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„Succession stages of the herbaceous layer in reforestation areas in southwestern Costa Rica“

Verfasst von / submitted by

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Summary (English)

The decline of forest cover today is mainly due to land use and the conversion of natural habitats into agriculturally used fields. Tropical forests are especially affected by this. In Neotropical countries such as Costa Rica and Puerto Rico, the forest cover was drastically reduced between the 70’s and 90’s of the last century for the conversion of the land into mainly pastures for cattle and, ultimately, meat production. Many of these pastures today are abandoned, which led to the regeneration of forests on these sites, either through natural processes or through active reforestation efforts. There are a multitude of studies about the succession of the vegetation on these types of areas. However, they mostly focus on trees and very little is known about herbaceous species and their development. In order to gain further insight into the herbaceous layer in tropical regions, five sectors of three reforestation areas of different ages within the COBIGA (Corredor Biológico La Gamba) project in the Golfo Dulce Region in Costa Rica where chosen to construct a chrono sequence of succession stages. The herbaceous layers inside these sectors were evaluated using the methods for vegetational assessments after Braun-Blanquet (1932, 1964) using 10 x 10 m plots. The data set was then analysed under various aspects such as the alpha and beta diversities as well as family composition inside the plots. The results showed that the herbaceous layers in the three reforestation areas were highly distinct in multiple aspects. First, the species and family compositions differed considerably from area to area. The family composition changed with age of the reforestation areas with noticeable trends for Poaceae, Cyperaceae, Araceae and Marantaceae to name examples. Floristically, all sampled plots were heterogenous and the majority of individual species covered only up to 1% of a given plot area. The alpha diversities of the plots were on average rather low throughout, meaning that the layers were not diverse in a general context. Beta diversity showed high species turnover rates when transitioning from one reforestation area to another. NMDS analyses showed that in terms of species composition and coverage, plots within the same reforestation area were more similar to each other than to plots in other areas. The results suggest that the herbaceous layer in the tropics shows similar developmental patterns as they are known from temperate regions with respect to plant diversity and overall distinctiveness of different forest succession stages. However, it is not clear if solely time or environmental conditions at the time when reforestation started were the main drivers of the development

of the herbaceous layer. Further investigations and observations are needed to clearly disentangle these potential driving forces.

1. Introduction

Tropical forests are one of the most biodiverse habitats in the world. They contribute 45% of the worlds forest cover and host about 60% of the world's vascular plant species (FAO, 2020b). Human wellbeing is closely related to tropical forests. Their diversity maintains gene pools for food and medicinal crops along with providing other resources such as timber, fuel, employment, and recreation (FAO, 2020b). However, with the downwards trend in global tree cover it cannot be excluded that the tropical forests and their diversity is endangered as well. The main reason for the loss in tropical forest cover is land use in form of deforestation for agricultural expansion (FAO, 2020b). Even if the overall loss in forest cover has been becoming less over the past three decades, the amount of forest recovered for the time span is still lower than the area that has been deforested overall (FAO, 2020b). An effective approach to reduce human effects on tropical forests would be to protect still existing primary forests, which harbour particularly high species diversities (Zimmerman *et al.*, 1995). A potential equally effective approach would be to forward the development of secondary forests (Wadsworth, 1987; Chazdon *et al.*, 2009). They harbour a huge potential when it comes to re-establishing tropical forests. Secondary forests have been shown to have the capability to regenerate to a state similar in structure and tree biomass to primary forests in only 40 to 85 years (Aide *et al.*, 2000; Oberleitner *et al.*, 2021). In contrast to this, it is known for forests in temperate regions that they reach a primary forest state usually only after centuries (Hilmers *et al.*, 2018).

According to the FAO (2020b), the main ways forests expand are natural expansion through e.g. abandoned farm land, reforestation (including assisted reforestation) and afforestation. Big potential contributors to natural regeneration in South America are abandoned pastures. The conversion of forests into pastures for cattle grazing and beef production has been the most abundant type of land use that has affected the ecosystem especially in the 70's and 90's of the last century (Aide *et al.*, 2000). Many of these areas eventually got abandoned due to their reduced productivity as well as socio-political and/ or economic changes (Thomlinson *et al.*, 1996). An example for natural forest regeneration through abandoned land being linked to economic changes would be Puerto Rico. When agricultural activity was at its peak in the 1940's, the forest cover for the country was at its lowest with 3%. As agriculture declined due to the shift of economic interest towards manufacturing, an increase in forest cover was observed with it reaching 34% in 1985 (Thomlinson *et al.*, 1996). In 2020 the forest cover for the country sat at around 56% (FAO, 2020a). Similarly, also Costa Rica's landscape has been historically affected by agriculture. An agricultural boom started in the eighteen hundredths with the production of mainly coffee (*Coffea arabica*) and banana (*Musa x paradisiaca*) (Janzen, 1983). Later, the cultivation of cacao (*Theobroma cacao*) became common as well. This boom also marks the beginnings of the United Fruit Company (an impactful agricultural company until the late 80's) in the country. After World War II agricultural production was still strong and dominated by the cultivation of sugar cane (*Saccharum officinale*). An extreme rise in beef production was noted in parallel (Janzen, 1983). The expansion and creation of pastureland led to a major rise in deforestation. The loss in forests was so severe that in 1976 it was said that if the deforestation would continue at the current rate, all of the remaining forest at the time would have been vanished until 1990 (Janzen, 1983). However, this did not happen due to multiple reasons. Like in Puerto Rico, the fluctuating beef prices during the 80's and 90's were one of the main reasons for pastures being abandoned along with efforts to industrialize the country and the widespread degradation of the soil on already established pastures (Healey, 2001). Further deforestation was also severely slowed down starting in 1996 due to a highly restricting forest law that got implemented in that year (Weber and Baumgartner, 2001). Over 400'000 hectares of pastures have been abandoned in the late 90's due to these events and most of these areas are now covered with secondary forest vegetation (Healey, 2001). Forest cover for the country has increased drastically in the past years which made Costa Rica a prime example of successful forest recovery as a result of government-led forest policies or initiatives (FAO, 2020b).

Because of the high number of abandoned pastures in Costa Rica, it would be beneficial to know how forests develop on such areas to facilitate and foster the re-expansion of tropical forests. There is a multitude of studies on this topic (e.g. Aide et al., 1995, 2000; Zimmerman et al., 1995; Healey, 2001; Sandor and Chazdon, 2014). However, most of these studies mainly focus on tree species with a DBH (Diameter at

Breast Height) bigger than 10 or 5 cm. Herbaceous species and treelets are notoriously neglected, especially in already established forests. This is understandable since herbaceous specious are most abundant and diverse in the early stages of succession, which is a typically rather short phase in a forest's lifespan (Finegan, 1992; Hilmers *et al.*, 2018). Forest succession is a continues and cyclic process that starts soon after an area becomes abandoned. After Egler (1954), at first, species with the fastest initial growth will dominate a newly opened area. These species typically tolerate only a small amount of shade and cannot regenerate beneath themselves, which is why their senescence quickly allows other species to dominate. Once these die out due to their own senescence or low-intensity disturbances (e.g. diseases, removal etc.) more long-lived species will dominate and persist for the longest time. For this idea Egler (1954) proposed the concept of "Initial floristics" in which most species, even the ones of later successional stages, invade a field soon after abandonment, for which there is evidence in other studies as well (Finegan, 1992). Finegan (1992) expands on Egler's contributions by defining three distinct phases of "ecology groups" (plants with different growth patterns) for forest succession in tropical regions (Fig 1.). The first phase consists of fast-growing herbaceous species that are dominant in their percentual biomass for the shortest time. This phase would partially overlap with the second phase of short-lived pioneers that are mostly shrubs and short-lived trees. Phase 3 species, which consist of long-lived pioneers such as tress, would then more slowly take over the phase 2 plants due to their growth pattern. Phase 1 and 2 species would only have a significant contribution to the plant biomass for roughly 10 to 20 years according to the model, while phase 3 species could be dominant for up to a century or more (Fig 1.). After phase 3, there could also be a potential phase 4, which would consist of shade tolerant tree species that would slowly grow in the understory during phase 3 and only become dominant with the eventual senescence of the phase 3 plants or by other means of their removal through e.g. disturbances, forestry, disease etc. (Finegan, 1992; Corlett, 1995; Healey, 2001). "Initial floristics" is also integrated in this model with representatives of each phase said to be present since the early or late stages of phase 1 (Fig. 1). Even if the contribution to the overall biomass of the herbaceous phase 1 plants during later stages is miniscule, their influence on the development of phase 3 and phase 2 vegetation should not be understated. It is possible that large-leafed members of the herbaceous families Cyclanthaceae, Araceae, Marantaceae and Heliconiaceae are important components of forest understories since the dense shade cast by large leaved representatives of these families may affect the abundance and distribution of tree seedlings (Denslow, 1987). It is also known from common, woody phase 3 species such as *Vochysia ferruginea* and *Brosimum utile* that they only start gaining dominance over a clearing when it has been first dominated by herbaceous species followed by short lived trees (Healey, 2001). The initial microclimate of an open area is also heavily influenced by herbaceous species, potentially facilitating, or inhibiting the establishment of other species in the first place (Uhl *et al.*, 1981; Posada, Aide and Cavelier, 2000). The density and persistence of the herbaceous cover can also delay the development of forests by several years acting as a filter towards woody species by shading of seeds or those not reaching the ground (Aide *et al.*, 1995, 2000). Correctly executed weeding is usually enough to solve the issue (Finegan, 1992).

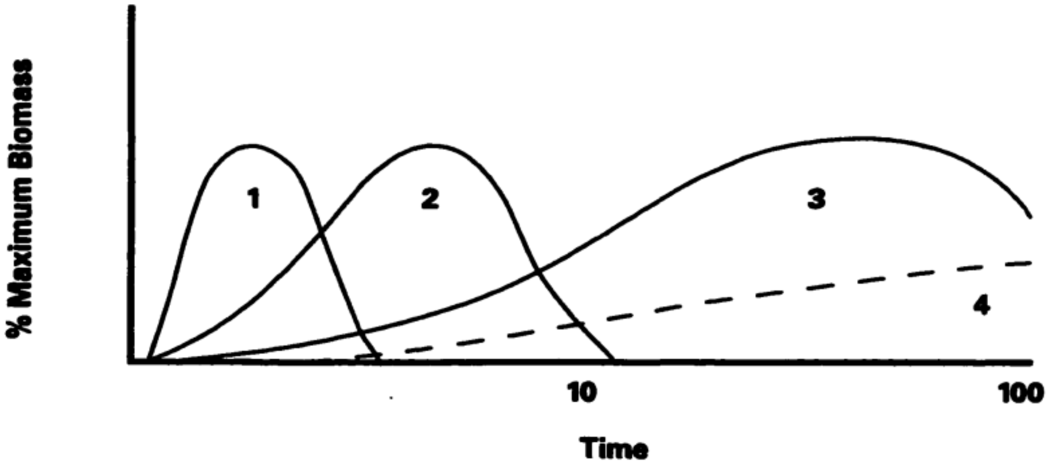

Figure 1: Schematic Model of forest development after Finegan (1992). The numbered graphs represent 3 phases of ecological plant groups with a theoretical fourth phase, which are defined by the growth patterns of plant species. Phase 4 is dotted due to it not being well-studied. Image taken from Healey (2001).

There are projects that try to counteract the past events of deforestation by afforestation and protection of secondary forests on pastures and other agricultural fields such as the COBIGA (Corredor Biólogico la Gamba) project in the Golfo Dulce region in Costa Rica (lagamba.at, 27.01.2023). The Golfo Dulce region is situated in the southwest of the province Puntarenas adjacent to the Panama border. Due to the geographical position of the region in Central America, as a bridge for flora and fauna between South and North America, a high diversity for both plants and animals can be found despite its relatively small range (Weber and Baumgartner, 2001). An estimated 3000 plant species including 700 tree species have been identified with a noticeable amount of endemism for the Golfo Dulce region (Weber and Baumgartner, 2001). The local flora also shows strong affinities to the Chocó region in north-western Columbia (Weber and Baumgartner, 2001). Thirteen types of ecosystems have been distinguished for the Golfo Dulce area with tropical wet forests being the most abundant especially in the lowlands (Weissenhofer *et al.*, 2008). These forests in the Golfo Dulce region represent one of the most least studied, species-rich ecosystems in Costa Rica and are the last remains of this type of forest on the pacific coast in the country (Weber and Baumgartner, 2001; Weissenhofer *et al.*, 2008). Two national parks can be found in the region: The Corcovado National Park, situated on the Osa Peninsula, and the Piedras Blancas National Park, which is also known as the Esquinas Forest. The latter park has been heavily influenced by past agricultural activities. In it, primary forest is still present mainly in hilly areas. However, almost the entirety of the flat areas was deforested in the past. Today only pastures and secondary forests are left in these spaces (Weber and Baumgartner, 2001). Generally, pastures are still very abundant in the entire region. Among other activities, the COBIGA project aims to buy these with the help of collaborators and donations for reforestation. The goal is to create a biological corridor that connects the forests of the Golfo Dulce region with forests of the nearby mountain range Fila Cal (lagamba.at, 27.01.2023; Weissenhofer *et al.*, 2019). The project started in 2007 and is ongoing with efforts to also combine COBIGA with the biological corridor AMISTOSA (Corredor biológico Amistosa). This will ensure the preservation of the local diversity by connecting the patchy forest areas (Weissenhofer *et al.*, 2019). The reforestation of different areas has been ongoing for several years allowing for the investigation of different forest succession stages.

The goal of this study is to gain knowledge on the development of the often-neglected herbaceous species of different successional stages of tropical secondary forest understories by utilizing the reforested areas of the COBIGA project. To gain insights into the species composition, vegetational assessments using the methods by Braun-Blanquet (1932, 1964) were performed. Using these assessments, both a floristic and a physiognomic reconstruction of the local herbaceous layers was carried out and in addition the alpha and beta diversity of the studied sectors was estimated.

2. Methods

2.1. Study areas

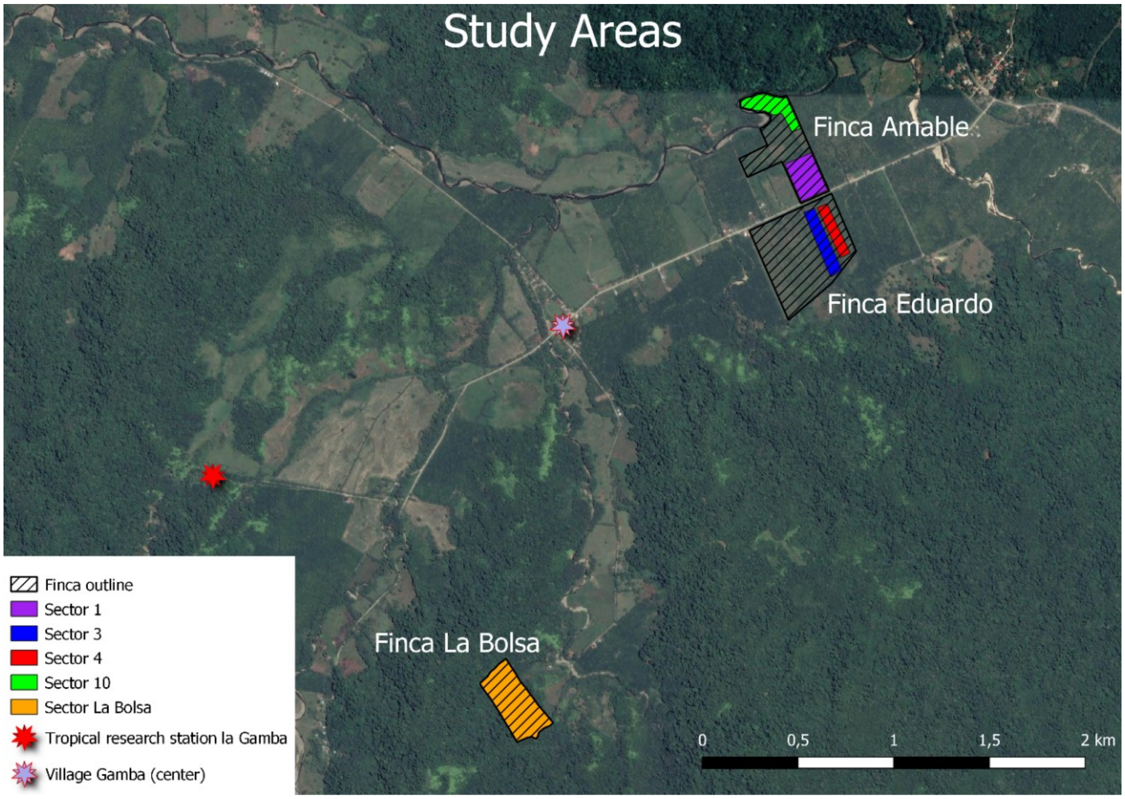

Figure 2: Location of the study areas of this project in Puntarenas, Costa Rica.

The study areas are situated in the lowland of the Golfo Dulce region in southwestern Costa Rica in close vicinity to the village Gamba (8.704334, -83.187588) which is located near the cities Río Claro and Golfito. A tropical day time climate is present with high amounts of precipitation and high monthly temperatures with little fluctuation throughout the year (Fig. 3). Mean annual precipitation can reach values of around 5938 mm to up to 6241 mm with no dry months (Fig. 3; Weber and Baumgartner, 2001; Weissenhofer and Huber, 2008). There are wet and dry seasons. However, the dry season is rather a time with less rain, since there is still up to 200 mm of precipitation in the driest months and 286 days of the year are generally classified as days with rain (Weber and Baumgartner, 2001; Weissenhofer and Huber, 2008). The dry season lasts from December to April and the wet season from May to November with the highest precipitation between September and October (Fig. 3). The daily sunshine average also depends on the season with three to four hours in the rainy season and up to eight hours in the dry season (Weber and Baumgartner, 2001). The average annual temperature is between 25 °C in forests and 27 °C on fields with months in the dry season tending to be hotter. Humidity is high with 88.3% on fields and 97.7% in forests (Weber and Baumgartner, 2001). The high humidity also leads to the formation of high amounts of mist usually in morning hours. These climatic and geographical conditions suggest that the main vegetation found in these lowland areas would be tropical wet forests (Janzen 1983). The estates used for this study were all part of the COBIGA project and are undergoing monitored reforestation. The three estates in question are the Finca Eduardo, Finca Amable, and Finca La Bolsa (Fig. 2). Each finca is divided into sectors by COBIGA to better manage and plan reforestation efforts (Fig. 2). The sectors that were investigated in this study had different reforestation ages when counting from the year where reforestation began (ages are given in 2.2.). Finca Eduardo holds the youngest sectors and Finca Amable sectors are of intermediate ages. La Bolsa is not divided into sectors as reforestation started in the same year for all areas on the estate (lagamba.at, 27.01.2023). As such, the whole Finca will be treated as one sector throughout this study (Fig. 2). It is also the oldest one out of all study areas. The fincas are flat, with the exception of La Bolsa, and are between 70 and 170 m in elevation. Based on previous assessments in the region, it is assumed that the soils of the fincas are most likely a form of inceptisol, which are moderately weathered soils that are characterized by moderate too high levels of nutrients and have a noticeable amount of secondary iron oxides (Weber and Baumgartner, 2001). In spite of these general similarities, the fincas differ in various aspects including e.g., previous agricultural use, local soil conditions, and surrounding vegetation and land.

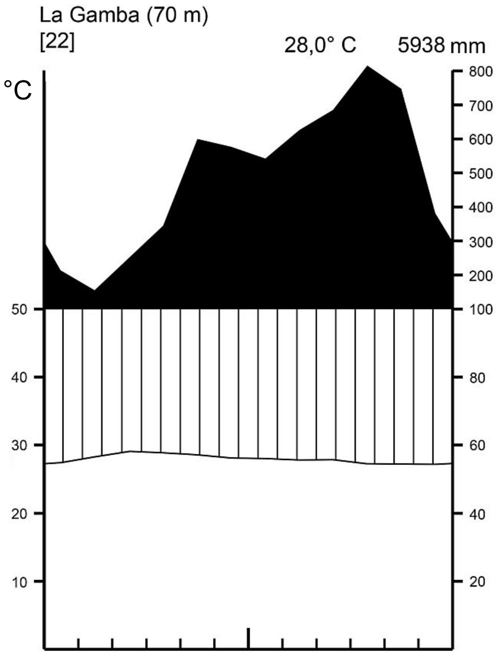

Figure 3: Climate chart (1998-2020) of the village Gamba, which is in close vicinity to the study areas. The graph in the centre of the graphic represents the course of the temperature (left scale, black line at the base of the white bars) throughout a year while the bars represent the precipitation (right scale). Up until 100 mm, the precipitation is represented as white bars. Everything above 100 mm is filled out in black. The mean annual temperature as well as the mean annual precipitation for the data collection period are given at the top of the Chart. Graphic created by Susanne Pamperl. Image taken from https://www.lagamba.at/forschung/wissenschaftliche-informationen/ (27.01.23)

Before reforestation, the Finca Eduardo was mainly used for agricultural purposes. At first, various crops were cultivated (*Musa sp., Manihot esculenta, Dioscorea trifida)* by the United Food Company and the Agro Arenal SA company starting in 1940 and lasting until 2015 (lagamba.at, 27.01.2023). The field lay fallow during the transition of ownership between the two companies in 1986 to 2000. From 2015 to 2020 most of the finca, including the areas that fall into today's sectors 3 and 4, was used as pasture for cattle. Other smaller parts were used for oil palm plantations (*Elaeis guineensis*). In 2020, COBIGA bought the finca for their projects and started with reforestation in the same year. Due to the recent acquirement, the vegetation of the finca is still open and meadows can still be found on most of the area (Fig. 4). In some parts, mainly the south-eastern area of sector 3, and along ditches, a dense shrub vegetation can be found consisting of e.g., *Piper aduncum*, *Mimosa pigra* and *Clidemia capitellata*. Trees such as *Senna reticulata*, *Miconia argentea,* and *Cecropia sp*. can be found in between as well. Sectors 3 and 4 are partially flooded especially during the rainy season. Ponds, puddles and naturally forming rivulets that can all persist for a couple of days can be encountered frequently after high amounts of precipitation. For this reason, the ground is wet or at least very moist for most of the time. The upper soil layers are very dense and clay-like because of the past use as pasture. This is also the reason why the water does not drain efficiently. Sunlight hits the ground with high intensity during the day, except in the overgrown areas. Palm plantations are bordering the finca in the northeast and southwest ends. In the southeast, it borders the forests of the Fila Gamba and on the northwest side, across a dirt road, the Finca Amable is located.

Figure 4: Exemplary study site on the Finca Eduardo (Sector 3, 2 years of age counting from when reforestation had started).

The Finca Amable differs considerably from the Finca Eduardo. There is already an established secondary forest with most trees (the majority planted) reaching an estimated 6 to 10 or more meters in height (Fig. 5). While the canopy is still patchy, the forest floor is being heavily shaded during the day, which leads to a noticeable cooler microclimate when compared to the Finca Eduardo. Forest gaps occur frequently, especially in the younger reforested areas. Similarly to the Finca Eduardo, the Finca Amable was an intensely used agricultural field that was turned into a pasture afterwards (lagamba.at, 27.01.2023). According to workers for COBIGA, who have known the area for many years, the agricultural use was very intense, more so than on the Finca Eduardo. Because of this, no forest remnants or overgrowth existed when reforestation efforts were started in 2013. Water was a major hindrance during the work because of the ground water level reaching the surface. For this reason, a network of drainage ditches was created. Despite these endeavours, the soil is to this day very wet to even muddy across the whole area. Flooding events are also very frequent. This is because, for one, the river Río Bonito is adjacent to the north of the Finca (Fig. 2). It overflows usually on multiple occasions throughout the year covering the northern parts of the Finca. This is also noticeable in the soil of those areas since lots of alluvial material and rocks can be found in the top layers. Furthermore, the forest also gets partially flooded after heavy rain. Oil palm plantations are bordering the northeast and the southwest side of the Finca. An actively used pasture can be found in the south. On the other side of the Río Bonito are the forests of the Piedras Blancas National Park.

Figure 5: Exemplary study site on the Finca Amable (Sector 10, 7 years of age counting from when reforestation had started).

The Finca La Bolsa is located 3 to 4 km to the southwest of the other two Fincas and lies at the head of the valley Quebrada Bolsa (Fig. 2). Like on the Finca Amable, a secondary forest can be found here as well (Fig. 6). However, due to its older age, the forest canopy is denser and gaps are seldom found. Structurally, this Finca differs clearly from the other two. On the one hand the area is not entirely flat but is characterized by a myriad of steep hills with the valleys in between being usually similarly flat as seen on the other two Fincas. On the other hand, there is also a creek that winds through the entire area. It might be for this reason that the soil conditions here are also somewhat similar to Finca Amable, with soils in some areas clearly being influenced by the overflow of the creek with high amounts of alluvial material and rocks. Most other parts are either very moist or more rarely muddy. For the soils here, it is known that they are high in iron and aluminium, low in nutrients and are on the acidic spectrum of the pH scale (lagamba.at, 27.01.2023). In the past, half of the area was used for growing crops while the other half was used as a pasture for cattle simultaneously. Still, patches of primary and secondary forests were present before reforestation efforts started in 2010, suggesting that the land use was less intense than for the Finca Eduardo and the Finca Amable. La Bolsa is surrounded by primary forests of the Piedras Blancas National Park as well as the primary forests of the Forest Reserve Golfito.

Figure 6: Exemplary study site on the Finca La Bolsa (12 years of age counting from when reforestation had started).

2.2. Field work

Field work took place from the middle of September 2022 until the end of October 2022, which marks the peak of the rainy season (Fig. 3). Five sectors were chosen (see section 2.1.) to construct a chrono sequence of study sites. On the Finca Eduardo, sector 4 and sector 3, which were one (planting in 2021) and two years old (planting in 2020) respectively, were picked (Fig. 2). These represented the youngest forest stages. The sectors selected on the Finca Amable were Sector 10, which was 7 years old (planting in 2015) and sector 1 which was nine years old (planting in 2013) (Fig. 2). Lastly the sector La Bolsa was chosen as the representative of an older forest stage since planting of trees started in 2010 (12 years old).

To sample the species composition of the herbaceous layers, four 10x10 m plots (100 m^2) were set randomly in each of the five sectors (20 plots in total) using the software QGIS (ver.3.28.1). Plots were labelled with an alphabetical ID ("a" to "t") following the ages of the sectors they were in. There was a minimum distance of 20 m between plots. To minimize edge effects such as potentially higher nutrient levels due to neighbouring farmland or higher moisture of the soil due to a nearby waterbody, the position of some of the randomly chosen plots was slightly adjusted. If a plot was randomly set within a 20-meter range of such a potential source of error, the plot was set up 20 m away from it in the field and the new coordinates were noted. The plots on the Finca la Bolsa were a special case. They were not set up as previously described. Since there was no reliable GPS signal available in the area, the position of the plots was estimated with a satellite map before setting them up. In addition, the above-described approach to minimize edge effects could not be followed due to the structure of the terrain (see 2.1.), which lead to plots mostly being at maximum 10 meters away from possible sources of error.

During the vegetation assessments, each herbaceous species was recorded and determined to species level when possible. At the same time, the abundance/coverage of each species inside a plot was estimated using the categorisations and methods by Braun-Blanquet (1964). An overview of the classification used can be found in Table 1. Herbaceous plants were defined as non-woody plants that were rooting in the ground, similarly to Poulsen (1996). This would exclude epiphytes but not hemi-epiphytes or other climbing herbaceous species as long as their roots were rooting in the soil of a plot and if most of their vegetative parts were inside the margins as well. Treelets and shrubs, on which the overwhelming majority of their shoots were not lignified (e.g. *Palicourea tomentosa*) and that were very abundant (e.g. *Piper hispidum*), were recorded as well. Taking these taxa not into account, would have made it impossible to obtain a true representation of the local vegetational layer inside a plot. Saplings of trees, treelets and woody shrubs were ignored. Ferns of which the family they belonged to could not be established unequivocally, were grouped under their respective orders. In this study, this was only needed for ferns belonging to the order Polypodiales which was treated as a family in the subsequent statistical analyses. Additionally, the vegetation structure and general descriptive characteristics of the environmental conditions such as the state of the soil were noted. An overview picture of each plot was taken as well. For plant identification, adequate literature was used (Hammel *et al.*, 2003; Weber and Baumgartner, 2001; Gargiullo and Magnuson, 2008) as well as the photo herbarium material present in the Tropical Research Station la Gamba. Pictures were also shown to experienced botanists, to help with the determinations.

Table 1: Categories for abundance/coverage and habit after Braun-Blanquet (1932). The coverage of a species in a given plot is the estimated area covered by the above ground plant organs of all individuals of that species in the plot when projected on to the ground. It has to be kept in mind that the percentages of area covered by each species do not have to add up to a 100% for any vegetational assessment as there can be multiple species assigned to e.g. category 5 for a plot if adequate.

Categories of abundance/coverage	**Description**
r	Only single individuals/ almost no cover
+	Sparsely or very sparsely present/<1%
1	Numerous individuals/ <5% but >1%
2	Any number of individuals/ 5-25%
3	Any number of individuals/ 25-50%
4	Any number of individuals/ 50-75%
5	Any number of individuals/ 75-100%

2.3. Alpha and beta diversity

The terms alpha and beta diversity, which highlight two different aspects of diversity, where first introduced by R. H. Whittaker (1960) together with gamma diversity which will not be further discussed in this work. He defined alpha diversity or primary diversity as “the richness in species of a particular stand or community, or a given stratum or group of organisms in a stand” (Whittaker, 1960). In other words, it is a measure to describe the species richness of a particular area of interest e.g., the absolute number of species of a particular area. Beta diversity, or secondary diversity, on the other hand, he defined as "the extent of change of community composition, or degree of community differentiation, in relation to a complex- gradient of environment, or a pattern of environments" (Whittaker, 1960).

Nowadays there are various methods to quantify alpha and beta diversity. For this study the Shannon-Wiener-index, or just Shannon-index, was chosen for alpha diversity which to this day is still widely applied and discussed (Sandor and Chazdon, 2014; Konopiński, 2020). It was introduced by C.E. Shannon in Shannon (1948) and has its origins in information theory, the general aim of which is to measure the degree of order/ disorder of a system (Tremp, 2005). The index represents a value describing the uncertainty of randomly choosing a species twice when drawing from a sample (Tremp, 2005). The magnitude of the index is infinite and depends on the maximum number of species present in a sample while the minimum number it can reach is 0 standing for complete certainty to draw a species twice. When looking at the formula (For. 1), the minimum and therefore the lowest alpha diversity is reached when there is only one species present. This leads to the relative proportion of the species P_i in the sample to become 1, which leads to the natural logarithm to become zero and therefore leads to the entire product to be 0 as well. The maximum diversity is reached when the term is equal to the natural logarithm of the total number of species (For. 2), which is only achievable when each species is evenly distributed within a sample. This also shows that the Evenness, the equality of species or uniformity of the sample, is integrated within the formula. The Evenness for Shannon is defined as the quotient between the index calculated (H') and the maximum possible index (H'_{max}) for that sample (For. 2). It can only reach numbers between 1 and 0 with one being a completely evenly distributed sample and 0 meaning that there is only one species contributing to the entire community. A maximum Evenness is reached when H' is the same as H'_{max} indicating that a maximum Evenness is only possible when the highest diversity is given, reflecting what was stated earlier. A benefit of using the Shannon-index is the comparability of the values when having multiple samples. If all the samples were taken in the same manner, a direct comparison of the diversities is possible.

Since beta diversity describes the change in species composition between areas of interest it can be easily described by calculating the species turnover rate along a chosen gradient. For this study, time was chosen as the gradient for the calculations. The formula can be found in For. 3. The Turnover rate can reach numbers between 0 and 1 and it describes the relative exchange in community members along any gradient. Only two areas at a time can be compared with each other. 0 implies that there was no change from one to the other area of interest while 1 signifies a complete substitution of the previous community. A hypothetical result of 0.5 would therefore mean an equal exchange of newly appearing species and old ones disappearing. High turnover rates would also stand for a big change in environment and conditions in the new area along the gradient. The rate does not indicate which species get exchanged, only how many (Tremp, 2005).

$$H' = -\sum_{i=1}^{s} p_i \cdot \ln(p_i) \quad with \quad p_i = \frac{n_i}{N}$$

H' = Diversity index
s = Number of species
p_i = Relative proportion of species i in the sample
N = Sum of the importance values of all species
n_i = Importance value of species i

Formula 1: Shannon-Wiener index, taken from Tremp (2005).

$$E = \frac{H'}{H'_{max}} \quad with \quad H'_{max} = \ln(s)$$

E = Evenness
H'= Current diversity index
H'_{max}=Theoretically possible maximum diversity index for the sample
s = Number of species

Formula 2: Evenness *E* dependent on the Shannon-Wiener index of a sample, taken from Tremp (2005)

$$T = \frac{A^{+}_{n_1;n_2} + A^{-}_{n_1;n_2}}{n_1 + n_2}$$

T= Species turnover rate
$A^{+}_{n1;n2}$= Number of species that newly appeared during the transition from sample 1 to sample 2
$A^{-}_{n1;n2}$= Number of species that disappeared during the transition from sample 1 to sample 2
n_1= Number of species in sample 1
n_2= Number of species in sample 2

Formula 3: Species turnover rate, here referred to as *T*, taken from Tremp (2005)

2.4. Data analyses

The data was analysed using Rstudio (ver. 2022.07.2+576, R 4.2.2). The most essential packages used were "vegan" (2.6-4), "ggplot2" (ver.3.3.0) and "BinMat" (ver. 0.1.5). First, two stacked bar plots were constructed in which the composition of the families on each plot would be demonstrated. One bar plot would visualize the percentual shares of the families in each sample plot. The other shows the absolute number of species found for each family on each sample plot. Only those families, for which more than one species was discovered on any given sample plot, were separated and appear as their own segments in the bars. The families that did not uphold this requirement were summarized in the extra category "other" to identify trends and more dominant families more easily. Next, to make further statements on the floristic structure of the plots, frequency diagrams were made with the bars representing the frequency for each category of coverage on a sample plot. In Braun-Blanquet (1932, 1964) it is stated that plots with higher frequencies in lower categories such as +, 1 and 2 and lower frequencies in the highest categories such as 4 and 5 have floristically non-homogenous vegetation. For plots where the opposite distribution of the frequencies is the case (higher frequencies in the highest categories and less in the lower categories) the vegetation is classified as floristically homogenous. These frequency diagrams are comparable due to them being the results of test plots of equal size. The diversity of the plots and sectors was numerically analysed by using the Shannon-Wiener index (H') for alpha diversity (For.1) and the species turnover rate (T) for beta diversity (For. 3). A midpoint conversion was applied for the categories of coverage after Tüxen und Ellenberg (1951) to give them numerical values and therefore making them usable as importance values for the Shannon-index (For.1). The alpha diversity on each plot, separated by sectors, was also visualized as a jitter plot to see the range of the values. The means of the indices as well as the theoretical maximum values (For.2) were added as well. To check if the H' values of each sector represent different samples, a Kruskal-Wallace test was done for a significance level of 0.05 and the Null-Hypothesis (H_0) "There is no difference in calculated Shannon-indices for the sectors". The turnover rates were calculated under the assumed gradient of time starting from the youngest sector to the oldest following the succession in order (For. 3). The rates for each transition where plotted. Lastly an NMDS analyses was executed using a PCoA ordination model in which plots would be grouped according to their similarities in their species composition and their respective coverages. The variables MDS1 and MDS2 were plotted in a scatter plot for visualisation. Potential clusters were marked inside the graphic.

3. Results

3.1. Species composition

In total, 122 species belonging to 43 families were found across all sample plots, with 91 species (~75%) being unique for one of the three Fincas. With 32 species each, the Finca Eduardo and the Finca La Bolsa had the same number of unique species and with 27, the Finca Amable had only five less. Likewise, the total numbers of species found on each finca are also in comparable ranges with no huge discrepancies. The Finca Eduardo showed a total of 57 species, Amable had 58 and La Bolsa had 47. Looking at the sectors in the order of age, the same trend continues. Sector 4 possessed 42 species, Sector 3 had 47, Sector 10 had 44, Sector 1 had 35 and La Bolsa, again, 47. There was a mean number of 22 ± 5 species found per sample plot. Out of the 43 families, 14 were represented by more than one species on any plot. These families contributed 75% or more to the overall species composition across the majority of the sample plots (Fig. 7). Members of the Rubiaceae and Poaceae were present on nearly every plot (Figs. 7,8). Poaceae were the most diverse family and dominant on the youngest sectors whereas one species, *Panicum laxum*, was the sole representative in the sectors older than two years. Of the Rubiaceae, solely *Sabicea villosa* was consistently found and was the only

Rubiaceae representative on sectors 10 and 1. Other noticeable groups are the Piperaceae and Polypodiales which were present in 75% or more of the plots. Their presence was more dominant the older a sector was. A reverse case can be found in Fabaceae which appeared on 80% of the plots (Figs. 7,8). However, the family is represented with relatively more species in the youngest sectors and loses prominence in older sectors. Acanthaceae are as well on 80% of the plots. Here, the species numbers stay rather consistent across plots despite the different ages with no noticeable trend visible (Figs. 7,8). Families present on 50-75% of the plots were Marantaceae, Araceae, Cyperaceae, and Heliconiaceae. Similarly to the Poaceae and Fabaceae, the Cyperaceae also have the greatest number of species and are most prominent on the youngest sectors with only one *Scleria* species representing the family on the older sites. Heliconiaceae, Araceae and Marantaceae have occasional appearances on the youngest plots in sectors 4 and 3 but are present on almost every other older plot. Araceae are special in that the number of species is positively correlated with sector age (Fig. 8). Six species of Araceae were found across all plots on the Finca Amable compared to nine on Finca La Bolsa, with only one shared species (Tables A2, A3). To compare to a family with similar abundance patterns on the plots, for Heliconiaceae only two species were encountered overall, *Heliconia latispatha* and *Heliconia wagneriana*, of which the former species appeared on all fincas. Figure 8 shows that the number of species for Marantaceae is increasing with the age of the study areas, similarly to Araceae, but not as prominently. However, when looking into the species lists (Tables A2, A3), it becomes apparent that Finca Amable and La Bolsa had the same absolute number of species for that family with the two fincas having three species in common. *Calathea lutea* was the most common species of Marantaceae and usually was accompanied by *Heliconia latispatha* on all fincas. Another noteworthy family was the Onagraceae of which in total three species were found, all part of the genus *Ludwigia*. They were only present in the sectors 4 and 3 of the Finca Eduardo and completely absent from all other fincas. For Asteraceae, Convolvulaceae and Verbenaceae no specific patterns were visible (Figs. 7,8). Compared to the other families, representatives of these three families occur rather sporadically and inconsistently, being present in 40% or less of the plots. They were also only represented with one to two distinct species in any given plot. The remaining 29 families, summarized in figures 7 and 8 as “Other”, still represent large parts of the family composition, averaging on an estimated 25% on each plot. Included in this group are typical tropical herbaceous plant families such as Orchidaceae, Bromeliaceae, Musaceae, Costaceae, Zingiberaceae and Passifloraceae. It also has to be noted that no one family is overwhelmingly dominant on any of the plots (e.g. taking up more than 50% of the total composition) implying that the communities are rather heterogenous.

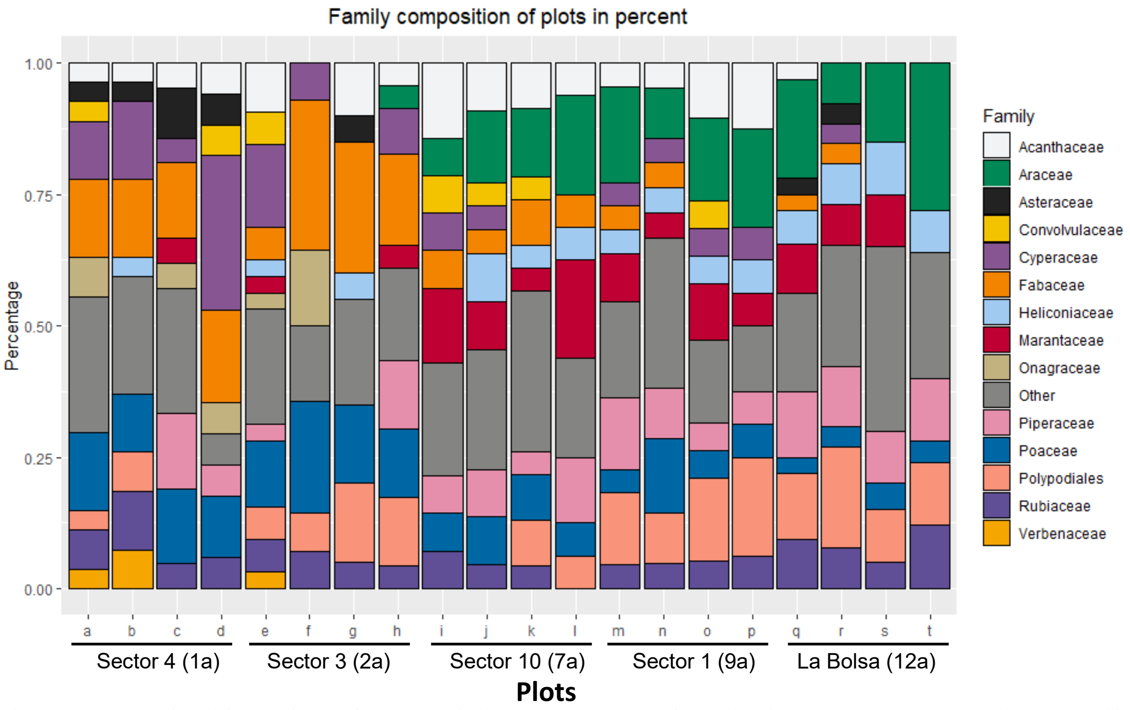

Figure 7: Stacked bar plot where each bar represents the absolute percentage a plant family contributed to the species composition on a given plot. The plots are ordered by age of the sectors they appeared in from youngest (on the left) to oldest (on the right). The letters on the x-axes are the IDs of each respective Plot. A set of four plots always belongs to one sector with a specific age. Belonging to the group “Other” (grey) are families that had less than two representative species on any of the plots.

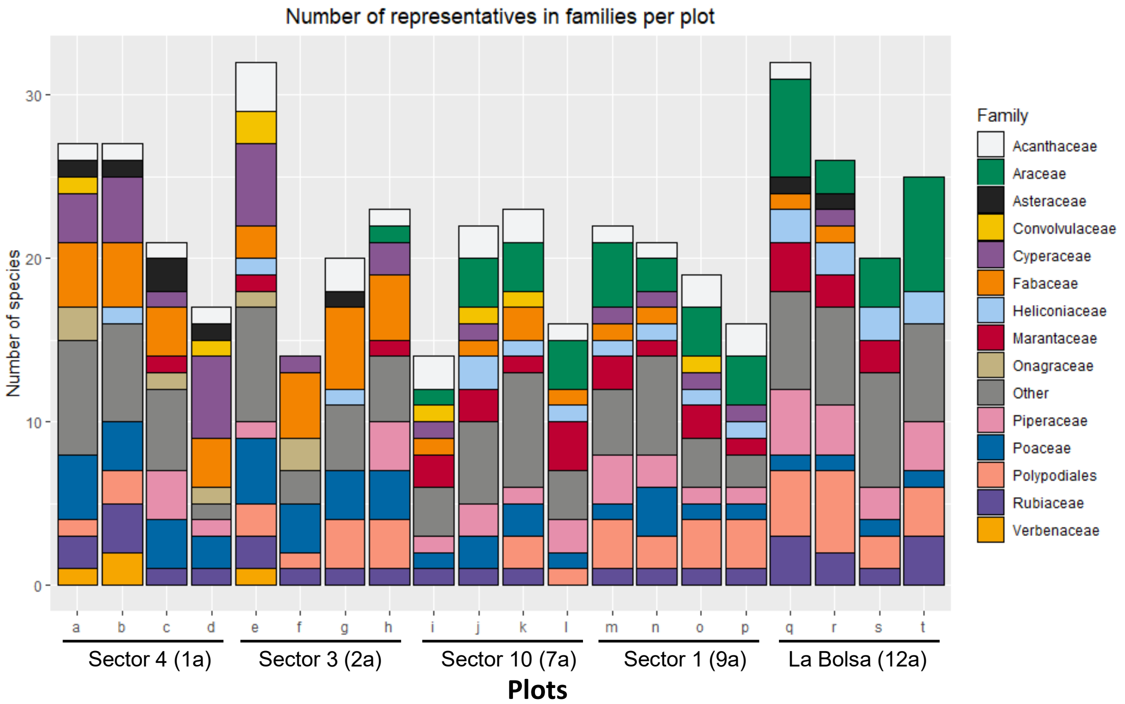

Figure 8: Stacked bar plot for the families present on each investigated plot quantified by their total number of representative species. The plots are ordered by age of the sectors they appeared in from youngest to oldest. A set of four plots always belongs to one sector with a specific age. The letters on the x-axes are the IDs of each respective Plot. Belonging to the group “Other” (grey) are families that had less than two representative species on any of the plots.

The floristic structure of the individual plots, based on the frequencies of each category of coverage, was also heterogenous throughout. Figure 9 shows that all of the plots predominantly had a variety of species with mostly minimal spread. In all plots the most represented categories of coverage were the lower ones such as r, +, and 1 while categories with the highest coverage such as 4 or 5 mostly appear as outliers with minor representation as seen for example in plots a, c, e, g, i, and o (Fig. 9). These examples also show that these types of outliers are not exclusive to any one finca or sector. The highest number of species that were categorised above, were found in sectors 3 and 4, followed by sector 1 then 10, and lastly La Bolsa. The plots in the older sectors such as sector 1 and La Bolsa are the most heterogenous, with around 90% of the species being categorised in either r or + meaning that the overwhelming majority of species covers less or around 1% of the 100 m^2 plot area. The outliers on the sectors of the Finca Eduardo in categories 4 and 5 are usually the same set of species: *Ischaemum timorense* (Poaceae, locally known as Ratana or Retana), *Panicum laxum* (Poaceae), and *Vigna longifolia* (Fabaceae). This is different for the plots on the sectors on the Finca Amable. The species that appear here in the higher categories were usually assigned to lower categories of coverage across all plots whereas the species mentioned for Finca Eduardo were almost certainly part of the highest categories when they were present. For example, on plot l and i in sector 10 of the Finca Amable, the species in question were *Hedychium coronarium* (Zingiberaceae) and *Diffenbachia aurantiaca* (Araceae) (Fig. 9). Even in the same sector they were usually assigned to categories 1 or 2 at maximum. *Piper hispidum* (Piperaceae), a species that was present on all sectors, was throughout the study mainly assigned to the intermediate categories 2 and 3. On sector 1 however on e.g. plot m, the species had cases of huge coverage on plots leading to it being assigned to 4 during the field work. The only species that regularly occurred with high coverage on plots on the Finca Amable was *Calathea lutea.* La Bolsa is the only location that does not show these kinds of outliers in the highest categories 4 and 5.

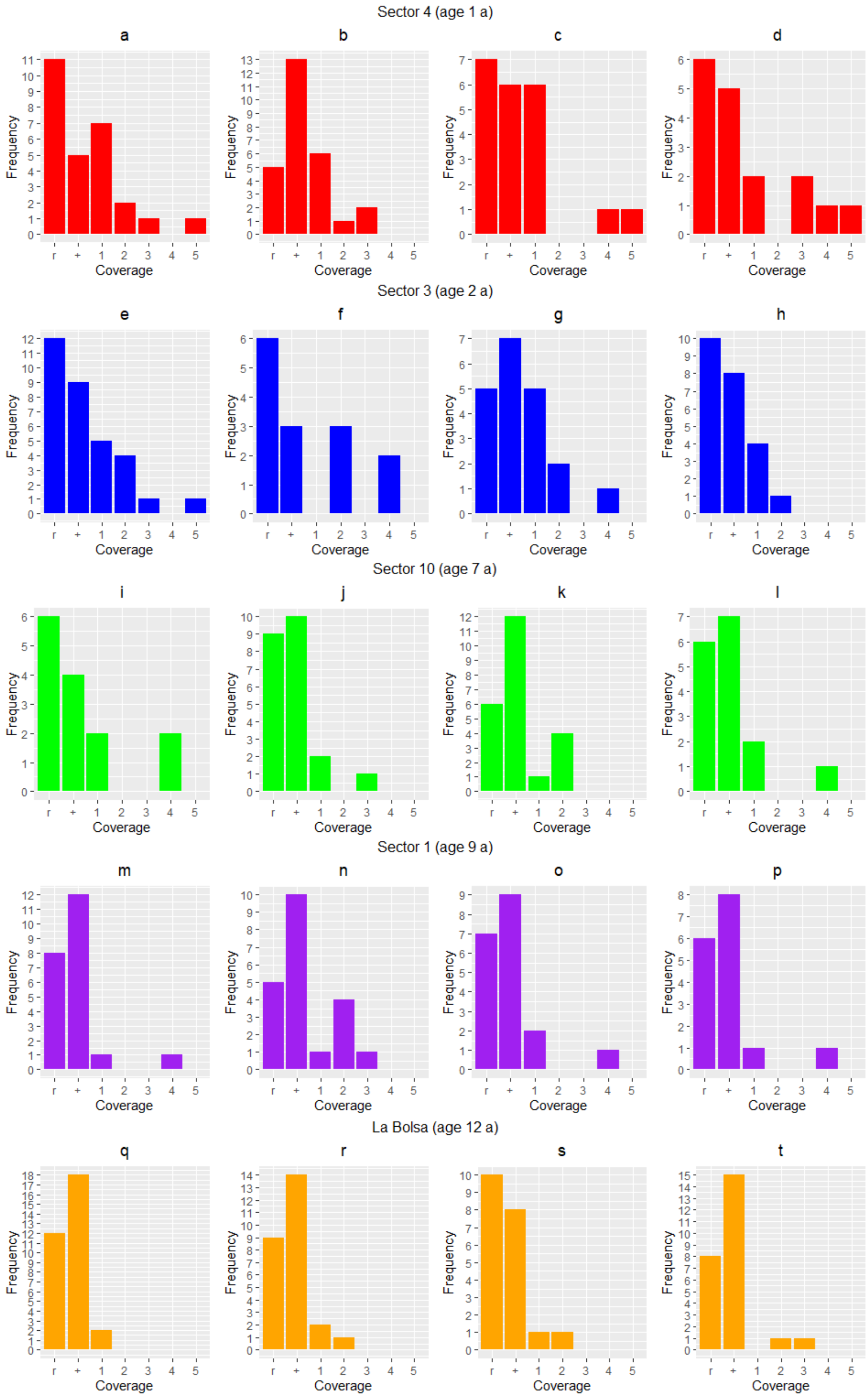

Figure 9: Frequency of each category after Braun-Blanquet (1964) on each investigated plot. Each bar represents the number of species found on that plot for that specific category of coverage. The colours of the bars represent the sectors the plots were situated in.

3.2. Diversity calculations

The Shannon-Indices for each plot as well as the means and standard deviations can be found in Table 2. Since every sector had the same area sampled and the data has been collected with identical methods, a direct comparison of the sectors' Shannon-indices as a measure of alpha diversity is possible. The overall highest mean diversity was calculated for the younger sectors (Fig. 10). Sector 3 had a mean index of 1.495 ± 0.191. Sector 4 is the second most diverse with a mean of 1.436 ± 0.227. The lowest diversities were recorded for the sectors with the intermediate ages, sectors one and ten with 0.671 ± 0.669 and 0.887 ± 0.530 respectively, roughly being half the values of sector 3 and 4. The oldest, La Bolsa, is in between with a Shannon-Index of 1.183 ± 0.590. It must be noted, that the standard deviations especially for sectors1, 10 and La Bolsa are rather high, e.g., for sector 1, the standard deviation is almost identical to the calculated mean index of the area (Tab. 2). This indicates a high variance of values. This is also visualised in figure 10. The calculated values are not consistently clustered together (Fig. 10). The figure also shows that for every sector there is at least one outlier present. The most numerically distant from the other indices can be found for sectors 1, 10 and La Bolsa. The Kruskal-Wallace test gave a p-value of 0.263 which is far greater than a significance level of 0.05 meaning that there is no difference in the Shannon-Indices between the sectors. The Evenness of each sector showed that most communities were uneven with the values ranging from a maximum of around 0.5 for sectors 3 and 4 to a minimum of around 0.2 for sector 1. Figure 10 illustrates, that the mean values of the theoretical maximum diversity indices and their respective error bars, as well as their data points are completely separate and do not overlap by a wide margin with the means of the original data. The maximum theoretical diversity indices for each sector are also fairly similar to each other with all values being close to 3 (Mean 3.057 ± 0.242), due to the similar numbers of species found on each sector overall. La Bolsa has the highest theoretical maximum, followed by sector 4, then sector 3, sector 1 and lastly, sector 10 (Tab. 2). Lastly, the theoretical maxima for all sectors are two to five times bigger in value than the calculated indices.

Table 2: Shannon-Index (H’) calculated for all four sample plots on each sector. All values were rounded to the third digit. The mean and standard deviation (sd) as well as the same values for the theoretical maximum of the index and the Evenness for each sector can be found in the last five rows. The Evenness was calculated by dividing the general means with their respective possible mean H'_{max}.

Plot	Sector 4	Sector 3	Sector 10	Sector 1	La Bolsa
H’ 1	1.561	1.777	0.887	0.317	2.023
H’ 2	1.633	1.397	0.629	1.669	1.159
H’ 3	1.119	1.362	1.625	0.428	0.740
H’ 4	1.432	1.444	0.405	0.268	0.808
Mean	1.436	1.495	0.887	0.671	1.183
Sd	0.227	0.191	0.530	0.669	0.590
Mean H'_{max}	3.118	3.059	2.910	2.963	3.235
Sd H'_{max}	0.224	0.342	0.242	0.141	0.193
E	0.461	0.489	0.305	0.226	0.366

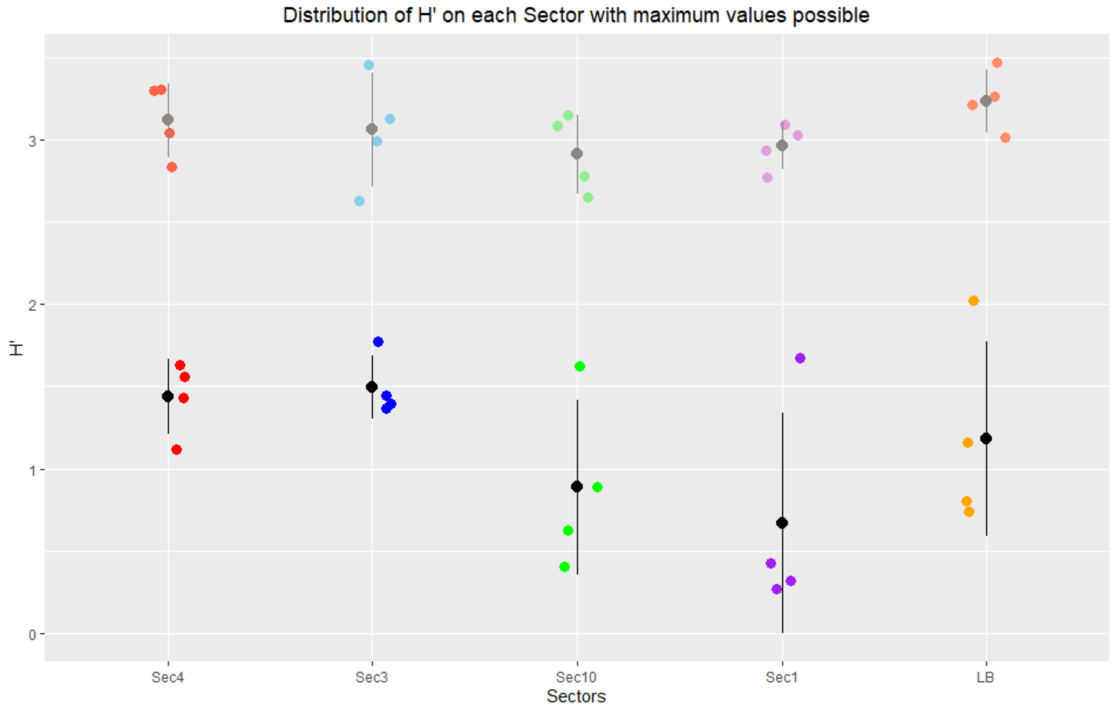

Figure 10: Jitter plot of the calculated Shannon-indices (H’) for each sample plot of each sector (fully coloured). The black dots with error bars represent the mean of their surrounding datapoints. The pale coloured data points and means above represent the theoretically possible max values of the Shannon-indices of the fully coloured data points. It must be kept in mind that the positions of the data points between the fully and pale coloured indices are not corelated which means, for example, that the lowest data points for maximum and calculated index do not necessarily represent the same plot. Sec=Sector, LB=La Bolsa

When it comes to quantifying the amount of difference in species community of the areas and therefore the beta diversity, the general trend is that the highest amounts of differences are present between areas that have an age gap of more than one year, which is especially true when transitioning from one finca to the other (Figs. 11, 12). Areas of similar ages do not have any noteworthy differences as seen in the turnover rate between the one-year-old and two-year-old sector on Finca Eduardo being the lowest with around 0.34. In contrast to this, a rather high change in species composition can be seen from the change from the two-year-old sector 3 to the seven-year-old sector 10, an age gap of 5 years. This is also the transition from the Finca Eduardo to the Finca Amable. The rate is nearly double to the previous entry indicating a rather big shift in species composition (Fig. 11). The rate of 0.59 demonstrates that an almost equal amount of new and old species is present with newer ones being slightly more dominant. The next transition from 7 to 9 years of age has an almost identical turnover rate of 0.58, even though the age gap is only two years, implying the same levels of changes in community composition as for the step from 2 to 7 years. For 9 to 12 years (age gap of 3 years), the turnover rate is around 0.88 which shows a major change in species composition with almost all previous species being replaced by new ones.

The NMDS analysis reflects as well, that the fincas are very distinct from each other in their species composition (Fig. 12). Firstly, almost all plots clearly cluster close together according to finca (except for four outlying plots) showing that plots of the same finca are more similar to each other in their species composition and their respective coverages than to plots of the others. The plots in the Finca Amable cluster are more intermixed than those in e.g. the Finca Eduardo (Fig. 12). The cluster size is also slightly bigger than for the other two fincas. Both facts demonstrate that in this case, there is a slightly higher difference between the data points of sector 10 and 1 compared to the other two clusters, reflecting the high turnover rate between the two sectors in Fig. 11. All clusters are, for the most part, equally numerically distant from each other, with the Eduardo cluster being slightly closer to the Finca Amable one. This also makes the La Bolsa cluster appear more isolated from the others.

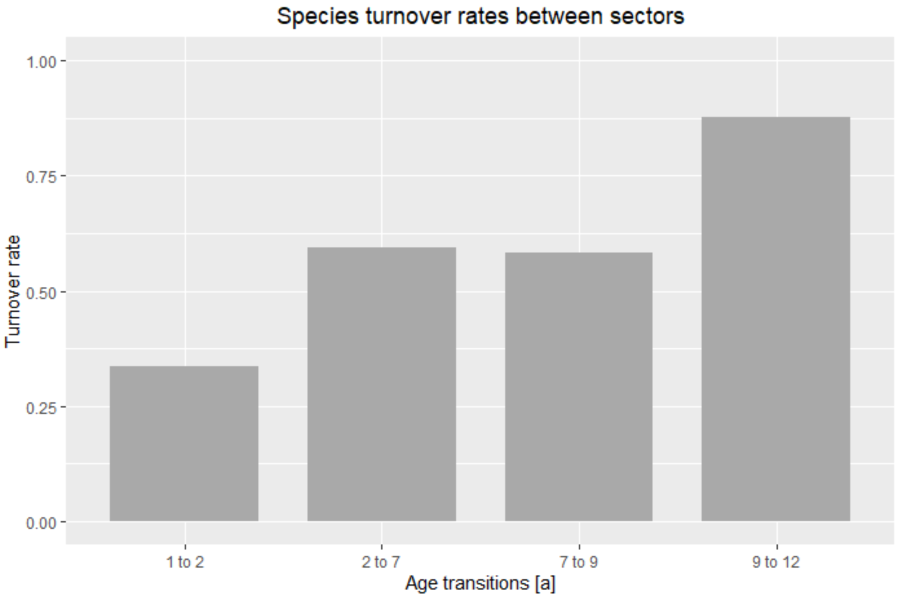

Figure 11: Species turnover rates between the investigated sectors. The rates were calculated under the gradient of time, starting from the youngest sector to the oldest.

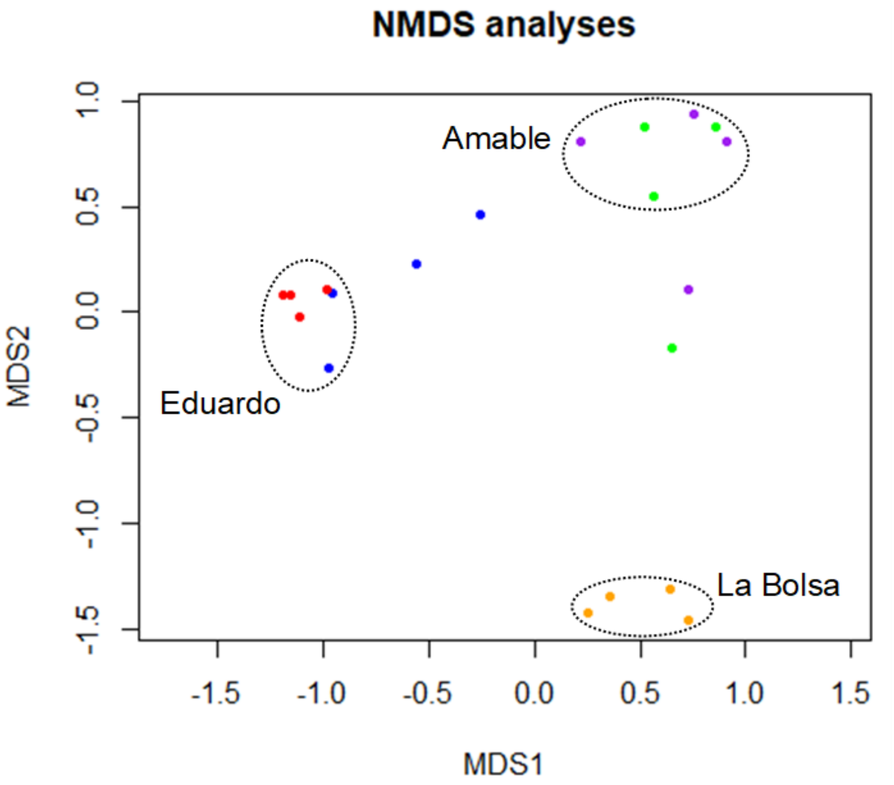

Figure 12: Graphical presentation of the NMDS analysis of the species found on each plot and their respective coverages categorised after Braun-Blanquet (1964). Each dot represents a sample plot. The colour of a dot stands for the sector the plot was on (blue=Sector 4, red=Sector 3, green= Sector 10, purple= Sector 1, orange= La Bolsa). The data points can be clustered into the respective finca (Eduardo, Amable, La Bolsa) they appeared in.

4.Discussion

4.1. Succession and herbaceous species diversity

Forest succession is a cyclic process with many distinct stages that differ greatly between each other (Meyer, Tabaku and v. Lupke, 2003; Hilmers *et al.*, 2018). Each stage has its own characteristics and assemblages of organisms. This is especially true for plants, with each stage showing the predominance of different species of plants of different growth types for both tropical and temperate regions (Egler, 1954; Finegan, 1992). Generally, for temperate forests, it is seen that the plant diversity (not just herbaceous species) follows a U-shaped curve throughout a forest's life span, meaning that diversity is highest in early and late stages of succession (Hilmers *et al.*, 2018). Adding to this is that the species compositions of early and late succession stages are more similar to each other than to any intermediate stage in temperate forests (Hilmers *et al.*, 2018). Furthermore, early and late stages of a forest harbour the most unique species (species exclusive to those stages) in temperate regions (Hilmers *et al.*, 2018). Most of these trends have been seen in this study as well. For one, the highest number of unique species was seen for youngest and comparably more advanced stages (see discussion below) too. Additionally, the calculated Shannon diversity indices were highest for oldest and youngest sectors, resembling a flat U-shaped curve (Fig. 10). The same trend was also observable for the maximum theoretical indices, but to a far lesser extent. Even so, the Kruskal-Wallis-Test resulted in a non-significant p-value. However, there is a high probability that this result could be a type II statistical error caused by rather low sample sizes and high variances within three of the five samples, which would make accepting the null hypothesis ("There is no difference in calculated Shannon-Indices for the sectors") false. Here it needs to be said that the low evenness of the samples as well as the maximum theoretical diversity indices being roughly two to five times bigger than the calculated mean indices point towards the herbaceous layers of all the sectors not being highly diverse in a general context. The reason for the unevenness can be derived from the frequencies of the categories of coverage on each plot (Fig. 10). Although they are a minority, the impact of species in higher categories of coverage (e.g. 2,3,4 and 5) on the diversity indices shows to be very significant and amplified based on the fact that the vast majority of species within a plot cover only up to 1% of a plots area. This causes a highly unequal ratio in species representation when outliers are present within a sample which therefore lowers the value of the Shannon index and evenness. In addition, observations during field work showed that sectors 1, 10, and La Bolsa had either large amounts of exposed ground and/ or were covered by woody species (e.g. trees), their leaf litter, branches and fallen stems as well as by young saplings or shoots. These factors would even further amplify the effects of a more abundant species on the diversity since there is even less ground that could be covered by other herbaceous species. While the vegetation was floristically heterogenous among the plots (Figs. 7, 9), the strong influence of a few particularly abundant species led to a homogenous physiognomic structure.

Coming back to the distinctness of forest stages in temperate regions (Hilmers *et al.*, 2018), it would seem that the same is applicable to tropical forests as well. Based on the fact that the NMDS analysis revealed distinct clusters for each finca as well as the highest species turnover rates being detected for transitions between the fincas, it is safe to say that each finca at the time of the study, truly was in a different succession stage. Arguably, sectors 1 and 10 on the Finca Amable might have represented different stages within a finca, with a high species turnover rate between the two sectors (Fig. 11). According to the NMDS analyses however, there is not enough of difference in species composition and coverages to support such a conclusion.

The state of a forest's canopy can also be used as a reference to determine in which succession stage a forest is in, e.g., with a homogenous canopy indicating that a forest has reached its regenerative peak or optimum stage (Meyer, Tabaku and v. Lupke, 2003). The optimum stage is also the longest phase in a forest's lifespan. Based on what was established in 2.1., with the Finca Eduardo being an open field with mainly herbs, the Finca Amable's canopy being patchy, and the Finca La Bolsa's being mostly closed, this would reemphasise that Finca Eduardo represents one of the earliest forest phases, Finca Amable represents an intermediate regenerating phase and Finca La Bolsa represents a phase at least very close to the optimum. This directly parallels the phases and descriptions for Finegan's (1992) model for forest succession in tropical regions, where mainly three forest phases are defined by the ecology types of the most dominant plant species. Phase 1 is characterised by fast growing herbs being dominant in biomass, then phase 2 by short-lived shrubs and trees dominating, and in phase 3 long-lived species such as trees that persist for the longest time. Phase 3 would therefore be equal to the optimum stage. This would mean that, when applied to Finegan's model, the Finca Eduardo is most definitely in phase 1 and the Finca La Bolsa in early phase 3. Since Finca Amable is not similar to any of the other two fincas, is in between the two in terms of age and has a still patchy canopy, it would imply that it is in phase 2.

With each finca representing one of the three phases in Finegan's (1992) model, the family composition of each plot would suggest that herbaceous species of certain families might be usable as potential indicator species to describe and determine in which phase the local vegetation is in. This would be a very useful approach as most herbaceous species are accessible on the ground and could represent an alternative to using mainly woody species whose size could represent a hindrance when it comes to reaching plant material for determination. The results of the present study show a dominance of Fabaceae, Poaceae and Cyperaceae on the Finca Eduardo. Species unique to this finca in said families might therefore be the most suitable as indicator species for phase 1. The genus *Ludwigia* of the Onagraceae was also exclusive to the same areas, making species of this genus ideal as indicators as well. However, the appearance of *Ludwigia* could be limited to regions that have similar climatic conditions as the Golfo Dulce Region due to the members of the genus mostly growing on open soils that are marshy and wet such as rice fields (Barua, 2010). Therefore, they would most likely not appear in tropical areas that are well drained or have low and less frequent precipitation as the Golfo Dulce region. For phase 2, it would most likely be species of Araceae, Heliconiaceae and Marantaceae, since these three families were for the most part not present on the Finca Eduardo and the Araceae composition on the Finca Amable largely different from that of the Finca La Bolsa. For the Finca La Bolsa, the most suited species as indicators for phase 3 would be of the Araceae, ferns of the order Polypodiales, Marantaceae and Piperaceae due to most species found being unique for that area (Table A3).

4.2. Factors of vegetation regeneration

As established in the previous sub-chapter, the herbaceous layers of the different forest stages do not seem to be very diverse in a general context. This could represent an observation for the herbaceous layers for the entire Golfo Dulce region overall, but it could also be bound to the fact, that all study areas were previously used agricultural farmland, for crop cultivations and as pastures for cattle. There are a variety of aspects established in subchapter 4.1. that point towards one of the driving forces for the structure and composition of the herbaceous vegetation to be time. These would include that all fincas are assignable to specific forest succession stages that typically develop over time as well as their species compositions paralleling the characteristics of temperate and tropical forest successional development. Further emphasizing time as the driving factor is an unpublished assessment of the species of a younger state of the Finca Amable from 2016 (personal communication with A. Weissenhofer), which shows that most species found during this earlier assessment were largely the same as the species found on the Finca Eduardo in the present study. However, there is a plethora of conditions bound to the environmental conditions and previous use of an area that can significantly influence the regeneration and diversity of a developing secondary forest on a pasture, making it implausible that time would be the sole factor for the state of the vegetation.

First, before COBIGA started with reforestation, all fincas were in different vegetational conditions and had undergone different kinds of previous use. According to long time workers of the COBIGA project, the entire field that is now the Finca Amable was devoid of any natural remnant vegetation, while the other two fincas were not when they were acquired. Finca Eduardo had remnants of secondary forests while Finca La Bolsa had patches of secondary forests as well as primary forests. For Finca Eduardo it is even known that it lay fallow for 14 years in the 80's and 90's which could have given time to the nutrient quality of the soil to recover from previous usage (lagamba.at, 27.01.23; Finegan, 1992). Furthermore, all fincas, even if they were all used for the same purposes, were managed with different intensity. From what is known of the remnant vegetation and from additional statements of long-time workers of COBIGA, it can be assumed that the Finca Amable has undergone the most intense, the Finca Eduardo less intense and the Finca La Bolsa the least intense use in the past. The hilly structure of the Finca La Bolsa might have also rendered it less suitable for more intense agriculture, since open areas on steep slopes would be less easily accessible for workers and machines. In general, in which way an area was used (e.g. use of heavy machinery, use of fire or excessive use of herbicides) and how long it was used (e.g. the period of grazing by cattle or for how long crops were cultivated) can influence the natural regeneration of an area once it gets abandoned (Finegan, 1992; Aide *et al.*, 2000; Healey, 2001). This could go as far as that the natural regeneration would not necessarily lead to the typical vegetation of an area (e.g. a forest) if the use was too intense or it could lead to a heavily altered ecosystems compared to the one that was there before the conversion of the land into an agricultural field (Finegan, 1992; Aide *et al.*, 2000). Additionally, the type of land use and its intensity can heavily delay the process of succession, which leads to different successional stages being reached by the vegetation much later than under less severe conditions (Finegan, 1992). Other studies have also shown that the previous types of land use of an area explain a large proportion of the variation in forest structure and composition both in temperate and tropical regions (Zimmerman et al., 1995). While some ecological characteristics of forests on previously intensely used lands such as nutrient cycling and water retention do mostly regenerate normally, the diversity recovers more slowly and could potentially need centuries for a complete regeneration in such areas, irrespective if the process is aided or not (Zimmerman *et al.*, 1995). These arguments would speak against the analysed herbaceous layers to be reliably reflective of the natural herbaceous vegetation of the Golfo Dulce region. And since the land use of the Finca Amable before acquisitions seems to have been most intense, it could explain why the calculated diversity indices where so low for its sectors compared to the others as well as why its canopy is rather patchy.

Not only the past use of an abandoned pasture, but also the environment during the early succession of the vegetation has to be considered as an impactful influence. Studies have shown that seed sources such as the area’s natural seed bank, remnant vegetation inside the area, and surrounding vegetation as well as sources of sprouts such as remnant tree trunks, can speed up the process of succession (Finegan, 1992; Aide *et al.*, 2000; Healey, 2001). Remnant vegetation such as remnant trees can also influence the species composition of its surroundings with effects detectable well after a forest’s establishment (Sandor and Chazdon, 2014). If the seed bank, surrounding and remnant vegetation are the main sources for the colonization of an abandoned pasture, it would be accurate to assume that the species composition inside the regenerating area will show affinities in its species composition and diversity to said sources. And with Eglers (1954) supported concept of “initial floristics” in mind, which states that most species, even the ones of later successional stages, invade a field soon after abandonment, these sources become all the more important at the beginning of the succession process for the species diversity of an area in the long term.

Due to all study areas being agriculturally used for well over 10 years right before COBIGA started their reforestation, the natural seed bank of the three fincas can likely be excluded as a source of potential colonizers during regeneration, since it effectively becomes destroyed on agricultural fields after only a couple of years of continuous use (Finca Amable, 27.01.23; Uhl et al., 1990; Aide et al., 2000). This, coupled with the fact that COBIGA exclusively plants trees and treelets (lagamba.at, 27.01.23), leaves only the remnant and surrounding vegetation as natural sources for colonizers for the herbaceous layer on the fincas.

The completely open Finca Amable, at the beginning of its reforestation, was exclusively surrounded by agricultural fields or pastures with the exception of an adjacent forest (Parts of the Piedras Blancas National Park) to the north of the finca. That forest however, is on the other side of a river, the Río Bonito (Fig. 2), making it far less probable for any dispersal of plant species into the finca by terrestrial means from that area. The dispersals of seeds and therefore the contribution to the species composition by means of water should be considered though, since floods, regularly occur due to the river overflowing. This could have been a possible contributor to the noticeable species turnover rate between sector 10 and 1 since sector 10 is directly adjacent to the Río Bonito. Dispersal of seeds from the Piedras Blancas forest by birds (ornithochorie) could still have been an important supplier of colonizing species. However, seed dispersal by birds into clear pastures without any perching opportunities, such as trees, is significantly lower into areas where perching possibilities exist (Holl, 1998). With no other remnant vegetation or diverse habitats present at the start of reforestation, it could be deduced that the regeneration of the forest's herbaceous species diversity is severely hampered, which would be another reason for the overall low diversity indices for sectors 1 and 10. Modes of seed dispersal that might not have been influenced strongly by the fincas initial vegetational structure are anemochory and other forms of zoochory, specifically epizoochorie by e.g. mammals (including stray dogs and cats from the nearby village), or seeds attached to the clothes of reforestation workers.

A very different starting point was to be found on the Finca La Bolsa. With plenty of remnant vegetation, representing sources of primary and secondary forest species as well as trees for perching birds, and the finca being directly adjacent and surrounded by primary forests, it is clear that the regeneration of its forests and by extension the diversity of its herbaceous layer was most likely much faster and advanced than on the Finca Amable by comparison. The colonization of the area by primary forest species also explains why the Finca La Bolsa cluster appears slightly more distinct in the NMDS analyses in relation to the other two fincas. It also explains why it had a very high species turnover rate between itself and sector 1 with around 0.9, implying an almost complete shift in species communities (Figs. 11, 12). Exactly which determined herbaceous species could be classified as typical for tropical primary forests did not become clear from the general literature of tropical forests in the region. Lastly, the Finca Eduardo's succession speed is most likely in-between the other two fincas, since, unlike Finca Amable, it had secondary vegetation in the beginning as well as a direct terrestrial connection to the forest of the Fila Gamba in the south-east and today's secondary forest of sector 1 of the Finca Amable in the north-west.

5. Conclusion

To conclude, this study has given first insights into the current status of the herbaceous species in three reforestation areas of the COBIGA project, with each of the herbaceous layers representing a different forest succession state, making them exemplary for future studies on the topic of succession. Generally, the herbaceous species diversity in these areas does not seem to be very high. Nevertheless, the herbaceous vegetation of the three areas showed a high level of uniqueness among each other. It is not clear if either the time since reforestation has started or the environment that was present at the start of the regeneration of the forest are the main driving factors for the species community compositions. The results of this study suggest that it was most likely a combination of both. To exclude either one of them, it would be necessary to continue surveying the vegetation with permanent plots if possible. Then it would become clear if e.g. the development of the vegetation on Finca Amable is hampered or not by its starting environment and its former intense agricultural use. Additionally, more frequent surveys would also lead to seeing if the younger fincas (Finca Eduardo, Finca Amable) would eventually be comparable to the older ones (Finca La Bolsa). To disentangle exactly what factors are more important to a forest's development, it would be helpful, to follow the succession of pastures with different remnant and surrounding vegetation right at the beginning of their abandonment as well as to make comparisons to forests that have not regenerated on agricultural land or pastures. If vegetational assessments should continue for the three fincas, it has to be made sure that more plots are taken into consideration to secure the statistical significance of the results and minimise variances. It should also be considered to include other environmental factors that were not assessable in detail during this study such as the structure and condition of the soil on each sector/plot to take their influence on the vegetation into account. Furthermore, more diversity indices than the Shannon-index could be applied to see if there are any that are more suitable for the type of samples, where the abundance of the vast majority of species is low. A more suited index would therefore not be as impacted by outliers as the Shannon-index was in this study. The methods by Braun-Blanquet (1932, 1964) were adequate for the study and turned out to be an efficient way of quantifying the herbaceous vegetation over the rather short study period. With more resources, it should be considered to use methods that could minimize the subjective aspect of the Braun-Blanquet categories.

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8. Attachments

Table A1: List of species determined for the Sectors 3 and 4 of the Finca Eduardo. The list is sorted by family. Species entries, that are spelled with the first three letters of the assigned family followed by an underscore, "sp", and a number were species where the determination was not possible or did not yield reliable results. They were labelled as such to integrate them in the statistical analysis and differentiate them as different species.

Sector 4	
Family	**Species**
Acanthaceae	*Lepidagathis alopecuroides* R.Br. ex Griseb.
Asteraceae	Ast_sp1
Asteraceae	Ast_sp2
Convolvulaceae	cf. *Merremia umbellata* Hallier f.
Convolvulaceae	Con_sp2
Cucurbitaceae	*Melothria pendula* L.
Cyperaceae	*Cyperus luzulae* (L.) Rottb. ex Retz.
Cyperaceae	*Eleocharis elegans* Roem. & Schult.
Cyperaceae	*Fimbristylis dichotoma* (L.) Vahl
Cyperaceae	*Kyllinga pumila* Michx.
Cyperaceae	*Scleria melaleuca* Rchb. ex Schltdl. & Cham.
Euphorbiaceae	*Caperonia palustris* A.St.-Hil.
Fabaceae	*Desmodium adscendens* (Sw.) DC.
Fabaceae	*Mimosa pigra* L.
Fabaceae	*Mimosa pudica* L.
Fabaceae	*Pueraria phaseoloides* (Roxb.) Benth.
Fabaceae	*Vigna longifolia* (Benth.) Verdc.
Heliconiaceae	*Heliconia latispatha* Benth.
Lamiaceae	*Hyptis obtusiflora* C.Presl ex Benth.
Marantaceae	*Calathea lutea* (Aubl.) Schult.
Onagraceae	*Ludwigia hyssopifolia* (G.Don) Exell
Onagraceae	*Ludwigia leptocarpa* (Nutt.) H.Hara
Onagraceae	*Ludwigia octovalvis* (Jacq.) P.H.Raven
Phyllanthaceae	*Phyllanthus urinaria* L.
Piperaceae	*Piper aduncum* L.
Piperaceae	*Piper auritum* Kunth
Piperaceae	*Piper hispidum* Sw.
Poaceae	*Homolepis aturensis* Chase
Poaceae	*Ischaemum timorense* Kunth
Poaceae	*Panicum laxum* Sw.
Poaceae	Poa_sp1
Polygonaceae	*Persicaria punctata* Small
Polypodiales	Pol_sp1
Pteridaceae	*Pityrogramma calomelanos* (L.) Link

Rubiaceae	*Oldenlandia lancifolia* DC.
Rubiaceae	*Sabicea villosa* Roem. & Schult.
Rubiaceae	*Spermacoce prostrata* Aubl.
Selaginellaceae	*Selaginella horizontalis* (C.Presl) Spring
Solanaceae	*Solanum volubile* Rusby
Verbenaceae	*Lantana trifolia* L.
Verbenaceae	Verb_sp1
Vitaceae	*Cissus verticilliata* (L.) Nicolson & C.E.Jarvis
Sector 3	
Family	**Species**
Acanthaceae	*Justicia comata* Lam.
Acanthaceae	*Lepidagathis alopecuroides* R.Br. ex Griseb.
Acanthaceae	*Ruellia blechum* L.
Araceae	Ara_sp1
Asteraceae	Ast_sp1
Caryophyllaceae	*Drymaria cordata* Willd. ex Schult.
Convolvulaceae	cf. *Ipomea* sp. All.
Convolvulaceae	Con_sp1
Cucurbitaceae	*Melothria pendula* L.
Cyperaceae	cf. *Scleria* sp. P.J.Bergius
Cyperaceae	*Cyperus luzulae* (L.) Rottb. ex Retz.
Cyperaceae	*Cyperus odoratus* L.
Cyperaceae	*Eleocharis elegans* Roem. & Schult.
Cyperaceae	*Rhynchospora* cf. *radicans* (Cham. & Schltdl.) H.Pfeiff.
Cyperaceae	*Scleria melaleuca* Rchb. ex Schltdl. & Cham.
Euphorbiaceae	*Acalypha arvensis* Poepp.
Euphorbiaceae	*Caperonia palustris* A.St.-Hil.
Fabaceae	*Desmodium adscendens* (Sw.) DC.
Fabaceae	*Mimosa pigra* L.
Fabaceae	*Mimosa pudica* L.
Fabaceae	*Pueraria phaseoloides* (Roxb.) Benth.
Fabaceae	*Vigna longifolia* (Benth.) Verdc.
Heliconiaceae	*Heliconia latispatha* Benth.
Lamiaceae	*Hyptis obtusiflora* C.Presl ex Benth.
Marantaceae	*Calathea lutea* (Aubl.) Schult.
Onagraceae	*Ludwigia leptocarpa* (Nutt.) H.Hara
Onagraceae	*Ludwigia octovalvis* (Jacq.) P.H.Raven
Phyllanthaceae	*Phyllanthus urinaria* L.
Piperaceae	*Piper aduncum* L.
Piperaceae	*Piper auritum* Kunth
Piperaceae	*Piper hispidum* Sw.
Poaceae	*Homolepis aturensis* Chase

Poaceae	*Ischaemum timorense* Kunth
Poaceae	*Luziola subintegra* Swallen
Poaceae	*Panicum laxum* Sw.
Poaceae	*Paspalum notatum* Flüggé
Poaceae	*Paspalum paniculatum* L.
Polypodiales	Pol_sp1
Pteridaceae	*Adiantum latifolium* Lam.
Pteridaceae	*Pityrogramma calomelanos* (L.) Link
Rubiaceae	*Oldenlandia lancifolia* DC.
Rubiaceae	*Sabicea villosa* Roem. & Schult.
Selaginellaceae	*Selaginella horizontalis* (C.Presl) Spring
Solanaceae	*Solanum volubile* Rusby
Thelypteridaceae	*Thelypteris serrata* (Cav.) Alston
Verbenaceae	Verb_sp1
Vitaceae	*Cissus verticiliata* (L.) Nicolson & C.E.Jarvis

Table A2: List of species determined for the Sectors 1 and 10 of the Finca Amable. The list is sorted by family. Species entries, that are spelled with the first three letters of the assigned family followed by "_sp" and a number were species where the determination was not possible or did not yield in reliable results. They were labelled as such to integrate them in the statistical analysis and differentiate them as distinct species.

Sector 10	
Family	**Species**
Acanthaceae	Aca_sp2
Acanthaceae	*Hygrophila costata* Nees & T.Nees
Acanthaceae	*Justicia comata* Lam.
Acanthaceae	*Lepidagathis alopecuroidea* R.Br. ex Griseb.
Acanthaceae	*Ruellia blechum* L.
Araceae	*Alocasia macrorrhizos* (L.) G.Don
Araceae	Ara_sp1
Araceae	*Dieffenbachia aurantiaca* Engl.
Araceae	*Syngonium hastiferum* (Standl. & L.O.Williams) Croat
Boraginaceae	*Cordia* sp. L.
Commelinaceae	Com_sp1
Convolvulaceae	Cf. *Merremia umbellata* Hallier f.
Cucurbitaceae	*Melothria pendula* L.
Cyclanthaceae	*Cyclanthus bipartitus* Poit. ex A.Rich.
Cyperaceae	cf. *Scleria* sp. P.J.Bergius
Dilleniaceae	*Doliocarpus* sp. Rol.
Fabaceae	*Desmodium adscendens* (Sw.) DC.
Fabaceae	Fab_sp1
Fabaceae	Fab_sp2

Heliconiaceae	*Heliconia latispatha* Benth.
Heliconiaceae	*Heliconia wagneriana* Petersen
Lamiaceae	*Hyptis obtusiflora* C.Presl ex Benth.
Marantaceae	*Calathea lutea* (Aubl.) Schult.
Marantaceae	*Goeppertia lasiophylla* (H.Kenn.) Borchs. & S.Suárez
Marantaceae	Mar_sp1
Marantaceae	Mar_sp2
Marantaceae	*Pleiostachya pruinosa* K.Schum.
Orchidaceae	Orc_sp1
Passifloraceae	*Passiflora* sp. L.
Phyllanthaceae	*Phyllanthus urinaria* L.
Piperaceae	Pip_sp1
Piperaceae	*Piper hispidum* Sw.
Poaceae	*Gynerium sagittatum* P.Beauv.
Poaceae	*Panicum laxum* Sw.
Poaceae	Poa_sp1
Polypodiales	Pol_sp1
Pteridaceae	*Adiantum latifolium* Lam.
Rubiaceae	*Sabicea villosa* Roem. & Schult.
Sapindaceae	*Paullinia serjaniifolia* Triana & Planch.
Selaginellaceae	*Selaginella horizontalis* (C.Presl) Spring
Solanaceae	*Solanum volubile* Rusby
Thelypteridaceae	*Thelypteris serrata* (Cav.) Alston
Vitaceae	*Cissus verticiliata* (L.) Nicolson & C.E.Jarvis
Zingiberaceae	*Hedychium coronarium* J.Koenig
Sector 1	
Family	**Species**
Acanthaceae	Aca_sp1
Acanthaceae	Aca_sp2
Acanthaceae	*Hygrophila costata* Nees & T.Nees
Acanthaceae	*Lepidagathis alopecuroides* R.Br. ex Griseb.
Alismataceae	*Limnocharis flava* (L.) Buchenau
Araceae	Ara_sp1
Araceae	Ara_sp2
Araceae	*Dieffenbachia aurantiaca* Engl.
Araceae	*Dieffenbachia picta* Schott
Bignoniaceae	cf. *Pleonotoma variabilis* Miers
Convolvulaceae	*Ipomoea trifida* G.Don
Cucurbitaceae	*Melothria pendula* L.
Cyperaceae	cf. *Scleria* sp. P.J.Bergius
Cyperaceae	*Scleria melaleuca* Rchb. ex Schltdl. & Cham.
Fabaceae	*Calopogonium caeruleum* (Benth.) Sauvalle

Heliconiaceae	*Heliconia latispatha* Benth.
Lamiaceae	*Hyptis obtusiflora* C.Presl ex Benth.
Marantaceae	*Calathea lutea* (Aubl.) Schult.
Marantaceae	Mar_sp1
Piperaceae	*Piper auritum* Kunth
Piperaceae	*Piper hispidum* Sw.
Piperaceae	*Piper peltatum* L.
Poaceae	*Panicum laxum* Sw.
Poaceae	*Paspalum paniculatum* L.
Poaceae	Poa_sp1
Polypodiales	Pol_sp1
Pontederiaceae	*Heteranthera reniformis* Ruiz & Pav.
Pteridaceae	*Adiantum latifolium* Lam.
Rubiaceae	*Sabicea villosa* Roem. & Schult.
Selaginellaceae	*Selaginella horizontalis* (C.Presl) Spring
Solanaceae	*Solanum volubile* Rusby
Thelypteridaceae	*Thelypteris serrata* (Cav.) Alston
Urticaceae	*Urera baccifera* (L.) Gaudich.
Zingiberaceae	*Hedychium coronarium* J.Koenig
Zingiberaceae	Zin_sp1

Table A3: List of species determined for the La Bolsa. The list is sorted by family. Species entries, that are spelled with the first three letters of the assigned family followed by "_sp" and a number were species where the determination was not possible or did not yield in reliable results. They were labelled as such to integrate them in the statistical analysis and differentiate them as distinct species.

La Bolsa	
Family	**Species**
Acanthaceae	Aca_sp4
Araceae	*Anthurium ochranthum* aff. *pluricostatum* K.Koch
Araceae	*Anthurium pentaphyllum* Kunth
Araceae	*Dieffenbachia burgeri* Croat & Grayum
Araceae	*Dieffenbachia concinna* Croat & Grayum
Araceae	*Dieffenbachia oerstedtii* Schott
Araceae	*Philodendron* cf. *opacum* Croat & Grayum
Araceae	*Philodendron sulcatum* K.Krause
Araceae	*Philodendron* sp. Schott
Araceae	*Syngonium hastiferum* (Standl. & L.O.Williams) Croat
Arecaceae	*Asterogyne martiana* H.Wendl. ex Drude
Asteraceae	*Micania guaco* Kunth
Bromeliaceae	Bro_sp1
Costaceae	*Costus pulverulentus* C.Presl

Cyclanthaceae	*Carludovica drudei* Mast.
Cyperaceae	cf. *Scleria.* sp. P.J.Bergius
Fabaceae	*Calopogonium caeruleum* (Benth.) Sauvalle
Gesneriaceae	*Episcia lilacina* Hanst.
Heliconiaceae	*Heliconia latispatha* Benth.
Heliconiaceae	*Heliconia wagneriana* Petersen
Marantaceae	*Calathea crotalifera* S.Watson
Marantaceae	*Calathea latifolia* (Willd. ex Körn.) Borchs. & S.Suárez
Marantaceae	*Calathea lutea* (Aubl.) Schult.
Marantaceae	Mar_sp1
Marantaceae	*Pleiostachya pruinosa* K.Schum.
Melastomataceae	*Aciotis rubricaulis* (Mart. ex DC.) Triana
Musaceae	*Musa* cf. *textilis* Née
Passifloraceae	*Passiflora costaricensis* Killip
Piperaceae	Pip_sp1
Piperaceae	Pip_sp2
Piperaceae	Pip_sp3
Piperaceae	Pip_sp4
Piperaceae	Pip_sp5
Piperaceae	*Piper hispidum* Sw.
Poaceae	*Panicum laxum* Sw.
Polypodiales	Pol_sp1
Polypodiales	Pol_sp2
Polypodiales	Pol_sp3
Polypodiales	Pol_sp4
Pteridaceae	*Adiantum latifolium* Lam.
Rubiaceae	*Palicourea tomentosa* (Aubl.) Borhidi
Rubiaceae	*Psychotria* cf. *deflexa* (DC.) Borhidi
Rubiaceae	*Psychotria racemosa* Rich.
Rubiaceae	*Sabicea villosa* Roem. & Schult.
Selaginellaceae	*Selaginella* sp. P.Beauv.
Thelypteridaceae	*Thelypteris serrata* (Cav.) Alston
Vitaceae	Vit_sp1

8.1. Summary (German)

Der heutige Rückgang der Waldbedeckung ist hauptsächlich auf Landnutzung und die Umwandlung dieser Flächen in landwirtschaftlich genutzte Gebiete zurückzuführen. Tropische Regenwälder sind hiervon besonders betroffen. In neotropischen Ländern wie Costa Rica und Puerto Rico wurde die Waldfläche in den 70er und 90er des letzten Jahrhunderts drastisch reduziert, um Viehweiden zu schaffen und die Fleischproduktion zu fördern. Viele dieser Weiden wurden im Laufe der Jahre wieder aufgelassen, was die Regenerierung der Wälder auf diesen Flächen ermöglichte, sei es durch natürliche Prozesse oder durch aktive Aufforstungen. Es gibt eine Vielzahl von Studien über die Sukzession der Vegetation auf solchen Flächen. Sie beziehen sich jedoch hauptsächlich auf Bäume und es wird nur sehr wenig über krautige Arten und deren Entwicklung berichtet. Um einen Einblick in die Krautschicht tropischer Wälder zu erhalten, wurden fünf Sektoren in drei unterschiedlich alten Wiederaufforstungsgebieten des COBIGA-Projekts (Corredor Biológico La Gamba) in der Golfo Dulce Region in Costa Rica ausgewählt, um eine Chronosequenz der krautigen Vegetation zu erstellen. Die Krautschicht innerhalb dieser Sektoren wurde mit den Methoden für Vegetationsaufnahmen nach Braun-Blanquet (1932, 1964) mit Hilfe von 10 x 10 m großen Plots durchgeführt. Die Daten wurden dann unter verschiedenen Aspekten wie der Alpha- und Beta-Diversität und der Familienzusammensetzung innerhalb der Plots analysiert. Die Ergebnisse zeigten, dass die Krautschichten der drei Wiederaufforstungsgebiete in mehrfacher Hinsicht sehr unterschiedlich sind. Zum einen unterschied sich die Familien- und Artenzusammensetzung deutlich von Gebiet zu Gebiet. Die Familienzusammensetzung änderte sich mit zunehmendem Alter mit erkennbaren Trends für beispielsweise Poaceae, Araceae und Marantaceae. Floristisch waren alle Plots heterogen und die Mehrzahl der einzelnen Arten bedeckte nur bis zu 1 % der Plot-Flächen. Die Alpha-Diversität der Plots war im Durchschnitt durchwegs eher gering, so dass die Diversität der Krautschicht als nicht besonders hoch eingeschätzt werden konnte. Die Beta-Diversität zeigte hohe Arten-Turnover-Raten beim Übergang von einem zum anderen Wiederaufforstungsgebiete. NMDS-Analysen zeigten, dass sich Plots innerhalb der gleichen Wiederaufforstungsflächen, in Bezug auf ihre Artenzusammensetzung und die Bedeckung durch bestimmte Arten, denen der gleichen Wiederaufforstungsfläche untereinander ähnlicher waren als im Vergleich zu Plots von anderen Flächen. Die

Ergebnisse legen nahe, dass die Krautschicht in den Tropen ähnlichen Trends folgt, wie sie aus gemäßigten Regionen bekannt sind. Es ist jedoch nicht klar, ob Zeit oder der Zustand der Flächen zu Beginn der Wiederaufforstung, die Hauptfaktoren für die Entwicklung auf den untersuchten Gebieten waren. Weitere Studien und Beobachtungen müssen durchgeführt werden, um ein differenzierteres Verständnis diese beiden möglichen Treiber der Entwicklung der Krautschicht auf Wiederaufforstungsflächen zu bekommen.