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„Recovery of Aboveground Biomass, Species Richness and Species Composition in Tropical Secondary Forests in SW Costa Rica“

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Master's thesis by Florian Oberleitner

Abstract

The conservational value of tropical secondary forests is much debated, as they comprise more than half of the world's tropical forests. They were found to have high biomass resilience and accumulate species at fast rates. However, many studies focussed on aboveground biomass recovery and findings for recovery rates are contradictory. We studied 12 secondary forests in the wet tropics of SW Costa Rica along a chronosequence of 55 years and evaluated the recovery of aboveground biomass, tree species richness and tree species composition in relation to nearby old-growth forests. We found fast rates of aboveground biomass accumulation, especially in the first years of succession. The studied forests showed an asymptotic aboveground biomass accumulation and recovered an average of 187 Mg/ha after 20 years with an accumulation rate of 9.35 Mg/ha/yr in the first 20 years. Species richness showed a rather linear accumulation. We could find species composition of secondary forests to approach old-growth species composition, yet, at a very slow rate only. Over 55 years, however, the studied secondary forests did neither fully recover aboveground biomass or species richness nor species composition. Moreover, we found a high variability of recovery rates among different secondary forests. Considering this variability and contradictory findings for the recovery of secondary forests among other studies, we conclude that the resilience of secondary forests is highly variable and, particularly regarding biodiversity, secondary forests have a limited conservation value.

Introduction

Tropical rainforests are among the ecosystems with the greatest biodiversity on earth (Myers 1990), they represent one of the most important terrestrial carbon storages (Dixon et al. 1994; Lugo and Brown 1992), and are a major carbon sink (Pan et al. 2011). However, recent research has shown that, other than expected, carbon sequestration rates of primary forests are declining (Brienen et al. 2015). Furthermore, degradation through deforestation and conversion of forests to agricultural lands is an ongoing problem in the tropics and leads to emissions of carbon, a loss of biodiversity and a loss of ecosystem functions alike (Oliver et al. 2015). Although the world wide net rate of loss of natural forest declined by half from 1990 to 2015, the vast majority of natural forest loss can still be found in the tropics, with a rate of 6.4 million hectares per year between 2010 and 2015 (Keenan et al. 2015).

Owing to the loss of old-growth forests, tropical secondary forests are receiving increasing attention. Secondary forests already comprise more than half of the world's tropical forests (FAO 2010) and potentially have a key role as major carbon sinks and reservoirs for biodiversity (Chazdon et al. 2016; Myers 1990). The importance of recovering forests has also been recognised by international policies resulting in ambitious initiatives such as the REDD+ mechanism.

Since regrowing forests are a main terrestrial carbon sink (Pan et al. 2011), much attention has been paid to the recovery of aboveground biomass (AGB) in tropical forests. In an extensive study, Poorter et al. (2016) have corroborated that tropical secondary forests are highly productive and resilient, recovering 90% of the biomass of old-growth forests in 66 years, on average. In another study, regrowing tropical secondary forests in the Latin American lowlands could sequester the amount of carbon emitted from fossil fuel use and industrial processes in this region between 1993 to 2014 in as little as 40 years (Chazdon et al. 2016). Hence, natural regeneration of forests was proposed to be an efficient, low-cost mechanism with a high carbon sequestration potential (Chazdon et al. 2016).

Concerns about the decline of tropical old-growth forests do not only relate to these ecosystems' carbon sequestration capacity but also to the imminent loss of their extraordinary biodiversity. Apart from ethical reasons, loss of biodiversity might also reduce ecosystem functionality and ecosystem service provision (Hooper et al. 2005; Naeem et al. 2012). In tropical forests, higher species richness was, for example, associated with an increase in ecosystem resilience after disturbances (Silver et al. 1996) and with higher carbon storage capacity (Bunker et al. 2005). The time until recovering secondary forests reach levels of biodiversity comparable to old-growth forests is debated. While some studies have found that species richness reaches old-growth levels after 25 to 30 years (Aide et al. 2000; Letcher and Chazdon 2009; Peña-Claros 2003), others report that it takes 50 years for tree species richness to recover, while epiphyte species richness did not recover at all within this time frame (Martin et al. 2013). These contrasting findings suggest that patterns of succession, especially regarding the regeneration of species communities, are potentially complex and probably depend on factors such as climate, soil conditions and the nature and intensity of natural disturbance regimes. As a consequence, successional pathways of individual forests are likely difficult to predict (Chazdon et al. 2007; Holl 2007; Norden et al. 2015; Poorter et al. 2016).

While pathways of aboveground biomass or biodiversity accumulation in re-growing tropical forests have often been studied separately, joint evaluations of biomass and biodiversity recovery are rare. As a consequence, few attempts have been made to include and relate AGB to species recovery and vice versa during secondary succession in tropical forests. Here, we undertake such a joint assessment and thereby addressed the following questions:

- How fast does aboveground biomass (AGB) accumulate during secondary succession? What factors influence AGB accumulation?
- How does tree diversity change during secondary succession? How long does it take secondary forests to reach old growth forest level in terms of tree species richness and until species composition of secondary forests converges with the composition of adjacent old-growth forests?
- Are recovery of AGB and species richness correlated, i.e. do fast-growing secondary forests also accumulate (tree) species rapidly?

We therefore estimated AGB, species richness and similarity of species composition to old-growth forests in 12 lowland secondary forests of different ages in a perhumid tropical area in Costa Rica. As tropical wet forests are generally more productive and have higher growth rates than other forests (Brown 1997; Chave et al. 2005), we hypothesized that AGB will generally accumulate fast and reach old-growth levels considerably earlier than the average 66 years reported by Poorter et al. (2016). Owing to these assumed high growth rates we hypothesized that species richness will also recover fast, yet with a delay relative to AGB accumulation due to gradual species replacement during secondary succession.

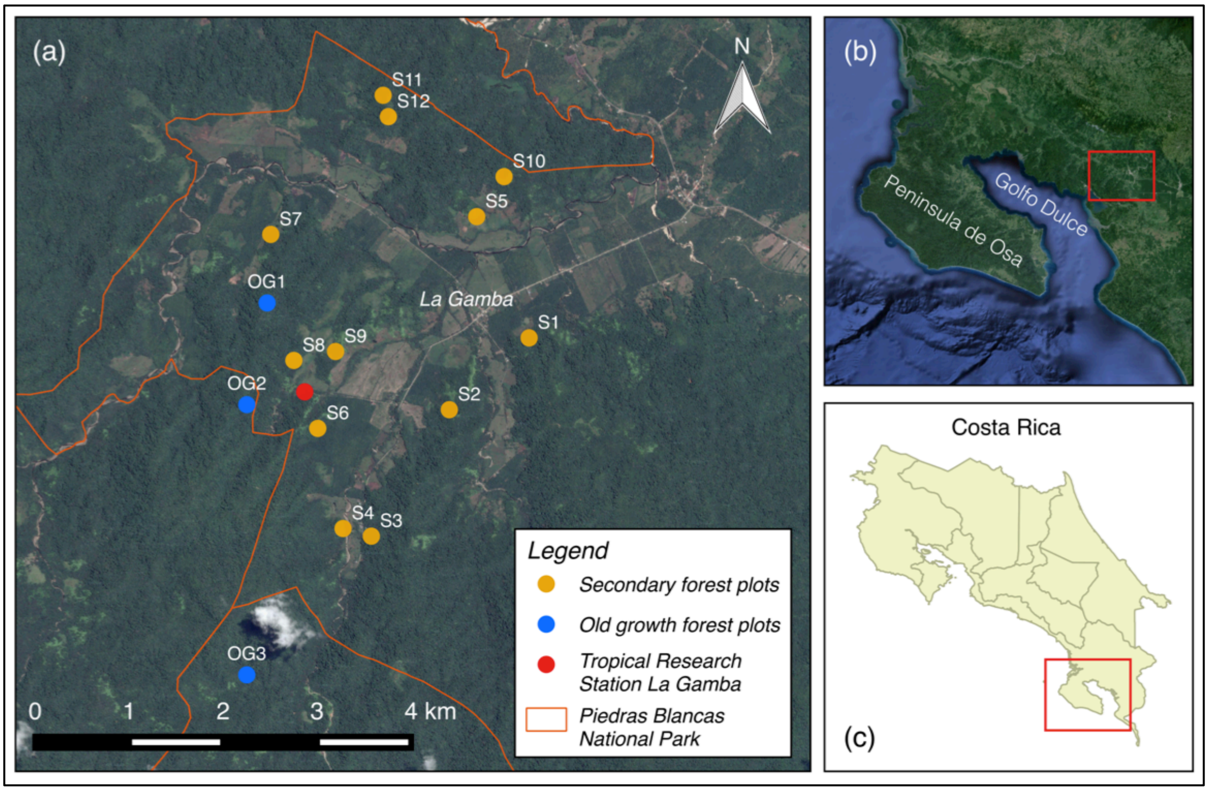

Figure 1: A map of the study area in indicating the study plots near (a) La Gamba in (b) the Golfo Dulce Region of (c) Costa Rica. For further information on plot characteristics see Appendix 2.

Materials & Methods

Study site

The 12 study sites are located in the vicinity of the Tropical Research Station La Gamba (8°42’03’’ N, 83°12’06’’ W) near Golfito, in the Golfo Dulce region of the Province of Puntarenas, SW Costa Rica (Fig. 1). The landscape is a matrix of primary and secondary forests, agricultural land and settlements. Agricultural areas are dominated by oil palm plantations and pastures and agricultural land is surrounded by patches of secondary forest, transitioning into primary forest (see Appendix 1). Forests are generally well preserved: the nearby Piedras Blancas National Park (148 km^2) and the Golfito Forest Reserve (13 km^2) protect large parts of the primary and secondary forests. Mean annual precipitation is 5911 mm with a short dry season and a pronounced wet season; mean annual temperature is 28.2°C, ranging from an average of 27°C in December to an average of 29.1°C in April and May (average from 1997 – 2015; data from the Tropical Research Station La Gamba). Hence this region is placed in the tropical lowland wet forest life zone (Holdridge 1967). The elevation ranges from 0 to 579 m.a.s.l.. Ultisols and Inceptisols are the main soil orders in this region (Chinchilla et al. 2012).

Data collection

Secondary forests were visually identified by the change of land cover on aerial photographs and satellite images from the years 1968, 1973, 1983, 1990, 1997, 2003, 2012 and 2014 using the software QGIS (QGIS Development Team 2015) and ArcGIS Desktop (ESRI 2011). Based on these changes of land cover in the sequence of aerial photographs and satellite images as well as on interviews with landowners the age of the secondary forests was estimated. To avoid edge effects, only forests with a minimum size of 1 ha were chosen for the study. To reduce the effect of slope on forest structure or species composition (Huber 2005), we only chose secondary forests on moderately steep slopes (13° and 37°) (see Appendix 2). Elevations were restricted to an interval of 100 m (80 – 165 m.a.s.l.). Given these constraints, 12 forests with times since abandonment ranging between 5 and 55 years were randomly chosen among all ages. Aerial photographs and satellite images were used to calculate forest cover in a 1 km radius around each plot (see Appendix 2). Images and interviews with landowners were used to determine land use before abandonment, which was either pastures or forests that were logged and left fallow (see Appendix 2).

Within each forest, a 500 m^2 plots was established and divided into 5 subplots of 100 m^2. Within the study plots all woody stems with a diameter at breast height (DBH) ≥ 2.5 cm were included in the inventory. We used a small DBH cut-off because only few large trees are found in young secondary forests. Trees were tagged, mapped, measured for DBH and identified to species level or in a few cases to genus level. Tree height was recorded for the 10 trees with the largest DBH in each plot. Multiple stems were recorded as single individuals with DBH measured for each stem. Stems were used to calculate AGB, while diversity calculations were based on individuals.

In addition, four soil samples were taken with a soil depth of 45 cm at random sites in each plot. Bulk soil samples were used to analyse soil pH ($CaCl_2$), base saturation (%), total amount of bases (cmol/kg), cation-exchange capacity (cmol/kg), carbon-to-nitrogen ratio, and soil organic content (%) as well as the fraction of sand and silt in the soils (%).

We used published data from three adjacent 1 ha primary forest plots as an old-growth reference for statistical analyses: the La Gamba slope and ravine primary forest plots from the Biodiversity and Ecosystem Functions (BDEF) project by Wanek et al. (2008) and the slope primary forest plot from Huber (2005) and Weissenhofer (2005). These primary forest plots are located in the Piedras Blancas National Park with an average distance of 2.6 km to our study sites (Fig. 1). Due to the short distance and the comparable topography these forests represent appropriate reference systems. In these three forests, 1 ha plots had originally been set up and subdivided into 100 subplots of 10 x 10 m2 each. All trees ≥ 10 cm DBH had been measured for DBH and height, and trees were identified to species or genus level. For detailed information see (Huber 2005; Wanek et al. 2008; Weissenhofer 2005).

Biomass allometry

Aboveground biomass (AGB) was calculated using a general allometric model for tropical wet forest trees (Chave et al. 2014):

$$AGB = \exp(-1.803 - 0.976*E + 0.976 * \log(WSG) + 2.673 * \log(DBH) - 0.0299*\log(DBH)^2)$$

with DBH in cm and E as a climate dependent parameter (E = -0.09591224 for the region).

One secondary forest included an exceptionally large tree (plot S1; Appendix 2). Some species may grow very fast, for others this is very unlikely, so that some trees are substantially older than the supposed age of the forest. In our opinion this tree can be seen as a remnant. We excluded the subplot with this remnant tree and calculated biomass for the 4 remaining subplots. For wood-specific gravity (WSG) we used data from central Panama (Hietz et al. 2013). For species that were not present in this dataset, we used data from a global wood dataset (Chave et al. 2009) or from the TRY plant traits database (Kattge et al. 2011). If no species data were available (34.1 % of the individuals), we used genus means first from Panama, and if not available then from the global dataset or TRY. If no data on the genus were available (7.5 % of the individuals), we used family-means. In the case of a few unidentified individuals and where no WSG data was available (2.6 % of the individuals) we used the mean WSG of all trees. The site-specific mean WSG was calculated as the WSG of each individual weighted by BA (Appendix 2).

Data analysis

All unidentified individuals as well as all individuals that could not be distinguished from others as morphospecies were excluded from the vegetation analyses (0.6 % of the individuals). For species richness, secondary forest data were treated separately for trees with DBH ≥ 10 cm to compare with the old-growth forest data. For AGB, species composition and similarity analyses of the vegetation all individuals DBH ≥ 2.5 cm were included. Two secondary forests turned out to be reforested with unknown species (plots S6 and S10; Appendix 2). Excluding these plots from the statistical analyses did not significantly change the results; the plots were therefore kept in the analyses.

Recovery of AGB over time was evaluated in a linear regression model, with log-transformed age as a predictor variable and AGB as the response variable. For species richness recovery a Poisson regression was applied, with log-transformed age as the predictor. To account for over-dispersion of the species count data, a quasi-likelihood model was used in the Poisson regression analysis of the species data (Quinn and Keough 2002). Transformations of the predictor variable age improved model fits in both cases, since AGB and species accumulation are expected to follow an asymptotic function. The models were used to predict AGB and species richness after 20 years of abandonment and calculate recovery rates for comparisons to published data.

To compare species richness and species composition of 1-ha plots from old-growth forests with 500 m2 plots from secondary forests, we used bootstrapping methods to calculate diversity indices. We randomly selected five 10 x 10 m subplots of old-growth forests 100 times, calculated species richness and species composition for each random selection and lastly calculated the mean of the 100 random samples for species richness. For species composition we compared each random old-growth sample to the secondary forests and calculated the mean values of all comparisons.

To account for the heterogeneity among secondary forest plots regarding AGB as well as species numbers, another more generalising approach was used. Plots were divided into four age groups: 0-13 years (N=4), 14-26 years (N=4) and 27+ years (N=4) since abandonment, as well as old-growth (OG; N=3). Each secondary forest group included 4 secondary forest plots; the old-growth group contained the three 1 ha primary forest plots described in the data collection section. Differences of AGB and species numbers between groups were analysed performing an ANOVA and Tukey's honest significance test for post-hoc pairwise comparison in R statistical software (R Core Team 2015). To account for variations in stem densities and rare species, species richness for age groups was also estimated by sample-based rarefaction (Colwell and Coddington 1994; Gotelli and Colwell 2011) using the 'vegan' package (Oksanen et al. 2015) R. Since statistical analyses with rarefied species numbers were similar, only results from absolute species counts are presented.

Non-metric multidimensional scaling (NMDS) was performed to visualize species composition of the study plots in a two-dimensional ordination space. An analysis of similarity (ANOSIM) was conducted with 999 permutations to test for differences in community composition between groups, with age groups as the grouping factor. NMDS and ANOSIM were implemented using the 'vegan' package in R. Similarity in terms of beta diversity was calculated as inverted Jaccard pair-wise dissimilarity using the 'betapart' package (Baselga et al. 2013) in R.

Mixed linear models were applied to test for effects of the other measured variables in addition to age on the response variables AGB and species richness. To test for the relative effect of variables that correlated with forest age (slope, soil pH, amount of sand, cation-exchange capacity and base saturation) variation partitioning methods were used performing redundancy analyses (RDA). Significances of variation partitioning analyses were calculated in ANOVAs. In addition to forest age as the main predictor, explanatory covariates in these analyses were: land use before abandonment, forest cover in a 1 km radius, slope, and different soil parameters: soil pH, base saturation, total amount of bases, cation-exchange capacity, carbon-to-nitrogen ratio, soil organic content, and the fraction of sand and silt in the soils (cf. data collection section).

Results

In total, 1184 unique stems belonging to 999 individuals were found in the 12 secondary forest plots. 124 different species belonging to 38 families were identified (see Appendix 3 for the species list). 25 individuals were only identified to genus level (13 genera), 5 individuals could not be identified at all. With the exception of the tree ferns *Cyathea microdonta* (DESV.) DOMIN, and *Alsophila* sp. R. BR. (both Cyatheaceae) all trees in the secondary forest inventory were angiosperms. All species found are native to the Golfo Dulce region with the exception of *Gmelina arborea* ROXB. (Lamiaceae), which was mainly found in one reforested plot (S10, Appendix 2 + 3), and two individuals in plot S9, with a reforested site nearby. Two young secondary forest plots (S11 and S12, Appendix 2) were monodominant stands of *Vochysia ferruginea* MART. (Vochysiaceae) and had a relatively high AGB. *Vochysia ferruginea* also dominated the canopy in two older plots (S2 and S7), where the undergrowth was more species rich than in plots S11 and S12.

Aboveground biomass

We found significant differences in AGB between age groups (One-way ANOVA, P = 0.005). A comparison of the single age groups showed that young secondary forests at the age of 0–13 years had significantly less biomass than older secondary forests of 27+ years of age and old-growth forests (Fig. 2a, Table 1). We could not find significant differences among all other groups (Fig. 2a, Table 1), however, indicating fast AGB accumulation in the first years of succession already. The results of the regression analysis also showed a rapid recovery of aboveground biomass in the beginning of succession (P = 0.001, R^2 = 0.58; Fig. 2b). Yet, predictions based on the regression model showed that AGB did not fully reach the level of old-growth forests in the same region (mean ± SE of 339 ± 30 Mg/ha; Fig. 2b). Calculations based on the fitted regression model showed that 20 years after abandonment 187 Mg AGB/ha had recovered; this equals to 55 % of old-growth forest AGB and an accumulation rate of 9.35 Mg AGB/ha/yr for the first 20 years of succession.

Species richness

Results of the analysis of age groups showed significant differences between age groups regarding species richness (One-way ANOVA, P = 0.002; Fig. 3a). In a pairwise comparison of age groups old-growth forests had significantly more species than secondary forests of any age class (Fig. 3a, Table 2) while secondary forests did not differ significantly from each other. Absolute species richness showed an almost linear accumulation in the Poisson regression analysis for all individuals (R^2 = 0.38, P = 0.043; Fig. 3b) and for individuals with a DBH ≥ 10 cm only (R^2 = 0.39, P = 0.025; Fig. 3c). Even though we could find a significant increase of species richness over time, levels of species richness comparable to old-growth forests (mean ± SE of 17.5 ± 0.5 species/500m^2) were not reached within 55 years post abandonment. By contrast, the near-linear relationships indicate that recovery of species richness is still in a relatively early phase even after 55 years.

Species composition

An overall analysis of similarity (ANOSIM) showed a significant difference in species composition between different age groups (P = 0.002, R = 0.44). A pairwise ANOSIM comparison of age groups showed that intermediate and older secondary forests had a species composition significantly different to the species composition of old-growth forests (Table 3). Young secondary forests, however, showed no significant difference to nearby old-growth forests. No difference in species composition between secondary forest age groups could be found.

Linear regression analysis showed that similarity to old-growth forests significantly increased with age (P= 0.004, R2 = 0.56; Fig. 3c). The NMDS stress level of 0.1 indicated a good representation of species composition of the study plots fairly in 2-dimensional ordination space (Fig. 4). Old-growth forests showed to be different from secondary forest and were grouped in the top left corner in NMDS plot. Species composition of

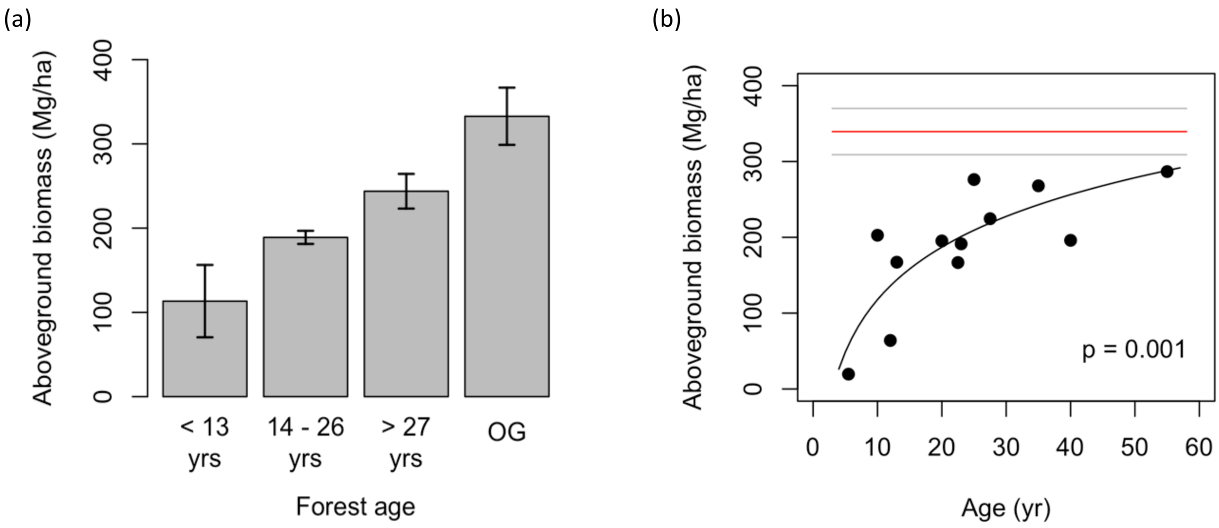

Figure 2: (a) Accumulation of aboveground biomass (AGB) by different age groups along succession. Grey bars indicate mean AGB value of the age group. Error bars indicate SE of the mean. For significance of differences in AGB see Table 1. (b) Relationship between aboveground biomass and stand age. Points represent secondary forest study plots along the chronosequence (N=12). Black line represents the regression trend line calculated with log-transformed age as the predictor (R^2 = 0.58). Red line and grey lines indicate mean ± SE AGB of nearby old-growth forests.

the two monodominant *Vochysia ferruginea* stands in plots S11 and S12 (10 and 13 yrs, respectively) was also reflected in the ordination as they grouped at the top right corner with the greatest distance to old-growth forests (Fig. 4). However, no general pattern of approximation of secondary forests towards old-growth forests along succession could be observed.

Effects of land use history, forest cover and soil parameters on AGB and species richness

In the constrained ordination, forest age showed significant effects on AGB and species richness ($P < 0.05$), explaining the largest part of the variances. Whatever covariate considered, however, we found no significant effects of covariates such as forest cover in a 1-km radius, land use before abandonment, soil parameters or abiotic site conditions on AGB or absolute species numbers ($P > 0.05$).

Due to uncertainties in determining land use before abandonment, we were only able to divide land use into two broad categories: pastures, with no more available details on intensity of use, and logged forests, that were left fallow immediately after logging. We could not find significant effects of land use history on species richness or AGB accumulation.

Some secondary forests had a relatively high amount of biomass at a young age, but at the same time a low number of species, suggesting a negative correlation between species richness and AGB. Therefore we also tested the number of species as a covariate to the main predictor age, but found no correlation between species richness and AGB.

TABLE 1: Significance of differences in aboveground biomass in secondary forests and old growth forests (OG) for different age groups. The table shows P values of post ANOVA pairwise comparisons by Tukey's honest significance test. (Values > 0.05 in bold)

	< 13 yr	14-26 yr	> 27 yr
14-26 yr	0.188		
> 27 yr	**0.048**	0.832	
OG	**0.003**	0.084	0.278

TABLE 2: Significance of differences in species richness (DBH > 10 cm) for different age groups of secondary forests and old growth forests (OG). The table shows P values of post ANOVA pairwise comparisons by Tukey's honest significance test. (Values > 0.05 in bold)

	< 13 yr	14-26 yr	> 27 yr
14-26 yr	0.479		
> 27 yr	0.265	0.965	
OG	**0.001**	**0.012**	**0.024**

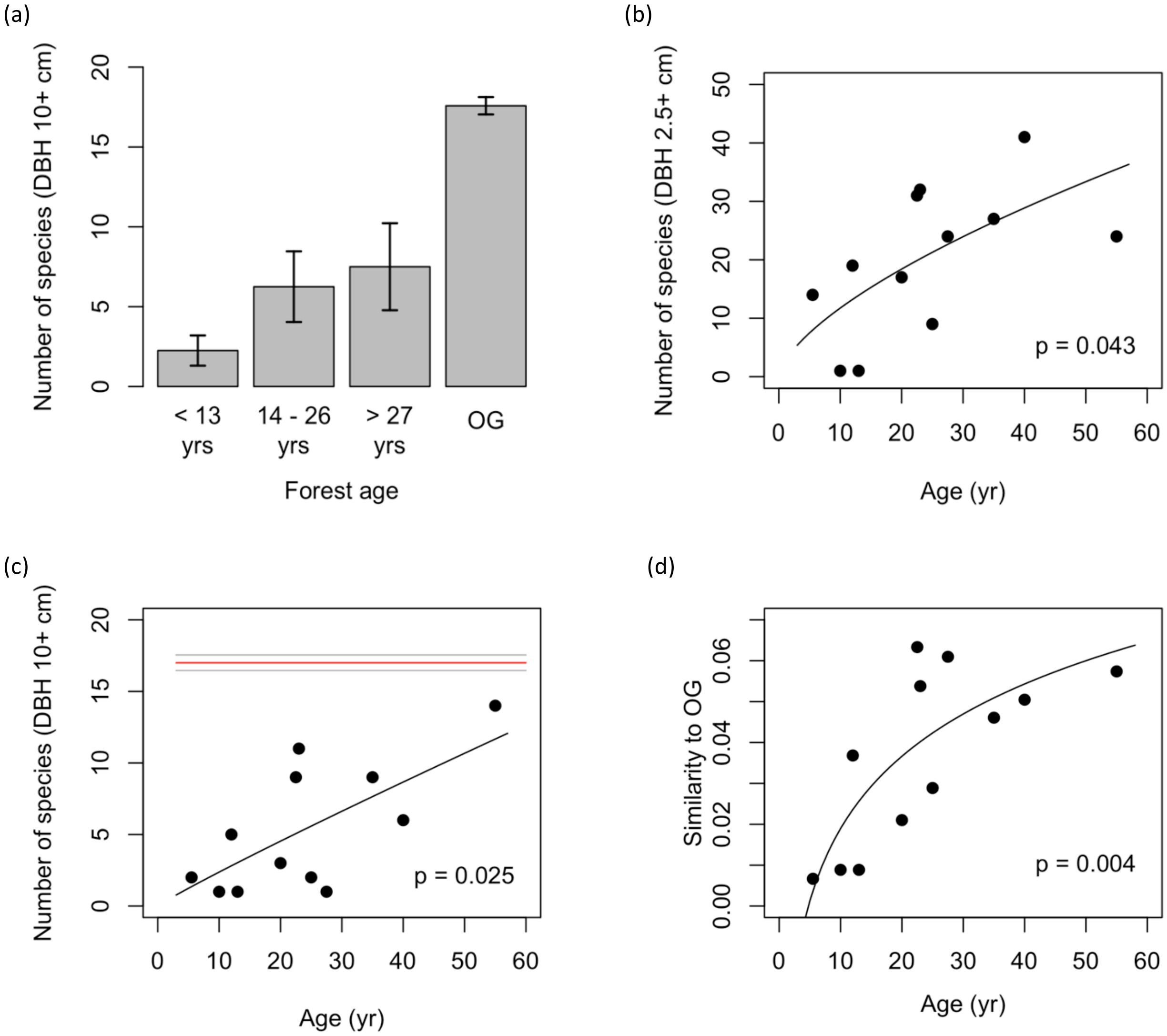

Figure 3: (a) Accumulation of species by different age groups along succession. Grey bars indicate mean number of species for the age group. Error bars indicate SE of the mean. (For significance of differences in species richness see Table 2). (b) Relationship between species richness and stand age for all individuals in secondary forest plots with a DBH ≥ 2.5 cm. Points represent secondary forest study plots along the chronosequence (N=12). Black line represents the Poisson regression trend line calculated with log-transformed age as the predictor (R^2 = 0.38). (c) Relationship between species richness and stand age for all individuals in secondary forest plots with a DBH ≥ 10 cm only. Points represent secondary forest study plots along the chronosequence (N=12). Black line represents the Poisson regression trend line calculated with log-transformed age as the predictor (R^2 = 0.38). Red line and grey lines indicate mean ± SE number of species of nearby old-growth forests. (d) Similarity of secondary forests to old-growth forests increases with stand age. Points represent Jaccard similarity values for secondary forest study plots along the chronosequence (N=12). Black line represents the regression trend line calculated with log-transformed age as the predictor (R^2 = 0.44)

Table 3: Significance of differences in species composition for different age groups groups of secondary forests and old growth forests (OG). The table shows P values ANOSIM pairwise comparisons of age groups. (Values > 0.05 in bold)

	< 13 yr	14-26 yr	> 27 yr
14-26 yr	0.247		
> 27 yr	0.162	0.346	
OG	0.097	**0.029**	**0.028**

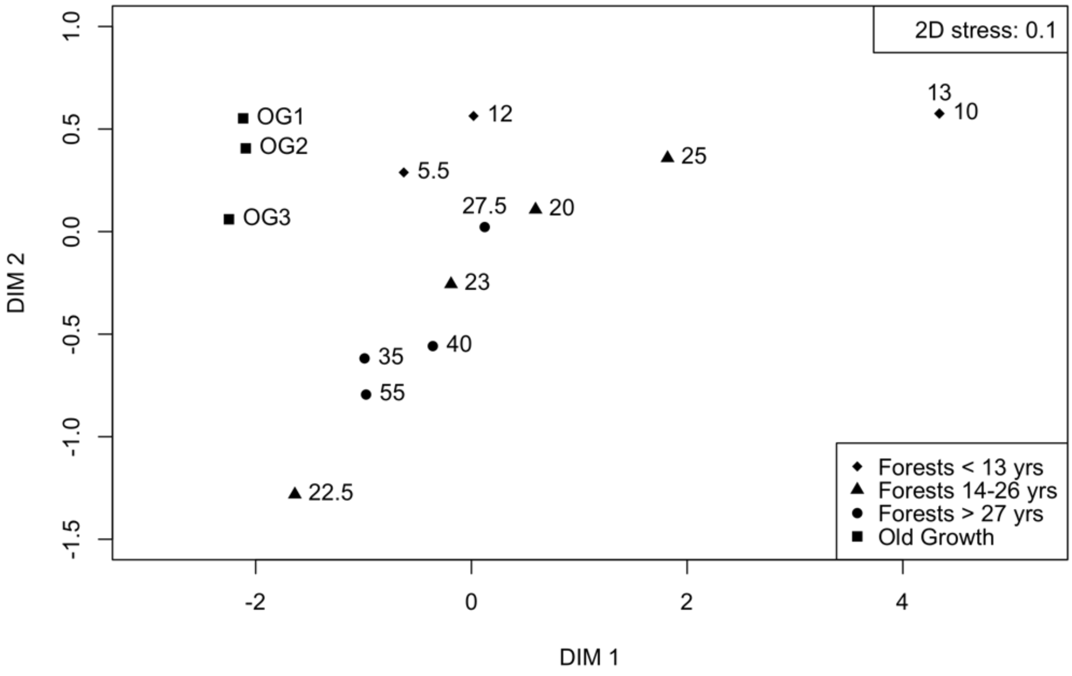

Figure 4: Non-metric multidimensional scaling (NMDS) plot of the 12 secondary forest plots and the 3 old-growth forest plots (OG 1-3) from our study. Numbers represent secondary forest age (also see Appendix 2).

Discussion

Aboveground biomass

In our study we found a rapid recovery of aboveground biomass, confirming other studies' findings for Neotropical secondary forest succession. When looking at the differences in AGB between age groups, only young secondary forests < 13 years showed to have less biomass than secondary forests > 27 years and old-growth forests, while all other groups were not significantly different from each other. When looking at the single plots in the regression analysis, the same pattern of fast recovery in the first years after abandonment appears. However, secondary forests did not fully recover and hence did not fully reach AGB levels of nearby old-growth forests within 55 years after abandonment.

In a recent study Poorter et al. (2016) concluded a high biomass resilience of tropical secondary forests. In their study they analysed AGB recovery in 45 forest sites and about 1500 forest plots all over the Neotropics and found that Neotropical secondary forests recovered on average 122 Mg/ha of AGB after 20 years, corresponding to 6.1 Mg/ha/yr, with significantly higher AGB levels (up to 225 Mg/ha after 20 years) with increasing water availability. A literature review of Silver et al. (2000) showed a very similar rate of 6.2 Mg/ha/yr during the first 20 years of succession in the Neotropics. At our study site we found AGB after 20 years at 187 Mg/ha and the recovery rate of 9.35 Mg/ha/yr to be much higher than the Neotropical average. Only few other studies (e.g. Broadbent et al. 2014; Vieira et al. 2003) found similar or higher biomass values at this age. The high biomass levels found in our study are best explained by the exceptionally high precipitation in our study region, that results in higher productivity (Clark et al. 2010; Poorter et al. 2016). However, in studies conducted in north-eastern Costa Rica, a study site comparable to our study site in terms of rainfall and seasonality, Chazdon et al. (2005) and Letcher and Chazdon (2009) found AGB levels to be lower than in our study, with about 172 and 145 Mg/ha (respectively; presented values are the biomass values recalculated by Poorter et al. (2016) with the allometric equation of Chave et al. (2014). Yet, after 20 years more biomass recovered relatively to old-growth (59 and 77 %, respectively) than in our study (55 %). Since aboveground biomass levels of old-growth forests in our region are comparatively high (Wanek et al. 2008), however, it hence takes longer to accumulate such amounts of biomass even if accumulation rates are exceptionally high. At the end of the observed succession, after 55 years, our plots had accumulated 84% of old-growth biomass, a value comparable to the average 90% reported by Poorter et al. (2016) for a time span of 66 years. As a corollary, fast accumulation rates apparently compensate for greater distance to old-growth AGB over time.

In contrast to our results, Letcher and Chazdon (2009) report that AGB values of second growth forests were soon comparable to those of old-growth forests. They even found a peak of AGB, exceeding old-growth level in intermediate to old aged secondary forests and other studies documented similar patterns (e.g. Denslow and Guzman 2000; Letcher and Chazdon 2009; Marin-Spiotta et al. 2007) mostly because of high abundance of long lived pioneer species and climax species at the same time (Mascaro et al. 2012). According to Mascaro et al. (2012) these patterns are mainly observed at small scales, with smaller plot sizes. Despite the small plot size of 0.05 ha in our study, our findings do not corroborate this hypothesis of a peak of biomass at intermediate ages. Rather, our data conform to a model of saturating biomass accumulation, fast at the beginning and levelling off towards the end of succession (Chazdon 2014; Finegan 1996).

Species richness

For our study site data of nearby old-growth was only available with a DBH threshold of 10 cm. We therefore analysed species richness data separately with thresholds set to DBH of 2.5 cm and, for comparison to old-growth, to 10 cm. The accumulation patterns we found in the regression analyses showed an almost linear accumulation for both DBH thresholds and that species richness did not fully recover in our chronosequence. If divided into age groups, we could see that each secondary forest group was significantly different from old-growth forests in terms of species numbers. Secondary forests, however, did not show significant differences among each other. This finding corroborates that species richness is accumulating relatively slowly. We note, however, that plots of similar ages had partly very different species numbers and hence species number accumulation has a considerable stochastic component – or at least one not explainable by the co-variates that we have used.

In a similar analysis, Letcher and Chazdon (2009) found secondary forests approaching old-growth species numbers much more quickly. In their study, these authors included all individuals with a DBH of more than 2.5 cm in both the secondary and the old-growth forests. This methodological difference may partly explain the contrasting results. Indeed, other studies also found that if smaller size classes are included in the analyses, old-growth species richness levels are reached faster during secondary succession (Denslow and Guzman 2000; Saldarriaga et al. 1988). This simply follows from the fact that small stems constitute a great part of the species richness in younger secondary forests, while in old secondary forests and old-growth forests larger stem classes make a much more important contribution to total species richness. Furthermore, few fast growing pioneer species dominate the large DBH size classes in early succession but it takes longer for species with a high maximum size to establish (Finegan 1996; Guariguata et al. 1997; Guariguata and Ostertag 2001). Nevertheless, even we accounted for young trees in the secondary forests, the secondary forests did not reach old-growth levels. It hence seems that the biodiversity accumulation rates observed at our sites are indeed slower than those reported by Letcher and Chazdon (2009).

Direct comparisons of species numbers to literature are difficult, since plot size, DBH thresholds and diversity indices vary among different studies due to a lack of standardization in data collection (Chazdon et al. 2007). Therefore many different patterns of species richness accumulation can be found among studies. Peña-Claros (2003) found species numbers with a DBH threshold of 1 cm to reach old-growth levels after as little as 20-25 years only. With the same threshold, Aide et al. (2000) showed that species richness was not significantly different to old-growth after 35-40 years. Other studies found species numbers in late successional stages to be even higher than in old-growth forests. Eggeling (1947), for example, found a peak for species in intermediate aged secondary forests with a DBH greater than 10 cm. Many chronosequence studies lack data from older secondary forests (50 + years) due to the availability of reliable information about older secondary forests (Chazdon et al. 2007; Holl 2007), which is also a drawback of our study. More data from older secondary forests and a focus on the late stages of succession would allow for a clearer picture of the transition from second growth to old-growth.

We found two forest plots (S11 and S12) to be dominated by one species only (*Vochysia ferruginea*). The pattern of monospecific dominance has been described for old-growth forests all over the tropics (Hart 1990; Hart et al. 1989; Torti et al. 2001). Peh et al. (2011) suggested a complex model of interactions and feedbacks that lead to longer lasting monodominance in old-growth forests. Evidence exists that monodominance by either invasive or non-invasive plant species in second growth may lead to an arrest of succession (Cohen et al. 1995; Fine 2002). However, little is known about monodominance during secondary succession. Personal observations in the seedling layer of these two plots documented a higher number of tree species that also occur in later successional stages this region. Furthermore the canopy of plots S2 and S7 were also dominated by *Vochysia ferruginea*, but had a much higher total number of species. In plot S2 we even found the highest species richness of our chronosequence (Appendix 2). Hence we conclude that monodominance of these 2 plots is only occurring for a restricted time during succession due to the fast growth of *Vochysia ferruginea* in the initial stage of recovery.

Other than expected, the young secondary forest age group including these two plots was not significantly different to old-growth forests regarding species composition. The ordination plot shows these study plots to be far distinct from other plots (Fig. 4). The other 2 plots in this age group (S5 and S9) were mainly dominated by early successional pioneer species. Yet they were placed even closer to old-growth than other secondary forests in ordination space. However, NMDS ordination showed no clear pattern of convergence in species composition of secondary forests with old-growth forests. These observations might be a reflection of different successional trajectories and different rates of recovery.

Species composition

Even though on a small scale, recovering forests were becoming more similar to old-growth in terms of species composition with time in our study Nevertheless, even the older secondary forests remained statistically significantly different from old-growth. The likelihood of secondary forest succession to arrive at the original species composition of old-growth is controversially debated (Chazdon 2008; Chazdon et al. 2007). Re-evaluating Eggeling’s (1947) data, Sheil (1999), for example, found that species composition indeed approached old-growth composition in a survey spanning 60 years of succession. Terborgh et al. (1996) found a similar pattern in an area with little or no disturbance of forest cover, and, more recently, Norden et al. (2009) showed that species composition of secondary forests clearly converged with species composition to old-growth forests. However, the latter authors documented that different trajectories were observed, with factors such as former land use, surrounding forest cover playing a modifying role. Letcher and Chazdon (2009) came to similar conclusions in a chronosequence study of 44 years. Guariguata et al. (1997) found that species composition in secondary forests was more similar to species composition in old-growth for small size classes (DBH ≥ 5 cm) than for bigger size classes (DBH ≥ 10 cm) only. This suggests that similarities are easier detectable if smaller size classes are included in a study. We included all individuals (DBH ≥ 2.5 cm) in the species composition analysis, but found no clear convergence of species composition towards old-growth forests. We therefore we suppose that, compared to AGB and species richness, recovery of old-growth species composition will take even longer if such convergence will ever occur at all.

Effects of co-variates

The recovery of forests can be affected by different site properties such as the availability of propagules from the surrounding vegetation (e.g. Aide et al. 1995; Holl 2007; Kammesheidt 2002) or the land use type and intensity before abandonment (Chazdon et al. 2007; Holl 2007; Jakovac et al. 2015; Silver et al. 2000). Especially in early stages and on strongly degraded land, succession can be delayed or even arrested due to the dominance of a few grass and shrub species (Kuusipalo et al. 1995; Otsamo 2000). Here, we incorporated different factors in addition to time to find explanations for variations in AGB and species richness. We propose that we could not find an effect of surrounding forest cover because forests in our study area are relatively well preserved. If secondary forests did not directly border old-growth, only smaller woodless gaps were between forest patches and continuous forests (see Fig. 1 and Appendix 1). As a corollary, propagule availability is probably similar among the plots included in this study. With respect to land use prior to abandonment we suppose that our categories were too rough to detect potential effects.

We propose that heterogeneity of plots along succession, regarding species composition, species richness and AGB alike, reflects different trajectories of succession. An underlying assumption of chronosequence studies is, however, that succession occurs as a single predictable trajectory along a defined time sequence, leading to a single stable climax forest (Chazdon 2008; Johnson and Miyanishi 2008; Walker et al. 2010; cf. Clements 1916; Egler 1954; Gleason 1917; Tansley 1935; White 1979; Whittaker 1953). This issue has also been addressed in several other Neotropical forest succession studies (e.g. Aide et al. 2000; Finegan 1996; Hubbell et al. 1999) with the general conclusion that succession is not a deterministic process that follows one trajectory only (Holl 2007; Norden et al. 2015). Therefore chronosequence studies face certain problems of applicability, for they do not sufficiently account for variations in gradients other than time since abandonment (Holl 2007). In our study this seems to be especially obvious regarding species composition. Furthermore, difficulties in documenting site conditions at the time of abandonment are among the common weaknesses of chronosequence studies (Chazdon et al. 2007; Holl 2007; Walker et al. 2010). This might lead to complicate the identifications of driving factors of succession. However, providing a space-for-time substitution, they are still an accurate option for studying general patterns of succession and relationships that drive the regrowth of tropical rainforests over long periods of time (Walker et al. 2010). More data of secondary forests, especially of older secondary forests, would have helped to fill gaps in our chronosequence and hence eliminate uncertainties in our study. Yet, we are confident that our major findings reflect secondary succession well in our chronosequence time frame.

Conclusion

We demonstrated that aboveground biomass is accumulating quickly in secondary forests. These results generally support the assumption of a high biomass resilience of tropical secondary forests, as suggested by Poorter et al. (2016). However, it takes longer for species richness to recover. Moreover, we could not find a clear convergence in species composition of secondary forests with old-growth forests. We strongly support the conclusions of other studies that secondary tropical forests should be main targets of conservation approaches as they are comparably resilient (Gehring et al. 2005; Letcher and Chazdon 2009; Norden et al. 2009; Poorter et al. 2016), play an important role in the tropics, as they amount to more than half of the world's tropical forests (FAO 2010) and provide important ecosystem functions and services (Hooper et al. 2005; Naeem et al. 2012). However, as Breugel et al. (2013) recently pointed out, the role of secondary forests for the conservation of floristic diversity is more limited than their importance for carbon sequestration. And even if properties like AGB and species richness recover at fast rates, it takes much longer for old-growth forests to regain such vital characteristics as primary forest species composition with diverse undergrowth, diverse epiphyte communities and a high animal diversity or old-growth forest dynamics and structure with big trees and high amounts of dead biomass. Hence the importance of conserving functioning old-growth forests shall not be traded off against a stronger focus on secondary forests.

Many questions remain as to what determines successional trajectories and what factors drive the recovery of tropical forests. Therefore we encourage further investigations in the complex mechanisms during tropical secondary forest succession, as they would help to identify and manage particularly valuable second and old-growth forests.

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Appendix 1: Overview of the landscape surrounding La Gamba

A photograph of the La Gamba landscape, with pastures and oil palm plantations bordering to secondary forests and old-growth forests on the hills. (Photo by Florian Oberleitner)

Appendix 2: Overview of the forests included in the study

Forest type	Age (yrs)	Site	AGB (Mg/ha)	BA (m^2/ha)	WSG	Species (DBH 2.5+)	Species (DBH 10+)	Lat.	Long.	Land-use	Forest Cover in 1-km radius (ha)	Elevation (m.a.s.l.)	Slope (°)
Secondary	5.5	S5	19.6	5.3	0.437	14	2	8.71753	-83.18537	pasture	149	80	20.9
forests	10	S11	202.7	29.6	0.415	1	1	8.72940	-83.19423	logged	266.4	162	13.4
	12	S9	64.0	11.4	0.514	19	5	8.70490	-83.19881	pasture	172.6	88	18.9
	13	S12	167.2	26.9	0.510	1	1	8.72738	-83.19376	logged	246.8	166	19.7
	20	S6	195.3	25.9	0.499	17	3	8.91639	-83.20806	pasture	176.5	116	31.4
	22,5	S4	166.7	22.2	0.374	31	9	8.68766	-83.19801	pasture	251.5	93	32.1
	23	S8	191.4	29.5	0.377	32	11	8.70385	-83.20277	pasture	211.1	107	29.0
	25	S10	276.2	46.3	0.386	9	2	8.72165	-83.18269	logged	220.9	151	24.4
	27.5	S7	224.6	33.7	0.528	24	1	8.71609	-83.2048	logged	166.4	119	23.4
	35	S3	268.0	32.0	0.374	27	9	8.68715	-83.19513	logged	260.4	113	29.4
	40	S2	196.1	29.1	0.399	41	6	8.69908	-83.18768	logged	146.4	123	24.3
	55	S1	286.7	30.2	0.522	24	14	8.70620	-83.18004	pasture	132.3	101	36.5
Primary	old-growth	OG1	306.5	31.5	0.533		16.6	8.68900	-83.20810				(Wanek et al. 2008)
forests	old-growth	OG2	291.8	30.1	0.527		17.7	8.67390	-83.20720		**Ref.:**		(Wanek et al. 2008)
	old-growth	OG3	400.1	35.5	0.552		18.4	8.68330	-83.20000				(Huber 2005; Weissenhofer 2005)

An overview of the age, name of the plot (Site), aboveground biomass (AGB), basal area (BA), site-specific average wood specific gravity (WSG; weighted by BA), number of species (per $500m^2$), latitude (Lat.), longitude (Long.), land-use before abandonment, forest cover in a 1-km radius, elevation and slope of the secondary forest and old-growth forest (OG) study plots.

Appendix 3: List of tree species identified in the secondary forests

Species	**Family**
Abarema adenophora	Fabaceae
Acacia allenii	Fabaceae
Albizia sp.	Fabaceae
Alchornea costaricensis	Euphorbiaceae
Alsophila sp.	Cyatheaeceae
Andira inermis	Fabaceae
Apeiba membranaceae	Malvaceae
Apeiba tibourbou	Malvaceae
Ardisia opegrapha	Primulaceae
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
Dendropanax arboreus	Araliaceae
Cyathea microdonta	Cyatheaceae
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
Hieronyma alchorneoides	Phyllanthaceae
Inga densiflora	Fabaceae
Inga jinicuil	Fabaceae
Inga oerstediana	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 trinervia	Melastomataceae
Mikania guaco	Asteraceae
Myriocarpa longipes	Urticaceae
Ochroma pyramidale	Malvaceae
Ocotea cernua	Lauraceae
Otoba novogranatensis	Myristicaceae
Palicourea guianensis	Rubiaceae
Pentagonia wendlandii	Rubiaceae
Perebea hispidula	Moraceae
Perrottetia sessiliflora	Dipentodontaceae
Piper aduncum	Piperaceae
Piper sp.	Piperaceae
Protium sp.	Burseraceae
Psychotria chiapensis	Rubiaceae
Psychotria cooperi	Rubiaceae
Psychotria elata	Rubiaceae

Psychotria solitudinum	Rubiaceae
Quiina schipii	Ochnaceae
Richeria obovata	Phyllanthaceae
Rinorea crenata	Violaceae
Senna reticulata	Fabaceae
Simarouba amara	Simaroubaceae
Simira maxonii	Rubiaceae
Siparuna andina	Siparunaceae
Sloanea sp.	Elaeocarpaceae
Solanum ravirosum	Solanaceae
Sorocea pubivena	Moraceae
Spondias mombin	Anacardiaceae
Sterculia apetala	Malvaceae
Symphonia globulifera	Clusiaceae
Terminalia amazonia	Combretaceae
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	Hypericaceae
Vismia guianensis	Hypericaceae
Vismia macrophylla	Hypericaceae
Vochysia allenii	Vochysiaceae
Vochysia ferruginea	Vochysiaceae
Zanthoxylum sp.	Rutaceae

Appendix 4: Abstract in German / Zusammenfassung

Tropische Sekundärwälder umfassen mehr als die Hälfte der tropischen Wälder der Welt, weshalb ihr Schutzwert lebhaft diskutiert wird. Studien belegen die große Biomasse-Resilienz und die schnelle Akkumulation von Arten. Viele Studien konzentrierten sich auf die Regeneration von Biomasse wobei die Ergebnisse bezüglich der Regenerationsraten widersprüchlich sind. Wir untersuchten 12 tropische Sekundärwälder in Süd-West Costa Rica In einer 55 Jahre umfassenden Chronosequenz und evaluierten die Regeneration von Biomasse, Anzahl von Baumarten und Zusammensetzung von Baumarten im Verhältnis zu nahegelegenen Primärwäldern. In den ersten Jahren der Sukzession fanden wir eine schnelle Anhäufung von Biomasse vor. Die Wälder zeigten eine asymptotische Zunahme von Biomasse und akkumulierten bereits nach 20 Jahren 187 t/ha. Dies entspricht einer Akkumulationsrate von 9.35 t/ha/a in den ersten 20 Jahren. Im Gegensatz dazu fanden wir eine lineare Akkumulation von Baumarten. Die Artzusammensetzung der Sekundärwälder näherte sich jener der Primärwälder nur sehr langsam an. In 55 Jahren konnten sich jedoch keine der untersuchten Eigenschaften vollständig regenerieren. Darüber hinaus fanden wir eine hohe Variabilität von Regenerationsraten zwischen den untersuchten Sekundärwäldern. Daraus schließen wir, dass die Resilienz von Sekundärwäldern sehr variabel ist und Sekundärwälder daher - besonders in Bezug auf Artenvielfalt - einen eingeschränkten Schutzwert haben.