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Master's Thesis

Natural regeneration of tropical wet secondary rainforests in lowlands of Southwest Costa Rica

submitted by Carola Egger

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Statutory declaration

I hereby declare that I am the sole author of this work. No assistance other than that which is permitted has been used. Ideas and quotes taken directly or indirectly from other sources are identified as such.

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Table of contents

Index of figures

Abstract

Current environmental challenges such as climate change and biodiversity loss call for immediate and effective action that builds on profound research. One of the most pressing issues of our time is the global loss of forest cover. Especially tropical rainforests are of high importance regarding biodiversity conservation, carbon storage and the provision of multiple other ecosystem services. As a large fraction of tropical forests are second-growth forests, their regeneration potential is receiving increasing attention. Several studies suggest that aboveground biomass and species richness can recover rapidly during the first years of natural regeneration. However, the regrowth of tropical forests is a complex issue that shows variations across sites and needs further research to understand its full potential.

This study investigated 12 tropical secondary lowland rainforest plots of 500 m^2 each at different sites in the La Gamba valley of Southwestern Costa Rica and their development within four years. Forest age ranged between 5 and 55 years in the initial year of observation. Aboveground biomass (AGB) as well as species richness and composition were analysed in 2015 and 2019 and compared with old-growth forests. Mortality, recruitment and leaf area index (LAI) were observed in 2019. Furthermore, the effects of previous land use on the regeneration pathway was investigated. The results revealed a rapid recovery of AGB reaching > 60 % of old-growth forest AGB after 25 years. Secondary forests accumulated up to 260.1 Mg / ha, while old-growth forests reached 322 Mg / ha on average. Species richness also increased fast, although slower than AGB. Up to 41 species were found per 500 m^2 plot and secondary forests had reached > 40 % of species numbers in old-growth forests after 25 years. While recruitment rates of the observed forests significantly declined over time, mortality showed a weaker negative correlation with age. No correlation was found between LAI and forest age or AGB.

The findings support the notion of a high regeneration potential of forests in tropical regions and point out the need for further research. Implications for forest management, reforestation and the support of natural regeneration are discussed. This study calls for researchers, decision-makers and practitioners to collaborate on finding holistic and sustainable solutions to tackle the issue of global forest loss.

Keywords: secondary forests, natural regeneration, aboveground biomass accumulation, biodiversity, forest succession, species richness

Zusammenfassung

Aktuelle Umweltherausforderungen wie Klimawandel und Biodiversitätsverlust erfordern unmittelbares und effektives Handeln, das auf fundierter Forschung basiert. Eines der akuten Probleme unserer Zeit ist der globale Verlust an Waldfläche. Besonders tropische Regenwälder sind von hoher Relevanz hinsichtlich Biodiversitätserhalt, Kohlenstoff-speicherung sowie vieler weiterer Ökosystemdienstleistungen. Da ein großer Anteil tropischer Wälder aus Sekundärwäldern besteht, erhält deren Regenerationspotential zunehmende Aufmerksamkeit. Mehrere Studien weisen darauf hin, dass sich die oberirdische Biomasse und das Artenreichtum innerhalb der ersten Jahre der Regenerierung schnell erholen kann. Allerdings ist das Nachwachsen tropischer Wälder eine komplexe Thematik, die Variationen zwischen Standorten aufweist und weiterer Forschung bedarf.

Diese Studie erforschte 12 Flächen von je 500 m^2 in tropischen Regenwäldern des La Gamba Tals im Südwesten Costa Ricas und deren Entwicklung innerhalb von 4 Jahren. Das Alter der Wälder reichte von 5 bis 55 Jahren im ersten Aufzeichnungsjahr. Oberirdische Biomasse, Artenvielfalt und Artenzusammensetzung wurden in den Jahren 2015 und 2019 analysiert und mit altgewachsenen Wäldern verglichen. Mortalität, Wachstum und Blattflächenindex wurden im Jahr 2019 aufgezeichnet. Zudem wurde der Effekt vorheriger Landnutzung auf den Regenerationsverlauf untersucht. Die Ergebnisse zeigten eine rasche Regenerierung der oberirdischen Biomasse, die > 60 % der Biomasse in altgewachsenen Wäldern nach 25 Jahren erreichte. Die Sekundärwälder akkumulierten bis zu 260,1 Mg / ha, während die altgewachsenen Wälder im Schnitt 247,5 Mg / ha erreichten. Auch die Artenvielfalt stieg in den ersten Jahren schnell an, jedoch langsamer als die Biomasse. Bis zu 41 Arten pro 500 m^2 Fläche wurden gefunden und die Sekundärwälder erreichten > 40 % der Artenanzahl in altgewachsenen Wäldern nach 25 Jahren. Während die Wachstumsraten der untersuchten Wälder mit zunehmendem Alter signifikant abnahmen, zeigten Mortalität und Alter eine schwächere, negative Korrelation. Der Blattflächenindex wies keine Korrelation mit der oberirdischen Biomasse oder dem Alter der Wälder auf.

Die Ergebnisse befürworten ein hohes Regenerationspotentials von Wäldern in tropischen Regionen und verdeutlichen die Notwendigkeit weiterer Studien. Schlussfolgerungen für Forstwirtschaft, Wiederaufforstung und die Unterstützung natürlicher Regeneration werden diskutiert. Diese Studie ruft Forscher, Entscheidungsträger und Mitwirkende dazu auf, zusammen an ganzheitlichen und nachhaltigen Lösungen für das Problem des globalen Verlustes an Waldfläche zu arbeiten.

1. Introduction

Tropical rainforests represent unique and significant ecosystems as they provide various ecosystem services and are highly relevant to climate dynamics and biodiversity conservation (Köhl et al., 2020; Leberger et al., 2020). The importance of tropical rainforests in the global carbon cycle is widely recognized since they embody major carbon sinks and sources (Aryal et al., 2014; d'Oliveira et al., 2011; Fonseca et al., 2011). Large amounts of carbon are stored in the aboveground biomass of these ecosystems (N'Guessan et al., 2019; Taylor et al., 2014). Furthermore, the biodiversity and species abundance that can be found in tropical rainforests is unprecedented (Zermeño-Hernández et al., 2016). These water abundant forests with little annual temperature changes and contain a high species richness consisting of a variety of trees, epiphytes and lianas as well as seedling, saplings and climbers in the understory layer (Hill and Hill, 2001). Primary tropical rainforests can enclose over 100 tree species per hectare, whereas most temperate forests do not exceed 30 tree species per hectare (Hill and Hill, 2001). Next to the diverse flora, tropical rainforests offer habitats for numerous animal species including insects, birds, mammals, reptiles, and amphibians (Hill and Hill, 2001; WWF, 2018).

The prevention of natural hazards, soil and erosion protection, nutrient availability and water purification are additional characteristics that raise the value of forest ecosystems (Köhl et al., 2015; Masiero et al., 2019). Moreover, forest benefits comprise social and economic dimensions regarding products that can be obtained from them and used for consumption or within the market economy. These forest goods reach from fuelwood and timber to non-timber forest products such as fruits and nuts, forage or medicinal plants (Masiero et al., 2019; Girão Rodrigues de Mello et al., 2020; Hermans-Neumann, 2016). Especially in the tropics, the provision of forest goods serving as livelihood source is fundamental for many communities (Brancalion et al., 2017).

Given these aspects, the high value of tropical rainforests and their implications for sustainability aspects are evident, allowing the conclusion that changes in global forest cover impact ecological, economic and social processes and structures (Masiero et al., 2019; Köhl et al., 2020; Hermans-Neumann, 2016). Since society and consequently our economy are embedded parts of the environment according to the nested dependencies model after Doppelt (2012), environmental protection has strong implications for future generations (FAO, 2015). Growth and degradation of the world's forests and human interaction with these ecosystems highly affect the two major sustainability challenges of our times, climate change and biodiversity loss (FAO, 2020).

Global forest cover has decreased substantially over the last decades with a forest loss of 178 million hectares between 1990 and 2020 (FAO, 2020). **Figure 1** shows the global forest expansion and deforestation over the past 30 years (FAO, 2020). The net annual rate of global forest area change decreased by 7.84 million hectares per year between 1990 and 2000, 5.17 million hectares per year between 2000 to 2010 and 4.74 million hectares per year between 2010 and 2020. Both forest expansion and deforestation rates have reduced over time, though deforestation continues to outweigh increases in forest cover (FAO, 2020).

Figure 1: Global forest expansion and deforestation for 1990–2020 (million hectares per year) (FAO, 2020)

A large part of the world's forests is located in the tropics comprising 45% of the total global forest area as shown in **Figure 2(a)** (FAO, 2020). The global distribution of changes in forest area shows high spatial variations depending on region and country (Leberger et al., 2020). The majority of forest losses occur in the Global South, whereas the Global North is mainly characterised by gains in forest area (FAO, 2016). **Figure 2(b)** displays the average net annual changes in forest area by climate domain from 1990 until 2015 (FAO, 2016). Forest losses occurred predominantly in tropical regions, where a high degree of land use conversion has taken place (FAO, 2016).

Growing and continuing deforestation and forest degradation have caused significant losses of primary forests and native vegetation and changed the global forest landscape over the past years (FAO, 2020; Villa et al., 2018). High deforestation rates in tropical regions are mainly a result of agricultural land use expansion due to the rapidly growing demand for agricultural products (FAO, 2020; Zermeño-Hernández et al., 2016). Large amounts of tropical forests have been cleared to enable the conversion to areas for animal husbandry and crop production. The FAO (2016) stated a net increase in agricultural land use area for 2000 until 2010. Timber extraction through logging represents a second anthropogenic driver for deforestation. Furthermore, droughts, wildfires and diseases cause forest losses in many regions (Leberger et al., 2020).

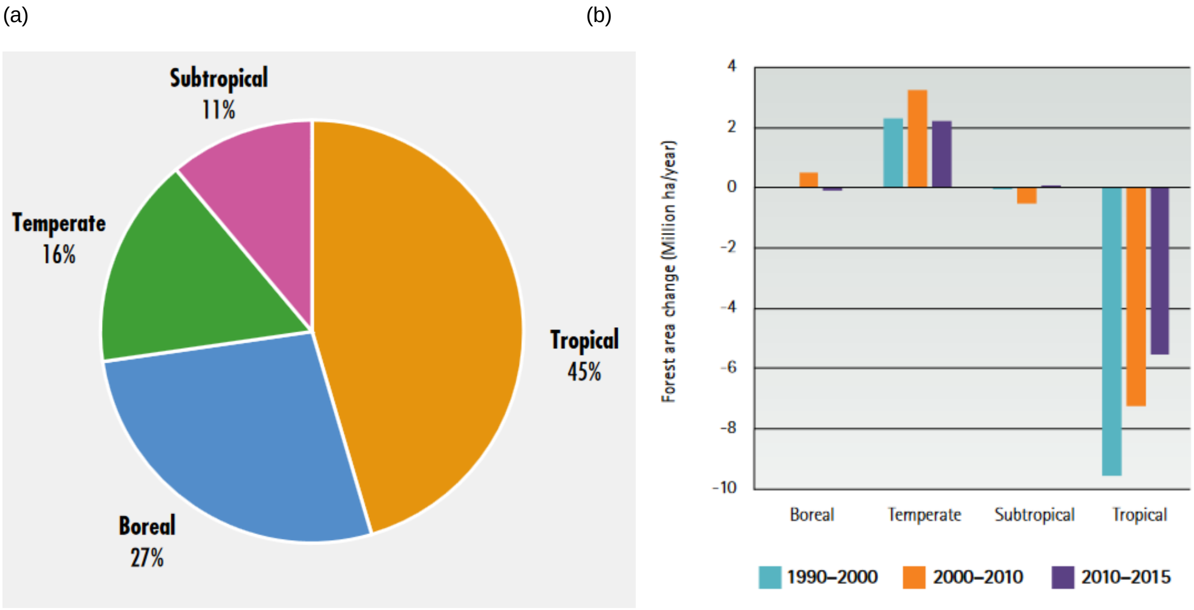


Figure 2: (a) Global forest area by climate domain in 2020 and (b) net annual average change in forest area by climate domain, 1990-2015 (FAO, 2015)

The observed forest losses have far-reaching environmental consequences. The reduction in tree cover contributes to a rise in atmospheric carbon dioxide levels and subsequently enhances climate change (Köhl et al., 2020). Nascimento and Laurance (2002) identified the deforestation of tropical forests as a main contributor to the release of major greenhouse gases in the atmosphere and consequently global warming. Furthermore, forest degradation can result in large-scale losses of biodiversity and causes a lack of habitat and biological corridors for various animal species (Hill et al., 2019; Rozendaal et al., 2019). **Figure 3** shows the global distribution of forest biodiversity significance for areas of forest loss between 2000 and 2018 (Hill et al., 2019). Forest biodiversity significance hereby implicates the contribution of each region to the distribution of various animal species. The highlighted areas (dark purple) show regions where decreases in forest cover led to an immense reduction in forest-dependent species (Hill et al., 2019). These significant locations are predominantly found in tropical regions including Central America, West Africa and Southeast Asia, matching the areas with the highest biodiversity and deforestation rates (FAO, 2020). Moreover, missing protection through forests leads to an increase in soil erosion, damages through natural hazards and a lack of soil nutrients (Masiero et al., 2019). In addition, the absence of socio-economic benefits through forest ecosystem services and goods are a concern for human well-being (Masiero et al., 2019; Köhl et al., 2015).

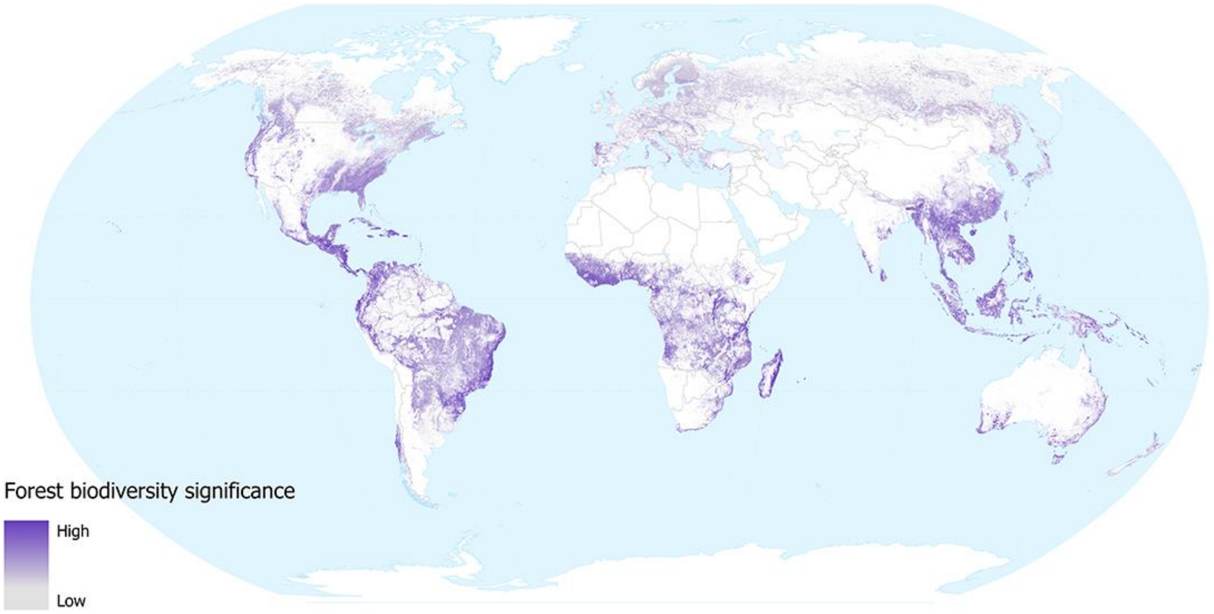


Figure 3: Forest biodiversity significance for areas of forest loss during 2000–2018 (Hill et al., 2019)

Nevertheless, forests can regrow and regenerate biomass as well as biodiversity after disturbances. Thereby, they build new, valuable ecosystems and regain their environmental and socio-economic importance and benefits (Chazdon, 2014; Zermeño-Hernández et al., 2016). These regrown forests are referred to as secondary, second-growth or regenerating forests (Chazdon, 2014; Chokkalingam and de Jong, 2001). These terms apply to forests post deforestation and full clearance as well as to forests regrowing after degradation, exploitation, and logging (Chazdon, 2014; FAO, 2020). Natural regeneration of such forests describes the naturally occurring patterns of regrowth that can be distinguished from the active human intervention that takes place when referring to reforestation and plantations (Chazdon, 2014; FAO, 2020; FAO, 2015). During regeneration, secondary forests undergo different stages of succession which entails changes in structure and species composition (Chazdon, 2014; Chua and Potts, 2018). Primary and old-growth forests have reached an almost steady state in which biomass and species composition only show little changes (Chazdon, 2014). In contrast, young secondary forests are characterized by high variations and constant development of new structures, though they have the potential to reach old-growth forest characteristics over time (Chazdon, 2014; Chua and Potts, 2018).

The FRA 2015 considers 93% of forest area globally as natural forests and 7% as plantation forests (FAO, 2015). Secondary forests of various age and in different phases of succession constitute a large part of the world's forest area (Abbas et al., 2019). 74% of all natural forests are categorized as secondary, regenerated forests, while primary forests comprise only 26% (FAO, 2015). The growing degradation of primary forest landscapes contributes to an increasing relevance of second growth (Chokkalingam and de Jong, 2001). Regenerating forests can contribute largely to an expansion in forest area and reduction of atmospheric CO_2 on a global scale (Chazdon, 2014). This enables additional solutions for the environmental challenges of our time, next to conservation efforts of primary forests and reforestation of fallow land (Chadzon, 2014). The potential of regeneration, after agricultural land is abandoned, is highly relevant in many regions of the tropics (Zermeño-Hernández et al., 2016).

Due to this, regenerating tropical rainforests are of increasing importance for scientific research, and studies investigating recovery patterns of these forests are in high demand (Chua and Potts, 2018; d'Oliveira et al., 2011). Secondary tropical rainforests can recover large amounts of their aboveground biomass (AGB) in a few decades and therefore have a high potential for carbon sequestration and mitigation of carbon emissions (Chazdon et al., 2016; Poorter et al., 2016). Furthermore, biodiversity and species richness show a high regeneration potential (Abbas et al., 2019). Nevertheless, the predictability of regeneration pace is limited since studies show large variations and uncertainties in recovery rates of both biomass and biodiversity (Abbas et al., 2019; Chua and Potts, 2018; Chazdon et al., 2016; Poorter et al., 2016). The potential of regrowth depends on a variety of factors including prior land use, type and intensity of disturbances, climate conditions and surrounding vegetation (Abbas et al., 2019; Chazdon, 2014; Hofhansl et al., 2014; Villa et al., 2018; Zermeño-Hernández et al., 2016). Little is known on the influencing parameters of observed developments of regenerating forests (Poorter et al., 2016).

In this regard, the study asks the following research questions:
RQ1: How fast does AGB accumulate in regenerating tropical secondary rainforests?
RQ2: What successional patterns and changes in species richness and composition can be identified?
RQ3: How does forest regeneration develop over time and do secondary forests converge towards the characteristics of old-growth forests?
RQ4: Which environmental factors determine growth and recovery rates?
RQ5: How do mortality and recruitment change forest structure and species composition?
RQ6: Is the present canopy cover related to forest age and AGB?
RQ7: Which conclusions can be drawn for conservation, restoration, and reforestation efforts?

For this purpose, 12 tropical secondary rainforest plots of different ages in the La Gamba valley of Southwest Costa Rica were investigated with regards to their natural regeneration potential.

While most studies on forest regeneration are based on chronosequences, where forests of different age are compared in a space-for-time substitution, observations over time are far less common (Chazdon, 2014; Guariguata and Ostertag, 2001; Villa et al., 2018). This study uses a combined approach by comparing forests of different age as a chronosequence, as well as observing single sites over a period of four years. Subjects of the investigation were the processes of natural regeneration and succession in secondary rainforests with a focus on biomass accumulation and species recovery. Furthermore, mortality and recruitment rates were calculated, and hemispherical photography was used to calculate leaf area indices and analyse canopy cover developments.

Consistent with the research questions stated above, the following hypotheses guided this research:
Hypothesis 1: AGB and species richness regenerate fast in secondary forests and converge towards values found in old-growth forests with increasing age, while species composition recovers at slower pace.
Hypothesis 2: Successional patterns vary across different forest sites depending on environmental parameters such as previous land use.
Hypothesis 3: Mortality and recruitment rates are highest in young secondary forests and change the species composition over time from secondary towards old-growth specialists.
Hypothesis 4: The leaf area index describing the present canopy cover in secondary forests is related to forest age and AGB.

2. Methods

2.1 Study area

The study area is located in the Golfo Dulce Region of Southwest Costa Rica, close to the city of Golfito, and surrounded by large parts of protected forest area. The observed sites are situated around the village of La Gamba (N 8°42''61', W 83°12'97''; height above sea level: 70 m) at the periphery of the Piedras Blancas National Park that comprises about 148 km^2. The park is part of to the Osa Conservation Area in the Puntarenas Province and holds a primary rainforest with a remarkable biodiversity (Weissenhofer et al., 2008). The research was conducted in the humid tropical secondary forest segments that spread along the La Gamba valley, alternating with primary forests, pastures, agricultural land, and homesteads. The main anthropogenic land use changes are reflected in large areas of pasture and oil palm plantations, representing important constituents of the local economy. The University of Vienna operates a research station close to the village (8°42’03’’ N, 83°12’06’’ W) which functioned as base, research facility and laboratory for this study.

The study site comprised 12 secondary forest plots in different forest segments of various age and succession stage. **Figure 4(a)** shows the location of these plots, in a radius of approximately 5 km around the village centre of La Gamba, and the borders of the Piedras Blancas National Park. Data of 15 old-growth forest plots of 1 ha each located in Costa Rica was available for comparison with secondary forests (Morera-Beita et al., 2019). The data set of the old-growth forest plots was used as reference values for AGB accumulation and species recovery in the secondary forest plots. **Figure 4(b) and (c)** indicate the location of the study area in the Golfo Dulce Region and within Costa Rica.

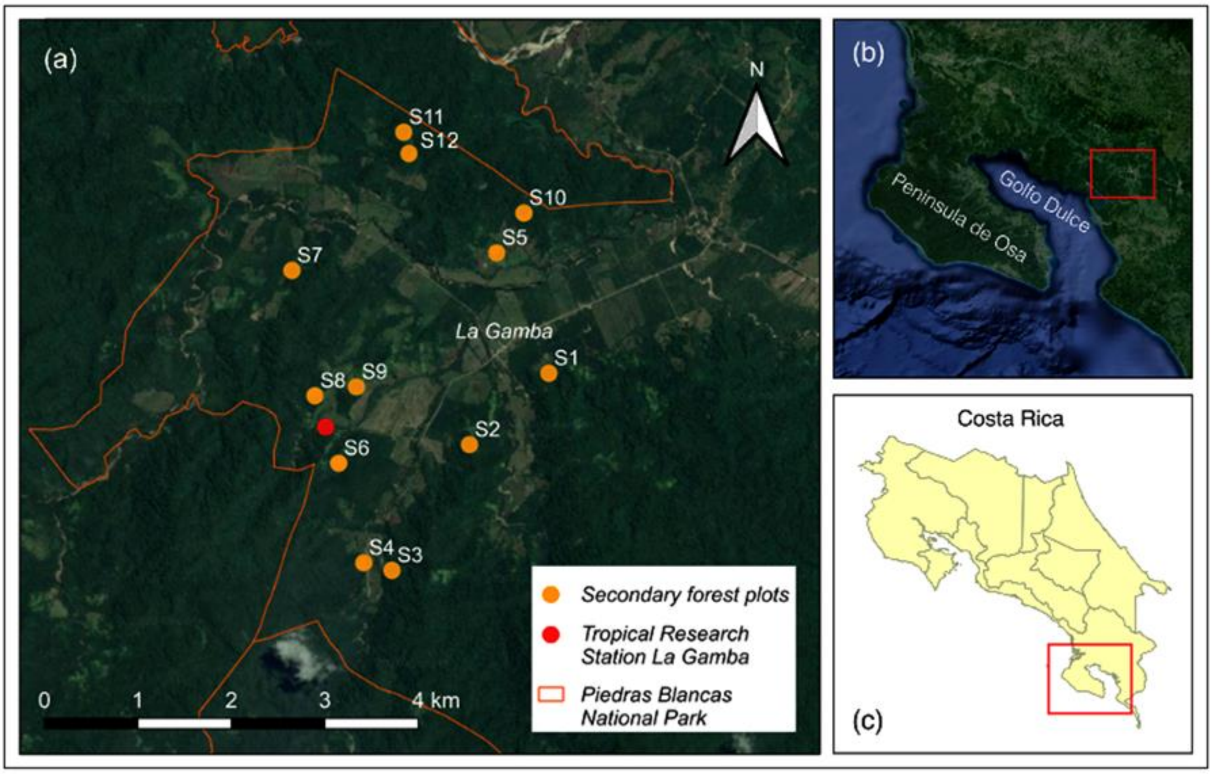
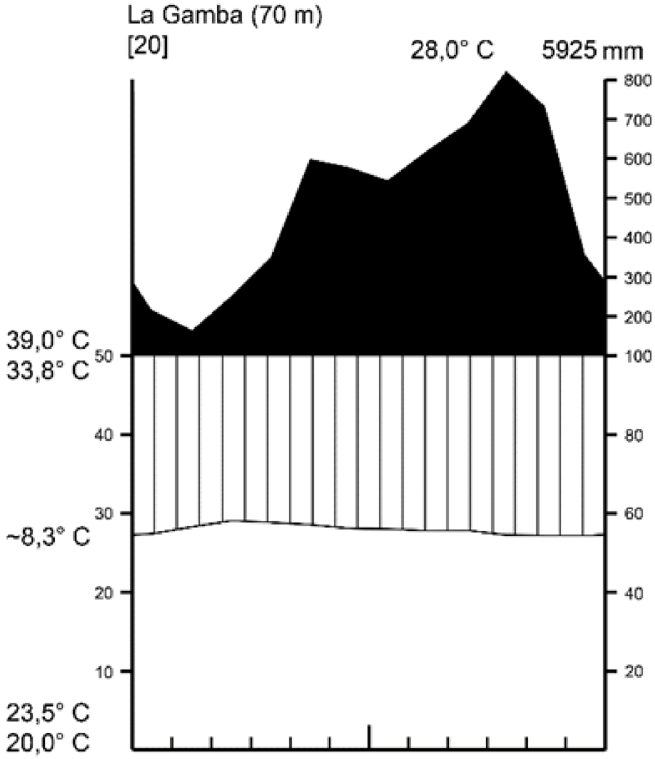


Figure 4: Location of the study area (a) around the village of La Gamba (b) in the Golfo Dulce Region (c) in Costa Rica (Oberleitner, 2016)

Figure 5 shows images of the La Gamba valley and its main land types including secondary and old-growth forests, oil palm plantations and pasture. Secondary forests are recognizable by the distinct yellow flowers in the canopy of the common pioneer tree *Vochysia ferruginea* that typically flowers in April and May aligning with the fieldwork period.

Figure 5: Impressions of the secondary forests with yellow flowered Vochysia ferruginea in the La Gamba valley alternating with oil palm plantations, pasture and old-growth forests



Quelle der Klimadaten: Tropenstation La Gamba, Diagramm erstellt von: Susanne Pamperl

Figure 6: Climate Diagram of La Gamba 1998 – 2019 based on average of measurements at the Tropical Research Station La Gamba (source: https://www.lagamba.at/tropenstation/wissenschaftliche-informationen)

The natural environment of the region is highly influenced by its humid tropical climate with steady high temperatures and abundant rainfall. **Figure 6** shows the climate diagram for La Gamba for 1998 until 2019 (average of measurements at the Tropical Research Station La Gamba). The climate data collected of the Tropical Research Station La Gamba shows a mean annual temperature of 28.3°C varying from 24°C in the night to 33°C during the day. The mean annual precipitation is 5880 mm with a short dry period between January and March and an enduring wet season with fewer variations throughout the rest of the year. The humidity is generally high with over 80% relative humidity and even higher levels within forest areas with an average of 97.7% (Weissenhofer et al., 2008). The occurrence and impact of strong winds in the area are categorized as small by Weissenhofer et al. (2008).

Figure 7 illustrates the environmental conditions of the study region and the surrounding area including the Golfo Dulce Region and the Osa Peninsula (Taylor et al., 2015). The environmental gradients indicate rainfall, soils, elevation, and geology. The primary soil types occurring in the study region are Ultisols with high acidity levels in advanced weathering stages, as well as less weathered Inceptisols in lower elevations (Hofhansl et al., 2014; Taylor et al., 2015). The forests investigated in our study are situated in lower elevations between 80 and 170 m above sea level and surrounded by more mountainous land. According to the life zones of Holdridge (1967), the secondary forests in the La Gamba Valley are categorized as tropical lowland wet forests. Geological substrates in the area are mainly basalt and volcanic sediments (Taylor et al., 2015).

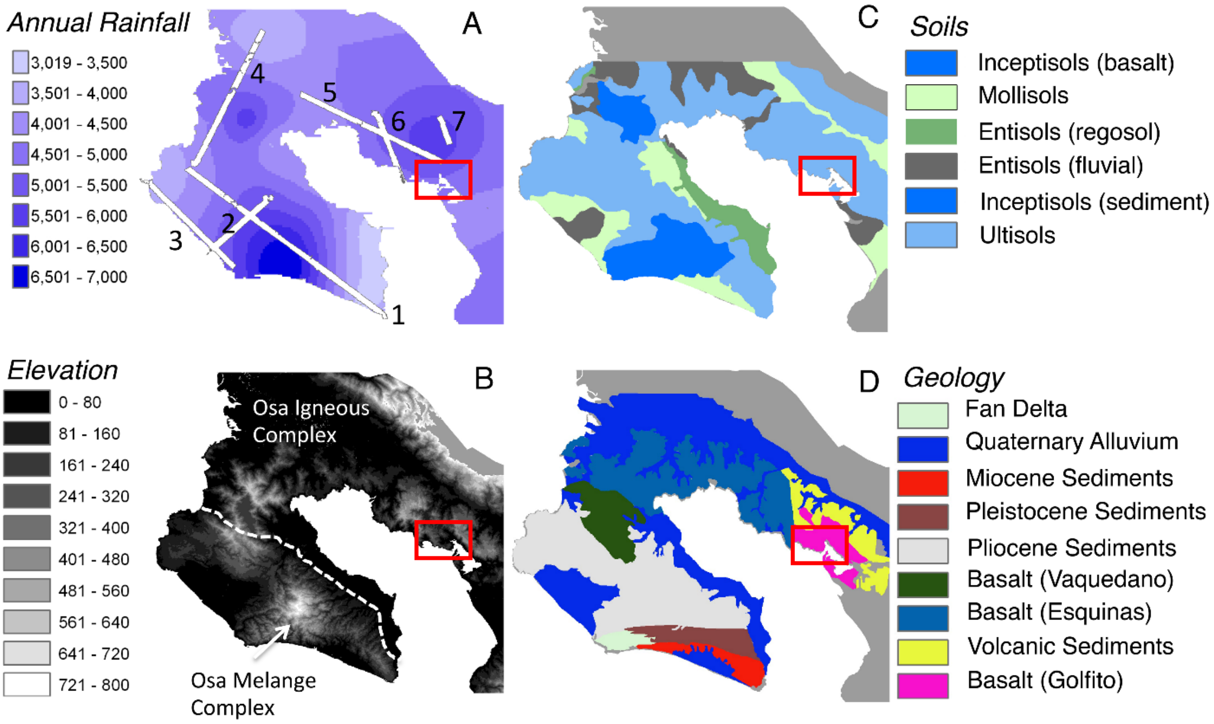


Figure 7: Environmental gradients of the Osa Peninsula and the Golfo Dulce Region with study area marked in red, detecting (A) annual rainfall (white lines caused by flight lines of observatory), (B) elevation, (C) occurring soil types and (D) geological substrates and sediments (Taylor et al., 2015)

2.2 Establishment of plots

The 12 individual forest plots comprised 500 m^2 each and were established in the year 2015. Secondary forests were identified using aerial photographs of 1960, 1968, 1973, 1983, 1990, and 1998 (Costa Rican Land Survey, Instituto Geográfico Nacional de Costa Rica) as well as satellite images of 2003, 2008 (Quickbird), 2012 and 2014 (GeoEye). These airborne images and additional interviews conducted with landowners were used to obtain the age and history of the sites. Forest age was either determined by landowner statements or image comparison in the software QGIS (QGIS_Development_Team 2020) depending on availability. For the image analysis, the median year between two images showing a change from non-forest to forest land was selected as year zero of forest regeneration. Land use prior to natural regeneration was categorized in two main groups, pasture and logging (Oberleitner, 2016).

Site selection criteria included a minimum forest size of 1 ha and a divergence in elevation up to 100 m within each plot. Forest age ranged from 5 to 55 years in 2015 with a slope between 7° and 43.2°. Restrictions of steepness and minimum forest dimensions were given to avoid data inconsistencies through side effects. The plots were situated 80 to 170 m above sea level.

Each plot was composed of five subplots that were laid out as 10 x 10 m squares assembled depending on suitability of terrain conditions and accessibility of the area (Oberleitner, 2016). **Figure 8** illustrates the setup and boundary conditions of the 12 secondary forest plots for an exemplary constellation of subplots that varied across sites.

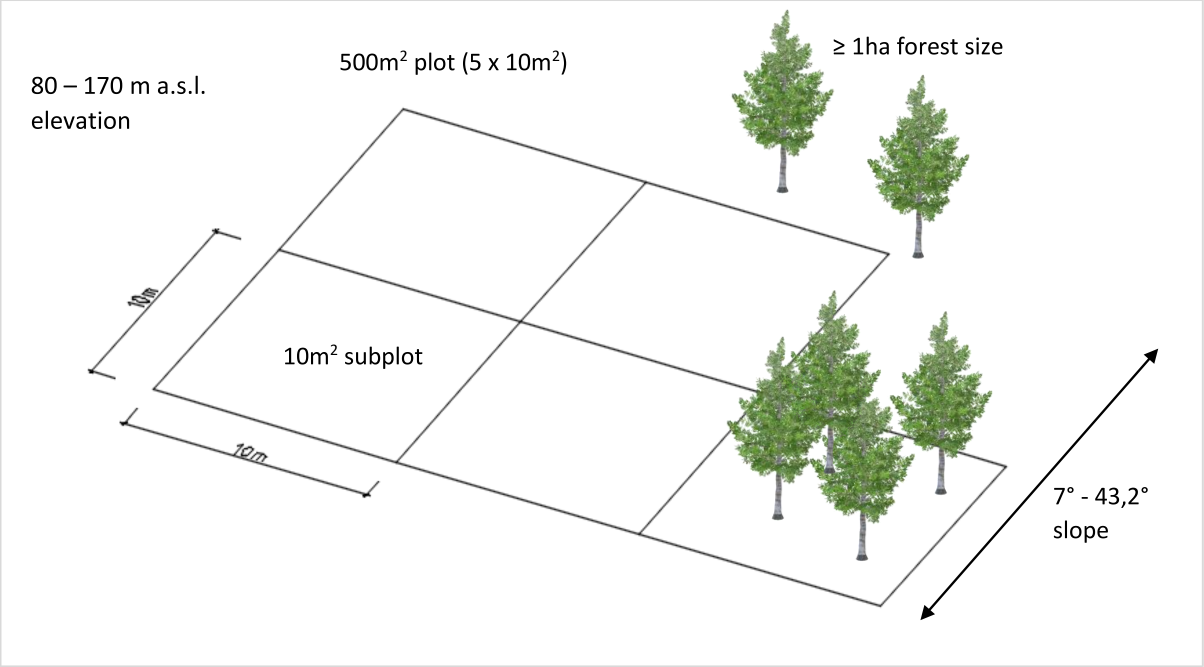


Figure 8: Secondary forest plot setup and characteristics with exemplary constellation of subplots

2.3 Data collection

An initial inventory of trees in all 12 plots was carried out in 2015 (Oberleitner, 2016). All woody plants within the plot with a diameter at breast height (DBH) ≥ 2.5 cm were documented. The DBH of woody plants up to 5 cm was measured with a sliding calliper, while the circumferences at breast height of trees over 5 cm were measured using a measuring tape. Next to DBH, family, genus and species of all recorded plants were determined as far as possible. Dead trees were measured and included in the inventory.

The coordinates of four corner points of each plot were recorded using a GPS device to trace back plot locations. Tree positions were surveyed within each subplot using a measuring tape from the subplot border lines. From these measurements, the position of each tree within the plots was calculated. The plots were additionally marked with poles on the edges of each subplot in 2015, and trees were equipped with number plates if diameters were above a minimum size to prevent larger tree damages or splitting of stems.

To assess the progress of biomass accumulation and succession over time, the same plots were remeasured in 2019 for a direct comparison with data from the previous study. I used a Garmin eTrex 10 GPS device to relocate the positions of the plots in 2019 with the documented plot coordinates that were available from the 2015 data set. Plot and tree markings, including poles and tags from 2015, were found in good condition in 2019, as shown in **Figure 9**, which enabled a consistent remeasurement of trees and comparison of data.

Figure 9: Condition of plots in 2019: (a) pole marker at plot corner, (b) retrievability of plot coordinates with GPS device, and (c) preservation of tree number tags

DBH of all woody plants recorded in 2015 were remeasured in 2019, insofar as they were retrievable. Dead and broken trees were documented and, if possible, measured. Trees that could not be found were furthermore marked as missing in the documentation. Data were directly compared on site with the inventory of 2015 and checked for plausibility. Species determination was revised to ensure accuracy of the data set. In addition, all newly grown trees with a DBH over 2.5 cm were measured and species were determined. Tree positions of newly grown trees were assessed with a TruPulse 360R laser rangefinder and inclinometer from a known reference point (tree with known position or corner point of a subplot). The newly included trees were equipped with tree tags for future references analogue to the initial study.

Next to the repetition of data collection methods applied in 2015, additional data was gathered in 2019 to enlarge the available information relevant to forest regeneration. Wood samples were collected from common tree species to calculate wood density. Core samples from stems were taken for trees > 10 cm DBH with an increment borer from the bark to the tree centre. For smaller trees, branch samples of 10 cm length were collected due to the likelihood of damages when using an increment borer. Four to five samples were collected from different individuals per species. The samples were processed in the laboratory facilities of the Tropical Research Station La Gamba. The tree bark was removed carefully with a knife from all samples. If the pith of the branch samples was larger than 2 mm in diameter, samples were split in half as shown in **Figure 10(a)**, and the pith was subsequently removed. Sample volumes were measured by submerging the individual sample pieces into a beaker filled with water on a scale and documenting the difference in weight through water displacement (**Figure 10(b)**).

Figure 10: Processing of wood samples in laboratory including (a) splitting of branch samples and (b) volume measurements with water displacement method

Unlike the procedure applied for branch samples, stem samples were cut into 2.5 cm sections and numbered according to their position from the cambium to the centre. The exact length of the sections was subsequently measured with a sliding calliper. Due to the standardized diameter of the increment borer, it was possible to calculate volumes from these measurements directly. All samples were stored in paper bags for further use and labelled with tree species, individual number, and plot number. The wood samples were left to dry in the oven at a temperature of 100-105°C for 72 hours. Afterwards, samples were weighed in the laboratory and wood density was calculated for all individuals.

In addition, digital hemispherical photographs of the canopy cover were taken to calculate gap fraction and leaf area index. Digital hemispherical photography is a commonly used method to describe the constitution of forest canopies and its characteristics (Chianucci et al., 2014). To take the photographs, a camera with an extreme wide-angle lens looking upwards was positioned perpendicular using a water level in a stand height of 1,50 m for each image. One picture was taken at each corner of every subplot, resulting in a number of 10-11 photographs per plot (depending on the subplot composition) and 139 photographs in total. **Figure 11** shows the positions of the camera for the hemispherical photograph acquisition in an exemplary subplot constellation.

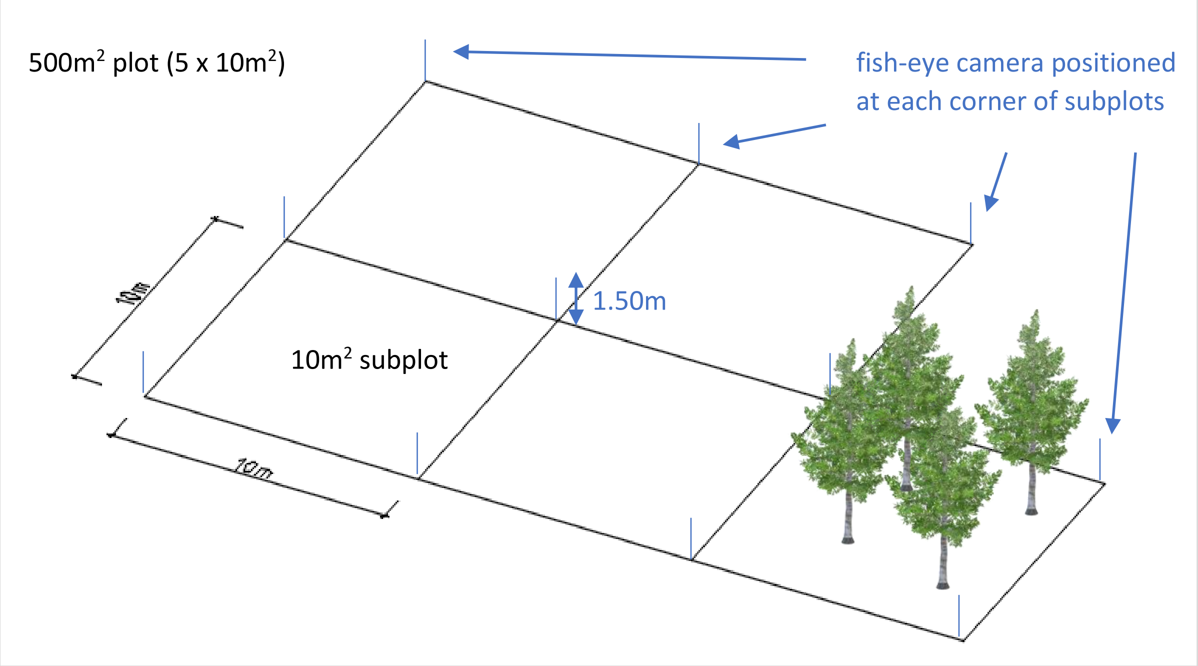


Figure 11: Camera positions for hemispherical photographs in exemplary plot setup

The pictures were captured with a Nikon Coolpix 995 camera with a fisheye lens on a monopod (**Figure 12(a)**). **Figure 12(b)** gives an example of a digital hemispherical photograph taken in one of the secondary forest study sites. Overexposed hemispherical photographs can lead to a misrepresentation of the observed canopy when using computer-based analysis (Beckschäfer et al., 2013) as applied in this study. Due to this incident, photographs were taken exclusively at sunrise, sundown or when the sky was cloudy to avoid direct sunlight and enable an image analysis as accurate as possible.

Figure 12: (a) Nikon Coolpix 995 camera setup with fisheye lens on monopod and (b) exemplary digital hemispherical photograph

2.4 Data analysis

2.4.1 Combined approach for temporal trend analysis

A chronosequence approach, combined with an over-time observation, was applied in this study for a complementary analysis of temporal changes. The chronosequence approach uses a space-for-time substitution method that enables an indirect observation of chronological developments (De Palma et al., 2018; Walker et al., 2010). Hereby, the assumption is made that forests of different ages with comparable environmental conditions undergo the same regeneration processes and therefore resemble different successional stages of a single forest (Chazdon, 2014; Mora et al., 2015). This approach allows an extensive data collection in a short period of time (Chazdon, 2014; Zhao et al., 2014a). However, the underlying assumption involves uncertainties since local disturbance regimes, environmental interactions and successional pathways can vary between sites (Chazdon, 2014; de Palma et al., 2018; Mora et al., 2015; Walker et al., 2010; Zhao et al., 2014b). When monitoring the same forest over time, such uncertainties and misleading data can be avoided (Chazdon, 2014; Walker et al., 2010; Zhao et al., 2014a). However, large-scale time series over long periods can be difficult to implement, require high financial resources and time, and are often impossible when forests are cleared again (Chazdon, 2014; Zhao et al., 2014a).

Chazdon (2014) and van Breugel et al. (2007) suggest a complementary combination of both approaches, as was implemented in this study. With regards to AGB and species recovery, we compared the sites of different successional stages with each other and additionally observed the single plots over the course of four years. Data were analysed by comparing the resulting trends and assessing whether the space-for-time trend seen in the data from 2015 was reflected in the changes between 2015 and 2019. With regards to the chronosequence, discrepancies between sites were interpreted with caution, and possible external factors causing variations were pointed out. However, the observation over time applied in this study was only performed over a relatively short time period. This calls for further observations in order to make conclusions of regeneration pathways with more certainty. Therefore, we suggest the continuation of this research as a longitudinal study with a data collection over several intervals.

2.4.2 Data cleaning

To provide transparency of data processing and cleaning, notable aspects of the inclusion and exclusion of data will be discussed in the following. Trees in all plots that were found dead in 2015 were removed from the data set. Individuals that showed highly unlikely growth were excluded from the analysis of tree growth. A particularly large tree of the species *Brosimum utile* with a DBH of 117 cm in 2019 was found in the secondary forest plot 1, subplot 3. Due to the large size of this tree individual, it was assumed to be an old-growth remnant tree that did not match the age of the secondary forest. Due to neighbouring effects, tree growth in the surrounding area is likely to have been affected by this old tree distorting the data on regeneration and succession. Given this incident, we decided to remove the subplot containing the large *Brosimum utile* from the data set and extrapolated the data of the remaining four subplots to 1 ha. At plots 6, 24 trees of the species *Calophyllum brasiliense* and at plot 10, 37 trees of the species *Gmelina arborea* were possibly planted. These species are typically used in reforested areas in the region. However, the exclusion of these plots did not change our results significantly, and the data was therefore included and used for further analysis. R version 3.6.4. (www.r-project.org) was used to perform data processing as well as statistical analysis.

2.4.3 Aboveground biomass estimation

A common allometric model by Chave et al. (2014), revised by Réjou-Méchain et al. (2017), was used to estimate AGB in the 12 study plots. The calculation without height measurements includes the variables DBH (D), wood specific gravity (ρ) and a climate constant (E) that varies depending on the site location. Consequently, the estimated AGB (AGB_{est}) can be determined by the following equation:

$$\mathrm{AGB}_{\mathrm{est}} = \exp[-1.803 - 0.976E + 0.976\ \ln(\rho) + 2.673\ \ln(D) - 0.029\ [\ln(D)]^2]$$

The climate parameter E has a value of -0.09591224 in the study region and was computed from the longitudinal and latitudinal gradients (lat = 8.6, lon = - 83.3). Wood specific gravity (WSG) was calculated from the on-site wood samples to the extent of availability. A preference was set on stem sample data compared to branch sample data, as the stem usually accounts for a predominant part of AGB, especially for larger trees. However, stem data was only used if more than two samples were available to generate an average. Otherwise, branch samples were included in the data analysis. For smaller trees, wood density was subsequently derived from branch samples. For species without local data, a data set from forests in Panama was used for calculation (Hietz et al., 2017). For species that were not included in either of these data sets, values provided by the Global Wood Density Database were used (Zanne et al., 2009). Community weighted mean (CWM) WSG was obtained by calculating the mean WSG of all individuals weighted by basal area (BA). The R package “biomass” was applied for calculating AGB values of the whole data set (Réjou-Méchain et al., 2017).

An alternative AGB calculation considering tree height, as additionally provided by Chave et al. (2014), was not possible due to the inaccessibility of such measurements, mainly as a result of closed canopy and hence a lack of visibility of treetops. However, the equation above is commonly used for the estimation of AGB and provides an improved model over the publication of Chave et al. (2005). A linear regression model with AGB ~ log(age) was fitted to the data to observe AGB accumulation over time. For comparison with old-growth forests, the contribution to AGB of species ranging from 2.5 cm to 10 cm DBH was estimated since only individuals > 10 cm DBH were included in the inventory of old-growth forests. Therefore, unpublished data from 100 m^2 subplots in three of the old-growth forests were used. The estimation suggested that these smaller trees add 3.7 % on average to total AGB. This share was subsequently added to the AGB of old-growth forests to allow an accurate comparison with secondary forests. The effects of age, previous land use type, forest cover in a 1 km radius, slope, and species numbers on AGB were tested using linear mixed-effects models in R statistical software. The data set of 2015 as well as 2019 was included and the year of observation used as random variable. Only significant parameters were kept in the final model which included age, forest cover and number of species for the AGB model.

2.4.4 Species richness

Species richness of secondary forest plots was derived from the number of species of all woody plants ≥ 2.5 cm DBH that were found in each plot at both censuses. The comparison of species richness within secondary forests and between census 1 and census 2 was performed including all individuals ≥ 2.5 cm DBH for each plot of 500 m^2 size. For the comparison with old-growth forests, only individuals > 10 cm DBH were included in the analysis to align secondary forests with old-growth forest plots where only trees > 10 cm DBH were documented and no data on smaller individuals were available. Furthermore, plot size of the 1-ha old-growth forest plots was adjusted to match the 500 m^2 secondary forest plots. Within the old-growth forests, 500 m^2 subplots were randomly drawn 100 times, and species richness and composition were determined for each of these subplots and averaged. As for AGB, the effects of different environmental parameters (age, prior land use, forest cover and slope) on species richness were tested using linear mixed-effects models. Significant factors in the final model included age as well as previous land use.

2.4.5 NMDS test for similarity analysis of species composition

The R package “vegan” was used to perform non-metric multidimensional scaling (NMDS) to identify similarities in species composition of secondary forests and old-growth forests. NMDS is an ordination technique for multivariate analysis that can be used to display a matrix of data (Davison, 1991). The analysed data is thereby presented as points in a two-dimensional space with the distance between these points indicating dissimilarities between the objects of observation (Davison, 1991; Shepard, 1966). In this study, dissimilarities of species composition between plots were analysed within the NDMS test using log transformed basal area (log(BA)) as species scores. Therefore, the data set had to be adjusted to compare secondary forest plots with old-growth forest plots due to the differences in plot size and included tree size classes. To create uniformity in plot size, random 500 m^2 subplots were selected, NDMS calculated 100 times, and average NMDS values taken for each plot. For standardisation of DBH inclusion range, trees of secondary forests < 10 cm DBH were included if they belonged to a species that had individuals > 10 cm DBH. Although these trees have not reached over 2.5 cm in DBH, they are likely to grow to this size due to their species characteristics.

2.4.6 Mortality and recruitment rates

For further analysis of forest dynamics and population changes, all trees ≥ 2.5 cm DBH were classified as individuals that were present and alive in both years of observation (surviving trees), new grown individuals since census 1 (recruited trees), and individuals that died in the timespan between census 1 and census 2 (died trees). Mortality and recruitment rates were derived from this data for each plot and compared across the sites of different ages. Furthermore, demographic rates were calculated for the ten most common tree species found in the 12 secondary forest plots. Calculation of the annual mortality rate (*M*) was performed using the following equation (Gomes et al., 2003):

$$\mathrm{M} = \{1 - [(\mathrm{N_0} - \mathrm{m})/\mathrm{N_0}]^{1/\Delta\mathrm{t}}\} \text{ x } 100\ [\%/\mathrm{year}]$$

with N_O indicating the population size at the first census in 2015, *m* expressing the number of dead individuals from the initial population and Δt indicating the time between the first census at time t_0 and the second census at time t_1 ($\Delta \mathrm{t} = \mathrm{t_1} - \mathrm{t_0}$). Recruitment rates (*R*) were calculated in a similar manner (Gomes et al., 2003) with the equation:

$$\mathrm{R} = \{[(\mathrm{N_0} + \mathrm{r})/\mathrm{N_0}]^{1/\Delta\mathrm{t}} - 1\} \text{ x } 100\ [\%/\mathrm{year}]$$

with *r* denoting the number of recruited, living individuals counted at the second census. Mortality and recruitment rates are expressed in percentage of the initial population per year. The developments of mortality and recruitment rates over time were evaluated using linear regression models. Effects of previous land use were tested additionally.

Furthermore, mortality and recruitment rates were related to the habitat specialization of species to secondary or old-growth forests. A data set, comprising a wide range of species and their occurrence in old-growth and secondary forests, was available for this analysis (Kleinschmidt et al., 2020). Observational data of species abundance in the two different habitats was derived from Letcher et al. (2015) for the Neotropics and from Morera-Beita et al. (2019) for local forests. Resulting from the number of individuals per species present in old-growth and secondary forests, a continuous variable for habitat specialization (*HS*), ranging from 0 to 1, was calculated (Kleinschmidt et al., 2020):

$$HS = \frac{total\ number\ of\ individuals\ occuring\ in\ OG\ forests}{total\ number\ of\ individuals\ occuring\ in\ OG\ and\ SG\ forests}$$

where a value of 0 indicates a species solely occurring in secondary forests, a value of 1 presents species only found in old-growth forests, and species occurring in both forest types are displayed on the scale in between. Peña-Claros (2003) provides a comparable index including forest age, which is, however, only available for fewer species due to the limited knowledge of forest age in many cases. Habitat specialization indices were used from species with a total abundance of > 20 individuals in all habitats. The correlation of mortality and recruitment with habitat specialization was analysed for a total population of > 10 individuals in the 12 observed secondary forest plots.

2.4.7 Hemispherical image analysis

The digital hemispheric photographs taken in all plots were used to estimate the gap fraction in the canopy and the leaf area index (LAI) for each site. For these calculations, the sections of visible sky on the hemispherical photographs need to be identified (Chianucci and Cutini, 2012). In the first step, the image-processing application ImageJ was used to classify the photographs into areas of sky and occlusion from vegetation using an individually adjusted threshold for each image. **Figure 13** shows three examples of hemispherical photographs in their original form (above) and after processing with threshold settings in ImageJ (below) dividing the image into black areas for covered and white areas for open sky.

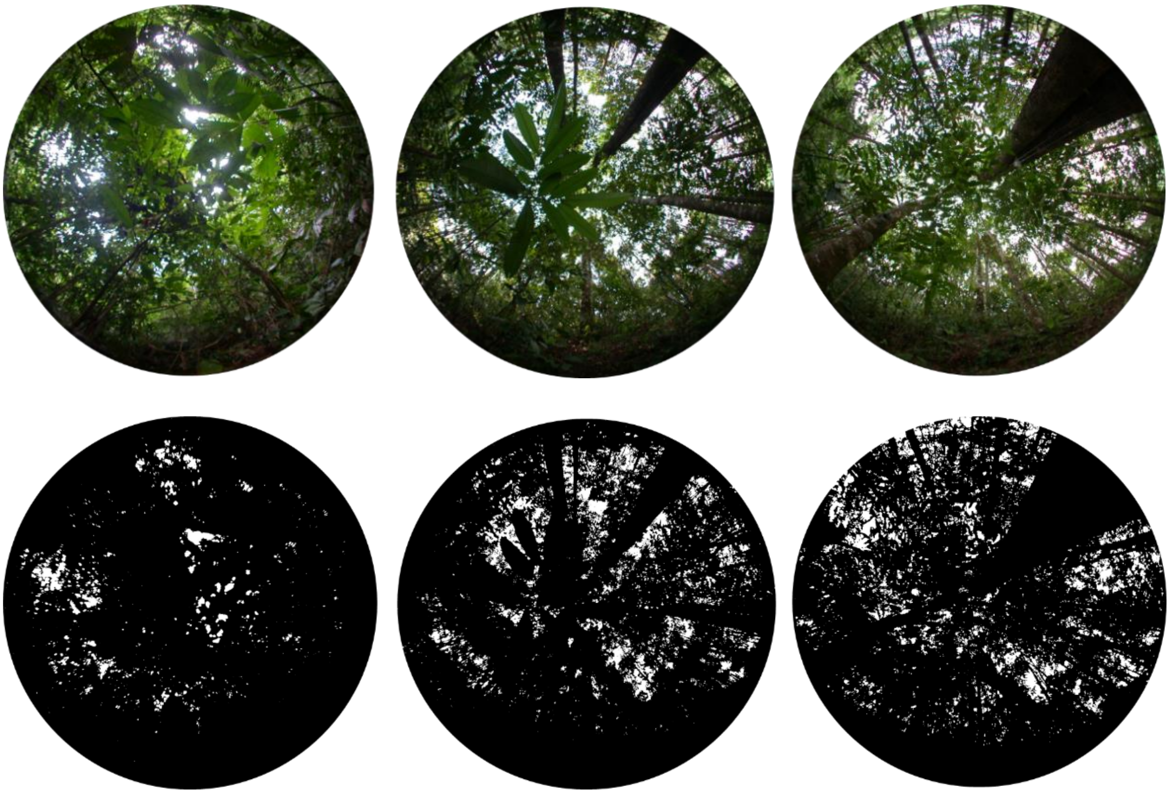


Figure 13: Original digital hemispherical photographs taken at study site (above) and edited images in processing program ImageJ with threshold value setting for covered (black) and open (white) sky (below)

Distortions of the images through water droplets or shadows were corrected if necessary, and non-representative photographs were excluded from the data set. Photographs were categorized as non-representative if a high distortion through large leaves of understory plants (i.e. *Carludovica palmata*) was present or the image showed a high level of overexposure that altered the representation of leaf area and open sky.

Proceeding with the edited images, a calculation of gap fraction and LAI was performed using the program Hemiview 2.1. In this process, the gap fraction is measured for multiple zenith angles (Chianucci and Cutini, 2012). **Figure 14** illustrates the projection of the captured canopy cover on the flat surface that equals the display on the resulting image (Gonsamo et al., 2013). Every point in the canopy cover (point M) can be displayed as a representing point on the two-dimensional surface (point M'). Thereby, all points in the canopy are represented by a specific zenith angle θ and azimuth φ (Chianucci and Cutini, 2012; Gonsamo et al., 2013).

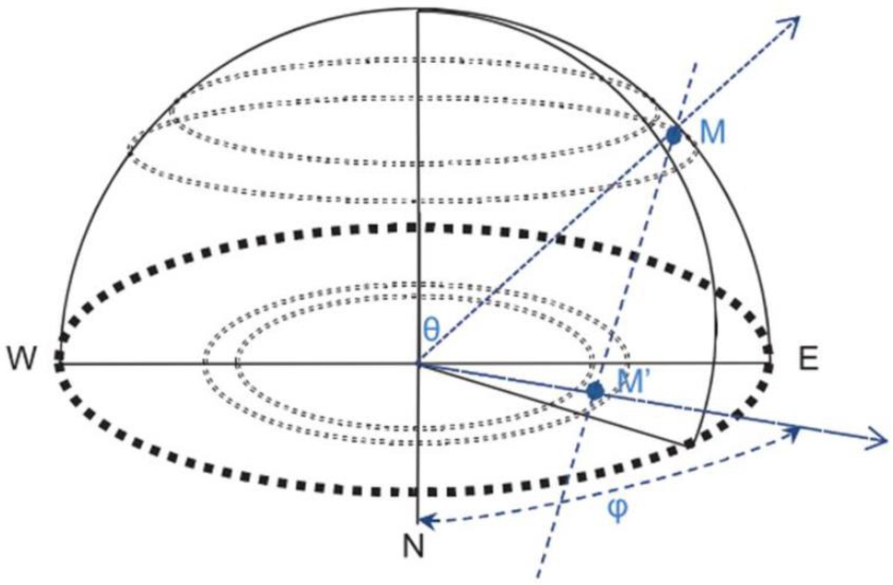


Figure 14: Projection of canopy cover on image created by fish eye lens (Gonsamo et al., 2013)

LAI can subsequently be derived from the Beer-Lambert law. The equation includes the gap fraction *P(θ)*, the zenith angle θ, and the G-function *G(θ)* that resembles the proportion of leaves that are projected perpendicular to the zenith angle onto the two dimensional surface (Chianucci and Cutini, 2012):

$$\mathrm{P}(\theta) = \exp\left(-\frac{\mathrm{G}(\theta)\mathrm{LAI}}{\cos(\theta)}\right)$$

With this underlying theory, LAI can be estimated with a modification of the Beer-Lambert law (Chianucci et al., 2014). Values for all hemispherical images were computed with Hemiview 2.1 and an average for each plot was taken to give a representative LAI value for every site. The settings within the program were tailored to the applied fisheye lens model, radius and position on the image.

3. Results

3.1 Overview of plot characteristics

The inventory of all secondary forests sites comprised an area of 6000 m^2 holding 135 species belonging to 45 families in 2019. A total of 1264 individuals with a DBH ≥ 2.5 cm was documented. In few cases, taxonomic identity of species could only be determined to genus level (49 individuals, 3.9 %) or could not be determined at all (10 individuals, 0.8 %). An overview of stand characteristics of all secondary forest plots is presented in tables enclosed in **Annex 1** for the year 2015 and **Annex 2** for the year 2019. AGB, species richness and composition, mortality and recruitment as well as LAI will be discussed in separate sections. Basal area (BA) for each plot reached values from 5.3 to 46.9 m^2 / ha in 2015 and 10.3 to 44.4 m^2 / ha in 2019. CWM-WSG differed between 0.33 and 0.51 g / cm^3 in both inventories. A regression of CWM-WSG with log(age) showed that forest age was not related to CMW-WSG ($p = 0.43$). Significantly higher CMW-WSG values than in secondary forests were obtained in old-growth forests with an average of 0.54 g / cm^3 ($p < 0.001$). Dominant tree species are presented in **Annex 1 and 2** as well as incorporated in the following short descriptions of each plot with *Vochysia ferruginea* as the most common species in many plots.

Before presenting the results of the statistical analysis, an overview of the 12 different study sites is provided in this chapter that elucidates characteristics and particularities of each plot. This serves to enable a better understanding of regeneration processes, specific disturbance regimes and environmental factors. It should be pointed out that some aspects mentioned in this section solely serve as additional information derived from on-site observations and are not reflected in further quantitative statistical analysis (i.e. abundance of lianas, understory ferns). These observations can nevertheless uncover a more detailed view on cause-effect relations regarding the regeneration of individual sites. In the following, short descriptions of each plot are given. A specification of forest age in the year 2019 and land use before natural regeneration is provided for each plot in brackets added to the respective caption.

Plot 1 *(59 years, pasture)*

Figure 15: Steep slope of plot 1 (top) and remnants of logged trees in subplot 1 (bottom)

Plot 1 was situated directly adjacent to a pasture area for cattle husbandry next to an oil palm plantation. The secondary forest in which the plot was established comprised a small river. Dominant tree species in this plot were *Chimarrhis latifolia* and *Guatteria chiriquiensis*. The site encompassed a multilayered, dense canopy. The plot was furthermore characterised by a predominantly steep slope that reached subplot gradients between 27° and 42.7° (**Figure 15, top**). As mentioned above, an extraordinarily large tree with a DBH of 117 cm was found in subplot 3 of plot 1 belonging to the species *Brosimum utile.* This tree was assumed to be an old remnant that was much older than the rest of the regenerating forest. Since the remnant is likely to have changed the surrounding regeneration pathway, the subplot was excluded from further calculations. As visible in **Figure 15 (bottom)**, many trees in subplot 1 were found to be logged along an aisle in 2019. Nevertheless, most of the stems could be located on the ground and the DBH measurements of the residuals were taken. It was not possible to gather further information on the logged trees and recreate the exact time of logging. However, cut surfaces appeared to be relatively fresh suggesting that measurements of cut stems reflect growth until census 2 reasonably accurate.

Plot 2 *(44 years, logged)*

The secondary forest in which plot 2 was set up bordered on a large oil palm plantation. Its topography was in most parts characterized by moderate slopes, compared to most secondary forest study sites, with a gradient ranging from 11° to 33.5°. **Figure 16 (top)** gives an impression of the multilayered, dense secondary forest. The site was characterised by a high population of the species *Tetrathylacium macrophyllum*, recognisable by its characteristic, long, narrow leaves in the tree crown (**Figure 16, bottom**). The upper canopy layer was dominated by *Vochysia ferruginea* and *Guatteria amplifolia*. At the border between subplot 4 and 5, a notable gap was found that differed substantially in tree density and light availability from the rest of the plot. The gap was documented in 2015 and remained present in 2019. It was most likely a result of a gap-phase disturbance such as the fall of a large tree. The gap was found in a longitudinal depression suggesting that erosion processes might have contributed to the disturbance regime.

Figure 16: Regeneration state of plot 2 in 2019 (top) and Tetrathylacium macrophyllum in the canopy of plot 2 (bottom)

Plot 3 and 4 *(39 and 26.5 years, logged and pasture)*

Plot 3 was established in a secondary forest next to a road through the La Gamba valley. The plot was located a few hundred meters up the slope from the roadside. Elevations in the horizontally arranged subplots created a slope ranging from 24.4° to 38.9°. Plot 4 was situated on the opposite side of the road across from plot 3 and showed a similar forest structure. Both plots were characterised by a dense, multilayered canopy, a profound understory layer as well as an abundance of lianas that did, however, not interfere with tree growth (**Figure 17**). The species *Carludovica palmata* was common in the understory of both plots. In contrast to plot 3, plot 4 was separated from the road by a large lawn and a river that flowed close to the forest. The slope gradient varied largely across the horizontally arranged subplots in plot 4. While subplot 1 was relatively plain with a slope of 8.5°, the incline became steeper over the plot's length reaching 43.2° in the last subplot. A gap was found in subplot 3 of plot 4 comprising many individuals of the species *Carludovica palmata*.

Figure 17: Regeneration state of plot 4 characterized by lianas and understory plants

Plot 5 *(9.5 years, pasture)*

The youngest of all study sites was located next to a small road and across from a large pasture area for cattle grazing. On one side, an area dominated by the fern *Dicranopteris pectinata* adjoined the plot. On the other side, the plot borders verged on a secondary forest dominated by *Vochysia ferruginea*. One half of the plot was completely overgrown with lianas, and trees were barely visible under the extensive growth (**Figure 18**). The two subplots 4 and 5, bordering on the fern area, were most affected by liana growth. The lianas bend down most young stems in this area almost completely (**Figure 19**) and reduced their growth, light availability and leaf development. Many of the trees documented in 2015 in this section of the plot could not be located in 2019 due to

Figure 18: Liana growth over trees in plot 5

Figure 19: Lianas bending down a tree in plot 5

the extensive spread of lianas. Furthermore, a high number of ferns was present that invaded from the plot boarder. The second half of the plot (subplot 1, 2, and parts of subplot 3) grew without such major disturbance, and tree individuals in this sector gained substantially in size. The plot borders of this area were merging into further secondary forest. Hence, two diverging states of regeneration were found in the same plot. Canopy cover subsequently differed as well in its characteristics. While lianas covered the sky to large parts in one section of the plot, the other section presented a canopy consisting of small, young tree crowns. Most subplots showed only slight inclines with a slope ranging from 14° to 21.5°. Subplot 5 presented an exception with a slope between 27.5° and 30.5°.

Plot 6 *(24 years, pasture)*

Figure 20: *Dicranopteris pectinata* in understory layer of the ascending slope of plot 6 and stems of *Calophyllum brasiliense* in the background

Plot 6 was reachable by crossing an oil palm plantation close to the Tropical Research Station La Gamba. The plot was located directly behind the oil palm plantation, where the slope became too steep for a continuation of the plantation, and natural regeneration of the forest was possible. Slope gradients were relatively steep varying between 29° to 37.5°. A high number of individuals of the species *Calophyllum brasiliense* was detected in the plot. This circumstance suggests that these species might have been planted. Two subplots showed a notable number of the fern *Dicranopteris pectinata* in the understory layer (**Figure 20**). The dominance of *Callophyllum brasiliense* and other high grown species like *Terminalia amazonia* and *Vochysia ferruginea* was reflected in the canopy and let a relatively high amount of light through.

Plot 7 *(31.5 years, logged)*

Figure 21: Tree stand composition and canopy of plot 7

Plot 7 verged on a pasture area which included a large remnant trees and was situated close to an oil palm plantation. The slope gradient increased upwards of the vertically arranged subplots from 11.5° in the lowest subplot to 30.5° in the highest subplot. Despite some large, tall grown *Vochysia ferruginea* individuals, the plot consisted almost exclusively of small and medium sized trees. Next to *Vochysia ferruginea, Psychotria elata* and *Siparuna andina* were common species at the site. The canopy was therefore dominated by *Vochysia ferruginea* in the upper layer, transmitting a substantial amount of light, and smaller, diverse trees in the lower layer (**Figure 21**). At the highest point of the plot a very large tree of the species *Vochysia ferruginea* had grown with two stems both exceeding 50 cm DBH. One of these branches died of in the period of 2015 until 2019 and fell in longitudinal direction down the slope, creating a localized disturbance in the plot. The tree's fall line reached across the whole length of the plot including all subplots in its disturbance regime. Subsequently, the tree fall took down several other individuals along its way that cracked under the weight and died as well.

Plot 8 *(27 years, pasture)*

Plot 8 was located next to a forest trail, built by the Tropical Research Station La Gamba, that leads through parts of primary rainforest and old-growth vegetation. **Figure 22** shows the trail

Figure 22: "La Torre Trail" of the Tropical Research Station La Gamba leading to plot 8

leading towards plot 8 as well as the surrounding vegetation. The observed site was fully surrounded by primary forest segments with old-growth tree species, and secondary forests dominated by *Vochysia ferruginea*. The site had a slope fluctuating between 19.5° and 37.5°. Within the plot, larger trees of the species *Vochysia ferruginea* with diameters > 50 cm DBH dominated the forest stand next to several individuals of *Cecropia sp.* and *Guatteria amplifolia*. The site was characterized by a multilayered, dense canopy.

Plot 9 *(16 years, pasture)*

Figure 23: Surrounding land of plot 9 dominated by the fern Dicranopteris pectinata

The surrounding vegetation of plot 9 consisted of abandoned land dominated by the pan-tropical fern *Dicranopteris pectinata*. The pervasive understory species overgrew the entire land around the observed forest site as seen in **Figure 23** and invaded the plot partly. The fern can arrest succession in regrowing secondary forests as has been observed in the region (Wyns, 2015). The plot had a gentle gradient ranging from 13° to 25°. Dominant tree species were *Miconia affinis, Miconia trinervia* and *Alchornea costaricensis*. The majority of trees at the young forest site were small, and only few species were able to establish larger individuals. The plot was characterised by an extremely high abundance of lianas that had bent down and suppressed the growth of many trees as visible in **Figure 24**. The high presence of lianas dominated the canopy and reduced light availability within the plot.

Figure 24: Excessive liana growth over trees and marker pole in plot 9

Plot 10 *(29 years, logged)*

Figure 25: Multilayered, dense forest stand of plot 10

Plot 10 was situated in a large secondary forest area. The plot itself was therefore fully surrounded by forest vegetation, while the whole forest bordered on oil palm plantations and pasture areas. **Figure 25** gives an impression of the regeneration state of plot 10 in 2019 characterized by tall grown stems alternating with smaller understory trees with narrow diameters. The site presented a multilayered, dense forest and canopy. The slope gradient at the site varied from 18° to 34.5°. A high number of *Gmelina arborea* was found in plot 10, a tree species that is commonly occurring in planted forests in the area. Concluding from this observation, plot 10 is, similar to plot 6, likely to contain planted individuals and might not be fully naturally regenerated. Other dominant species were the common pioneer tree *Vochysia ferruginea* and the understory tree *Miconia affinis*.

Plot 11 and 12 *(14 and 17 years, logged)*

Figure 26: Vochysia ferruginea dominated plot 11 with more diverse understory layer

Plot 11 and 12 were located in the same area and showed similar characteristics to each other. They were positioned far into the forest and therefore surrounded by secondary forest vegetation. Other land uses nearby consisted of oil palm plantations and pastures for cattle husbandry. The 14 year old plot 11 presented the second youngest of all sites and the lowest gradient with a range between 7° and 17°. Plot 12 was the third youngest site with slopes between 12° and 32.5° The two secondary forests differed largely from the other observed sites in their forest structure and species composition. A monoculture of the pioneer tree *Vochysia ferruginea* had established in both plots as observed in 2015. Individuals in the more diverse understory layer started to grow over 2.5 cm DBH at census 2 in 2019 leading to an increase of species numbers. While the individuals of *Vochysia ferruginea* grew very tall, the understory layer did not exceed heights of approximately 2.5 m to 3.0 m (**Figure 26**). The most common understory tree species in both plots was, by far, *Psychotria elata*.

3.2 Aboveground biomass

The DBH measurements of all 1264 tree individuals showed a size range from the threshold of 2.5 cm to 62 cm DBH (excluding the remnant tree in plot 1 with 117 cm DBH) in 2019. **Figure 27** shows the DBH measurements taken for all trees ≥ 2.5 cm DBH within the plot borders. Measurements of 2019 were compared with the values of 2015 to evaluate changes in DBH for the range of tree sizes. The red line displays a 1:1 ratio and thereby represents zero growth between 2015 and 2019. Consequently, points lying above the line generally suggest an increase in DBH and points below the line suggest a decrease in DBH. Most trees showed notable increases in DBH between 2015 and 2019. Especially larger trees experienced substantial growth, while most of the smaller trees showed slight increases in DBH. Few individuals in the smaller size classes had exceptional gains in DBH. Some trees furthermore experienced slight declines. A decline in DBH can, in most cases, be explained by tree bark that has worn off over the years which commonly occurs in tropical wet rainforest given the prevailing weather conditions.

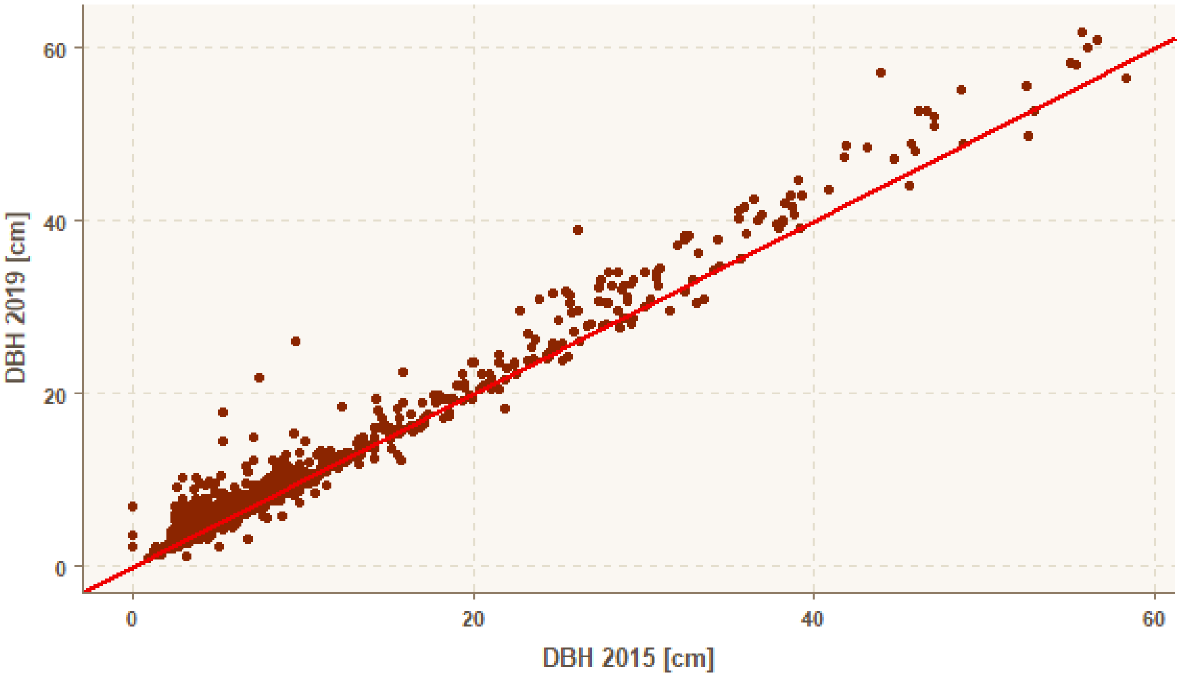


Figure 27: Comparison of diameter at breast height (DBH) between 2015 and 2019, points represent tree individuals within the 12 study plots, 1:1 red line indicates zero change in DBH

Resulting from the DBH measurements taken in 2015 and 2019, AGB accumulation was calculated for both years. **Figure 28** gives an overview of the 12 plots, indicated by plot age in 2019, and their AGB accumulation between 2015 and 2019. The accumulated AGB is thereby displayed for different tree diameters within each plot. Young trees with small diameters generally showed little AGB accumulation, while larger trees in older forests increased significantly more in AGB ($p < 0.001$). Nevertheless, the results show notable variations across the 12 study plots. The youngest plots comprised predominantly small trees < 10 cm DBH with little growth, and the largest tree did not exceed 24 cm DBH in 2019. While the third oldest plot with 16 years showed a similar size distribution, the two *Vochysia ferruginea* dominated plots of 14 and 17 years of age demonstrated higher AGB growth and larger tree diameters. Forests older than 20 years showed a higher number of larger trees ($p < 0.001$). The highest AGB growth per individual was found in the 27 year old plot belonging to a *Vochysia ferruginea* individual of 57 cm DBH.

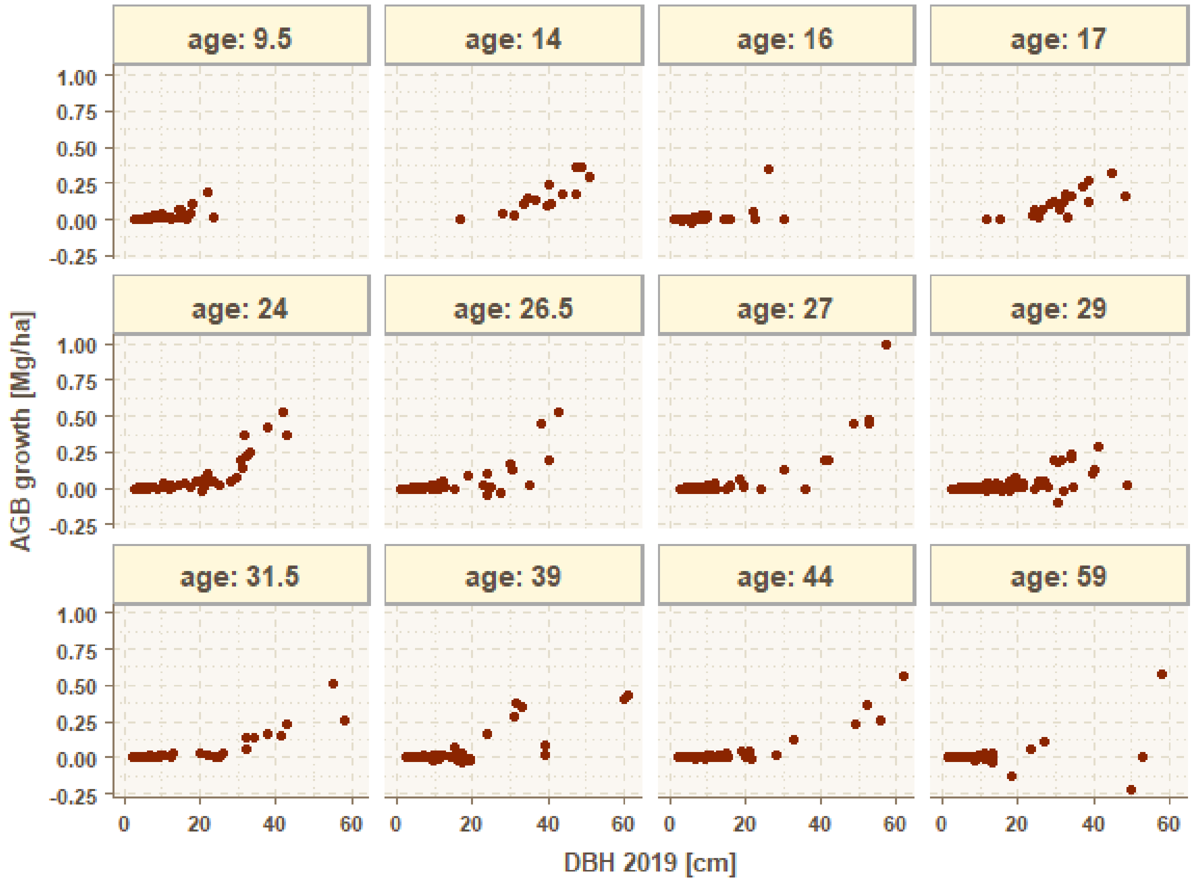


Figure 28: Aboveground biomass accumulation 2015-2019 grouped by plot age (2019) for different tree diameters (2019)

Figure 29 illustrates the total AGB per hectare in secondary forests in relation to forest age for the years 2015 and 2019. Land use prior to regeneration was divided into pasture and logging. AGB of old-growth forests was included for comparison with secondary forests. The smallest AGB was found in the youngest forest with 16.9 Mg / ha after 9.5 years of regeneration. The highest AGB of secondary forests was 260.1 Mg / ha in 2015 and 249.0 Mg / ha in 2019 in plot 10 which had been regrowing for 29 years. The oldest secondary forest with 59 years of age accumulated 219.6 Mg / ha until 2019, experiencing a decrease from the 2015 value of 234.2 Mg / ha. AGB accumulation in old-growth forest plots was 322 Mg / ha on average with a standard deviation of 74.5 Mg / ha. The highest AGB accumulations in secondary forests were converging towards AGB in old-growth forests. Mean values from the 12 forest sites indicate that > 50 % of AGB in old-growth forest had recovered after 20 years of regeneration and > 60 % after 25 years.

Most secondary forests recovered a notable amount of biomass since the beginning of the regeneration process and a clear increase of AGB with age was found ($p < 0.001$, **Annex 3**). The fitted regression model for AGB ~ log(age) ($R^2 = 0.42$, $p < 0.001$) resulted in two highly similar regression curves for 2015 and 2019. Consequently, predictions for AGB accumulation made from the chronosequence analysis in 2015 were confirmed by the data collected four years later. As the overall trend shows, AGB accumulated rapidly within the first years of regeneration. The findings indicate that, after more than 50 years of recovery, AGB of secondary forests can reach the lower threshold of old-growth forests at 247.5 Mg / ha.

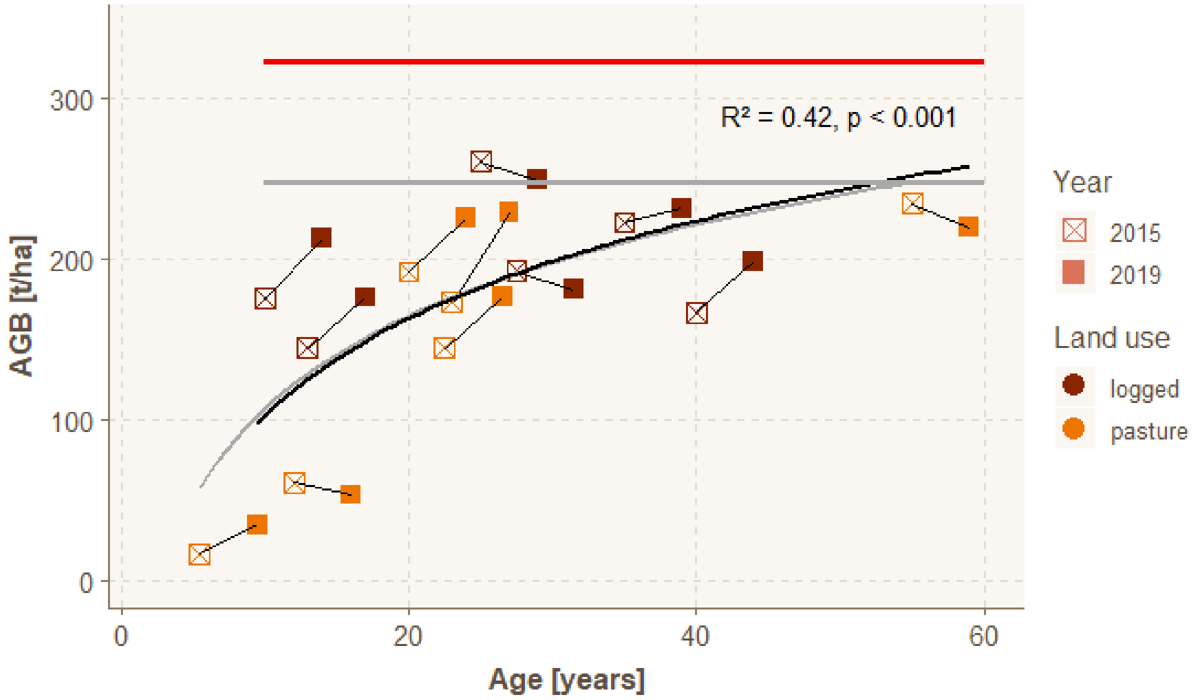


Figure 29: Estimated AGB in relation to forest age for the years 2015 (empty squares) and 2019 (filled squares) with resulting regressions for AGB ~ log(age) for both years. Difference in land use (pasture and logging) are indicated by colour (orange and brown). AGB values of old-growth forests are illustrated by red (average) and grey (- SD value) lines for comparison.

Despite the overall increase of AGB with age, considerable variations occurred between the different sites. Exceptionally fast accumulation of AGB was observed in the young forest plots 11 and 12 (14 and 17 years old in 2019), where the dominant pioneer tree *Vochysia ferruguinea* showed rapid growth in diameter. While several plots showed rapid regeneration of AGB within the four years, others experienced only slight inclines or declines of AGB values between the inventories. In total, four of the 12 sites decreased in AGB (plot 1, 7, 9, 10) due to the death of trees outweighing growth, whereas the remaining plots increased in AGB due to prevailing tree growth and recruitment. Decreases were found, inter alia, in the oldest site, the site with the highest overall AGB and one of the youngest sites. AGB accumulation did not differ significantly between the two land use types pasture and logging. **Annex 3** shows the environmental parameters that had a significant effect on AGB and the number of species resulting from the tested linear mixed-effects models. Age, forest cover and number of species showed significant effects on AGB.

3.3 Species richness and composition

Among the 135 species ≥ 2.5 cm DBH recorded at the 12 study sites, the most abundant species were *Vochysia ferruginea*, *Tetrathylacium macrophyllum, Psychotria solitudinum*, *Miconia affinis, Miconia trinervia*, *Psychotria elata, Siparuna andina, Gmelina arborea, Myriocarpa longipes* and *Alchornea costaricensis*. **Annex 4** provides a list of all species found in the secondary forest plots. **Figure 30** shows the observed number of species per plot in 2015 and 2019 and their distribution across forest age. Species richness increased significantly with forest age ($p < 0.001$, **Annex 3**). In contrast to AGB, the regeneration of species proceeded slower and varied largely across sites. While most plots experienced an increase in the number of species, some showed no change or slight declines.

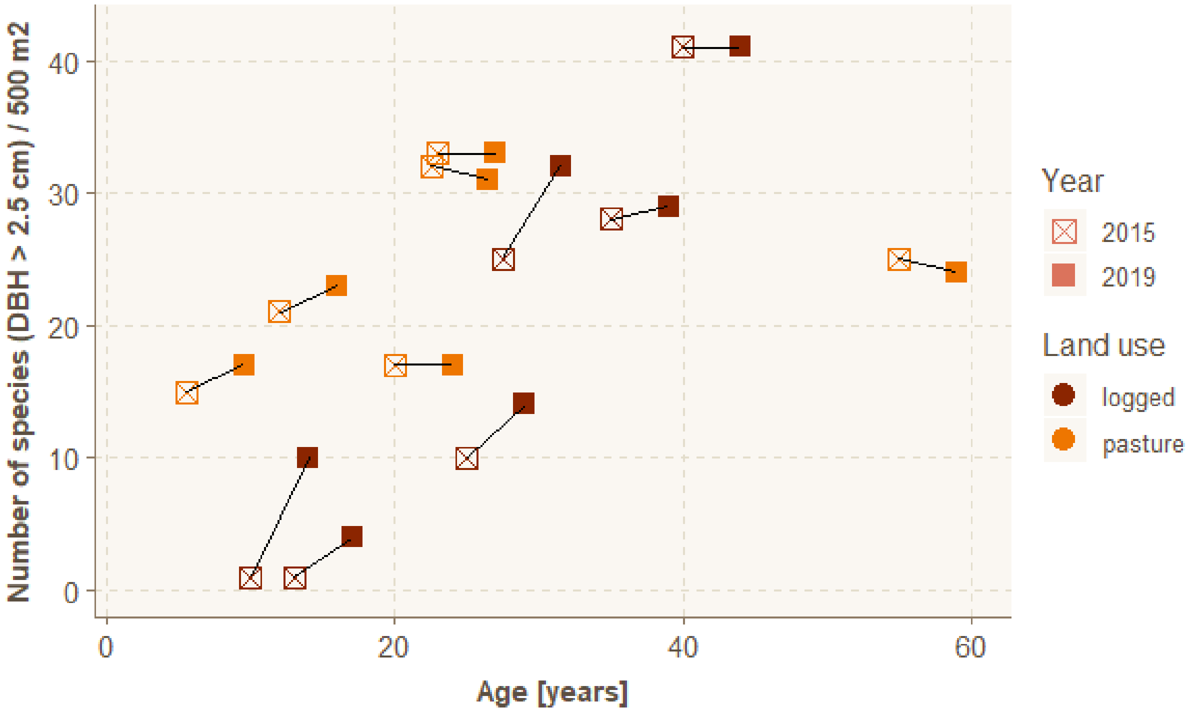


Figure 30: Number of species per secondary forest plot of 500 m² related to forests age for species with a DBH ≥ 2.5 cm

The lowest species richness was found in the two sites dominated by *Vochysia ferruginea* (plot 11 and 12), where the pioneer tree was the only tree species occurring in 2015. Increases in species number in 2019 in both plots occurred due to the more diverse understory layer reaching a DBH ≥ 2.5 cm. The highest species number was found in plot 2 (44 years old) with 41 species and no change in the number of species between the two documented years. Species richness regenerated more rapidly in plots post pasture than post logging ($p < 0.001$, **Annex 3**). A higher number of species had been established in young plots following pasture after only few years of regrowth. Forests after logging were more frequently dominated by

Vochysia ferruginea resulting in a lower number of species in those plots. The pioneer tree was dominant in the plots 2, 7, 11 and 12 that regenerated following logging and in plot 8 following pasture.

Figure 31 displays the number of species per 500 m^2 limited to individuals > 10 cm DBH for comparison with old-growth forests where only trees exceeding this threshold were registered. As for species ≥ 2.5 cm, an increase of species number with forest age was observed. However, for trees > 10 cm DBH, a greater difference in species recovery between logged forests and forests post pasture was detected. Species gains were significantly higher for forest formerly used as pasture ($p < 0.001$). Plots after logging showed no increases in species richness in four cases between 2015 and 2019 and small increases in two cases. In contrast, plots following pasture showed increases in five cases and a decrease in one case.

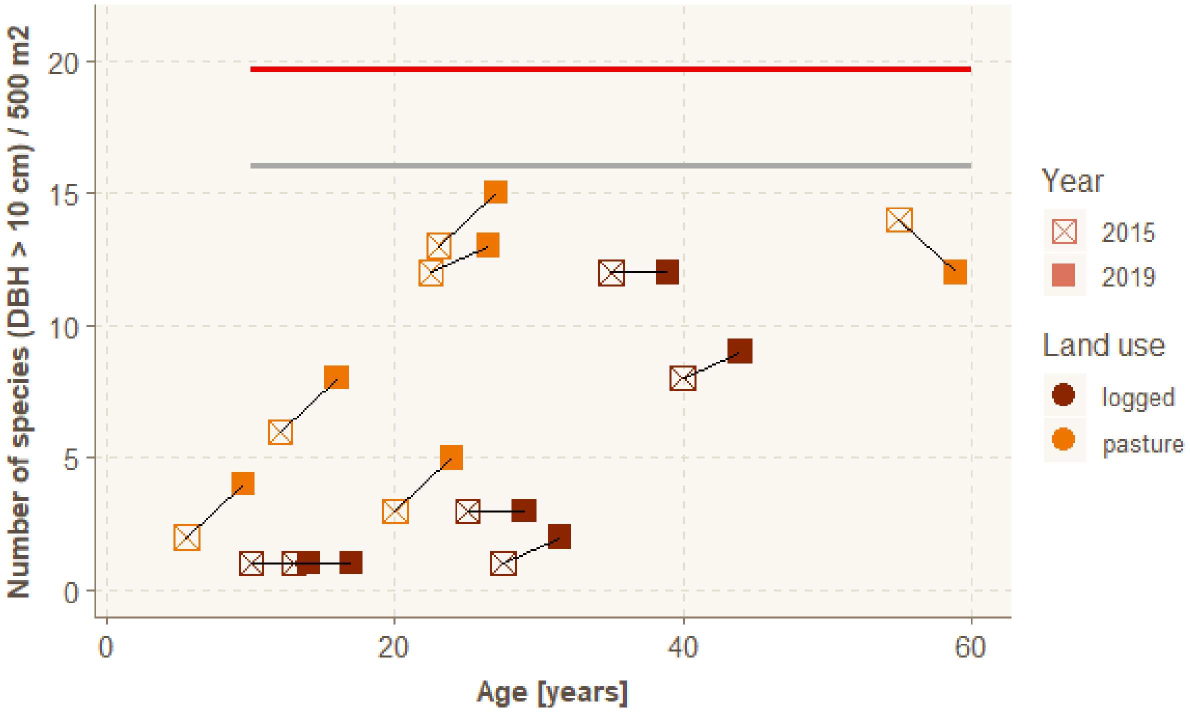


Figure 31: Number of species per secondary forest plot of 500 m² related to forests age for species with a DBH > 10 cm and comparison with randomly drawn 500 m² subplots in old-growth forests. Red line indicates average species number per 500 m² of 15 old-growth forests, grey lines indicate average - SD value.

The average number of species in the 15 old-growth forests plots was 19.6 per 500 m^2 with a standard deviation of 3.4. Secondary forests plots had between 1 and 15 species. Even older secondary forests did not yet reach species numbers typical old-growth forests. Secondary forests recovered > 30 % of species numbers in old-growth forests after 20 years and > 40 % after 25 years. Consequently, species richness in secondary forests converged slower towards old-growth forests than AGB.

The NMDS test results, displayed in **Figure 32**, illustrate the degree of similarity in species composition between the 12 secondary forest plots and the 15 old-growth forest plots. The test was performed for all species included in the inventory but did not differ notably when including only species with a DBH > 10 cm. The NMDS showed a visible distinction in species composition between old-growth forests and secondary forests. Along the axis MDS 1 the two forest types were clearly separated from each other, while the distribution of secondary forest plots along axis MDS 2 showed more variations.

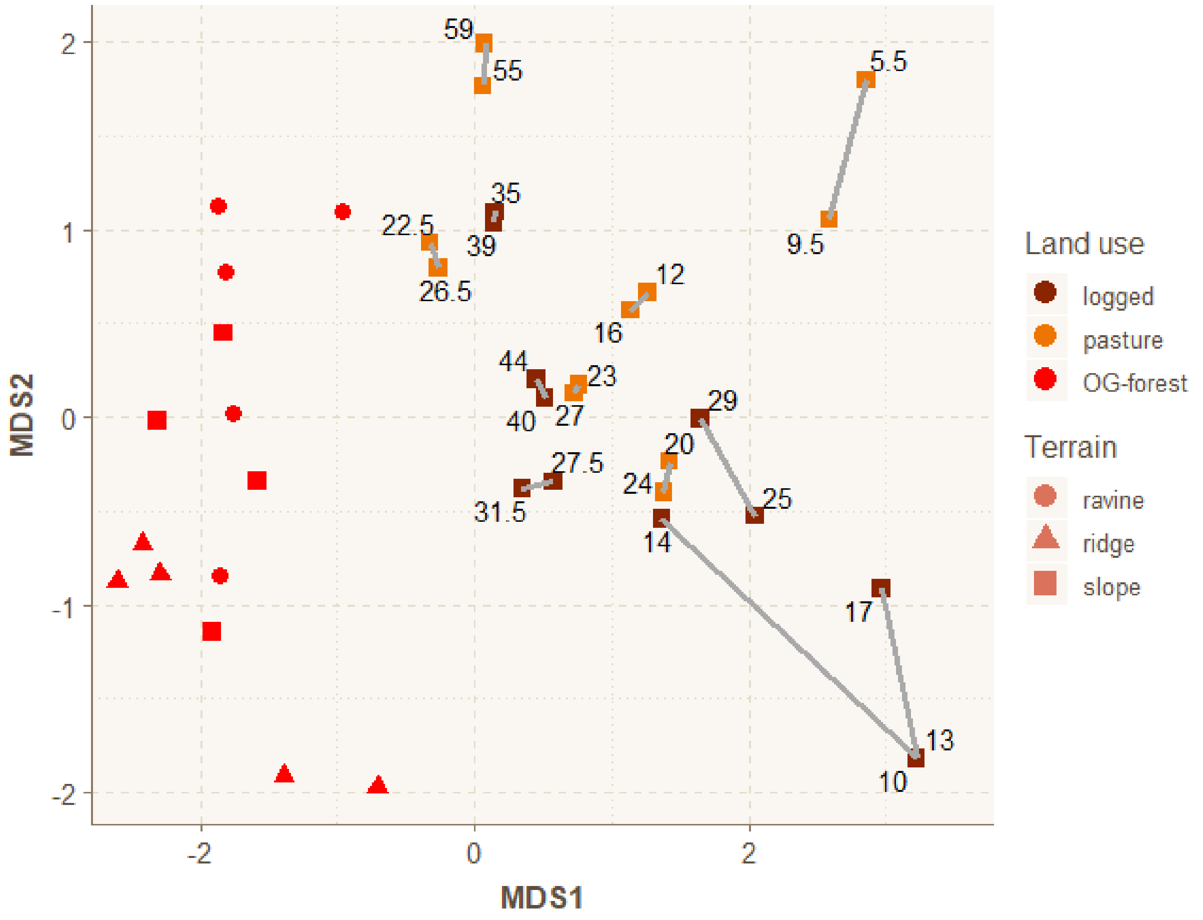


Figure 32: NMDS Test for all 12 secondary forest plots and 15 old-growth forest plots indicating similarity of species composition. Numbers indicate forest age and grey lines connect the same secondary forest plots in the two different years of observation.

Old-growth forest mostly position in the lower left of the two dimensional scale, while the projection of secondary forests spread widely over the right section. Species composition converged more towards those of old-growth forests with increasing age of secondary forests. The approximation was evident for the over-time observation as well as the chronosequence. However, even for older secondary forests, the NMDS showed clear distances between secondary and old-growth forests. While younger secondary forests experienced a large shift towards old-growth forests within the four years, older sites showed only little changes.

3.4 Mortality and recruitment

In the 12 secondary forest study plots, a total number of 175 individuals belonging to 55 species were found dead or missing at census 2. The census included all trees that died in the timespan between 2015 and 2019. Individuals that were already dead in 2015 were excluded from the data set, whereas trees documented at census 1 that were missing at census 2 were assumed to be dead. 296 newly recruited individuals belonging to 60 species that reached a DBH ≥ 2.5 cm were counted at the second census. 847 individuals of 119 species survived both censuses.

Figure 33 shows the calculated mortality rates per plot in relation to age for all 12 secondary forest sites. A weak, but statistically not significant correlation between mortality and stand age was found (p = 0.14 for mortality ~ log(age)). Mortality rates varied across the study plots. The highest mortality rate was detected in the youngest plot with 8.7 % per year. A high number of trees were found dead in this plot in 2019 under the vast number of lianas. Another outlier with a rate of 6.5 % per year was presented by plot 7 where the large tree fall caused a significant disturbance and the death of many trees. The *Vochysia ferruginea* and *Gmelina arborea* dominated plot 10 furthermore showed high mortality with 7.5 % per year. Many trees were found dead or missing in this plot at the second census. The plots with the highest mortality rates were all associated with prior land use as pasture, while the lowest mortality rates were detected in forests regenerating after logging. A considerable correlation between mortality and land use was found, though the results were statistically not significant (p = 0.06).

Figure 34 displays the recruitment rates of the secondary forest plots in relation to forest age. Recruitment rates significantly declined with increasing forest age (p = 0.04 for recruitment ~ log(age)). A strikingly high recruitment rate was found in the 14 year old plot 11. However, the high rate resulted exclusively from the recruitment of small understory species that comprise a relatively high number of individuals compared to the otherwise sparse number of surviving trees of the species *Vochysia ferruginea*. Nevertheless, while recruited trees proportionally accounted for a substantial share of individuals in this plot, they contributed very little to the forest stand in terms of AGB. Their DBH often barely surpasses 2.5 cm, whereas the high grown *Vochysia ferruginea* individuals reach diameters up to 51 cm. While the highest recruitment rate occurred for a forest after logging and the lowest for a forest following pasture, the results for the different land use types were otherwise mixed, and no correlation of land use with recruitment rate was found (p = 0.78).

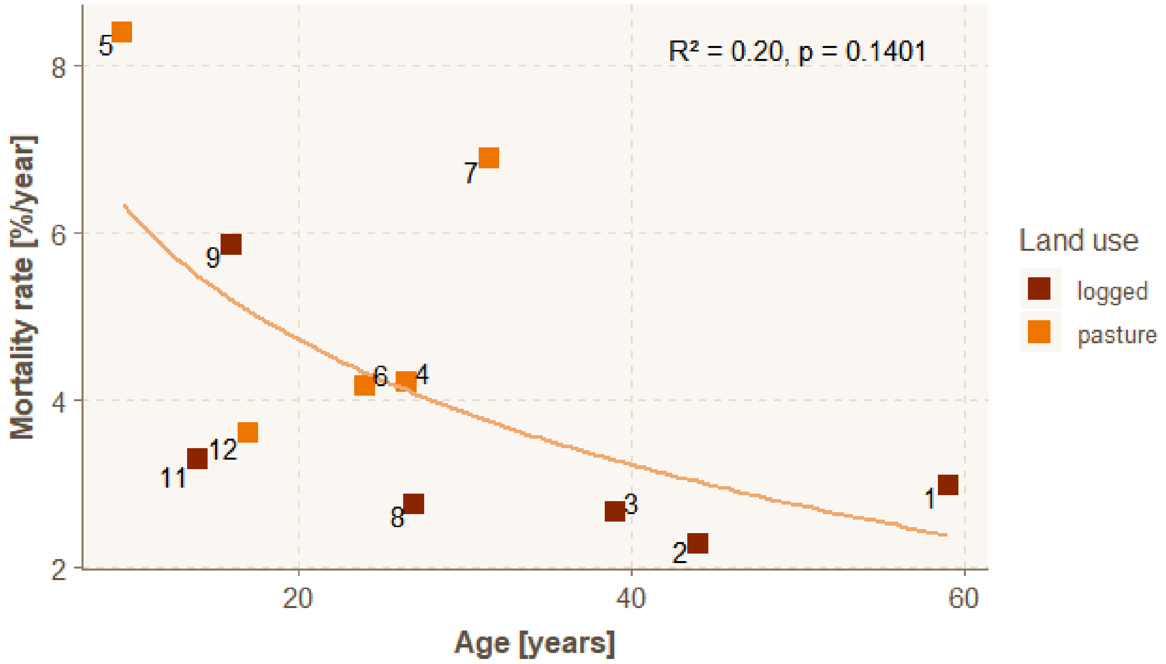


Figure 33: Mortality rates for the 12 secondary forest study plots in relation to forest age. Red line represents the regression mortality ~ log(age), numbers indicate plot ID.

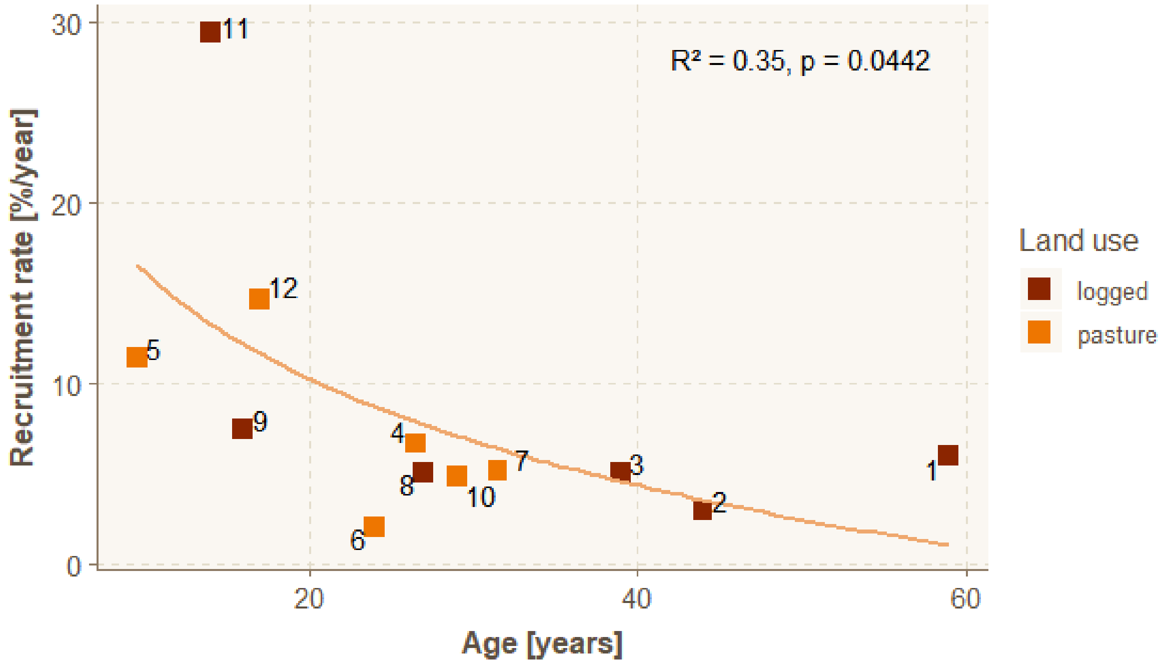


Figure 34: Recruitment rates for the 12 secondary forest sites in relation to forest age. Red line represents the regression recruitment ~ log(age), numbers indicate plot ID.

Mortality and recruitment rates of the 10 most common species are shown in **Figure 35**. *Psychotria elata* showed the highest recruitment rate with 20.0 % per year. The highest mortality rate of 9.6 % per year and the second highest recruitment rate of 12.8 % per year occurred for the population of *Alchornea costaricensis*. Interestingly, the population of *Gmelina arborea* had one of the highest mortality rates of 8.9 % per year, while its recruitment rate showed the lowest value of the 10 observed species with under 1 % per year. This suggests that the non-native, possibly planted tree species might become extinct. The most common tree species *Vochysia ferruginea* showed a moderate mortality rate of 4.4 % per year and a low recruitment rate of 2.0% per year. The lowest mortality rate with 0.3 % per year was found in the population of the third most common species *Tetrathylacium macrophyllum*. The average mortality rate across the 10 most common species was 5.8 % per year, while the average recruitment rate was 6.5 % per year. Overall, recruitment and mortality were not correlated (p = 0.84).

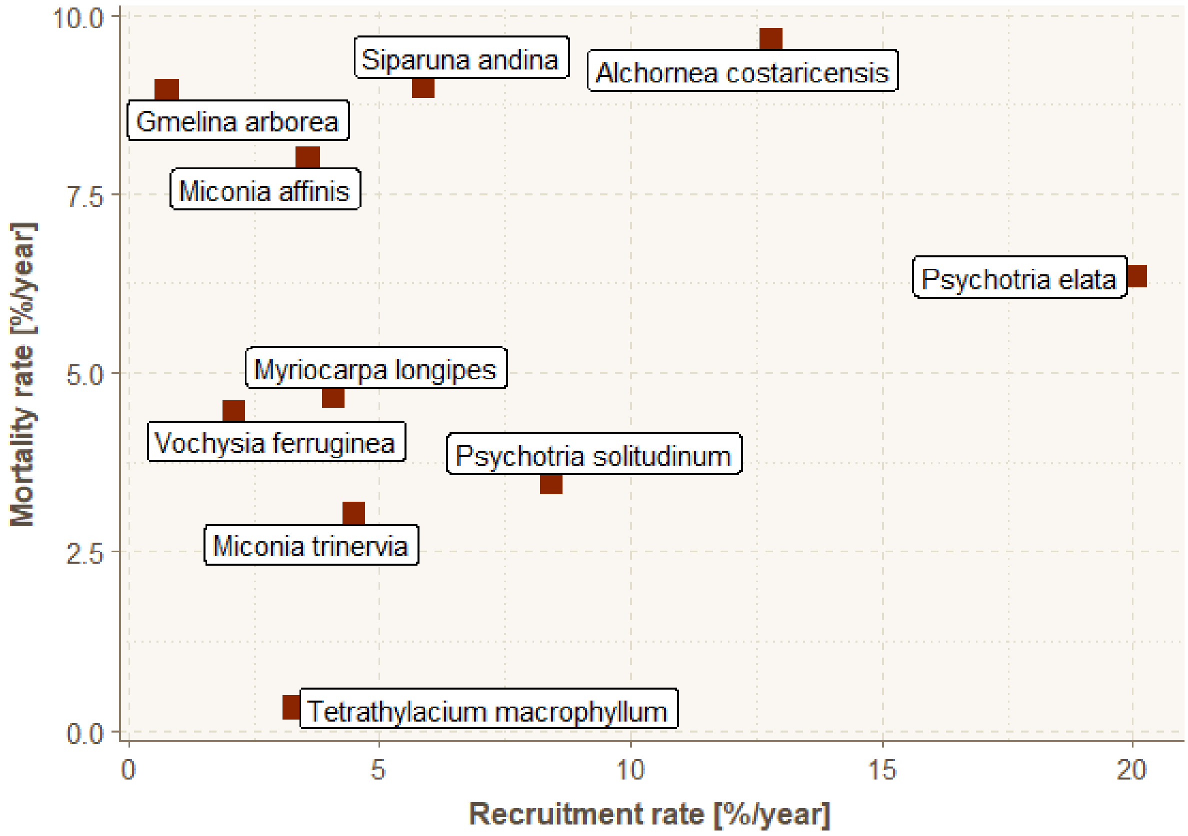


Figure 35: Recruitment vs. mortality rates for the ten most common species in the 12 secondary forest study plots.

Figure 36 shows the habitat specialization on a range from 0 (only occurring in secondary forests) to 1 (only occurring in old-growth forests) in relation to mortality and recruitment rates for species in secondary forest plots with a population > 10 individuals in the secondary forest plots studied and with > 20 individuals in the old-growth vs secondary forest dataset. Most of the observed species were primarily found in secondary forest habitats, while only two species were predominantly found in old-growth forests. The highest affiliation to old-growth forests was 0.72 for *Otoba novogranatensis*. Consequently, no species that was solely found in old-growth forests occurred within the given limits. Only the two species *Otoba novogranatensis* and *Calophyllum brasiliense* had a habitat specialization index above 0.5, while all other species held indices below this threshold. The highest mortality and recruitment rates were generally found for species with lower habitat indices, though no significant correlation with habitat specialization was identified (p = 0.15 for mortality ~ HS, p = 0.35 for recruitment ~ HS). The highest mortality rate was found for the species *Ochroma pyramidale* with 22.9 % per year and a HS value of 0.07 indicating that individuals of the species grow primarily in secondary forest habitats. The high mortality rate of this species was attributed to a large part to many individuals in plot 5 that died underneath severe liana growth. *Miconia argentea*, another species predominantly found in secondary forests (HS = 0.08), showed the highest recruitment rate with 46.9 % per year.

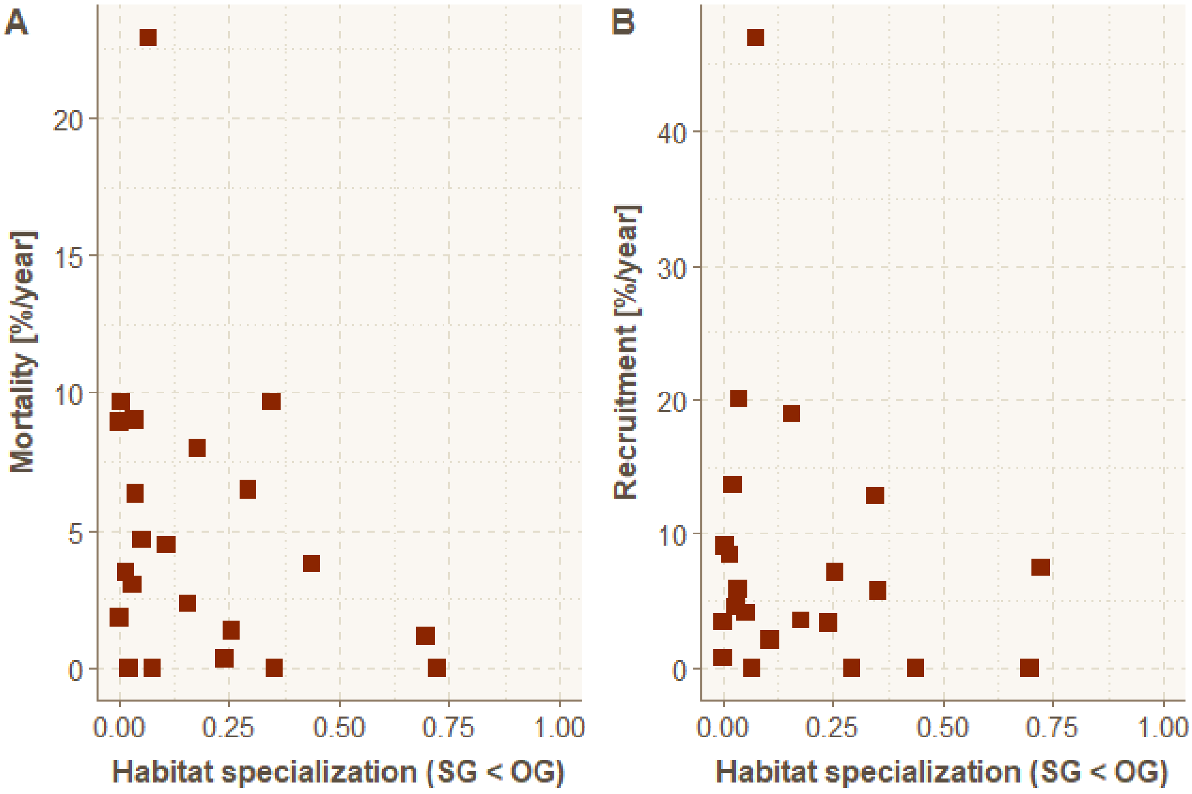


Figure 36: Habitat specialization on a scale from 0 (only occurring in secondary forest) to 1 (only occurring in old-growth forests) in relation to (A) mortality rates and (B) recruitment rates of species found in secondary forest plots with a population > 10 individuals and a habitat observation of > 20 individuals

3.5 Canopy cover

Leaf area indices for all 12 secondary forest plots were taken only in the year 2019 and not in OG forest plots. Therefore, no over-time observation of canopy cover development and no comparison with OG forests was possible. Subsequently, the analysis of canopy developments is limited to the space-for-time substitution within the chronosequence and analysing the correlation of leaf area index with the estimated AGB of each plot. **Figure 36(a)** demonstrates the results for LAI in each of the 12 secondary forest plots in relation to forest age. The results were highly variable and no correlation between LAI and secondary forests age could be found (p = 0.61). LAI in relation to AGB showed equally high variability (**Figure 37(b)**) and no patterns of LAI development with increasing AGB could be identified (p = 0.59). Plots with a multilayered, dense canopy cover present in all subplots showed the highest LAI with values > 3.0 (Plot 3, 4, 8, 10). The youngest forest had a relatively high LAI for its young age with a value of 2.89. Plots 11 and 12 differed largely in LAI, although their forest structure was very similar with monodominant *Vochysia ferruginea* in the upper canopy. The highest LAI with 3.87 was found in the secondary forest with the largest AGB of 249.0 Mg / ha. However, the two lowest LAI values were found in forest plots with a comparably high AGB accumulation > 200 Mg / ha.

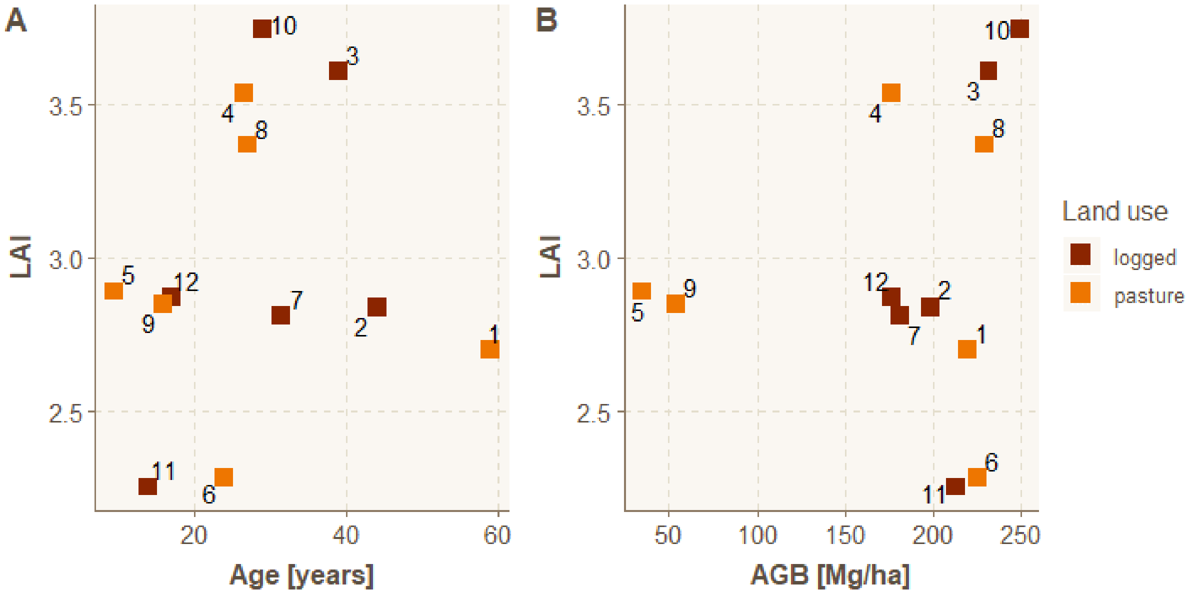


Figure 37: Leaf area indices (LAI) for 2019 for each plot in relation to (a) forest age since regeneration (state of 2019) and (b) aboveground biomass (AGB)

4. Discussion

4.1 Limitations of the study

The combination of the two complementary approaches applied in this study reduced uncertainties in the temporal analysis. Furthermore, plot markings were found in excellent condition at census 2, allowing a second data collection with a high level of accuracy. However, some essential limitations of this study need to be pointed out. First, the established plots only covered a relatively small size of 500 m^2 each. It is questionable whether this section reflects the represented forest in an accurate manner. Extending the plot size to 1 ha could increase the level of precision of the data and allow a direct comparison with old-growth forests and other studies of larger scale, without the need to extrapolate values and subsequently introduce noise. However, this would require considerably more resources and was not possible in our case since the study was timely and financially limited. Moreover, widening the plot size would have been difficult in many of the sites that were characterised by a challenging terrain and encompassed steep slopes and impassable areas. If these obstacles could be overcome, such an undertaking would provide a possibility for further research in the future.

Second, the observation period only encloses a fragment of the whole regeneration process. We solely collected data at two points in time comprising a period of 4 years. A longitudinal study with repeated measures would allow a better observation of developments and a more precise prediction for the natural regeneration patterns of tropical forests. The long-term continuation of this research is intended and measures such as labelling all trees and the careful documentation of the conducted fieldwork were implemented to enable this.

Third, only specific parameters were observed and measured in this study. Natural regeneration processes of forest ecosystems are subject to complex interactions with their environment and depend on a various parameters determining successional pathways (Chazdon, 2014; N'Guessan et al., 2019). Forest succession is driven by many abiotic and biotic factors that influence how a forest evolves and changes its constitution (Chazdon, 2014). Those factors include climate, landscape, prior land use, disturbances and interactions within and beyond the borders of the forest ecosystem (Chazdon, 2014; N'Guessan et al., 2019; Zermeño-Hernández et al., 2016). Viewing forests as a dynamic, interwoven system is a critical point in evaluating secondary forest regeneration (Chazdon, 2014). In our study, knowledge of prior land use as well as forest age was limited by the scarcity of information that was possible to obtain. Besides that, various other factors, such as soil parameters, surrounding landscape characteristics or neighbouring effects between tree individuals have not been included in this research due to limited resources. However, these aspects might have a significant impact on regeneration pathways that cannot be fully unravelled by this research.

Despite the mentioned limitations, this study provides valuable insights into the dynamics of natural regeneration in tropical secondary rainforests and supports the importance of this field and can point to the need for further research.

4.2 Aboveground biomass

The results of this study indicate a fast accumulation of AGB in the observed secondary forest plots within a few years after the initiation of the regeneration process which supports Hypothesis 1. This suggests a high potential for biomass recovery in naturally regenerated tropical rainforests and subsequently offers possibilities for carbon sequestration in the AGB of secondary forests. These findings align with several studies conducted in neotropical forests that possessed comparable characteristics and environmental conditions (*i.e.* Chazdon et al., 2016; Letcher and Chazdon, 2009; Marín-Spiotta et al., 2007; Poorter et al., 2016). A large-scale study by Poorter et al. (2016) compiling 1,500 secondary forest plots at 45 different sites showed an average AGB recovery of 122 Mg / ha after 20 years. A direct comparison of results for forests that were subject to high precipitation conditions showed strong similarities to our study. While Poorter et al. (2016) stated a biomass recovery of 160 Mg/ha (60% of old-growth biomass) after 20 years in those forests, our results for the same timespan accounted for 164 Mg (52% of old-growth biomass). It should, however, be kept in mind that big data sets need to be analysed very critically and uncertainties might remain in large-scale studies such as provided by Poorter et al. (2016).

Letcher and Chazdon (2009) found that secondary forests in northeastern Costa Rica recovered a significant amount of biomass after 21-30 years that almost reached old-growth forest values. In addition, Marín-Spiotta et al. (2007) encountered AGB accumulation rates to be highest and peaking during the first 20 years of regeneration resulting in a high carbon sequestration potential. An approximately logarithmic trend of AGB accumulation with age was confirmed by many studies (Aryal et al., 2017; Kenzo et al., 2010; Poorter et al., 2016). These findings agree with our data trend that showed similar patterns with a strong increase of AGB in the first years of regeneration that levelled off over time.

Hiratsuka et al. (2006) conclude in their study on naturally regenerated forests in Indonesia that recovery of AGB is largely determined by the dominant tree species present within each site. Our results support this theory, especially regarding the particularly fast AGB accumulation in plot 11 and 12, where the pioneer tree *Vochysia ferruginea* clearly dominated. Each site showed different regrowth patterns and dominant tree species resulting in variations between the plots as assumed in Hypothesis 2. Decreases in AGB in four of the 12 study sites can mostly be attributed to high tree mortality or mortality of larger trees and significant forest disturbances such as disruptive tree falls (i.e. in plot 7). Similar declines in AGB due to mortality within the dynamic forest matrix have been observed by other studies, mostly in advanced stages of regeneration, contributing to an overall decreasing AGB accumulation rate with age (Hiratsuka et al., 2006; Hu et al., 2020). The declining AGB in the young plot 9 is likely caused by severe liana growth that built a heavy, thick layer over the canopy, resulting in reduced tree growth and death. Similar conditions were found in two subplots of plot 5, but the undisturbed growth of the remaining subplots outweighed those losses and led to a net positive AGB accumulation. Several studies have shown the negative effect of a high abundance and growth of lianas on AGB accumulation of trees as the woody vines compete for water and light resources and can suppress tree growth (Meunier et al., 2020; van der Heijden and Phillips, 2009). Effects of lianas will further be discussed under section 4.4 regarding mortality and under section 4.5 in terms of light availability.

The analysis showed no correlation of AGB with prior land use. Contrary to these findings, land use history is widely acknowledged as one of the determinants of regrowth (Chazdon, 2014; Letcher and Chazdon, 2009) which has been confirmed by many studies (*i.e.* Kammesheidt, 2002; Steininger, 2000; Wandelli and Fearnside, 2015). Nevertheless, research on the influence of previous land use on AGB shows mixed results. Poorter et al. (2016) did not find a significant correlation of AGB accumulation with previous land use, which was categorized as pasture or shifting cultivation. Similarly, Letcher and Chazdon (2009) could not detect a linkage regarding biomass recovery. In contrast, Wandelli and Fearnside (2015), who observed 15 forests following agricultural land use and 9 forests following pasture, detected considerable impacts of land use history. AGB accumulation rates were much slower for abandoned pastoral areas and the frequency of burning during agricultural land use affected regrowth negatively. Silver et al. (2000) observed reforested sites after clearing next to pasture and agricultural sites. AGB accumulation was highest in former agricultural areas followed by pasture. A small part of the inventory consisted of cleared sites that showed the lowest AGB growth curve. It should be noted that the intensity of land use can furthermore have a significant effect on AGB and carbon sequestration (Silver et al., 2000; Wandelli and Fearnside, 2015). Uhl et al. (1988) observed a 40% higher AGB in secondary forests following low intensive pasture farming than in forests formerly subject to high intensity pasture. More research on the land use history in the observed study area in cooperation with local landowners could reveal patterns that might be unknown so far and give relevant implications on the impact of anthropogenic activities.

4.3 Species richness and composition

The analysis of species richness showed an overall increase in the study plots with forest age, although the results displayed strong variations across sites. These results support Hypothesis 1 and 2. The increment of species richness with stand age is consistent with comparable studies on species recovery in tropical secondary forests. Abbas et al. (2019) and Peña-Claros (2003) found a fast increase in species numbers during the first two decades of regeneration, while species gains slowed down in later stages of succession. Similarly, Villa et al. (2018) reported steadily rising species numbers over a period of 20 years, although secondary forests were only observed in early stages of succession in this study.

While our inventory comprised all species ≥ 2.5 cm DBH, it was only possible to include individuals ≥ 10 cm DBH in the comparison with old-growth forests due to the availability of data. This poses a limitation of our research and renders comparisons with other studies difficult. While some sites converged towards species numbers of old-growth forests within little more than 20 years, non could exceed the diversity in old-growth forests and most forest plots retained at substantially lower levels. In comparison, Villa et al. (2018) documented individuals ≥ 5 cm DBH in 45 secondary forest plots that reached up to 70% of old-growth forest species richness within only 20 years. Peña-Claros (2003) included very small trees ≥ 1 cm DBH in their inventory, which resulted in species numbers comparable to old-growth forests after no more than 25 years. Letcher and Chazdon (2009) described species richness in secondary forests achieving old-growth forest values after 30 years for woody plants ≥ 2.5 cm DBH. The lower levels of species recovery found in our study might result from the differences in tree size class. Especially in early stages of succession, species with small diameters add a major part to species richness (Guariguata et al. 1997; Letcher and Chazdon, 2009; Peña-Claros, 2003). If smaller trees are included in the inventory, species richness is more likely to shift towards old-growth forest levels (Guariguata and Ostertag, 2001). The higher species richness due to the inclusion of smaller tree sizes might then implicate a greater convergence towards old-growth forests, even though these trees will take a long time to reach substantial size, and the forest structure cannot provide similar habitats to old-growth forests (Letcher and Chazdon, 2009). Considering the size classes included in the analysis is therefore an important point in evaluating the potential of species recovery. Moreover, the mentioned studies varied in methodological approach which could cause discrepancies of results when comparing secondary forests to old-growth sites.

The results for species ≥ 10 cm revealed notable differences between the two types of previous land use (pasture and logging). Forests regrowing after pastoral land use recovered more species within the four years and comprised higher species numbers along the chronosequence compared to forests past logging. Species increases in logged sites for species ≥ 2.5 cm DBH mostly stemmed from smaller individuals. In contrast to AGB, these results suggest a correlation with land use history. The findings agree with the broadly recognized case that previous land use impacts species regeneration (Chazdon, 2014; Pascarella et al., 2000; Purata, 1986), although in other studies a significantly stronger correlation could be drawn compared to our analysis (*i.e.* Mesquita et al., 2001; Pascarella et al., 2000; Purata, 1986). As in our case, Letcher and Chazdon (2009) found influences of land use history on species regeneration, but not on AGB.

The high variability of species richness between the plots might be caused by several reasons. Given the study’s limitations, the small plot size is likely to affect the analysis, since a larger scale is critical to ensure an accurate picture of forest regeneration (Letcher and Chazdon, 2009). Besides methodological aspects, differences between the sites within the chronosequence could explain variability in species richness. Chazdon (2014) identified five main causes that introduce diverging successional pathways, namely site availability, species pool, species traits and intra- or interspecific species interactions. In example, the availability and dispersal of seeds have high impacts on species richness in secondary forests (Chazdon, 2014; Guariguata and Ostertag, 2001; Mesquita et al., 2001) and depend, inter alia, on the existence of nearby primary forests (Mesquita et al., 2001) and biotic or abiotic factors (*i.e.* birds, mammals, seed rain) that can enable dispersal (Palma et al., 2021). Furthermore, spatial parameters, climatic conditions and soil properties in the region fluctuate and can alter successional pathways (Hofhansl et al., 2014).

The same effects could likewise explain variations in species composition resulting from the NMDS test. While secondary forests spread relatively widely across the NMDS scales, old-growth forests showed more similarity to each other. This might partly be related to the larger plot size of 1 ha in old-growth forests that is likely to reduce noise compared to the smaller secondary forest plots. However, similar differences in species composition between secondary forest plots were found by comparable studies (*i.e.* Abbas et al., 2019; Letcher and

Chazdon, 2009; Peña-Claros, 2003). Furthermore, plots within a chronosequence tend to show more variations than single site observations over time (Chazdon et al., 2007).

Even though species composition of secondary forests generally became more similar to old-growth forests with age, a clear distance remained between the two forest types. This agrees with Hypothesis 1 and fosters the findings of several other studies indicating that species composition shifts very slowly towards old-growth forests, whereas species richness develops significantly faster (*i.e.* Finegan, 1996; Rozendaal et al., 2019; Swaine and Hall, 1983; Uhl, 1987). Nonetheless, results on species composition in tropical secondary forests differ largely across studies (Chazdon et al., 2007). Terborgh et al. (1996) as well as Sheil (1999), re-evaluating a study by Eggeling (1947), both reported species secondary forest succession in Peru and Uganda approximating the species composition found in old-growth forests. Differences in environmental parameters, particularities of the study regions and methodological approaches might lead to these variations. This calls for further research on the evolution of species composition in secondary forests and illustrates that our current understanding is not sufficient to predict successional trajectories.

4.4 Mortality and recruitment

The results suggest that mortality decreases over time, though no significant correlation with age was found and results showed relatively large variations. Recruitment and mortality rates of the 12 study sites were highest in the early years of regeneration, supporting Hypothesis 3. Recruitment rates continuously decreased over time and showed a significant correlation with age. Research on the dynamics in secondary forests caused by mortality and recruitment is characterized by variations, illustrating the complexity of changes in these ecosystems (Chazdon, 2014). During the early stages of succession, secondary forests go through constant changes in stand composition characterized by death and new growth of trees (Chazdon, 2014). As secondary forest succession progresses, mortality and recruitment of species continue to change the forest composition (Chazdon, 2014; van Breugel et al., 2007). Lebrija-Trejos et al. (2010) observed mortality and recruitment in tropical dry forests in Mexico along a chronosequence spanning the first 60 years of succession. As in our study, recruitment was highest in young forests, though experiencing a faster decline within the first 20 years of succession and levelling off towards advanced forest ages. The initially low mortality increased until peaking after 15 years and steadily decreased thenceforth towards later stages of succession. Van Breugel et al. (2006) found high mortality in early years and rapid changes in forest structure occurring during young ages that decreased significantly with increasing forest age resulting from a balance between growth and mortality. Van Breugel et al. (2007) proposed that recruitment of pioneer species under an established canopy could be enabled by high mortality in young forests. Chazdon et al. (2005) described large variations in forest structure due to mortality and recruitment in Costa Rican forests. They also reported dynamics in younger forests to be larger than in older secondary forest sites.

The distribution of dead trees across the range of DBH measurements showed that mortality was predominantly occurring for smaller individuals. This agrees with other studies that found the highest mortality levels in the smallest tree size class (Chazdon et al., 2005; Mascaro et al., 2004). Chazdon et al. (2005) and van Breugel et al. (2006) attributed the death of a high number of stems in early years of succession to the suppression of small pioneer trees. The results of this study support this case, especially regarding the young plots 5 and 9 where a high number of small sized trees died under the liana dominated canopy. In contrast, the two *Vochysia ferruginea* dominated plots 11 and 12, that were likewise among the younger forests and showed no suppression of smaller trees, demonstrated considerably lower mortality rates. Many studies have shown that liana infestation in the tree canopy enhances tree mortality significantly (*i.e.* Schnitzer et al. 2005; van der Heijden and Phillips 2009; Ingwell et al.; 2010). Ingwell et al. (2010) reported the death of twice as much tree individuals interfered by liana infestation in the crown (> 75%) in comparison to unobstructed trees.

The pioneer species *Vochysia ferruginea* and *Gmelina arborea*, two of the most common species in the study plots, showed negligibly low recruitment rates, while mortality rates were moderate to high. This could point to the theory that early stages of succession in young secondary forests are usually characterized by the growth of many pioneer tree species, while shade-tolerant species become more dominant in later stages (van Breugel et al., 2007). Uhl (1987) showed high mortality rates of abundant pioneer species after few years of succession. Furthermore, the small understory species *Miconia affinis* and *Psychotria elata* showed high mortality rates which agrees with findings of Chazdon et al. (2005) who listed these species under the ones with the highest mortality rates of small sized trees. However, they reported considerably higher rates than in our case. Additionally, the hypothesis of the suppression of smaller trees, as introduced above (Chazdon et al. (2005); van Breugel et al. (2006), is reinforced by the high mortality of the small sized populations of *Miconia affinis, Psychotria elata* and *Siparuna andina*. However, *Miconia trinervia* and *Psychotria solitudinum* showed lower mortality, even though they were in the same size category and developed under a closed canopy.

The observed habitat specialization in the secondary forests of common species with a population > 20 individuals showed a tendency towards second-growth specialists and very few species predominantly occurring in old-growth forests. High mortality and recruitment both occurred mostly for species specialized in secondary forest habitats. These results illustrate that, even though species richness generally increased through forest dynamics, mortality and recruitment did not yet shift species composition towards old-growth forest species contrary to the assumption made in Hypothesis 3. Due to the continuity that characterizes forest succession (Chazdon, 2014), we did not want to classify species in static categories of old-growth, second-growth and generalist species, but rather display them on a gradual scale depending on their occurrence in different habitats. Early studies categorized species into pioneer and non-pioneer species (Swaine and Hall, 1983; Uhl, 1987) and further subdivided non-pioneer species into early secondary, late secondary and climax species (Budowski, 1965; de Oliveira, 2002). Many studies have shown that the accumulation of old-growth species in secondary forests requires a very long time (Finegan, 1996; Rozendaal et al., 2019; Swaine and Hall, 1983; Uhl, 1987). Corresponding to similar research, this study supports the need to safeguard both secondary and old-growth forests for the conservation and restoration of biodiversity in tropical forests. However, literature on the development of species composition shows controversies. Van Breugel et al. (2007) found large variations between sites regarding changes in species composition of recruited and dead trees. While in some plots shade-tolerant species were recruited and pioneer species died, other plots continued to recruit many pioneer trees. Kappelle et al. (1996) identified a considerable portion of old-growth species in secondary forests within the first 20 years of succession, whereas Saldarriaga et al. (1988) did not find any old-growth species in forests of similar ages.

4.5 Canopy cover

The evaluation of hemispherical photographs showed no correlation of LAI with age or AGB. These results contradict Hypothesis 4 and strongly disagree with other studies (*i.e.* Feldpausch et al., 2005; Kalácska et al., 2004; Kenzo et al., 2010). Kalácska et al. (2004) measured LAI in tropical wet forests in Costa Rica similar to our study area and reported an exponential incline of LAI with progressing successional stage. Kenzo et al. (2010) found a steady increase of LAI with age and especially steep inclines of LAI values in the initial years of regeneration in forests after shifting cultivation in Malaysia. A similar development was shown by Feldpausch et al. (2005) for Brazilian secondary forests post pasture with continuously rising LAI values during early years of succession. However, they only observed young forests up to 14 years of age and LAI of the canopy layer already levelled off towards forest ages of 12-14 years. In addition, Feldpausch et al. (2005) described a pronounced positive correlation of LAI with total AGB.

The exceptionally large variations of LAI between plots might partly stem from differences in forest structure and hence canopy characteristics of the sites. The observations made in each plot can help understand canopy dynamics to some extent. The youngest plot in the chronosequence had a high LAI for its age. This value most likely occurred due to the excessive abundance of lianas in approximately half of the plot and the thereby lowered percentage of open sky and light transmission. The same relationship can be drawn for the 16-year-old plot 9 where lianas overgrew the entire site. The highly similar forest structure of plot 11 and 12 would appear to suggest a consequently comparable LAI. However, this was not the case. A second observation of hemispherical photographs showed that there were more and larger gaps between trees in the canopy visible in the images of plot 11 compared to plot 12 despite the similarities in structure and composition.

Discrepancies of LAI results might also result from methodological aspects. The gap-fraction-based method applied in this study represents an indirect measurement of leaf area index by mapping the whole canopy (Bréda, 2003). This implies that, besides leaves, other parts of the forests are displayed, such as stems and branches (Bréda, 2003). This could further explain differences between plot 11 and 12 given that gaps between trees were large and flooded with light, but stems had substantial diameters appearing in the photographs in varying degrees. Next to that, sloping terrain represents a particular case when examining hemispherical images (España et al., 2008). Since all 12 study sites were located on slopes with varying gradients, a resulting slope effect on LAI values is inevitable and needs to be considered (Bréda, 2003; España et al., 2008; Walter and Torquebiau, 2000). This effect occurs due to the visibility of the terrain in the hemispherical images that distorts the representation of the canopy. Walter and Torquebiau (2000) point out the need to correct such a slope effect for gradients > 15-20°, while España et al. (2008) showed significant impacts for gradients > 25°. Slope gradients exceeding these thresholds were present at a majority of the observed sites in this study. Methodologies for slope correction and computation approaches are proposed and evaluated by various literature (Duursma et al., 2003; España et al., 2008; Montes et al., 2007; Walter and Torquebiau, 2000). These could provide a remedy for slope effects on LAI measurements in this study and reduce noisy data.

Furthermore, it should be noted that taking hemispherical photographs at ideal lighting conditions posed a challenge. The remote location of some sites and distance to larger paths or roads hindered the accessibility before sunrise or return route after sundown. Most pictures were hence taken during the day and ideally under cloudy sky conditions. However, it cannot be ruled out that some photographs might be subject to overexposure and partly misrepresent the open sky. This can lead to errors in the estimation of the gap fraction and hence LAI calculations. Manual adjustments of photographic exposure can correct such errors to some degree (Beckschäfer et al., 2013). Nevertheless, even though photographs were taken and processed to the best of our knowledge, it should be mentioned that the applied method might be error-prone in this aspect.

In addition, the quantitative synthesis of the different sites introduced uncertainties that could enhance variations. In contrast to the preceding analyses, canopy cover was only observed in 2019. Therefore, results solely rely on the space-for-time substitution of the chronosequence. As annotated above, the chronosequence approach is limited by the circumstance that different forests might undergo individual changes that make a direct comparison difficult (Chazdon, 2014; De Palma et al., 2018; Walker et al., 2010). This hence implies that analyses of chronosequences are vulnerable to possible deviations in climatic conditions, soil properties or other site-specific factors impacting the regeneration pathway (De Palma et al., 2018; Mora et al., 2015; Zhao et al., 2014b). Repeating measures at the study sites in reasonable time intervals might provide results allowing further conclusions on the relationship between LAI and age in the future.

4.6 Practical implications

Naturally regenerated secondary forests offer a wide range of opportunities and environmental as well as socio-economic benefits (Chazdon et al., 2016; Chazdon et al., 2020). Those include carbon sequestration, biodiversity conservation, the provision of forest goods to improve livelihoods and economies, as well as multiple other ecosystem services (Chazdon et al., 2016; Chazdon et al., 2020; Masiero et al., 2019). Investigating the successional pathways of tropical forests can yield important knowledge for forest management, restoration and the provisioning of ecosystem services and goods (Guariguata and Ostertag, 2001). Reforestation measures are often cost- and labour-intensive and consequently limited on financial resources (Brancalion et al., 2017). In contrast, the combination of sustainable forest management, natural regeneration and the prevention of forest degradation delivers solutions for increasing forest cover at low cost (Chazdon et al., 2016). However, the advantages of natural regeneration are often not recognized with regards to the design of forest restoration (Chokkalingam et al., 2018).

Our study showed a high regeneration potential for tropical secondary forests and thereby supports measures for secondary forest restoration. Simply allowing secondary forests to regenerate naturally provides a straightforward and effective restoration strategy (Aide et al., 2001; Chazdon et al., 2016). This process can take place assisted or unassisted (Chazdon et al., 2020). Small management intervention might be a valuable addition to assist the natural regeneration process depending on the situation. In our case, the suppression of tree growth by lianas had major impacts on forest regeneration. Wyns (2015) furthermore showed arrested succession by the fern *Dicranopteris pectinata* in the same study area. Freeing forests of lianas and cutting ferns that suppress growth could outline a small management intervention that could significantly impact natural regeneration. Our results, confirming several others (Finegan, 1996; Rozendaal et al., 2019; Swaine and Hall, 1983; Uhl, 1987), indicate that recovery of species composition proceeds very slowly and old-growth species might not be recruited until late stages of secondary forest succession. If restoration of these old-growth species is intended, enrichment planting can assist the regeneration process and promote species composition (Aide et al., 2001; Weissenhofer et al., 2019).

Depending on the state of degradation and the requested outcomes, larger and more cost-intensive interventions might be necessary (Aide et al., 2001). In some areas, natural regeneration cannot take place or might take very long due to the depletion of seed banks or compaction of soils (Weissenhofer et al., 2019). Furthermore, seed availability is a highly important factor determining the success of forest regeneration (Aide, 2001; Chazdon, 2014; Chokkalingam et al., 2018). The conservation of primary forests is hence not only of major importance due to the valuable ecosystem they represent (Barlow et al., 2007; Kosmos et al., 2017), but also essential for seed availability in nearby regenerating forests (Aide, 2001; Chazdon, 2014; Chokkalingam et al., 2018).

In the observed study region, the Tropical Research Station La Gamba initiated the project COBIGA (Corredor Biológico La Gamba) which focuses on the creation of a biological corridor that connects the lowland tropical rainforests of the Golfo Dulce region with the mountainous rainforests of Fila Cal (Weissenhofer et al., 2019). It is integrated into the larger project AMISTOSA that aims at connecting the Osa Peninsula with the La Amistad International Park. **Annex 4** shows a map of the region and its initiatives for biological corridors (provided by the Tropical Research Station La Gamba). These initiatives focus on reforestation, forest restoration and sustainable forest management (Weissenhofer et al., 2019). As Weissenhofer et al. (2019) point out, natural succession is promoted within COBIGA in areas were seed availability is given. In contrast, plantings are introduced where natural regrowth is hindered.

This study provides a valuable addition to emphasize the inclusion of naturally regenerated forests into such projects and integrate secondary forest areas into biological corridor planning. Moreover, new knowledge on successional pathways of local natural forests can be used as valuable input to improve reforestation design. Furthermore, the inclusion of the local community in decision-making processes is a key factor in the implementation of such projects (Chokkalingam et al., 2018). Intense and efficient collaboration of project initiators, facilitators and researchers with local landowners of secondary forest patches or potential regeneration areas could result in successful conservation and restoration efforts, while also providing socio-economic benefits for the community.

Besides these research findings, integrating traditional knowledge into scientific conclusions can provide useful implications for forest restoration and new opportunities for participatory forest management (Wangpakapattanawong et al., 2010). Indigenous people have managed the rainforest for several thousand years in a way that adjusts to its natural cycle and makes full regeneration possible (Chazdon, 2014; Ogar et al., 2020). However, the ever-growing consumption of our modern-day society has led to an exploitation of these ecosystems and a shortening of necessary regeneration time that would need to be applied in shifting cultivations (Chazdon, 2014; Chokkalingam et al., 2018). Moreover, indigenous people often bring expertise on environmental processes and the use and growth of native species (Wangpakapattanawong et al., 2010). Too little attention is paid to valuable indigenous insights and some of the ancient knowledge has already been lost (Chazdon, 2014; Ogar et al., 2020).

Natural regeneration lies at the interface between forest conservation and restoration (Arroyo-Rodriguez et al., 2017; Chazdon, 2019). Holistic strategies that integrate environmental, social and economic aspects can result in successful, sustainable and long-lasting forest regrowth (Chazdon and Brancalion, 2019). However, the realization of naturally regenerated areas faces barriers in an economic and policy-related context, and holistic solutions are poorly represented and lacking support by policy-makers (Chazdon et al., 2020; Chazdon and Brancalion, 2019). In conclusion, this research makes a plea for researchers, decision-makers and practitioners in forest landscape restoration to continuously provide incentives, improve strategies and further innovations that are truly effective and yield multidimensional benefits.

5. Conclusion

This study showed that AGB accumulates fast in tropical secondary rainforests and can reach quantities close to old-growth forests within the first 60 years of regeneration. Even though species richness recovered slower than AGB, a considerable and increasing number of species were able to establish with forest age. These findings illustrate the high potential of natural regeneration in secondary forests. They furthermore confirm the significance of these ecosystems for carbon sequestration, biodiversity conservation and the provision of valuable ecosystem services. On the other hand, our findings support the case that species composition can take a long time to regenerate and become comparable to the forest structure of old-grown forests. Moreover, secondary forests in our study failed to recruit old-growth species in the observed timespan. Consequently, the conservation of old-growth forests as well as the restoration of secondary forests are both crucial points for conserving biodiversity in forest ecosystems.

Despite the limitations of our study, we could demonstrate that natural regeneration of forest ecosystems is a multidimensional process that depends on a variety of environmental parameters and shows unique pathways for individual sites. This research emphasizes the need for long-term observations of permanent plots in addition to standalone chronosequence studies that might be misleading. Variations in our results and differences in relevant literature demonstrate how limited our knowledge and understanding still is. This calls for more in-depth research on the complex interactions in tropical rainforests and determinants of regrowth and successional pathways.

Resulting from our findings, a strong case is made for the appreciation of second growth as an opportunity for forest restoration and the recovery of valuable ecosystems that have been subject to environmental degradation, largely through anthropogenic activities. Research on secondary forests that leverages our current understanding can provide important implications for conservation and restoration efforts as well as the design of active reforestation. Moreover, insights into natural regeneration processes allow us to find ways of living in accordance with nature and maintaining natural resources, while still benefiting from multiple ecosystem services.

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Appendix

Annex 1: Stand characteristics of secondary forest plots for 2015 with basal area (BA), above-ground biomass (AGB), community-weighted mean wood specific gravity (CWM.WSG)

PLOT	AGE (YRS)	SPECIES > 10 CM DBH	SPECIES > 2.5 CM DBH	BA (M^2/HA)	AGB (MG/HA)	HEIGHT (M)	CWM.WSG (G/CM3)	DOMINANT TREES
P5	5.5	2	15	5.3	16.9	6.2	0.357	Jacaranda copaia, Alchornea costaricensis, Trichospermum grewiifolium
P11	10	1	1	29.6	175.2	23.8	0.326	Vochysia ferruginea
P9	12	6	21	11.5	61.4	7.9	0.514	Miconia affinis, Ficus pertusa, A. costaricensis
P12	13	1	1	26.9	144.7	21.7	0.326	V. ferruginea
P6	20	3	17	25.9	192.0	9.8	0.514	Calophyllum brasiliense, Terminalia amazonia, V. ferruginea
P4	22.5	12	32	21.4	144.7	9.5	0.482	Spondias mombin, Guatteria chiriquiensis, Inga sp.
P8	23	13	33	29.8	173.0	9.0	0.387	V. ferruginea, Guatteria amplifolia, Cecropia sp.
P10	25	3	10	46.7	260.1	11.4	0.378	Gmelina arborea, V. ferruginea, M. affinis
P7	27.5	1	25	33.7	192.2	8.4	0.342	V. ferruginea, Psychotria elata, Siparuna andina
P3	35	12	28	32.1	222.7	10.3	0.434	G. chiriquiensis, Apeiba membranaceae, Tetrathylacium macrophyllum
P2	40	8	41	29.1	166.7	9.0	0.387	V. ferruginea, T. macrophyllum, G. amplifolia
P1	55	14	25	30.2	234.2	9.4	0.450	Chimarrhis latifolia, G. chiriquiensis, Inga jinicuil

Annex 2: Stand characteristics of secondary forest plots for 2019 with basal area (BA), above-ground biomass (AGB), community-weighted mean wood specific gravity (CWM.WSG)

PLOT	AGE (YRS)	SPECIES > 10 CM DBH	SPECIES > 2.5 CM DBH	BA (M^2/HA)	AGB (MG/HA)	HEIGHT (M)	WSG (G/CM^3)	LAI	MORT (%/YEAR)	RECR (%/YEAR)	DOMINANT TREES
P5	9.5	4	17	10.3	35.3	7.5	0.385	2.89	8.73	11.41	Jacaranda copaia, Alchornea costaricensis, Trichospermum grewiifolium
P11	14	1	10	34.7	212.9	11.8	0.329	2.25	3.28	30.21	Vochysia ferruginea
P9	16	8	23	10.2	53.8	7.9	0.513	2.85	5.28	7.62	Miconia affinis, Ficus pertusa, A. costaricensis
P12	17	1	4	31.0	176.1	15.2	0.328	2.87	3.60	14.64	V. ferruginea
P6	24	5	17	28.9	225.3	10.5	0.508	2.28	4.17	2.04	Calophyllum brasiliense, Terminalia amazonia, V. ferruginea
P4	26.5	13	31	24.3	176.4	9.4	0.492	3.54	3.69	6.80	Spondias mombin, Guatteria chiriquiensis, Inga sp.
P8	27	15	33	37.5	228.6	9.1	0.381	3.37	2.55	5.17	V. ferruginea, Guatteria amplifolia, Cecropia sp.
P10	29	3	14	44.4	249.0	11.1	0.369	3.75	7.54	5.00	Gmelina arborea, V. ferruginea, M. affinis
P7	31.5	2	32	31.8	181.0	8.6	0.349	2.81	6.47	5.23	V. ferruginea, Psychotria elata, Siparuna andina
P3	39	12	29	31.1	231.5	9.6	0.466	3.61	2.10	5.12	G. chiriquiensis, Apeiba membranaceae, Tetrathylacium macrophyllum
P2	44	9	41	33.5	198.3	9.3	0.384	2.84	2.05	2.76	V. ferruginea, T. macrophyllum, G. amplifolia
P1	59	12	24	26.6	219.6	9.0	0.490	2.7	3.28	7.18	Chimarrhis latifolia, G. chiriquiensis, Inga jinicuil

Annex 3: Results of linear mixed-effects model analysis of significant environmental parameters effecting AGB and species richness

	Model parameter	*Estimate*	*Standard Error*	*t value*	*p value*
AGB	Age	120.55	14.45	8.34	0.0000
	Number of species	1.45	0.47	3.06	0.0043
	Forest cover	-2.50	0.77	-3.24	0.0064
	Model parameter	*Estimate*	*Standard Error*	*z value*	*p value*
Number of species	Age	2.01	0.22	9.20	< 2e-16
	Land use	6.31	0.82	7.67	1.74e-14
	Age × Land use	-1.79	0.24	-7.547	4.47e-14

Annex 4: List of species found in the 12 secondary forest plots including number of individuals found in the year 2019 (latest observation)

SPECIES	**FAMILY**
Abarema adenophora	Fabaceae
Acacia allenii	Fabaceae
Aiouea obscura	Lauraceae
Albizia sp.	Fabaceae
Alchornea costaricensis	Euphorbiaceae
Alsophila sp.	Cyatheaceae
Andira inermis	Fabaceae
Apeiba membranaceae	Malvaceae
Apeiba tibourbou	Malvaceae
Ardisia opegrapha	Myrsinaceae
Ardisia sp.	Mirsinaceae
Brosimum guianense	Moraceae
Brosimum lactenscens	Moraceae
Brosimum utile	Moraceae
Calophyllum brasiliense	Calophyllaceae
Calophyllum longifolium	Calophyllaceae
Carapa guianensis	Meliaceae
Carpotroche platyptera	Achariaceae
Casearia arborea	Salicaceae
Casearia arguta	Salicaceae
Casearia sp.	Salicaceae
Casearia sylvestris	Salicaceae
Casearia tacanensis	Salicaceae

Castilla ulei	Moraceae
Cecropia sp.	Urticaceae
Chimarrhis latifolia	Rubiaceae
Chomelia barbata	Rubiaceae
Chrysochlamys glauca	Clusiaceae
Clidemia densiflora	Melastomataceae
Cojoba sophorocarpa	Fabaceae
Compsoneura sprucei	Myristicaceae
Conostegia lasiopoda	Melastomataceae
Conostegia xalapensis	Melastomataceae
Croton schiedeanus	Euphorbiaceae
Cyathea microdonta	Cyatheaceae
Davilla nitida	Dilleniaceae
Dendropanax arboreus	Araliaceae
Dendropanax ravenii	Araliaceae
Dialium guianense	Fabaceae
Duroia costaricensis	Rubiaceae
Ficus pertusa	Moraceae
Ficus sp.	Moraceae
Ficus tonduzii	Moraceae
Gmelina arborea	Lamiaceae
Gonzalagunia rudis	Rubiaceae
Grias cauliflora	Lecythidaceae
Guarea bullata	Meliaceae
Guarea corticosa	Meliaceae
Guarea kunthiana	Meliaceae
Guatteria amplifolia	Annonaceae
Guatteria chiriquiensis	Annonaceae
Hampea appendiculata	Malvaceae
Hasseltia floribunda	Salicaceae
Herrania purpurea	Malvaceae
Hieronyma alchorneoides	Phyllanthaceae
Huberodendron allenii	Bombacaceae
Inga densiflora	Fabaceae
Inga jinicuil	Fabaceae
Inga oerstediana	Fabaceae
Inga pezizifera	Fabaceae
Inga samanensis	Fabaceae
Inga sp.	Fabaceae
Inga vera	Fabaceae
Isertia laevis	Rubiaceae
Jacaranda copaia	Bignoniaceae
Lacistema aggregatum	Lacistemataceae
Laetia procera	Salicaceae

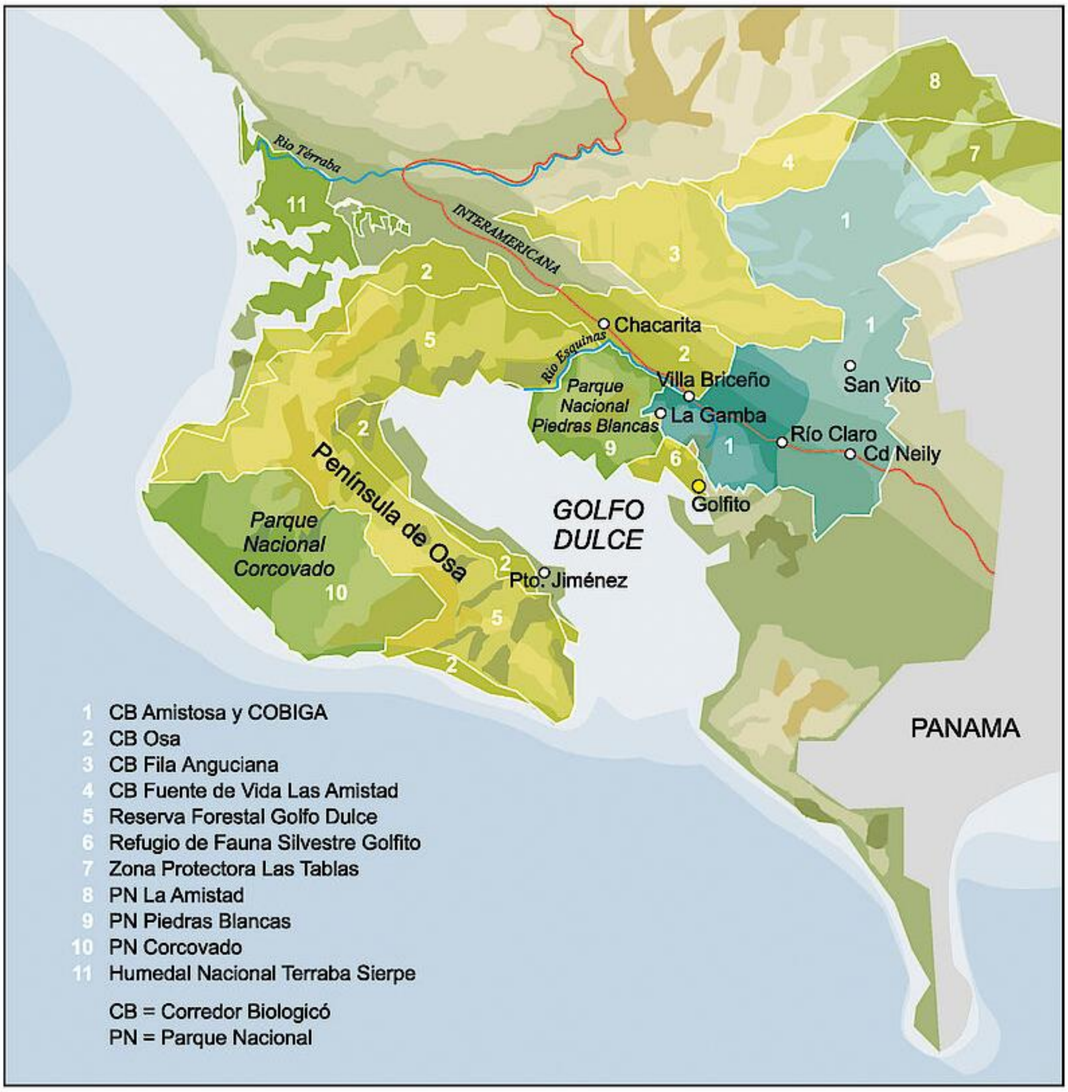
Licaria sp.	Lauraceae
Lonchocarpus sp.	Fabaceae
Luehea seemannii	Malvaceae
Mabea piriri	Euphorbiaceae
Marila laxiflora	Calophyllaceae
Miconia affinis	Melastomataceae
Miconia argentea	Melastomataceae
Miconia gracilis	Melastomataceae
Miconia macrophylla	Melastomataceae
Miconia prasina	Melastomataceae
Miconia schlimmii	Melastomataceae
Miconia sp.	Melastomataceae
Miconia trinerva	Melastomataceae
Miconia trinervia	Melastomataceae
Mikania guaco	Asteraceae
Myriocarpa longipes	Urticaceae
Ochroma pyramidale	Malvaceae
Ocotea cernua	Lauraceae
Otoba novogranatensis	Myristicaceae
Palicourea guianensis	Rubiaceae
Pentagonia wendlandii	Moraceae
Perebea hispidula	Moraceae
Perrottetia sessiliflora	Dipentodontaceae
Piper aduncum	Piperaceae
Piper hispidum	Piperaceae
Piper sp.	Piperaceae
Protium sp.	Burseraceae
Psychotria chiapensis	Rubiaceae
Psychotria cooperi	Rubiaceae
Psychotria elata	Rubiaceae
Psychotria solitudinum	Rubiaceae
Quiina schipii	Ochnaceae
Richeria obovata	Euphorbiaceae
Rinorea crenata	Violaceae
Senna reticulata	Fabaceae
Simarouba amara	Simaroubaceae
Simira maxonii	Rubiaceae
Siparuna andina	Siparunaceae
Siparuna andina	Siparunaceae
Siparuna guianensis	Siparunaceae
Sloanea sp.	Eleocarpaceae
Solanum ravirosum	Solanaceae
Sorocea pubivena	Moraceae
Spondias mombin	Anacardiaceae

Sterculia apetala	Malvaceae
Symphonia globulifera	Clusiaceae
Terminalia amazonia	Combreataceae
Terminalia bucidoides	Combretaceae
Terminalia catappa	Combretaceae
Tetragastris panamensis	Burseraceae
Tetrathylacium macrophyllum	Salicaceae
Tocoyena pittieri	Rubiaceae
Tovomita stylosa	Clusiaceae
Trichilia hirta	Meliaceae
Trichilia septentrionalis	Meliaceae
Trichospermum grewiifolium	Malvaceae
Virola guatemalensis	Myristicaceae
Virola koschnyi	Myristicaceae
Virola sebifera	Myristicaceae
Virola surinamensis	Myristicaceae
Vismia baccifera	Clusiaceae
Vismia guianensis	Clusiaceae
Vismia macrophylla	Clusiaceae
Vochysia allenii	Vochysiaceae
Vochysia ferruginea	Vochysiaceae
Zanthoxylum sp.	Rutaceae

Annex 5: Map of the biological corridors in Southwest Costa Rica including the Osa Peninsula and the Golfo Dulce Region (source: https://www.regenwald.at/cobiga/cobiga)

Biologischer Korridor La Gamba COBIGA

AmistOsa Biologischer Korridor



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