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„Development of spontaneous vegetation in reforested areas in La Gamba, Costa Rica"

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Abstract

In this thesis spontaneous vegetation growth in two reforestation areas on former pastureland near the village La Gamba, Costa Rica, was investigated. Spontaneous vegetation here includes all natural woody vegetation that has established since the start of reforestation in addition to the planted trees. Studies concerning the spontaneous vegetation in reforestation trials are scarce but of great importance as they provide insights on how fast species are arriving and establishing spontaneously and to what extent they contribute to biomass and biodiversity. These findings can be incorporated into future planting designs of reforestation areas and help to improve the management of such areas. The field work for this study was conducted on the two reforestation sites Finca Amable and Finca La Bolsa from March – May 2019. All spontaneous woody vegetation with a diameter at breast height (DBH) > 2 cm was measured and individuals with a DBH between 1-2 cm were counted. In the planted research area on Finca Amable 5122 spontaneous individuals (69 species) were recorded and 290 spontaneous individuals (23 species) could be observed in the five control plots without planted trees. In the six plots on Finca La Bolsa 129 spontaneous individuals (34 species) were detected. The calculated above ground biomass (AGB) of the spontaneous vegetation in the planted area on Finca Amable was 12.4 t/ha and 17.1 t/ha in the control plots. The AGB of the spontaneous vegetation on Finca La Bolsa was 10 t/ha. The mean spontaneous basal area and the mean number of spontaneous individuals per 100 m^2 were both higher on Finca La Bolsa than on Finca Amable but only the difference in the number of individuals was significant. In both reforestation sites pioneer species accounted for most of the overall spontaneous growth. The total number of spontaneous species found was higher in the planted plots compared to the control plots and higher on Finca Amable compared to Finca La Bolsa. However, this is mainly due to the small number of control plots on Finca Amable and of survey plots on Finca La Bolsa compared to the number of planted plots on Finca Amable. The Shannon- and Simpson index provide an exactly inverted picture, being both higher in the control plots (2.35 and 0.85, respectively) compared to the planted plots (2.11 and 0.79) and on Finca La Bolsa (3.02 and 0.92) compared to Finca Amable. In contrast to the situation four years ago (Jackman, 2016), the average basal area, the average number of spontaneous species and the average number of spontaneous individuals were higher in the control plots on Finca Amable than in the planted plots. This could be due to the lack of competition from the planted trees but is remarkable in light of the strong growth of herbaceous vegetation in the control plots. The identity of the spontaneous trees is highly significantly non-randomly related to the species of planted trees. The influence of the size of the planted trees on the spontaneous vegetation showed a weak but significant correlation between the planted basal area and the basal area of the spontaneous vegetation. The distance and size of neighbouring trees was used to calculate a shade index (SI), which was weakly negatively correlated with the spontaneous basal area. Contrary to expectations, the mechanism of seed dispersal was not different between trees growing in control plots versus under planted trees and also did not differ between the two sites. In all cases zoochory was by far the most common. The comparison of the functional traits of the planted and spontaneous trees resulted in significant differences for leaf thickness, leaf dry matter content (LDMC) and branch wood density.

Keywords: Reforestation, spontaneous vegetation, Costa Rica, biodiversity, succession, dispersal mode, aboveground biomass, functional traits

Zusammenfassung

In dieser Masterarbeit wurde die Spontanvegetation auf zwei Wiederbewaldungsflächen auf ehemaligen Viehweiden in der Nähe des Dorfes La Gamba, Costa Rica, untersucht. Die Spontanvegetation umfasst hier die gesamte holzige natürliche Vegetation, die sich seit Beginn der Wiederbewaldung zusätzlich zu den gepflanzten Bäumen entwickelt hat. Untersuchungen zur Spontanvegetation auf Wiederbewaldungsflächen sind selten, aber von großer Bedeutung, da sie Aufschluss darüber geben, wie schnell sich spontane Arten ansiedeln und etablieren und in welchem Ausmaß sie zur Biomasse und Biodiversität beitragen. Diese Erkenntnisse können in zukünftige Pflanzpläne von Wiederbewaldungsflächen einfließen und helfen, das Management dieser Flächen zu verbessern. Die Feldarbeiten wurden auf den beiden Wiederbewaldungsflächen Finca Amable und Finca La Bolsa von März - Mai 2019 durchgeführt. Alle spontanen Gehölze mit einem Durchmesser auf Brusthöhe (BHD) > 2 cm wurden gemessen und Individuen mit einem BHD zwischen 1-2 cm wurden gezählt. In dem bepflanzten Untersuchungsgebiet auf der Finca Amable wurden 5122 spontane Individuen (69 Arten) erfasst und in den fünf Kontroll-Plots ohne Baumpflanzungen konnten 290 spontane Individuen (23 Arten) beobachtet werden. In den sechs Untersuchungs-Plots auf der Finca La Bolsa wurden 129 spontane Individuen (34 Arten) nachgewiesen. Die berechnete oberirdische Biomasse der Spontanvegetation in der bepflanzten Fläche auf der Finca Amable betrug 12.4 t/ha und in den Kontroll-Plots 17.1 t/ha. Die oberirdische Biomasse der Spontanvegetation auf der Finca La Bolsa betrug 10 t/ha. Sowohl die mittlere spontane Basalfläche als auch die mittlere Anzahl der spontanen Individuen pro 100 m^2 waren auf der Finca La Bolsa höher als auf der Finca Amable, aber nur der Unterschied in der Anzahl der Individuen war signifikant. In beiden Wiederbewaldungsflächen waren Pionierarten für den größten Teil des gesamten spontanen Wachstums verantwortlich. Die Gesamtzahl der gefundenen spontanen Arten war in den bepflanzten Plots höher als in den Kontrollplots und auf der Finca Amable höher als auf der Finca La Bolsa. Dies ist jedoch hauptsächlich auf die geringe Anzahl von Kontrollplots auf der Finca Amable und auf die geringe Anzahl an Untersuchungsplots auf der Finca La Bolsa im Vergleich zur Anzahl der bepflanzten Plots auf der Finca Amable zurückzuführen. Der Shannon- und der Simpson-Index ergeben ein genau umgekehrtes Bild, da beide sowohl in den Kontrollplots (2.35 bzw. 0.85) im Vergleich zu den bepflanzten Plots (2.11 und 0.79) als auch auf der Finca La Bolsa (3.02 und 0.92) im Vergleich zur Finca Amable höher liegen.

Im Gegensatz zu der Situation vor vier Jahren (Jackman, 2016) waren die durchschnittliche Basalfläche, die durchschnittliche Anzahl der Spontanarten und die durchschnittliche Anzahl der spontanen Individuen in den Kontrollplots auf der Finca Amable höher als in den bepflanzten Plots. Dies könnte auf die fehlende Konkurrenz durch die gepflanzten Bäume zurückzuführen sein, ist aber angesichts des starken Wachstums der Krautvegetation in den Kontrollplots bemerkenswert. Die Identität der Spontanvegetation ist hoch signifikant nicht zufällig mit den gepflanzten Baumarten verbunden. Der Einfluss der Größe der gepflanzten Bäume auf die Spontanvegetation zeigte eine schwache, aber signifikante Korrelation zwischen der Basalfläche der gepflanzten Bäume und der Basalfläche der Spontanvegetation. Aus dem Abstand und der Größe der benachbarten Bäume wurde ein Schattenindex (SI) berechnet, der schwach negativ mit der Basalfläche der Spontanvegetation korrelierte. Entgegen der Erwartungen unterschieden sich die Samenverbreitungsmechanismen nicht zwischen den beiden Plot-Typen auf der Finca Amable und auch nicht zwischen den beiden Wiederbewaldungsflächen. In allen Fällen war Zoochorie bei weitem der häufigste Verbreitungsmodus. Der Vergleich der funktionellen Merkmale der gepflanzten und spontanen Bäume ergab signifikante Unterschiede in der Blattdicke, dem Blatttrockenmassegehalt und der Astholzdichte.

Schlagwörter: Wiederbewaldung, Spontanvegetation, Costa Rica, Sukzession, Samenverbreitungsmechanismen, oberirdische Biomasse, funktionelle Eigenschaften

I. Introduction

In Latin America, the main underlying causes for deforestation are forest clearings for pasture land and commercial agriculture (van Andel and Aronson 2012). Despite the continuing high rates of deforestation and the degradation of forests worldwide, forest cover is increasing in some countries. Costa Rica is one of these countries and, according to the global forest resources assessment (FRA) 2015, forest cover increased by 0.3% between 1990 and 2015. The forest area in Costa Rica consists of 65.8 % primary forest, 33.4 % other naturally regenerated forests and 0.6 % planted forest area.(FAO 2015)

The Golfo Dulce region in the southwest of Costa Rica is botanically one of the most diverse regions of Central America with about 2700 plant species. More than 700 tree species are found in this region, that make up one quarter of all tree species present in Costa Rica (Weissenhofer 2008). The region is therefore particularly important for conservation and the reforestation projects within the biological corridor La Gamba (COBIGA) aim to maintain biodiversity by connecting isolated forest areas.

Protecting existing rainforests as well as converting deforested areas back to forests either through natural regeneration or through active reforestation has become a key instrument of international plans for biodiversity conservation and against climate change (Caughlin et al. 2016). The cost of restoration varies greatly depending on the different methods used. Natural regeneration is usually less costly, whereas active reforestation requires high costs for planting and caring for trees in order to accelerate ecological succession (Crouzeilles et al. 2017).

Plots of active reforestation and natural succession are monitored near La Gamba (Schnetzer 2014, Wyns 2015, Feldmeier 2016, Oberleitner 2016) and have been studied elsewhere (Saldarriaga et al. 1988, Uhl et al. 1988, Mesquita et al. 2001, Reid et al. 2015). If the decision is for active planting, important questions are, how many and which tree species should be planted and at which densities. With time other trees will regenerate spontaneously and in the long term these trees will replace the planted ones. Depending on how fast this happens, the management of the reforestation sites can be adapted to obtain a fast recovery of biodiversity and biomass or optimize the investment of available funds.

Where previous agricultural land-use has been rather extensive with primary or secondary forests and animal dispersers nearby to ensure a diverse seed input, spontaneous natural regeneration may be the most rapid and most affordable path to restore forests. One study on abandoned pastures in Puerto Rico showed that after 30 to 40 years of natural regeneration, secondary forests have developed that are comparable to mature forests on the island in terms of biodiversity and biomass (Chazdon 2008). Saldarriaga et al. (1988) showed in their study of a long-term chronosequence of forest succession in the upper Rio Negro region of Colombia and Venezuela that stands of 20 to 40 years had a similar species richness compared to mature forest and Rozendaal et al. (2019) came to comparable results using the data from 56 chronosequence sites of Neotropical secondary forests.

A difficulty for the regeneration of forest on agricultural lands can be that the light availability is much higher compared to forests, as well as other differences in microclimate and the soil. Especially seedlings of late successional stages that regenerate in the forest understory might face reduced survival and limited growth under these microclimatic conditions (van Andel and Aronson 2012). Additionally, the rate of development of natural regrowth can be constrained by depleted soil seed-banks and therefore regeneration is depending on seed dispersal from external sources (Wijdeven and Kuzee 2000, Reid et al. 2015, Shoo et al. 2016).

Studies in the Australian wet tropics concluded that active replanting can achieve a faster increase in biomass and diversity of the regenerating forest compared to natural succession. Species richness of trees and shrubs aggregated much faster in plantings than in natural regrowth (Shoo et al. 2016). Specifically, trees provide a structure that encourages seed dispersal by birds and shade out light-demanding herbaceous species (Holl 1999).

However, not all forms of reforestation result in an increase in biodiversity (Lamb et al. 2005, Chazdon 2008). Industrial monoculture tree plantations are a popular form of forest restoration in tropical countries, but they bring various problems with them. They may facilitate the establishment of invasive species or develop into forests with a species composition that differs from naturally developed forests and thus do not provide the same amount of ecological services (e.g. biodiversity; (Lamb et al. 2005, Chazdon 2008). It is therefore of great importance to make decisions about the aim of the reforestation project when selecting tree species.

Spontaneous woody vegetation on the reforestation site Finca Amable in La Gamba, Costa Rica, has been previously recorded in 2016 (Jackman) and in 2018 (Kopper et al.). Spontaneous vegetation includes all the natural woody vegetation that has developed since the start of reforestation. Accordingly, the reforested area consists of planted trees and spontaneous vegetation. The trees planted included both pioneer tree species as well as tree species of late successional stages (Weber 2001). We were therefore asking if under these circumstances spontaneous species would be pioneers only or include late successional species that either germinate from seeds of planted trees or might already find a suitable habitat for regeneration below the fast-developing canopy.

The composition of spontaneous vegetation is related to the stage of succession and changes continuously up to the climax stage (Saldarriaga et al. 1988). The replacement of species during secondary succession is often explained by the adaptation of species to changing light conditions, reflecting a compromise in plant design (Bazzaz and Pickett 1980). Fast-growing species with rapid resource acquisition prosper at the high light environment of early successional stages, while slow-growing, resource-preserving species dominate under the low light environment of late successional stages (Lohbeck et al. 2013).

The number of species with high growth rates (pioneers) decreases with stand age, while late successional forest species colonize the area slowly. During the first ten to twenty years of succession, pioneer species tend to be dominant and after thirty to forty years, they are replaced by groups of other fast-growing and more persistent species (Saldarriaga et al. 1988). One argument for the active planting of trees from late successional stages is therefore that the forest will pass through the young pioneer stage more quickly and thus the development towards a mature rainforest can be accelerated (Martínez-Garza and Howe 2003, Lamb et al. 2005).

Plant functional traits are the characteristics that define ecological strategies and determine how plants react to environmental factors (Pérez-Harguindeguy et al. 2013). In this study, we focus on six leaf and wood traits that are important for light acquisition and resource conservation. Especially specific leaf area (SLA) and wood density (WD) are often used to characterize plant-growth strategies (Huang et al. 2018). The collection of functional traits intends to show possible differences in the characteristics of the trees planted and the spontaneous vegetation.

With this study we want to find out how fast species are arriving and establishing spontaneously and quantify their contribution to biodiversity and biomass. Thereby, this research will provide new insights regarding the efficiency of reforestation projects and possible future planting designs.

Specifically, this study addressed the following research questions:

1. What is the present composition of spontaneous vegetation on the reforestation site Finca Amable and how did it change compared to surveys in 2016 and 2018?
2. Does spontaneous vegetation differ between the planted plots and the unplanted control plots with mainly pasture grass on Finca Amable?
3. Does the identity and size of planted trees affect spontaneous growth?
4. Are planted trees already regenerating?
5. Which dispersal mode is most common among the spontaneous species and are there differences between planted and control plots on Finca Amable or between Finca Amable and Finca La Bolsa?
6. Do functional traits differ between planted and spontaneous species?
7. To what extent do the two reforestation areas Finca Amable and Finca La Bolsa differ regarding their spontaneous vegetation?

II. Material and Methods

2.1 Site Descriptions

Both study sites, Finca Amable and Finca La Bolsa, are in the vicinity of the Tropical Research Station La Gamba (N 8°42.61', W 83°12.97), in the Golfo Dulce region of the Province of Puntarenas, South West Costa Rica (Fig. 1). High rates of precipitation are common for the entire Golfo Dulce region and annual precipitation is around 6,000 millimeters. The average annual temperature is 28.3°C. The Golfo Dulce region is botanically one of the most diverse areas in Central America (Weissenhofer 2008, Kohlmann et al. 2010)

Figure 1: Overview map – Surroundings of Finca Amable and Finca La Bolsa (Source of aerial photo: Google Earth, aerial photo date: 3/5/2015)

2.1.1 Finca Amable

The reforestation site Finca Amable is a former cattle pasture close to the village of La Gamba with a size of 14.5 hectares. It borders a palm plantation to the east, a dirt road and pastures belonging to a local farm to the south, pastures, a smaller dirt road and another palm plantation to the west and the river “Rio Bonito” to the north. The river is the limit of the Piedras Blancas National Park. The closest nearby forest lies within the Piedras Blancas National Park in approximately 400 m from the rear sectors (Fig. 2). The site is therefore not in direct contact with either primary or secondary forests. The terrain is level with an average elevation of 65 meters above sea level. To attenuate the effects of flooding, due to heavy rainfall during the rainy season and the proximity of the river “Rio Bonito”, drainage ditches run along the sector borders. The whole site was divided into 12 sectors with a total of 56 study plots plus 5 control plots where no planting and no maintenance occurred (Fig. 2).

Each study plot consists of 36 individual trees planted in a 6 x 6 grid. The species chosen for the reforestation of the study plots can be categorized into the following three groups: legumes, low-wood density, and high-wood density. The three groups were paired in all combinations for future studies on the effect of functional diversity on succession and ecosystem properties. The five control plots have the same size as the study plots and were also divided into 36 subplots of the same size.

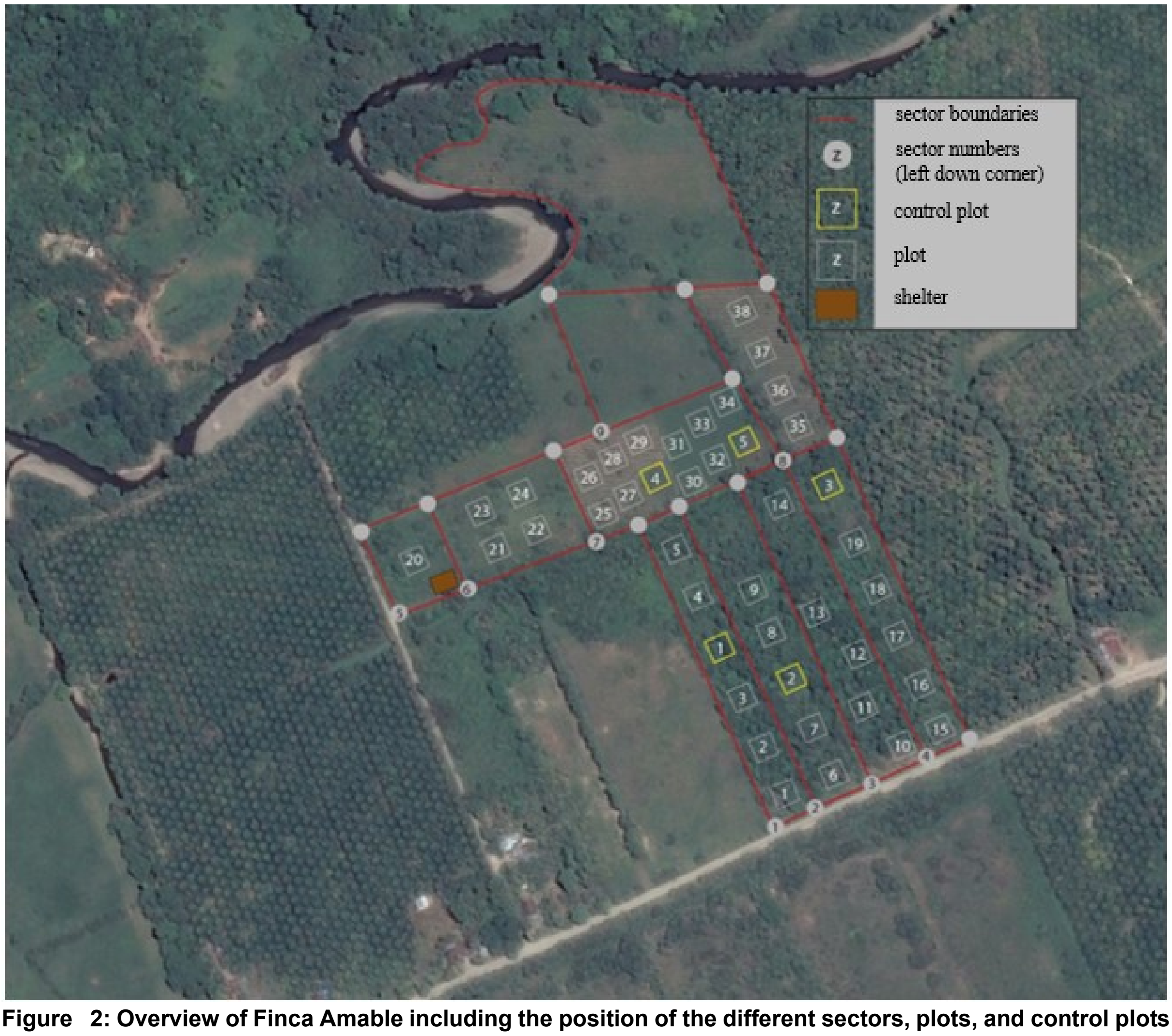


Figure 2: Overview of Finca Amable including the position of the different sectors, plots, and control plots (Source of aerial photo: Google Earth, aerial photo date: 3/5/2015)

From 2012 to 2015, a total of 10700 trees from over 100 indigenous tree species were planted on the site, with unsuccessful individuals being replanted. Trees were planted in rows and columns with a distance between rows of 4m and between columns of 3.5m (Fig. 5).

Between the sectors 1 - 4 and 5 - 8 runs a canal that divides the whole site into two areas of different character. The sectors bordering the local road were planted earlier and received more maintenance measures (e.g. cutting of lianas), and therefore mostly have taller trees and a more closed canopy that suppresses a herbaceous ground vegetation. In many parts of sectors 5 - 12 the canopy is more open and trees are smaller, so that growth of herbs is stronger and these - in part - suppressed the growth of trees (Fig. 3). Thus, herbaceous species, especially the pasture grass *Braccharia sp.,* can still be predominant.

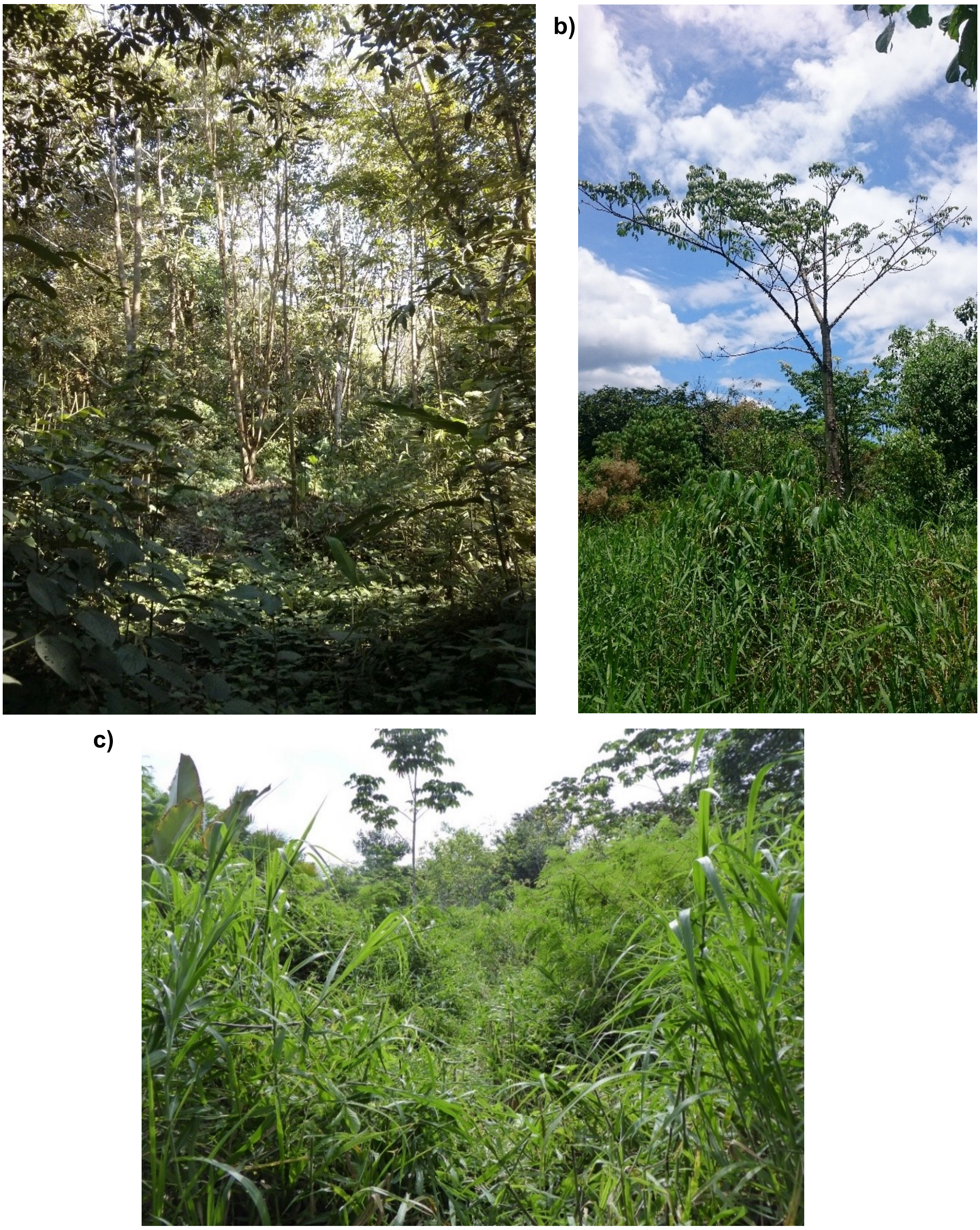


Figure 3: Impressions of Finca Amable. a) front sectors © Peter Hietz, b) dense grass cover in sector 7 © Hannah Böhmer, c) control plot C4 in sector 7 © Hannah Böhmer

2.1.2 Finca La Bolsa

The Finca La Bolsa is an older reforestation area established in 2010 and lies approximately 2 kilometers outside the village of La Gamba. Before the reforestation, the area was used as a pasture for cattle and for the cultivation of fruit and timber trees. These trees were not cut before the reforestation started and older trees such as *Psidium guajava, Citrus sp.,* and *Theobroma cacao* can be found throughout the site.

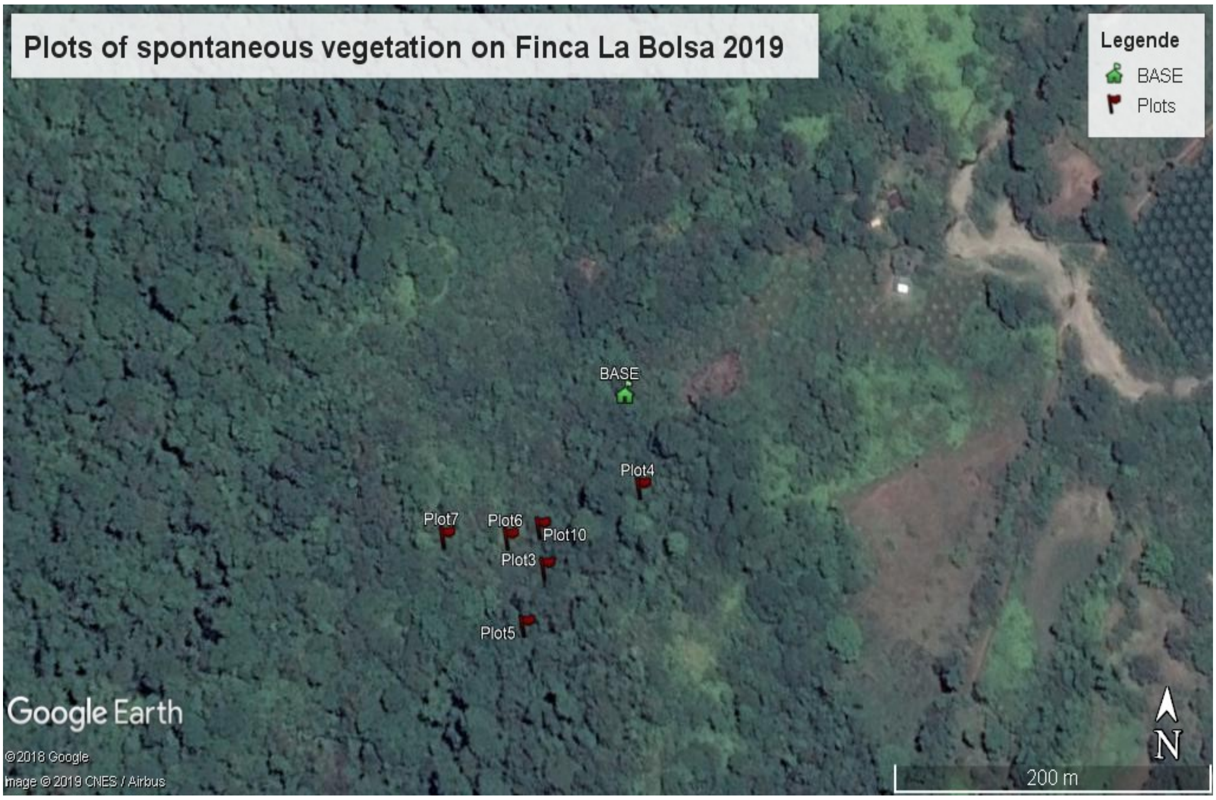


Figure 4: Location of the six study plots on Finca La Bolsa (Source of aerial photo: Google Earth, aerial photo date: 3/5/2015)

The Finca has a size of 13.6 hectares on which 6065 trees from over 113 native species were planted in 2010 (Weissenhofer et al. 2016). Maintenance was carried out until 2012 to ensure the survival of the young trees and dead trees were replaced. The terrain is extremely heterogenous regarding the topography, inclination, and exposition. The altitude ranges from 86m to 140m above sea level. Flat areas are rather scarce and can be largely found along the meandering stream through the site. Steep slopes with an inclination up to 60° are not uncommon. The area was divided into 13 sectors and trees were planted in rows with a distance between rows of 3.5m and a distance between trees of 3m.

2.2 Data Collection and processing

2.2.1 Diameter at Breast Height (DBH) Measurements

The field work was conducted in the dry season from March 7th to May 5th 2019. Data collection on Finca Amable occurred in the sectors 1 to 8 (7 hectares), including 38 plots, 5 control plots, as well as around all other trees planted in these sectors. Due to available planting scheme maps, orientation in the field and locating planted tree species proved to be relatively easy - with an exception of sectors with a high grass cover - and allowed a clear assignment of the spontaneous vegetation to a specific tree with its surrounding subplot. A subplot is considered the $14m^2$ area around each planted tree with the halfway points between neighboring trees setting the subplot boundaries (Fig. 5).

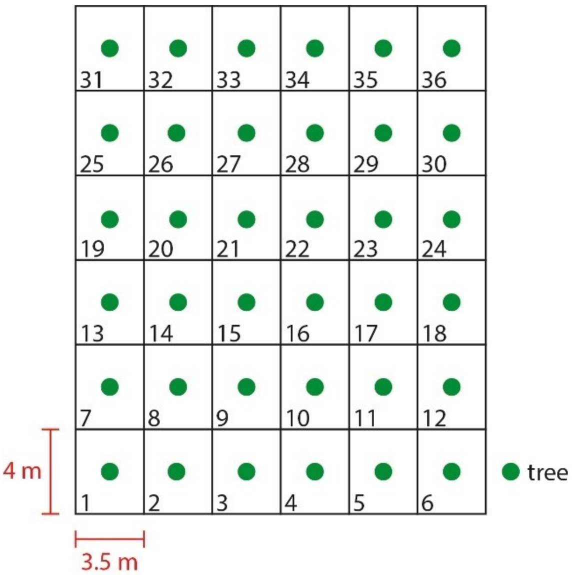


Figure 5: Plot design Finca Amable (Planting scheme)

Each study plot consists of 36 planted trees and numbering of the subplots starts in the bottom left corner of the plot and increases from left to right as shown in Figure 5. Control plots were treated in the same way and subplots of the same size, as in the study plots, were created using a measuring tape and barrier tape.

On the Finca La Bolsa, spontaneous vegetation was last surveyed in 2016 and 10 plots (10m x 10m) were created in the past. Despite having the previous coordinates, it was impossible to find the exact plot positions of 2016 due to GPS inaccuracies, changed species composition, and missing data.

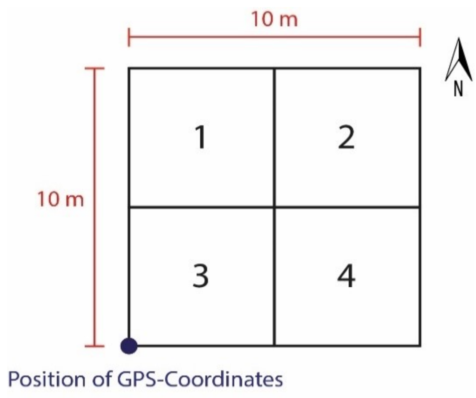


Figure 6: Plot design Finca La Bolsa

Six new plots with a size of $100m^2$ each were created near the old plots using measuring tape (Fig. 4). Each plot was then split into four subplots (Fig. 6). Since orientation on the site and identifying particular planted trees was a difficult task, a design differing from the one on Finca Amable was chosen.

All spontaneous woody species with a diameter at breast height (DBH) > 2 cm were measured in each subplot. For diameters up to 5 cm, a vernier caliper was used and for diameters over 5 cm, the circumference was determined with a measuring tape and afterwards converted to DBH (= circumference / π). In the case of substantial branching below breast height (1.3m), diameters of all branches or stems were measured at 1.3 m, and a DBH was calculated that corresponds to the sum of the cross-sectional areas. Spontaneous individuals with a DBH between 1 – 2 cm were counted, but not measured and played a role in assessing the biodiversity of the area. If a species could not be identified directly in the field, pictures and samples were taken and brought back to the research station for further identification with the help of literature.

2.2.2 Functional Traits

In order to perform a functional traits analysis, branch and leaf samples of the most common spontaneous species were collected on Finca Amable using a pole pruner. For each species, three branch and leaf samples were taken from different individuals. As far as it was possible for understory vegetation sun-exposed leaves were sampled, preferably only samples from healthy leaves. Branch samples were taken with a pole pruner from branches with a diameter between 1 and 2 cm. Leaves and branches were collected during the morning hours and afterwards brought back to the laboratory.

Starting with fresh leaves, the chlorophyll content was measured on each leaf at six different points, half-way between the mid-rib and the margin, using the SPAD 502 Plus Chlorophyll Meter (Konika Minolta, Osaka, Japan). The device then displayed the average value that was noted for each leaf.

In a next step, the petioles of the leaves were removed before scanning them with a desktop scanner with a resolution of 300 dots per inch (dpi). If a leaf was too large to fit on the scanner, it was cut to multiple parts. Leaflets were scanned separately.

For the determination of saturation weight, leaf thickness and leaf toughness, the leaves were first saturated. The leaves were put between wet tissue and left to saturate in a dark place at c. 20° C for 24 hours. Afterwards, they were blotted dry and the fresh weight was determined with an electronic balance to 1 mg. The leaf thickness was measured using the Digital Outside Micrometer IP65 (ACCUD Europe, Vienna, Austria), avoiding major veins and averaging from two measurements per leaf. The measurement of the leaf toughness was conducted on a 5 x 1 cm piece of the leaf that was cut parallel to the midrib. The piece was put between the two clamps of the FK25 forcegauge (Sauter, Balingen, Germany) and the value being displayed at the tear point of the leaf was recorded.

The leaves were then put in a drying oven for 48 hours at 80°C and the dry weight was measured.

For the calculation of the wood density the water displacement method was used (Pérez-Harguindeguy et al. 2013). Firstly, the bark was removed from the branches. If the diameter of the pith was over 2 mm, the branch was split, and the pith was removed. The green volume was measured by submerging the debarked branch sample in a beaker filled with water to determine the change in weight. The samples were then put in a dryer at the temperature of 80°C for 72 hours. Subsequently, the dry weight was measured accordingly, and the wood density was calculated as g dry weight / cm^3 green volume.

2.2.3 Seed Dispersal

The dispersal mode of the spontaneous species was obtained from literature (Estrada 1986, Weber 2001, Schembera 2004, Kimmel et al. 2010, Sandor 2012, Hecht et al. 2013, Jackman 2016) and botanical databases such as TRY (https://www.try-db.org/TryWeb/Home.php, Kattge et al. 2011) or the Seed Information Database (SID, http://data.kew.org/sid/). In cases where the dispersal mode was not available, the characteristics of the seeds were examined in order to infer the dispersal mode as wind or animal dispersed. While having wings or plumes is an attribute often found on wind dispersed diaspores (Thomson and Neal 1989), animal dispersed seeds mostly have hooks, sticky surfaces or edible coverings (Fenner 2000). The size and weight of the seeds may also indicate the dispersal mode.

2.2.4 Above ground biomass (AGB)

The calculation of the above ground biomass was done with the BIOMASS R-package, which uses the allometric model of Chave et al. (2014). Variables for the allometric model to calculate AGB are tree diameter, wood density and tree height. The DBH was measured in the field as explained above. Values for the wood density of the various taxa were extracted automatically from the global wood density (GWD) database (Zanne et al. 2016). Because tree heights were not measured in the field, a generic height-diameter model, based on a single bioclimatic predictor, was used. The bioclimatic predictor is obtained using the coordinates of the reforestation sites (-83.1,8.6). (Réjou-Méchain et al. 2017)

2.2.5 Shade Index (SI)

The shade under any planted tree depends on the size of this tree and the size and distance of neighbouring trees. Given that it was not possible to quantify this for all trees, a simple quantitative shade index (SI) was calculated as SI = Σ (DBH^2 / distance$^{0.5}$) with DBH in cm and distance in m and the distances of the closest planted tree set to 3 m. Trees within a 10 m radius around each planted tree were included in the calculation of the SI.

2.2.6 Diversity measures (biodiversity indices)

Differences in species diversity of the planted plots and the control plots as well as of Finca Amable and Finca La Bolsa were analysed using the iNEXT-package in R (Hsieh et al. 2016). The goal of this package is to design a diversity accumulation curve as a function of sample size (m) (Chao et al. 2014). For abundance data the sample size is simply the number of individuals. Based on a reference sample of size n, an interpolated diversity estimator is used for any rarefied sample of size m < n and an extrapolated diversity estimator is used for any enlarged sample of size n + m (Chao et al. 2014). The sample-size-based rarefaction/extrapolation curve includes therefore a rarefaction and an extrapolation part that both join at the reference point (actual reference sample size with the observed species richness). For the 38 plots on Finca Amable 40 equally spaced knots (samples sizes) between 1 and 2736 (= 2 x 1368, double the reference sample size) were selected by default. Diversity estimates were computed for each of these 40 knots.

Besides this visualization of species richness, Shannon diversity (H, H_{max} and E_H) and Simpson diversity were calculated to draw conclusions about the species richness and evenness. Species richness refers to the number of different species in a given area and is strongly dependent on sampling size and sampling effort. However, diversity depends not only on richness, but also on evenness. Evenness compares the similarity of the population size of each of the species present.

The Shannon index is a measure of diversity within a group of species, taking into account both, the number of species and abundance (number of individuals per species). In contrast to species richness, the Shannon index is therefore less dependent on sampling size (La Luz de Maza et al. 2002). The following equation was used to calculate the Shannon diversity (H): $H = -\sum_{i=1}^{R} pi \ln pi$ where: pi = proportion of individuals belonging to the ith species and R = total number of species present. Higher values stand for a more diverse species composition, with more equal abundancies of species. The maximum diversity a community can achieve when all species are equally common with the given number of species sampled (H_{max}) was calculated as $H_{max} = \ln R$. The evenness of the sampled community was then determined by: $E_H = H / H_{max}$. The value of E_H lies between zero and one and the closer E_H to zero, the more irregular is the species distribution in the sample area.

The Simpson Index is, alongside the Shannon Index and the evenness calculated from it, one of the most frequently used diversity indices. It expresses the probability that two individuals randomly selected from all individuals in a sample do not belong to the same species. Simpson diversity was calculated as: $D = 1 - \left(\frac{\sum n(n-1)}{\sum N(N-1)}\right)$ where N = total number of individual organisms (all species combined) and n = number of individuals of a particular species. D assumes values between zero and one and the greater the diversity, the closer D to one.

2.2.7 Statistical Analysis

The data were entered into Microsoft Office Excel sheets, the statistical analysis was performed in R version 3.6.1 (Team R. Core 2019) and Past3 (Hammer et al. 2001).

To test if species randomly established under planted tree species, the ten most abundant planted and spontaneous species were first selected using a Pivot-table and then a Pearson`s Chi-squared test was performed, testing the number of spontaneous individuals being found in the subplots of the planted species.

Next, I tested if the size of the spontaneous trees (measured as the total basal area in a subplot) was related to the basal area of planted trees next to which the spontaneous plants had established. Possible assumptions are that the growth of spontaneous individuals under shady conditions is worse if they compete for resources, or that the shade is beneficial because it provides a more suitable microclimate or suppresses the emergence of herbaceous species and thus helps the establishment of spontaneous vegetation. Another hypothesis is that larger trees are more inviting for birds to sit on them, which can increase seed input. The data were first examined for normal distribution using the Shapiro-Wilk normality test. Since a normal distribution was not given, Spearman's rank correlation test was used to determine the correlation. Both, the connection between the planted basal area and the spontaneous basal area and between the planted basal area and the number of spontaneous individuals per subplot were also investigated, using Spearman's rank correlation test.

Research question 4 was, if planted trees are already regenerating. More precisely, did the planted trees produce seeds that already germinated and reached a DBH greater than 1 cm, so that they could be observed during the data collection. This would only be expected in planted species that had already become fertile and their seedlings should be more common next to the same species (ideally fertile individuals).

Wilcoxon rank sum tests were used to determine differences in spontaneous basal area, number of spontaneous individuals and number of spontaneous species between the planted plots and control plots on Finca Amble and between plots on Finca Amable and Finca La Bolsa. For the analysis of the species composition in the plots and the control plots, as well as in the plots on Finca La Bolsa, a non-metric multidimensional scaling (NMDS) was calculated. NMDS uses ranking data instead of metric values. The proximity between the points in the NMDS represents the similarity of the species composition of the plots.

Further, it was tested if functional traits (leaf thickness, leaf toughness, leaf dry matter content (LDMC), specific leaf area (SLA), chlorophyll content and WD) are significantly different between the spontaneous trees recorded and planted species. Planted trees included a large variety of local forest species, whereas spontaneous species must have been filtered from the local species pool by their ability to arrive and establish under the specific local conditions. Traits from planted species, which included several that had also established spontaneously, had been obtained by Evelyn Ersthofer (unpubl.) and in previous studies (Hackl 2016, Kreinecker 2016). Traits of individuals that were present in spontaneous as well as planted trees were only counted for the calculation of spontaneous mean-values. So far hardly any of the planted trees apparently had reproduced locally, so the presence of these species in the pool of spontaneous species was not because they also had been planted. Wilcoxon rank sum tests with continuity correction were used to compare trait values between the two groups because the data was not normally distributed and a principal component analysis was calculated for visualization, using six traits for 33 species that had established spontaneously and 40 species that had not.

III. Results

3.1 Finca Amable

3.1.1 Spontaneous species distribution, basal area and biomass

In the studied area a total of 5122 individuals of spontaneous woody vegetation were recorded, of which 1991 had a diameter at breast height over 2 cm. The individuals belong to 69 different species, representing 24 plant families (Table 1).

Figure 7 shows the distribution of the ten most abundant spontaneous species in the studied area on Finca Amable. All these species - except for *Croton schiedeanus* and *Piper friedrichsthalii* - were represented in all sectors.

If one considers the different distribution patterns of the species, it is noticeable that *Acalypha diversifolia*, *Cecropia obtusifolia*, *Conostegia subcrustulata*, *Croton schiedeanus*, *Miconia argentea*, *Piper hispidum* and *Urera baccifera* have more individuals in sectors 1 to 4 than in sectors 5 to 8 and that *Miconia schlimii*, *Piper aduncum* and *Piper friedrichsthalii* have exactly the opposite distribution pattern. The non-uniform distribution across the area studied (particularly between the front and rear sectors) was particularly pronounced in *Croton schiedeanus*, *Piper aduncum*, *Piper friedrichsthalii* and *Urera baccifera*. (Fig. 7)

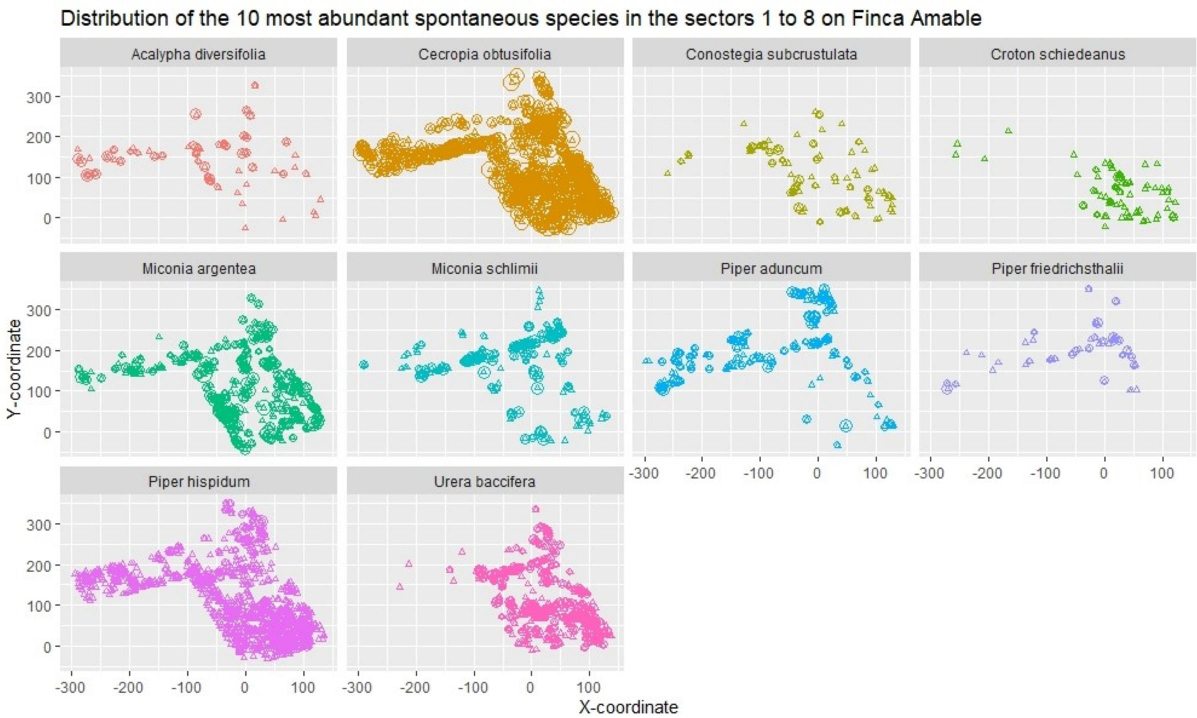


Figure 7: Distribution of the 10 most common spontaneous species on Finca Amable. (Circles represent individuals with a dbh over 2 cm and larger individuals are drawn with larger circles, triangles represent individuals with a dbh under 2 cm.)

Table 1: Spontaneous woody species found on Finca Amable including the basal area, above ground biomass (AGB) and the number of individuals (n). Species without BA data had no individual > 2 cm DBH

Spontaneous species	Family	Basal area [cm^2]	AGB [kg]	n
Cecropia obtusifolia	*Urticaceae*	142756	66803	751
Miconia argentea	*Melastomataceae*	10445	6816	408
Luehea seemannii	*Malvaceae*	5194	3054	46
Miconia schlimii	*Melastomataceae*	4639	2770	216
Piper aduncum	*Piperaceae*	2873	986	160
Urera baccifera	*Urticaceae*	2861	304	789
Apeiba tibourbou	*Malvaceae*	1885	597	9
Ficus maxima	*Moraceae*	1621	867	12
Ficus sp.	*Moraceae*	1217	487	51
Piper hispidum	*Piperaceae*	1156	329	2048
Erythrina fusca	*Fabaceae*	1100	411	22
Senna reticulata	*Fabaceae*	1019	406	58
Vernonia patens	*Asteraceae*	1011	356	24
Acalypha diversifolia	*Euphorbiaceae*	959	244	68
Ochroma pyramidale	*Malvaceae*	867	273	1
Psidium guajava	*Myrtaceae*	730	502	10
Piper friedrichsthalii	*Piperaceae*	429	125	59
Conostegia subcrustulata	*Melastomataceae*	354	87	79
Piper auritum	*Piperaceae*	348	87	39
Schizolobium parahyba	*Fabaceae*	269	130	1
Vismia baccifera	*Hypericaceae*	268	116	6
Spondias mombin	*Anacardiaceae*	213	86	5
Albizia saman	*Fabaceae*	209	132	1
Anacardium excelsum	*Anacardiaceae*	185	82	22
Croton schiedeanus	*Euphorbiaceae*	170	70	85
Annona sp.	*Annonaceae*	113	63	1
Inga sp.	*Fabaceae*	94	40	7
Guatteria chiriquiensis	*Annonaceae*	83	22	26
Carica sp.	*Caricaceae*	75	15	1
Simarouba amara	*Simaroubaceae*	62	17	3
unknown 1	-	57	-	1
Tachigali versicolor	*Fabaceae*	49	21	1
Platymiscium curuense	*Fabaceae*	48	27	3
Bunchosia nitida	*Malpighiaceae*	48	17	20
Eugenia sp.	*Myrtaceae*	47	27	1
Nectandra sp.	*Lauraceae*	42	19	1
Bursera simaruba	*Burseraceae*	36	9	1
Cornutia pyramidata	*Lamiaceae*	33	14	1
Palicourea sp.	*Rubiaceae*	29	6	22
Ficus insipida	*Moraceae*	27	7	2

Spontaneous species	Family	Basal area [cm²]	*AGB [kg]*	n
Cedrela odorata	*Meliaceae*	25	6	3
Ocotea insularis	*Lauraceae*	25	7	13
Brosimum utile	*Moraceae*	23	8	1
Amphitecna isthmica	*Bignoniaceae*	14	4	1
unknown 2	-	14	-	1
Sorocea sp.	*Moraceae*	13	4	1
Cestrum sp.	*Solanaceae*	13	2	4
unknown 3	-	12	-	5
Perebea sp.	*Moraceae*	11	3	2
Solanum cf.	*Solanaceae*	11	2	1
Theobroma cacao	*Malvaceae*	11	2	1
Sapium laurifolium	*Euphorbiaceae*	10	2	2
Macrolobium hartshornii	*Fabaceae*	9	3	1
Castilla tunu	*Moraceae*	7	2	4
Pentagonia sp.	*Rubiaceae*	5	1	1
Xylopia sp.	*Annonaceae*	5	1	1
Tetragastris panamensis	*Burseraceae*	5	1	1
Lonchocarpus macrophyllus	*Fabaceae*	4	1	2
Vitex cooperi	*Lamiaceae*	3	1	1
Andira inermis	*Fabaceae*	-	-	1
Carapa guianensis	*Meliaceae*	-	-	1
Caryocar costaricense	*Caryocaraceae*	-	-	1
Guatteria amplifolia	*Annonaceae*	-	-	3
Hieronyma alchorneoides	*Phyllanthaceae*	-	-	2
Ocotea sp.	*Lauraceae*	-	-	3
Posoqueria sp.	*Rubiaceae*	-	-	1
Tectona grandis	*Lamiaceae*	-	-	1
unknown 4	-	-	-	1
unknown 5	*Myrtaceae*	-	-	1

Three out of the ten most common spontaneous species belong to the family *Melastomataceae*, three to *Piperaceae*, two species belong to *Euphorbiaceae* and another two to *Urticaceae*.

Cecropia obtusifolia had by far the largest basal area (142756 cm^2) and thus constitutes most of the spontaneous growth. *Miconia argentea* accounts the second largest basal area with 10445 cm^2, or less than a tenth of the basal area of *Cecropia obtusifolia*. (Table 1)

Throughout the study area 37 % of the measured woody spontaneous vegetation had a basal area < 10 cm^2 but there were also 75 individuals with a basal area > 500 cm^2. Out of these 75 largest individuals, 67 belong to the species *Cecropia obtusifolia* and the others are individuals of *Luehea seemannii*, *Apeiba tibourbou, Miconia argentea*, *Ochroma pyramidale* and *Ficus maxima*. However, the one large individual of *Ficus maxima* very likely had germinated before the start of planting in 2012. The calculated total above-ground biomass of spontaneous vegetation in the sectors 1 - 8 was 86.5 t or 12.4 t/ha.

3.1.2 Does the species of trees planted affect spontaneous growth?

First, it was tested whether the proportion of spontaneous individuals found in the subplots of the ten most frequently planted species corresponded to the frequency of the ten most common planted species or was non-random. (Table 2)

Table 2: Number of individuals for the ten most frequently planted trees and the number of spontaneous individuals in subplots of these species.

	Anacardium excelsum	*Astronium graveolens*	*Cedrela odorata*	*Croton schiedeanus*	*Hieronyma alchorneoides*	*Inga sp.*	*Lonchocarpus macrophyllus*	*Platymiscium curuense*	*Vitex cooperi*	*Zygia longifolia*	Total of individuals
nr. of trees planted	157	152	151	187	188	160	169	198	159	214	1735
nr of spontaneous individuals in subplots of these species	190	123	166	137	164	241	229	265	170	234	1919
spontaneous/planted	1.2	0.8	1.1	0.7	0.9	1.5	1.4	1.3	1.1	1.1	1.1

The chi-squared test (χ^2) showed that the number of spontaneous individuals growing in subplots of the various most common planted trees is significantly not proportional ($\chi^2 = 43.466$, DF = 9, p = 1.8×10^{-6}) to the number of trees planted. Some species therefore have a higher or lower number of spontaneous individuals in their subplots than expected by chance, which raises the question of whether there are species-species interactions between the planted trees and the spontaneous individuals.

To test if some species established significantly more or less under certain planted trees, I compared the ten most common planted species with the ten most common spontaneous species. (Table 3)

The ten most common planted species in sectors 1 to 8 are *Zygia longifolia* (214 individuals), *Platymiscium curuense* (198), *Hieronyma alchorneoides* (188), *Croton schiedeanus* (187), *Lonchocarpus macrophyllus* (169), *Inga sp.* (160), *Vitex cooperi* (159), *Anacardium excelsum* (157), *Astronium graveolens* (152) and *Cedrela odorata* (151). Out of these ten most abundant planted species, four belong to *Fabaceae,* two to *Anacardiaceae*, and one each to *Lamiaceae, Euphorbiaceae, Meliaceae* and *Phyllanthaceae*.

Table 3: Correlation of the ten most abundant planted species and the ten most abundant spontaneous species in sectors 1 to 8 on Finca Amable (columns represent the ten most abundant planted species, rows the ten most abundant spontaneous species and values are in percent of the total of the spontaneous individuals per species)

Spontaneous species	Planted species											
	Anacardium excelsum	*Astronium graveolens*	*Cedrela odorata*	*Croton schiedeanus*	*Hieronyma alchorneoides*	*Inga sp.*	*Lonchocarpus macrophyllus*	*Platymiscium curuense*	*Vitex cooperi*	*Zygia longifolia*	Percentage of all other planted trees	Total of individuals
Acalypha diversifolia	5.9	1.5	2.9	0.0	1.5	8.8	2.9	2.9	1.5	7.4	64.7	68
Cecropia obtusifolia	2.3	2.4	2.4	2.0	2.9	2.3	5.1	4.1	2.8	4.5	69.2	751
Conostegia subcrustulata	2.5	1.3	2.5	3.8	5.1	6.3	1.3	3.8	2.5	5.1	65.8	79
Croton schiedeanus	0.0	2.4	8.2	7.1	3.5	2.4	2.4	2.4	4.7	2.4	64.5	85
Miconia argentea	2.9	3.9	2.9	7.1	4.4	5.6	3.2	5.4	2.7	5.9	56	408
Miconia schlimii	3.7	1.4	2.8	2.8	6.0	10.2	4.6	4.6	3.7	3.2	57	216
Piper aduncum	6.3	0.6	0.6	1.3	3.1	1.9	5.6	5.6	5.0	3.1	66.9	160
Piper friedrichsthalii	0.0	0.0	3.4	1.7	15.3	6.8	3.4	10.2	3.4	6.8	49	59
Piper hispidum	4.2	2.7	3.6	2.7	2.9	5.5	4.8	6.1	3.2	5.4	58.9	2048
Urera baccifera	5.4	2.4	3.8	1.3	1.8	3.3	3.5	4.1	3.9	3.3	67.2	789
Percentage of total of individuals	2.72	2.63	2.61	3.24	3.25	2.77	2.92	3.43	2.75	3.70	69.98	

The ten most abundant spontaneous species in the studied area are *Piper hispidum* (2048 individuals), *Urera baccifera* (789), *Cecropia obtusifolia* (751), *Miconia argentea* (408), *Miconia schlimii* (216), *Piper aduncum* (160), *Croton schiedeanus* (85), *Conostegia subcrustulata* (79), *Acalypha diversifolia* (68) and *Piper friedrichsthalii* (59).

Combined these individuals of the ten most abundant spontaneous species make up 91 % of the spontaneous vegetation found on Finca Amable, whereby the individuals of the ten most common planted trees only account for 30 % of the total of planted trees in the surveyed area. Table 3 above shows per row, how many percent of the spontaneous species can be found in the subplots of the ten most common planted trees. *Acalypha diversifolia,* for example, can be found to 8.8 % in subplots with *Inga sp.* and to 7.4 % in subplots with *Zygia longifolia.* Randomly distributed, the proportion growing together with *Zygia longifolia* would be the same as the proportion of *Zygia longifolia* on all other planted tree individuals (3.7%).

The chi-squared test (χ^2) showed that the distribution is highly significantly non-random ($\chi^2 =$ 167.4, DF = 81, p = 5.7 x 10^{-8}).That means spontaneous species were found next to planted species with a higher or lower proportion than expected by random distribution.

Generally, the values are all rather low and range between 0 and 15.3 %. Some higher percentages include the presence of *Piper friedrichsthalii* in subplots with *Hieronyma alchorneoides* (15.3 %) and *Platymiscium curuense* (10.2 %) and the occurrence of *Miconia schlimii* in subplots with *Inga sp.* (10.2 %). Conversely, no individual of *Acalypha diversifolia* was found next to *Croton schiedeanus*, no individual of *Croton schiedeanus* next to *Anacardium excelsum* and no individual of *Piper friedrichsthalii* was detected next to *Anacardium excelsum* and next to *Astronium graveolens*.

3.1.3 Effect of planted tree size

The size (measured as the basal area) of the planted trees was weakly but significantly positively correlated with the basal area of the spontaneous vegetation per subplot (Fig. 8a, Spearman's rho = 0.0463, p = 0.005)

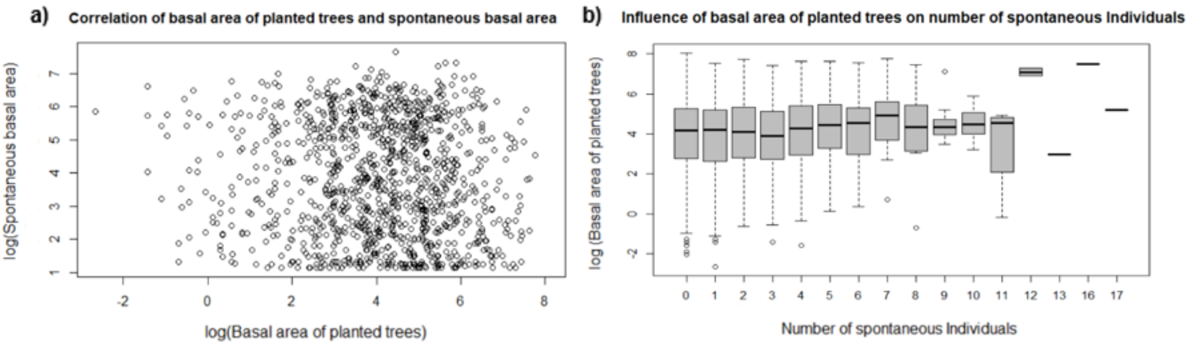


Figure 8: Plot of the correlation of basal area of planted trees and spontaneous basal area (a) and box-plot of the influence of basal area of planted trees on number of spontaneous individuals (b). (log-values were used for a better visualization)

However, the number of spontaneous individuals was not related to the size of the planted trees (Fig. 8b, Spearman's rho = 0.0218, p = 0.186).

3.1.4 Shade index

The shade index (SI) was calculated using a 10 meters radius around each planted tree. Higher values result from more and/or larger trees in the vicinity of the subplot, creating more shady conditions in the subplot itself.

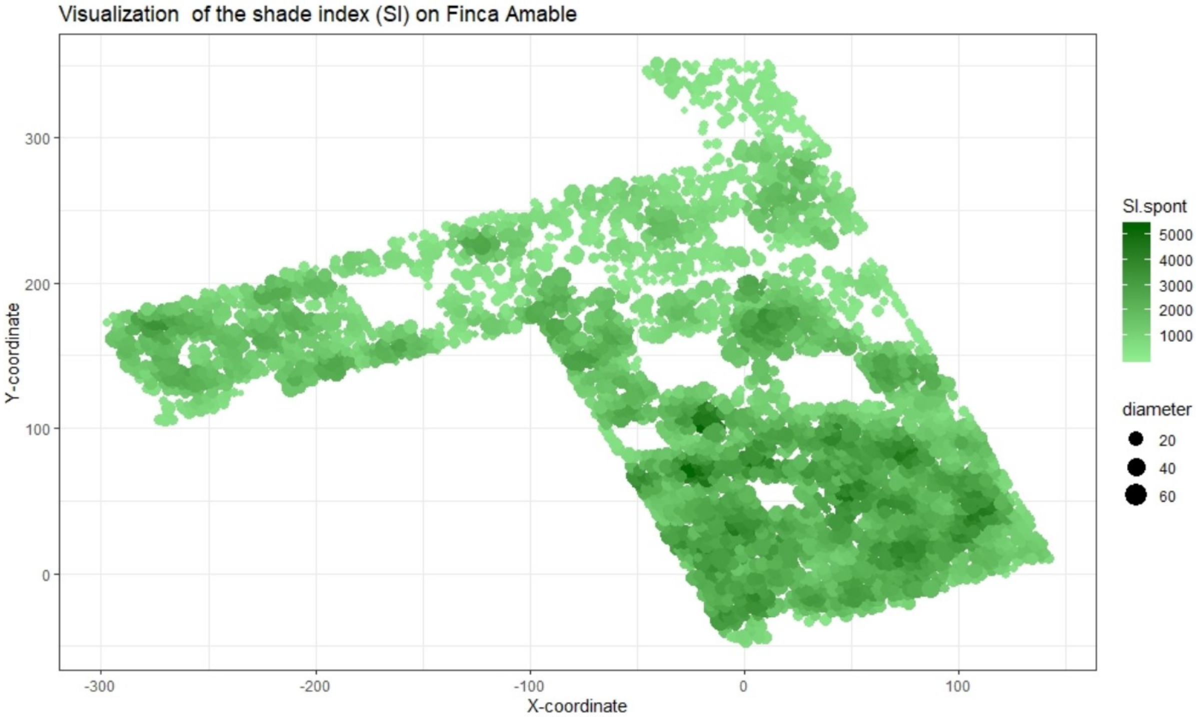
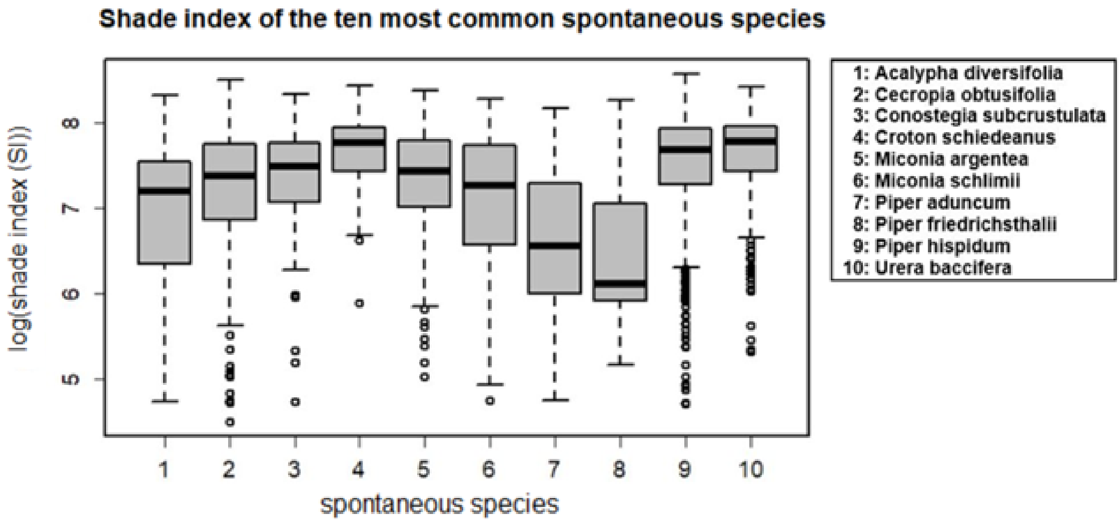


Figure 9: Visualization of the shade index (SI) on Finca Amable

Figure 9 gives an overview of the shade index and thus canopy cover on Finca Amable. As trees are larger especially in sectors 1- 4, but also in parts of sector 5 and 6, this results in higher SI-values and therefore less light-availability for the spontaneous vegetation.



	1	2	3	4	5	6	7	8	9	10
Mean SI	1356	1691	1754	2281	1762	1473	976	866	2131	2288

Figure 10: Boxplot showing the shade Index (SI) of the ten most common spontaneous species. A table of mean values per species is included. (log-values were used for a better visualization)

Croton schiedeanus, *Piper hispidum* and *Urera baccifera* seem to prefer more shady conditions, whereas *Piper aduncum* and *Piper friedrichsthalii* were found in more open areas (Fig. 10).

Different spontaneous species were growing under significantly different crown cover, calculated as the shade index (ANOVA, p = < 2 x 10^{-16}, DF = 68). The relationship between species and shade index was also significant (p = < 2 x 10^{-16}, DF = 47) when only trees in sectors 1-4 were compared, which had been planted somewhat earlier and where the composition of spontaneous trees may also differ for other reasons (see below). Testing the effect of neighbouring trees on the spontaneous basal area per subplot with Spearman's rank correlation test resulted in a significant but very weak negative correlation, meaning higher values of the shade index result in lower values of the spontaneous basal area (Spearman's rho = -0.173288, p =2.2 x 10^{-16}). (Fig. 11)

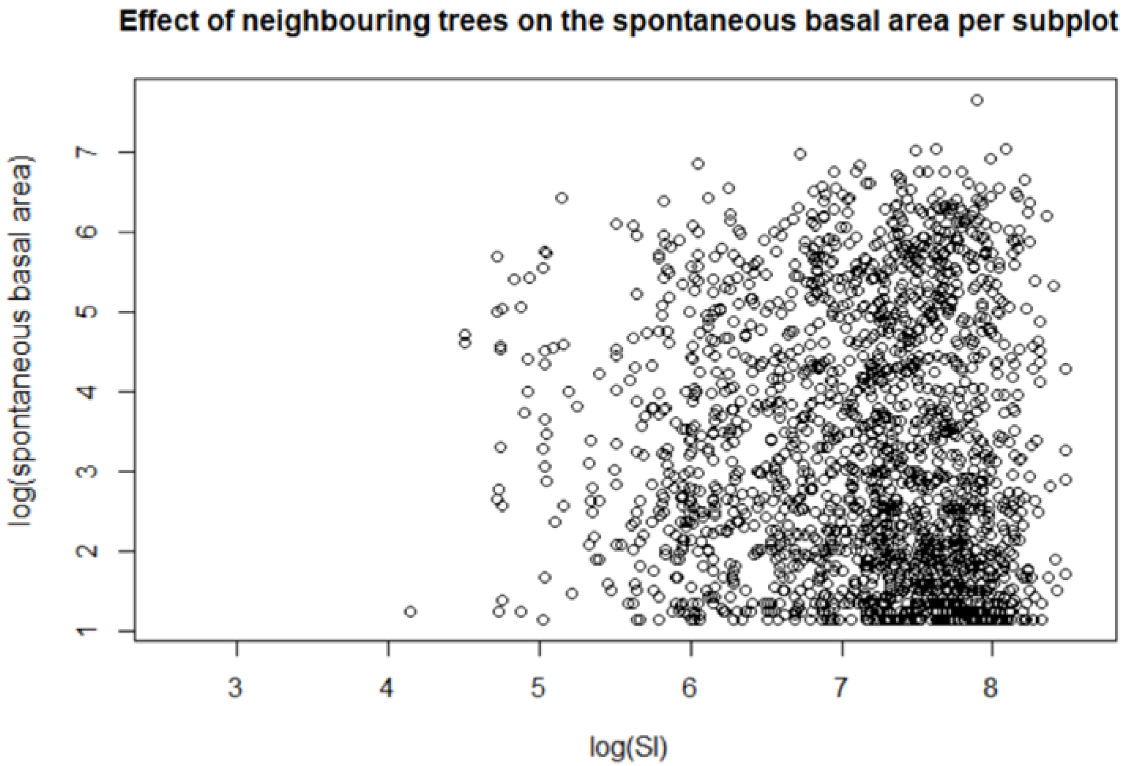


Figure 11: Effect of neighbouring trees (Shade Index) on the spontaneous basal area per subplot (log-values were used for a better visualization)

3.1.5 Impact of fertile planted trees on spontaneous vegetation

In the field it often proved quite challenging to identify the fertility of planted trees either due to their height and therefore poor visibility or because of inconspicuous fruits and flowers and strong liana growth. Despite these difficulties, 184 individuals of all the planted trees in sector 1 to 8 were detected being fertile, and 3279 individuals were observed being non-fertile.

As shown in Table 4 below, individuals of 25 planted tree species had already become fertile. However, for only 12 of these species, spontaneous individuals were recorded, and no rejuvenation of the planted trees could be observed directly in the same sub-plots as the fertile planted trees.

Table 4: Frequency of fertile planted tree species in sector 1 to 8 on Finca Amable and number of spontaneous individuals of the same species in the study-area (the red underlined species are fertile species that can be found among the spontaneous species)

Fertile planted tree species	*n*	*Number of spontaneous individuals*
Inga sp.	71	7
Inga oerstediana	30	-
Posoqueria sp.	27	1
Apeiba tibourbou	11	9
Elaeis guineensis	9	-
Tocoyena pittieri	9	-
Bunchosia nitida	5	20
Anacardium excelsum	2	22
Genipa americana	2	-
Luehea seemannii	2	46
Tetragastris panamensis	2	1
Acacia allenii	1	-
Albizia saman	1	1
Amphitecna isthmica	1	1
Astronium graveolens	1	
Guarea guidonia	1	-
Guatteria amplifolia	1	3
Guatteria sp.	1	-
Inga barbourii	1	-
Inga densiflora	1	-
Inga pezizifera	1	-
Ocotea insularis	1	13
Swartzia panamensis	1	-
Trichospermum mexicanum	1	-
Vitex cooperi	1	1

Species that were both found in the spontaneous vegetation and in the planted trees, without the planted trees being noticeable fertile, are included in Table 5 below. Especially the rejuvenation of *Croton schiedeanus* is remarkable, which was found in large numbers in the undergrowth. This might be the only species that spreads from planted trees, but here the presence of fertile individuals appears to have been missed due to the above-mentioned reasons.

Table 5: Table of species that appear both in the spontaneous vegetation and in the planted trees. Planted trees of these species were not observed being fertile.

Species	**Number of spontaneous individuals**	**Number of planted individuals**
Croton schiedeanus	85	187
Ficus sp.	51	29
Erythrina fusca	22	6
Ficus maxima	12	5
Spondias mombin	5	91
Castilla tunu	4	98
Cedrela odorata	3	151
Platymiscium curuense	3	198
Simarouba amara	3	90
Hieronyma alchorneoides	2	188
Lonchocarpus macrophyllus	2	169
Sapium laurifolium	2	50
Andira inermis	1	36
Brosimum utile	1	144
Bursera simaruba	1	64
Carapa guianensis	1	47
Caryocar costaricense	1	19
Macrolobium hartshornii	1	31
Ochroma pyramidale	1	26
Tachigali versicolor	1	103
Schizolobium parahyba	1	41

3.1.6 Dispersal mode

Out of the 64 identified spontaneous species on Finca Ambale, 47 use zoochory as a mechanism to disperse their seeds, ten species are wind-dispersed (anemochorous) and three species are autochorous. Concerning the remaining four species, each use a combination of different dispersal-modes: zoochory/autochory occurs twice and zoochory/hydrochory as well as anemochory/hydrochory are represented in only one species.

At the level of individuals (5113 individuals), zoochory was by far the most common mechanism of dispersal (94 %), while only 3 % were autochorous and 2.7 % anemochorous. (Fig. 12)

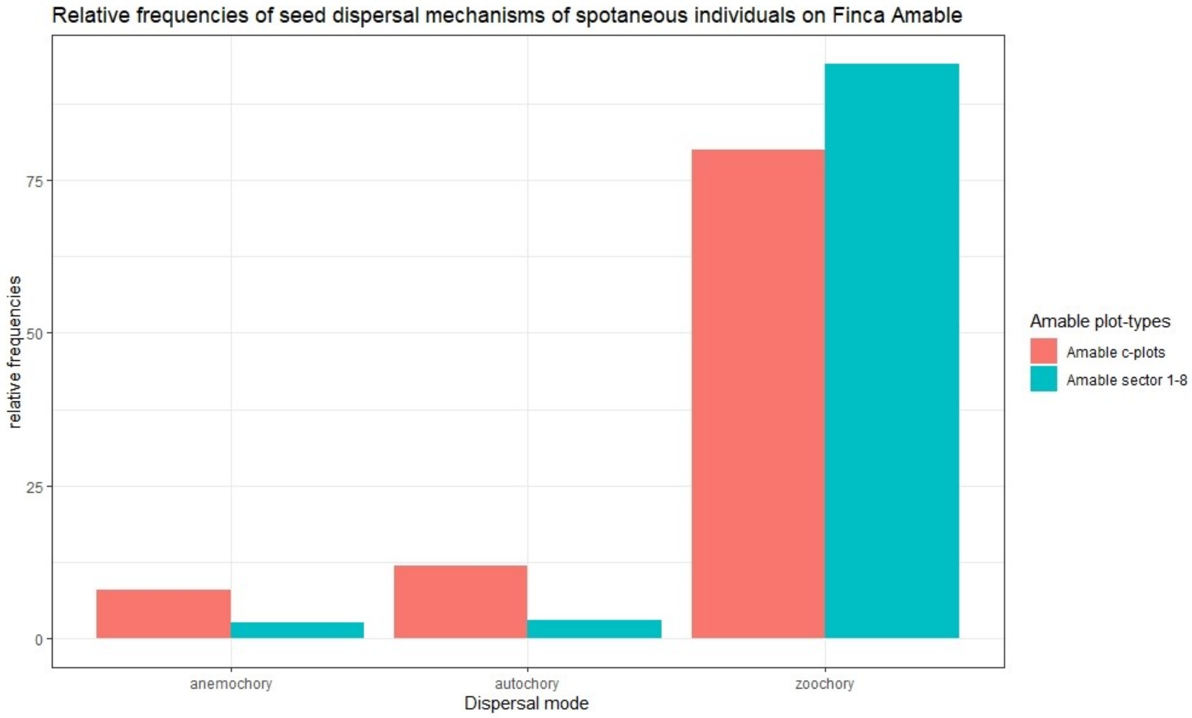


Figure 12: Proportion (%) of seed dispersal mechanisms of spontaneous individuals in the sectors 1-8 and in control (c) plots without planted trees on Finca Amable

Within the five control plots on Finca Amable 21 spontaneous woody species were observed using three different dispersal modes. Zoochory was most common in 15 of the 21 species, anemochory was second with 4 species and autochory was found in 2 species. At the individual level (285 individuals) 80 % were zoochorous, 12 % autochorous and 8 % anemochorous (Fig. 12).

Animal distribution is by far the most common seed dispersal mode in both planted and control plots, but anemochorous and autochorous species were found to be more common in control plots compared to the plots with planted trees. A chi-squared test (χ^2) confirmed a significant difference between the proportion of zoochorous, anemochorous and autochorous spontaneous individuals in planted plots and control plots ($\chi^2 =$ 10.1, DF = 2, p = 0.006).

3.1.7 Comparison of planted plots and control plots

The mean spontaneous basal area per plot (1 - 38) was 2 ± 2 cm^2 / m^2. However, the mean spontaneous basal area (BA) of the plots 1 - 19 in sectors 1 - 4 (3 ± 2 cm^2 / m^2) was significantly higher (Wilcoxon rank sum test: W = 54, p = 0.0004) than of the plots 20 - 38 in sectors 5 - 8 (1 ± 1 cm^2 / m^2). (Table 7)

The mean value of the spontaneous basal area of the control plots (C1-C5) was 3 ± 3 cm^2 / m^2. Similar to spontaneous vegetation below planted trees, control plots C1-C3 in sectors 1 - 4 had a significantly higher (Welch Two Sample t-test: t = -5.4, df = 2.2, p = 0.03) mean basal area of 5 ± 1.5 cm^2 / m^2, than C4 and C5 (0.4 ± 0.2 cm^2 / m^2) in the rear part of Finca Amable. (Table 6)

Table 6: Spontaneous vegetation on Finca Amable in control plots (C1-C5)

Plot	species	families	individuals > 2 cm	individuals < 2 cm	Total individuals	basal area [cm^2]	AGB [kg]
C1	14	9	33	57	90	3028	1431
C2	10	6	32	71	103	1778	861
C3	13	7	21	17	38	3188	1892
C4	6	4	8	24	32	286	95
C5	9	5	6	21	27	114	33

Comparing the spontaneous basal area of the plots and the control plots, it is noticeable that the mean value of the plots is lower than that of the control plots (Fig. 13). Examining more closely, how the comparatively high spontaneous basal area of the control plots C1, C2 and C3 is created, the following can be seen:

In C1, the majority of the total basal area falls to only eight individuals, each with a basal area > 100 cm^2. Six of these individuals are *Cecropia obtusifolia* and account for 79% of the basal area. In C2 three individuals of *Cecropia obtusifolia* with a basal area > 100 cm^2 account for 85 % of the basal area. In C3 five individuals with a basal area >100 cm^2 were found. Two of these belong to the species *Luehea seemannii* and constitute 32 % of the basal area. Also mentionable is one *Ochroma pyramidale* that makes up 20 % of the total basal area and the large *Ficus sp.* (possibly present before the trees were planted) that represents 36 %.

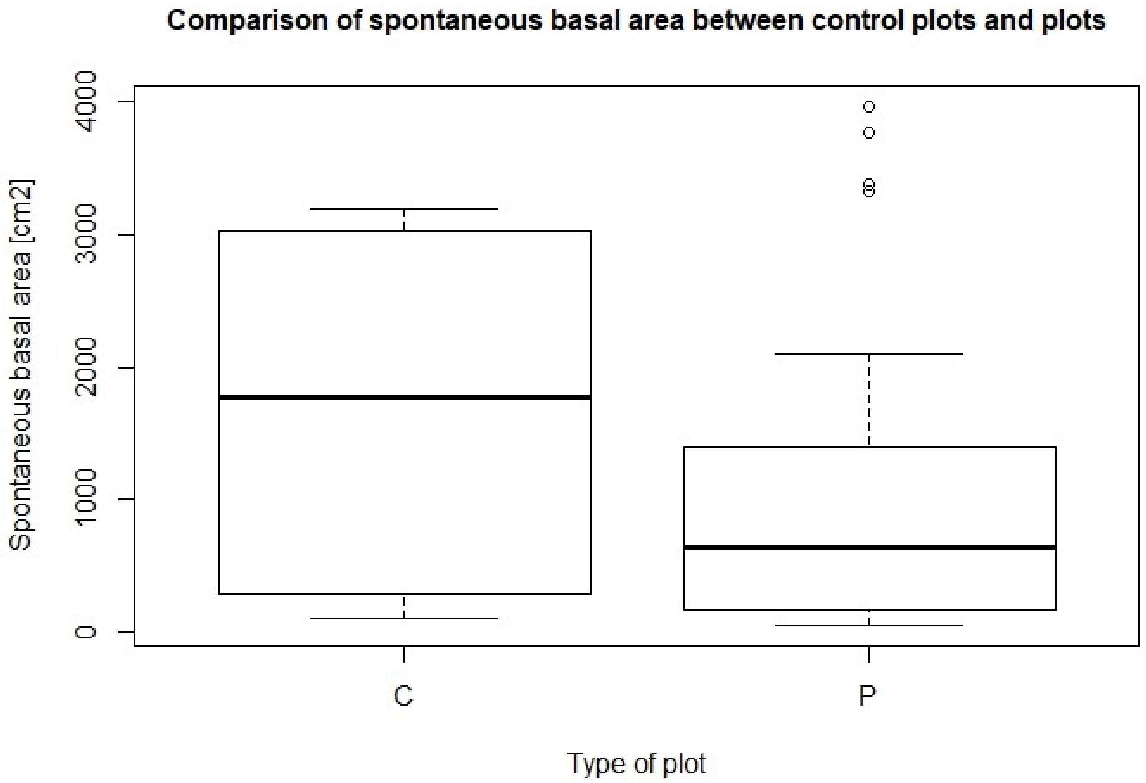


Figure 13: Boxplot – Comparison of spontaneous basal area between plots (P) with and control plots (C) without planted trees on Finca Amable

The mean basal area of the trees planted was also significantly higher (Wilcoxon rank sum test: W = 35, p = 8.525 x 10^{-6}) in the plots of sectors 1 – 4 (11 ± 4 cm^2 / m^2) than in the plots of sectors 5 – 8 (5 ± 3 cm^2 / m^2). (Table 7)

In total 1368 individuals from 38 species, belonging to 20 plant families, were recorded in the 38 planted plots. As the layout of plot 37 was very unclear, almost all planted trees from the planting scheme could not be found. For this reason, the spontaneous vegetation in plot 37 could not be surveyed. Plot 37 was therefore subsequently removed and not used in the analysis. Per plot, there were 2 – 13 (average 6.92) species and 3 – 140 (average 37) individuals.

In the control plots 290 individuals from 23 species were found. The number of spontaneous species ranged from 6 to 14 (mean 10.4) and the number of individuals from 27 and 103 (mean 58). Both, the mean number of spontaneous species and the mean number of spontaneous individuals were higher in the control plots than in the planted plots. (Table 8)

Table 8 summarizes the statistical results of the Wilcoxon rank sum tests with continuity correction which were used to compare the spontaneous basal area, the number of spontaneous species and the number of spontaneous individuals of planted plots and control plots. Out of these three tested characteristics only the number of spontaneous species differed significantly ($p < 0.05$) between the two different plot types.

Table 7: Spontaneous vegetation on Finca Amable in planted plots 1 - 38 (sectors 1 - 8)

Plot	species	families	individuals > 2 cm	individuals < 2 cm	Total individuals	Spontaneous basal area [cm²]	Spontaneous AGB [kg]	Planted basal area [cm²]
1	7	6	9	33	42	639	324	8133
2	6	3	17	17	34	1694	997	6173
3	10	7	11	18	29	735	343	4557
4	8	5	5	19	24	398	156	3220
5	8	5	10	52	62	1146	959	6474
6	5	4	8	22	30	3372	2090	4691
7	6	5	5	35	40	617	265	5413
8	9	7	29	61	90	1175	406	9115
9	8	4	10	24	34	1168	576	8528
10	8	5	9	50	59	771	329	5770
11	8	6	9	39	48	638	222	4205
12	7	6	16	84	100	1309	599	2771
13	11	6	11	48	59	1391	710	6048
14	4	3	2	10	12	90	53	7626
15	9	6	30	19	49	3959	1843	4216
16	13	10	40	100	140	1636	796	7999
17	9	8	23	26	49	3327	1416	2443
18	6	5	31	11	42	3765	1711	2640
19	12	10	29	41	70	2035	949	5980
20	6	5	4	14	18	726	361	2470
21	8	5	13	16	29	2098	996	3339
22	10	8	15	27	42	1238	505	1281
23	8	6	14	42	56	301	89	5536
24	6	4	6	11	17	247	92	2266
25	8	4	26	9	35	1517	607	925
26	3	2	2	2	4	61	16	1478
27	8	5	26	24	50	562	196	4925
28	4	3	2	3	5	68	19	2953
29	4	4	3	1	4	174	55	717
30	7	3	5	6	11	69	17	576
31	2	2	3	0	3	134	43	1139
32	6	3	7	3	10	84	21	2751
33	3	2	2	1	3	61	0.5	3072
34	5	3	16	7	23	620	234	1264
35	8	6	15	10	25	535	221	2947
36	3	3	2	2	4	77	23	2664
38	3	2	11	5	16	91	18	1357

Table 8: Results of Wilcoxon rank sum tests with continuity correction comparing characteristics of plots and control plots

	Mean of planted plots	Mean of control plots	W-value	p-value
Spontaneous basal area [cm²]	1041	1679	121	0.37
Number of spontaneous species	6.92	10.4	155	0.025
Number of spontaneous individuals	37	58	129.5	0.221

While the total number of species was greater in planted than in control plots, there were fewer control plots and thus fewer individuals and species. The species accumulation curve did not differ (Fig. 14).

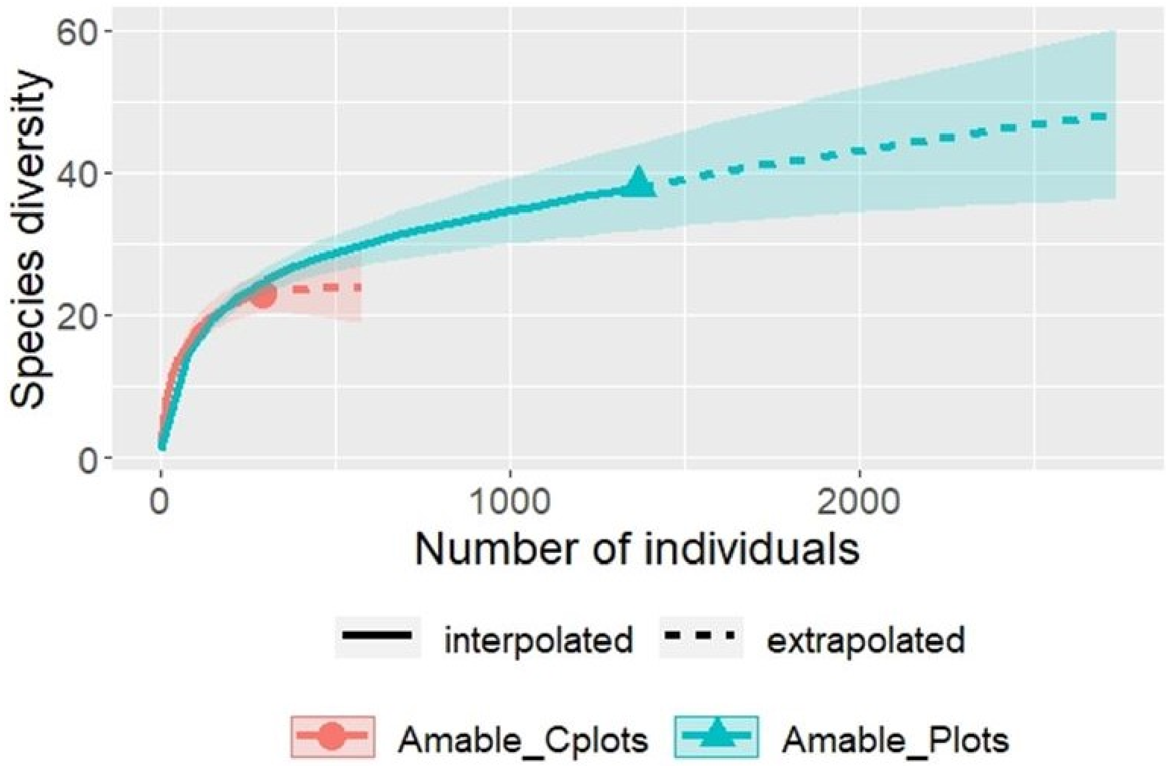


Figure 14: Species richness of sample-size-based rarefaction and extrapolation (dotted lines) sampling curves with 95% confidence intervals (shaded areas) for the 38 plots and the 5 control plots on Finca Amable

The observed Shannon and Simpson diversity indices were higher in control than in planted plots (Table 9). However, H_{max} was higher in the planted plots than in the control plots.

Table 9: Results of the three diversity orders of the plots and control plots on Finca Amable - Species richness, Shannon diversity and Simpson diversity

	planted plots			control plots		
Species richness		38			23	
Shannon diversity (H; H_{max}; E_H)	2.11	3.64	0.58	2.35	3.14	0.75
Simpson diversity		0.79			0.85	

For the analysis of the species composition in the plots and the control plots a non-metric multidimensional scaling (NMDS) was calculated (Fig. 15). The proximity between the points represents the similarity of the species composition of the plots. The closer two points are to each other, the more similar is the species composition of the plots, and the further away they are, the more different. The stress value can be seen as a measure for the quality of an ordination and should be below 20 % (<0.2). In this case the stress value was 0.18.

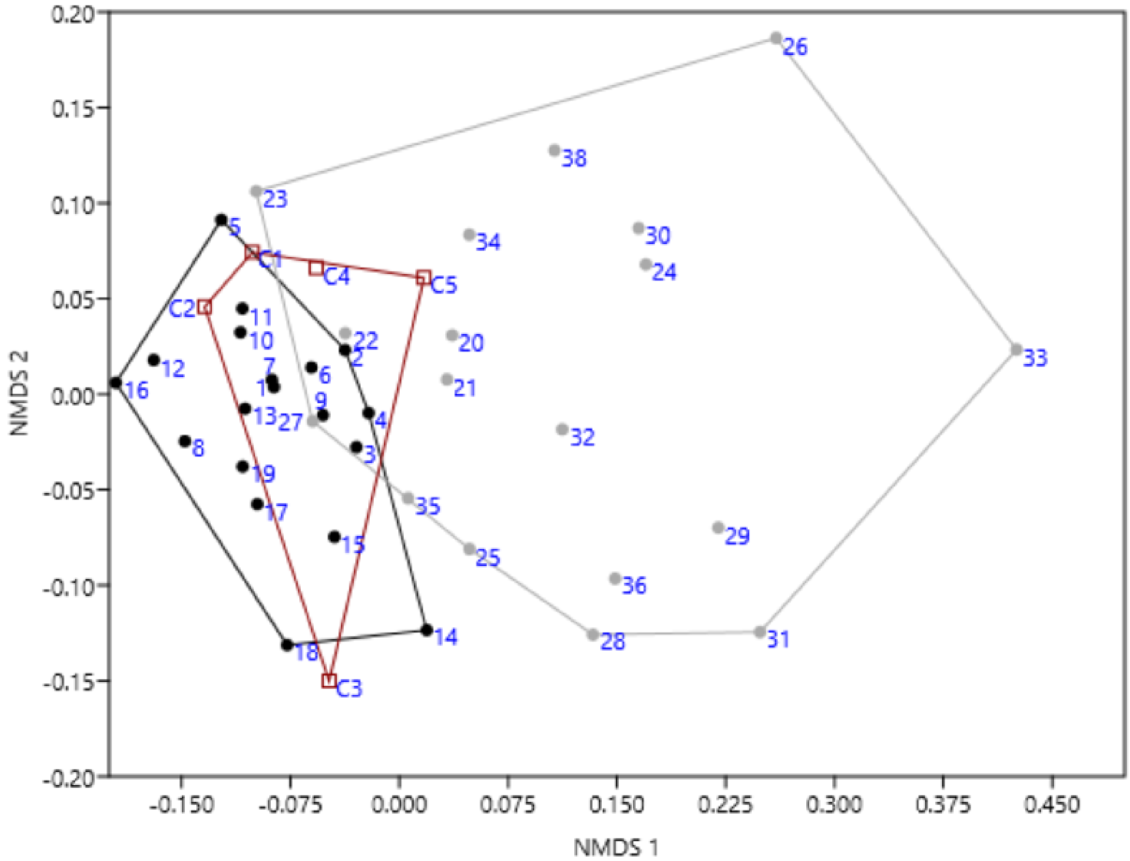


Figure 15: NMDS including the 38 plots (black dots: plot 1-19; grey dots: plot 20-38) and 5 control plots (C1-C5: red colour)

Species composition of plots 1 - 19 was quite similar and mostly different from plots 20 -38. The control plots C1 – C3 had a similar species composition to the planted plots of the front sectors and the control plots C4 and C5 had a more similar species composition to the planted plots from the rear sectors. C 3 differs in its species composition from all other control plots. The five most common species in the control plots were *Piper hispidum* (98 individuals), *Miconia argentea* (32), *Croton schiedeanus* (31), *Urera baccifera* (20) and *Cecropia obtusifolia* (19). All of these are gap-colonizing pioneer species. Besides the mentioned woody plants, the five control plots, especially C4 and C5, were strongly dominated by the grass *Brachiaria sp.* and the small shrub *Mimosa pudica*.

3.1.8 Functional traits of the spontaneous species

For 37 out of 69 spontaneous species on Finca Amable, functional leaf traits were collected and compared with data from 46 planted species. Wood traits were recorded for 35 spontaneous species and 42 planted species.

Table 10: Results of Wilcoxon rank sum tests with continuity correction comparing functional traits of spontaneous and planted species

	Mean of spontaneous species	Mean of planted species	W-value	p-value
Leaf thickness [mm]	0.26	0.22	596.5	0.02
Leaf toughness [N/cm]	3.6	3.9	874.5	0.43
Chlorophyll (SPAD units)	46.6	45	802	0.66
LDMC [mg g^{-1}]	324	376	1168	0.003
SLA [m^2 kg^{-1}]	18	16	781	0.64
Branch wood density [g / cm3]	0.4	0.5	1065	0.0006

Table 10 summarizes results of Wilcoxon rank sum tests with continuity correction. Significant differences (p-value < 0.05) between the spontaneous and planted species were found for leaf thickness, leaf dry matter content (LDMC) and branch wood density. Leaf thickness was significantly lower in the planted species compared to the spontaneous species and LDMC and branch wood density were significantly higher in the planted species compared to the spontaneous species. Not significant were the differences in leaf toughness, chlorophyll content and SLA.

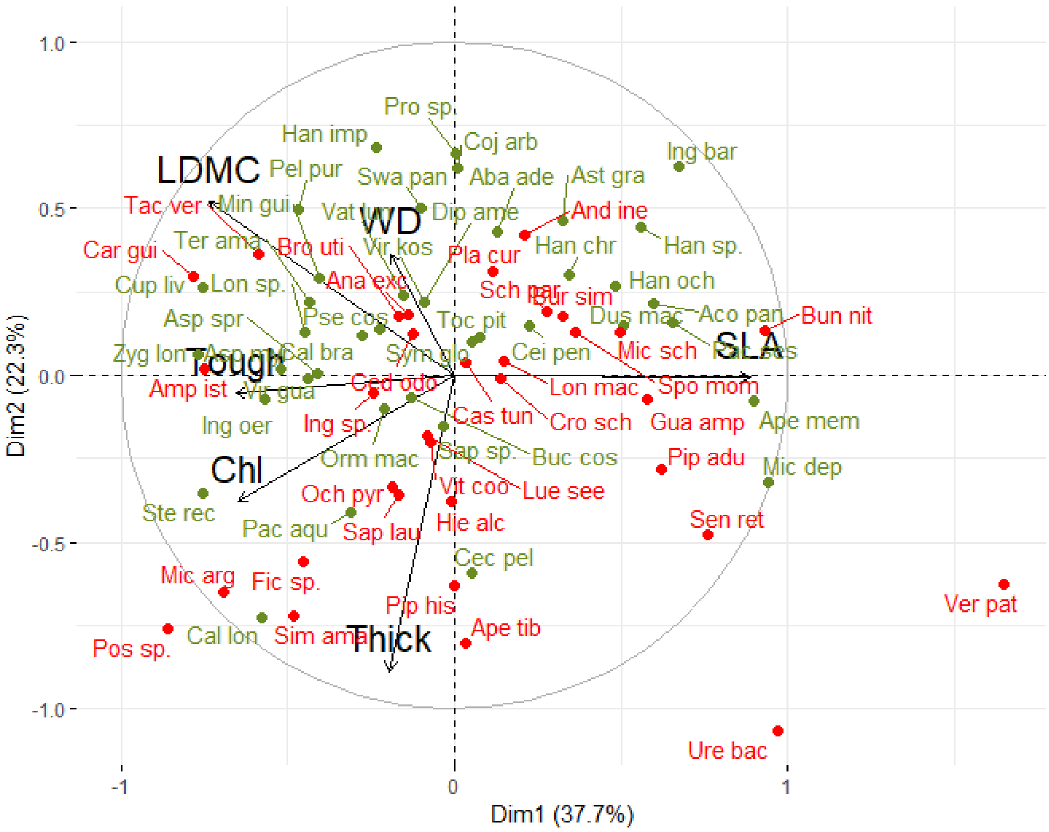


Figure 16: PCA of the collected functional traits for spontaneous (red) and planted species (green).

To test, if spontaneously establishing species differed in their combination of traits from trees, that had not established so far (but were planted at the same location), a principal component analysis (PCA) was calculated. The PCA is a common way to display correlations of many variables. In Figure 16 the first two main components are shown. The arrows indicate, to which main component a variable loads how strongly. “SLA” only contributes to axis 1, whereas “Thick” mainly loads on axis 2.

3.1.9 Comparison of spontaneous vegetation in the years 2016, 2018 and 2019

The comparison of the spontaneous basal area per plot showed that the total basal area of the plots 1 – 19, including the control plots C1 - C5, was highest in 2019 and lowest in 2016.

Table 11: Comparison of the spontaneous basal area [cm^2] per plot from the years 2016, 2018 and 2019

Plot	Basal area [cm^2]/ year		
	2016	**2018**	**2019**
1	13	503	684
2	1580	1867	1694
3	578	586	735
4	228	654	398
5	929	1332	1146
6	2925	3340	3372
7	574	472	617
8	368	1207	1175
9	1021	1295	1168
10	257	595	771
11	117	435	638
12	515	1044	1309
13	599	1230	1391
14	236	80	90
15	1189	3336	3959
16	774	1258	1636
17	1105	2908	3327
18	790	3278	3765
19	1126	1801	2035
C1	66	1119	3028
C2	1112	2012	1778
C3	173	2552	3188
C4	0	247	286
C5	3	35	114
Total	**16279**	**33186**	**38305**

In 17 out of 24 plots and control plots the highest spontaneous basal area could be found in 2019. Of the remaining 7 plots, the highest spontaneous basal area per plot was observed 6 times in 2018 and one time in 2016. (Table 11) One reason for the differences in basal area per plot between the years were the slightly different survey methods. In 2016 and 2018, individuals that most likely germinated on Finca Amable before the start of active reforestation were also recorded. Subsequently, particularly remarkable individuals (concerning the basal area) were removed from the data from previous years, but for minor variations, this was not always possible.

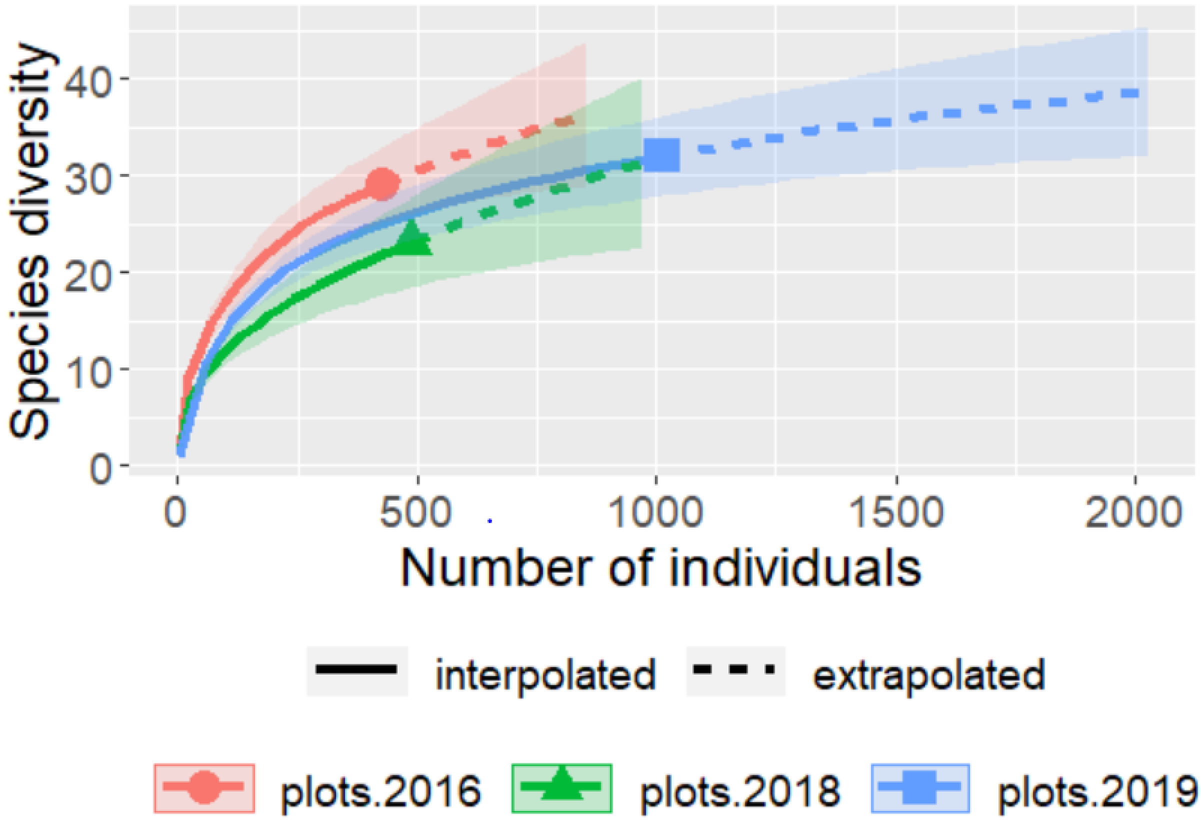


Figure 17: Species richness of sample-size-based rarefaction and extrapolation (dotted lines) sampling curves with 95% confidence intervals (shaded areas) of the plots 1-19 on Finca Amable in the years 2016, 2018 and 2019

The comparison of the species diversity between the three years in the planted plots (Fig. 17) showed that the observed number of species (species richness) was highest in 2019 (32), followed by 2016 (29) and 2018 (23). The species accumulation curves differed in their gradient on account of the higher number of spontaneous individuals in 2019 (1013) compared to 2018 (486) and 2016 (427). The species accumulation curve was steepest in 2016, followed by 2019 and 2018.

In the control plots the highest number of individuals and species was found in 2019 with 290 individuals belonging to 23 species. In 2018, 77 individuals of 18 species were observed and in 2016, 63 individuals out of 12 species. The steepest species accumulation curve could be observed in 2018, followed by 2019 and 2016. (Fig.18)

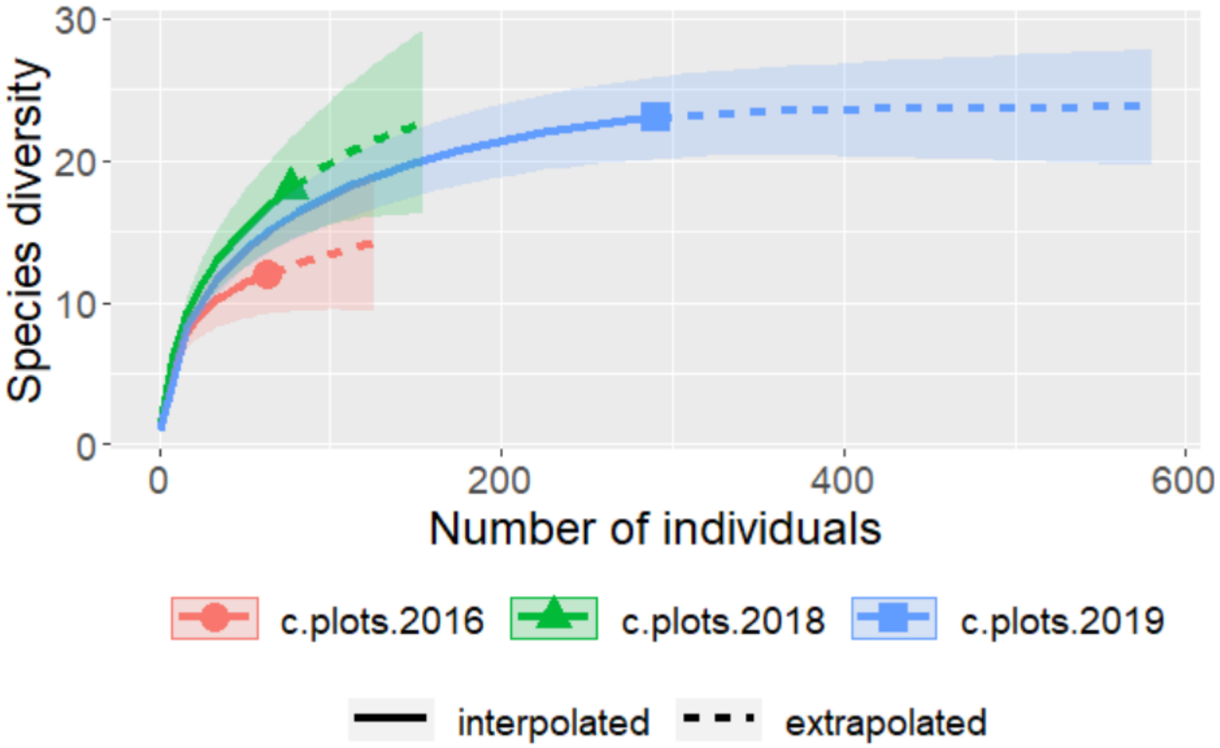


Figure 18: Species richness of sample-size-based rarefaction and extrapolation (dotted lines) sampling curves with 95% confidence intervals (shaded areas) of the control plots (C1-C5) on Finca Amable in the years 2016, 2018 and 2019

The observed Shannon and Simpson diversity indices of the plots 1 - 19 were both highest in 2016 (2.35/0.87), whereas of the control plots they were highest in 2018 (2.49/0.91). (Table 12)

Table 12: Comparison of the three diversity orders (Species richness, Shannon diversity and Simpson diversity) of the plots 1 - 19 and the control-plots C1 - C5 on Finca Amable in the years 2016, 2018 and 2019

	2016		2018		2019	
	plots	c-plots	plots	c-plots	plots	c-plots
Species richness	29	12	23	18	32	23
Shannon diversity	2.35	2.17	1.86	2.49	1.88	2.35
Simpson diversity	0.87	0.88	0.79	0.91	0.79	0.85

3.2 Finca La Bolsa

3.2.1 Spontaneous species, basal area and biomass

As already mentioned in the methods, data collection on Finca La Bolsa proved to be not as straightforward as on Finca Amable. It was not always clear, which species grew spontaneously and which species were planted or already existed in the area before planting. The results presented here should therefore be viewed more critically.

Table 13: Spontaneous species found in the 6 plots on Finca La Bolsa including the basal area, above ground biomass and the number of individuals (n). Species without BA had no individual > 2 cm DBH

Spontaneous species	Family	Basal area [cm²]	AGB [kg]	n
Unknown_B	-	521	-	4
Unknown_B1	-	474	-	1
Miconia sp.	*Melastomataceae*	278	157	8
Miconia schlimii	*Melastomataceae*	264	140	7
Cecropia obtusifolia	*Urticaceae*	146	47	2
Guatteria chiriquiensis	*Annonaceae*	140	46	30
Gliricidia sepium	*Fabaceae*	112	63	2
Unknown_B4	-	88	-	3
Conostegia subcrustulata	*Melastomataceae*	84	39	4
Carapa guianensis	*Meliaceae*	44	15	4
Terminalia sp.	*Combretaceae*	43	13	6
Apeiba sp.	*Malvaceae*	41	9	1
Qualea polychroma	*Vochysiaceae*	26	11	1
Acalypha sp.	*Euphorbiaceae*	17	3	3
Unknown_B6	-	11	-	1
Vochysia allenii	*Vochysiaceae*	10	2	4
Theobroma cacao	*Malvaceae*	9	2	4
Calophyllum sp.	*Calophyllaceae*	9	2	2
Simarouba amara	*Simaroubaceae*	9	2	1
Cedrela odorata	*Meliaceae*	8	2	1
Sapindaceae	*Sapindaceae*	8	-	1
Guatteria amplifolia	*Annonaceae*	7	2	2
Cupania sp.	*Sapindaceae*	6	2	10
Casearia sp.	*Salicaceae*	4	1	1
Inga sp.	*Fabaceae*	3	1	1
Castilla tunu	*Moraceae*	3	1	3
Guatteria sp.	*Annonaceae*	-	-	2
Ocotea insularis	*Lauraceae*	-	-	1
Piper hispidum	*Piperaceae*	-	-	6
Piper sp.	*Piperaceae*	-	-	1
Psychotria sp.	*Rubiaceae*	-	-	7
Qualea sp.	*Vochysiaceae*	-	-	1
Tetrathylacium macrophyllum	*Salicaceae*	-	-	2
Vochysia sp.	*Vochysiaceae*	-	-	2

A total of 173 individuals were recorded in the six 100 m^2 plots on Finca La Bolsa. Of these 173 individuals, 129 were assigned to spontaneous vegetation (70 individuals with a dbh > 2 cm) and 44 to planted vegetation or plantation remnants. The 129 individuals of spontaneous vegetation belong to 34 different species out of 17 plant families.

Guatteria chiriquiensis was the most abundant with 30 individuals, followed by *Cupania sp.* with ten individuals and *Miconia sp.* with eight. Two unidentified species accounted for 42% of the total spontaneous basal area (together 995 cm^2), followed by *Miconia sp.* (278 cm^2). 54% of all measured spontaneous individuals had a basal area < 10 cm^2 and only 4 individuals had a basal area > 100 cm^2. (Table 13)

The six plots on Finca La Bolsa were very heterogeneous. Plot 3 is situated between streams, two larger individuals of *Theobroma cacao* as plantation remnants are present and subplot 4 is bordered by an *Acacia* grove. Plot 4 lies above the steep bank of the stream, consisting of a flat part and a steeper area. Plot 5 is facing north-east, towards the south-east the plot borders a slope and in subplot 1 many trees were uprooted. Plot 6 is strongly fern dominated. Plot 7 is located at the base of a slope and parts of the plot reach into the slope area. Plot 10 is in flat terrain with a high abundance of ferns and larger individuals of *Cedrela odorata* and *Citrus sp.*.

The lowest number of spontaneous individuals and basal area of spontaneous species were found in plot 6, the highest number of spontaneous individuals in plot 7 and the largest spontaneous basal area in plot 10. (Table 14)

Table 14: Spontaneous vegetation data on Finca La Bolsa per plot

Plot	species	families	individuals > 2 cm	individuals < 2 cm	Total individuals	Spontaneous basal area [cm²]	AGB [kg]	Planted basal area [cm²]
3	11	9	11	7	18	336	128	1055
4	13	10	14	15	29	258	121	1209
5	11	7	15	2	17	390	153	521
6	4	4	3	6	9	38	14	1181
7	10	7	16	15	31	337	117	1596
10	7	5	11	14	25	1006	25	3224

3.2.2 Dispersal mode

Out of the 29 spontaneous species, identified on Finca La Bolsa, 20 are zoochorous, five species are wind-dispersed, two species adopt a combination of zoochory/anemochory and one species each use autochory or a combination of zoochory/autochory.

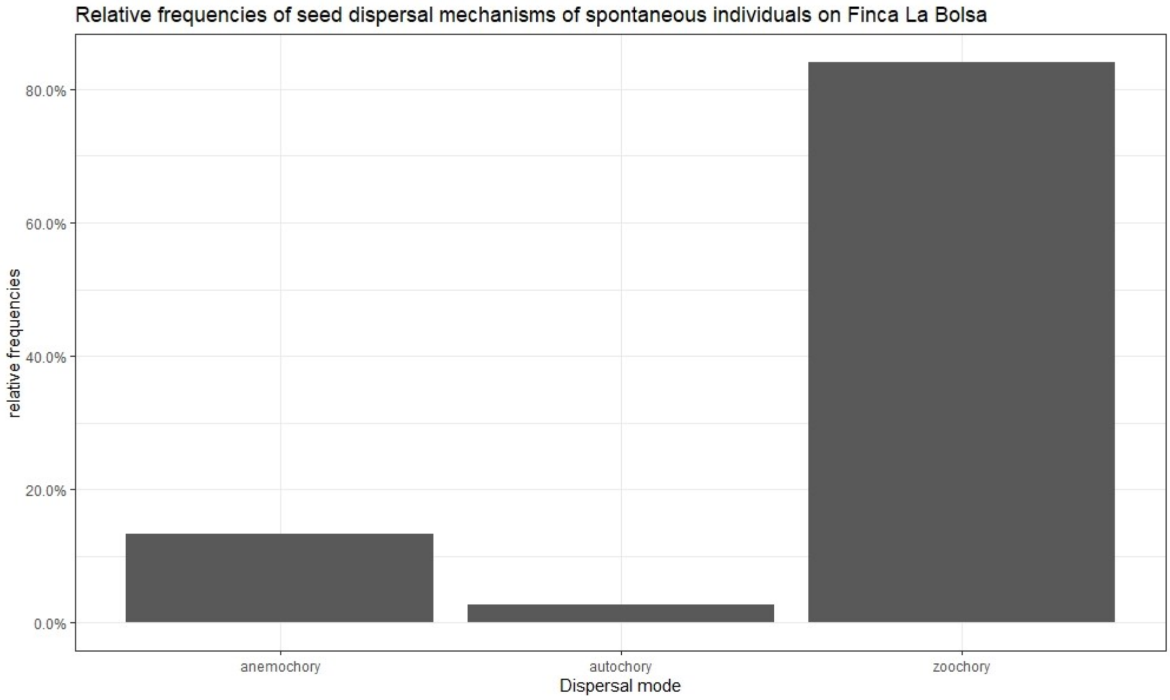


Figure 19: Relative frequencies of seed dispersal mechanisms of spontaneous individuals on Finca La Bolsa

At the individual level (119 individuals) 80 % are zoochorous, 13 % anemochorous and 2.5 % autochorous. (Fig. 19)

3.3 Comparison of Finca Amable and Finca La Bolsa

For the comparison, the 37 planted plots on Finca Amable with an area of 18648 m^2 (37 x 504 m^2) and the 6 plots on Finca La Bolsa with an area of 600 m^2 (6 x 100 m^2), were used. Keeping in mind the different plot size as well as the different number of plots on Finca Amable and Finca La Bolsa, the following approach was adopted to compare the spontaneous basal area and the number of spontaneous individuals:

The values of the basal area per plot and the number of individuals per plot on Finca Amable were divided by 5.04 to result in values per 100 m^2 in order to be comparable with the plot size of Finca La Bolsa. Both, the mean basal area as well as the number of spontaneous individuals were lower on Finca Amable than on Finca La Bolsa. The results of the Wilcoxon rank sum tests with continuity correction only showed a significant difference (p-value < 0.05) for the number of spontaneous individuals between the two different reforestation sites. (Table 15)

Table 15: Results of Wilcoxon rank sum tests with continuity correction comparing characteristics of the two reforestation sites Finca Amable and Finca La Bolsa

	Mean of Amable	Mean of La Bolsa	W-value	p-value
Spontaneous basal area [$cm^2/100m^2$]	203	394	170	0.058
Number of spontaneous individuals [$n/100m^2$]	7.48	21.5	209	0.0012

The spontaneous aboveground biomass of the sectors 1 - 8 on Finca Amable was 86.5 tonnes or 12.4 tonnes/hectare. The spontaneous AGB of the 37 planted plots was 18.3 tonnes, which resulted in 0.98 kg/m^2. In the five control plots the AGB amounted to 4.3 tonnes, which is 1.7 kg/m^2. On Finca La Bolsa the AGB of the six plots was 0.6 tonnes, leading to 0.93 kg/m^2.

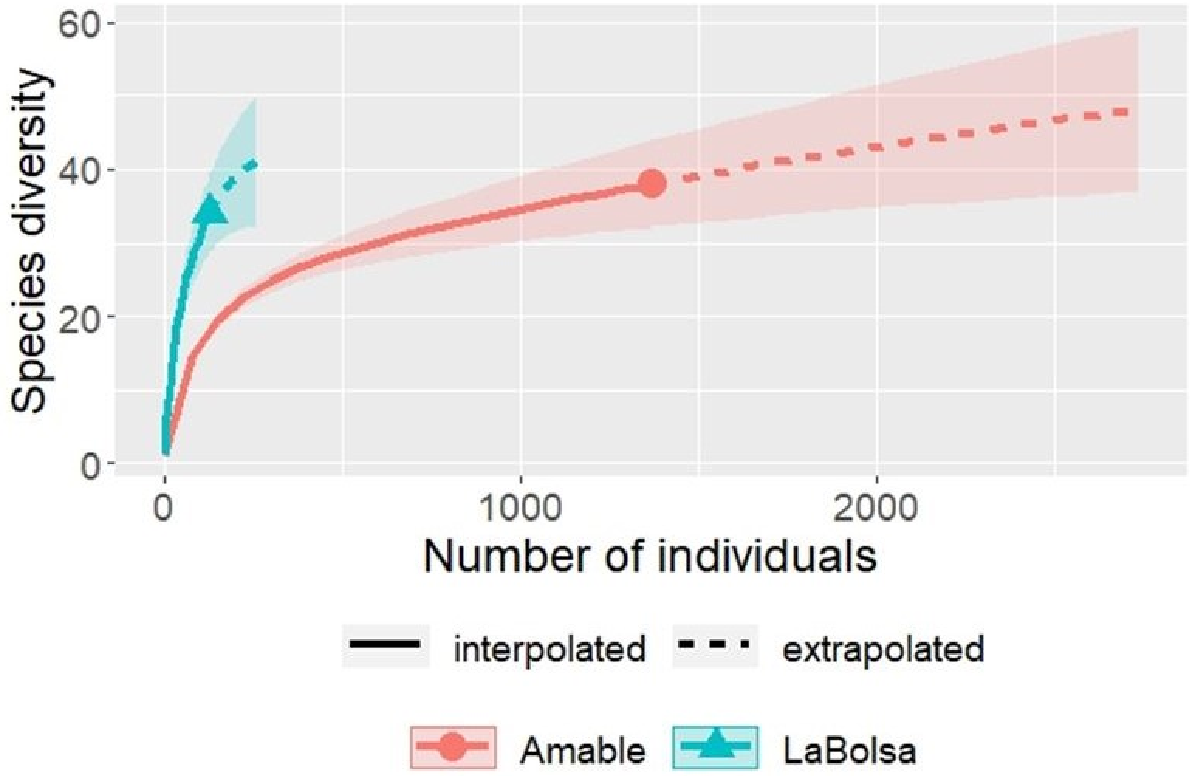


Figure 20: Species richness of sample-size-based rarefaction and extrapolation (dotted lines) sampling curves with 95% confidence intervals (shaded areas) for the 38 plots on Finca Amable and the 6 plots on Finca La Bolsa

While the total number of species was greater on Finca Amable than on Finca La Bolsa, there were fewer and smaller plots on Finca La Bolsa and thus fewer individuals and species. The species accumulation curve of Finca La Bolsa was much steeper than that of Finca Amable (Fig. 20) and also the Shannon and Simpson diversity indices were higher on Finca La Bolsa than on Finca Amable (Table 16).

Table 16: Results of the three diversity orders of the plots on Finca Amable and Finca La Bolsa - Species richness, Shannon diversity and Simpson diversity

	Finca Amable			Finca La Bolsa		
Species richness		38			34	
Shannon diversity (H; H_{max}; E_H)	2.11	3.64	0.58	3.02	3.53	0.86
Simpson diversity		0.79			0.92	

Species composition of both plot types on Finca Amable was different from the six plots on Finca La Bolsa (Fig. 21). In general, most species on Finca La Bolsa had very low abundances. The five most common species in the plots on Finca La Bolsa were *Guatteria chiriquiensis* (30), *Cupania sp.* (10), *Miconia sp.* (8), *Miconia schlimii* (7) and *Psychotria sp.* (7). In comparison, the five most common species of the planted plots on Finca Amable were *Piper hispidum* (521), *Urera baccifera* (268), *Cecropia obtusifolia* (184), *Miconia argentea* (94) and *Miconia schlimii* (50).

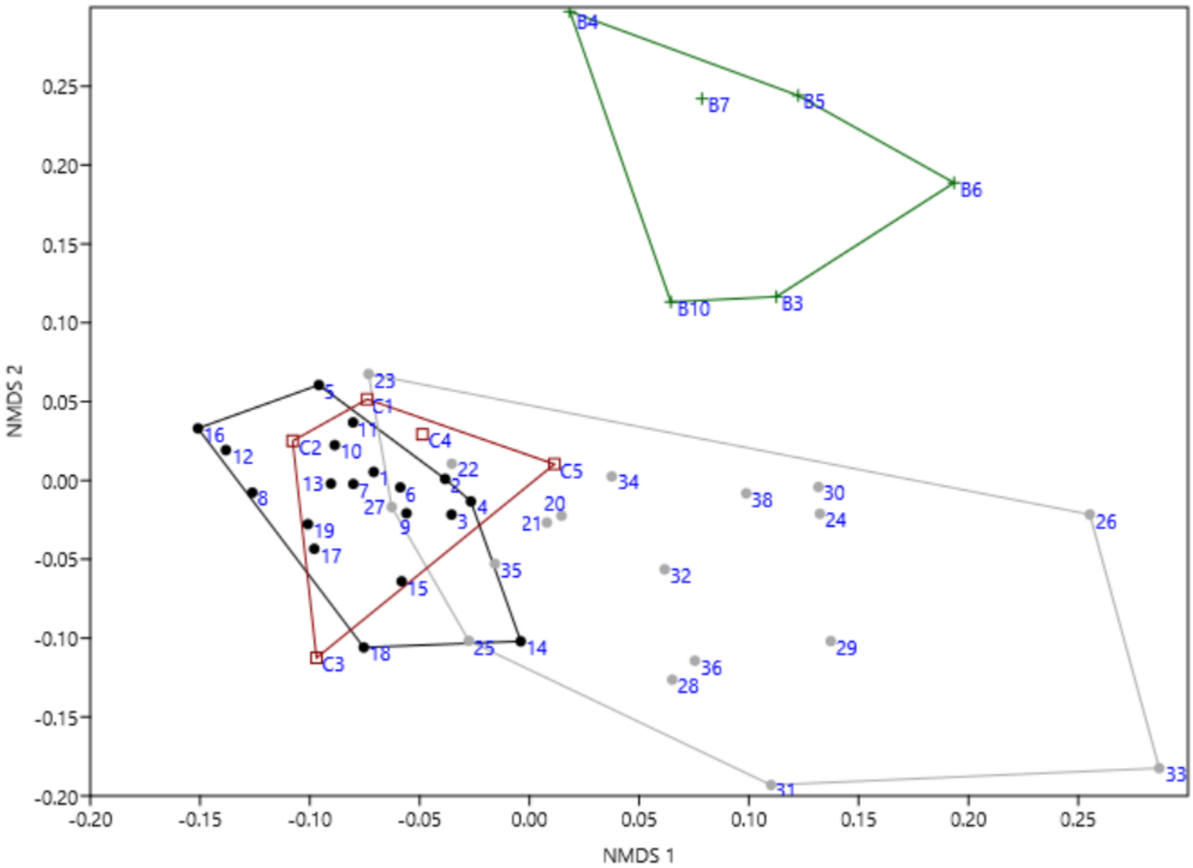


Figure 21: NMDS including the 38 plots (black dots: plot 1-19; grey dots: plot 20-38) and 5 control plots (C1-C5: red colour) of Finca Amable and the 6 plots (B1-B6: green colour) of Finca La Bolsa

IV. Discussion

4.1 Spontaneous species composition and growth

4.1.1 Finca Amable

Tree seed density of pasture seed banks is much lower compared to the seed banks of secondary forests. Forest regeneration on abandoned pastures is therefore often limited by a lack of tree seed availability (Wijdeven and Kuzee 2000). Most studies identified limited seed dispersal, herbaceous competition, seed predation, poor soil conditions and the extent and state of surrounding forests as the main constraints to the establishment of trees in former tropical pastures (Holl et al. 2000, Zimmerman et al. 2000, Martínez-Garza and Howe 2003, Hooper et al. 2005, Lamb et al. 2005, Günter et al. 2006, Muñiz-Castro et al. 2006, Letcher and Chazdon 2009, Caughlin et al. 2016). Due to many years of use as pastures, the seed banks on both Finca Amable and Finca La Bolsa must have been depleted, which was one of the main reasons for the active reforestation (Crouzeilles et al. 2017). Since the start of tree plantings in 2012, a lot has changed on Finca Amable and the former pasture area is increasingly looking more forest-like.

The spontaneous species composition on Finca Amable consisted mainly of pioneer species such as *Piper hispidum*, *Cecropia obtusifolia* or *Miconia argentea*. These species are fast growing and better adapted to sunlight exposure (Hilje et al. 2015). Pioneer species tend to be dominant during the first ten to twenty years of succession (Saldarriaga et al. 1988). In contrast, the proportion of pioneer tree species in old-growth tropical forests is generally only up to 15 % (Dalling and Brown 2009). Especially *Cecropia obtusifolia* attracts a number of different seed dispersing animals that may introduce forest seeds from later successional stages to the area (Wieland et al. 2011). In addition *Cecropia obtusifolia* is supposed to be beneficial for soil fertility (Diemont et al. 2011). Typical shade-tolerant climax species of secondary forests in Costa Rica, such as *Brosimum utile* or *Carapa guianensis* (Weber 2001), were generally rare, but could be found sporadically in the spontaneous vegetation of the planted area on Finca Amable.

Spontaneous woody vegetation growth on Finca Amable, measured as the spontaneous basal area, was noticeable worse in the rear sectors than in the front ones. This was the case in both, the planted plots and the control plots. Also, the growth of the planted trees was slower in the rear sectors compared to the sectors in the front. Since the control plots are the same age as the planted ones, this suggests that further back the tree growth is generally worse. This is therefore not (only) because trees were less tended to or planted at a later time. The very strong growth of herbaceous species in the rear sectors compared to the front sectors, especially of the grass *Brachiaria sp.,* might be one of the reasons for this. Wieland et al. (2011) state that forest succession in anthropogenically altered landscapes can be delayed, based on the dominance of competitive initial colonizers. Guariguata et al. (1995) also came to the conclusion that herbaceous competition has a major influence on the initial invasion of woody species and one study in a seasonal montane wet forest in southern Costa Rica showed that less than 1 % of all seedlings of early successional tree species survived in grass patches (Holl 2002). Grasses can impact tree seedling survival and growth in several ways, including shading, below-ground competition for water and nutrients, or through allelopathic chemicals (Holl 2002, Holz et al. 2009). In order to identify other possible causes for this observation, further studies of biotic and abiotic environmental factors - such as soil properties - should be carried out on Finca Amable.

The results of the aboveground biomass calculations on Finca Amable are in line with other studies. Lugo et al. (2004) state that the rate of aboveground biomass accumulation is lower in restored forests compared to natural succession, especially in the first decades of forest establishment. Letcher and Chazdon (2009) and Poorter et al. (2016) calculated an AGB around 69 tonnes/ha in secondary forests < 15 years of age. The calculated AGB of the spontaneous vegetation for the 37 planted plots at an age of c. 7 years on Finca Amable was only 9.8 tonnes/ha. After approximately five years the mean AGB of the planted trees on Finca Amable had reached 36.4 t/ha (Hietz et al. 2019) and thus the spontaneous individuals with a total AGB of 9.8 t/ha in the 37 plots do not represent such an irrelevant proportion.

The five control plots, especially C4 and C5, were strongly dominated by various grass species, like for example *Brachiaria sp.,* and the shrub *Mimosa pudica*, which may have affected the composition of the woody flora. Surprisingly, both, the mean spontaneous basal area and the average number of spontaneous woody species and individuals, were higher in the control plots than in the planted plots on Finca Amable. This result contrasts with other studies (Holl et al. 2000, Holl 2002, Hooper et al. 2005, Wieland et al. 2011, Jackman 2016). A similar study in the north-central part of Costa Rica showed that dense herbaceous vegetation inhibits woody growth and no woody seedlings could be observed after one year in the control plots (Guariguata et al. 1995).

However, seed predation was seen to be higher under shrubs and small trees because of the reduced grass cover which increases the likelihood of foraging animals to find seeds (Holl 2002). Reduced predation stress in the control plots could therefore be a reason for greater spontaneous vegetation growth, although this is likely not a main reason. The lack of competition from planted trees could be another reason. Further research is necessary to identify other possible causes.

4.1.2 Finca La Bolsa

Zimmerman et al. (2000) and Günter et al. (2006) mentioned that the distance to the nearest forest edge has a negative impact on the number of species and on the number of seeds in the seed bank. Since the Finca La Bolsa is surrounded, to a large extent, by secondary forest, it is not surprising that the development of the reforestation area to a closed forest went fast compared to Finca Amable. The sighting of various groups of monkeys and numerous birds at Finca La Bolsa can be an evidence for progressive structural diversity and of better connection to intact forests. More specialized dispersal animals such as primates, ground-living mammals and larger birds and bats, which inhabit mature forests, are rare visitors to early secondary vegetation and prefer to roam in more mature forests (Wieland et al. 2011, Hilje et al. 2015).

During data collection several fallen trees could be observed on Finca La Bolsa. These gaps create space for the establishment of woody species (Brokaw 1987), whereas fern dominance has been observed in many forest gaps (Butler et al. 2008). Overall the terrain on La Bolsa was very heterogeneous. Robinson et al. (2015) state that the topography can influence succession by changing the edaphic conditions and Chazdon and Guariguata (2016) point out that topographic variation results in spatial heterogeneity and creates diverse environmental conditions for species recruitment and survival. Therefore, it was not surprising that the species composition differed between the six investigation plots. A substantial proportion of the species recorded was only found in one or two of the six surveyed plots. The most frequent observed species was *Guatteria chiriquiensis*, a medium sized tree that is typically found in the understory of riverine forests in the Golfo Dulce region (Weber 2001). *Cupania sp.* and *Miconia sp.* were also quite common. Species of the genera *Miconia* are typical pioneer species of the region (Weber 2001).

The location of the plots was chosen to reflect the heterogeneity of the environmental conditions. However, the selection of the fern dominated plot number 6, for example, has a negative effect on the average values of woody spontaneous growth. As mentioned, the results of spontaneous vegetation growth at Finca La Bolsa should be viewed with caution, as it was not always clear if an individual had been planted or whether it had grown spontaneously since the beginning of reforestation in 2010.

4.2 Biodiversity

Shannon and Simpson indices, as well as species richness, were calculated for both plot types on Finca Amable and on Finca La Bolsa. This section focuses mainly on the results of the Shannon index. The Shannon index usually takes on values between 1.5 and 3.5 and rarely exceeds 4.5 (La Luz de Maza et al. 2002). Shannon indeces obtained for the understory vegetation in species-rich neotropical rain forests were H = 3.65 (Barro Colorado Island, Panama) and H = 5.59 (Yasuni National Park, Ecuador; LaFrankie et al. 2006), which is substantially higher than for Finca Amable (H = 2.11) and La Bolsa (H = 3.02).

Some studies showed, that the presence of surrounding forests increases seed availability and thus woody stem density and diversity in forest restoration sites (Mesquita et al. 2001, Günter et al. 2006, Robiglio and Sinclair 2011, Robinson et al. 2015, Caughlin et al. 2016). In fact, both the Shannon and the Simpson index of the spontaneous vegetation were higher on Finca La Bolsa than on Finca Amable. One case study in a secondary forest on an abandoned cattle pasture in the tropical mountain rain forest of southern Ecuador showed a comparable Shannon index with an average of H = 2.03. The average number of species per plot was higher in the secondary forest established by natural succession than on the two reforestation sites Finca Amable and Finca La Bolsa. (Günter et al. 2006)

While the recorded number of species was higher on Finca Amable than on Finca La Bolsa this is due to the much larger area surveyed on Finca Amable. This species accumulation curve (Fig. 19) suggests that the potential number of species is much higher in the older reforestation site surrounded by natural forests.

4.3 Effects of identity and size of planted trees on spontaneous growth

Shrubs may compete strongly with planted trees for resources (Guariguata et al. 1995), potentially inhibiting tree growth. Conversely, planted trees might also compete with and negatively affect spontaneous vegetation, preventing germination or generally slowing down their growth (Myster 2004).

Alternatively, planted trees might be beneficial for the growth of spontaneous vegetation. They may prevent the emergence of competing grasses by forming a closed canopy and thus create a cooler micro-climate (Haggar et al. 1997, Diemont et al. 2011, Caughlin et al. 2016). In addition, they can attract seed-dispersing birds to the area by providing fruits and perches (Medellin and Gaona 1999, Hooper et al. 2005, Heelemann et al. 2012). Some planted trees, especially legumes, can also improve the soil conditions by fixing nitrogen. In general, disproportionally high densities of spontaneous individuals were growing next to the three legumes species *Inga sp.*, *Lonchocarpus macrophyllus* and *Platymiscium curuense*. A correlation of the ten most frequently planted species with the ten most abundant spontaneous species also showed a preference for legumes. *Inga sp.* both increases the nitrogen content in the soil and attracts seed dispersing animals by producing large fruits (Myster 2004, Reid et al. 2015). This shows that the identity of the planted trees does indeed have an influence on the developing spontaneous vegetation.

In this study a very weak but significant positive correlation was detected between the size of planted trees and the spontaneous basal area. This suggests that spontaneous vegetation growth tends to be better underneath larger individuals. Since an inverse result was obtained by including larger neighbouring trees (section 4.4 below), I conclude, that shadier conditions are not the reason for this observation. Rather, I assume that the growth conditions in subplots, where larger planted trees could develop, were better overall, and therefore the spontaneous vegetation in these subplots also had a higher basal area. Another factor might be that more seeds and seed species are being dispersed under tall trees than underneath smaller trees (Duncan and Chapman 1999). Overall, the correlation between the basal area of the planted trees and the spontaneous basal area as well as between the shade index and the spontaneous basal area was very weak. Moreover, the two results were contradictory. It is therefore not clear how the size of the planted trees influences the spontaneous vegetation growth. Further research is needed to clarify the size effect.

4.4 Shade Index

In some species seed-germination is regulated by light. Seeds that require light for germination are called positive photoblastic. *Cecropia obtusifolia* for example needs hours of light for germination and is thus often found in forest gaps, where the sunlight occurs more predictably and lasts for longer time period (Bazzaz and Pickett 1980, Vazquez-Yanes and Orozco-Segovia 1993). It can therefore be assumed that the death of planted trees or clear areas in the control plots favour the germination of *Cecropia obtusifolia*. Since the last investigation of the spontaneous vegetation on the Finca Amable, an increase in the number of *Cecropia obtusifolia* has been observed, including the control plots. Species in the genus *Piper* grow in contrasting habitats in the forest and also require different light quality and quantity for germination. Some species are able to germinate in more shady areas with a low red-light/far-red-light ratio, whereas others need long periods of light with a high red-light/far-red-light ratio that can be found in forest gaps or outside the forest. (Vazquez-Yanes and Orozco-Segovia 1993) *Piper hispidum* prefers more shady conditions, whereas *Piper aduncum* and *Piper friedrichsthalii* were found in more open areas. In general, light availability is one of the most important environmental factors for the growth of tropical rainforest trees (Rüger et al. 2011). As climax species are already present through active reforestation, the germination of some common pioneer species might already be limited in subplots with a dense canopy. This would explain the significant, but weakly negative correlation between the shade index and the spontaneous basal area.

4.5 Fertility of planted trees

During field work, 184 individuals of 25 planted tree species were observed being fertile. Most of the fertile individuals were planted in 2012 and only a few trees, planted in 2014, already showed signs of being fertile. For 12 out of the 25 fertile planted tree species spontaneous individuals with a DBH > 1 cm could be detected. However, it is not clear whether the spontaneous individuals developed from seeds of the fertile tree species or were introduced otherwise to the area.

The fertility of planted trees is important for the development of the Finca Amable through reproduction within the site and by attracting seed-dispersing animals through food resources (Thomas et al. 1988, Hooper et al. 2005, Caughlin et al. 2016). Birds visiting fruiting trees might bring seeds of other species with them, in which case you would expect more seedlings close to fertile zoochorous trees. This aspect was not tested in the present study but would be interesting to verify in future studies concerning the spontaneous vegetation on Finca Amable.

Particularly remarkable was the rejuvenation of *Croton schiedeanus*, whereby no fertile planted individuals were recorded although this may have been missed during the field survey. Alternatively, seeds of *Croton* might have persisted in the soil during the use as a pasture. Dalling and Brown (2009) found that viable seeds of *Croton* had persistence in the soil seed bank of tropical forests for up to 38 years.

4.6 Seed dispersal:

Seeds of rainforest trees have the tendency to germinate quickly after dissemination without dormancy (Vazquez-Yanes and Orozco-Segovia 1993). Most of them become nonviable in the soil seed bank within a year after deforestation. By contrast, seeds of many pioneers including *Cecropia* and *Piper* have seeds that can be dormant for more than a year (Vazquez-Yanes and Orozco-Segovia 1993).

The seed rain in deforested areas relies on several landscape features, including the spatial layout of the remaining seed sources, the density and type of seed-distributing animals, and the strength and direction of the wind (Günter et al. 2006, Caughlin et al. 2016). A turning point in secondary succession is canopy closure because it implies that trees have successfully outperformed herbaceous species for light resources. The seed density in a reforestation site is likely to increase with increasing canopy cover, due to reproduction within the site and directed dispersal, as tree canopy attracts seed-dispersing animals. (Myster 2004, Hooper et al. 2005, Heelemann et al. 2012, Reid et al. 2015, Caughlin et al. 2016)

The majority of all identified spontaneous species in the sectors 1 - 8 on Finca Amable were dispersed by animals. The same goes for the spontaneous individuals, found in the five control plots and in the six sample plots on Finca La Bolsa. Frugivore-assisted dispersal is crucial for most tree species in tropical forests worldwide (Duncan and Chapman 1999). A study in the Australian wet tropics uplands showed that 83 % of the tree and shrub species are animal dispersed (Shoo et al. 2016). K. D. Holl also comes to this conclusion and states in her article “Restoration of tropical forests” that the primary dispersal mode in tropical rain forests is through animals (van Andel and Aronson 2012). During the two months of field work many different bird species could be observed on Finca Amable, which is showing that birds are present to act as seed dispersers. On Finca La Bolsa, in addition to birds, monkeys, wild peccary and jaguarundis were observed that also disperse seeds.

Wind dispersed species are often found in more open areas (Zimmerman et al. 2000) and thus it was expected to find a higher proportion of wind dispersed species in the control plots. As mentioned in the previous paragraph, the majority of tropical seeds are adapted to animal distribution, yet many tropical birds and mammals avoid open areas (Holl 1999) due to the lack of food resources or suitable perching sites and a higher risk of predation (Kelm et al. 2008). The proportion of wind dispersed species in the control plots was higher than in the planted plots, but not as pronounced as originally assumed. The denser vegetation in form of planted trees and spontaneous species, surrounding the control plots and the overall small size of the control plots, are probably the reason that anemochory does not play such an important role. The forest canopy has a high influence on wind speeds and most seeds just fall to the ground where air movement is hindered (Seidler and Plotkin 2006). This considerably reduces the dispersion radius of wind-dispersed species. As the Finca Amable is surrounded by anthropogenically changed landscapes and the nearest forest is at a distance of 400 meters, fewer wind-dispersed seeds will reach the site. On Finca La Bolsa the percentage of wind dispersed species was higher than in planted as well as control plots on Finca Amable. This could be due to the surrounding secondary forests that include wind-dispersed tree species whose seeds got blown on to the Finca La Bolsa. Individuals of *Terminalia sp*. and *Vochysia sp.* contributed to the comparatively higher proportion of wind-dispersed species on Finca La Bolsa.

Autochory was only found in three species on Finca Amable and Finca La Bolsa. Autochorous seeds generally drop close to the mother tree and it is difficult to see how these would arrive on Finca Amable. According to Estrada (1986), Sandor (2012) and TRY Plant trait database *Acalypha diversifolia*, *Brosimum utile* and *Croton schiedeanus* are autochorous, though at least the seeds of *Brosimum utile* have a fleshy coating and very likely are also zoochorous. It is therefore possible that some species use zoochory as a dispersal mechanism in addition to autochory, which would further increase the proportion of animal-dispersed seeds.

4.7 Functional traits

Tree species used in restoration plantings often do not represent the full range of functional traits found in natural regrowth forests (Crouzeilles et al. 2017). Nonetheless, a comparison of the following six functional traits between spontaneous vegetation and planted tree species was carried out: SLA, LDMC, leaf thickness, leaf toughness, chlorophyll content and branch wood density.

Specific leaf area (SLA) is calculated from the leaf area divided by the dry mass of the leaf and is linked to phenology and growth efficiency (Sakschewski et al. 2016). It can also be seen as a function of leaf dry-matter content (LDMC) and leaf thickness and both factors can contribute to the SLA to varying degrees (Pérez-Harguindeguy et al. 2013). The higher SLA of the spontaneous individuals compared to the planted trees suggests the production of cheaper leaves of the predominant pioneer tree species in the spontaneous vegetation (Bazzaz and Pickett 1980, Sakschewski et al. 2016).

Leaf dry-matter content (LDMC) is the leaf dry mass divided by the saturated fresh weight of the leaf. The LDMC is indirectly related to the leaf thickness (Pérez-Harguindeguy et al. 2013) and it is assumed that the LDMC and leaf thickness correlate negatively. This was also shown in this study by the comparatively higher LDMC in the planted trees and the simultaneously lower leaf thickness. In addition, leaves with a higher LDMC tend to be relatively tougher than leaves with a lower LDMC (Pérez-Harguindeguy et al. 2013).

Contrary to expectations, the individuals of the spontaneous vegetation had on average a significantly higher leaf thickness. However, the leaf toughness was on average higher in the planted trees despite the lower leaf thickness. This contrasts with results from other studies, where a positive correlation between leaf thickness and leaf toughness is mentioned (Hackl 2016). Physically stronger leaves are better protected against abiotic and biotic damages, contributing to longer leaf lifespans. This explains the higher leave toughness of the planted trees and means that the planted trees invest more carbon in structural protection of the photosynthetic tissue than pioneer species (Pérez-Harguindeguy et al. 2013).

The chlorophyll content represents the light capture efficiency per unit leaf area, which is relevant for individuals growing in the shade (Lohbeck 2014). It was therefore not surprising, that the spontaneous individuals had a higher chlorophyll content, as they grow in the undergrowth of the planted trees.

The mean wood density of spontaneous species was significantly lower than of planted species, which is consistent with other studies. In general, the wood density of pioneer species is lower compared to tree species of late successional stages because they tend to invest in light wood for faster growth, rather than mechanical strength or long-term defence (Bazzaz and Pickett 1980, Pérez-Harguindeguy et al. 2013, Hietz et al. 2017).

V. Conclusion

The woody vegetation regenerating spontaneously on Finca Amable and the Finca La Bolsa is typical for regenerating forests with gap or pioneer species dominating at both sites. The former cattle pasture Finca La Bolsa is already in an advanced stage of development and a closed forest with lianas and partly dense undergrowth had developed. The local conditions on Finca La Bolsa were very heterogeneous and the general occurrence of spontaneous species and frequency differed greatly throughout the area. Overall more shady conditions were encountered on Finca La Bolsa but there were also gaps in the forest, which were mostly dominated by ferns. The sighting of various groups of monkeys and numerous birds at Finca La Bolsa can be an evidence for progressive structural diversity. On Finca Amable the overall development of planted as well as spontaneous trees differed between the front sectors and the rear sectors. In the front sectors a forest with a mixture of very light undergrowth and denser areas is developing. In the rear sectors, especially in parts of the sectors 6 - 8, there were some areas with closed canopy, but most of the area was characterized by high and dense grass cover with planted trees in between and sporadic spontaneous vegetation. Since the Finca La Bolsa is surrounded to a large extent by secondary forest and reforestation planting was in 2010, it was not surprising that a higher biodiversity and evenness could be detected on Finca La Bolsa. Apart from different ages, the difference in species composition of the spontaneous vegetation on the two Fincas likely results from different surroundings, different seed banks and different site characteristics in general. Contrary to original assumptions, average spontaneous vegetation growth was greater in the control plots than in the planted plots on Finca Amable. For future studies concerning spontaneous vegetation on reforestation sites it would be interesting, to have a more equal number of planted plots and control plots, in order to be able to draw more precise conclusions from the effect of planted trees on spontaneous vegetation in comparison to natural succession on degraded pasture land. An equal number of plots and control plots would also improve statistical analyses. Overall, both reforestation sites are developing well and are thus not only contributing to landscape connectivity and to the preservation of biodiversity but also functioning as carbon sinks.

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Appendix

Appendix 1: Dispersal mode of the spontaneous species found on Finca Amable and on Finca La Bolsa

Spontaneous species	Dispersal mode	Source
Acalypha diversifolia	autochory	(Estrada 1986)
Acalypha sp.	autochory	(Hecht et al. 2013)
Albizia saman	zoochory, autochory	(Lagarrigue and Lagarrigue)
Amphitecna isthmica	zoochory, hydrochory	(Weber 2001)
Anacardium excelsum	zoochory	TRY (Future Earth, Max Planck Institute for Biogeochemistry, iDiv 2019)
Andira inermis	zoochory	TRY
Annona sp.	zoochory	(Weber 2001)
Apeiba sp.	zoochory	TRY
Apeiba tibourbou	zoochory	(Jackman 2016)
Brosimum utile	autochory	TRY
Bunchosia nitida	zoochory	(Weber 2001)
Bursera simaruba	zoochory	TRY
Calophyllum sp.	zoochory	TRY
Carapa guianensis	zoochory, autochory	TRY
Carica sp.	zoochory	(Weber 2001), (Hecht et al. 2013)
Caryocar costaricense	zoochory	(Sandor 2012)
Casearia sp.	zoochory	TRY
Castilla tunu	zoochory	(Sandor 2012)
Cecropia obtusifolia	zoochory	TRY
Cedrela odorata	anemochory	TRY
Cestrum sp.	zoochory	seed observation
Conostegia subcrustulata	zoochory	(Jackman 2016)
Cornutia pyramidata	zoochory	fruit observation
Croton schiedeanus	autochory	(Sandor 2012)
Cupania sp.	zoochory	(Kimmel et al. 2010)
Erythrina fusca	zoochory	(Hecht et al. 2013)
Eugenia sp.	zoochory	(Weber 2001), (Kimmel et al. 2010)
Ficus insipida	zoochory	TRY
Ficus maxima	zoochory	(Jackman 2016)
Ficus sp.	zoochory	(Jackman 2016)
Gliricidia sepium	anemochory	(Jackman 2016)
Guatteria amplifolia	zoochory	(Weber 2001)
Guatteria chiriquiensis	zoochory	(Weber 2001)
Guatteria sp.	zoochory	(Weber 2001)
Hieronyma alchorneoides	zoochory	(Sandor 2012)
Inga sp.	zoochory	TRY
Lonchocarpus macrophyllus	anemochory	(Schembera 2004), (Sandor 2012)
Luehea seemannii	anemochory	TRY
Macrolobium hartshornii	anemochory	(Schembera 2004)
Miconia argentea	zoochory	TRY
Miconia schlimii	zoochory	(Jackman 2016)
Miconia sp.	zoochory	TRY
Nectandra sp.	zoochory	(Weber 2001), (Hecht et al. 2013)
Ochroma pyramidale	anemochory	TRY

Spontaneous species	**Dispersal mode**	**Source**
Ocotea insularis	zoochory	(Hecht et al. 2013)
Ocotea sp.	zoochory	(Hecht et al. 2013)
Palicourea sp.	zoochory	(Weber 2001), (Hecht et al. 2013)
Pentagonia sp.	zoochory	(Weber 2001), (Hecht et al. 2013)
Perebea sp.	zoochory	(Weber 2001), (Hecht et al. 2013)
Piper aduncum	zoochory	(Jackman 2016), (Weber 2001)
Piper auritum	zoochory	(Jackman 2016), (Weber 2001)
Piper friedrichsthalii	zoochory	(Jackman 2016), (Weber 2001)
Piper hispidum	zoochory	(Jackman 2016), (Weber 2001)
Piper sp.	zoochory	(Jackman 2016), (Weber 2001)
Platymiscium curuense	anemochory	(Schembera 2004)
Posoqueria sp.	zoochory	TRY
Psidium guajava	zoochory	(Jackman 2016)
Psychotria sp.	zoochory	TRY
Qualea polychroma	semachory	(Weber 2001)
Qualea sp.	semachory	(Weber 2001)
Sapium laurifolium	zoochory	(Sandor 2012)
Sapium sp.	zoochory	(Sandor 2012)
Schizolobium parahyba	anemochory	(Jackman 2016), (Schembera 2004)
Senna reticulata	anemochory	(Jackman 2016)
Simarouba amara	zoochory	TRY
Solanum cf.	zoochory	(Hecht et al. 2013)
Sorocea sp.	zoochory	(Hecht et al. 2013)
Spondias mombin	zoochory	TRY
Tachigali versicolor	anemochory	TRY
Tectona grandis	anemochory, hydrochory	(Orwa et al. 2009)
Terminalia sp.	anemochory	TRY, (Hecht et al. 2013)
Tetragastris panamensis	zoochory	TRY
Tetrathylacium macrophyllum	zoochory	(Weber 2001), (Sandor 2012)
Theobroma cacao	zoochory	TRY
Urera baccifera	zoochory	(Jackman 2016)
Vernonia patens	anemochory	(Jackman 2016)
Vismia baccifera	zoochory	(Jackman 2016)
Vitex cooperi	zoochory	(Sandor 2012), fruit observation
Vochysia allenii	anemochory	TRY, (Weber 2001)
Vochysia sp.	anemochory	TRY, (Weber 2001)
Xylopia sp.	zoochory	(Weber 2001), (Hecht et al. 2013)

STATUTORY DECLARATION

I declare that I have authored the master thesis “Development of spontaneous vegetation in reforested areas in La Gamba, Costa Rica” independently and that I have not used other than the declared sources. I have explicitly marked all material which has been quoted either literally or by content from the used sources.

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date	signature