (Lewis et al. 2004)

To evaluate height and dbh growth, and canopy area, we selected two points in time: ages of 4 and 8.5 y, so we could evaluate how species were performing in these distinct forest development phases for each variable. We calculated the canopy area based on the two field measurements of the crown width, considering that it has an ellipse form (Eq. 2)

$CA = (\pi * C1/2 * C2/2)$ *(Eq. 2)*

Where CA = crown area of the individual (m^2), C1 and C2 = crown longitudinal and transversal length to the planting line (m).

We ranked height, dbh, and canopy cover based on average for each species in the selected years. We then selected the top ten species for each variable and both ages. We also built a rank with all variables together, we established three classes for each variable (canopy cover, total height, diameter growth and survival), based on Table 3 and then assigned a weigh for each class; high values weighed 15 points, intermediate values weighed 10 points and low values weighed 5 points.

Table 3: Classes for each variable used to build a general species rank.

Canopy cover	
High canopy cover	species with crown area higher than 5 m^2 at 4 years and higher than 15 m^2 at 8 years
Intermediate canopy cover	crown area from 1m^2 - 5m^2 at 4y and >5m^2 - 15m^2 at 8y

Low canopy cover	crown area bellow 1m² at 4y and bellow 5m² at 8y
Total height	
High height growth	height >5m at 4y and >10m at 8y
Intermediate height growth	height from 3m up to 5m at 4y and >5 m at 8y
Low height growth	height lower than 3m at 4 y and lower than 5m at 8y
Diameter growth	
High diameter growth	dbh > 5cm at 4y and >10cm at 8y
Intermediate diameter growth	dbh up to 5cm at 4y and up to 10 cm at 8y
Low diameter growth	no individual has reached minimum dbh of 5cm at 4y and 8y
Survival	
High survival	species with annual mortality rate up to 1%
Intermediate survival	annual mortality rate from 1-2%
Low survival	annual mortality rate > 2%

2.4.3 Frost effect analysis

Temperature data was downloaded from a local station website, located 1 km from the study site (GEBIOMET 2022) for years 2011 to 2019, when monitoring took place. We detected a total of five seasonal frost events (temperatures below 0°C) which occurred in Jun-Jul 2011 (06/28/2011 and 07/04/2011), Jul-Aug 2013 (07/24/2013 and 08/28/2013), Jun 2016 (12/6/2016), Jul/2017 (18/07/2017) and Jun-Jul 2019 (6/7/2019 and 7/7/2019). Frost occurrence before the following measurement or replanting were accounted for and considered a frost event. We considered the nine measurements in the field, as well as the replanting, to evaluate individual's response to frost and in order to do that, we tracked when the individual died (species status), how large it was in the census before death (based on rcd), and if there was a frost before that measurement or not. If an individual died and was replanted, the death was also accounted for, and a new individual was added to the database for the sapling replanted. To understand frost's influence on mortality we fitted a generalized linear mixed-effects model with mortality (whether the species died or not, 0 or 1) as a response variable of frost occurrence, and added lag of rcd (the last measurement before death) as a fixed effect, and subplot nested in plot, frost occurrence, and species as random effects (Eq. 3).

mortality ~ frost occurrence + lagRCD + (1|plot:subplot) + (frost occurrence|species)(Eq. 3)

3. Results

3.1. Which species had the best survival, growth, and canopy cover?

3.1.1 Survival

Filling species with the lowest mortality rates were *Schinus terebinthifolia, Solanum mauritianum, Guazuma ulmifolia,* and *Bauhinia forficata*, while the highest mortality rates were from individuals of *Alchornea triplinervia*, *Piptadenia gonoacantha*, *Croton floribundus* and *Mimosa scabrella*, in this order (Appendix II). Overall, higher values for annual mortality rates were found up to two years after planting, where we could observe up to 9% of *A. triplinervia* saplings dying one year after planting (Figure 12).

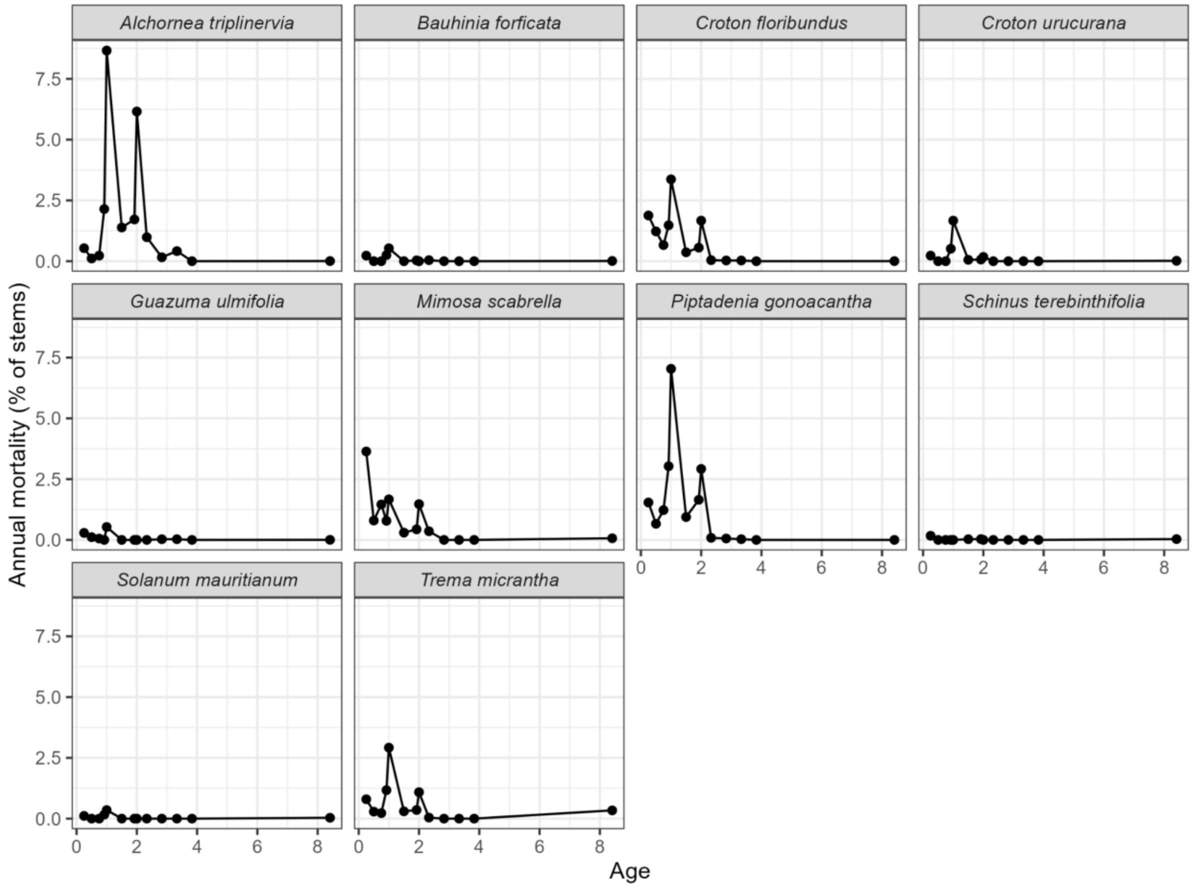

Figure 12: Annual mortality rate for filling species from 0 to 8.5 years in percentage of saplings.

Among the 70 species evaluated, 11 had no mortality, which means that 100% of the planted individuals survived during the first 8.5 years, and all these species belonged to the diversity group: *Albizia polycephala*, *Allophyllus edulis*, *Balfourodendron riedelianum*, *Cedrela fissilis*, *Myrceugenia euosma*, *Eugenia pyriformis*, *Eugenia uniflora*, *Gymnanthes klotzschiana*, *Lafoensia pacari*, *Lonchocarpus* sp., and *Podocarpus* sp. (see Appendix II). On the other hand, the ten diversity species with the highest mortality rates were *Annona cacans*, *Jaracatia spinosa*, *Myrsine coriacea*, *Ilex paraguariensis*, *Monteverdia aquifolia*, *Sloanea hirsuta*, *Erythrina falcata*, *Trichilia clausenni*, *Cabralea canjarana* and *Cupania vernalis*, (Figure 13).

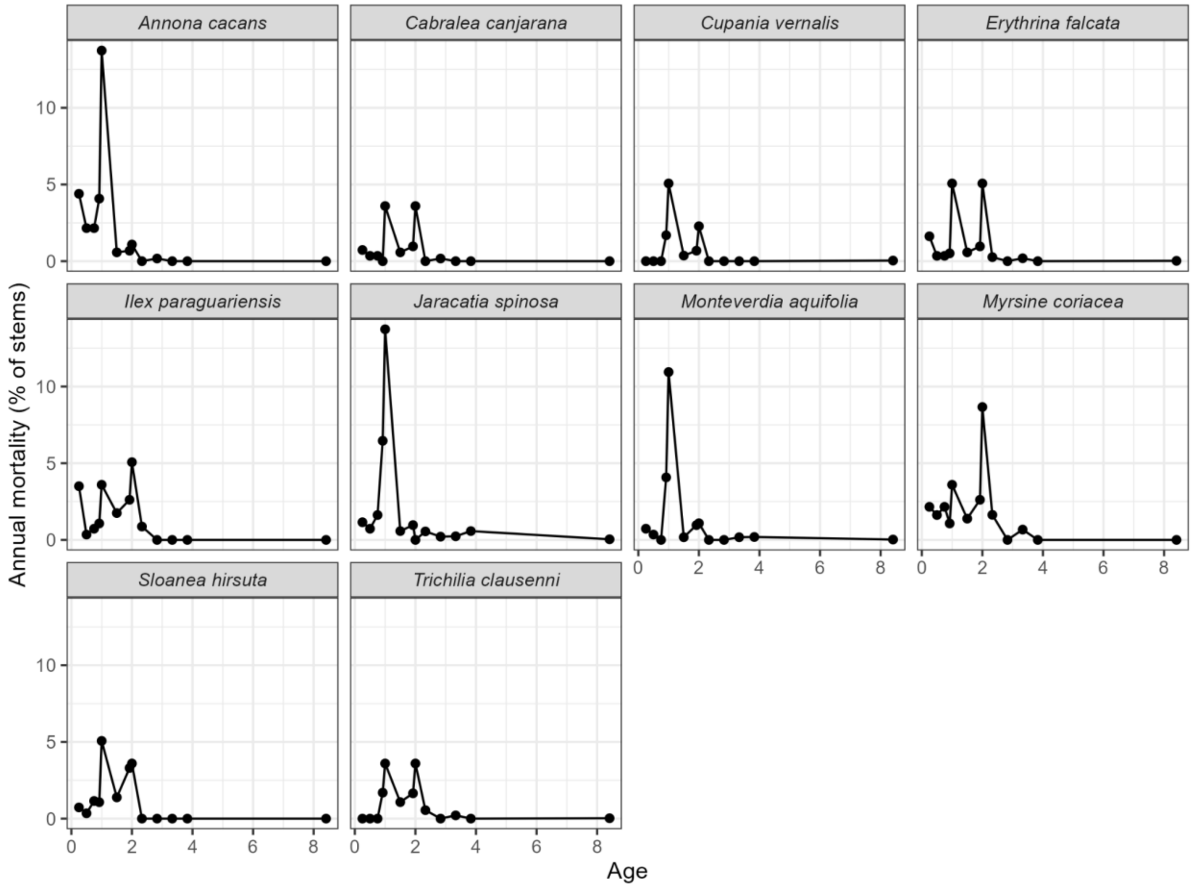

Figure 13: Ten highest annual mortality rates for diversity species from 0 to 8.5 years. Blue lines indicate the local polynomial regression.

For diversity species, higher mortality rates were observed up to 2 years after planting, however, we could observe higher percentages when compared to filling species, where *A. cacans* and *J. spinosa* for example, reached an annual mortality around 14% of one year after planting.

3.1.2 Growth

We selected the top 10 species in height growth for ages 4 and 8.5 y, and we could see a shift between groups and species through time (Table 4).

Table 4: Total height growth rank at 4 and 8.5 years for the first ten species ranked at each age.

4 years			**8.5 years**		
Species	**Group**	**Height (m)**	**Species**	**Group**	**Height (m)**
Croton urucurana	filling	7.04 ± 1.15	*Guazuma ulmifolia*	filling	12.3 ± 3.62
Trema micrantha	filling	6.73 ± 1.72	*Croton floribundus*	filling	11.8 ± 3.7
Mimosa scabrella	filling	6.71 ± 2.70	*Albizia polycephala*	diversity	11.6 ± 2.35
Guazuma ulmifolia	filling	6.58 ± 1.97	*Inga vera*	diversity	10.3 ± 2.72
Solanum mauritianum	filling	6.38 ± 1.01	*Croton urucurana*	filling	9.54 ± 3.30
Peltophorum dubium	diversity	5.99 ± 1.12	*Peltophorum dubium*	diversity	9.38 ± 1.78
Croton floribundus	filling	5.94 ± 2.08	*Piptadenia gonoacantha*	filling	9.38 ± 4.66
Zanthoxylum rhoifolium	diversity	5.76 ± 2.26	*Ceiba speciosa*	diversity	8.79 ± 2.98
Ceiba speciosa	diversity	4.96 ± 1.19	*Solanum mauritianum*	filling	8.45 ± 3.99
Ficus enormis	diversity	4.85 ± 0.956	*Zanthoxylum rhoifolium*	diversity	8.28 ± 4.07

At 4 y, the first five species with the highest height average were from the filling group, however at 8 y, it changed to only three filling species in the top five. *C. urucurana* was the tallest species at 4 y and *G. ulmifolia* was the tallest at 8.5 y. At 4y, there were six species from the filling group and four from the diversity group among the top ten rank, changing to five from each group at 8.5 y. At 8.5 y, the filling species *Trema micrantha* and *Mimosa scabrella* which were in second and third position at four years were not among the top ten anymore.

Regarding to dbh growth, at both ages, the top ten had six filling species, and four diversity species, however, we could see a shift in positions and species at 8.5 y (Table 5).

Table 5: Dbh growth rank at 4 and 8.5 years for the first ten species ranked at each age.

4 years			**8.5 years**		
Species	**Group**	**DBH (cm)**	**Species**	**Group**	**DBH (cm)**
Croton urucurana	filling	19.8 ± 7.13	*Guazuma ulmifolia*	filling	24.2 ± 8.68
Solanum mauritianum	filling	16.1 ± 3.77	*Croton urucurana*	filling	24.0 ± 11.6
Mimosa scabrella	filling	14.6 ± 8.07	*Croton floribundus*	filling	20.7 ± 9.96
Trema micrantha	filling	14.6 ± 7.54	*Inga vera*	diversity	19.6 ± 7.59
Guazuma ulmifolia	filling	12.1 ± 6.53	*Mimosa scabrella*	filling	16.1 ± 13.2
Croton floribundus	filling	9.77 ± 7.33	*Albizia polycephala*	diversity	15.0 ± 4.14
Inga vera	diversity	8.82 ± 4.68	*Ficus enormis*	diversity	14.3 ± 5.10
Zanthoxylum rhoifolium	diversity	8.16 ± 4.82	*Solanum mauritianum*	filling	14.3 ± 7.62
Peltophorum dubium	diversity	7.68 ± 2.27	*Piptadenia gonoacantha*	filling	12.3 ± 9.40
Ceiba speciosa	diversity	6.41 ± 4.13	*Peltophorum dubium*	diversity	11.8 ± 2.71

The largest species in dbh at 4 y was *C. urucurana*, and at 8.5 y it was *G. ulmifolia* the same species as seen for height. Again as seen for the height average, *T. micrantha* also declined in average dbh growth and left the top ten after 4.5 years. *M. scabrella* only lost a few positions, as mortality was not as frequent for this species, but a decline in the number of stems rather than total individual death, was observed in the field.

3.1.3 Canopy cover - crown area

We selected the top 10 species for each age: at 4 y, *C. urucurana* presented the largest canopy area, followed by *T. micrantha*, *S. mauritianum*, *M. scabrella*, *I. vera*, *S. terebinthifolia*, *C. floribundus*, *G. ulmifolia*, *Celtis* sp., and *Moquiniastrum polymorphum*, in this order (Table 6).

Table 6: Canopy area rank at 4 and 8.5 years for the first ten species ranked at each age.

4 years			**8.5 years**		
Species	**Group**	**Canopy area (m^2)**	**Species**	**Group**	**Canopy area (m^2)**
Croton urucurana	filling	32.5 ± 16.6	*Guazuma ulmifolia*	filling	45.7 ± 28.8
Trema micrantha	filling	29.5 ± 14.7	*Croton urucurana*	filling	43.9 ± 42.2
Solanum mauritianum	filling	26.8 ± 9.71	*Albizia polycephala*	diversity	36.1 ± 14.1
Mimosa scabrella	filling	20.5 ± 12.7	*Inga vera*	diversity	30.9 ± 24.8
Inga vera	diversity	15.8 ± 6.76	*Croton floribundus*	filling	29.0 ± 21.8
Schinus terebinthifolia	filling	14.7 ± 5.67	*Moquiniastrum polymorphum*	diversity	24.3 ± 8.73
Croton floribundus	filling	13.9 ± 8.32	*Mimosa scabrella*	filling	23.7 ± 22.3
Guazuma ulmifolia	filling	13.9 ± 6.35	*Calliandra tweedii*	diversity	19.0 ± 13.3
Celtis sp.	diversity	10.8 ± 9.13	*Piptadenia gonoacantha*	filling	18.2 ± 16.7
Moquiniastrum polymorphum	diversity	9.64 ± 3.01	*Parapiptadenia rigida*	diversity	16.8 ± 7.35

At 8.5 years, *G. ulmifolia* had the largest canopy area followed by *C. urucurana*, *A. polycephala*, *I. vera*, *C. floribundus*, *M. polymorphum*, *M. scabrella*, *C. tweedii*, *P. gonoacantha*, and *P. rigida*, in this order (Table 5). Only five filling species were in the top 10 rank at 8.5 y, and the species with the highest crown area (*Guazuma ulmifolia*) was in the eighth position at 4 y. *T. micrantha* and *S. mauritianum* that were in the second and third position at 4 y, were not in the top ten anymore at 8.5 y.

3.1.4 Species performance classification

We then created a general attribute classification with the 70 species studied and weighed each variable according to Table 3 thresholds, which can help the selection of more suitable species according to the restoration goals (Table 7).

Table 7: High (blue), intermediate (yellow) and low (red) species performance for crown area (CA), height (H), diameter (DBH) and survival (S).

Species	Ecological group	Rank	CA 4y	CA 8y	H 4y	H 8y	DBH 4y	DBH 8y	S
Croton floribundus	filling	105	● (blue)	● (blue)	▲ (blue)	▲ (blue)	● (blue)	● (blue)	✚ (blue)
Guazuma ulmifolia	filling	105	● (blue)	● (blue)	▲ (blue)	▲ (blue)	● (blue)	● (blue)	✚ (blue)
Croton urucurana	filling	100	● (blue)	● (blue)	▲ (blue)	▲ (yellow)	● (blue)	● (blue)	✚ (blue)
Inga vera	diversity	100	● (blue)	● (blue)	▲ (yellow)	▲ (blue)	● (blue)	● (blue)	✚ (blue)
Mimosa scabrella	filling	100	● (blue)	● (blue)	▲ (blue)	▲ (yellow)	● (blue)	● (blue)	✚ (blue)
Solanum mauritianum	filling	100	● (blue)	● (blue)	▲ (blue)	▲ (yellow)	● (blue)	● (blue)	✚ (blue)
Albizia polycephala	diversity	95	● (blue)	● (blue)	▲ (yellow)	▲ (blue)	● (yellow)	● (blue)	✚ (blue)
Peltophorum dubium	diversity	95	● (blue)	● (yellow)	▲ (blue)	▲ (yellow)	● (blue)	● (blue)	✚ (blue)
Lafoensia pacari	diversity	90	● (blue)	● (blue)	▲ (yellow)	▲ (yellow)	● (yellow)	● (blue)	✚ (blue)
Moquiniastrum polymorphum	diversity	90	● (blue)	● (blue)	▲ (yellow)	▲ (yellow)	● (yellow)	● (blue)	✚ (blue)
Schinus terebinthifolia	filling	90	● (blue)	● (blue)	▲ (yellow)	▲ (yellow)	● (yellow)	● (blue)	✚ (blue)
Zanthoxylum rhoifolium	diversity	90	● (blue)	● (yellow)	▲ (blue)	▲ (yellow)	● (blue)	● (yellow)	✚ (blue)
Ficus enormis	diversity	85	● (blue)	● (yellow)	▲ (yellow)	▲ (yellow)	● (yellow)	● (blue)	✚ (blue)
Gymnanthes schottiana	diversity	85	● (blue)	● (blue)	▲ (yellow)	▲ (yellow)	● (yellow)	● (yellow)	✚ (blue)
Parapiptadenia rigida	diversity	85	● (blue)	● (blue)	▲ (yellow)	▲ (yellow)	● (yellow)	● (yellow)	✚ (blue)

Bauhinia forficata	filling	80	Blue	Yellow	Yellow	Yellow	Yellow	Yellow	Blue
Ceiba speciosa	diversity	80	Yellow	Red	Yellow	Yellow	Blue	Blue	Blue
Cordia trichotoma	diversity	80	Blue	Yellow	Yellow	Yellow	Yellow	Yellow	Blue
Gymnanthes klotzschiana	diversity	80	Blue	Yellow	Yellow	Red	Yellow	Blue	Blue
Piptadenia gonoacantha	filling	80	Yellow	Blue	Yellow	Yellow	Yellow	Blue	Yellow
Trema micrantha	filling	80	Blue	Red	Blue	Red	Blue	Yellow	Blue
Araucaria angustifolia	diversity	75	Yellow	Yellow	Yellow	Yellow	Yellow	Yellow	Blue
Balfourodendron riedelianum	diversity	75	Yellow	Yellow	Yellow	Yellow	Yellow	Yellow	Blue
Cassia leptophylla	diversity	75	Yellow	Yellow	Yellow	Yellow	Yellow	Yellow	Blue
Lonchocarpus	diversity	75	Blue	Yellow	Yellow	Yellow	Red	Yellow	Blue
Cedrela fissilis	diversity	70	Blue	Red	Red	Yellow	Yellow	Yellow	Blue
***Celtis* sp.**	diversity	70	Blue	Yellow	Yellow	Red	Red	Yellow	Blue
Cordia americana	diversity	70	Yellow	Yellow	Yellow	Yellow	Red	Yellow	Blue
Handroanthus chrysotrichus	diversity	70	Yellow	Yellow	Yellow	Yellow	Red	Yellow	Blue
Machaerim stipitatum	diversity	70	Yellow	Yellow	Yellow	Yellow	Red	Yellow	Blue
***Podocarpus* sp.**	diversity	70	Yellow	Yellow	Yellow	Yellow	Red	Yellow	Blue
Prunus myrtifolia	diversity	70	Yellow	Red	Yellow	Yellow	Yellow	Yellow	Blue
Ruprechtia laxiflora	diversity	70	Yellow	Yellow	Yellow	Yellow	Red	Yellow	Blue
Allophyllus edulis	diversity	65	Yellow	Yellow	Red	Yellow	Red	Yellow	Blue
Calliandra tweedii	diversity	65	Blue	Blue	Red	Red	Red	Red	Blue
Diatenopteryx sorbifolia	diversity	65	Yellow	Yellow	Red	Yellow	Red	Yellow	Blue
Psidium cattleyanum	diversity	65	Yellow	Yellow	Red	Yellow	Red	Yellow	Blue
Casearia decandra	diversity	60	Yellow	Yellow	Red	Red	Red	Yellow	Blue
Cinnamodendron dinisii	diversity	60	Yellow	Yellow	Red	Red	Red	Yellow	Blue
Eugenia pyriformis	diversity	60	Yellow	Red	Red	Yellow	Red	Yellow	Blue
Eugenia uniflora	diversity	60	Yellow	Yellow	Red	Yellow	Red	Red	Blue
Myrsine umbellata	diversity	60	Red	Yellow	Red	Yellow	Red	Yellow	Blue
Ocotea puberula	diversity	60	Yellow	Yellow	Red	Red	Red	Yellow	Blue
Strychnos brasiliensis	diversity	60	Yellow	Yellow	Red	Red	Red	Yellow	Blue
***Xylosma* sp.**	diversity	60	Yellow	Yellow	Yellow	Red	Red	Red	Blue
Alchornea triplinervia	filling	55	Yellow	Red	Red	Red	Yellow	Yellow	Yellow
Butia capitata	diversity	55	Yellow	Yellow	Red	Red	Red	Red	Blue
Cabralea canjarana	diversity	55	Red	Red	Red	Yellow	Red	Yellow	Blue
Campomanesia guazumifolia	diversity	55	Yellow	Red	Red	Red	Red	Yellow	Blue
Erythrina falcata	diversity	55	Yellow	Red	Red	Red	Yellow	Yellow	Yellow
Galesia integrifolia	diversity	55	Yellow	Red	Red	Red	Red	Yellow	Blue
Jacaranda micrantha	diversity	55	Red	Red	Red	Yellow	Red	Yellow	Blue
Myrsine coriacea	diversity	55	Yellow	Red	Red	Red	Yellow	Yellow	Yellow
Syagrus romanzoffiana	diversity	55	Red	Yellow	Red	Red	Red	Yellow	Blue
Campomanesia xanthocarpa	diversity	50	Yellow	Red	Red	Red	Red	Red	Blue
cf. Myrceugenia euosma	diversity	50	Yellow	Red	Red	Red	Red	Red	Blue
Cupania vernalis	diversity	50	Red	Red	Red	Red	Red	Yellow	Blue
Eugenia involucrata	diversity	50	Red	Red	Red	Red	Red	Red	Blue

Myrcianthes pungens	diversity	50	●	●	▲	▲	●	●	✚
Ocotea porosa	diversity	50	●	●	▲	▲	●	●	✚
Aspidosperma polyneuron	diversity	45	●	●	▲	▲	●	●	✚
Ilex paraguariensis	diversity	45	●	●	▲	▲	●	●	✚
Plinia peruviana	diversity	45	●	●	▲	▲	●	●	✚
Randia ferox	diversity	45	●	●	▲	▲	●	●	✚
Sloanea hirsuta	diversity	45	●	●	▲	▲	●	●	✚
Trichilia clausenni	diversity	45	●	●	▲	▲	●	●	✚
Vitex megapotamica	diversity	45	●	●	▲	▲	●	●	✚
Annona cacans	diversity	40	●	●	▲	▲	●	●	✚
Jaracatia spinosa	diversity	40	●	●	▲	▲	●	●	✚
Monteverdia aquifolia	diversity	40	●	●	▲	▲	●	●	✚

3.2 How was the accuracy of the classification in ecological groups - "filling" and "diversity" species?

PCA was used to cluster species in a species group space based on growth variables. The first two axes explained 93.56% of the variation among species (see Appendix III). During the first years (0.5 to 4 y), four filling species had a well-defined faster growth when compared to other filling and diversity species: *Croton urucurana*, *Mimosa scabrella*, *Solanum mauritianum*, and *Trema micrantha* (Figure 14). In contrast, two filling species (*Piptadenia gonoacantha* and *Alchornea triplinervia*) were clustered with the diversity species, and 14 diversity species were clustered with other filling species.

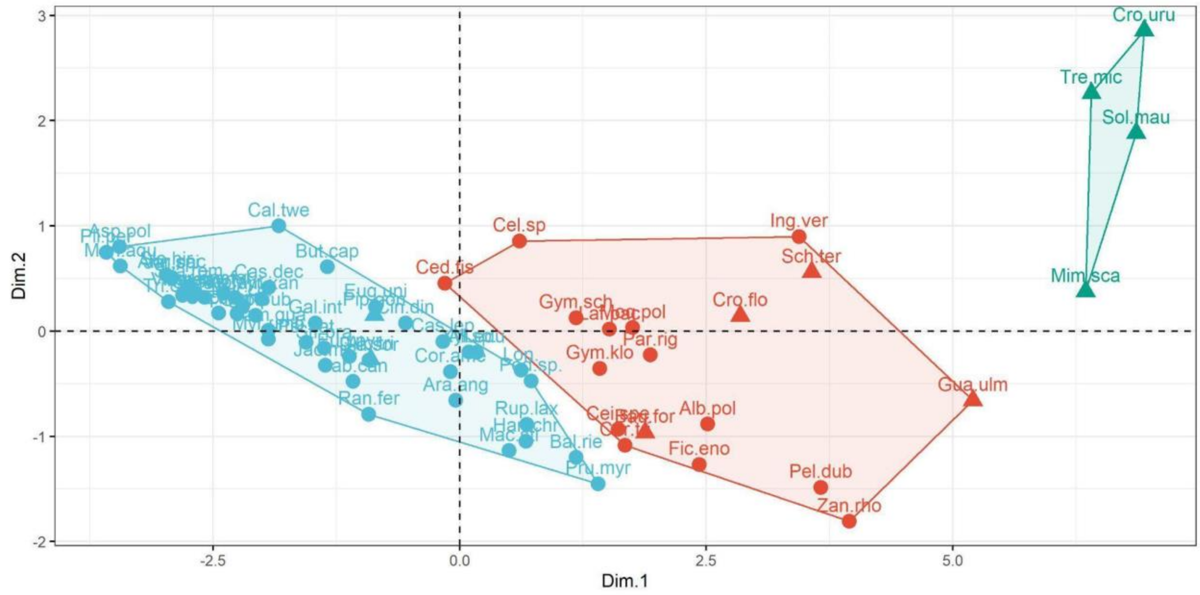

Figure 14.: Principal component analysis (PCA) plots with growth rates in ages 0.5 to 4 y, using an average per species among the 70 species tested. Circles indicate diversity species while triangles indicate filling species. Each color represents a different cluster.

For the second period, from age 4.5 up to 8.5 y, the first two axes explained 76.39% of the variation among species (see Appendix III), and we could notice some changes in the clusters, and a shift in the composition of species (Figure 15)

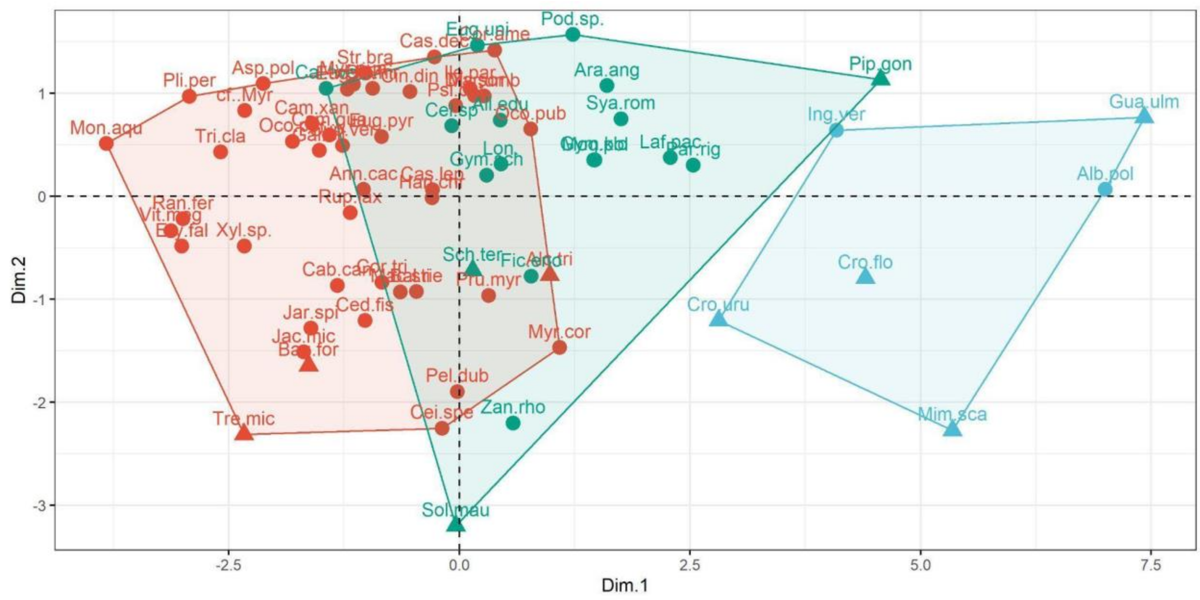

Figure 15.: Principal component analysis (PCA) plots with growth rates in ages 4.5 to 8.5 y, using an average per species among the 70 species tested. Circles indicate diversity species while triangles indicate filling species. Each color represents a different cluster.

For the first cluster, *T. micrantha* and *S. mauritianum* were not present anymore, and *T. micrantha* was classified as the third, slower-growing group. As the plantation ages, the species level differences begin to be less distinct compared to the earlier stage. *Inga vera* and *Albizia polycephala* were clustered with filling species by this age, presenting similar growth, distancing them from the diversity group species. *C. floribundus* and *G. ulmifolia* were the two filling species that joined the faster growing group at 8.5 y.

3.3 Which species were most affected by frost?

Overall, frost occurrence had an effect on species mortality ($p = 0.007$, Table 8): the community mean was positive, which means that the chance of a sapling dying after a frost event is greater than during a non-frost interval. We found that greater rcd before death reduced the odds of mortality ($p < 0.001$, Table 8). However, species were affected differently by frost, being more or less sensitive to die after a frost (see Appendix V).

Table 8: Generalized linear mixed-effects model outputs.

Predictors	*Odds Ratios*	*CI*	*p*
(Intercept)	0.02	0.01 – 0.03	**<0.001**
Frost	1.73	1.16 – 2.58	**0.007**
RCD	0.94	0.92 – 0.96	**<0.001**
Random Effects			
σ^2	3.29		
$\tau_{00\ \mathrm{species}}$	1.98		
$\tau_{00\ \mathrm{Plot:Subplot}}$	0.02		
$\tau_{11\ \mathrm{species.frost}}$	1.36		

$\rho_{01\ species}$	-0.34
ICC	0.38
N_{Plot}	4
$N_{Subplot}$	3
$N_{species}$	70
Observations	10679
Marginal R^2 / Conditional R^2	0.025 / 0.393

The ten species most sensitive to frost occurrence, which means those that have more chance of dying after a frost, were *Trema micrantha, Solanum mauritianum, Mimosa scabrella, Schinus terebinthifolia, Celtis* sp., *Croton urucurana, Campomanesia guazumifolia, Bauhinia forficata, Jaracatia spinosa, Randia ferox*, in descending order, meaning that frost occurrence was negatively related to these species survival. From the species most sensitive to frost, six are filling species and four are diversity species.

The ten species least sensitive to frost were *Cassia leptophylla*, *Aspidosperma polyneuron*, *Araucaria angustifolia*, *Sloanea hirsuta*, *Cabralea canjarana*, *Ilex paraguariensis*, *Ceiba speciosa*, *Myrsine coriacea*, *Plinia peruviana* and *Ocotea puberula*, in descending order, all species belong to the diversity species group. As the model suggested, average mortality rates were higher after frost (Figure 16).

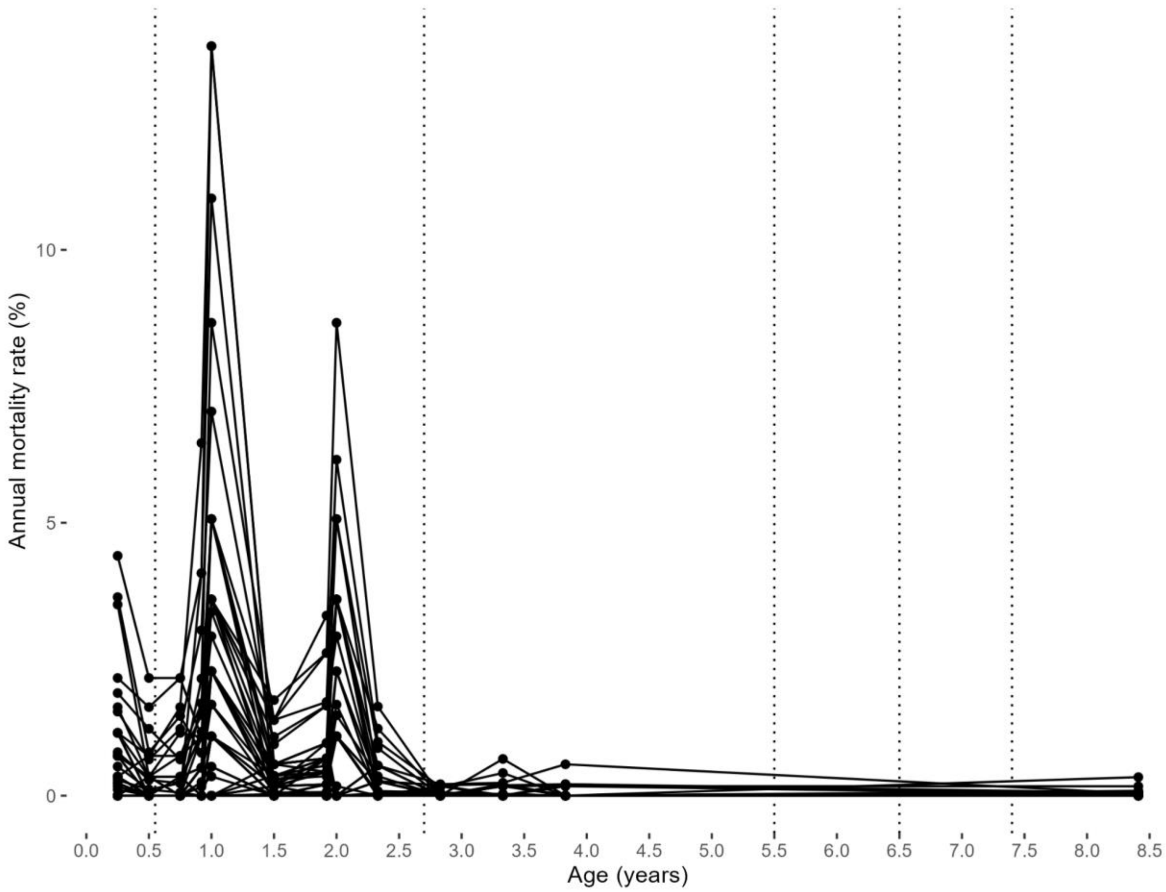

Figure 16: Annual mortality rate for each of the 70 species at all ages. Horizontal lines are species, and dotted vertical lines indicate frost events.

However, saplings did not die right after a frost, but a few months after the event (higher mortality was around 6 months later), what can be related to field observations, where at first sight a plant is without leaves and do not seem to be dead, however a few months later death is confirmed.

4. Discussion

4.1 Which species had the best survival, growth, and canopy cover?

Species vary in their performance, however, when setting restoration attributes like survival, height and dbh growth, crown area, as well as frost susceptibility, we can help guide species selection for projects in our region.

For species with higher mortality, we noted that early years' mortality rates were higher, which agrees with other studies (Grossnickle 2012; Charles et al. 2018) suggesting that saplings are more susceptible to environmental field factors. Forest dieback or increasing mortality of tree species can be also related to extreme climate events such as drought, flooding, and heat stress (Menezes-Silva et al. 2019): frosts could be considered an extreme event, associated with the occurrence of more rigorous winters, negatively affecting saplings survival at early ages in our site (see 4.3). We could also observe a second peak for mortality for a few species 2 years after planting. When we look at annual mortality rates, it is expected for a tropical forest to have an annual probability of mortality from 1-2% (Sheil and May 1996), and despite the high rates of mortality up to two years after planting, the average for species mortality rate along the 8.5 years was as expected, with a maximum of 2.2% (see Appendix II). In our study, filling species had overall lower mortality rates when compared to diversity species, consistent with a study of tree species growing in a tropical pasture, where pioneer species had lower mortality rates when compared to non-pioneer species up to 3.5 years after planting (Martínez-Garza et al. 2013).

Although the survival rates of diversity species in our study may have been affected by the low number of repetitions (12 individuals), it can still be helpful because mortality data is not available for many of these sixty species, however, we recommend that more studies should be performed for these species. Furthermore, understanding which factors drove the high mortality rates up to two years is important to improve the performance of these species in the field.

Regarding height growth, the top five species at 4 years were filling species, however, at 8.5 years, the species *T. micrantha* and *M. scabrella* were not among the top 10 anymore. We observed in the field that many *T. micrantha* individuals were already dead and many *M. scabrella* individuals were presenting decay, fewer stems, and smaller crowns, evidencing a quite short life cycle, even for filling species. We could already see a shift from a dominance of filling species to diversity species being more competitive at 8.5 years, where *Albizia polycephala* and *Inga vera* were in the top 5 species regarding height growth. The same shift was observed in dbh for *I. vera* occupying the fourth position in the rank at 8.5 years. Based on other studies of Atlantic Forest restoration sites, it takes from seven up to 30 years to reach a reference site value for height, which would be around 8 to 10 m (Londe et al. 2020), values that all top ten species, filling and diversity ones, have already reached at 8.5 years in our restoration site. A shift in dominance between filling and diversity species is expected in the future, where diversity species will persist (Brokaw and Scheiner 1989), while filling species grow faster in the early years. However, we could already see a shift of some filling species dying at 8.5 years and diversity species competing with the long-lived filling ones.

When we evaluated crown area growth we wanted to see if filling species rapidly covered the restoration site. As expected, most of the best growing species were from the filling group, however, three were from the diversity group. This means that the other three filling species, *Bauhinia forficata*, *Piptadenia gonoacantha* and *Alchornea triplinervia* which occupied, respectively, the twenty-first, twenty-six and forty-third positions in the rank, did not grow as expected at early stages. These three filling species did not perform as expected in the initial restoration process in our field conditions, which would be to have large crowns that help shading and provide a more suitable place for diversity species to grow. Therefore, *B. forficata*, *P. gonoacantha* and *A. triplinervia* should not be recommended for this purpose, since they were not among the top 10 larger canopy areas at 4 years. Even though *P.*

gonoacantha was among the top at 8.5 years we believe that this fast closure is more important and expected at early years, where, as we could see, species mortality is higher, even more for diversity species, which could be related to these species not having adequate conditions to grow.

Our species performance rank, based on all variables evaluated, can be used to select species with best performance for the variables of interest. We caution that we do not imply that species with slower values for some variable should not be used, because a high number of species, including filling and diversity groups, should be considered in order to reach biodiversity goals. However, what we propose is that the use of this rank can be of help for practitioners select species for restoration, based on specific goals, in addition, among seventy species, the best ones can be chosen for more efficient restorations while maintaining a highly diverse restoration project.

4.2 How was the accuracy of the classification in ecological groups - "filling" and "diversity" species?

When planting species in filling and diversity groups, the goal we expect is that the filling species will provide faster canopy closure - in our case up to 4 years - inhibiting exotic grasses invasion and facilitating environmental conditions for the development of diversity species, and a shift is expected in the future, where diversity species will last longer. The species that presented larger canopy closure at an early stage were *C. urucurana*, *T. micrantha*, *M. scabrella* and *S. mauritianum*, standing out when compared to other species, and we can highlight that these four species are important filling species and should be used for restoration in our region.

Some filling species did not present characteristics that were expected for this group, and some diversity species had filling species growth patterns. The two filling species that were clustered with diversity species, *Piptadenia gonoacantha* and *Alchornea triplinervia*, and the 14 diversity species that were clustered with filling species, suggest that a new classification may be needed for our region, in order to relate these species development with our specific climatic conditions. *P. gonoacantha* is a pioneer species that does not have a filling species potential at early ages, and could be more correctly used in the diversity group as recommended by Paraná state, São Paulo state and Embrapa list of species for restoration (Barbosa et al. 2017; EMBRAPA 2023; IAT 2023); however, around 8 years its crown area was large, reaching an average of 18.18 m² and occupying the 9th position in the crown area rank. *A. triplinervia* however, is widely classified as a filling species (Barbosa et al., 2017; EMBRAPA 2023; IAT 2023) and presented a crown area average of 4.03 m² after 8.5 years, really small when compared to other filling species.

The diversity species that outstand in growth at 8.5 years were *I. vera* and *A. polycephala*. *I. vera* is classified as filling for the Paraná state species list (IAT 2023) while for the national list (EMBRAPA 2023), it is classified as a diversity species. *A. polycephala* is the opposite, classified by EMBRAPA as a filling species and by IAT as a diversity species, in our study it presented higher growth only after 8.5 years, when it reached the third position for crown area.

Species classification as filling and diversity groups could vary locally, which implies that a more region-specific classification is important, and more field studies evaluating these species performance are needed in order to have an accurate classification for each Brazilian mesoregion.

4.3 Which species were most affected by frost?

Frost effects could be really important in maintaining subtropical ecosystems, because forest types transitions could be shaped by climatic factors such as frost, by killing species that are less resistant to frost (Whitecross et al. 2012; Bojórquez et al. 2019; Araujo Frangipani et al. 2021). Besides climate change effects on temperature in general results in the rise of global temperatures, it also causes an increase of extreme events such as frost (IPCC 2018).

Frosts could play an important role on seedlings establishment, because mortality will impact restoration initial costs with replantings and also affect the later success of restoration efforts. Based on our analysis, we do not suggest the use of *Trema micrantha, Solanum mauritianum*, *Mimosa scabrella*, *Schinus terebinthifolia*, *Celtis* sp, *Croton urucurana, Campomanesia guazumifolia*, *Bauhinia forficata*, *Jaracatia spinosa*, *Randia ferox* in areas prone to freezing temperatures (see Appendix V). We found the following species less sensible to frosts, and are recommended for the use on restoration projects where frost could be an issue: *Cassia leptophylla*, *Aspidosperma polyneuron*, *Araucaria angustifolia*, *Sloanea hirsuta*, *Cabralea canjarana*, *Ilex paraguariensis*, *Ceiba speciosa*, *Myrsine coriacea*, *Plinia peruviana*, *Ocotea puberula* among other species (see Appendix V). We are aware that other factors could cause plant mortality and could have influenced tree mortality in addition to frost events, particularly in the last measurement, where three frost events occurred and only one measurement in a four-year interval, however, our model frost occurrence and tree size explained almost 40% of data variation in our model of mortality (Table 7) suggesting frost is an important factor in the success of species in this region. Attempting to restore areas that will be more resilient in the future should consider the use of more frost resistant species where frosts can be a problem, such as in our region. Among other desirable attributes, frost resistance can also be evaluated when choosing species for restoration, and knowing the performance of these 70 native species related to frost sensibility should help to accomplish this goal.

4.4 Management recommendations

Based on the findings of this study, we recommend that the following filling species should be prioritized for restoration projects in our region: *C. floribundus*, *G. ulmifolia*, *C. urucurana*, *T. micrantha*, *S. mauritianum*, and *M. scabrela*, being the last four even more recommended when there is a need for a fast shading. For the diversity species group, the following should be used: *I. vera*, *A. polycephala*, *P. dubium*, *L. pacari*, *M. polymorphum*, *Z. rhoifolium*, *F. enormis*, *G. schottiana*, *P. rigida*, and *C. speciosa*.

5. Conclusions

Forest restoration success will depend, among other factors, in which selected species will have the best performance, higher survival and faster growth, outstanding ecological barriers that can be present in a degraded area. Usually faster canopy coverage is aimed to improve environmental conditions and allow other species to establish and grow, while worsening the chance of invasive grasses to thrive, and thereby accelerating the restoration process. Both filling and diversity groups presented species with great growth and survival. Species should be chosen based on restoration goals and site specificities such as frost occurrence and our study can serve as a basis for choosing these best performance species.

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CHAPTER 3 - Assessing long-term outcomes of a high-diversity restoration plantation: species strategies and stand performance after 8.5 years

Abstract

The aim of our study was to evaluate the effectiveness of a high-diversity plantation restoration using an ecological groups method. We investigated how growth strategies vary among species groups and within groups, how was the evolution of canopy closure over time and which successional stage the stand has reached after 8.5 years. We found differences in growth strategies among and within groups, however, most filling species invested more in crown area and height, while *B. forficata* and *A. triplinervia* invested in height only, keeping small crowns. Most diversity species invested more in height than dbh, and *I. vera* and *A. polycephala* diversity species invested more in crown area, similar to filling species. Our high diversity stand reached a closed canopy four years after plantation. After 8.5 years, the stand reached an initial successional stage, suggesting that it will take more successional time to reach an intermediate forest stage.

1. Introduction

The goal of forest restoration is to bring back the ecological functions, biodiversity and resilience of forests that have been altered by human activities such as deforestation, land use change, and other forms of degradation. Restoration ecology has evolved over the years, incorporating more ecological understanding of natural forest succession into restoration projects, and this involved selecting and distributing species based on their ecological groups, as defined by Budowski (1965), that classified species into pioneer, early secondary, late secondary and climax based on their ecological characteristics and strategies.

Ecological groups are related to the classification of species based on shared attributes, such as their role in the ecosystem or their physical characteristics as shade tolerance or seeds aspects (Swaine and Whitmore 1988). This can be used to understand how different species interact with one another and how they contribute to the overall ecosystem functioning. A redundancy of attributes may be an important insurance for restoration sites, where a greater variety of species offers a wider range of conditions, and also multiple species perform similar roles, insuring that important ecological functions are maintained and higher diversity will be present, leading to a restored ecosystem functioning and increased resilience against disturbances (Lawton and Brown 1994).

Within the pioneer species group there is a range of species that vary in their lifespan, from short-lived to long-lived species; this implies that short-lived species will be smaller in size compared to long-lived ones (Whitmore 1989) and that there can be a lot of variation even within a single species group. Another classification of species, this one applied to restoration projects, is based on “filling” and “diversity” species groups, aiming for fast canopy recovery in a short time period: filling species are fast-growing pioneers species that are planted to promote soil covering as fast as possible, suppressing invasive grasses and exotic weeds and facilitating the understory recovery; diversity species group include late-successional species, or even pioneer species with poor soil coverage, these species bring diversity to the restoration site, and promote the long term maintenance of forest structure, adding functional diversity (Nave and Rodrigues 2007; Rodrigues et al. 2009).

Even though it is possible an overall classification into groups with similar characteristics, it is important to note that singular species may reveal different growth strategies based on specific ecosystems and resources availability. Additionally, species may shift their growth strategies over time in response to changing environmental conditions (Rüger et al. 2011). Understanding these growth patterns and how different species allocate their resources can be useful for informing restoration efforts and for selecting species that are best suited for different types of restoration projects. How tall a mature species will be for example, associated with crown architecture, may be a good indicator of this species strategy to reach canopy (Iida et al. 2011).

It is important to evaluate long-term restoration outcomes because monitoring is necessary to determine if the restoration project has been successful in achieving initial goals and also if the restored ecosystem is sustainable over time (Wortley et al. 2013). When long-term outcomes are evaluated, it is possible to identify the most successful restoration techniques and strategies and this information can then be used to inform and improve restoration efforts.

The aim of our study was to evaluate the effectiveness of a high-diversity plantation restoration method using filling and diversity ecological groups. After 8.5 years, we assessed whether the stand achieved the desired restoration outcomes based on metrics such as canopy closure, average height, average diameter (dbh) and basal area. Additionally, we analyzed the growth strategies of species focusing on crown area and height relationship and also crown area and dbh relationship. The questions we aimed to answer include: 1) How do growth strategies vary among species groups and within groups? 2) How was the evolution of canopy closure in a high-diversity plantation? and 3) What successional stage has the stand reached after 8.5 years?

2. Methods

2.1 Study site

Our experimental site was established in October 2010 at the Federal University of Technology – Parana, Dois Vizinhos, Brazil (25º41’44” - 25º41’49” S; 53º06’23” - 53º06’07”

W) (Figure 17). The climate is humid subtropical, with an average annual precipitation of 2,044 mm (without water deficit), the average annual temperature is 19.2°C with at least one frost every two years, altitude ranges from 495 to 504 m and the vegetation is an Atlantic Forest ecotone between *Araucaria* Forest and Seasonal Semideciduous Forest (Bechara et al., 2021; IBGE 2004).

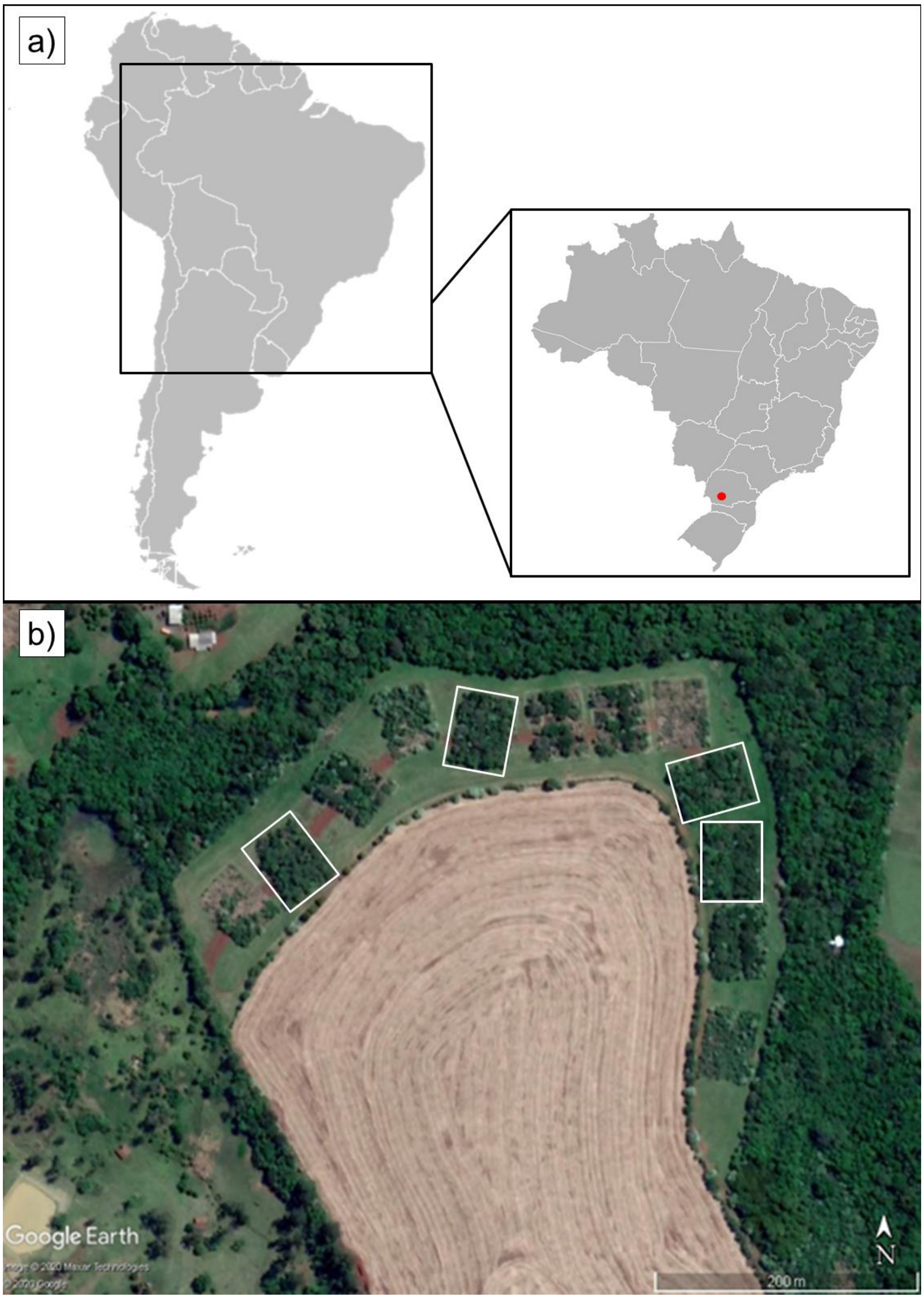

Figure 17: a) Study site location in Brazil, the red dot shows the specific site location. b) Plots used in this study are indicated in white rectangles.

2.2 Experimental design

The experiment started with the application of herbicide in the total area, followed by soil preparation including planting lines. Seedlings were planted with fertilization (360 g of NPK 5-20-10), irrigation with 3 l of hydrated gel in the pits, mulching cardboards, and systematic control of cutting ants. These forestry operations were maintained semiannually up to the third year. The restoration method was based on Rodrigues et al. (2009), who classified species into two ecological groups: 1) filling species - early pioneers with faster growth and shading; and 2) diversity - slow-growth non pioneer species; the species selection and classification on each group was based on the literature and field experts considering also regional development of each species. We selected and classified 10 filling species and 60 diversity species (see Appendix I).

Planting spacing design was 3 m between rows and 2 m within the row (total of 1,666 plants per hectare) and the two species ecological groups were intercalated in the row and within rows. The planting was conducted in a systematic way, where each species was planted at the same spot in each plot, with a total of four plots of 40 x 54 m (Figure 18), and inside each plot, there were three repetitions for the species design, totaling 8,640 m². We planted 360 seedlings in each plot (180 seedlings of filling species and 180 seedlings of diversity species), bringing to a total of 1,440 individuals. In total, filling species had 72 seedling repetitions, and diversity species had 12 repetitions.

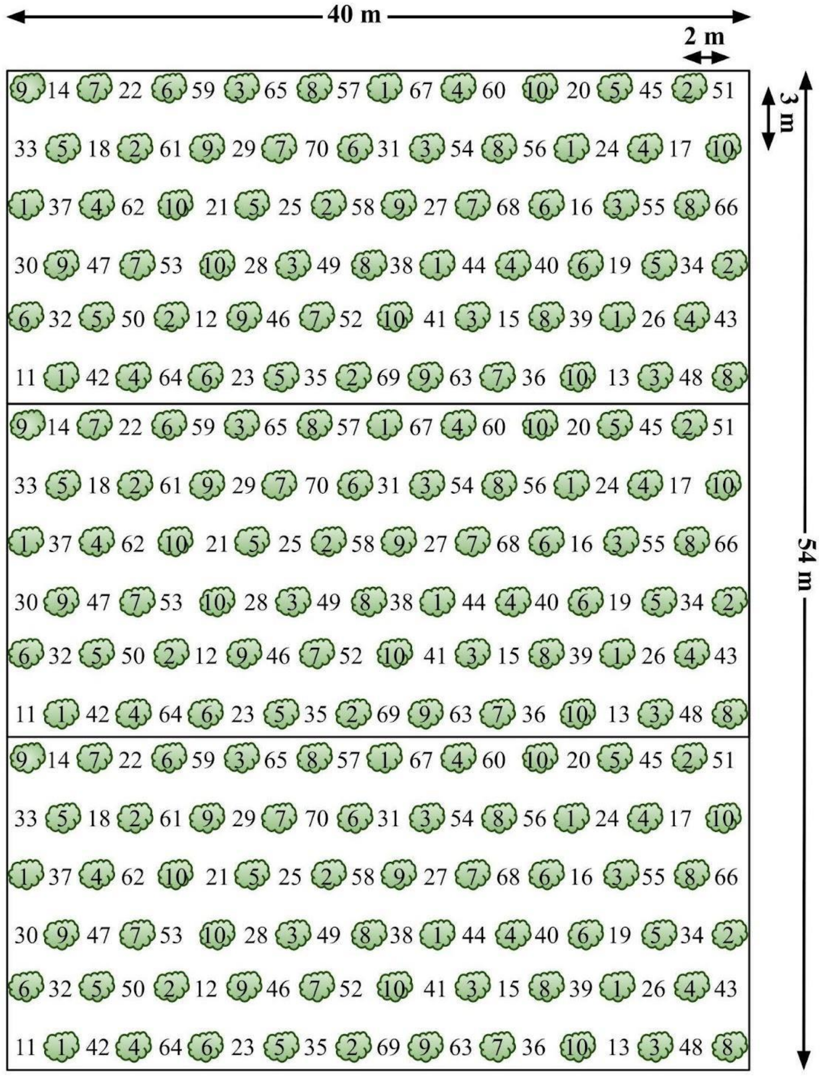

Figure 18: Planting method using filling (green crowns) and diversity species ecological groups. Each number refers to a different species.

2.3 Tree sampling

Seedlings monitoring started in Jun 2011 (six months after planting), followed by Nov 2011, Jun 2012, Nov 2012, May 2013, Nov 2013, Jun 2014, Dec 2014, and finally Aug 2019. Every individual was measured considering: i) dbh (> 5 cm dbh) or root collar diameter (rcd; if dbh < 5cm); ii) total height (m); and iii) crown area (m^2), using two perpendicular measurements for each tree. Mortality was also quantified, and replaced seedlings were tracked through time and its age was reconsidered setting back to its planting time. Replantings occurred three times, from age 0,5 y to age 2 y (Mar 2011, Sep 2011, Dec 2011, Nov 2012).

2.4 Data analysis

All analyses were performed in R software 4.1.1 (R Core Team 2020) using the following packages: dplyr (Wickham et al. 2022) , ggplot2 (Wickham et al. 2019), and data.table (Dowle and Srinivasan 2021). We also tested for edge effects of the plots on dbh, total height and crown area and it was not significant ($p>0.05$).

2.4.1 Allometry

We evaluated the relationship between height, dbh and crown area for all species. In order to do that, we calculated the canopy area based on the measurements of crown diameter taken in the field (Eq. 1):

$CA = ((\pi * C1/2 * C2/2)$ *(Eq.1)*

Where, CA = crown area of the individual (m^2), C1 and C2 = perpendicular crown lengths (m). We then plotted all the individuals from every age measured using height versus crown area and dbh versus crown area.

2.4.2 Height and dbh thresholds

In order to estimate the stand successional stage, we plotted species distributions for dbh and height values. We evaluated it only at 8.5 years because we aimed to estimate the successional stage the stand achieved by this age. We added thresholds for each successional stage based on Brazil's national legislation that defines these stages for Parana state (CONAMA, 1994). We only used structure (dbh and height) values for reference and did not consider other floristic aspects of the stand. According to this legislation: i) the early successional stage, is when species have a height average <= 10 m and dbh <= 15 cm; ii) the intermediate successional stage is defined by individuals with height from 8 to 17 m and dbh from 10 to 40 cm; and iii) the late successional stage (old-growth forest) is characterized by heights > 15 m and dbh from 20 to 60 cm.

2.4.3 Basal area

We calculated basal area for each individual, using the following equation:

$$g = \pi * dbh^2/40000$$

We summed the basal area for all the individuals for each measurement, which gave us the stand basal area and basal area per hectare, for each monitoring age.

2.4.4 Canopy cover

In order to evaluate canopy cover evolution, we built maps for each plot based on crown area measurements for each individual and compared them through time. For that we related the specific position of each individual in the plot as described in Figure 18, giving a x and y position for each individual, based on spacing between and within rows.

3. Results

3.1 How do growth strategies vary among species groups and within groups?

Among filling species, we could observe differences in growth strategies within the species group, where some species invested more in height and others more in crown area (Figure 19).

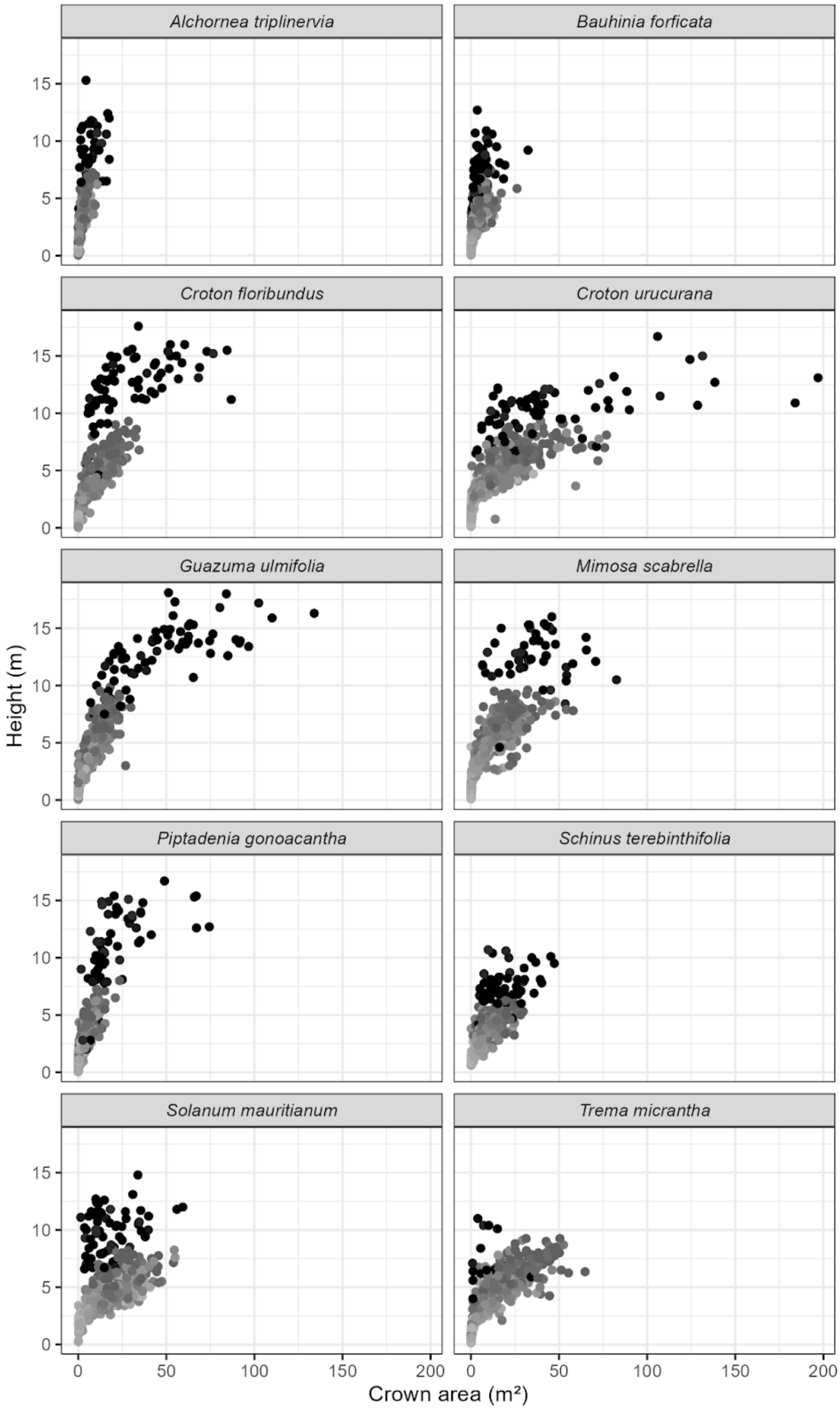

Figure 19: Height (m) vs crown area (m²) relationship for filling species from ages 0.5 to 8.5 y in a subtropical Atlantic forest, Brazil. Ages are represented by gray scale, where light gray are initial ages, and black indicates age 8.5 y.

Solanum mauritianum, *Trema micrantha* and *Schinus terebinthifolia* were investing more in crown area earlier (up to four years) when compared to the other filling species, however, they did not reach heights much above 10 m, and *T. micrantha* e started to stabilize growth and even having a decay after 8.5 years. *Alchornea triplinervia* and *Bauhinia forficata* invested more in height, but did not get too high, and had small crown areas, which is not desirable for filling species in restoration. *Piptadenia gonoacantha* reached an intermediate level, where it invested in height and also in crown area (but to a lesser extent). This species was very peculiar in the field, because some individuals were really small, around 1 m tall after 8.5 years while others were reaching more than 15 m at the same age, so its overall performance could be explained by the variation within individuals of the same species. The species that invested more in both, crown area and height were *Guazuma ulmifolia*, *Croton floribundus, Croton urucurana*, and *Mimosa scabrela*, and we highlight the first two for having two individuals reaching the biggest crown areas, higher than 100 m² up to almost 200 m².

When comparing dbh growth vs crown area growth at the same ages, we can also capture some temporal changes for the filling species and the differences within the species group (Figure 20).

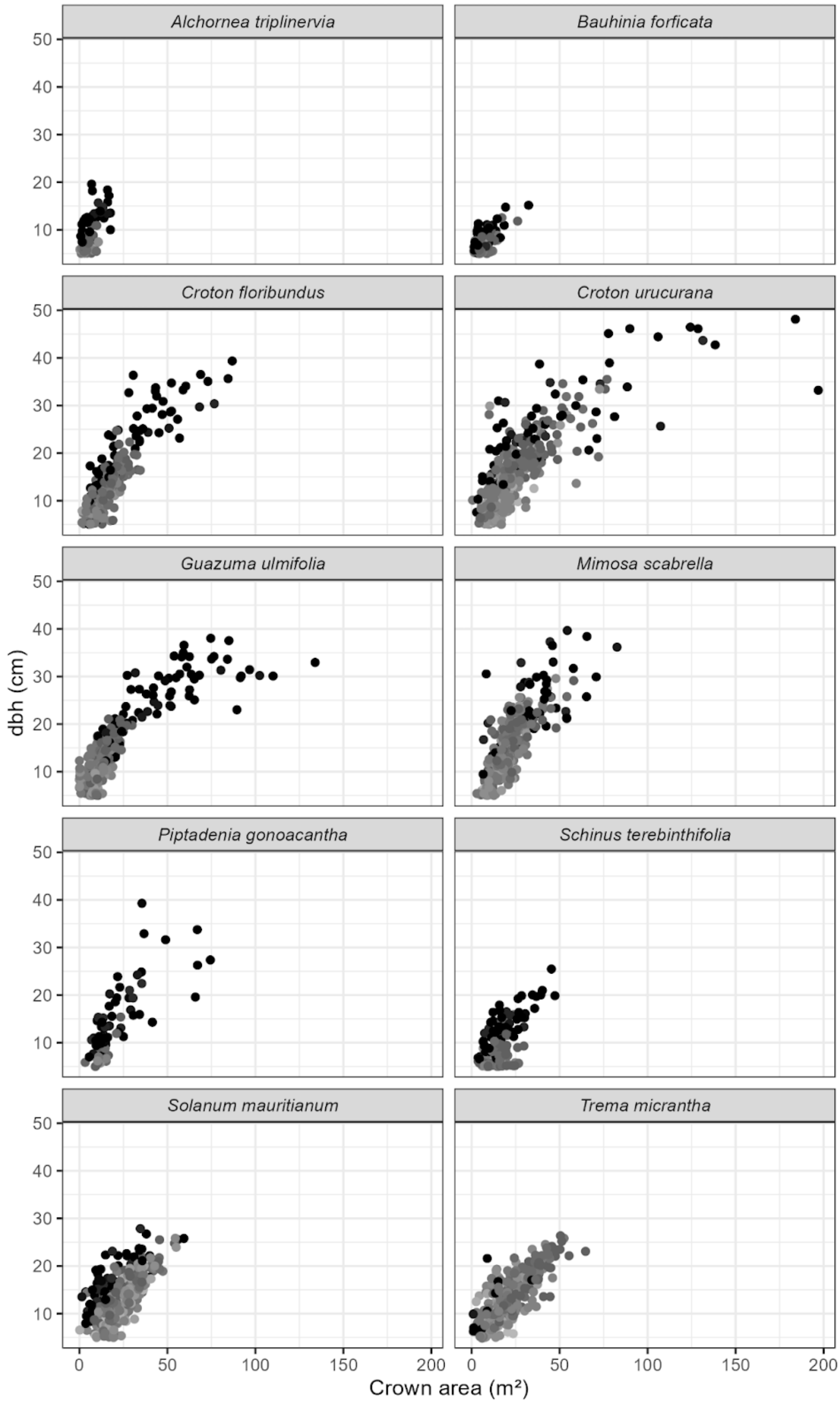

Figure 20: Dbh (cm) vs crown area (m²) relationship for filling species from ages 0.5 to 8.5 years in a subtropical Atlantic forest, Brazil. Ages are represented by gray scale, where light gray are initial ages, and black indicates age 8.5 y.

Contrasting with the height measurements, *B. forficata* and *A. triplinervia* did not invest as much in dbh as they did in height, reaching slow sizes for dbh with max values of 15-20 cm after 8.5 years. *S. terebinthifolia* had slower dbh growth, however it kept growing even after 8.5 years, contrasting with *T. micrantha* and *S. mauritianum* that presented some decay after 8.5 years, where dbh values were smaller than the years before. *G. ulmifolia*, *C. floribundus, C. urucurana*, and *M. scabrela* invested a lot in dbh growth, as they did in height, however at 8.5 y *M. scabrela* was already presenting some decay for dbh (by losing trunks) not as clear for height. *P. gonoacantha* presented the same variation pattern we could observe in height, with some individuals smaller than the most, however, overall individuals were investing in dbh growth, mostly at 8.5 y.

Among the diversity species group, most species invested more in height at first and did not grow a lot up to 8.5 years after planting, however, some species performed differently (Figure 21).

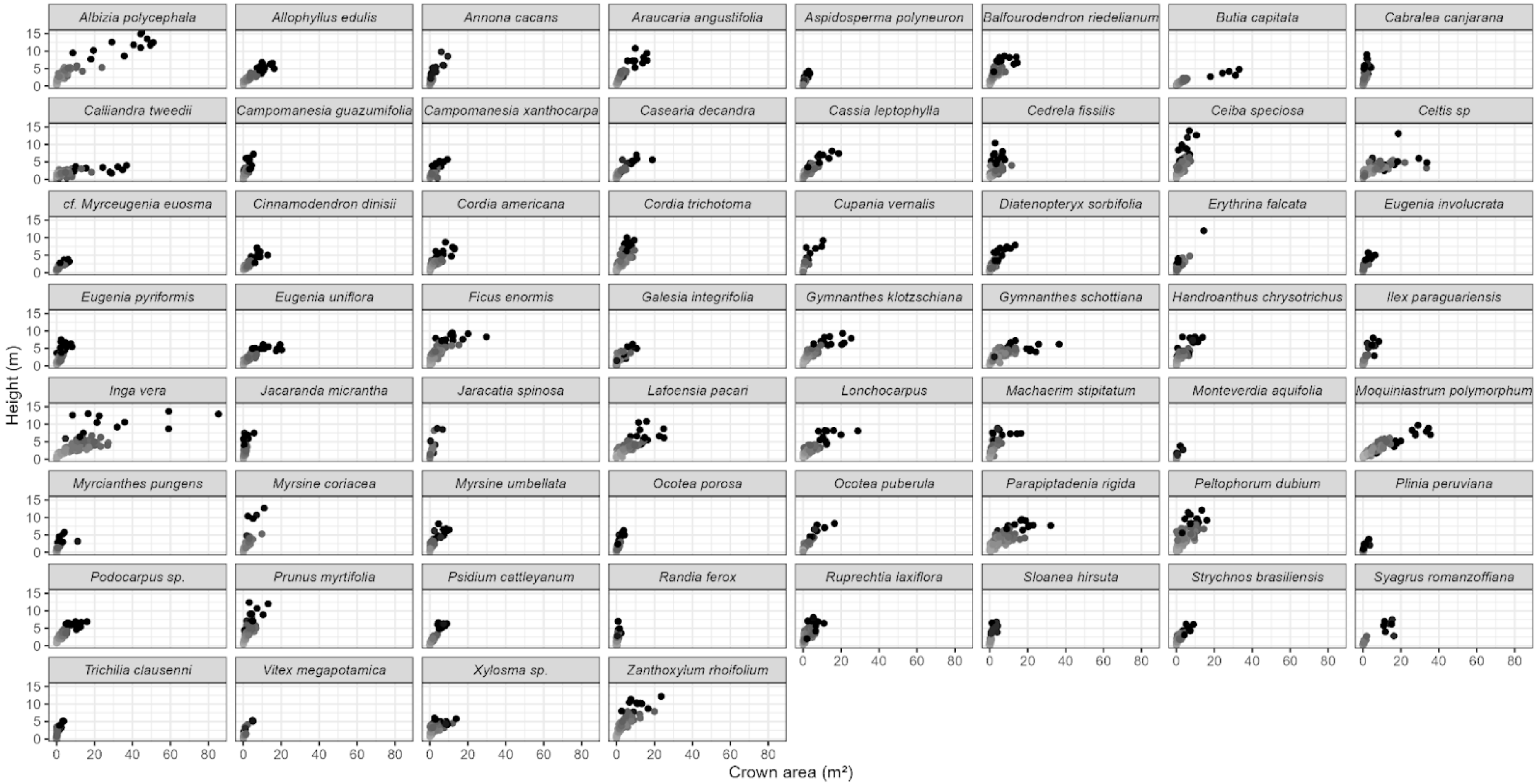

Figure 21: Height (m) vs crown area (m²) relationship for diversity species from ages 0.5 to 8.5 in a subtropical Atlantic forest, Brazil. Ages are represented by grey scale, where light grey are initial ages, and black indicates age 8.5 y.

Albizia polycephala and *Inga vera* can be highlighted because some individuals presented larger crown areas of 50 up to 80 m², and reached heights up to 15 m, growing more than any other diversity species. Regarding crown area, *Ficus enormis*, *Zanthoxylum rhoifolium*, *Lafoensia pacari*, *Gymnanthes klotzschiana*, *Gymnantes schottiana*, *Lonchocarpus*, *Moquinastrum polymorphum*, *Parapiptadenia rigida*, *Celtis* sp., *Butia capitata*, and *Calliandra tweedii*, invested more in crown area when compared to other diversity species. *C. tweedii* is a shrub, with its crown growing up to 40 m² after 8.5 years, however, because of its life form, it did not reach heights above 5 m. *B. capitata* is a small palm, and it also reached crown areas of up to 30-40 m² however heights were below 5 m. The other diversity species were varying with some growing taller than others but with closer values and usually heights not above 10 m after 8.5 years.

Regarding dbh growth vs crown area, fewer diversity species could be highlighted and 13 species had not reached the minimum dbh threshold of 5 cm, being excluded from the analysis (Figure 22), they were: *Vitex megapotamica, Xylosma sp., Randia ferox, Plinia peruviana, Monteverdia aquifolia, Myrceugenia euosma, Eugenia uniflora, Eugenia involucrata, Campomanesia xanthocarpa, Butia capitata, Aspidosperma polyneuron, Calliandra tweedii, Trichilia clausennii*.

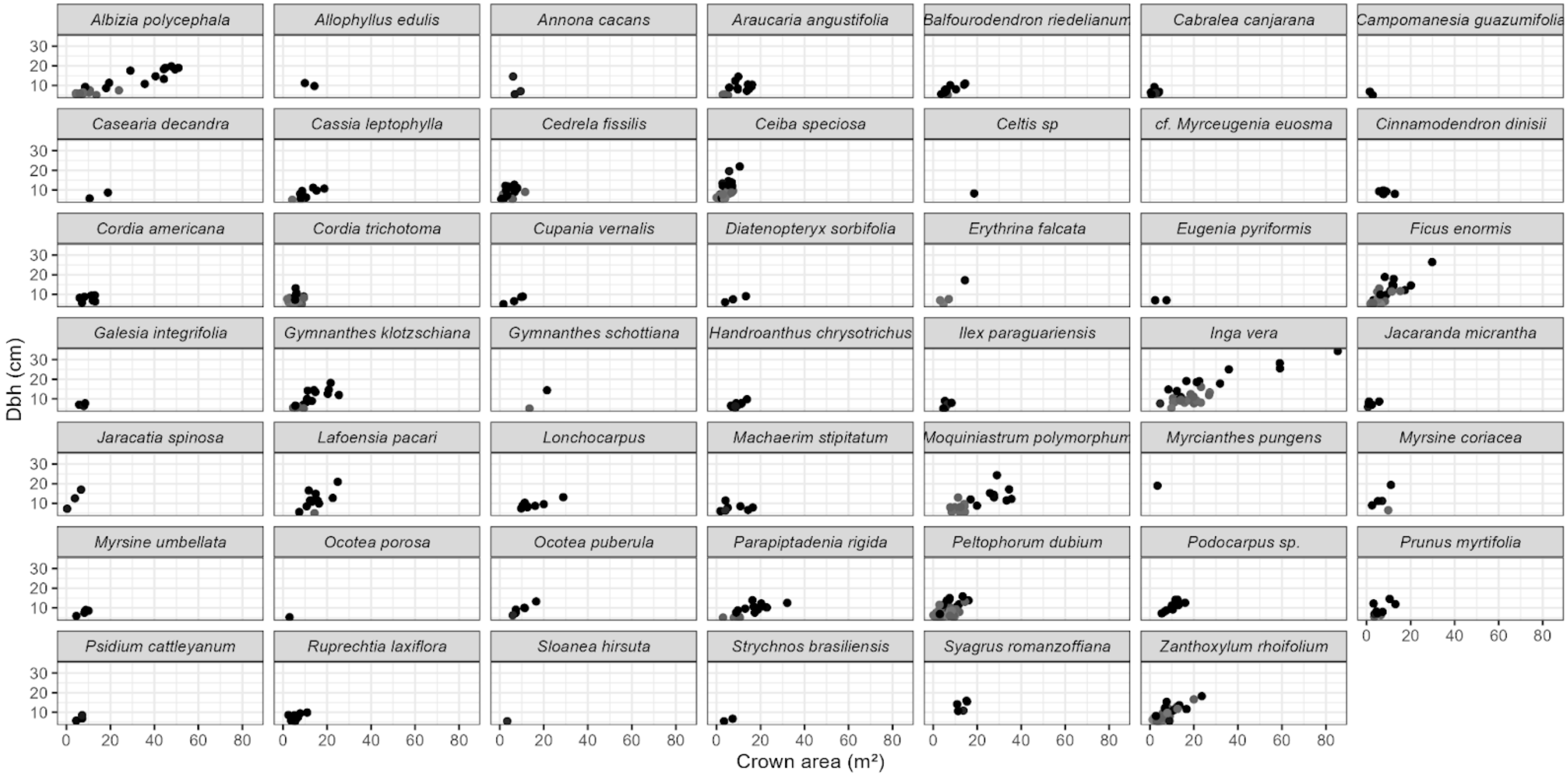

Figure 22: Dbh (m) vs crown area (m²) relationship for diversity species from ages 0.5 to 8.5 y in a subtropical Atlantic forest, Brazil. Ages are represented by grey scale, where light grey are initial ages, and black indicates age 8.5 y.

A. polycephala invested less in dbh than it did in height growth, however it was still larger than overall diversity species, reaching up to 20 cm of dbh. Besides that, *I. vera, F. enormis* and *M. polymorphum*, could be highlighted for investing more in dbh growth, from 25 up to 35 cm, when compared to other diversity species, where in most cases only a few individuals had reached dbh threshold of 5 cm even after 8.5 years.

3.2 How was the evolution of canopy closure in a high diversity restoration?

Overall, canopy area in all plots was similar through time, where filling species were dominating canopy up to 2014, 4 years after planting. In 2019 some diversity species started to reach larger crown areas. Dynamics among the plots were a bit different, but overall all plots reached a closed canopy at 4 years, with only small gaps, and even after 8.5 years plots 3 and 4 had small gaps on the canopy (Figure 23).

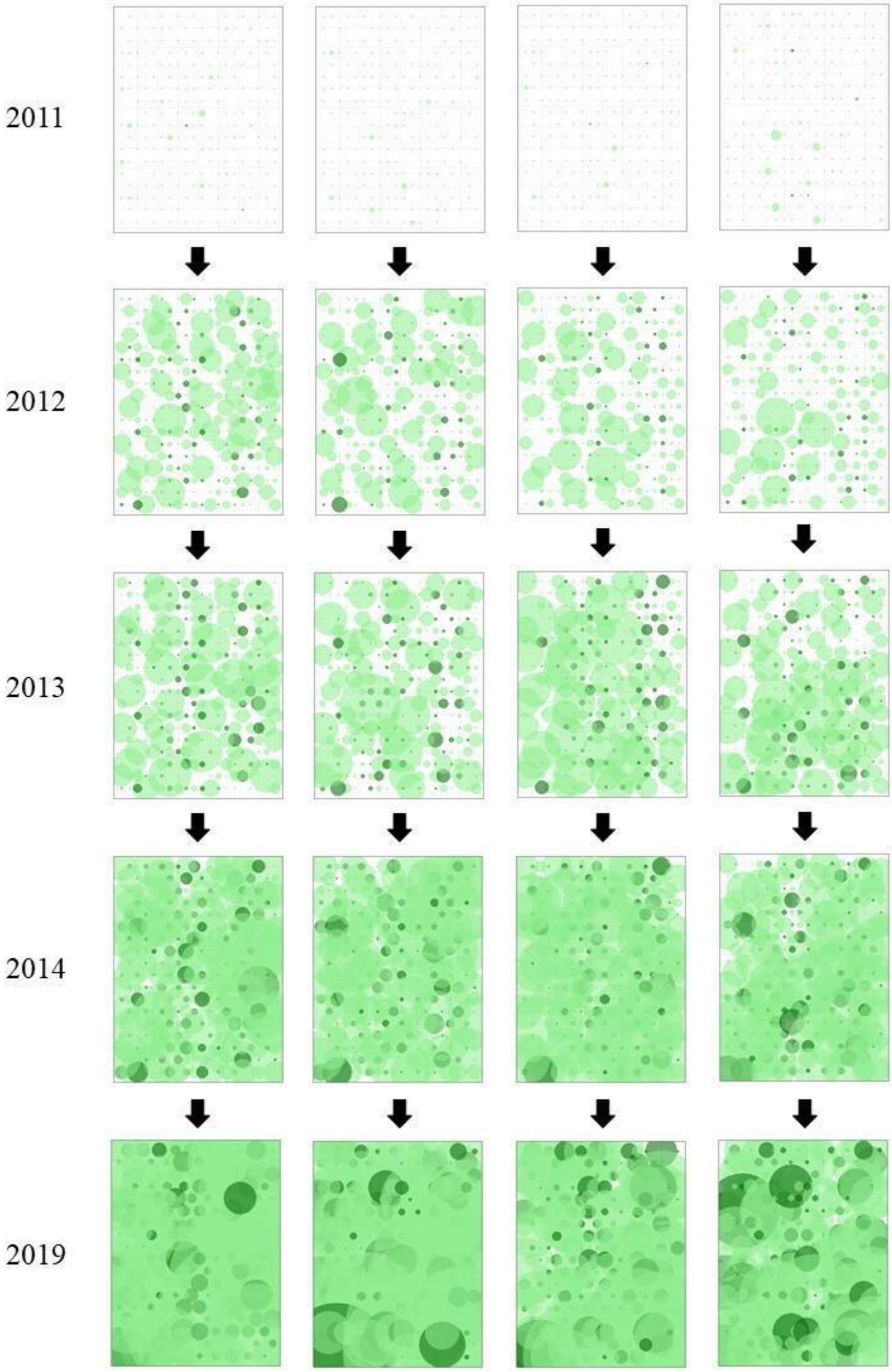

Figure 23: Canopy closure evolution for each plot (40 x 54 m), plots 1 to 4 are illustrated from left to right, from years 2011 to 2019 at ages 1, 2, 3, 4 and 8.5 years, based on crown area for each individual.

When we look at canopy area for all plots through time, we can see that the pattern of increasing canopy area with age was true for many individuals, but we do not see a huge increase in crown area from 2014 to 2019. We also can point that plots 3 and 4 reached smaller higher values for canopy area when compared to plots 1 and 2, where a few individuals reached up to 200 m² (Figure 24).

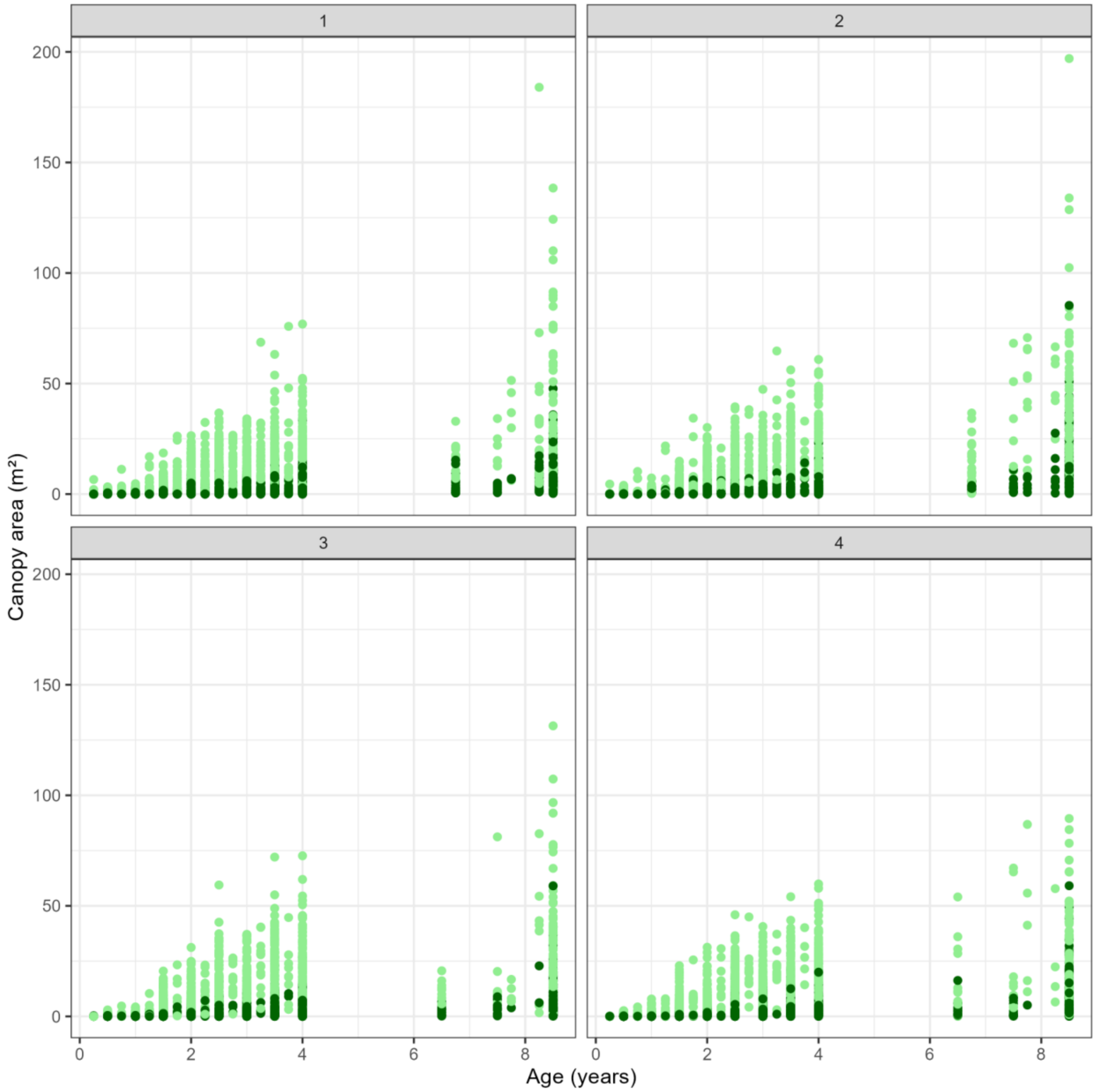

Figure 24: Canopy area for each plot (1-4) through time. Light green dots indicate filling species and darker green dots indicate diversity species.

3.3 What successional stage has the stand reached after 8.5 years?

Based on height distribution, at 8.5 years, the stand has achieved an early succession stage, however, we can already see a transition to the intermediate succession stage (Figure 25).

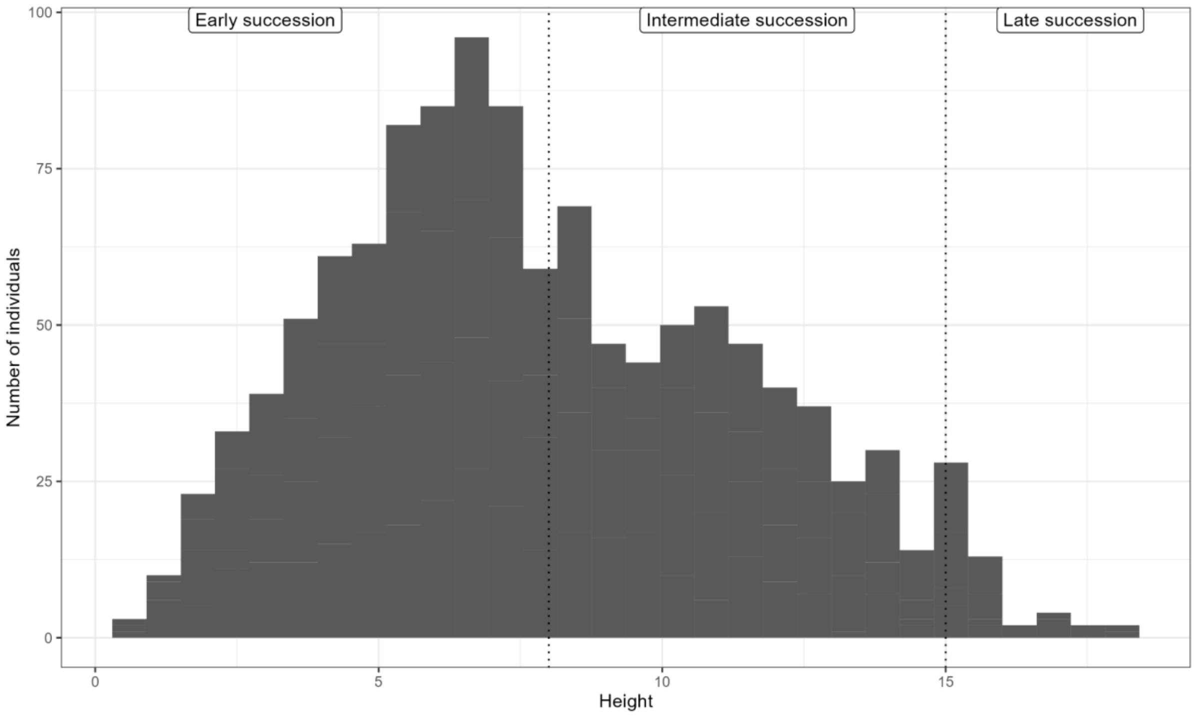

Figure 25: Individuals' height at 8.5 years for the entire stand (1,440 individuals). Dotted line represents thresholds for successional stages based on the Brazilian national legislation for Parana state (CONAMA, 1994).

Based on Parana resolution, most or 71% (860) of the individuals had heights smaller than 10 m, while 43% (513) individuals were from 8 up to 10 m height (Table 9).

Table 9: Height and dbh individuals (Ind.) distribution at 8.5 years comparing CONAMA (1994) resolutions n. 2, n. 4 and n. 33.

Succession	**Paraná**					
	Height (m)	**Ind.**	**Dbh (cm)**	**Ind.**	**Basal area (m^2/ha)**	**Pop.**

Early	<= 10	860	<= 15	854	<= 20	24.05
Intermediate	8 – 17	513	10 - 40	552	15-35	
Late	> 15	34	20 - 60	216	>30	
Succession	**Santa Catarina**					
	Height (m)	**Ind.**	**Dbh (cm)**	**Ind.**	**Basal area (m^2/ha)**	**Pop.**
Early	<= 4	170	<= 8	531	<= 8	24.05
Intermediate	4 - 12	850	8 - 15	323	8 - 15	
Late	12 - 20	178	15 - 25	344	15 - 20	
Succession	**Rio Grande do Sul**					
	Height (m)	**Ind.**	**Dbh (cm)**	**Ind.**	**Basal area (m^2/ha)**	**Pop.**
Early	<= 3	91	<= 8	531	-	-
Intermediate	3 - 8	589	8 - 15	323	-	
Late	> 8	518	> 15	344	-	

Considering dbh minimum threshold, most individuals (71%, 854) would be in the early stage of succession with dbh up to 15 cm (Figure 26), which includes individuals that did not reach the minimum dbh yet (<5 cm). However, the stand has 46% (552) of the individuals in the intermediate stage parameters with dbh from 10 up to 40 (Table 9). Total of individuals was 1,440, however, 242 individuals were dead at this age, and the total of alive individuals was 1,198.

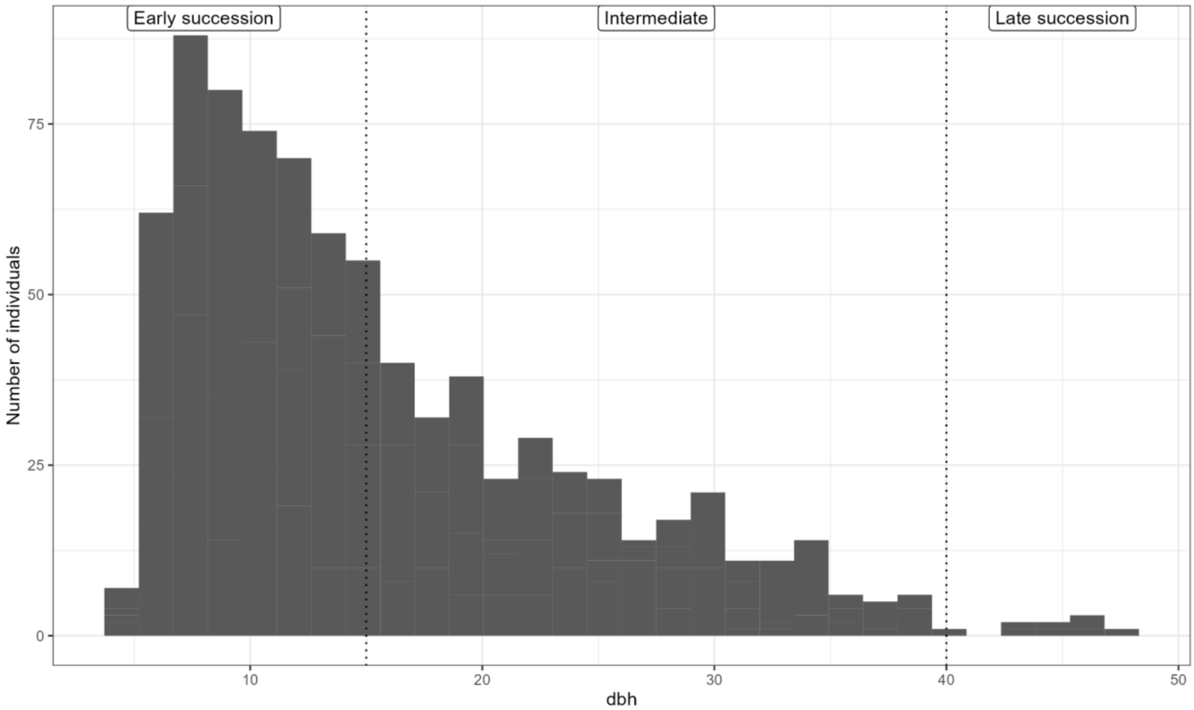

Figure 26: Individuals dbh (cm) thresholds at 8.5 years for the entire stand (1,440 individuals), the dotted line represents thresholds for successional stages based on the Brazilian national legislation for Parana state (CONAMA, 1994).

Regarding basal area, individuals started to reach the minimum dbh threshold only 2 years after planting (Nov 2012) with a basal area of 1.10 m²/ha (Table 10).

Table 10: Basal area for each age assessed from 0.5 to 8.5 years.

Plantation age in years (monitoring date)	**Basal area (m²/ha)**
0.5 (Jun 2011)	0
1 (Nov 2011)	0
1.5 (Jun2012)	0
2 (Nov 2012)	1.10
2.5 (May 2013)	3.46
3 (Nov 2013)	4.68
3.5 (Jun 2014)	8.87
4 (Dec 2014)	11.58

8.5 (Aug 2019)	24.05

After 8.5 years the stand basal area reached 24.05 m²/ha, and increases varied from annual increases of 3.5 m² up to almost 7 m² increasing annually, reaching intermediate successional stage values for basal area.

However, when analyzing parameters for the successional stages of Atlantic Forest we looked at the parameters for other states from the South region of Brazil as well, and comparing these parameters, besides being the same biome, and similar regions, we can see a vast difference among parameters (Table 9) where the same restoration site in other state would be considered in an intermediate successional stage. Considering the Parana state resolution and based on these three parameters (dbh, height and basal area), we can estimate that the stand has achieved an early successional stage 8.5 years after planting and it is transitioning to an intermediate stage, as we can see for basal area values.

4. Discussion

4.1 How do growth strategies vary among species groups and within groups?

We anticipated that filling species would share similar growth patterns as they were chosen with the goal of quickly and effectively filling the site with larger crowns when compared with other pioneer species, investing more in crown area. However, we could observe that *A. triplinervia* and *B. forficata* did not follow this pattern, investing more in height and with crowns smaller than 25 m² even after 8.5 y. *S. terebinthifolia* invested in crown area in early succession but it did not invest as much in height.

When we relate dbh with crown area, dbh could indicate the individual tree decay, because once an individual loses a trunk of many sprouts, total dbh will be smaller than it was the year before. *T. micrantha* and *S. mauritianum* and even a few individuals of *M. scabrella* presented dbh decay at 8.5 years, where smaller values for dbh can be seen when compared to early years, we do not see the same pattern for height because even though they were losing trunks, height was not affected in the same intensity. It seems that these very sprouted (after frosts) trees are naturally selecting the best trunks over time.

As the forest ecosystem undergoes succession the pioneer species tend to be gradually replaced by climax species; however, some pioneer species have the ability to persist even in the later stages of succession (Holm and Kellomäki 1984). From the pioneer species we selected for the filling group and based on our results we can state that *S. mauritianum*, *T. micrantha* and *M. scabrella* are typical pioneer species that were outgrowing during early succession, however at 8.5 y presented already some decay, where heights and dbh were lower when compared to early years, due to the loss of trunks and death of the individuals. C. *urucurana* also invested a lot in crown area in early years, however, it has not presented any decay until 8.5 years, which could indicate that it could have a longer lifespan when compared to typical pioneers, persisting after the initial phase of restoration has been completed. *C. floribundus* and *G. ulmifolia* could also fit into more persistent pioneer species, having reached substantial values for height and dbh and keep growing even during the intermediate succession phase. *P. gonoacantha* presented a lot of variability within the species, which could be related to seedlings quality, and makes it difficult to find a pattern for the species growth strategy.

When we refer to diversity species, their growth pattern tends to be slower. However, despite being adapted to growth under low light conditions, where resources can be scarce, these species have the ability to modify their growth pattern positively under open situations such as gaps in the forest canopy (Boojh and Ramakrishnan 1982). *Albizia polycephala* and *Inga vera* were two species classified as diversity species that distinguished growth in crown area and even in height, which could indicate that this is the pattern of these species growth in our region, since most individuals of these species followed this pattern and not only a few. Overall, diversity species invested more in height than in dbh, and not much in crown area up to 8.5 years after restoration, which could be explained by the high density of individuals, planted in 3 by 2 meters spacing.

The dichotomy filling and diversity species is limited in accurately representing the complex and diverse patterns of succession, mostly due to the significant diversity observed in the established phase of non-pioneer species, as well as the wide range of tree species and forests sites that contribute to successional patterns (Brzeziecki and Kienast 1994) which makes even more important to describe these growth strategies for these 70 native species in our region.

4.2 How was the evolution of canopy closure?

The physical structure of a canopy evolves over time, shaped by various factors such as climate, environmental conditions, species composition, past disturbances, and the stage of succession (Atkins et al. 2018). Considering Atlantic Forest studies, canopy cover of restored areas reached averages equal to reference sites only after 12 up to 55 years after restoration (Londe et al. 2020). In our study, the stand reached a closed canopy after four years, when only small gaps could be seen.

Besides that, plots 3 and 4 were closing canopy earlier than plots one and two up to three years, however at four and 8.5 years, these plots had more gaps in the canopy than plots one and two. This could be related to management actions of mowing and herbicide spraying that were applied up to the third year (to control invasive species), while all plots were managed, plots three and four were specially dominated by invasive grasses in the understory, which can have contributed by making it more difficult to close the canopy once management actions were not present anymore and grasses were outgrowing trees. This may suggest that management actions in restoration projects with severe invasion issues should be extended for longer than three years.

4.3 What successional stage has the stand reached after 8.5 years?

After 8.5 years the stand achieved a basal area of 24.05 m²/ha, which indicates that restoration is progressing towards reference values even earlier than expected, as a review of Atlantic forest restoration studies shows that restoration sites usually take anywhere from 10 to more than 50 years after restoration to reach reference basal areas of 30 to 40 m²/ha (Londe et al. 2020). When considering height, it takes from 7 up to 30 years after planting to reach reference values of 8 to 10 m (Londe et al. 2020), while in our site 71% of the individuals have already reached the reference height for early stage, of up to 10 m at 8.5 years.

We are aware that only height, dbh and basal area are not enough to classify a successional stage, since it is a complex and dynamic concept that involves changes in species composition, structure, and function over time and it is also influenced by multiple factors such as disturbance history, environmental conditions, and biotic interactions, additionally, we only considered planted individuals, and regeneration should also be considered when classifying a forest successional stage. Nonetheless, dbh and height can provide some indication of successional stage in a forest stand, since they are generally used to assess the development and structure of a forest stand over time.

We would like to draw attention to the differences in classifications for successional stages for each state, we believe that more similar estimates should be considered, and that these resolutions should be reviewed in order to have more accurate successional stages classifications for the Atlantic Forest biome.

5. Conclusions

Our results showed that there were differences in growth strategies among and within species groups. Most filling species invested more in crown area and height, while two filling species invested primarily in height, resulting in smaller crowns. On the other hand, most diversity species invested more in height than diameter, and two diversity species invested more in crown area, which was similar to filling species growth pattern. The high diversity stand reached a closed canopy four years after plantation, indicating a relatively quick successional stage transition. After 8.5 years, the stand reached an early successional stage in transition to an intermediate stage, which suggested that this technique is reaching desirable outcomes.

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FINAL CONSIDERATIONS

The study on tree species selection for carbon storage found several key insights. Firstly, choosing the best performing species could lead to a doubling of carbon storage at the same age. Filling species stored more carbon than diversity species, up to 8.5 years after planting. Combining fast and slow-growth species increased carbon storage over time.

Up to four years after planting, filling species dominated the top ten ranking in terms of growth in height, diameter at breast height, and crown area. However, after 8.5 years, diversity species made up half of the top ten ranking. The filling species *T. micrantha*, *S. mauritianum*, *M. scabrella* and *C. urucurana* grew faster than the rest from one to four years, but the difference was less distinct after 8.5 years. Frost was found to have a negative impact on species survival, and higher mortality rates were observed within the first two years after planting.

In terms of growth patterns, typical filling species invested more in crown area and height, while diversity species invested more in height than diameter or crown area. Canopy closure occurred four years after plantation, and by 8.5 years the stand had achieved an early successional stage, in transition to an intermediate stage.

APPENDIX

Appendix I- Higher performance 16 species selected are indicated by subscript numbers 1 to 16 in descending order; filling scenario included species with subscript numbers [1, 2, 3, 4, 6, 7, 13]; diversity scenario included species with subscript numbers [5, 8, 9, 10, 11, 12, 14, 15, 16]; 5 filling + 5 diversity scenario included species with subscript numbers [1, 2, 3, 4, 5, 6, 8, 9, 10, 11]; and 7 filling + 9 diversity scenario included all 16 higher performance species. * indicates species that did not reach the dbh threshold by 8.5 years. The average of the total carbon is indicated for each species, followed by the standard deviation. N indicates the number given to the species on the map.

Species	Author	N	Species Group	Average of Total Carbon (t/ha ± SD) 2012.2	2013.1	2013.2	2014.1	2014.2	2019
Alchornea triplinervia	(Spreng.) Müll.Arg.	1	filling	-	0.44 ±1.85	0.75 ±2.54	2.47 ±4.55	4.04 ±6.9	19.94 ±24.57
Bauhinia forficata	Link	2	filling	-	0.19 ±1.6	0.98 ±2.98	4.16 ±6.08	5.99 ±6.82	12.67 ±11.52
[3]*Croton floribundus*	Spreng.	3	filling	0.16 ±1.4	6.11 ±10.05	9 ±12.9	20.79 ±22.7	32.52 ±31.55	138.95 ±107.97
[2]*Croton urucurana*	Baill.	4	filling	7.36 ±13.33	24.28 ±22.57	31.78 ±27.68	66.66 ±45.12	94.05 ±60.57	171.68 ±150.73
[1]*Guazuma ulmifolia*	Lam.	5	filling	2.47 ±5.01	15.54 ±12.08	18.27 ±13.44	29.45 ±23.05	41.33 ±29.76	173.77 ±101.08
[4]*Mimosa scabrella*	Benth.	6	filling	2.23 ±5.49	12.35 ±16.05	21.24 ±24.09	50.03 ±41.55	61.15 ±47.34	110.54 ±111.64
[6]*Piptadenia gonoacantha*	(Mart.) J.F.Macbr.	7	filling	-	0.14 ±1.22	0.15 ±1.29	1.1 ±4.62	2.17 ±7.63	62.93 ±80.88
[13]*Schinus terebinthifolia*	Raddi	8	filling	-	0.85 ±3.15	1.05 ±3.73	6.37 ±9.67	8.62 ±11.11	34.05 ±31.13
[7]*Solanum mauritianum*	Scop.	9	filling	13.96 ±11.49	23.89 ±15.2	33.39 ±17.77	46.88 ±23.15	57.34 ±27.41	62.89 ±47.8
Trema micrantha	(L.) Blume.	10	filling	9.66 ±10.46	24.63 ±18.8	26.79 ±22.6	47.67 ±33.21	58.01 ±40.39	5.9 ±16.72
[8]*Albizia polycephala*	(Benth.) Killip ex Record	11	diversity	-	-	-	2.9 ±4.32	5.67 ±5.33	62.45 ±32.78
Allophyllus edulis	(A.St.-Hil. et al.) Hieron. ex Niederl.	12	diversity	-	-	-	-	-	4.05 ±9.56
Annona cacans	Warm.	13	diversity	-	-	-	-	-	5.99 ±14.67
Araucaria angustifolia	(Bertol.) Kuntze	14	diversity	-	-	-	-	2.4 ±3.55	19.86 ±14.07
**Aspidosperma polyneuron*	Müll.Arg.	15	diversity	-	-	-	-	-	-
Balfourodendron	(Engl.)	16	diversity	-	-	-	0.6	0.62	12.75

riedelianum	Engl.						±2.07	±2.15	±9.63
**Butia capitata*	(Mart.) Becc.	17	diversity	-	-	-	-	-	-
Cabralea canjarana	(Vell.) Mart.	18	diversity	-	-	-	-	-	8.71 ±6.2
**Calliandra tweedii*	Benth.	19	diversity	-	-	-	-	-	-
Campomanesia guazumifolia	(Cambess.) O.Berg	20	diversity	-	-	-	-	-	1.57 ±3.76
**Campomanesia xanthocarpa*	(Mart) O.Berg	21	diversity	-	-	-	-	-	-
Casearia decandra	Jacq.	22	diversity	-	-	-	-	-	2.12 ±5.24
Cassia leptophylla	Vogel	23	diversity	-	-	-	0.56 ±1.95	0.57 ±1.97	12.79 ±9.68
Cedrela fissilis	Vell.	24	diversity	-	-	-	1.02 ±3.52	2.62 ±5.26	22.37 ±9.07
[10]*Ceiba speciosa*	(A.St.-Hil.) Ravenna	25	diversity	-	1.34 ±3.18	1.5 ±3.51	9.3 ±6.99	12.69 ±9.26	40.76 ±37.37
Celtis sp	L.	26	diversity	-	-	-	-	-	1.63 ±5.66
Cinnamodendron dinisii	Schwacke	27	diversity	-	-	-	-	-	8.52 ±9.1
Cordia americana	(L.) Gottschling & J.S.Mill.	28	diversity	-	-	-	-	-	8.71 ±8.45
Cordia trichotoma	(Vell.) Arráb. ex Steud.	29	diversity	-	1.22 ±2.85	1.54 ±3.62	4.77 ±6.11	6.19 ±7.21	14.11 ±12.03
Cupania vernalis	Cambess.	30	diversity	-	-	-	-	-	4.7 ±7.6
Diatenopteryx sorbifolia	Radlk.	31	diversity	-	-	-	-	-	3.57 ±6.82
Erythrina falcata	Benth.	32	diversity	-	-	0.56 ±1.94	0.93 ±3.22	1.09 ±3.78	6.26 ±21.7
**Eugenia involucrata*	DC.	33	diversity	-	-	-	-	-	-
Eugenia pyriformis	Cambess.	34	diversity	-	-	-	-	-	2.04 ±4.76
**Eugenia uniflora*	L.	35	diversity	-	-	-	-	-	-
[9]*Ficus enormis*	Mart. ex Miq.	36	diversity	-	0.56 ±1.96	2.16 ±5.05	5.94 ±10.71	9.6 ±11.55	51.55 ±37.47
Galesia integrifolia	(Spreng.) Harms	37	diversity	-	-	-	-	-	3 ±5.5
[15]*Gymnanthes klotzschiana*	Müll.Arg.	38	diversity	-	-	-	0.64 ±2.2	2.05 ±3.73	33.1 ±17.79
Gymnanthes schottiana	Müll.Arg.	39	diversity	-	-	-	-	0.6 ±2.07	3.41 ±11.81
Handroanthus chrysotrichus	(Mart. ex DC.)	40	diversity	-	-	-	-	-	9.74 ±6.96

	Mattos								
Ilex paraguariensis	A.St.-Hil.	41	diversity	-	-	-	-	-	5.13 ±7.05
[5]*Inga vera*	Willd.	42	diversity	-	-	0.59 ±2.03	10.81 ±11.06	20.67 ±14.42	106.91 ±81.39
Jacaranda micrantha	Cham.	43	diversity	-	-	-	-	-	5.86 ±7.53
Jaracatia spinosa	(Aubl.) A.DC.	44	diversity	-	-	-	-	-	9.54 ±20.62
[14]*Lafoensia pacari*	A.St.-Hil	45	diversity	-	-	-	-	0.58 ±2.02	33.95 ±26.6
Lonchocarpus	Kunth	46	diversity	-	-	-	-	-	13.94 ±12.24
Machaerim stipitatum	Vogel	47	diversity	-	-	-	-	-	9.28 ±9.79
**Monteverdia aquifolia*	(Mart.) Biral	48	diversity	-	-	-	-	-	-
[11]*Moquiniastrum polymorphum*	(Less.) G. Sancho	49	diversity	-	-	-	4.96 ±6.94	7.57 ±10.96	37.4 ±37.99
**Myrceugenia euosma*	(O.Berg) D.Legrand	50	diversity	-	-	-	-	-	-
Myrcianthes pungens	(O.Berg) D.Legrand	51	diversity	-	-	-	-	-	5.93 ±20.54
Myrsine coriacea	(Sw.) R.Br. ex Roem. & Schult.	52	diversity	-	-	-	-	0.86 ±2.97	15.05 ±28.78
Myrsine umbellata	Mart.	53	diversity	-	-	-	-	-	6.22 ±7.95
Ocotea porosa	(Nees & Mart.) Barroso	54	diversity	-	-	-	-	-	0.63 ±2.17
Ocotea puberula	(Rich.) Nees	55	diversity	-	-	-	-	-	10.72 ±13.24
Parapiptadenia rigida	(Benth.) Brenan	56	diversity	-	-	-	0.59 ±2.03	1.84 ±3.34	23.39 ±11.68
[12]*Peltophorum dubium*	(Spreng.) Taub.	57	diversity	-	3.25 ±5.08	3.41 ±5.46	12.28 ±7.66	14.97 ±8.56	35.84 ±15.71
**Plinia peruviana*	(Poir.) Govaerts	58	diversity	-	-	-	-	-	-
Podocarpus	L'Hér. ex Pers.	59	diversity	-	-	-	-	-	21.39 ±13.88
Prunus myrtifolia	(L.) Urb.	60	diversity	-	-	-	1.61 ±3.83	2.23 ±5.4	15.45 ±17.57
Psidium cf. cattleyanum	Sabine	61	diversity	-	-	-	-	-	3.11 ±5.89
**Randia ferox*	(Cham. & Schltdl.) DC.	62	diversity	-	-	-	-	-	-
Ruprechtia laxiflora	Meisn.	63	diversity	-	-	-	-	-	10.96 ±7.74

Sloanea hirsuta	(Schott) Planch. ex Benth.	64	diversity	-	-	-	-	-	0.67 ±2.33
Strychnos brasiliensis	(Spreng.) Mart.	65	diversity	-	-	-	-	-	1.51 ±3.59
Syagrus romanzoffiana	(Cham.) Glassman	66	diversity	-	-	-	-	-	16.44 ±21.85
**Trichilia clausenni*	C.DC.	67	diversity	-	-	-	-	-	-
**Vitex megapotamica*	(Spreng.) Moldenke	68	diversity	-	-	-	-	-	-
**Xylosma sp.*	G.Forst.	69	diversity	-	-	-	-	-	-
[16]*Zanthoxylum rhoifolium*	Lam.	70	diversity	0.59 ±2.03	2.57 ±4.69	6 ±6.95	12.6 ±11.21	19.9 ±16.89	31.8 ±24.37

Appendix II - Species annual mortality rate average for all ages.

Species	Group	Annual mortality rate (average)	SD
Annona cacans	diversity	2.234	3.775
Jaracatia spinosa	diversity	2.066	3.888
Myrsine coriacea	diversity	1.967	2.285
Alchornea triplinervia	filling	1.732	2.661
Ilex paraguariensis	diversity	1.504	1.682
Piptadenia gonoacantha	filling	1.476	1.977
Monteverdia aquifolia	diversity	1.439	3.059
Sloanea hirsuta	diversity	1.281	1.664
Erythrina falcata	diversity	1.153	1.794
Trichilia clausenni	diversity	0.954	1.327
Croton floribundus	filling	0.870	1.016
Mimosa scabrella	filling	0.844	1.029
Cabralea canjarana	diversity	0.795	1.282
Cupania vernalis	diversity	0.779	1.485
Ocotea puberula	diversity	0.753	1.074
Galesia integrifolia	diversity	0.672	1.411
Myrsine umbellata	diversity	0.609	1.097
Syagrus romanzoffiana	diversity	0.582	0.671
Trema micrantha	filling	0.579	0.808
Jacaranda micrantha	diversity	0.482	0.668
Myrcianthes pungens	diversity	0.464	0.664
Prunus myrtifolia	diversity	0.354	0.629
Araucaria angustifolia	diversity	0.353	0.656
Ceiba speciosa	diversity	0.303	0.994
Ocotea porosa	diversity	0.292	0.434
Psidium cattleyanum	diversity	0.241	0.634
Gymnanthes schottiana	diversity	0.216	0.636
Xylosma sp.	diversity	0.215	0.636
Croton urucurana	filling	0.210	0.463
Vitex megapotamica	diversity	0.203	0.333
Aspidosperma polyneuron	diversity	0.191	0.328
Parapiptadenia rigida	diversity	0.179	0.361
Cassia leptophylla	diversity	0.175	0.632
Plinia peruviana	diversity	0.164	0.297
Casearia decandra	diversity	0.147	0.320
Butia capitata	diversity	0.145	0.237
Zanthoxylum rhoifolium	diversity	0.138	0.320
Celtis sp.	diversity	0.128	0.321
Campomanesia xanthocarpa	diversity	0.120	0.304
Inga vera	diversity	0.113	0.301
Handroanthus chrysotrichus	diversity	0.110	0.309
Machaerim stipitatum	diversity	0.100	0.302
Cordia trichotoma	diversity	0.089	0.319
Randia ferox	diversity	0.088	0.301
Bauhinia forficata	filling	0.084	0.160
Guazuma ulmifolia	filling	0.081	0.158
Ficus enormis	diversity	0.056	0.202
Eugenia involucrata	diversity	0.056	0.113

Solanum mauritianum	filling	0.051	0.105
Cinnamodendron dinisii	diversity	0.043	0.108
Campomanesia guazumifolia	diversity	0.032	0.097
Cordia americana	diversity	0.027	0.097
Diatenopteryx sorbifolia	diversity	0.027	0.097
Moquiniastrum polymorphum	diversity	0.027	0.097
Peltophorum dubium	diversity	0.027	0.097
Ruprechtia laxiflora	diversity	0.027	0.097
Strychnos brasiliensis	diversity	0.027	0.097
Schinus terebinthifolia	filling	0.020	0.047
Calliandra tweedii	diversity	0.001	0.005
Albizia polycephala	diversity	0	-
Allophyllus edulis	diversity	0	-
Balfourodendron riedelianum	diversity	0	-
Cedrela fissilis	diversity	0	-
Myrceugenia euosma	diversity	0	-
Eugenia pyriformis	diversity	0	-
Eugenia uniflora	diversity	0	-
Gymnanthes klotzschiana	diversity	0	-
Lafoensia pacari	diversity	0	-
Lonchocarpus	diversity	0	-
Podocarpus sp.	diversity	0	-

Appendix III - Grouping analysis a) 1-4 years and b) 4.5-8.5 years PCA data.

a)

Variable	**PC1**	**PC2**
RCD.rs	12.855	1.035
Total.height.rs	12.769	13.479
CrownA.rs	10.812	36.534
CrownH.rs	12.540	9.099
RCD.s	12.660	0.388
Total.height.s	13.741	2.728
CrownA.s	11.457	32.197
CrownH.s	13.162	4.537
Eigenvalues	6.846	0.638
Variance contribution (%)	85.585	7.975
Cumulative variance contribution rate (%)	85.585	93.560

b)

Variable	**PC1**	**PC2**
RCD.rs	8.999	5.957
Total.height.rs	12.889	2.799
CrownA.rs	13.334	8.591
CrownH.rs	5.567	49.658
RCD.s	14.477	9.835
Total.height.s	13.970	21.318
CrownA.s	14.506	0.839
CrownH.s	16.256	1.000
Eigenvalues	4.902	1.209
Variance contribution (%)	61.271	15.120
Cumulative variance contribution rate (%)	61.271	76.391

Appendix IV: Species performance followed by ranking position for each variable. CA = crown area, RP = ranking position, H = height, DBH = diameter at breast height.

Species	Species Group	CA 4y	RP	CA 8y	RP	H 4y	RP	H 8y	RP	DBH 4y	RP	DBH 8y	RP
Albizia polycephala	diversity	8.32	14º	36.08	3º	4.49	16º	11.61	3º	3.62	14º	14.96	6º
Alchornea triplinervia	filling	2.35	41º	4.03	49º	2.62	40º	4.88	41º	2.18	17º	6.14	24º
Allophyllus edulis	diversity	4.77	26º	11.07	21º	2.97	34º	5.38	35º	0.00	-	1.74	47º
Annona cacans	diversity	0.70	60º	3.56	52º	1.71	52º	4.81	43º	0.00	-	2.26	42º
Araucaria angustifolia	diversity	2.67	38º	10.17	22º	3.24	32º	6.59	23º	1.75	18º	8.18	20º
Aspidosperma polyneuron	diversity	0.47	65º	1.60	63º	0.89	68º	2.35	64º	0.00	-	0.00	-
Balfourodendron riedelianum	diversity	3.87	32º	7.62	30º	4.46	18º	7.25	16º	0.44	26º	6.12	25º
Bauhinia forficata	filling	6.15	19º	5.79	37º	4.69	13º	6.83	20º	3.51	16º	5.86	26º
Butia capitata	diversity	1.98	45º	11.25	20º	1.09	64º	1.60	67º	0.00	-	0.00	-
Cabralea canjarana	diversity	0.98	53º	2.01	60º	2.23	44º	5.48	34º	0.00	-	5.03	31º
Calliandra tweedii	diversity	6.74	17º	19.02	8º	1.94	49º	2.61	62º	0.00	-	0.00	-
Campomanesia guazumifolia	diversity	1.20	51º	2.36	56º	1.65	54º	3.55	56º	0.00	-	0.99	54º
Campomanesia xanthocarpa	diversity	1.85	47º	3.92	51º	1.68	53º	3.91	54º	0.00	-	0.00	-
Casearia decandra	diversity	2.44	39º	7.68	29º	2.20	46º	4.66	44º	0.00	-	1.19	51º
Cassia leptophylla	diversity	4.61	27º	9.11	25º	3.10	33º	5.88	30º	0.42	27º	6.25	22º
Cedrela fissilis	diversity	5.63	20º	4.50	43º	2.75	38º	6.62	22º	1.64	19º	9.68	17º
Ceiba speciosa	diversity	4.45	28º	4.42	46º	4.96	9º	8.79	8º	6.41	10º	11.11	13º
Celtis sp	diversity	10.82	9º	12.58	18º	3.60	29º	4.21	50º	0.00	-	0.69	55º
cf. Myrceugenia euosma	diversity	1.47	49º	4.39	47º	1.58	56º	2.88	59º	0.00	-	0.00	-
Cinnamodendron dinisii	diversity	3.85	33º	7.18	32º	2.78	37º	4.88	42º	0.00	-	4.36	35º
Cordia americana	diversity	3.55	34º	7.87	28º	3.60	30º	5.90	29º	0.00	-	4.57	33º
Cordia trichotoma	diversity	5.05	23º	5.41	42º	4.64	14º	7.50	14º	3.53	15º	6.33	21º
Croton floribundus	filling	13.94	7º	28.98	5º	5.94	7º	11.78	2º	9.77	6º	20.73	3º
Croton urucurana	filling	32.54	1º	43.87	2º	7.04	1º	9.54	5º	19.75	1º	24.00	2º
Cupania vernalis	diversity	0.69	61º	3.19	53º	1.46	60º	4.07	52º	0.00	-	2.43	41º
Diatenopteryx sorbifolia	diversity	2.36	40º	6.48	33º	2.58	42º	6.00	28º	0.00	-	1.89	44º
Erythrina falcata	diversity	1.10	52º	1.63	62º	1.24	63º	2.67	61º	0.64	24º	1.43	50º
Eugenia involucrata	diversity	0.73	56º	3.08	54º	1.72	51º	4.21	51º	0.00	-	0.00	-
Eugenia pyriformis	diversity	2.14	42º	4.09	48º	2.65	39º	5.59	33º	0.00	-	1.17	52º
Eugenia uniflora	diversity	4.37	29º	12.09	19º	2.79	36º	5.01	38º	0.00	-	0.00	-

Ficus enormis	diversity	5.60	21º	12.71	16º	4.85	10º	8.09	12º	4.92	11º	14.32	7º
Galesia integrifolia	diversity	2.06	44º	4.44	45º	2.40	43º	3.69	55º	0.00	-	1.77	46º
Guazuma ulmifolia	filling	13.85	8º	45.69	1º	6.58	4º	12.30	1º	12.08	5º	24.18	1º
Gymnanthes klotzschiana	diversity	6.44	18º	14.79	15º	4.45	19º	7.10	19º	1.39	20º	11.72	11º
Gymnanthes schottiana	diversity	9.49	11º	15.46	13º	4.40	20º	4.38	48º	0.42	28º	1.73	48º
Handroanthus chrysotrichus	diversity	4.08	31º	7.51	31º	3.61	28º	6.63	21º	0.00	-	5.33	30º
Ilex paraguariensis	diversity	0.71	59º	3.92	50º	1.38	61º	4.42	47º	0.00	-	2.86	40º
Inga vera	diversity	15.83	5º	30.91	4º	4.75	12º	10.28	4º	8.82	7º	19.57	4º
Jacaranda micrantha	diversity	0.97	54º	1.27	65º	2.17	48º	5.03	37º	0.00	-	3.14	38º
Jaracatia spinosa	diversity	0.45	66º	1.29	64º	1.58	57º	2.37	63º	0.00	-	3.07	39º
Lafoensia pacari	diversity	8.18	15º	15.74	11º	3.96	22º	7.17	18º	0.42	29º	11.19	12º
Lonchocarpus	diversity	5.52	22º	12.66	17º	3.52	31º	6.50	24º	0.00	-	6.23	23º
Machaerim stipitatum	diversity	2.68	37º	6.20	35º	3.94	23º	7.18	17º	0.00	-	4.56	34º
Mimosa scabrella	filling	20.46	4º	23.70	7º	6.71	3º	8.17	11º	14.63	3º	16.11	5º
Monteverdia aquifolia	diversity	0.12	70º	0.73	70º	0.76	69º	1.36	70º	0.00	-	0.00	-
Moquiniastrum polymorphum	diversity	9.64	10º	24.29	6º	3.86	24º	6.36	25º	4.41	12º	10.73	14º
Myrcianthes pungens	diversity	0.51	64º	2.35	57º	0.95	67º	2.93	58º	0.00	-	1.58	49º
Myrsine coriacea	diversity	1.77	48º	2.30	58º	1.56	58º	4.03	53º	0.54	25º	4.23	36º
Myrsine umbellata	diversity	0.93	55º	5.82	36º	2.20	45º	5.38	36º	0.00	-	3.27	37º
Ocotea porosa	diversity	0.72	58º	2.36	55º	1.64	55º	4.43	46º	0.00	-	0.44	57º
Ocotea puberula	diversity	1.45	50º	5.64	39º	1.74	50º	4.35	49º	0.00	-	4.66	32º
Parapiptadenia rigida	diversity	9.35	12º	16.79	10º	4.51	15º	7.79	13º	1.29	21º	9.40	18º
Peltophorum dubium	diversity	9.25	13º	8.59	26º	5.99	6º	9.38	6º	7.68	9º	11.84	10º
Piptadenia gonoacantha	filling	4.98	24º	18.18	9º	3.74	26º	9.38	7º	0.99	23º	12.32	9º
Plinia peruviana	diversity	0.19	68º	1.16	67º	0.53	70º	1.76	66º	0.00	-	0.00	-
Podocarpus sp.	diversity	4.17	30º	9.44	24º	3.81	25º	6.19	27º	0.00	-	8.85	19º
Prunus myrtifolia	diversity	3.14	36º	4.45	44º	4.49	17º	7.31	15º	1.21	22º	5.73	28º
Psidium cattleyanum	diversity	1.90	46º	6.41	34º	2.19	47º	5.74	31º	0.00	-	1.77	45º
Randia ferox	diversity	0.73	57º	0.74	69º	2.95	35º	2.84	60º	0.00	-	0.00	-
Ruprechtia laxiflora	diversity	3.45	35º	5.65	38º	3.99	21º	5.73	32º	0.00	-	5.81	27º
Schinus terebinthifolia	filling	14.72	6º	15.71	12º	4.81	11º	6.27	26º	4.36	13º	10.23	15º
Sloanea hirsuta	diversity	0.38	67º	2.14	59º	1.54	59º	4.91	40º	0.00	-	0.46	56º

Solanum mauritianum	filling	26.82	3º	15.39	14º	6.38	5º	8.45	9º	16.08	2º	14.25	8º
Strychnos brasiliensis	diversity	2.07	43º	5.48	41º	2.59	41º	4.55	45º	0.00	-	1.02	53º
Syagrus romanzoffiana	diversity	0.58	62º	7.88	27º	1.09	65º	3.30	57º	0.00	-	5.59	29º
Trema micrantha	filling	29.47	2º	1.89	61º	6.73	2º	1.55	68º	14.58	4º	2.01	43º
Trichilia clausenni	diversity	0.13	69º	1.25	66º	1.03	66º	2.20	65º	0.00	-	0.00	-
Vitex megapotamica	diversity	0.53	63º	1.04	68º	1.25	62º	1.53	69º	0.00	-	0.00	-
Xylosma sp.	diversity	4.96	25º	5.63	40º	3.61	27º	4.93	39º	0.00	-	0.00	-
Zanthoxylum rhoifolium	diversity	7.22	16º	9.48	23º	5.76	8º	8.28	10º	8.16	8º	9.94	16º

Appendix V - Estimates of random effects, deviation from population-level average predicted response with the response predicted for each particular species. Intercept column is the baseline mortality, whether there is a frost or not. Frost column shows the increase or not of the odds of dying if a frost event occurs. Higher the number, higher the odds of dying after a frost in relation to the community response, lower the number, lower the odds of dying after a frost in relation to the community response.

Species	(Intercept)	frost
Trema micrantha	0.111602	2.995128
Solanum mauritianum	-0.96279	2.036113
Mimosa scabrella	0.545335	1.603918
Schinus terebinthifolia	-0.81898	1.436911
Celtis sp	-0.18248	1.303971
Croton urucurana	-0.27606	1.078044
Campomanesia guazumifolia	-0.35808	1.07623
Bauhinia forficata	-1.03799	1.022669
Jaracatia spinosa	2.225814	0.857635
Randia ferox	0.212702	0.643765
Annona cacans	1.523692	0.575632
Vitex megapotamica	1.344013	0.568834
Parapiptadenia rigida	-0.6508	0.452533
Calliandra tweedii	-0.73874	0.440282
Croton floribundus	0.901217	0.410693
Zanthoxylum rhoifolium	0.265398	0.393148
Cupania vernalis	1.095185	0.368862
Gymnanthes schottiana	0.180432	0.357924
Galesia integrifolia	0.721135	0.330875
Syagrus romanzoffiana	1.468456	0.203755
Piptadenia gonoacantha	1.80705	0.196657
Myrcianthes pungens	0.634672	0.034353
Monteverdia aquifolia	1.99823	0.012222
Prunus myrtifolia	0.706853	0.006988
Psidium cattleyanum	-0.0588	-0.01274
Xylosma sp.	0.028036	-0.01335
Peltophorum dubium	-1.04175	-0.05351
Cedrela fissilis	-1.02318	-0.05507
Ficus enormis	-1.0766	-0.0553
Albizia polycephala	-1.08785	-0.05659
Cordia trichotoma	-1.07225	-0.05998
Lafoensia pacari	-1.06592	-0.06034
Alchornea triplinervia	1.998378	-0.06195
Gymnanthes klotzschiana	-1.06342	-0.06249
Moquiniastrum polymorphum	-1.0777	-0.06334
Balfourodendron riedelianum	-1.09691	-0.06359
Ruprechtia laxiflora	-1.09004	-0.06508
Podocarpus sp.	-1.0789	-0.06525
Allophyllus edulis	-1.11602	-0.06583
Diatenopteryx sorbifolia	-1.14569	-0.06626

Eugenia uniflora	-1.13924	-0.06629
Lonchocarpus	-1.09903	-0.06649
Cordia americana	-1.09736	-0.06667
Eugenia pyriformis	-1.13228	-0.06826
Strychnos brasiliensis	-1.14962	-0.06928
cf. Myrceugenia euosma	-1.15552	-0.071
Butia capitata	1.539529	-0.07354
Guazuma ulmifolia	-0.49714	-0.22179
Trichilia clausenni	1.731275	-0.26295
Casearia decandra	0.473596	-0.36918
Ocotea porosa	0.456132	-0.3739
Myrsine umbellata	0.558351	-0.39511
Jacaranda micrantha	1.294839	-0.45881
Inga vera	-0.16307	-0.50045
Handroanthus chrysotrichus	-0.2536	-0.50164
Cinnamodendron dinisii	-0.22781	-0.50444
Machaerim stipitatum	-0.26903	-0.50517
Campomanesia xanthocarpa	-0.24111	-0.50543
Eugenia involucrata	-0.29549	-0.51108
Erythrina falcata	1.619808	-0.70686
Cassia leptophylla	0.351319	-0.83508
Aspidosperma polyneuron	1.150628	-0.83587
Araucaria angustifolia	0.400907	-0.84967
Sloanea hirsuta	2.337211	-0.85295
Cabralea canjarana	1.277037	-0.88249
Ilex paraguariensis	1.968742	-0.9681
Ceiba speciosa	0.955093	-1.08134
Myrsine coriacea	2.910481	-1.0933
Plinia peruviana	1.306204	-1.4355
Ocotea puberula	1.959144	-1.74921