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# Recovery of aboveground biomass, species richness and composition in tropical secondary forests in SW Costa Rica



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### ABSTRACT

Tropical secondary forests comprise about half of the world's tropical forests and are important as carbon sinks and to conserve biodiversity. Their rate of recovery varies widely; however, particularly older secondary forests are difficult to date so that the recovery rate is uncertain. As a consequence, factors affecting recovery are difficult to analyse. We used aerial surveys going back to 1968 to date 12 secondary forests in the wet tropics of SW Costa Rica and evaluated the recovery of aboveground biomass, tree species richness and tree species composition in relation to nearby old-growth forests and previous land use. To confirm the validity of the spacefor-time substitution, the plots were re-censused after four years. We found fast rates of aboveground biomass accumulation, especially in the first years of succession. After 20 years AGB had reached c. 164 Mg/ha equivalent to 52% of the biomass in old-growth forests in the region. Species richness increased at a slower pace and had reached c. 31% of old-growth forests after 20 years. Recovery rates differed substantially among forests, with biomass at least initially recovering faster in forests after clearcuts whereas species numbers increased faster in forests recovering from pastures. Biomass recovery was positively related to the forest cover in the vicinity and negatively to species richness, whereas species richness was related to soil parameters. The change during the four years between the censuses is broadly in line with the initial chronosequence. While the recovery of tropical secondary forests has been studied in many places, our study shows that various environmental parameters affect the speed of recovery, which is important to include in efforts to manage and restore tropical landscapes.

### 1. Introduction

Tropical rainforests are the terrestrial ecosystems with the highest biodiversity on earth (Myers 1990) and function as an important carbon sink (Dixon et al. 1994; Pan et al. 2011). Degradation through deforestation and conversion of forests to agricultural land is ongoing and leads to emissions of carbon, and the loss of biodiversity and ecosystem functions (Oliver et al. 2015). Although the world wide net loss rate of natural forest declined, the vast majority of natural forest loss can still be found in the tropics, with a loss of 6.4 million hectares per year between 2010 and 2015 (Keenan et al. 2015).

While the carbon sink capacity of old-growth forests is limited and is declining in the Amazon (Hubau et al. 2020), regrowing forests often

have high rates of biomass accumulation and thus carbon sequestration and therefore are receiving increasing attention (Chazdon 2014). They comprise about half of the world's tropical forests (FAO 2015) and also play an important role as reservoirs for biodiversity (Chazdon et al. 2016). The importance of recovering forests for climate mitigation is widely acknowledged and the magnitude of their contribution is being discussed (Bastin et al. 2019; Lewis et al. 2019).

Because in tropical forests a large fraction of carbon is stored in the aboveground biomass (AGB) of trees and allometric models permit a relatively easy estimation of it (Chave et al. 2014), much attention has been paid to the recovery of AGB in tropical forests. An extensive data set corroborated that tropical secondary forests are highly productive and resilient, recovering on average 90% of the biomass of old-growth

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forests in 66 years (Poorter et al. 2016). However, this synthesis study also showed a tremendous variation. Some of this variation is due to differences in rainfall but much remains unexplained. Some uncertainty may also result from the difficulty of knowing the age or previous land use of regrowing forests, particularly in older secondary forests where information is often obtained by seeking local knowledge.

Tropical regions harbour the majority of global species (Barlow et al. 2018) and old-growth rainforests are particularly rich in tree species (Sullivan et al. 2017). Apart from the importance of conserving biodiversity per se, the loss of diversity may also reduce important ecosystem functions and services (Hooper et al. 2005; Poorter et al. 2015). In tropical forests, higher tree species richness was also associated with an increase in ecosystem resilience after disturbance (Silver et al. 1996). The time until recovering secondary forests reach levels of tree diversity comparable to old-growth forests is highly variable. While some studies have found species richness similar to old-growth forests after only 25-30 years (Peña-Claros 2003; Letcher & Chazdon 2009b), others reported that it takes substantially longer and that the recovery of species richness is slower than that of biomass. A recent analysis of 56 neotropical chronosequences found that, on average, after only 20 years 80% of old-growth forest species richness was restored but only 34% of the species composition (Rozendaal et al. 2019). As with AGB, the variation among sites was very large and was correlated with environmental variables such as water availability but uncorrelated with soil fertility or prior land use.

Although the often fast recovery of tropical biomass and biodiversity in secondary forests is encouraging, the poor predictability of recovery rates limits strategies to optimize the management of tropical landscapes (Melo et al. 2013; Molin et al. 2018). Low predictability may arise from the stochastic nature of forest succession (Norden et al. 2015) but may also be due to the limited records of factors potentially affecting succession, including the age of the forest, previous land use and the nature and intensity of prior disturbance. Forest recovery over time is frequently studied by comparing plots differing in age, an approach called space-for-time substitution. This may, however, mix forests that are on different successional trajectories. To analyze the idiosyncrasies of successional trajectories and to test the validity of the space-for-time substitution, plots can be re-sampled over time (Mesquita et al. 2015; Norden et al. 2015).

More data on the pathways of succession together with information on the factors that might explain differences in speed and trajectories are hence important to optimize the restoration of tropical forests, if these are to contribute substantially to the ambition to restore 350 million ha of degraded land by 2030 (Holl 2017, www.bonnchallenge.org). To address this need, we here used aerial photographs dating back to 1960 to locate and date the age of 12 secondary forests in a perhumid lowland area in Costa Rica. For these forests, we analysed AGB accumulation, tree diversity and the similarity to nearby oldgrowth forests in relationship with forest age, soil characteristics, surrounding forest cover and previous land use and compared the speed of succession with other published data.

### 2. Materials& methods

### 2.1. Study region

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 secondary forests of various ages and remnants of primary forests. Larger tracts of primary forest are not far away as the area borders the Piedras Blancas National Park (Fig. 1). Mean annual precipitation is 5910 mm with a short dry season during which mean monthly rainfall

is still > 100 mm. Mean annual temperature is 28.2 °C, ranging from an average of 27 °C in December to 29.1 °C in April and May (average from 1997 to 2015 measured at the Tropical Research Station La Gamba). Soils in the region are mostly Ultisols and Inceptisols (Mata Chinchilla & Sandoval Chacón 2016). Aboveground biomass and tree diversity of old-growth forests in the region has been studied in several 1-ha plots (Hofhansl et al. 2020) and AGB was also estimated by airborne Light Detection and Ranging (Taylor et al. 2015), which was partially calibrated on the 1-ha plots. These studies showed that regional AGB is high compared to other neotropical forests, probably because of relatively fertile soils in the geologically active area. In addition to soil fertility, AGB is controlled by topography and to a smaller extent by regional variation in climate (Taylor et al. 2015; Hofhansl et al. 2020).

### 2.2. Site selection and data collection

To estimate the age of secondary forests, we used aerial photographs from the Costa Rican land survey (Instituto Geográfico Nacional de Costa Rica) for the years 1960, 1968, 1973, 1983, 1990, and 1998, Quickbird satellite images for the years 2003 and 2008 and Geo Eye satellite images for the years 2012 and 2014. These were visually compared using the software QGIS (QGIS Development Team, 2020) to identify pastures and secondary forests in each image. Based on the aerial images, there were no large trees left on the plots, though one larger individual was apparently overlooked and the subplot later excluded from the analysis. If no more reliable information was obtained by interviewing landowners, secondary forest succession was assumed to have started in the median year between a photograph showing no tree cover and the first one showing tree cover at a particular site. To avoid edge effects, only forests with a current minimum size of 1 ha were chosen for the study. We selected 12 sites with times since the start of secondary forest succession ranging between 5 and 55 years in 2015. The sites are located at elevations between 80 and 170 m and at slopes from 13 to 36° as the flat areas in the region are generally used for cultivation. A vegetation map of the area (Weissenhofer et al. 2008) based on aerial photographs and satellite images from 1998 and 2003, respectively, was used to calculate forest cover in a 1 km radius around each plot (Table 1). Images and interviews with landowners were used to determine the land use before abandonment, which was either pasture or forest that had been logged and left to regrow.

Within each forest site, a 500 m<sup>2</sup> plot was established and divided into 5 subplots of 100 m<sup>2</sup>. In February – April 2015 and again in 2019 we measured diameter at breast height (DBH) of all woody stems with  $DBH \ge 2.5$  cm. Trees were tagged, mapped, and species identified. Tree height was recorded for the 10 trees with the largest DBH in each plot using a Vertex IV hypsometer (Haglöf, Sweden). 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. One secondary forest included an exceptionally large tree that we believe must have been a remnant from a previous forest so we excluded the 100 m<sup>2</sup> subplot that included this tree from all calculations and analyses. Dead trees and lianas were excluded from the analysis. Lianas require different and more laborious methods to estimate biomass (Schnitzer et al. 2008), contribute relatively little to AGB (< 2%of self-supporting plants across a forest age gradient, Letcher & Chazdon 2009a), and were also excluded from the reference old-growth forests data.

Four soil samples were taken with a 8-cm diameter root corer from 0 to 15 cm at random points in each plot and fresh bulk soil samples were sieved to 2 mm. Soil pH was measured in water and in 10 mM CaCl<sub>2</sub> slurries (weight:volume = 1:5) using a calibrated ISFET-electrode (Sentron Argus). Effective cation exchange capacity (CEC) was determined following ÖNORM L 1086-2, based on the extraction of 5 g air-dried soil with 100 mL BaCl<sub>2</sub> solution at actual soil pH value and measurement of exchangeable Ca, Mg, K, Na, Fe, Mn and Al by



Fig. 1. Location of secondary forest plots in the study area near La Gamba in the Golfo Dulce Region of Costa Rica.

inductively coupled plasma spectrometry (ICP) at BOKU University, Vienna. Base saturation (BS<sub>eff</sub>) was calculated as BS<sub>eff</sub> (%) = ( $\Sigma$ base cations / ( $\Sigma$ base cations + exchangeable acidity)) × 100. Total soil N and soil organic carbon (SOC) contents were determined after homogenizing the samples using a ball mill (Retsch MM2000) with an Elemental Analyzer (EA 1110, CE Instruments) coupled to an isotope ratio mass spectrometer at the University of Vienna (Delta<sup>Plus</sup>, Thermo Fisher). Soil texture was measured using a modified micro-pipette method (Miller & Miller 1987), where air dried soil samples (4 g) were suspended with 40 mL 5% sodium hexametaphosphate and shaken overnight.

### 2.3. Data analysis

Aboveground biomass (AGB) was calculated using a general allometric model for tropical wet forest trees (Réjou-Méchain et al. 2017). Wood specific gravity (WSG) was obtained from 5.15-mm increment cores collected locally (accounting for 64% of basal area - BA) or in Panama (Hietz et al. 2017; 21.22% of BA) since these data were obtained in a standardized way. WSG for species not in the regional datasets were obtained from a global dataset (Zanne et al. 2009). If species-wise WSG data were not available, we used genus means (8.6% of BA), family means (0.7%) or a dataset mean (2.9%). The community-weighted mean (CWM) WSG was calculated as the mean WSG of all individuals weighted by BA. For comparison with old-growth forests, we used data from 15 nearby 1-ha primary forest plots in the region where trees  $\geq$  10 cm DBH had been measured (Hofhansl et al. 2020, Fig. 1).

To compare species richness with old-growth forests, only trees with DBH  $\geq 10$  cm were used as this was the size-threshold for the regional OG forests for which data were available. To estimate the contribution of trees < 10 cm DBH to AGB of OG forests, unpublished data of trees 2.5 – 10 cm DBH from 100 m<sup>2</sup> subplots in three of the OG forests were analysed. Scaled to 1 ha, these small trees represent between 2.3 and 5.8% (average 3.7%) of the AGB of trees  $\geq 10$  cm. We thus added 3.7% to the AGB of Costa Rican OG forests for comparison with secondary forest AGB. Two secondary forests turned out to have a number of trees that may have been planted (*Calophyllum brasiliense* in plot S6 and *Gmelina arborea* in plot S10), but these do not stand out in AGB or species composition and were therefore kept in the analyses. To

Table	1

Secondary	forest plots sampled	in the region of La	Gamba, SW Costa	Rica. SOC: soil organic carbon,	C/N: bulk soil C/N ratio,	CEC: cation exchange capacity.
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Site	Age (yrs)	Previous land-use	Lon.	Lat.	Slope (°)	Elevation (m.a.s.l.)	Forest in 1 km radius (%)	Sand (%)	Silt (%)	pН	SOC (mg/g)	C/N ratio	CEC (mmol/kg)	Base saturation (%)
S5	5.5	pasture	-83.185	8.718	20.9	80	47	8.1	27.4	3.5	25.7	9.5	8.8	12.5
S11	10	logged	-83.194	8.729	13.4	162	85	10.5	43.7	3.7	36.0	11.5	13.1	37.7
S9	12	pasture	-83.199	8.705	18.9	88	55	9.3	87.6	3.7	25.0	9.7	7.4	21.8
S12	13	logged	-83.194	8.727	19.7	166	79	5.1	26.9	3.7	40.7	11.5	8.9	3.7
S6	20	pasture	-83.208	8.916	31.4	116	56	8.9	50.1	4.0	28.9	10.8	10.6	45.7
S4	22.5	pasture	-83.198	8.688	32.1	93	80	15.3	51.4	4.3	23.6	9.8	24.9	76.6
S8	23	pasture	-83.203	8.704	29	107	67	5.0	73.4	3.7	22.7	10.4	8.5	36.8
S10	25	logged	-83.183	8.722	24.4	151	70	12.5	37.6	3.7	32.0	10.3	15.2	33.4
S7	27.5	logged	-83.205	8.716	23.4	119	53	9.7	72.1	3.6	30.2	10.8	7.6	28.7
S3	35	logged	-83.195	8.687	29.4	113	83	19.0	52.4	4.8	40.5	10.4	36.7	75.3
S2	40	logged	-83.188	8.699	24.3	123	47	18.4	65.0	3.7	29.8	10.0	10.5	43.4
S1	55	pasture	-83.180	8.706	36.5	101	42	20.6	53.3	4.4	26.4	11.0	28.8	61.3

compare species richness and species composition of 1 ha plots from old-growth forests with 500 m<sup>2</sup> plots from secondary forests, we used bootstrapping to calculate diversity indices. We randomly selected 500 m<sup>2</sup> subplots of old-growth forests 100 times, calculated species richness and species composition for each random selection and the mean of the 100 random samples for species richness. To compare similarity in terms of beta diversity, we calculated the inverted Jaccard pair-wise dissimilarity index using the R package 'betapart'. For comparison with old-growth forests the mean for the 100 random draws was used.

Non-metric multidimensional scaling (NMDS) was calculated using the R package "vegan" with log(BA) as species scores to visualize species composition of the study plots in a two-dimensional ordination space. The smaller secondary forest plots were compared with 1 ha old growth plots by randomly drawing 500 m<sup>2</sup> subplots in the latter, calculating NMDS 100 times, and averaging NMDS scores per plot. Minimum DBH was 10 cm in the old growth plots but 2.5 cm in the secondary forest plots. We tested the effect of variable size-thresholds by calculating NMDS with all trees or only with trees  $\geq$  10 cm DBH.

The first census used a space-for-time substitution approach whereby the different ages of plots are thought to represent the speed and direction of change in individual plots. To test if this is indeed the case we used data from the second census to visualize if the change over four years in individual plots corresponds to the expected trends based on the space-for-time approach.

Mixed effect models were used to test for effects of age and other plot parameters on the response variables AGB and species richness. We included census data from 2015 and 2019 and used year as a random variable. To avoid overparameterization of the models with soil parameters that are often correlated, we calculated a principal component analysis (PCA) with the soil parameters pH, C:N ratio, SOC, CEC, base saturation, total bases, sand, silt and clay content and used the first two principal components in the model. PC1 is correlated with CEC, total bases, base saturation and pH, and PC2 is mainly related to silt/clay, soil C:N and SOC \*\*\*(Fig. A.1, Table A.2). In addition to soil parameters, plot variables that entered the models were log(age), slope, land use before abandonment (either pasture or clearcut) and forest cover in a 1 km radius. The AGB model also included the number of species. Initial full models were reduced stepwise until only significant factors remained. All statistical analyses were calculated with R 3.5.1 (www.r-project.org).

### 3. Results

In total, 1264 individuals, belonging to 135 different species and 45 families were found in the 12 secondary forest plots. Ten individuals could not be identified at all and 49 individuals were only identified to genus level. With the exception of 16 tree ferns (Cyathea microdonta and Alsophila sp.) all trees in the secondary forest inventory were angiosperms. In five forests between 10 and 40 years Vochysia ferruginea was the dominant tree species (by BA); in two of these (10 and 13 years) it was monodominant in 2015 with no other woody plants  $\geq$  2.5 cm DBH recorded. Stem density ranged between 320 and 2840 stems  $\geq$  2.5 cm DBH / ha (120 and 1020 stems  $\geq$  10 cm) and BA ranged between 5.3 and  $46.9 \text{ m}^2$  / ha. CWM WSG in secondary forest plots (0.33–0.51) was not related to forest age (p = 0.43 for a regression with log(age)), but average CWM WSG across secondary forest plots (0.41) was significantly (p < 0.001) lower than in OG forests (0.54). CWM WSG in secondary forests did not differ between 2015 (0.408) and 2019 (0.416).

### 3.1. Aboveground biomass

AGB ranged between 16.9 Mg / ha for the youngest site to 260.1 Mg / ha in a 25-yr-old forest dominated by *V. ferruginea*. While AGB significantly increased with age (Fig. 2a, Table 2), there was substantial

variation in AGB that was not explained by age. Between 2015 and 2019 AGB increased in eight forest plots but decreased in four plots as large trees died. Overall, biomass accumulation over time is nearly identical when using the 2015 or the 2019 dataset (black and grey regression lines in Fig. 2a). By comparison, AGB recorded in 15 1 ha plots of old-growth forests in the region was 322 (SD: 75) Mg/ha. AGB in some of secondary forests was in the range of old-growth forests after little more than 20 years. On average, secondary forests had reached 164 Mg/ha or 52% of old-growth AGB after 20 years and would reach 90% after 85 years.

In addition to age, the speed of biomass recovery was positively related to forest cover within a radius of 1 km and negatively related to the number of species (Table 3). Soil parameters and prior land use had no significant effect on AGB.

### 3.2. Species diversity and composition

The number of species per area also increased with age, but the increase was more variable than for AGB. In particular, plots that were previously used as pastures increased species number faster, at least initially, than forests that were logged and then left to regrow, with a significant age × land use interaction on species recovery (Fig. 2b and 2c, Table 3). The pattern of species recovery was similar when looking at trees  $\geq 2.5$  cm or 10 cm DBH, but we can directly compare only the number of trees  $\geq 10$  cm in our plots to OG-forests. Additionally, soil PC2 (which scales with soil C:N, SOC and silt/clay content) was significantly related to species numbers. Four of the forests after clearcuts were dominated by *V. ferruginea*, whereas this species dominated only one forest after pasture.

Species richness per plot accumulated at a slower pace than AGB. A regression with age suggests that after 20 years c. 31% of the diversity of trees  $\geq 10$  cm DBH had been recovered. We did not estimate the time to recover 90% of species as this would require extrapolating far beyond our data range. From 2015 to 2019 species richness increased in nearly all plots and the rate of species increase within these four years corresponds to the space-for-time substitution that the initial survey would suggest (Fig. 2b and 2c). Interestingly, the increase in the number of species  $\geq 10$  cm DBH was particularly slow in forests after clearcut.

With age the secondary forests also became more similar to oldgrowth forests in the region though the similarity for the oldest plot remained low (Fig. 2d). Species composition, as analysed by NMDS, of secondary forests differed from that of old growth forests and separated clearly along MDS1. Older secondary forests were more similar to oldgrowth forests and as far as a trend was observed between 2015 and 2019, the species composition also became more similar to mature forests within these four years. The NMDS changed little when including only trees  $\geq$  10 cm DBH from OG and SG forests (Fig. A.3).

### 4. Discussion

### 4.1. Aboveground biomass

We found a rapid recovery of aboveground biomass, confirming other studies on Neotropical secondary forest succession (Silver et al. 2000; Letcher & Chazdon 2009b; Poorter et al. 2016). The much larger dataset compiled by Poorter et al. includes some implausible values (> 300 Mg/ha at 3 years; recovery to > 300% AGB of OG forests), but their average biomass accumulation (c 160 Mg/ha or 60% of OG biomass after 20 years in high rainfall regions) agrees closely with our data (164 Mg and 52%, respectively). Given the variation in AGB in secondary as well as in OG forests, some had reached biomass values within the range of old-growth forests in little more than 20 years. The small plot size likely introduced some noise in the plot-level AGB estimate, but the comparison among plots shows a clear age trend and our data do not appear to be noisier than secondary forest AGB data from



**Fig. 2.** Relationship between stand age and aboveground biomass (a), the number of tree species > 2.5 cm DBH recorded in 500 m<sup>2</sup> secondary forest plots (b), the number of species > 10 cm DBH (c), and the Jaccard similarity values compared to old-growth forests (d). The same sites censused in 2015 (circles) and 2019 (triangles) are connected by lines. Yellow symbols represent sites that were previously used as pasture, green symbols represent sites where the forest had been logged but not used for cultivation or cattle. The grey and black curves in (a) are regressions for AGB  $\sim \log(age)$  for data from 2015 and 2019, respectively. Horizontal lines represent comparable values for old-growth forests in the region, red lines are the mean of 15 plots, the grey line the mean - 1SD. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 2											
Stand characteristics of secondary	forest plot	ts for 2015. BA	: basal area,	AGB: above-g	round biomass,	CWM.WSG: comm	unity-weig	ted mean	wood sr	becific g	gravity.

Site	Age (yrs)	Species > 10 cm DBH	Species > 2.5 cm DBH	BA (m <sup>2</sup> / ha)	AGB (Mg/ ha)	Height (m)	CWM.WSG (g/ cm3)	dominant trees
S5	5.5	2	14	5.3	16.9	6.2	0.357	Jacaranda copaia, Alchornea costaricensis, Trichospermum grewiifolium
S11	10	1	1	29.6	175.2	23.8	0.326	Vochysia ferruginea
S9	12	5	19	11.5	61.4	7.9	0.514	Miconia affinis, Ficus pertusa, A. costaricensis
S12	13	1	1	26.9	144.7	21.7	0.326	V. ferruginea
S6	20	3	17	25.9	192.0	9.8	0.514	Calophyllum brasiliense, Terminalia amazonia, V.
								ferruginea
S4	22.5	9	31	21.4	144.7	9.5	0.482	Spondias mombin, Guatteria chiriquiensis, Inga sp.
<b>S</b> 8	23	11	32	29.8	173.0	9.0	0.387	V. ferruginea, Guatteria amplifolia, Cecropia sp.
S10	25	2	9	46.7	260.1	11.4	0.378	Gmelina arborea, V. ferruginea, M. affinis
S7	27.5	1	24	33.7	192.2	8.4	0.342	V. ferruginea, Psychotria elata, Siparuna andina
<b>S</b> 3	35	9	27	32.1	222.7	10.3	0.434	G. chiriquiensis, Apeiba membranaceae,
								Tetrathylacium macrophyllum
S2	40	6	41	29.1	166.7	9.0	0.387	V. ferruginea, T. macrophyllum, G. amplifolia
S1	55	14	24	30.2	234.2	9.4	0.450	Chimarrhis latifolia, G. chiriquiensis, Inga jinicuil

### Table 3

Variables with significant effects on above-ground biomass and species richness in secondary forests. PC2 is the second principal component of a PCA with soil parameters and related to the CN ratio, SOC and clay/silt content.

Above-ground biomass								
	Estimate	t-value	р					
Age	120.55	8.34	0.0000					
Forest cover	1.45	3.06	0.0064					
Nr. species	-2.50	-3.24	0.0043					
Number of tree species								
	Estimate	z value	р					
Age	1.71	7.38	1.62e-13					
Land use	5.13	5.74	9.36e-09					
Soil PC2	0.15	3.79	0.00015					
Age $\times$ land use	-1.50	-5.92	3.24e-09					

larger plots (e.g., Poorter et al. 2016).

Each forest plot has its specific environment and history that may explain differences in biomass accumulation, in addition to chance events such as the death of larger trees. So far, very few studies have tried to analyse the effect of environmental variables on secondary forest recovery. This is likely limited by the fewer secondary forest datasets compared to OG forests and the fact that the - often imprecisely known - forest age needs to be controlled for. Soil nutrients have been shown to affect tropical forest carbon pools (Lewis et al. 2013; Hofhansl et al. 2020) and growth (Soong et al. 2020) though not all analyses found significant effects (Poorter et al. 2017). Also fertilization studies have shown an effect of N and P addition to biomass growth in young secondary forests (Davidson et al. 2004) and an earth system model suggests nutrient limitation can reduce the carbon sink capacity of regrowing forests (Wang et al. 2015). It would thus be logical to expect an effect of soil nutrients on biomass recovery, but in our study we also found no significant effect of soil fertility, although soil nutrients were directly measured and the variation in soil properties was substantial (CEC ranging between 7.4 and 36.7 mmol / kg and base saturation between 12.5 and 76.6%, 1). A comparison of neotropical secondary forest plots also found no effect of CEC on absolute biomass but a small significant effect on biomass relative to nearby OG forests (Poorter et al. 2016), although that study did not use plot-level soil data but globally gridded estimates.

As in our study, an analysis of neotropical succession (Poorter et al. 2016) found no significant effect of previous land use on biomass recovery after 20 years. Another analysis of 134 plots with differences in prior land use (Silver et al. 2000) found a marginally significant effect with the highest AGB in forests succeeding agriculture and the lowest after abandoned clearcuts, although the sites in this study are a heterogeneous compilation and include few abandoned clearcuts.

Interestingly, there was a positive effect of the forest cover within a 1-km radius and a negative effect of species diversity on AGB accumulation (Table 3). The latter may be explained by the presence of *V. ferruginea* in several forests, which has high growth rates but becomes strongly dominant suppressing competing species in early successional forest.

### 4.2. Species richness

For our study site data of comparable old-growth forests were only available with a DBH threshold of 10 cm. In addition to analysing species richness for trees  $\geq 2.5$  cm DBH, we therefore also analysed species richness for trees  $\geq 10$  cm to compare with old-growth forest plots. Similar to AGB, species richness also increased with age, but reached levels similar to OG forests at a slower pace than biomass. The increase was also slower than reported in other studies. In a study in Costa Rica, which included all trees  $\geq 2.5$  cm DBH in both the secondary and the OG forests, secondary forests had reached species numbers similar to OG forests after about 40 years (Letcher & Chazdon

2009b). Other studies also found that if smaller size classes were included in the analyses, old-growth species richness levels are reached faster during secondary succession (Denslow and Guzman 2000; Saldarriaga et al. 1988). Using a DBH threshold of 1 cm species numbers reached old-growth forest levels after as little as 20–25 years in Bolivia (Peña-Claros 2003) and after c. 35–40 years in Puerto Rico (Aide et al. 2000). This may follow from the fact that small stems constitute a larger part of species richness in younger forests, while in old forests larger stem classes contribute more 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 larger maximum size to establish (Finegan 1996; Guariguata et al. 1997; Guariguata and Ostertag 2001) and for slow-growing species to reach the size limit.

Differences between our results and the findings of others may also stem from the way species numbers are calculated and compared. Rozendaal et al. (2019) used rarefaction to compare species numbers for a fixed number of stems (25 stems), so the upper limit is set to 25 species and a strong dominance of a few species will produce lower diversity estimates, no matter how high the total number of species actually is. Letcher & Chazdon (2009) used a fixed plot size and EstimateS (Colwell 1997) to estimate species numbers independent of the number of stems (or stem density) whereas we used a fixed plot size with variable density. Depending on plot size, stem density, the number of individuals drawn and evenness these approaches will yield different species number estimates apart from the potential pool of available species. This may partly explain different patterns of species richness accumulation reported.

Using a uniform method, we found that various factors affect species accumulation. Notably, forests after clearcuts had, at least initially (with a significant age  $\times$  land use interaction, Table 3), lower species numbers than forests regrowing after pasture abandonment, which again may be explained by the dominance of V. ferruginea in the former. In two plots there was no other species  $\geq 2.5$  cm DBH in 2015 (Fig. 2b). Monospecific dominance has been described also for a few tropical oldgrowth forests (Hart, 1990; Hart et al., 1989; Torti et al., 2001) and Peh et al. (2011) suggested a complex model of interactions and feedbacks that may lead to longer-lasting monodominance. Little is known about monodominance during secondary succession, which may be by invasive or non-invasive plant species (Cohen et al. 1995; Fine 2002). One study in Uganda found that species numbers may decline in late successional stages as succession converges towards a natural monodominant forest (Sheil, 1999). In the seedling layer of the two monodominant plots a number of tree species that also occur in later successional stage were observed in 2015 and indeed the number of species  $\geq 2.5$  cm had increased by 2019.

While soil parameters were not significantly correlated with AGB, soil affected species recovery with the number of species being negatively related to the PCA axis driven by SOC, soil C:N and clay content, although not with PCA 1 which was related to CEC and base saturation. Soil fertility has been found to promote species richness in tropical OG forests (Laurance et al., 2010), but we are not aware of any study confirming its effect on tree species diversity in secondary forests.

### 4.3. Species composition

To some extent the large variation in species composition among SG forests may also be an effect of small plot sizes on which rare species may be missing. This may also explain the rather large spread of SG forests relative to OG forests in the NMDS. Also, owing to the high variability in geology and topography, regional species turnover is high and composition and structure of OG forests are also variable (Morera-Beita et al. 2019; Hofhansl et al. 2020). This may complicate a comparison of species composition with secondary forests clustered around one location. However, NMDS of OG forests (Fig. 3 and Morera-Beita et al. 2019) across the region showed that slope forests from different



**Fig. 3.** Non-metric multidimensional scaling (NMDS) of the 12 secondary forest plots and 15 oldgrowth forest plots. Surveys of the same plots in 2015 and 2019 are connected by lines. Numbers next to symbols represent the age of the secondary forests. Old-growth forests were located either on ridges, slopes or ravines (see Hofhansl et al. 2020), the secondary forests all on slope positions.

localities are more similar to each other than to forests in other topographic positions from the same locality. The SG forests studied are all on slopes and differ from all OG forests, on slopes or other positions.

Recovering forests were becoming more similar to old-growth in terms of species composition with time, but even the oldest secondary forests still differed from OG forests. Indeed after the first 20–30 years it was not clear that successional forests continued to become more similar to OG forests (Fig. 2). Also while the younger forests tended to become more similar to OG forests after four years, for forests > 30 years old the change in species composition over four years was minor.

The likelihood and speed of secondary forest succession arriving at the species composition of old-growth is controversial (Chazdon 2008; Chazdon et al. 2007). Re-evaluating data from Uganda spanning 60 years of succession (Eggeling 1947) it was shown that species composition approached that of old-growth forests (Sheil et al. 1999). The analysis of an extensive dataset from multiple plots that were repeatedly censused in seven regions in the neotropics, suggests a substantial stochastic element in successional trajectories (Norden et al. 2015). This analysis accounted for previous land use, but other factors such as soil nutrients were not included although these may also affect species diversity (Table 3). While we do not question that random processes affect successional trajectories, we do not think that the unexplained variation should be interpreted as stochasticity in systems with imperfect knowledge of potentially significant drivers. Detecting true stochasticity in systems as complex as tropical forest succession may require conditions that are impossible to find in natural systems but perhaps could be created in carefully designed experiments. What is feasible is a better prediction of successional pathways if we understand environmental factors better, which calls for a thorough documentation of site and local conditions.

Using space-for-time substitution to study successional pathways obviously carries the risk that plots not only differ in age but also in other factors that may affect growth or species composition. The dataset presented by Norden and colleagues include many plots repeatedly censused over many years and shows that biomass and species density do not necessarily converge. In our dataset a second census after four years resulted in essentially the same biomass : age relationship as the first census (Fig. 2a). At least in the first years species composition of successions starting from pasture or clearcut did converge somewhat (Fig. 3), but we cannot say for how long legacies of prior land use will remain.

Understanding the idiosyncrasies of successional pathways may require a careful analysis of biotic and abiotic factors. A study from central Amazonia (Mesquita et al. 2015), which was similar to the present one, also followed succession after clearcut or pasture and provides a striking contrasts with our results. After 30 years, forests succeeding pastures clearly differed from forests originating from abandoned clearcuts and vegetation composition did not appear to be converging. In contrast to our study, Amazonian forests after clearcuts had substantially higher species numbers than forests after pasture. Both studies were conducted not far from closed forests, so seed availability should not be a strong limitation or at least not explain the differences. In the Amazonian study, clearcuts were soon dominated by Cecropia, a widespread neotropical pioneer, which died in the second decade and gave way to a more diverse community. By contrast, abandoned Amazonian pastures were soon dominated by Vismia, which resprouts after fire and suppresses other species. By contrast, in the La Gamba plots studied abandoned pastures are not strongly dominated by single species, whereas on nutrient poor ridges and slopes Vochysia ferruginea can become very dominant and is longer-lived than Cecropia. Also, in our study area with annual rainfall more than twice as high as in central Amazonia, fires are virtually absent. In La Gamba Cecropia does become dominant in flat terrain, but such locations are generally not abandoned and were thus not available for the present study. If we could have included such areas, the outcome might well have been different.

### 5. Conclusion

The fact that regrowing tropical forests recover biomass fast and species diversity somewhat slower is now well established and was confirmed by our study. Although our dataset is limited in size, we could show that recovery is also controlled by environmental factors and prior land use. Such controls might be expected, data that document their effects are often not available, which limits our understanding of forest recovery, ecosystem dynamics, carbon sequestration and landscape management. Remote sensing products are increasingly available at sufficient resolution to permit a more precise dating of secondary forests. Climate data of sufficient detail can be obtained from available databases, but the accuracy of global soil datasets is probably too low to account for the small-scale variation that may explain differences between study plots. We therefore call on researchers working in secondary forests to include soil analyses for their sites, preferably following standard methodology. While this may not produce significant effects for a single study comparing a few plots within a region, it would provide valuable input to larger scale (meta-)analyses.

### **Declaration of Competing Interest**

The authors have no conflict of interest to declare.

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### Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2020.118580.

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