Restoring the Chocó: Growth and Survival of Native Chocoan Trees Using Different Propagation Methods

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ABSTRACT

The Chocó region is one of the most biodiverse places on the planet and has been identified as a priority area for conservation due to its high levels of endemism and diversity, currently threatened by the ongoing loss of forest cover. In this context, establishing baseline data on the survival and growth rates of native species can contribute to the design of effective ecological restoration strategies in the region.

With this objective, we evaluated the establishment capacity of 28 native species propagated from large cuttings. The results showed that survival depended primarily on species identity, suggesting that propagation capacity by this method is associated with intrinsic adaptations. Although the use of large cuttings is a more economical method than using seedlings, there are certain limitations, such as the fact that not all species can be propagated by this method or the requirement of a high number of donors in order not to affect genetic variability.

Additionally, the survival and growth rates of 23 native species (seven of them endemic to the Ecuadorian Chocó) were documented in a restoration experiment based on the applied nucleation strategy. The results showed high variability among species, while edaphic factors such as more acidic, less dense soils with gentle slopes and eastward exposure favored growth and survival. Pioneer species such as *Castilla elastica*, *Ficus tonduzii*, and *Cecropia sp.* promoted the development of highly diverse plantations, possibly by acting as nurse species. Finally, plantations with a higher density of islands (each composed of 25 individuals) showed increased growth rates, which could reflect competitive or facilitative interactions between individuals.

This thesis presents key insights into the performance of various propagation methods and provides a scientific foundation to inform future forest restoration efforts in the Ecuadorian Chocó.

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GENERAL AUDIENCE ABSTRACT

The Chocó region boasts extraordinary biodiversity, making it a site of great importance for conservation. However, high rates of deforestation have considerably reduced its area. The use of large cuttings is presented as a propagation method capable of rapidly producing fruit and ground cover. With this objective, we evaluated the survival capacity of 28 native species. The results show that this method is not effective for all species and that its success depends on the specific characteristics of each one. Even so, this method proved more economical than the use of seedlings, and the application of rooting hormones could improve survival.

Additionally, we evaluated the growth rate of 23 native species, providing basic information on their development during the first two years of establishment. We identified that both survival and growth vary according to the species, but we did not find a direct relationship between the two. We also observed that species such as *Castilla elastica*, *Ficus tonduzii*, and *Cecropia sp*. favored the development of more diverse plantations by facilitating resource acquisition. Finally, we found that plantations with a higher density of islands showed higher growth, possibly due to competitive or collaborative interactions between the species present within and around the plantations.

DEDICATION

I dedicate this thesis to my family in Mexico and friends for their love and constant support throughout my career.

Dedico este trabajo de tesis a mi familia en México y amigos por su cariño y apoyo constante durante toda mi carrera.

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Chapter 1: Review of literature

1.1 Biodiversity Loss

The biodiversity loss has become one of the most pressing environmental challenges of the 21st century. The effects are so great that current extinction rates are estimated to be a thousand times higher than natural extinction rates (Pimm et al., 2014). However, assisting species that are at risk of extinction is particularly complex; in the case of plants, only 21% of known species have been assessed, and among endemic species, 58% have not yet been assessed (Gallagher et al., 2023). The main causes of biodiversity loss are habitat loss, we can find habitat loss, overexploitation of resources, the introduction of invasive species, pollution, and climate change (Díaz et al., 2019).

1.2 Topical Forest and Biodiversity Hotspots

1.2.1 Tropical Forest

Tropical forests are the most diverse terrestrial ecosystems on the planet, harboring more than half of all terrestrial vertebrate species and a remarkable degree of endemism (Pillay et al., 2022). Despite their ecological importance, it is estimated that less than 50% of tropical forests remain today (Lewis et al., 2015; Malhi et al., 2014). Their degradation continues to increase due to multiple anthropogenic pressures, such as logging, fires, and edge effects, which cause significant losses of carbon and biodiversity (Bourgoin et al., 2024). Consequently, ecosystem recovery times are becoming increasingly prolonged.

This problem is exacerbated by the growing demand for tropical forest products and the accelerating impacts of climate change, factors that increase the risk of continued and severe degradation (Lewis et al., 2015). Therefore, forest conservation is not only an environmental

concern but also a social and economic necessity, as between 1.2 and 1.5 billion people depend directly on forest ecosystems for their livelihoods (Vira et al., 2015). Investing in tropical forest restoration thus represents not only a strategy for conserving biodiversity but also a way to promote climate change mitigation, adaptation, and water security (Brancalion et al., 2019; Lewis, 2006). Failure to act now could lead to irreversible losses of these vital ecosystems (Malhi et al., 2014).

1.2.2 Biodiversity Hotspots

Although biodiversity loss is an urgent problem, the resources available for its mitigation are limited, making it impossible to act simultaneously in all regions of the planet. Therefore, identifying priority areas for conservation has become an essential strategy. To this end, Myers (1988) proposed the concept of biodiversity hotspots, defining them as regions with exceptional levels of endemism facing intense habitat loss. In their initial study, this author and other researchers identified 25 regions that, despite occupying less than 2.5% of the Earth's land surface, harbored nearly a third of all known species of vascular plants and vertebrates (Myers, 1988; Myers et al., 2000).

Subsequently, the hotspot definition was formalized to include regions containing at least 1,500 endemic species of vascular plants and that have lost at least 70% of their original vegetation (CEPF, 2025). Based on these criteria, the total number of globally recognized biodiversity hotspots has expanded to 36 (Hrdina & Romportl, 2017).

1.3 The Chocó region

1.3.1 Description

Within the extensive number of biodiversity hotspots, we find the Tumbes–Chocó–Magdalena region, one of the first 25 described by Myers et al (2000). Characterized by its high

biodiversity, high level of endemism, and the constant loss of its forest cover (Mittermeier, 2005; Myers et al., 2000), this region extends from southern Panama, along the Pacific coast of Colombia, Ecuador, to northwestern Peru, covering approximately 187,500 km² (WWF, 2025).

Despite being geologically young, this region exhibits a high level of endemism, which is usually attributed to its biogeographical isolation caused by the drastic elevation changes of the Andean Cordillera (Conservation International, 2007; Gentry, 1982). Within this hotspot, the Chocó biogeographical region constitutes a large part of the territory, being particularly characterized by its high diversity of flora (Gentry, 1986).

1.3.3 Ecological importance

The Chocó region is often recognized for its high biodiversity and high annual rainfall, which can range from 3,000 to 11,700 mm, making it the second-wettest region on the planet (Banerjee et al., 2012; Pérez-Escobar et al., 2019). Several studies have identified a positive correlation between average annual rainfall and species richness, reinforcing the importance of the water regime in maintaining tropical biodiversity (Copete et al., 2019; Gentry, 1986; Pérez-Escobar et al., 2019).

Thanks to its unique geographical characteristics and the complex interaction between biotic and abiotic factors, the Chocó has positioned itself as the ninth most biodiverse region on the planet, harboring a high number of endemic species (Gentry, 1982, 1986; Pérez-Escobar et al., 2019). Therefore, failing to protect the high diversity of species present in this region could lead to the extinction of species that we will not be able to recover.

1.3.4 Threats to its conservation

However, despite the region's high biological value, the Chocó is highly threatened by a constant loss of its area, with agriculture, livestock farming, mining, and urbanization being the main causes of deforestation. Additionally, reforestation efforts do not tend to support long-term conservation because they are not very widespread (Fagua et al., 2019). The fragmentation of this ecosystem has been so severe that in western Ecuador, it was estimated that only 4% of the original cover remained (Dodson & Gentry, 1991). Therefore, there is an urgent need to conserve and restore highly vulnerable sites in the region.

1.3.5 Justification

This manuscript aims to contribute to the planning of ecological restoration strategies in the Chocó region. To this end, it evaluates the effectiveness of using large cuttings and seedlings as propagation methods, with the objective of identifying the survival rates of different species according to the method employed.

Additionally, it analyzes the growth rates of endemic species, many of which lack documented information on their early development. The results of this study are intended to serve as a baseline to guide future restoration and conservation efforts in this highly threatened region.

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Chapter 2: Assay of native Chocoan trees for their capacity to regenerate from large cuttings

2.1 Abstract

Deforestation has severely impacted the Chocó region of western Ecuador and Colombia and assessing mechanisms to enrich and accelerate the process of forest recovery are needed. Large cuttings (i.e., ≥4m) is a propagation method that can promote the establishment of native species and, at the same time, positively influence the landscape in the short term by providing rapid canopy cover, early fruit production, and a means to outcompete other plants. However, not all plant species can be easily established using this method, so identifying which species are suitable for this approach could benefit future projects in the region. This study used 4 plots to evaluate the survival and development of 28 native tree species in the region (six individuals of each species per plot, N: 672) that were established using 3-4-meter cuttings. Overall survival was low (13.2%), but several widespread Neotropical species used as living fences performed well. *Erythrina poeppigiana* and *Trichanthera gigantea* did not experience mortality, while *Spondias mombin* and *Gliricidia sepium* showed viable survival rates of 95.8% and 62.5%, respectively, using this propagation method. Additionally, two of these species were able to produce fruits, and one was able to produce flowers within a year after the cuttings were established. The ability to resprout has been linked to an adaptation to disturbances such as hurricanes; the low number of species capable of surviving this propagation method in the Chocó could be linked to the lack of this type of disturbance. Therefore, understanding what makes these species so able to establish under this propagation method could help to identify other potential candidates that haven't been used as living fences.

2.2 Keywords

Chocó region, giant stakes, tropical forest restoration, living fence, plant propagation.

2.3 Introduction

The Chocó region stretches from Panama to Ecuador along the western edge of the South American. Despite occupying <0.2% of Earth's land surface, the Choco hosts nearly 3% of the world's basal plant species. The combination of high endemism and high habitat alternation makes this region one of the world's hottest biodiversity hotspots (Pérez-Escobar et al., 2019; Christenhusz et al., 2017; Myers et al., 2000). Despite its remarkable biological diversity, this region has been increasingly affected by deforestation, primarily driven by the expansion of activities such as infrastructure development, mining, logging, and agriculture (Fagua et al., 2019). Particularly in the western region of Ecuador, deforestation processes have caused only approximately 4.4% of primary forests to remain in this region (Dodson & Gentry, 1991). Considering this, restoring the Chocó region becomes an even more challenging task. Maintaining the high biodiversity of endemic species in a region where deforestation limits their availability requires the use of various restoration methods.

Due to this, the use of propagation methods that accelerate the development of the canopy cover could benefit restoration projects in this region. The establishment of living fences usually employs the use of large cuttings as the main propagation method, which is why it has become a common practice in different regions of the world. Compared to the use of seedlings, large cuttings do not require the costs associated with germination or acclimatization processes, and depending on the length of the cutting, the access of the individuals to resources can be facilitated. In addition, some species can develop an early canopy or a faster production of fruits (Granzow-De la Cerda,

1999; Harvey et al., 2005; Zahawi & Holl, 2009), which makes this propagation method very attractive for restoration efforts that wish to incorporate these advantages. The high level of endemism in this region presents an opportunity to study this propagation method with species that have not been evaluated in this way before. At the same time, identifying native Chocoan species capable of being propagated by this method could establish a baseline of species that can easily escape competition with other plants, changing habitat structure quickly by attracting seed dispersers and reducing the cost associated with maintenance (Zahawi, 2005; Zahawi & Holl, 2009; Fuentealba & Martínez-Ramos, 2014).

This study evaluates the ability of 28 native and endemic species from the Chocó region of western Ecuador to establish as large cuttings (≥3 - 4m), so they could be identified as potential tools for restoration efforts developed in the region.

2.4 Methods

2.4.1 Study area

This study took place in northwestern Ecuador, within the reserve of the Fundación para la Conservación de los Andes Tropicales (FCAT), which has a total of 607 hectares dedicated to the conservation and restoration of the Chocó region. As this reserve is located within this biodiversity hotspot, the Köppen classification considers it a tropical rain forest (Peel et al., 2007; Beck et al., 2023). Despite its ecological importance, the surrounding landscape is significantly influenced by human activities, including cocoa, banana, African palm, and cattle pastures (Castro et al., 2013). In 2024, the year presents an accumulated precipitation of 1,5070.8 mm (FCAT & USFQ, 2024), which was marked by high seasonality from January to May. However, this value is below the

average annual rainfall of 2,000-3,000 mm reported at the Bilsa biological station located 8 km away (Charlat et al., 2000; Jongsma et al., 2014).

2.4.2 Experimental design

The experiment was established in January 2024. Four plots previously used for agriculture were selected, two of which had been used for pasture and two for cacao. Plots were 20×20 m and were selected to represent the regional variation in climate, elevation, and soil quality. Two of these plots were selected near the FCAT station and have an elevation between 500-520 masl. The two remaining plots were located next to Laguna De Cube and share an approximate elevation of between 300 and 330 masl.

2.4.3 Species

We selected 28 native tree species to assay based on local ecological knowledge, prior studies, and the availability of mature donor trees. We planted six individuals per species per plot (N = 672 stakes). Taking into account the results obtained by Zahawi in previous experiments located in Costa Rica (Zahawi, 2008), it was decided to use larger stakes (3-4 meters long, with a minimum diameter of 5 cm) to increase the chance of survival, promote the rapid growth of plant structures, generating an early habitat in a degraded landscape (Zahawi, 2008; Zahawi & Holl, 2009; Pulido-Santacruz & Renjifo, 2011; Zahawi & Reid, 2018). The mean length of the large cuttings established in the experiment was 3.67 meters (min: 2.21 and max: 4.87 m), (Appendix A Table 1).

Once the large cuttings were obtained, the branches were removed from the trunk, and a pointed cut was made at the base to facilitate their establishment. Following the local custom of

using live cuttings for fence posts, the cuttings were left to rest for 15 days in the shade to seal their wounds and encourage early root development. Each cutting was planted in a hole approximately 50 cm deep.

The planting process took place during the rainy season (Jan-Feb 2024) to promote the establishment of individuals in our experiment.

2.4.4 Monitoring

We monitored the survival, size, and reproductive development of stakes after four months and 16 months. The variables collected were survival, phenology (presence of flowers and/or fruits), type of resprout, which seeks to classify individuals according to the height at which the regrowth emerged on the stake (Appendix A Figure 2), height [cm] (used to estimate the growth of cuttings over time and it corresponds to the maximum height of the apex with respect to the ground), diameter at breast height (DBH) [cm], and longest canopy diameter and its corresponding perpendicular diameter [m]. These previous values were collected to estimate the canopy area [m2], assuming an oval shape. Phenology data were collected monthly since the fourth month and also included the approximate number of fruits per tree was reported.

2.4.5 Soil sampling

Given this, five soil samples were analyzed per plot to better understand the differences between them. The collection was done using a slide hammer soil sampler, which, using a soil auger head as an attachment, we extracted soil cylinders with a diameter of 5 cm and a height of 15 cm. Four of the samples were extracted at approximately 1.5 meters from each corner, and the

last one was in the center. Each sample was sealed in an airtight bag and refrigerated to reduce the degradation of organic matter before analysis.

The soil samples were analyzed at the AQUA-BIO Lab facilities, located at the Universidad San Francisco de Quito (USFQ). Twelve different soil analyses were performed (Appendix A Table 2), including soil texture (FAO, 2016), bulk density (g/cm3), pH, organic matter (%), Total Kjeldahl Nitrogen (TKN), concentration of magnesium (mg Mg/kg), calcium (mg Ca/kg), phosphate (mg PO4/kg), phosphorus (mg P/kg), sulfate (mg SO4/kg), and sulfur (mg S/kg) using Hach calmagite colorimetric method.

2.4.6 Data Analysis

We used a permutational multivariate analysis of variance (PERMANOVA) to evaluate soil parameters between the study plots, so we could account for these environmental factors in the growth rate models. Considering a Euclidean distance for the values, we used the R package vegan, function adonis2 (Oksanen et al., 2001), and subsequently we performed a pairwise comparison between plots using the package *pairwiseAdonis* with the function *pairwise.adonis* (Martinez Arbizu, P., 2017). Additionally, we performed a Principal Component Analysis (PCA) to understand these differences (Appendix A Figure 3), using the *prcomp* function from the R package stats (R Core Team, 2025), based on the parameters listed in Table 2. 1.

To determine the most important drivers of species survival, multiple general linear models were compared to identify the best simple model, using the corrected Akaike Information Criterion (AICc) value as the main selection criterion (Appendix A Table 3). The built models used the species and the initial characteristics of each individual before planting (length and DBH)

The growth models used a linear model and also required multiple comparisons to identify the best model. The constructed models used the species of the individuals and the axes of the PCA that were associated with the soil parameters of each plot as predictors. The *lm* function was used, and again, the selection was based on the AICc values obtained from each comparison.

Species with only one individual were excluded from the growth analyses, as they consistently showed basal regrowth that prevented DBH measurements and affected height models.

2.4.7 Economic comparison

The costs associated with the establishment of this experiment and a comparable restoration project conducted within the FCAT Reserve were estimated. Expense records from both projects, together with the total number of working days, were used to estimate the overall costs. For the seedling-based restoration, expenses included seed collection, nursery establishment, site preparation, planting (N = 2,900 individuals), and maintenance activities carried out between 2022 and 2024. Additional materials required for these tasks included plastic bags for seedling transport, brush cutter replacements, fuel, and other consumables. Similarly, the costs associated with the establishment of cuttings included plot preparation, collection of plant material, transportation, planting (N = 672 individuals), and maintenance activities conducted between 2024 and 2025. As with the seedling project, material costs were also considered, including chainsaw files, machetes, fuel, and other field supplies. Using this information, the cost per individual and the cost per establish individual were estimated, accounting for final survival rates recorded at the end of each project.

2.5 Results

2.5.1 Survival

Stake survival after four months was exceedingly low (22.17%). Corresponding to this percentage, we can see that only 16 species showed any sign of survival (Figure 2. 1), of which 74.50% of the surviving individuals show signs of resprouts. Subsequently, the evaluation corresponding to 16 months after the establishment of the experiment showed a decline in survival to 13.24% and a reduction in the number of species to seven (Figure 2. 1). The selected model used species identity as the only fixed effect, explaining 87.6% of the variation in survival. Subsequent analyses were performed to explore whether initial characteristics (stake length and DBH) could explain survival rates, considering species effect as random in survival rates greater than 0% and less than 100%. However, none of these models proved to provide an explanation of variance focused on initial characteristics.

18 months after planting *Erythrina poeppigiana* and *Trichanthera gigantea* had 100% survival rates. In contrast, *Spondias mombin* and *Gliricidia sepium* presented survival rates of 95.83% and 62.50%, respectively. Finally, *Pouteria torta, Ficus crassiuscula,* and *Aniba magnifica* presented a low survival with only one individual of each on the whole experiment, representing a 4.17% survival rate.

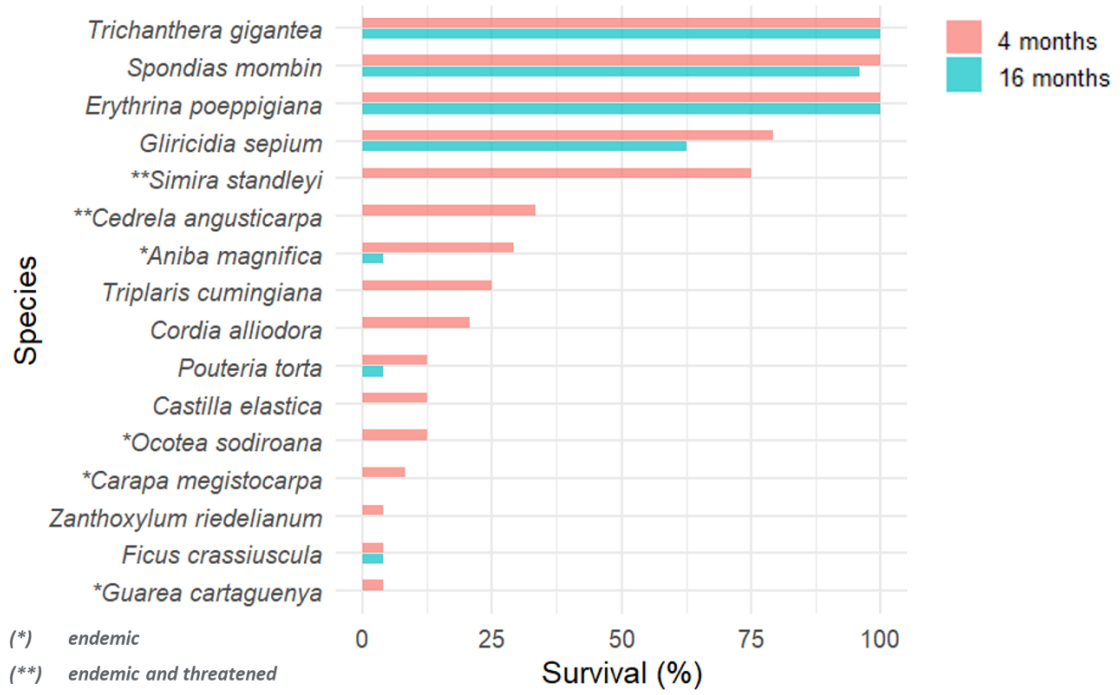

Figure 2. 1.- Survival of large cuttings of 28 native Chocoan trees over 16 months (2024-2025). Only species with survival >0% are shown. The following species had 0% survival: Coussapoa villosa*,* Coccoloba obovata*,* Castilla tunu, Miconia brevitheca, Otoba gordoniifolia, Pentagonia macrophylla*,* Pouteria capacifolia*,* Quararibea casasecae, Chrysochlamys nicaraguensis, Virola dixonii, Virola elongata, Vismia panamensis. *Scientific names were confirmed using the https://www.tropicos.org portal*

A total of 57 individuals died between the two monitoring periods, although 43.86% of them had already produced some form of regrowth before dying. During the second evaluation, four individuals were carefully extracted on-site, corresponding to two micro-endemic species of the region. In *Cedrela angusticarpa*, all individuals that remained alive at the four-month evaluation had developed some regrowth. In contrast, none of the surviving *Simira standleyi* individuals showed evidence of regrowth, despite appearing in good condition. In both species, the extracted cuttings revealed no evidence of root formation (Figure 2. 2).

Resprouting 4-mo-old stake.

Death of resprouts in an 8-mo-old stake.

A large cutting that was unable to develop roots after 14

Figure 2. 2.- Example of Cedrela angusticarpa *capable of resprouting from large cuttings but unable to develop roots. The first image shows a healthy cutting with active shoot growth, the second depicts leaf loss after initial sprouting, and the third illustrates an individual of the same species that failed to produce roots.*

2.5.2 Soil properties

The PERMANOVA analysis indicates that the physicochemical characteristics of the plots are significantly different ($F = 3.59$, $R^2 = 0.42$, $p = 0.035$), based on Euclidean distance with 999 permutations. A homogeneity test was subsequently performed using analysis of variance (ANOVA) ($p = 0.49$), raising confidence that each plot has a distinct composition. However, individual comparisons between plots didn't show a significant difference after adjusting the p-value with the Holm method. This could suggest that differences may be concentrated in a subset of groups or that there are complex patterns that cannot be captured by individual comparisons.

Comparisons corresponding to plots 1 and 4, and plots 4 and 3, presented marginally significant results (adjusted p= 0.06, R2= 0.50, and adjusted p= 0.14, R2= 0.34, respectively).

Table 2. 1.- Mean soil physicochemical properties per plot, based on analyses conducted by the AQUA-BIO Laboratory (USFQ).

Plot number	***Plot 1***	***Plot 2***	***Plot 3***	***Plot 4***
pH	6.94 ± 0.07	6.96 ± 0.09	7.45 ± 0.18	6.87 ± 0.13
TKN (% N total)	0.93 ± 0.31	1.17 ± 0.55	3.26 ± 0.21	0.59 ± 0.41
Organic Matter (%)	9.84 ± 0.68	10.78 ± 0.87	11.39 ± 0.79	11.26 ± 0.54
Magnesium (mg Mg^{2+}/Kg)	36.21 ± 4.99	22.88 ± 2.15	45.19 ± 8.62	22.88 ± 1.54
Calcium (mg Ca^{2+}/Kg)	59.92 ± 9.76	80.79 ± 20.73	56.47 ± 21.69	126.12 ± 10.09
Phosphate (mg PO_4/Kg)	63.72 ± 21.28	48.78 ± 9.87	103.77 ± 35.5	49.95 ± 5.58
Sulfate (mg SO_4/Kg)	639 ± 157.64	1629 ± 340.43	1026 ± 94.74	1827 ± 339.29
Bulk density (g/cm^3)	0.36 ± 0.01	0.33 ± 0.01	0.29 ± 0.01	0.28 ± 0.03

The results obtained from the PCA allowed the marginal differences between the plots to be visualized, increasing confidence in their environmental differences. Additionally, its axes were able to jointly explain 60.6% of the variance (PCA1: 39.7%, PCA2: 20.9%). Axis 1 was mainly associated with variables such as Mg2+, pH, TKN, PO4, and Ca2+. Axis 2 was mainly associated with variables such as organic matter, bulk density, and SO4 (Appendix A Figure 3).

2.5.3 Growth and Canopy

Species were initially tested as a random effect but did not improve model performance due to low survival and limited interspecific variation. It was therefore included as a fixed effect along with the PCA axes in the final growth models.

The selected model that best explains year diameter growth included both axes of the PCA. However, the overall fit of the model explained only a small percentage of the variance in the data (R^2 = 0.145). Soils with higher concentrations of calcium, sulfate (SO4), and organic matter showed a positive effect on diameter growth, as indicated by the significant positive coefficients of both PCA axes (β = 0.16).

Subsequently, the selected height growth model included both PCA axes as well as the use of the species factor (R^2 = 0.62). Showing that height growth depends on the species and associating greater growth in soils with higher calcium concentrations (PCA 1, β = 0.007) and higher bulk density values (PCA 2, β = -0.011). The growth rates for each species are found in Table 2. 2.

Table 2. 2.- Growth rates and canopy cover of native species planted as large cuttings in western Ecuador with more than one survivor. Species with only one surviving individual show growth rates: Aniba magnifica *(n=1, DBH rate= 0 cm, height= 0.52 m & canopy cover= 0.13 m2),* Ficus crassiuscula *(n=1, DBH rate= -0.2 cm, height= 0.60 m & canopy cover= 0.29 m2), and* Pouteria torta *(n=1, DBH rate= -0.6 cm, height= 0.63 m & canopy cover= 0.12 m2).*

Species	**Number of individuals**	**DBH growth rate [cm/ year]**		**Height growth rate [m/year]**		**Canopy cover [m^2/ year]**	
Erythrina poeppigiana	*24*	0.54	± 0.88	1.56	± 0.82	3.68	± 2.28
Gliricidia sepium	*15*	0.52	± 0.66	2.23	± 0.55	8.54	± 4.31
Spondias mombin	*23*	0.48	± 0.99	0.25	± 0.45	1.39	± 0.87
Trichanthera gigantea	*24*	0.57	± 0.51	0.95	± 0.45	5.71	± 1.86

Because canopy cover was positively and significantly correlated with monthly height growth rate (r = 0.60, p < 0.0001), no models were developed. These results suggest that canopy cover and individual vertical growth are closely related.

G. sepium had the largest canopy growth, expanding to 8.54 ± 4.31 m² by 16 months. On the other hand, *T. gigantea* presented the second largest canopy cover with 5.71 ± 1.86 m². *E. poeppigiana* is closer to a circular shape on its canopy and presents a mean value of 3.68 ± 2.28 m². Finally, *S. mombin* presented the smallest canopy cover of 1.39 ± 0.87 m² (Figure 2. 3).

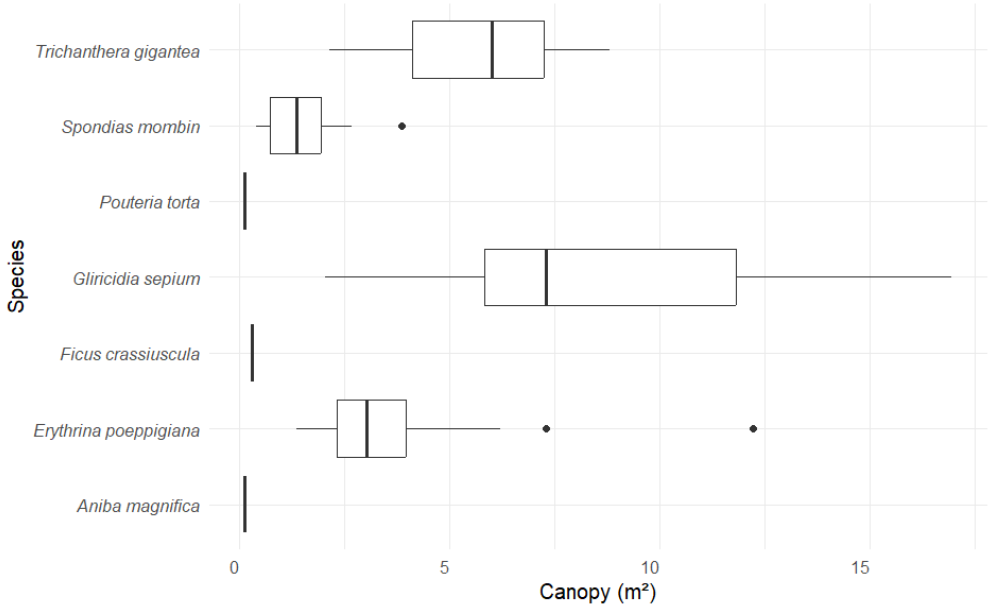

Figure 2. 3.- Canopy Area [m2] of the surviving species after 14 months of their establishment.

2.5.4 Phenology

No flowers were identified in *T. gigantea* during monthly monitoring; however, this species showed the first signs of a phenological cycle eight months after establishment, evidenced by the presence of fruits, with a total of two individuals. Subsequently, two individuals of *E. poeppigiana* produced flowers and fruits in the tenth month, while *G. sepium* began producing flowers from the eleventh month with a total of 2 individuals (Appendix A Figure 4).

2.5.5 Cost

The costs associated with the use of seedlings were estimated at USD 21.16 per individual, whereas the use of large cuttings resulted in a lower initial cost of USD 16.13 per individual. However, the restoration project that employed seedlings achieved a survival rate of 82.1%, leading to a final cost of USD 25.79 per successfully established individual. In contrast, due to the low survival observed in the large cutting method, the final cost per established individual was considerably higher, reaching USD 121.78.

2.6 Discussion

The ability of certain species to resprout has been considered a strategic adaptation that favors their survival under different disturbance regimes (Bond & Midgley, 2001). In tropical forests with a high incidence of hurricanes, the ability to generate resprouts promotes rapid regeneration of the vegetation cover and the persistence of affected individuals (Basnet, 1993; Bond & Midgley, 2001; Poorter et al., 2010). Some studies have been able to link the generation of resprouts with the presence of hurricanes in the Caribbean (Van Bloem et al., 2007). This mechanism could be key in determining the capacity of different species to be propagated through the use of large cuttings.

In contrast, hurricanes do not occur in the Ecuadorian Chocó because the effects of the Earth's rotation are weak near the Equator (Steenkamp et al., 2019). As a result, this adaptive strategy may be less frequent among species present in this region, which could explain the low number of species that were able to be propagated by this method. Additionally, the four species that did establish have wide distribution ranges across much of the Neotropics (According to the

GBIF 2025 database), suggesting the presence that these adaptive traits could not be shared by species with a smaller distribution range in Chocó.

This interpretation is consistent with our findings, which show that species identity was the primary factor determining survival. However, previous studies have also demonstrated the impact of initial characteristics being significant, demonstrating that the use of larger (2-3 meters) and thicker (4.5-6 cm) cuttings favors the development and survival of species such as *G. sepium* (Zahawi, 2005). The difference in these results may be due to the initial characteristics of our cuttings not being sufficiently distinct to demonstrate what was established in previous studies.

There is still a significant gap between our current knowledge and the actual number of species that can be propagated through this method. In the Caribbean, South America, and Central America, 95% of living fences correspond to just eight species, despite the fact that more than 100 have been recorded as capable of being propagated using this method (Harvey et al., 2004). Evaluating the viability of additional species is therefore crucial to broadening the range of tools available for restoration.

When we compare survival rates by species in other studies located in the Neotropics, our individuals showed similar survival and development rates. Efforts *with E. poeppigiana* and *G. sepium* have yielded survival rates above 90% and 50%, respectively (Zahawi, 2005, 2008; Zahawi & Holl, 2009), which is consistent with our results. However, contrary to our study, the literature shows that *E. poeppigiana* has quicker and more extensive canopies than *G. sepium* (Zahawi & Holl, 2009). This difference may be due to the timing of the experiments or to the developmental capabilities of each species in different regions. On the other hand, according to the literature, efforts made with S. mombin have resulted in low survival rates (<50%) (Granzow-De la Cerda, 1999; Zahawi, 2005; Douterlungne et al., 2015). By contrast, our survival rate exceeded 90%,

which may be due to the annual rainfall, as some studies have indicated, species of the same genus used as living fences tend to thrive in drier regions (Harvey et al., 2004). Considering the studies carried out by Zahawi (2005) and Douterlungne et al. (2015) were conducted in regions with an average nearly double what was present in FCAT during the year 2024, this could be a determining factor in the survival of this species; however, more information is required to confirm this assumption. Finally, regarding T. gigantea, studies conducted in Colombia using cuttings approximately 2 meters tall showed a considerably low survival rate of 34% (Díaz-Páez et al., 2022). However, these results also contrast with those obtained in other studies, which describe that even using smaller cuttings can achieve high survival rates. Ensuring the presence of 3-4 nodes per cutting appears to be a key factor in propagating this species. (Moreno & Guerrero, 2005; Espinosa et al., 2013).

Although the success of this propagation method largely depends on the characteristics of each species, it is possible that this process can be improved by using hormones that promote root development before the establishment of cuttings (Bonfil-Sanders et al., 2007).

Regarding cost comparisons, some studies conducted in Costa Rica have shown that this propagation method can be up to ten times cheaper than using seedlings (Zahawi & Holl, 2009). However, our results indicate that although the costs per individual are indeed lower, the cost difference compared to the use of seedlings on a reforestation project within the same reserve is not as substantial. The results become less promising if we compare the cost associated with surviving individuals, making this method of propagation unviable. Nevertheless, given that some species exhibited relatively high survival rates, prioritizing these species could substantially reduce overall project costs and enhance the economic viability of this propagation approach in tropical restoration initiatives.

2.7 Conclusions

Although previous studies have shown that the initial conditions of large stakes can influence individual survival, the use of 3–4 m stakes in our study did not show an effect on individual survival. This suggests that survival capacity depends primarily on the adaptive traits specific to each species rather than on stake size. Resprouting capacity has been described as an evolutionary adaptation to recurrent disturbances such as hurricanes, which favor rapid canopy regeneration. However, this adaptation may be absent in the Ecuadorian Chocó, where such disturbances are not present, which could explain the low resprouting capacity observed in local species. On the other hand, the high diversity of species presents in this region and the low number of individuals that were able to establish themselves could be related to the number of species that were evaluated. Therefore, in order to evaluate both hypotheses, further studies are still needed.

The species that were able to be propagated by this method showed similar survival and growth rates in other regions of the Neotropics, and three of these were able to produce flowers and/or fruits within the first year of establishment. This demonstrates the feasibility of using this propagation method for the establishment of these species, confirming their suitability for use in the Chocó.

Using this propagation method offers significant advantages over seedlings, primarily due to its lower cost per individual and the rapid vegetation coverage it can provide. However, using stakes taller than four meters can limit the extent of reforested areas due to the size and handling of each individual. Even so, selecting species with a high survival rate could favor projects that combine different propagation methods, optimizing both costs and restoration effectiveness.

Additionally, the use of rooting hormones could enhance the establishment success of other species of interest.

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Chapter 3: Growth and survival patterns in native Chocoan trees: Impacts on growth and survival on applied nucleation plantations

3.1 Abstract

This study evaluates the growth and survival rates of 23 native Chocoan trees during their first two years of development. Within these development descriptions, we can find seven endemic species of the region, among which we highlight *Exarata chocoensis, Matisia palenquiana, Pouteria juanguillermensis*, and *Virola dixonii*, among others. The individuals were established in an applied nucleation experiment, which included variations in plot composition to generate different levels of fruit availability, species diversity, and island density. Our results showed clear differences in plant survival based on species and planting year, and to a lesser extent, on soil characteristics and topography. Furthermore, plantations with high diversity exhibited higher growth rates, favored by the presence of pioneer species such as *Castilla elastica, Ficus tonduzii,* and *Cecropia obtusifolia*. Similarly, growth was enhanced in plots with a higher island density, suggesting that the spatial configuration of the plantations can influence the performance of the established species. These results could favor the planning of restoration efforts in the Chocó region, considering the variability in survival and development in the establishment of these species as seedlings.

3.2 Keywords

Ecuador; Chocó Region; Tropical Forest Restoration; Reforestation; Seedlings.

3.3 Introduction

The high level of endemism, combined with the great variety of species, positions the Chocó region as one of the most diverse places on earth (Christenhusz et al., 2017; Myers et al., 2000). Thanks to its climate and geographical location, this region has become home to a wide variety of plant species, including ~2,750 endemic species (Among these, we can find locally endemic species that have distribution areas smaller than 20,000 km2), and hosts more than 11,000 species (Pérez-Escobar et al., 2019; Christenhusz et al., 2017; Zachos & Habel, 2011; Dodson & Gentry, 1991). However, its high biodiversity has not prevented this region from being exploited in various ways, resulting in a high rate of deforestation caused by human activities such as livestock farming, agriculture, mining, urbanization, timber harvesting, and armed conflicts (Fagua et al., 2019a; Fagua & Ramsey, 2019; Sierra & Stallings, 1998). While in many cases, vegetation can recover after land abandonment, there is a spatial correlation between reforestation and deforestation that hinders the long-term preservation of these forests (Fagua et al., 2019b). In the specific case of Western Ecuador, deforestation has caused a great fragmentation of this ecosystem to such an extent that less than 4% of the original forest cover remains in the region (Dodson & Gentry, 1991; Fagua et al., 2019a; Fagua & Ramsey, 2019). As a result, many species have begun to go locally extinct, and even more are now endangered. According to predictive models, the number of threatened and endangered species will likely increase in the coming years. Failing to act now would mean the extinction of many more (Palacios & Jaramillo, 2016; Brooks et al., 2002; Dodson & Gentry, 1991).

Nonetheless, restoring a region like the Chocó presents numerous challenges that must be considered, such as political factors, governance processes, lack of funding, and the need to account for the high biodiversity of species present in the region (Wiegant et al., 2020). In addition

to these limitations, in areas with high biodiversity, it is common to find a lack of knowledge regarding the survival and growth rates of the species present. In the Chocó region specifically, there are still many undescribed species that are difficult to identify in taxonomic databases (Gentry, 1986).

Generating baseline information on the growth and survival rates of native species is fundamental for guiding ecological restoration efforts. This data allows us to understand how species respond to local environmental conditions and to predict the long-term outcomes of restoration projects. However, this information remains limited, especially for endemic species, which are often restricted to unique ecological contexts and can exhibit high variability in their growth and survival (Holl et al., 2022; Rodrigues et al., 2009; Schlichting, 1986). Therefore, generating new in situ data is essential to reduce this knowledge gap, improve restoration planning, and anticipate potential changes in biodiversity and carbon stocks at a regional scale (Mesa-Sierra et al., 2025; Rüger et al., 2011).

To address the lack of knowledge about species development in this region, the growth and survival of seedlings of 23 native species, seven of them endemic, were monitored. These seedlings were established within a restoration project evaluating the effects of nucleation on forest regeneration. This ecological restoration method aims to accelerate natural succession by creating small plantations or “islands” of vegetation within a plot, which act as focal points for seed dispersers and facilitate the recruitment of new species (Corbin & Holl, 2012; Holl et al., 2020). In this sense, the present study not only aims to establish a baseline for the survival and growth of the evaluated species but also to identify the potential effects of the different treatments associated with this restoration method on their development.

3.4 Methods

3.4.1 Study site

This study was conducted in the province of Esmeraldas, Ecuador, within the "Fundación para la Conservación de los Andes Tropicales" (FCAT) reserve [17N 648517.08 E 41267.38 N; elevation 250-500 masl], on 600-ha dedicated to conservation and restoration. Meteorological data for the Bilsa Reserve, located approximately 8 km from FCAT, shows an annual rainfall that varies between 2,000 and 3,000 mm (Charlat et al., 2000; Jongsma et al., 2014). In contrast, records from the meteorological station at FCAT show notably lower annual accumulations for the years 2022 and 2024, with totals of 1,421.3 mm and 1,570.8 mm, respectively (FCAT & USFQ, 2024).

The landscape where this experiment is located is 1.5 km away from the largest patch of vegetation (Bilsa Biological Station; 3,000 ha) and is nested in a matrix of old-growth and secondary forests at 250-500 m elevation.

3.4.2 Study design

The study evaluated the survival and growth of 23 native tree species established across 12 plots (each approximately 1.65 ha) with a total area of 19.8 ha. Each plot ach plot was randomly assigned a combination of three experimental factors that determined the composition and structure of the planting: (1) fruiting traits of planted pioneer species [two levels: low and high fruit availability], (2) richness of planted tree species [two levels: low richness with four species and high richness with 19 species], and (3) density of planted tree islands [three levels: low with four islands per plot, medium with nine islands per plot and high with 16 islands per plot] (Figure 3. 2). The different combinations of these treatments generated 12 combinations assigned to each of the plots (Figure 3. 1). The effect of these treatments on the growth was also evaluated.

Plot	Fruit availability	Tree island density	Tree diversity
1	Low	Low	Low
2	High	Low	High
3	High	Low	Low
4	High	High	Low
5	Low	High	High
6	High	Med.	High
7	Low	Med.	High
8	Low	High	Low
9	Low	Low	High
10	High	Med.	Low
11	High	High	High
12	Low	Med.	Low

Figure 3. 1.- Treatments used in each one of the plots present in the applied nucleation experiment.

The selection of these factors was based on ongoing assessments that aimed to evaluate the impacts of these factors on the use of applied nucleation plantations to restore this region. This strategy seeks to avoid the need for large plantations by establishing small patches of vegetation that favor the ecological succession of the surroundings by attracting seed dispersers that can recruit new species (Corbin & Holl, 2012).

Due to these variables, the number of individuals on each plot depends on the factor that determines the density of tree islands; however, each island has the same dimensions (15×15 m, 225 m2) and contains a total of 25 tree seedlings. This gives us a total of 2,900 trees of 23 different species.

Before the experiment was conducted, the presence of livestock was removed, and the areas where the individuals would be established were cleared of vegetation and treated with glyphosate to reduce competition. On the other hand, the establishment of each island required the delimitation of each plot and island using high-precision GPS, followed by a vegetation clearing process and treatment with glyphosate to reduce competition. Due to the scale of the project, the planting

process took place in two phases: in 2022 (when 1,193 trees were planted during the second quarter of the year) and in 2023 (when the remaining 1,707 trees were planted) [N=2,900]. To accelerate the growth process, some species were propagated using cuttings (*Erythrina berteroana*, *Trichanthera gigantea,* and *Spondias mombin*).

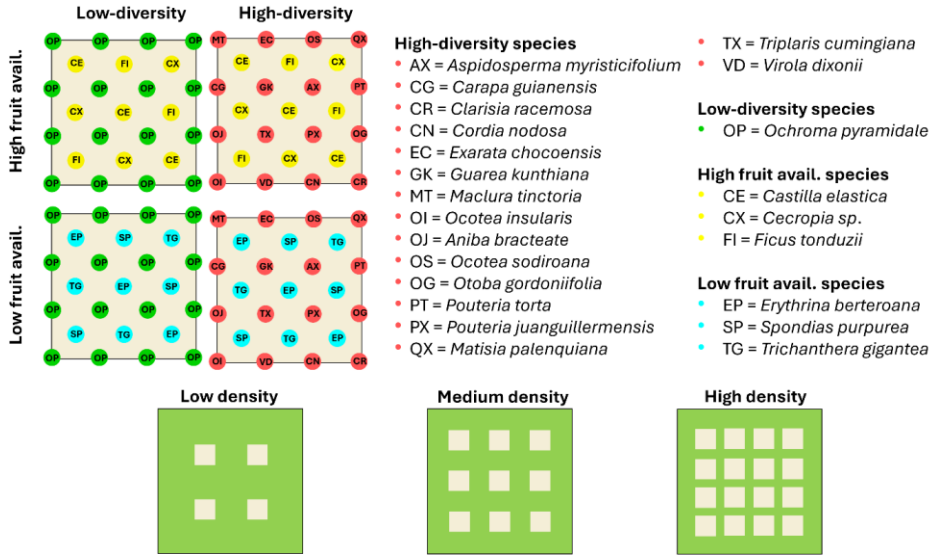

Figure 3. 2.- Planting design according to the assigned treatments. Colors indicate the fruit-availability level and species-diversity treatment associated with each species. Island density is represented by the number of planted islands per plot.

3.4.4 Species Selection

To determine which species were suitable to meet both levels of the treatments, fruit availability, and species diversity, we consulted with several naturalists and botanists in the region. High fruit availability was defined as species that rapidly produce copious endozoochorous fruits (*Castilla elastica* and *Ficus tonduzii*; Moraceae) and have a high abundance of seeds (*Cecropia obtusifolia, Cecropia insignis*; Urticaceae). In contrast, low fruit availability included species with

other seed dispersal syndromes (*Trichanthera gigantea*, Acanthaceae, dispersed by wind), colored seeds that provide no reward (*Erythrina berteroana*, Fabaceae), or species capable of producing larger fruits that are not eaten by animals and are produced in smaller quantities (*Spondias mombin*; Anacardiaceae). Low diversity plots combined pioneer species associated with the previous treatment and the presence of only one additional species (*Ochroma pyramidale*, Malvaceae). In contrast, plots with high biodiversity featured a variety of 16 species, from 10 families (Appendix B Table 1). However, given the characteristics of the experiment, none of the 12 individual treatments contained all 23 species used (Appendix B Table 2).

3.4.5 Soil sampling

In the summer of 2021, before tree planting, fourteen soil samples were taken on sites corresponding to plots 1-6 using a soil probe at a depth of 0-10 cm. The samples were later analyzed at the Universidad San Francisco de Quito (USFQ) for pH, dry weight, water content, and bulk density.

3.4.6 Monitoring

The monitoring was designed to evaluate the survival and development of each individual annually over two years. Therefore, data collection for the first planting took place from 2022 to 2024, and for the second planting from 2023 to 2025. During each monitory event, survival growth, and phenological data were recorded. Survival was considered successful when individuals remained alive throughout the entire monitoring period. Growth was measured through height [cm] and was measured from the base of the tree (on the downslope side) to the apex of the tree, using metric tape, a telescopic pole or a laser rangefinder for individuals exceeding 8 meters in height.

For phenology, the presence or absence of buds, flowers, and/or fruits was registered along with a brief description and the approximate number of fruits, if it was possible to determine it

3.4.7 Data Analysis

3.4.7.1 Soil

Average values of the soil parameters corresponding to the islands present in plots 1-6 were obtained through interpolation using ArcGIS Pro software. While ideally a single interpolation method would have been used, not all variables exhibited clear spatial patterns. Therefore, a mixed approach was adopted: Kriging was applied for pH, water content, and dry weight, while for bulk density, where a geostatistical model could not be fitted, Inverse Distance Weighting (IDW) was used.

In April 2023, a drone equipped with LiDAR sensors was used to generate a digital elevation model (DEM) and, from this, create slope and aspect maps, which were included as parameters to consider for each island. Since aspect is expressed in degrees, its north and east components were calculated by converting the raster values to radians and applying the cosine and sine functions, respectively. Finally, the Zonal Statistics as Table tool in ArcGIS Pro was used to obtain the average values for each parameter, including slope and the north and east components of aspect.

To assess the effect of soil parameters (pH, bulk density, water content, dry weight, slope, and north and east aspect) on the species' survival and growth, we used a principal component analysis (PCA) to reduce the complexity of the parameters considered and summarize the information into a smaller number of axes. This was done using the *prcomp* function present in the R package stats (R Core Team, 2025).

3.4.7.2 Survival

Survival analyses were performed using generalized linear mixed-effects models using a binomial distribution. Each model was constructed with the *glmer* function from the *lme4* package (Bates et al., 2015). The fixed effects considered for model comparison included species identity, planting year, and the soil environmental parameters of each island represented by both axes of the PCA. The random effect accounted for variation among islands, using the island identification code (island ID) as a grouping factor. The best simple model was selected based on the lowest Corrected Akaike Information Criterion (AICc) value, the $\Delta AICc < 2$, and the Akaike weight (wi) (Appendix B Table 3).

3.4.7.2 Height growth

For the height growth, we performed a model comparison using linear mixed-effects models built with the *lmer* function present in the *lme4* package. The comparison of growth models used the same variables as the survival models for both fixed and random effects. Similarly, AICc, $\Delta AICc$, and *wi* were used to determine the best simple model (Appendix B Table 4).

3.4.7.3 Effects of species growth rate on survival

The relationship between species growth and survival was evaluated using correlation tests and linear models. Spearman and Pearson correlations were used to determine the direction and magnitude of both variables using the *cor_spear* and *cor_pear* functions, respectively, available in the base R package stats. Subsequently, the *lm* function was used to generate a simple linear model using the annual growth rate as a fixed effect to predict average survival per species.

3.4.7.4 Treatment effects on growth

To evaluate the effects of the treatments on individual growth, we built three linear mixed models that were fitted using the *lmer* function.

The first model evaluated the impact of species diversity and island density on the growth of pioneer species used in the fruit availability treatment. Fixed effects were species identity, species diversity, and island density, while island ID was included as a random effect. To improve the model performance, we used a log transformation on the annual growth rate of the individuals.

The second model focused on the low-diversity plots where only the presence of *Ochroma pyramidale* is found (excluding pioneer species from the fruit availability treatment). In this case, fruit availability and island density were the fixed effects, and island ID served again as a random effect.

The third model applied the same fixed effects (fruit availability and island density) but was restricted to high-diversity plots containing 16 species (excluding the presence of pioneers). Here, species identity was also included as a fixed effect, and island ID remained the random factor. Similar to the first model, we performed a log transformation on the annual growth rate to improve fitness.

To address potential spatial correlation, we compared multiple generalized least squares (GLS) models incorporating alternative spatial correlation structures (Appendix B Table 5). We used the function *gls* present in the nlme package (Mixed-Effects Models in S and S-PLUS, 2000). The coordinates used to determine the spatial correlation corresponded to those of the centroid of each island and were captured using the Universal Transverse Mercator (UTM) system. Model selection was based on the lowest Akaike Information Criterion (AIC) value. Models that showed signs of spatial correlation were verified using Moran's test, with the *moran.test* function from the

spdep package (Bivand, 2022). This test was applied to the residuals of the mixed model (*lmer*) and used a spatial weights matrix constructed from the UTM coordinates of each island centroid, considering neighbors within a distance threshold defined according to the experimental design. The significance of Moran's statistic allowed us to assess whether there was residual spatial dependence not captured by the random effects included in the model.

3.5 Results

3.5.1 Soil Sampling

The results of the PCA analysis showed slight differences between the plots; however, the two principal components together explained 65.5% of the variance (PCA1: 49.1%, PCA2: 16.4%). The variables associated with PCA1 were soil dry weight, water content, north aspect (related to the orientation of each plot), and bulk density. On the other hand, the variables associated with PCA2 were pH, east aspect (also related to plot orientation), and slope.

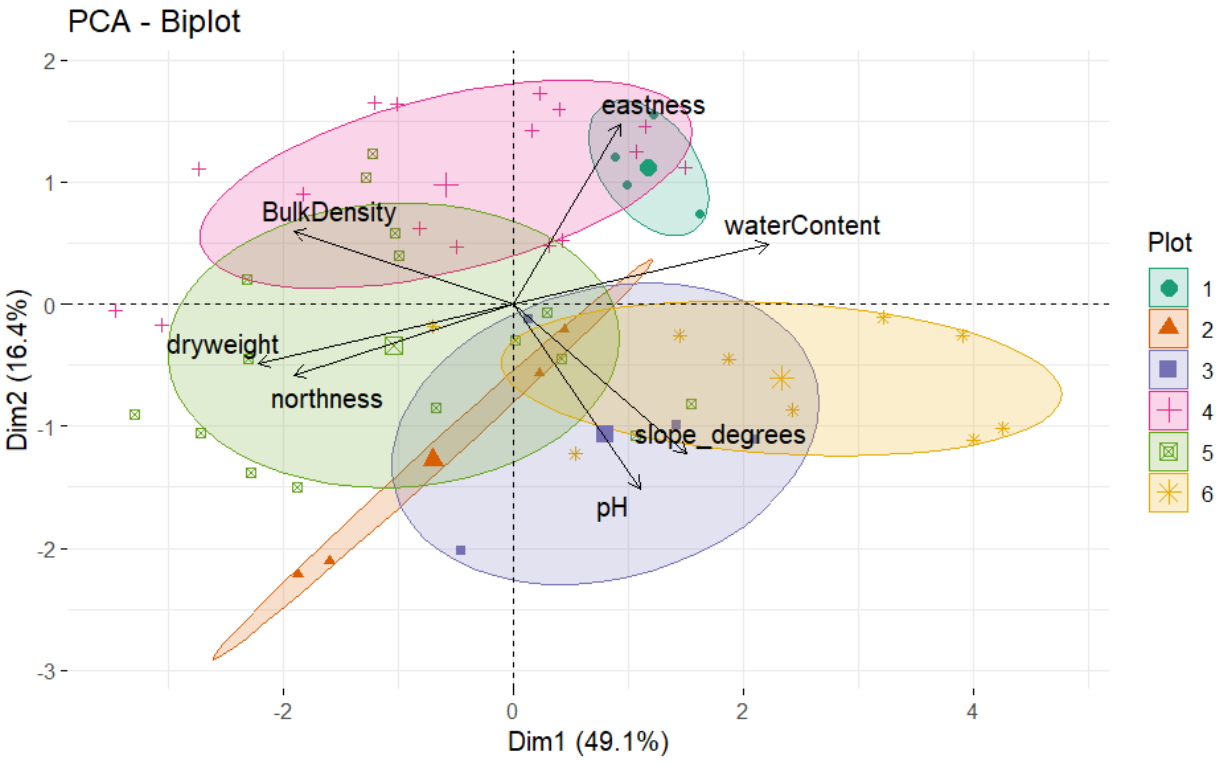

Figure 3. 3.- Principal Component Analysis of environmental parameters, showing their distribution across islands and associated plots.

3.5.2 Survival

The overall survival rate across the experiment was relatively high (82.20%, ranging from 43.10% to 98.27% between species). With the vast majority of the species (19/23) exceeding 80% survival (Figure 3. 4).

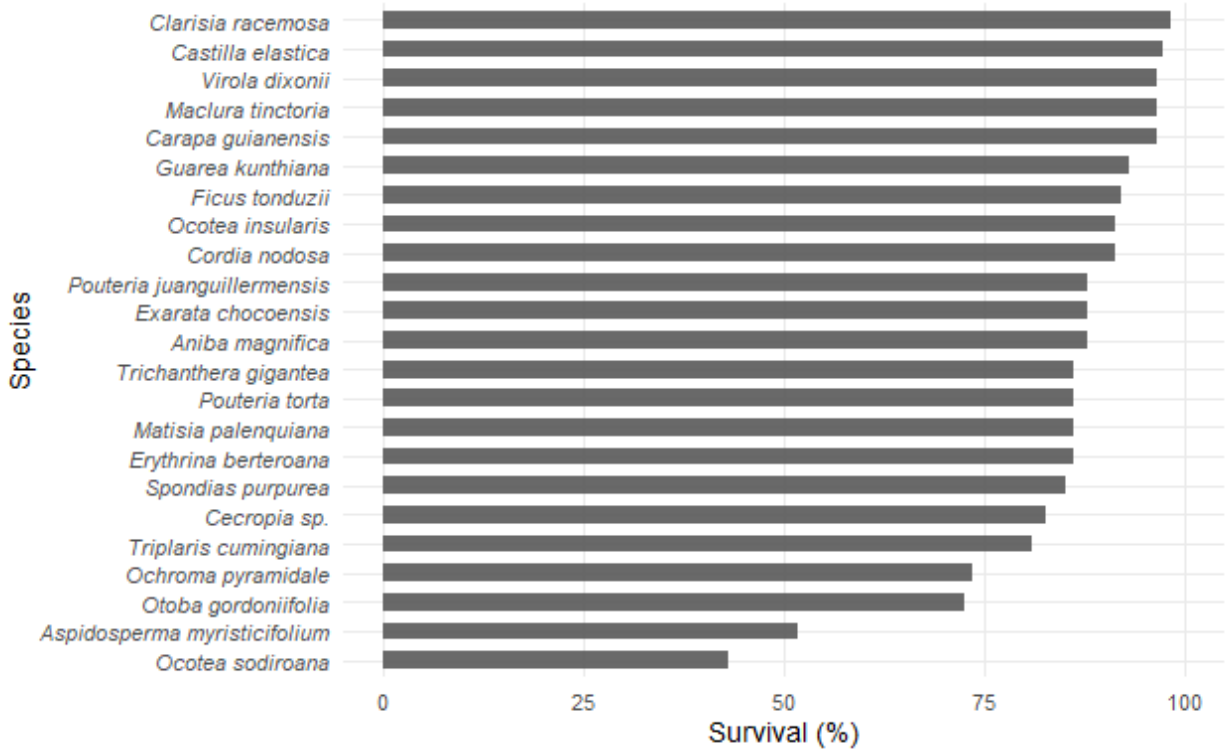

Figure 3. 4.- Survival rate of 23 native species from Chocó over 2 years (2022-2024 and 2023-2025)

Although simpler models were evaluated, they showed similar ΔAICc values and wi, differing only in the inclusion of one of the PCA axes (Appendix B Table 3). Therefore, the model that includes all the fixed effects was selected (ΔAICc = 0, wi = 0.51), explaining 25.9% of the marginal variance in the survival (conditional R^2: 0.35). Survival rates varied across species and

were influenced by the year of planting. Specifically, plantations made in 2023 had an 85% reduction in survival odds compared to 2022 (β = -1.92, odds ratio = 0.15), indicating a substantial decline in survival performance across species. In contrast, survival tended to increase on islands with lower dry weight and bulk density values, higher water content, and a southern aspect (PCA1 β = 0.12, odds ratio = 1.11). Similarly, islands with more acidic soils, gentler slopes, and an eastern aspect also favored survival (PCA2 β = 0.17, odds ratio = 1.18).

3.5.3 Growth rate

Growth rates varied among species. Pioneer species, such as *Ochroma pyramidale*, exhibited very rapid growth rates, averaging over 341.54 cm in height per year. In contrast, late-successional species such as *Aspidosperma myristicifolium* exhibited a growth rate of 9.82 cm per year (Appendix B Table 1).

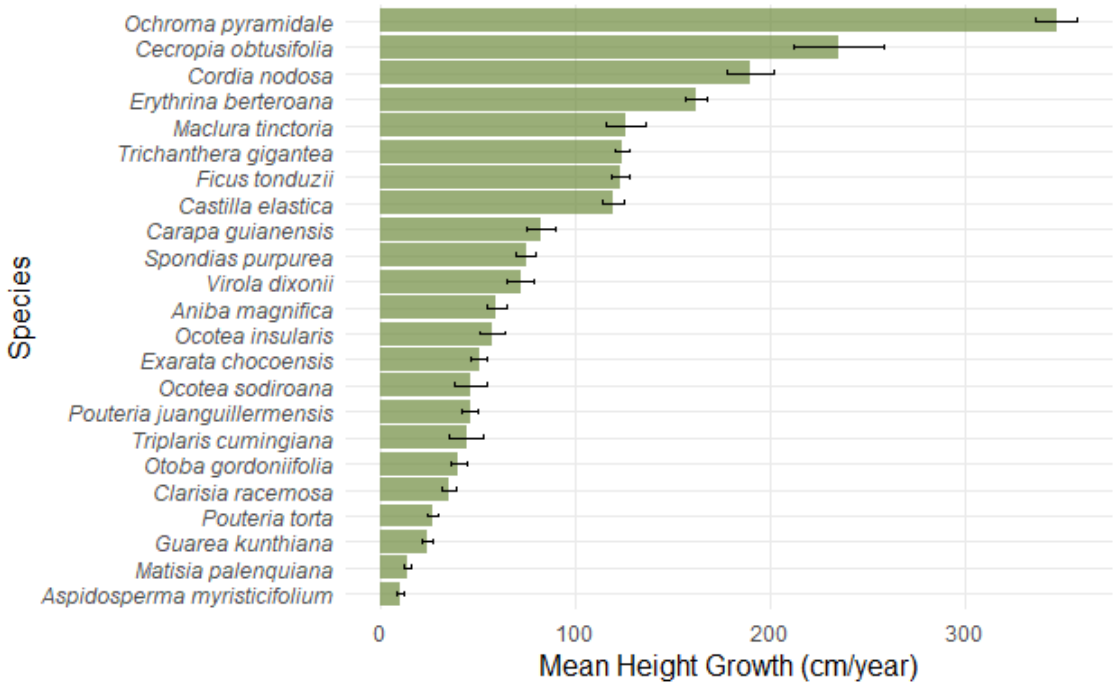

Figure 3. 5.- Average monthly height growth rate of 23 native species of the Ecuadorian Chocó, over a two-year period after being established as seedlings.

As with the survival analysis, the best-supported growth model included all fixed effects since no simpler model improved the fit (ΔAICc = 0, wi = 0.96). The selected model was able to explain 60% of the variance present in the data (Appendix B Table 4). The results of this model showed that the growth rate varied across the species and was influenced by the planting year and both axes of the PCA. Individuals established in 2023 grew an average of -63.46 cm less annually compared to 2022, adjusted for species and PCA axes. Islands with lower dry weight values and bulk density, higher water content, and a south aspect showed a positive effect on individual growth (PCA1, $\beta = 8.32$). Similarly, more acidic soils with lower slopes and an east aspect were also associated with greater growth (PCA2, $\beta = 8.81$).

3.5.4 Effects of growth on survival

No significant relationship was detected between the average annual growth rates of each species and their survival over two years (Spearman rho = 0.25, p = 0.24, Pearson cor = 0.13, p = 0.54). The linear model indicated a negligible effect of growth rates on the survival of each species (p = 0.54).

3.5.5 Treatment effect on height growth

The model generated to describe the growth of pioneer species showed no significant effects from the treatments evaluated. No differences in growth were detected associated with the level of species diversity (p = 0.47) or the density of islands per plot (p = 0.14). The GLS model selected to assess the presence of spatial autocorrelation used an exponential structure, which showed no spatial correlation (range = 18.25, nugget = 0.76). The estimated range indicates that

the spatial correlation extends to approximately 18.3 meters, while the nugget value close to 1 suggests that most of the variability occurs at smaller, non-spatial scales.

The model describing the growth of *O. pyramidale* also showed no significant effects of fruit availability treatments (ANOVA, $p = 0.09$) or plot density (ANOVA, $p = 0.13$). The GLS model with a rational quadratic structure showed a slight spatial correlation signal due to the high rank obtained and a nugget value closer to 1 (range = 194.51, nugget = 0.48); however, Moran's test confirmed the absence of spatial dependence (Moran's $I = -0.004$, $p = 0.58$).

On the other hand, the model describing growth rates in high-diversity plantations showed significant effects from both treatments. Individuals established in plots with high fruit availability grew on average 29% more than those in plots with low availability ($\beta = 0.26$, $p = 0.02$). Similarly, plots with medium island density showed 46% greater growth ($\beta = 0.38$, $p = 0.03$), while those with high density showed a 66% increase compared to those with low density ($\beta = 0.50$, $p < 0.01$). The associated GLS model, with a rational quadratic structure, did not show significant spatial autocorrelation (range = 106.20, nugget = 0.89); however, since the range could have overlaps with other plots, we ran a Moran's test that confirmed the absence of spatial dependence (Moran's $I = 0.41$, $p = 0.38$).

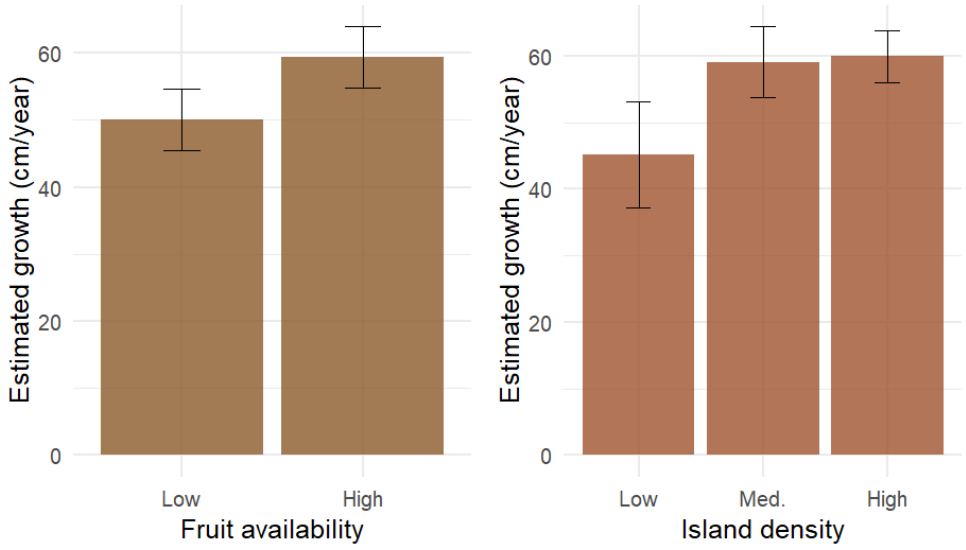

Figure 3. 6.- Change in growth rates with planting treatment.

3.6 Discussion

Survival and growth capacities vary depending on the species and the successional stage to which they belong. The use of the same propagation method does not guarantee comparable survival rates between species, and in various tropical regions, species identity has been shown to be the main determinant of both survival and growth (Zhang et al., 2025). Consequently, marked differences can be observed in the survival and growth of different species (Álvarez-Aquino & Williams-Linera, 2012). Therefore, differences in survival rates, such as those presented in our study with *Ocotea sodiroana* (43.10%) and *Clarisia racemosa* (98.28%), have been reported in other plantations that evaluate the survival of different native species (Álvarez-Aquino & Williams-Linera, 2012; Marquez Torres & Martínez-Garza, 2022). Similarly, growth rates vary widely, and they can depend on various factors such as the availability of resources and the stage of succession to which the species belongs (Dalling et al., 2004; Díaz-Talamantes et al., 2025;

Scalon et al., 2022a): late-successional species such as *Aspidosperma myristicifolium* showed growth rates up to 35 times lower than *Ochroma pyramidale*, a pioneer species.

However, even within the same species, local conditions and treatments can generate variability in survival and growth rates (Mesa-Sierra et al., 2025). A clear example is O. *pyramidale*, a species widely distributed in the Neotropics, which has shown growth rates ranging from 1.8 to 4.5 m during the first year (Francis, 2000) and slower growth in plantations established outside its native range, such as in Malaysia (Wycherley & Mitchell, 1962). In our study, the growth rates of *O. pyramidale* were relatively high, but within the expected range. However, the variation among individuals was notable, with annual increases ranging from as little as 3 cm to more than 7 m. Similar variability has been reported in tropical plantations in southern Mexico, where *O. pyramidale* showed distinct growth responses under different management and maintenance regimes (Douterlungne et al., 2008).

In our analysis, growth rates did not show a significant effect on individual survival, suggesting that other factors, such as soil conditions and environmental variations between establishment years, better explain the observed patterns. However, previous studies have documented different trends depending on the functional group or site conditions. In pioneer species, a higher growth rate can coincide with high survival, especially in open and well-managed sites (Álvarez-Aquino & Williams-Linera, 2012). In contrast, in late-successional species, a high growth rate can compromise persistence, since slow-growing species tend to invest more resources in defense and structure, which favors their long-term survival (Scalon et al., 2022b). Additionally, large-scale analyses have strengthened this latter trend by linking growth rate to climate. Slow-growing species tend to have deeper roots, smaller leaves, and denser wood, which favors their survival in sites with limited resources. In contrast to these qualities, fast-growing species tend to

have reduced survival rates in the face of water scarcity (Johnson et al., 2018). These trends, although not evident in our study, highlight the importance of considering both functional traits and local environmental conditions to understand the mechanisms that determine survival in tropical restoration projects.

The different treatments applied in the experiment did not show significant effects on the growth of *O. pyramidale* or other pioneer species; however, significant effects were observed in plantations with high species diversity. The presence of pioneer species associated with high fruit availability (*Castilla elastica*, *Ficus tonduzii*, and *Cecropia obtusifolia*) positively influenced the overall growth of the plantations. In comparison, these species showed higher survival and growth rates than those linked to low fruit availability. Nevertheless, both groups possess distinct functional characteristics that could have influenced the development of their respective plantations. *C. elastica* and *F. tonduzii*, for example, are species that can exceed 25 m in height and, even in early stages, generate a dense vegetation cover capable of providing shade, promoting moisture retention, reducing competition with grasses, and serving as a "nurse tree" for other species (Cottee-Jones et al., 2016; Custodio-Rodríguez et al., 2022; Fonseca Da Silva, 2015; Richard, 2024; Tropicos, 2025). In contrast, *C. obtusifolia* is not characterized by developing a dense crown (CONABIO, n.d.), but it maintains a mutualistic relationship with ants of the genus *Azteca*. These ants feed on sugary secretions produced by the tree and, in return, defend their host from some herbivores (Marting et al., 2018). However, since they obtain their food mainly from the *Cecropia* they inhabit, it cannot be assumed that their presence can reduce herbivory in neighboring trees (Hurley, 2011; Schupp, 1986).

In contrast, species such as *Erythrina berteroana* and *Trichanthera gigantea* contribute primarily to soil enrichment through nitrogen fixation, but their less developed structure limits

their ability to provide shade or reduce competition with grasses (López & Zeledón Duarte, 2016; Orwa et al., 2009; Rosales, 1997). *Spondias mombin*, on the other hand, offers a distinct ecological value by attracting seed dispersers through its production of fleshy fruits (Adler & Kielpinski, 2000; Mandujano et al., 1994; Méndez-Toribio et al., 2014). These functional differences with the other group of pioneers could be some of the reasons why differences were found between the two levels of this treatment; however, a more detailed evaluation of the ecological mechanisms involved would be necessary to confirm this.

Plots with higher island density exhibited greater growth rates, regardless of species. This trend could be related to some type of competition or facilitation in resource acquisition favored by denser configurations. Based on this, we propose two hypotheses. First, the effects of growth based on island density could be determined primarily by the proximity of established individuals, which can generate facilitating or competitive interactions depending on the spatial scale (Salazar Villegas et al., 2023). Second, we theorize that growth could be influenced by the dynamics of ruderal vegetation colonizing the space between islands. In high-density plots, the smaller open area between islands could favor faster and denser colonization by ruderal vegetation, thus increasing competition for resources. Conversely, in more open configurations (with distances of up to 30 m between islands), colonization processes will be slower, reducing competition and possibly generating more stable conditions for the growth of established individuals. Furthermore, the spatial structure and identity of neighbors can modify patterns of coexistence and competition without depending exclusively on the availability of resources, but rather on the spatial organization of the plantations (Falade, 2023).

However, this assessment did not allow for measuring changes in resource availability or vegetation cover in the vicinity of the established islands. Therefore, future studies analyzing

growth under different treatments should consider variations in resource availability and the causes associated with these changes.

3.7 Conclusion

The survival and growth rates of the evaluated species showed significant differences depending on the species and the environmental conditions under which the individuals were established. No significant relationship was identified between survival and growth rates; however, larger-scale studies have reported a negative trend when considering functional traits associated with survival, such as wood density or root depth. On the other hand, establishing plots with a higher density of islands had a positive effect on the growth of the individuals. This pattern could be due to modifications in the patterns of coexistence and competition, both among the individuals present in the plantations and with the surrounding vegetation that grows around the islands.

3.8 Acknowledgments

We would like to thank the FCAT team members for their support in establishing this experiment, especially Medardo Quiñonez and Domingo Cabrera, who were crucial to the monitoring processes. We also thank Rachel Wolf-Smith, John Huston, and Lillie Henthorne for their collaboration in the early monitoring processes and data collection

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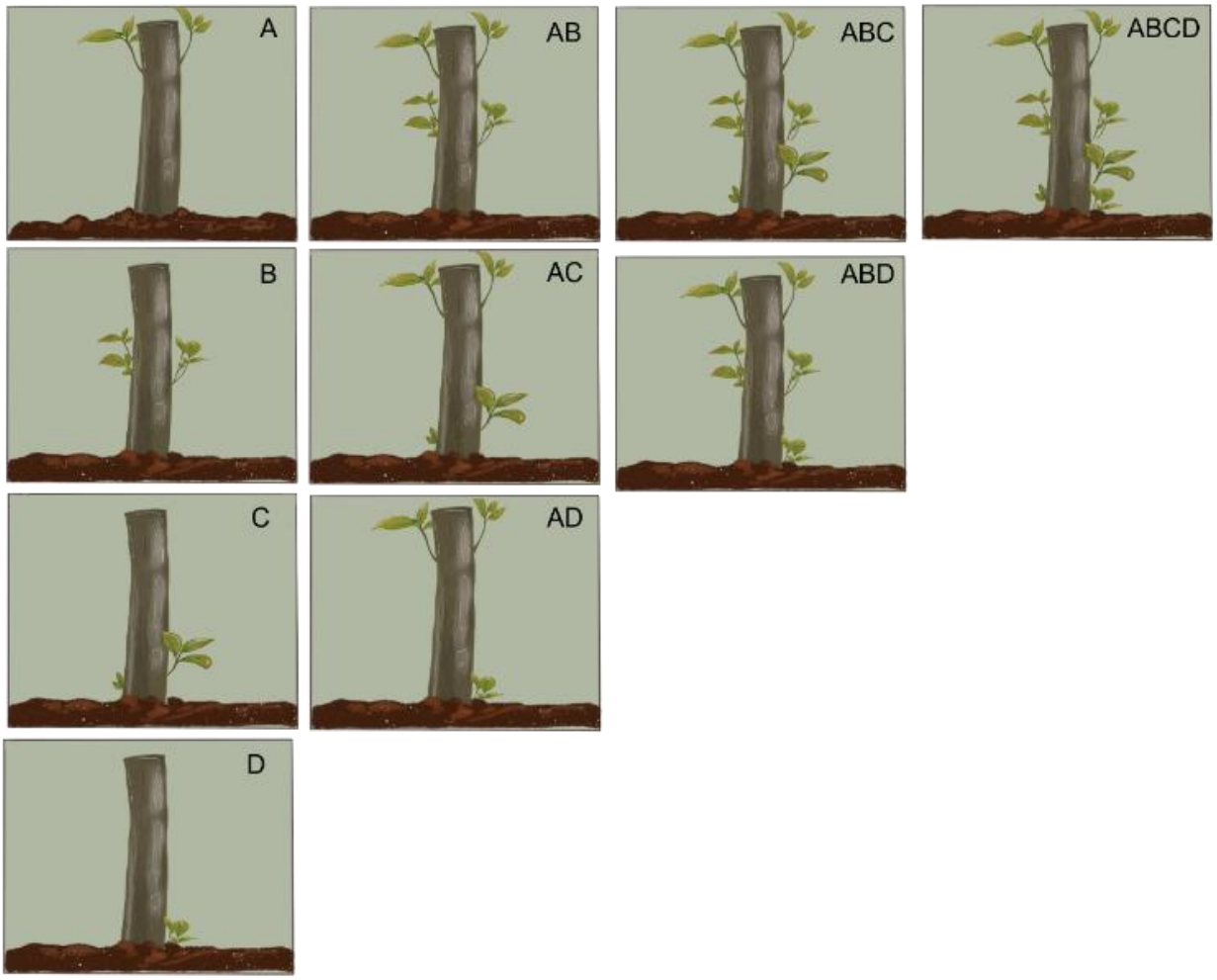
4. Appendix A: Chapter 2 Supplemental Materials

Appendix A Figure 1.- Giant stakes, (A) Large cutting of Trichanthera gigantea that after 5 months shows healthy sprouts. (B) Large cutting that despite being alive has not shown any sprouts. (C) Plot establishment with 168 giant stakes of 28 species.



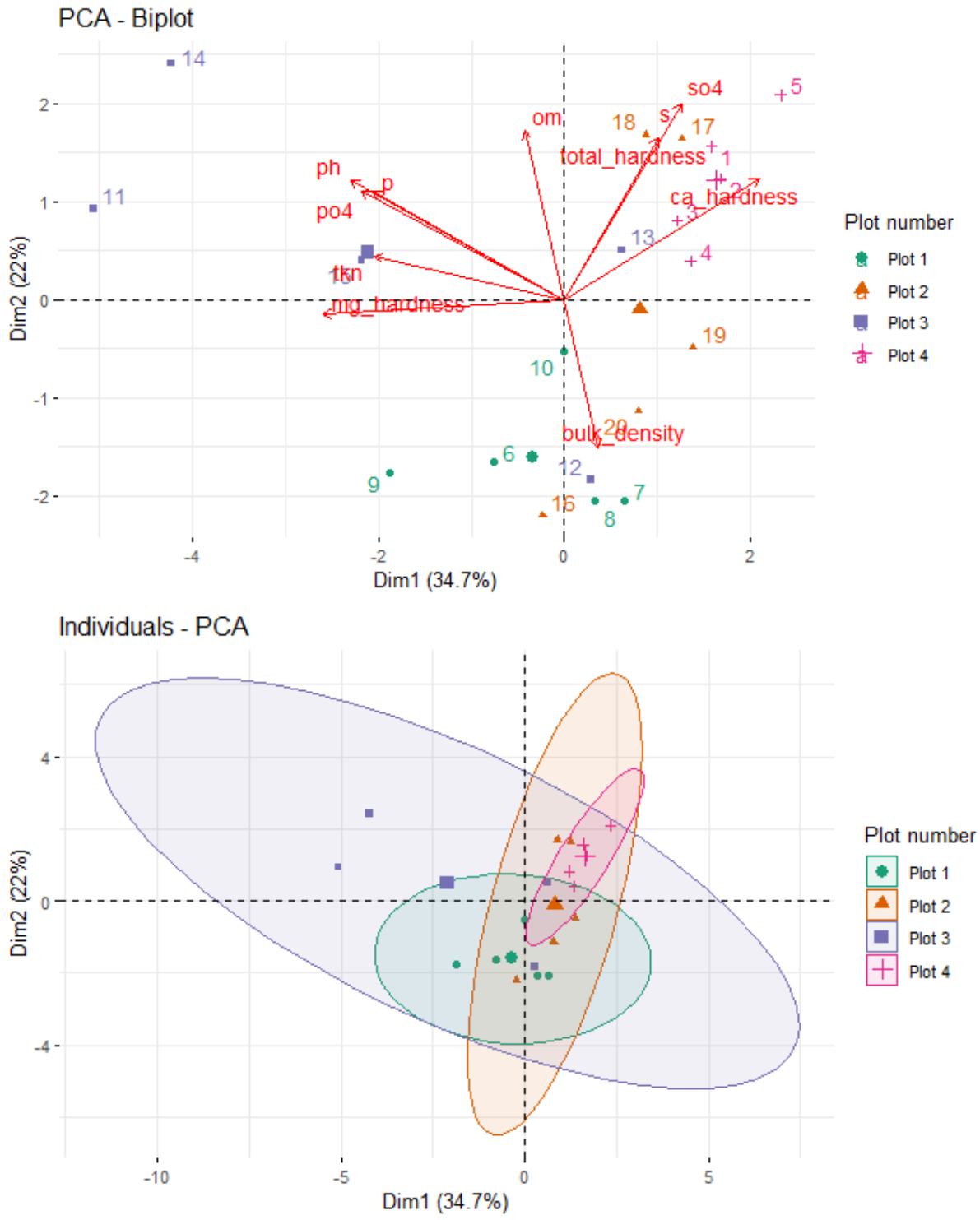
Appendix A Figure 2.- Types of regrowth that can occur in the stem of each individual present in the giant stakes experiment. Figure A shows sprouting in the first 30 cm of the stem. Figure B shows sprouting in the middle of the stem, excluding the first and last 30 cm. Figure C shows sprouting in the last 30 cm of the stem above the ground. Figure D shows sprouting from the stem that emerged below the ground. The remaining figures illustrate some of the possible combinations that could occur in each individual.

Appendix A Table 1.- Initial characteristics of 28 native Chocoan tree species planted as large cuttings in northwestern Ecuador (Scientific names obtained from https://www.tropicos.org/Home.aspx). Diameter at Breast Height (DBH)

Scientific name	***Family***	***Mean Length and (range) [m]***	***Mean DBH and (range) [cm]***
Aniba magnifica	Lauraceae	3.82 (2.8–4.64)	8.96 (5.3–15.1)
Coussapoa villosa	Urticaceae	3.62 (2.21–4.4)	6.83 (4.5–10.4)
Cedrela angusticarpa	Meliaceae	3.21 (2.6–3.94)	7.77 (4.5–13.3)
Castilla elastica	Moraceae	4.03 (3.52–4.47)	8.72 (6.1–12.5)
Cordia alliodora	Boraginaceae	3.72 (3.1–4.56)	10.4 (5.6–14.1)
Coccoloba obovata	Polygonaceae	3.96 (2.88–4.56)	7.16 (4.4–12.1)
Carapa megistocarpa	Meliaceae	3.46 (2.8–4.32)	8.23 (3.7–15.2)
Castilla tunu	Moraceae	3.76 (3.04–4.49)	8.58 (5–13.9)
Erythrina poeppigiana	Fabaceae	3.57 (2.9–4.36)	8.16 (4.6–15.9)
Ficus crassiuscula	Moraceae	3.51 (2.89–4.13)	8.78 (4.3–13.7)
Guarea cartaguenya	Meliaceae	3.64 (2.99–4.36)	6.97 (3.3–14.4)
Gliricidia sepium	Fabaceae	3.19 (2.84–3.82)	7.7 (4.1–12.5)
Miconia brevitheca	Melastomataceae	3.75 (2.94–4.7)	8.41 (6–14.2)
Otoba gordoniifolia	Myristicaceae	3.68 (2.75–4.69)	9.22 (5.7–19.2)
Ocotea sodiroana	Lauraceae	3.63 (2.99–4.33)	9.83 (5.5–18.6)
Pentagonia macrophylla	Rubiaceae	3.69 (2.63–4.37)	6.8 (4.3–12.3)
Pouteria torta	Sapotaceae	3.78 (2.83–4.26)	7.95 (3.8–11.5)
Pouteria sp.	Sapotaceae	3.94 (3.26–4.36)	7.1 (5.3–10)
Quararibea casasecae	Malvaceae	3.49 (2.9–4.39)	7.66 (4.5–12.6)
Chrysochlamys nicaraguensis	Clusiaceae	3.5 (2.43–4.39)	7.75 (4.2–15.4)
Simira standleyi	Rubiaceae	3.66 (2.84–4.2)	8.55 (3.7–14.6)
Spondias mombin	Anacardiaceae	3.35 (2.77–4.5)	6.25 (3.7–10.3)
Trichanthera gigantea	Caprifoliaceae	3.45 (2.79–3.99)	7.41 (4.2–14.1)
Triplaris cumingiana	Polygonaceae	3.77 (3.13–4.67)	9.99 (4.7–14.9)
Virola dixonii	Myristicaceae	4.12 (3.37–4.66)	7.83 (5.3–13.1)
Virola elongata	Myristicaceae	3.59 (2.55–4.25)	9.35 (5.2–13.2)
Vismia panamensis	Hypericaceae	3.87 (3.12–4.7)	8.61 (4.9–13.7)
Zanthoxylum riedelianum	Rutaceae	3.89 (3.14–4.87)	7.16 (4.9–11.8)

Appendix A Table 2.- Methods used for the characterization of soil samples.

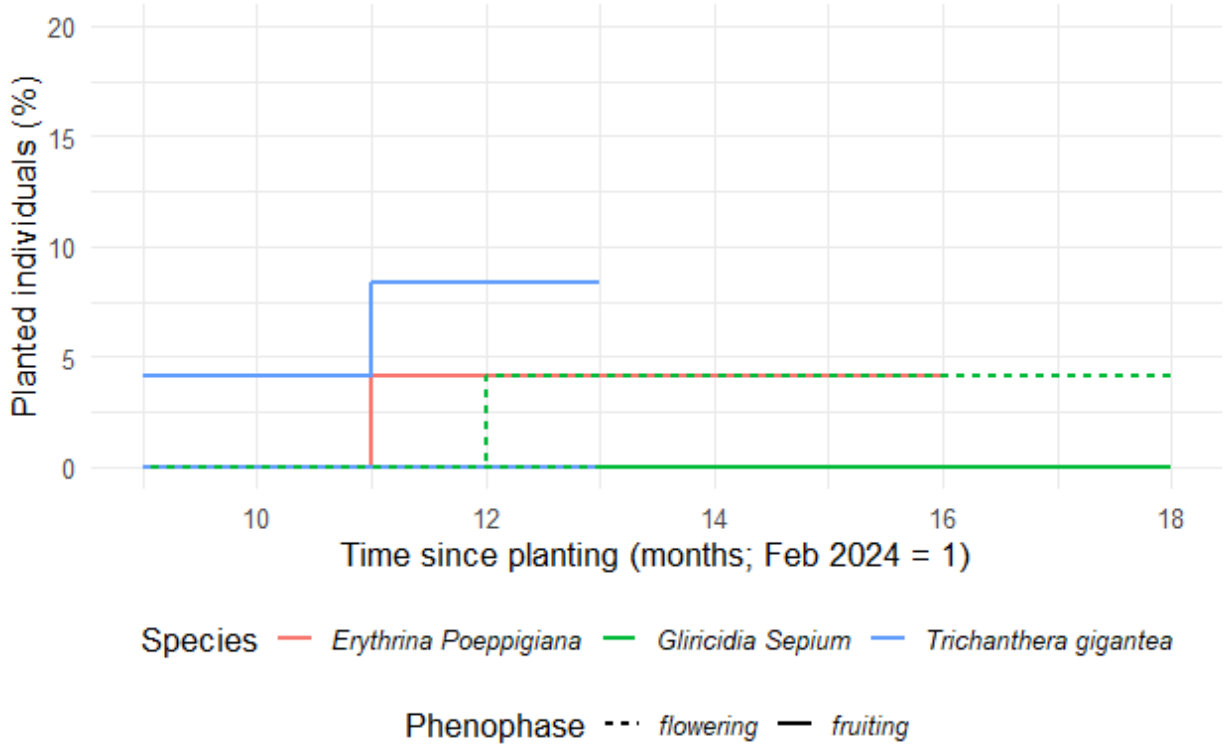
Soil analysis	Method used
Soil texture	FAO, Soil texture, manipulative test
pH	SM 4500 H
TKN (% N total)	Kjeldahl method
Organic Mater (%)	SM 2540 G - Calcination Method
Magnesium Hardness (mg CaCO3/L)	Calmagite colorimetric method 8030 HACH
Calcium Hardness (mg CaCO3/L)	
Total Hardness (mg CaCO3/L)	
Phosphate (mg PO4/L)	SM 4500-P E
Phosphorus (mg P/L)	
Sulfate (mg SO4/L)	SM4500-SO42-E
Sulfur (mg S/L)	



Appendix A Figure 3.- Principal Component Analysis (PCA) showing the distribution of physicochemical characteristics of each plot.

Appendix A Table 3.- Model comparison process. Survival and growth (height and DBH) models used species identity, initial characteristics before planting of each individual, and physicochemical characteristics of each plot related to both axes of a principal component analysis (PCA) as fixed effects. Each model includes the number of estimated parameters (K), explained deviance (% dev.), log-likelihood (Log L), Akaike Information Criterion (AIC), corrected Akaike Information Criterion (AICc), Akaike difference (Δi), and Akaike weight (wi). Model fit (% dev.), corresponds to the proportion of deviance explained relative to the null model. Selected models are bold.

Model	K	% dev.	Log(L)	AIC	AICc	Δi	wi
Survival							
Specie [factor]	**28**	**87.63**	**-248.49**	**121.01**	**123.54**	**0.00**	**0.48**
Length [numeric variables]	2	5.43	-258.64	500.98	500.99	377.46	0.00
DBH [n. variables]	2	1.56	-32.51	521.29	521.31	397.77	0.00
Specie [factor] + Length [n. variables]	29	87.79	-32.08	122.16	124.87	1.33	0.25
Specie [factor] + DBH [n. variables]	29	87.66	-32.42	122.84	125.55	2.01	0.17
Length [n. variables] + DBH [n. variables]	3	8.22	-241.15	488.30	488.34	364.80	0.00
Specie [factor] + Length [n. variables] + DBH [n. variables]	30	87.87	-31.87	123.74	126.65	3.11	0.10
Null	1	0.00	-262.75	527.50	527.51	403.97	0.00
DBH growth rate							
Specie [factor]	4	0.92	-79.74	167.49	167.99	14.64	0.00
PCA1 [n. variables]	2	8.77	-76.28	156.55	156.70	3.35	0.15
PCA2 [n. variables]	2	2.75	-78.96	161.92	162.07	8.71	0.01
Specie [factor] + PCA1 [n. variables]	5	9.88	-75.76	161.52	162.29	8.93	0.01
Specie [factor] + PCA2 [n. variables]	5	3.69	-78.55	167.11	167.88	14.52	0.00
PCA1 [n. variables] + PCA2 [n. variables]	**3**	**14.55**	**-73.53**	**153.06**	**153.36**	**0.00**	**0.78**
Specie [factor] + PCA1 [n. variables] + PCA2 [n. variables]	6	15.72	-72.95	157.90	158.99	5.63	0.05
Null	1	0.00	-80.13	162.26	162.31	8.96	0.01
Height growth rate							
Specie [factor]	4	57.60	136.57	-265.14	-264.65	6.02	0.03
PCA1 [n. variables]	2	2.64	100.82	-197.65	-197.50	73.16	0.00
PCA2 [n. variables]	2	2.01	100.55	-197.09	-196.95	73.72	0.00
Specie [factor] + PCA1 [n. variables]	5	60.56	139.67	-269.35	-268.60	2.06	0.19
Specie [factor] + PCA2 [n. variables]	5	60.72	139.85	-269.71	-268.96	1.71	0.23
PCA1 [n. variables] + PCA2 [n. variables]	3	3.77	101.33	-196.65	-196.36	74.30	0.00
Specie [factor] + PCA1 [n. variables] + PCA 2 [n. variables]	**6**	**62.51**	**141.86**	**-271.73**	**-270.66**	**0.00**	**0.55**
Null	1	0.00	99.67	-197.34	-197.30	73.37	0.00



Appendix A Figure 4.- Reproductive phenology of three species from October 2024 to July 2025. Monthly presence of flowering and fruiting.

5. Appendix B: Chapter 3 Supplemental Materials

Appendix B Table 1.- Species used in the experiment with their respective family, origin status, average survival rates, and growth rates with standard error. Scientific names were confirmed using the https://tropicos.org/home portal. Origin status was referenced using the Tumbes–Chocó–Magdalena biodiversity hotspot and corroborated using the https://www.gbif.org/ portal.

Species	Family	Status	Survival rate	Height growth (cm/year)	Number of individuals
Aniba magnifica	Lauraceae	Native	87.93%	59.03 ± 5	58
Aspidosperma myristicifolium	Apocynaceae	Native	51.72%	9.82 ± 1.84	58
Carapa guianensis	Meliaceae	Native	96.55%	82.22 ± 7.22	58
Castilla elastica	Moraceae	Native	97.13%	118.97 ± 5.73	174
*Cecropia sp.**	Urticaceae	Native	82.76%	234.82 ± 22.97	174
Clarisia racemosa	Moraceae	Native	98.28%	35.16 ± 3.7	58
Cordia nodosa	Cordiaceae	Native	91.38%	189.11 ± 11.95	58
Erythrina berteroana	Fabaceae	Native	86.21%	161.38 ± 5.54	174
Exarata chocoensis	Schlegeliaceae	Endemic	87.93%	50.17 ± 4.52	58
Ficus tonduzii	Moraceae	Native	91.95%	122.98 ± 4.74	174
Guarea kunthiana	Meliaceae	Native	93.10%	23.7 ± 3.07	58
Maclura tinctoria	Moraceae	Native	96.55%	125.87 ± 10.28	58
Matisia palenquiana	Malvaceae	Endemic	86.21%	13.53 ± 1.99	58
Ochroma pyramidale	Malvaceae	Native	73.38%	346.56 ± 10.89	928
Ocotea insularis	Lauraceae	Native	91.38%	57.03 ± 6.63	58
Ocotea sodiroana	Lauraceae	Endemic	43.10%	45.74 ± 8.49	58
Otoba gordoniifolia	Myristicaceae	Endemic	72.41%	39.71 ± 4.35	58
Pouteria juanguillermensis	Sapotaceae	Endemic	87.93%	45.64 ± 4.42	58
Pouteria torta	Sapotaceae	Native	86.21%	26.36 ± 3.02	58
Spondias purpurea	Anacardiaceae	Native	85.06%	74.57 ± 5.13	174
Trichanthera gigantea	Acanthaceae	Native	86.21%	123.68 ± 4.02	174
Triplaris cumingiana	Polygonaceae	Native	81.03%	43.69 ± 9.19	58
Virola dixonii	Myristicaceae	Endemic	96.55%	71.48 ± 6.61	58
Total number of individuals					2900

**Note: Within the Cecropia plantations, two distinct species (Cecropia obtusifolia and Cecropia insignis) were accidentally established. Each species was identified among the surviving individuals; therefore, the survival rate reflects the survival of both species, while the growth rate refers to the more common species, Cecropia obtusifolia.*

Appendix B Table 2.- Total number of individuals planted for each of the treatments.

Species	Treatment						
	Fruit availability		Tree island density			Tree diversity	
	Low	High	Low	Med.	High	Low	High
Aspidosperma myristicifolium	29	29	8	18	32	0	58
Castilla elastica	0	174	24	54	96	87	87
Carapa guianensis	29	29	8	18	32	0	58
Cordia nodosa	29	29	8	18	32	0	58
Clarisia racemosa	29	29	8	18	32	0	58
Cecropia sp.	0	174	24	54	96	87	87
Exarata chocoensis	29	29	8	18	32	0	58
Erythrina poeppigiana	174	0	24	54	96	87	87
Ficus tonduzii	0	174	24	54	96	87	87
Guarea kunthiana	29	29	8	18	32	0	58
Maclura tinctoria	29	29	8	18	32	0	58
Otoba gordoniifolia	29	29	8	18	32	0	58
Ocotea insularis	29	29	8	18	32	0	58
Aniba magnifica	29	29	8	18	32	0	58
Ochroma pyramidale	464	464	128	288	512	928	0
Ocotea sodiroana	29	29	8	18	32	0	58
Pouteria torta	29	29	8	18	32	0	58
Pouteria juanguillermensis	29	29	8	18	32	0	58
Matisia palenquiana	29	29	8	18	32	0	58
Spondias purpurea	174	0	24	54	96	87	87
Trichanthera gigantea	174	0	24	54	96	87	87
Triplaris cumingiana	29	29	8	18	32	0	58
Virola dixonii	29	29	8	18	32	0	58

Appendix B Table 3.- Model comparison process. Survival models used species year of planting and environmental traits related to both axis of a principal component analysis (PCA) as fixed effects. Each model includes the number of estimated parameters (K), explained deviance (% dev.), log-likelihood (Log L), corrected Akaike Information Criterion (AICc), Akaike difference (Δi), and Akaike weight (wi). Model fit (% dev.), corresponds to the proportion of deviance explained relative to the null model. Selected model is in bold.

Model	K	% dev.	Log(L)	AICc	Δi	wi
Survival						
Specie [factor]	23	12.93	-477.71	957.42	43.72	0.00
Year [factor]	2	3.58	-522.44	1046.87	133.18	0.00
PCA1 [numeric variables]	2	-0.14	-537.62	1077.25	163.56	0.00
PCA2 [numeric variables]	2	-0.03	-539.64	1081.29	167.60	0.00
Specie [factor] + Year [factor]	24	17.27	-457.75	917.49	3.80	0.08
Specie [factor] + PCA1 [numeric variables]	24	12.79	-476.56	955.12	41.43	0.00
Specie [factor] + PCA2 [numeric variables]	24	13.07	-476.91	955.82	42.13	0.00
Year [factor] + PCA1 [numeric variables]	3	3.43	-520.12	1042.24	128.55	0.00
Year [factor] + PCA2 [numeric variables]	3	3.56	-522.38	1046.76	133.07	0.00
PCA1 [numeric variables] + PCA2 [numeric variables]	3	-0.17	-537.56	1077.12	163.43	0.00
Specie [factor] + Year [factor] + PCA1 [numeric variables]	25	17.16	-456.61	915.21	1.52	0.24
Specie [factor] + Year [factor] + PCA2 [numeric variables]	25	17.42	-456.95	915.91	2.22	0.17
Specie [factor] + PCA1 [numeric variables] + PCA2 [numeric variables]	25	12.95	-475.80	953.60	39.91	0.00
Year [factor] + PCA1 [numeric variables] + PCA2 [numeric variables]	4	3.40	-520.06	1042.12	128.43	0.00
Specie [factor] + Year [factor] + PCA1 [numeric variables] + PCA2 [numeric variables]	**26**	**17.33**	**-455.84**	**913.69**	**0.00**	**0.51**
Null	1	0.00	-539.70	1081.41	167.72	0.00

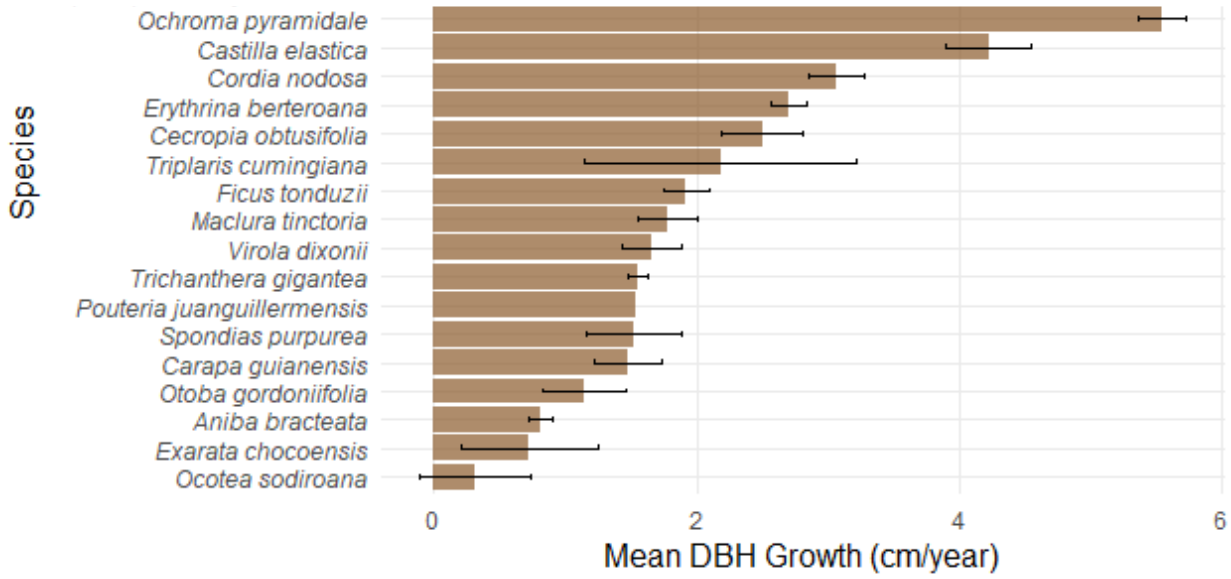
Appendix B Table 4.- Model comparison process. Average height growth per year models used species year of planting and environmental traits related to both axis of a principal component analysis (PCA) as fixed effects. Each model includes the number of estimated parameters (K), marginal R^2 (R_m^2), log-likelihood (Log L), corrected Akaike Information Criterion (AICc), Akaike difference (Δi), and Akaike weight (wi). Model fit (% dev.), corresponds to the proportion of deviance explained relative to the null model. Selected model is in bold.

Model	K	R_m^2	Log(L)	AICc	Δi	wi
Height grow rate						
Specie [factor]	23	0.59	-5434.03	10870.05	35.47	0.00
Year [factor]	2	0.01	-5860.32	11722.64	888.06	0.00
PCA1 [numeric variables]	2	0.01	-5864.73	11731.47	896.89	0.00
PCA2 [numeric variables]	2	0.11	-5856.14	11714.29	879.71	0.00
Specie [factor] + Year [factor]	24	0.59	-5424.09	10850.19	15.61	0.00
Specie [factor] + PCA1 [numeric variables]	24	0.60	-5430.07	10862.15	27.57	0.00
Specie [factor] + PCA2 [numeric variables]	24	0.60	-5430.34	10862.68	28.10	0.00
Year [factor] + PCA1 [numeric variables]	3	0.02	-5856.55	11715.10	880.52	0.00
Year [factor] + PCA2 [numeric variables]	3	0.12	-5848.42	11698.84	864.26	0.00
PCA1 [numeric variables] + PCA2 [numeric variables]	3	0.12	-5852.32	11706.64	872.06	0.00
Specie [factor] + Year [factor] + PCA1 [numeric variables]	25	0.59	-5419.90	10841.80	7.22	0.03
Specie [factor] + Year [factor] + PCA2 [numeric variables]	25	0.60	-5420.50	10843.00	8.42	0.01
Specie [factor] + PCA1 [numeric variables] + PCA2 [numeric variables]	25	0.61	-5426.37	10854.74	20.16	0.00
Year [factor] + PCA1 [numeric variables] + PCA2 [numeric variables]	4	0.13	-5844.52	11691.03	856.45	0.00
Specie [factor] + Year [factor] + PCA1 [numeric variables] + PCA2 [numeric variables]	**26**	**0.60**	**-5416.29**	**10834.58**	**0.00**	**0.96**
Null	1	0.00	-5868.44	11738.88	904.30	0.00

Appendix B Table 5.- Model comparison process of Generalized Least Squares models to evaluate spatial correlation. Average height growth per year models used different correlation structures. Each model includes the number of estimated parameters (K), log-likelihood (Log L), Akaike Information Criterion (AIC) and Akaike difference (Δi). The models that evaluated the effect of treatments on the growth of high and low diversity plantations required a logarithmic transformation in the response variable.

Model	Correlation structure	K	Log(L)	AIC	Δi
Effect of treatments on height growth of pioneer species					
Specie [factor] + Tree diversity [factor] + Tree island density [factor]	Null	20	-1026.00	2072.01	93.15
Specie [factor] + Tree diversity [factor] + Tree island density [factor]	Spherical	22	-1026.00	2076.01	97.15
Specie [factor] + Tree diversity [factor] + Tree island density [factor]	Linear	22	-1026.00	2076.01	97.15
Specie [factor] + Tree diversity [factor] + Tree island density [factor]	**Rational Quadratic**	**22**	**-977.43**	**1978.85**	**0.00**
Specie [factor] + Tree diversity [factor] + Tree island density [factor]	Gaussian	22	-1026.00	2076.01	97.15
Specie [factor] + Tree diversity [factor] + Tree island density [factor]	Exponential	22	-977.61	1979.22	0.37
Effect of treatments on height growth of low-biodiversity plantations*					
Specie [factor] + Fruit availability [factor] + Tree island density [factor]	Null	20	-999.77	4589.07	96.62
Specie [factor] + Fruit availability [factor] + Tree island density [factor]	Spherical	22	-999.77	4593.07	100.62
Specie [factor] + Fruit availability [factor] + Tree island density [factor]	Linear	22	-999.77	4593.07	100.62
Specie [factor] + Fruit availability [factor] + Tree island density [factor]	Rational Quadratic	22	-982.38	4492.58	0.13
Specie [factor] + Fruit availability [factor] + Tree island density [factor]	Gaussian	22	-986.71	4593.07	100.62
Specie [factor] + Fruit availability [factor] + Tree island density [factor]	**Exponential**	**22**	**-981.12**	**4492.45**	**0.00**
Effect of treatments on height growth for high-biodiversity plantations					
Specie [factor] + Fruit availability [factor] + Tree island density [factor]	Null	20	-999.77	2039.53	33.29
Specie [factor] + Fruit availability [factor] + Tree island density [factor]	Spherical	22	-999.77	2043.53	37.29
Specie [factor] + Fruit availability [factor] + Tree island density [factor]	Linear	22	-999.77	2043.54	37.30
Specie [factor] + Fruit availability [factor] + Tree island density [factor]	Rational Quadratic	22	-982.38	2008.76	2.52
Specie [factor] + Fruit availability [factor] + Tree island density [factor]	Gaussian	22	-986.71	2017.41	11.18
Specie [factor] + Fruit availability [factor] + Tree island density [factor]	**Exponential**	**22**	**-981.12**	**2006.24**	**0.00**

*Note: The low-diversity plantation model describes the growth of only *Ochroma pyramidale.*



Appendix B Figure 1.- Average annual DBH growth rate of 16 native species of the Ecuadorian Chocó, over two years after being established as seedlings.