Demographic drivers of tree biomass change during secondary succession in northeastern Costa Rica

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Abstract. Second-growth tropical forests are an important global carbon sink. As current knowledge on biomass accumulation during secondary succession is heavily based on chronosequence studies, direct estimates of annual rates of biomass accumulation in monitored stands are largely unavailable. We evaluated the contributions of tree diameter increment, recruitment, and mortality to annual tree biomass change during succession for three groups of tree species: second-growth (SG) specialists, generalists, and old-growth (OG) specialists. We monitored six second-growth tropical forests that varied in stand age and two old-growth forests in northeastern Costa Rica. We monitored these over a period of 8 to 16 years. To assess rates of biomass change during secondary succession, we compared standing biomass and biomass dynamics between second-growth forest stages and old-growth forest, and evaluated the effect of stand age on standing biomass and biomass dynamics in second-growth forests.

Standing tree biomass increased with stand age during succession, whereas the rate of biomass change decreased. Biomass change was largely driven by tree diameter increment and mortality, with a minor contribution from recruitment. The relative importance of these demographic drivers shifted over succession. Biomass gain due to tree diameter increment decreased with stand age, whereas biomass loss due to mortality increased. In the age range of our second-growth forests, 10–41 years, SG specialists dominated tree biomass in second-growth forests. SG specialists, and to a lesser extent generalists, also dominated stand-level biomass increase due to tree diameter increment, whereas SG specialists largely accounted for decreases in biomass due to mortality.

Our results indicate that tree growth is largely driving biomass dynamics early in succession, whereas both growth and mortality are important later in succession. Biomass dynamics are largely accounted for by a few SG specialists and one generalist species, *Pentaclethra macroloba*. To assess the generality of our results, similar long-term studies should be compared across tropical forest landscapes.

Key words: biomass accumulation; forest dynamics; generalists; La Selva Biological Station, Costa Rica; old-growth vs. second-growth forest; specialists; successional groups; tree demography; tropical forest succession; wet tropical forest.

Introduction

Second-growth forests now comprise more than half of the total tropical forest area worldwide (FAO 2010), and this percentage is expected to increase in the future. Thus, second-growth forests represent a major global carbon sink, because they cover a substantial area and rapidly accumulate aboveground biomass (Pan et al. 2011, Eva et al. 2012). Most of the current knowledge on biomass accumulation during secondary succession is based on chronosequence studies (e.g., Silver et al. 2000, Martin et al. 2013; but see Feldpausch et al. 2007), in which rates of change with stand age are inferred from a comparison of static data from forest stands of different ages, a "space-for-time" substitution (Pickett 1989, Hughes et al. 1999, Walker et al. 2010). Chronosequence studies across the tropics demonstrate rapid increases in aboveground biomass during the first 40–50 years of secondary forest succession, followed by either a slow, asymptotic increase toward old-growth values (Brown and Lugo 1990, Guariguata and Ostertag 2001), or a peak in biomass at intermediate stand ages (e.g., Marín-Spiotta et al. 2007, Letcher and Chazdon 2009, Mascaro et al. 2012). Chronosequence data show that annual rates of biomass accumulation decrease with stand age during succession (e.g., Silver et al. 2000, Chazdon 2014). In old-growth forests, annual rates of biomass change are typically lower than in second-growth forests (Valencia et al. 2009), as biomass gains from growth and recruitment largely balance biomass losses through mortality in small-scale gap disturbances (cf. Feeley et al. 2007, Chambers et al. 2013).

The demographic processes underlying temporal patterns of biomass accumulation in secondary forests remain unknown, because these cannot be inferred from chronosequence studies. Change in aboveground living tree biomass (ΔAGTB; per hectare per year) is the net result of three demographic processes: biomass gain from growth of living trees, biomass gain from recruitment of trees, and biomass loss through tree mortality. During secondary succession, stands are initially dominated by early-successional species that colonize under high-light conditions and exhibit high growth rates. Over time, dominance gradually shifts toward shade-tolerant, slower growing late-successional species that establish beneath a closed canopy (Gómez-Pompa and Vázquez-Yanes 1981, Finegan 1996). In temperate forests, succession has been proposed to occur in different stages, where both early- and late-successional species establish during stand initiation, followed by a rapid increase in basal area of early-successional species, subsequent thinning of trees ("stem exclusion" or "thinning" stage), followed by a slow transition from early- to late-successional species in the canopy ("understory reinitiation" or "transition" stage; Peet and Christensen 1987, Oliver and Larson 1996). Stand changes during secondary succession in tropical forests follow a similar pattern (Denslow and Guzman 2000, Chazdon 2008b, Chazdon 2014). Dominance of short-lived pioneer species has been hypothesized to occur in second-growth forests up to ~20 years old, whereas long-lived pioneers are expected to dominate until a stand age of ~100–150 years (Finegan 1996, Guariguata and Ostertag 2001).

Few studies have assessed changes in tree demographic rates during stand development. Early in succession, rates of tree growth and recruitment are high when both pioneer species and shade-tolerant species establish (van Breugel et al. 2006), and mortality occurs at early stages when small, suppressed trees die (e.g., Chazdon et al. 2005, van Breugel et al. 2006), as well as later in succession when larger pioneer trees die (Saldarriaga et al. 1988). Tree growth rates are expected to decrease with stand age as a result of canopy closure, which increases competition for resources (e.g., Uriarte et al. 2004), and drives a shift toward slow-growing, more shade-tolerant species (Chazdon et al. 2010). In older second-growth forest (~55 years after abandonment), however, dynamics are typically still faster than in old-growth forest (e.g., Brearley et al. 2004). Stand dynamics models, however, largely describe stand development processes based on stem replacement, and thus stem density, rather than in terms of biomass accumulation. Although growth of large, fast-growing trees has been suggested to be the main driver of increasing basal area and biomass (Chazdon et al. 2007, 2010), the relative contributions of demographic processes to biomass change during secondary tropical forest succession remain poorly understood.

Here, we used annual diameter measurements of trees ≥ 5 cm diameter at breast height (dbh) in six second-growth and two old-growth plots in northeastern Costa Rica to assess temporal changes in the rate of biomass change during secondary succession by monitoring plots of different stand ages over time, spanning 10–41 years after abandonment of cattle pasture. We examined the contribution of three groups of tree species, second-growth (SG) specialists, generalists, and old-growth (OG) specialists (Chazdon et al. 2011), to standing biomass and biomass change. Specifically, we tested the following hypotheses: (1) aboveground standing tree biomass (AGTB) will increase from second-growth to old-growth forest and with stand age in second-growth forests; (2) SG specialists, which consist of short- and long-lived pioneer species, will dominate standing biomass in second-growth forests, followed by generalists, whereas in old-growth forests, OG specialists, thus late-successional species, and generalists will account for most of the standing biomass (cf. Fig. 1); (3) rates of annual biomass change (ΔAGTB) will decrease over succession, due to a decrease in biomass change attributed to diameter increment (ΔAGTB$_{incr}$), and an increase in biomass change attributed to mortality (ΔAGTB$_{mort}$); and (4) diameter increment of SG specialists and generalists will be the main driver of biomass change in second-growth forests, whereas OG specialists will play a minor role. Recruitment will be of larger importance during the stand initiation stage, which is estimated to last until ~10 years of age in our study sites (Chazdon 2008b), i.e., before the start of our study (Fig. 1). Mortality of small trees during the stand initiation stage will most likely not result in large biomass losses, but we predict that biomass loss due to mortality of large canopy trees will contribute more strongly to biomass change during the stem exclusion stage, which is estimated to be associated with stand ages from 10–25 years in our study site (Chazdon 2008b; Fig. 1).

METHODS

Study sites and annual censuses

The study was conducted in six secondary tropical wet forest stands initially 10–25 years old, and two old-growth forest stands in and around La Selva Biological Station, Sarapiquí province, Costa Rica (Table 1). Mean annual rainfall is 3800 mm and mean annual temperature is 26°C at La Selva (McDade and Hartshorn 1994). All sites were located in a landscape matrix consisting of old-growth forests, second-growth forests, and agricultural areas (Table 1). Land-use history was similar across the six second-growth sites (Table 1). All sites were cleared for pasture, and in five of the six sites grazing occurred, but in one of the stands, remnant trees were present (FEB; Table 1). Additional information on the study sites can be found in Chazdon et al. (2005), Norden et al. (2009), and Norden et al. (2012).
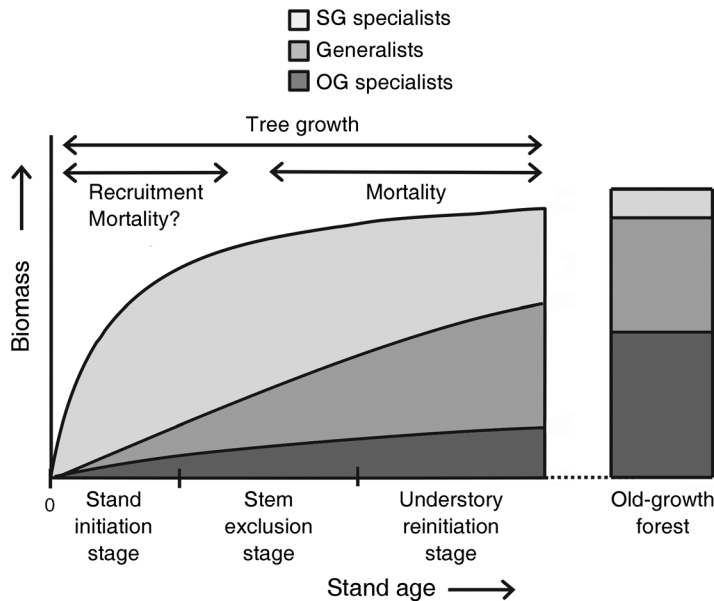
Fig. 1. Conceptual scheme of biomass accumulation with stand age during secondary succession, and contributions of specialist and generalist groups. Tree diameter increment (growth) is expected to be the major driver of biomass change during succession, whereas tree recruitment is likely to be important during the stand initiation stage, and tree mortality is important later in the stem exclusion stage. The stand initiation stage is expected to range from 0 to 10 years, the stem exclusion stage from 10 to 25 years, and the understory reinitiation stage from 25 to 200 years in our study site in Costa Rica (Chazdon 2008b). SG specialist is second-growth specialist; OG specialist is old-growth specialist.

All tree stems ≥ 5 cm diameter at breast height (dbh) or above stem abnormalities (buttresses or stilt roots) were annually censused since 1997 or 2005 until 2013 in a 1 ha-plot in each site, leading to a range in stand age from 10 to 41 years across all plot–age combinations for the second-growth forests (Table 1). Tree species were classified as SG specialist, generalist, OG specialist, or "too rare to classify" based on their estimated relative abundance in second-growth and old-growth forests of the area, using a multinomial modeling approach (Chazdon et al. 2011). Palm species were regarded as a separate group, because they have low wood density and an unbranched growth form, with substantially lower biomass for a given stem diameter compared to dicot trees. Lianas were excluded from our analysis.

Calculation of tree biomass

We used allometric equations based on dbh and wood specific gravity (WSG), where possible, to calculate tree biomass (dry mass). Average, species-specific WSG was measured as the ratio of dry mass to green volume, from cores or discs of trees ranging from 5 to 60 cm dbh of 174 species (Plourde et al., in press; A. DeFrancesco and R. L. Chazdon, unpublished data). Green volume was measured with the water displacement method; then wood samples were dried at 103–105°C for 24–48 h before dry mass was determined (Plourde et al., in press). For palm species, we used values from Rich (1987). We used allometric equations developed for secondary forest tree species in Panama to estimate tree biomass of trees ≤25 cm dbh in the six second-growth sites (van Breugel et al. 2011), as allometric equations developed for old-growth forests substantially overestimate the biomass of trees in second-growth forest (van Breugel et al. 2011). No allometric equations for second-growth forests in Costa Rica are available, but 11 out of the 26 species used to establish the allometric equations for Panama are also present in our study sites, as well as congenerics for another eight species. These 19 species comprised, on average, 13–34% (25% on average) of the standing basal area across years in our six second-

TABLE 1. Characteristics of the study sites in Costa Rica.

Site	Location	Previous land use	Year plot established	Initial stand age (yr)	Landscape matrix
Lindero Sur (LSUR)	La Selva	pasture	1997	12	adjacent to old-growth forest
Tirimbina (TIR)	Tirimbina	pasture	1997	15	pasture and second-growth forest
Lindero El Peje secondary (LEPS)	La Selva	pasture	1997	20	adjacent to old-growth forest
Cuatro Ríos (CR)	La Virgen de Sarapiquí	cleared, no grazing	1997	25	pasture and second-growth forest
Juan Enríquez (JE)	Chilamate	pasture	2005	10	pasture and second-growth forest
Finca El Bejuco (FEB)	Chilamate	pasture with remnant trees	2005	10	pasture and second-growth forest
Lindero El Peje primary (LEPP)	La Selva	none	2005	mature	old-growth forest
Selva Verde (SV)	Chilamate	none	2005	mature	pasture and second-growth forest

growth sites. For the two old-growth forest sites, and trees ≥25 cm dbh in second-growth forests, we used general equations developed for wet tropical forests (Brown 1997, Chave et al. 2005). For species for which WSG data were available, we used allometric equations that incorporated WSG in both the second-growth and old-growth sites (Chave et al. 2005, van Breugel et al. 2011); otherwise, we used an allometric equation based on dbh only (Brown 1997, van Breugel et al. 2011). For palms, we used the same allometric equations as for trees (cf. Clark and Clark 2000). This may lead to a slight overestimate of palm biomass, despite the inclusion of actual WSG values for the palm species in the equations. We calculated total aboveground tree biomass (AGTB) per 1-ha plot for each year from either 1997 or 2005 to 2013, as well as the change in AGTB (ΔAGTB) from either 1997 or 2005 to 2012. In addition, we calculated the components of ΔAGTB derived from tree diameter increment (ΔAGTB$_{incr}$), tree recruitment (ΔAGTB$_{recr}$), and tree mortality (ΔAGTB$_{mort}$) per 1-ha plot for each year. All demographic rates were expressed at the stem level; ΔAGTB$_{recr}$ comprised the change in biomass resulting from stems that reached 5 cm dbh in that year, whereas ΔAGTB$_{mort}$ was composed of stems ≥5 cm dbh that died in that year.

STATISTICAL ANALYSIS

We compared total AGTB and AGTB per specialist group across three stand age classes: 10–24 years after abandonment, 25–41 years after abandonment (25–40 years for ΔAGTB and its demographic components), and old-growth, using linear mixed-effects models with site as a random effect. We used Tukey's HSD tests to assess significance of differences in AGTB between stand age classes. Similarly, we compared ΔAGTB, and its demographic components ΔAGTB$_{incr}$, ΔAGTB$_{recr}$, and ΔAGTB$_{mort}$, across the three stand age classes. We log$_{10}$-transformed ΔAGTB$_{recr}$ and ΔAGTB$_{mort}$ before all analyses to meet assumptions of normality and homoscedasticity. We expressed the contribution of the specialist groups to AGTB, ΔAGTB$_{incr}$, ΔAGTB$_{recr}$, and ΔAGTB$_{mort}$ for the three stand age classes, by calculating a percentage based on the totals across all sites and years.

We related AGTB, ΔAGTB, and its demographic components ΔAGTB$_{incr}$, ΔAGTB$_{recr}$, and ΔAGTB$_{mort}$, to stand age using linear mixed-effects models for the six second-growth sites. We modeled AGTB as a function of ln(stand age) to account for possible nonlinear effects of stand age. We included ln(stand age) as a fixed effect, and included a random intercept and slope per site. For ΔAGTB and its demographic components, we included stand age as a fixed effect, and only a random intercept per site, because including a random slope did not improve model fits. We assessed whether the effect of stand age, or ln(stand age), was significant by comparing each model with a model with only an intercept as fixed effect, using Aikaike's information criterion (AIC). We considered

models to be equally supported if the difference in AIC was less than two units (Burnham and Anderson 2002). If the two models were equally supported, we regarded the intercept-only model as the best model. We calculated the marginal (m) and the conditional (c) R^2 following Nakagawa and Schielzeth (2013); R_c^2 indicates the variance explained by both fixed and random effects (conditional), whereas R_m^2 indicates the variance explained by fixed effects only (marginal). All analyses were performed in R version 3.0.1 (R Development Core Team 2013). Mixed-effects models were performed using the 'lme4' package (Bates et al. 2011).

RESULTS

As predicted, aboveground living tree biomass (AGTB) increased from 104.02 ± 3.72 Mg/ha (mean ± SE) in the first age class of 10–24 years, to 154.42 ± 4.32 Mg/ha in the second age class (25–41 years), and was greatest, 217.79 ± 2.81 Mg/ha, in the old-growth class (Fig. 2a). In the first age class (10–24 yr), SG specialists contributed 56% of AGTB, whereas generalists contributed 25%. In the second age class (25–41 yr), similarly, SG specialists and generalists accounted for 56% and 29%, respectively, of AGTB (Fig. 2b). In the old-growth class, in contrast, generalists (39%) and OG specialists (33%) accounted for most of the standing tree biomass (Fig. 2b). Palms and species that were too rare to classify contributed little to AGTB in the second-growth classes, but species that were too rare to classify contributed substantially to AGTB in the old-growth class (19%; Fig. 2b). In both second-growth forest and old-growth forest, AGTB of generalists was mostly accounted for by a single species, *Pentaclethra macroloba*. In general, few species dominated AGTB in the second-growth stand age classes. In the first age class, 47% of AGTB consisted of the generalist *Pentaclethra macroloba*, and the SG specialists *Vochysia ferruginea*, *Goethalsia meiantha*, and *Simarouba amara* (Appendix). Similarly, in the second age class, the generalist *Pentaclethra macroloba*, and the SG specialists *Vochysia ferruginea*, *Goethalsia meiantha*, and *Simarouba amara*, accounted for 52% of AGTB (see Appendix).

Annual tree biomass change (ΔAGTB) was highest (4.02 ± 0.27 Mg·ha^{-1}·yr^{-1}, mean ± SE) in the first stand age class (10–24 yr), decreased from the first to the second age class (25–40 yr; 1.64 ± 0.34 Mg·ha^{-1}·yr^{-1}), and remained low in old-growth forests (1.52 ± 0.34 Mg·ha^{-1}·yr^{-1}; see Fig. 3a). Tree biomass change (ΔAGTB) was mostly driven by tree diameter increment in all three age classes, followed by tree mortality, with a minor contribution from tree recruitment (Fig. 3b–d). Biomass change as a consequence of tree diameter increment (ΔAGTB$_{incr}$) decreased from the second-growth stand age classes to old-growth forest (Fig. 3b). Biomass lost through mortality (ΔAGTB$_{mort}$) increased from the first to the second age class in the second-growth forests, whereas ΔAGTB$_{mort}$ for old-growth forest was intermediate (Fig. 3d).
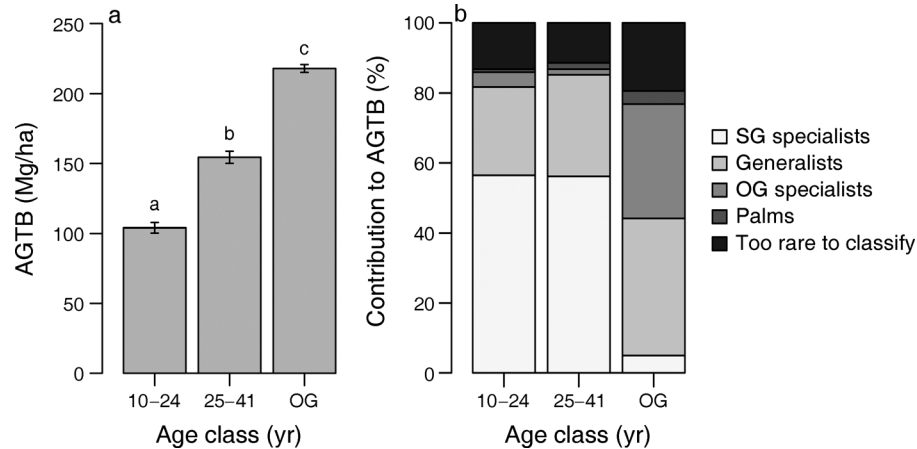
FIG. 2. (a) Standing tree biomass (AGTB, aboveground living tree biomass, mean ± SE) for three stand age classes for all tree species in a tropical wet forest in Costa Rica; different lowercase letters above bars indicate significant differences at $P < 0.05$. (b) Percentage contribution of specialist and generalist groups to AGTB. OG is old-growth forest of unknown age; SG specialist is second-growth specialist; OG specialist is old-growth specialist.

Annual tree biomass change was mostly driven by SG specialists and generalists in the two second-growth age classes, and by OG specialists and generalists in old-growth forest. SG specialists accounted for 60% and 50% of $\Delta AGTB_{incr}$, and 59% and 63% of $\Delta AGTB_{mort}$, in the first and the second age class, respectively (Fig. 4a, c). Similarly, these two groups also contributed most to $\Delta AGTB_{recr}$ (Fig. 4b), but palm species also contributed 15% and 23% in the first and the second age class to $\Delta AGTB_{recr}$, respectively (Fig. 4b). Generalists contributed 29% and 36% to $\Delta AGTB_{incr}$, and 15% and 20% to $\Delta AGTB_{mort}$, in the first and the second age class,
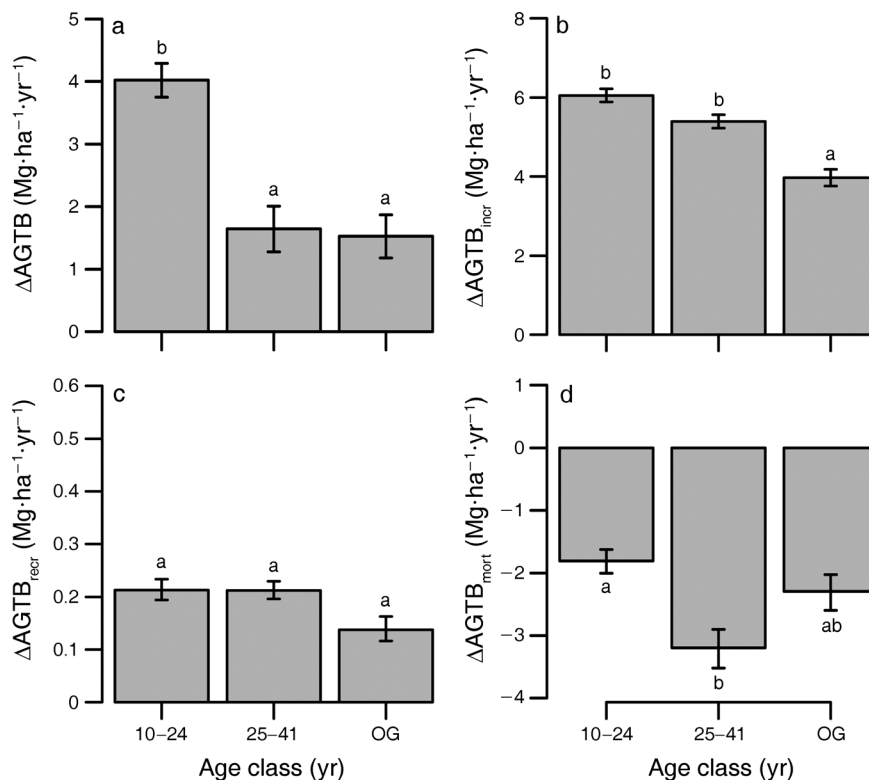

FIG. 3. (a) Aboveground living tree biomass (mean ± SE) change ($\Delta AGTB$) and biomass change resulting from (b) tree diameter increment ($\Delta AGTB_{incr}$), (c) from tree recruitment ($\Delta AGTB_{recr}$), and (d) from tree mortality ($\Delta AGTB_{mort}$) for all tree species across three stand age classes in a Costa Rican tropical wet forest. For biomass change resulting from tree recruitment and tree mortality, back-transformed means are shown. OG is old-growth forest of unknown age.
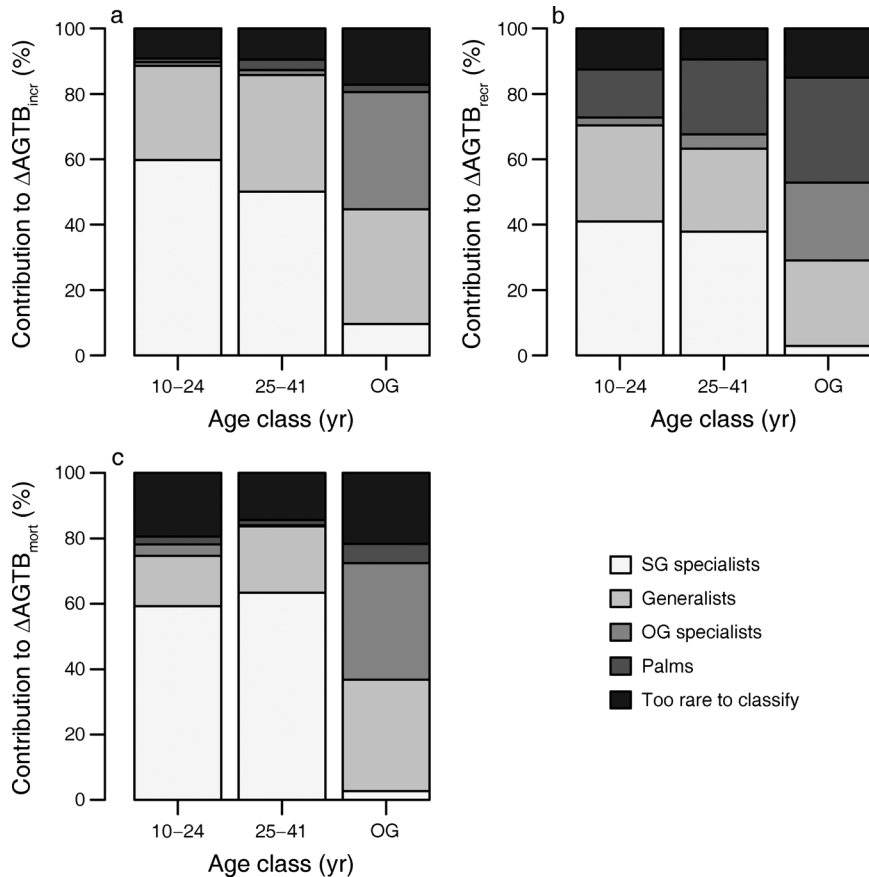
FIG. 4.   Contributions of specialist and generalist groups to biomass change due to (a) tree diameter increment ($\Delta AGTB_{incr}$), (b) tree recruitment ($\Delta AGTB_{recr}$), and (c) tree mortality ($\Delta AGTB_{mort}$) for three stand age classes for all tree species in a tropical wet forest in Costa Rica. OG is old-growth forest of unknown age. SG specialist is second-growth specialist; OG specialist is old-growth specialist.

respectively (Fig. 4a, c). In the old-growth class, OG specialists and generalists contributed equally to biomass change resulting from tree growth and mortality (Fig. 4a, c). Palms barely contributed to $\Delta AGTB_{incr}$ and $\Delta AGTB_{mort}$ in any of the age classes (Fig. 4). Species too rare to classify, however, contributed 9–17% to $\Delta AGTB_{incr}$ and 14–22% to $\Delta AGTB_{mort}$ across the three age classes (Fig. 4).

Changes in AGTB through growth and mortality were largely driven by a few dominant species in the second-growth forests. The generalist *Pentaclethra macroloba* accounted for the largest share of $\Delta AGTB_{incr}$ (16–18% of $\Delta AGTB_{incr}$) in both age classes in second-growth forests, followed by the SG specialists *Vochysia ferruginea* and *Goethalsia meiantha* in the first age class, and *Laetia procera*, *Vochysia ferruginea*, *Xylopia sericophylla*, *Cordia bicolor*, and *Goethalsia meiantha* in the second age class (Appendix). The SG specialists *Miconia affinis* (19% of $\Delta AGTB_{mort}$), *Vochysia ferruginea*, and *Goethalsia meiantha*, and generalist *Pentaclethra macroloba* contributed most to mortality in the first age class (Appendix). Similarly, the largest share of biomass loss in the second age class was composed of SG specialists

Goethalsia meiantha, *Vochysia ferruginea*, *Cordia bicolor*, and *Casearia arborea*, and also generalists *Pentaclethra macroloba* and *Inga pezizifera* (Appendix).

Aboveground tree biomass increased significantly, nonlinearly with stand age in the second-growth forests (Fig. 5a). Two sites, FEB (initial stand age of 10 years) and CR (initial stand age of 25 years), had relatively high initial biomass, probably due to the presence of remnant trees, and lower prior land-use intensity, respectively (cf. Table 1). Total $\Delta AGTB$ decreased significantly and linearly with stand age, although $\Delta AGTB$ was highly variable across years (Table 2, Fig. 5b). The decrease in $\Delta AGTB$ with stand age resulted from a significant increase in biomass loss through mortality ($\Delta AGTB_{mort}$), and a significant decrease in biomass change resulting from tree diameter increment ($\Delta AGTB_{incr}$) (Table 2, Fig. 5d, e). Biomass change due to tree recruitment ($\Delta AGTB_{recr}$) was not significantly related to stand age (Fig. 5c). The amount of variation in $\Delta AGTB$ and $\Delta AGTB_{mort}$ that was explained by the fixed and random effects was equal to the amount explained by the fixed effects only. For $\Delta AGTB_{incr}$ and $\Delta AGTB_{recr}$, however, R_c^2 was larger
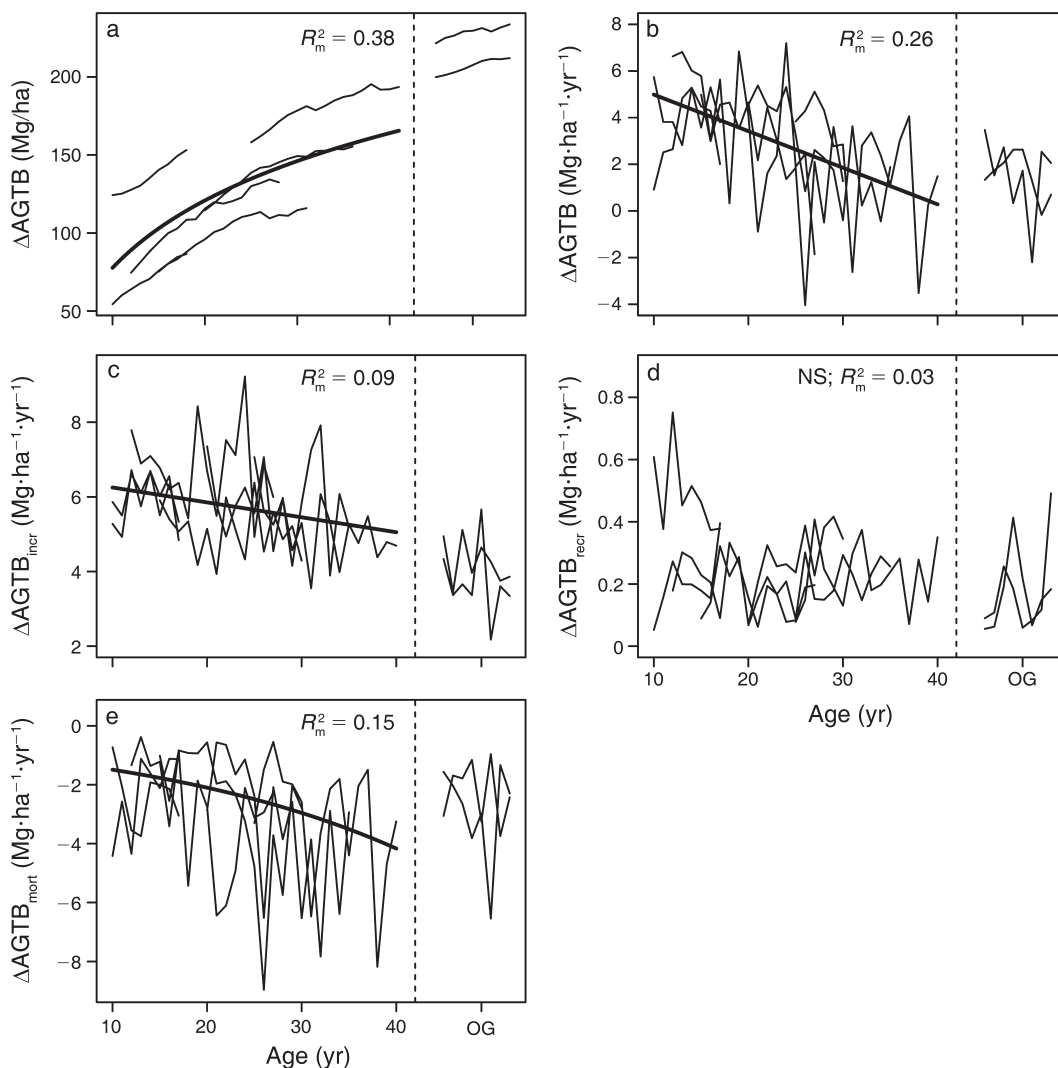
FIG. 5. Trajectories of standing tree biomass, and biomass dynamics for six second-growth and two old-growth 1-ha plots in tropical wet forest in Costa Rica. (a) Tree biomass (AGTB); (b) annual biomass change (ΔAGTB); (c) biomass change due to tree diameter increment (ΔAGTB$_{incr}$); (d) biomass change due to tree recruitment (ΔAGTB$_{recr}$); (e) biomass change due to tree mortality (ΔAGTB$_{mort}$). Lines indicate significant ($P < 0.05$), predicted relationships from the mixed-effects model, with associated R_m^2 (fixed effects only) values.

TABLE 2. Modeling results for standing biomass (AGTB), biomass change (ΔAGTB), and its demographic components.

| Variable | Predictor | AGE/ln(AGE) | | | Intercept only |
		ΔAIC	R_c^2	R_m^2	ΔAIC
AGTB	ln(AGE)	**0.00**	**0.99**	**0.38**	23.08
ΔAGTB	AGE	**0.00**	**0.26**	**0.26**	21.39
ΔAGTB$_{incr}$	AGE	**0.00**	**0.28**	**0.09**	2.21
ΔAGTB$_{recr}$	AGE	0.89	0.38	0.03	**0.00**
ΔAGTB$_{mort}$	AGE	**0.00**	**0.15**	**0.15**	10.77

Notes: Standing biomass (AGTB, aboveground living tree biomass), biomass change (ΔAGTB), and its demographic components, growth (incr), recruitment (recr), and mortality (mort), were modeled as a linear function of either ln-transformed stand age (ln(AGE)), or stand age (AGE), in second-growth forests in Costa Rica. For each variable, we compared the linear model with a model with only an intercept to assess significance of the fixed effect. The deviation in AIC (Aikaike's information criterion) units from the best model (ΔAIC) is indicated. The conditional R^2 (R_c^2, both fixed and random effects), and the marginal R^2 (R_m^2, fixed effects only) are indicated. The best models are indicated in boldface.

than R_m^2, indicating that most of the variation in these demographic components of biomass change was due to differences across sites (random effect), rather than to stand age (fixed effect).

DISCUSSION

Changes in AGTB over succession

In wet tropical forests in Costa Rica, aboveground living tree biomass (AGTB) increased with stand age in second-growth forests, and also from second-growth forests to old-growth, supporting hypothesis 1. In old-growth forests, AGTB is substantially higher than in second-growth forests, and chronosequence studies across the tropics show an increase in AGTB with stand age in second-growth forests (Saldarriaga et al. 1988, Alves et al. 1997, Hughes et al. 1999, Aide et al. 2000, Feldpausch et al. 2004, Gehring et al. 2005, Marín-Spiotta et al. 2007, Kauffman et al. 2009, Letcher and Chazdon 2009, Martin et al. 2013). In our study, standing tree biomass increased nonlinearly with stand age in second-growth forests that are 10–41 years old, which agrees with results of some chronosequence studies (e.g., Gehring et al. 2005). Others, however, found a linear increase in biomass with stand age in second-growth forests up to ~20 years old (Alves et al. 1997) or ~40 years old (Saldarriaga et al. 1988). These differences could also be due to the fact that our youngest forest was 10 years old, and that we thus lack the strong, probably linear, increase in biomass during the first 10 years of succession. Standing biomass in our second-growth forests is comparable to values from other tropical forests of the same age (cf. Brown and Lugo 1990, Silver et al. 2000), although values reported from a previous study in the same region in Costa Rica were higher than in our study (Letcher and Chazdon 2009). This may be partly due to the use of allometric equations constructed for old-growth forests in Letcher and Chazdon (2009), which tend to overestimate biomass of second-growth tree species (van Breugel et al. 2011). In our old-growth sites, aboveground tree biomass (AGTB) was, on average, 218 Mg/ha, slightly higher than AGTB estimates at La Selva from Clark and Clark (2000), which may be a result of the higher point-of-measurement in the stem in their study.

Consistent with hypothesis 2, SG specialists dominated tree biomass early in succession, followed by generalists, whereas in old-growth forests, both generalists and OG specialists dominated standing tree biomass. Thus, our results confirm a shift from pioneer species to shade-tolerant species during secondary succession (e.g., Saldarriaga et al. 1988, Brown and Lugo 1990, Chazdon 2008b), and suggest that stand composition in terms of biomass largely followed predictions from stand dynamics models based on changes in stem density (cf. Peet and Christensen 1987, Oliver and Larson 1996). Further, our results clearly show that OG specialists establish early in succession (cf. Fig. 4b), in agreement with findings of other studies

(Peña-Claros 2003, van Breugel et al. 2007), but contribute little to AGTB second-growth forests.

Rates of tree biomass change over succession

As expected, rates of annual biomass change (ΔAGTB) decreased from the first to the second age class, and significantly decreased with stand age in second-growth forests, supporting the notion that rates of biomass accumulation decrease through succession (e.g., Brown and Lugo 1990, Silver et al. 2000). Annual rates of biomass accumulation in our second-growth forests broadly agree with values estimated from chronosequence studies over a similar range of stand ages in wet Neotropical second-growth forests (Silver et al. 2000, Marín-Spiotta et al. 2008). Surprisingly, ΔAGTB in old-growth forests was positive. Hence, biomass increased over the course of our study, and did not significantly differ from ΔAGTB in second-growth forests 25–40 years old. Other temporal studies of old-growth tropical forests also show increases in above-ground tree biomass (e.g., Baker et al. 2004, Phillips et al. 2008). Causes of increasing biomass in old-growth forests remain heavily debated, and have been attributed to a fertilization effect of increasing CO_2 (e.g., Lewis et al. 2009) or to recovery from past disturbances (Chave et al. 2008, Fisher et al. 2008). The large fluctuation in ΔAGTB across years in our 1-ha plots agrees with results of Chambers et al. (2013), in which biomass at small spatial scales strongly fluctuates across years due to gap dynamics. Biomass loss through mortality of large trees can cause a rapid decrease in biomass, whereas biomass increase through recruitment and growth occurs on a considerably longer time scale (cf. Rutishauser et al. 2010). Thus, small-scale disturbances can lead to increases in ΔAGTB in the old-growth forest plots, through increased diameter growth rates.

Tree growth and mortality drive biomass dynamics in second-growth forests

The decrease in ΔAGTB with stand age in second-growth forests resulted from decreasing tree diameter increment and increasing biomass loss from tree mortality, consistent with hypothesis 2. Contrary to expectations, we found that both tree growth and mortality of a few species of SG specialists, and of the generalist *Pentaclethra macroloba* to a lesser extent, rather than tree growth alone, drove tree biomass change. Our results disagree with previous results from our study area, where increasing basal area, but decreasing stem density, suggested that the tree diameter increment of canopy and emergent tree species would be the major driver of the increase in basal area, rather than recruitment or mortality (Chazdon et al. 2010). Tree diameter increment probably decreases as a consequence of the closing canopy, and thus increased competition (cf. Uriarte et al. 2004), which may eventually also lead to increased tree mortality (cf. Wright et al. 2010). The high biomass loss through tree mortality in the second-

growth forests ranging from 25–40 years in stand age in our study reflects mortality of larger trees of pioneer species that reached their maximum life span after ~30 years. The decrease in biomass of fast-growing tree species probably also contributed to the decrease in biomass change resulting from tree diameter increment with stand age in second-growth forests. Other studies in the upper Rio Negro (Saldarriaga et al. 1988) and in Panama (Lang and Knight 1983, Milton et al. 1994), similarly, found high mortality of larger trees of long-lived pioneer species in second-growth forests ranging in age from 40 to ~100 years. High mortality rates during early stages of succession, as observed in our study sites by Chazdon et al. (2005), in Mexico (van Breugel et al. 2006), and in Brazil (Feldpausch et al. 2007), do not appear to be strong drivers of biomass change. In those cases, mortality was concentrated in small trees of early-successional species that could not survive shading early in succession, whereas in our study we also captured mortality later in succession. Tree recruitment was a minor component of biomass change in our study, as most trees reached 5 cm dbh earlier in succession, in stands less than 10 years old. Recruitment is likely to be a major driver of tree biomass accumulation during stand initiation, and of forest recovery after small-scale disturbances (Carreño-Rocabado et al. 2012).

In our study area, the generalist *Pentaclethra macroloba* was the dominant species in terms of standing biomass in second-growth forests, as well as in old-growth forest (results not shown), and accounted for a large part of the biomass accumulation in second-growth forests. One possible reason for its success could be its potential capacity for atmospheric nitrogen fixation, which could strongly enhance rates of biomass accumulation (cf. Batterman et al. 2013). Actual rates of nitrogen fixation in *Pentaclethra macroloba* or other legumes in these study areas have not yet been assessed.

Implications

Our results highlight the importance of high diameter increment rates of a few SG specialists and the generalist *Pentaclethra macroloba* for tree biomass accumulation in young second-growth forests (10–24 years old), but these fast growth rates trade off against high biomass loss through mortality in older second-growth forests (25–40 years old; cf. Chazdon 2014). Our results suggest that, ultimately, long-term accumulation of tree biomass is sustained by recruitment of OG specialists into large tree size classes, despite the low growth rates of these species (Chazdon et al. 2010). Increasing the stem density and growth of OG specialists in young second-growth forests through enrichment planting and silvicultural treatments (Chazdon 2008a) may be a more effective method for increasing rates of carbon storage than planting fast-growing, but relatively short-lived, pioneer species. In addition, planting nitrogen-fixing species may enhance rates of biomass accumulation

throughout succession because N_2-fixing species rapidly accumulate biomass and may provide large part of the nitrogen needed for biomass accumulation in the system (Batterman et al. 2013). To assess the generality of our results, similar long-term studies should be compared across tropical forest landscapes.

LITERATURE CITED

Aide, T. M., J. K. Zimmerman, J. B. Pascarella, L. Rivera, and H. Marcano-Vega. 2000. Forest regeneration in a chronosequence of tropical abandoned pastures: Implications for restoration ecology. Restoration Ecology 8:328–338.

Alves, D. S., J. V. Soares, S. Amaral, E. M. K. Mello, S. A. S. Almeida, O. F. DaSilva, and A. M. Silveira. 1997. Biomass of primary and secondary vegetation in Rondonia, Western Brazilian Amazon. Global Change Biology 3:451–461.

Baker, T. R., et al. 2004. Increasing biomass in Amazonian forest plots. Philosophical Transactions of the Royal Society B 359:353–365.

Bates, D., M. Maechler, and B. Bolker. 2011. lme4: Linear mixed-effects models using S4 classes. R package version 0.999375-39. http://cran.r-project.org/web/packages/lme4/index.html

Batterman, S. A., L. O. Hedin, M. van Breugel, J. Ransijn, D. Craven, and J. S. Hall. 2013. Tropical carbon sink depends upon N_2 fixation and biodiversity. Nature 502:224–227.

Brearley, F. Q., S. Prajadinata, P. S. Kidd, J. Proctor, and Suriantata. 2004. Structure and floristics of an old secondary rain forest in Central Kalimantan, Indonesia, and a comparison with adjacent primary forest. Forest Ecology and Management 195:385–397.

Brown, S. 1997. Estimating biomass and biomass change of tropical forests. FAO Forestry Paper 134. Food and Agriculture Organization of the United Nations, Rome, Italy.

Brown, S., and A. E. Lugo. 1990. Tropical secondary forests. Journal of Tropical Ecology 6:1–32.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Springer, New York, New York, USA.

Carreño-Rocabado, G., M. Peña-Claros, F. Bongers, A. Alarcón, J. C. Licona, and L. Poorter. 2012. Effects of disturbance intensity on species and functional diversity in a tropical forest. Journal of Ecology 100:1453–1463.

Chambers, J. Q., R. I. Negron-Juarez, D. M. Marra, A. Di Vittorio, J. Tews, D. Roberts, G. Ribeiro, S. E. Trumbore, and N. Higuchi. 2013. The steady-state mosaic of disturbance and succession across an old-growth Central Amazon forest landscape. Proceedings of the National Academy of Sciences USA 110:3949–3954.

Chave, J., et al. 2005. Tree allometry and improved estimation of carbon stocks and balance in tropical forests. Oecologia 145:87–99.

Chave, J., et al. 2008. Assessing evidence for a pervasive alteration in tropical tree communities. PLoS Biology 6:455–462.

Chazdon, R. L. 2008a. Beyond deforestation: Restoring forests and ecosystem services on degraded lands. Science 320:1458–1460.

Chazdon, R. L. 2008b. Chance and determinism in tropical forest succession. Pages 402–426 in W. P. Carson and S. A. Schnitzer, editors. Tropical forest community ecology. Wiley-Blackwell, Chichester, UK.

Chazdon, R. L. 2014. Second growth: The promise of tropical forest regeneration in an age of deforestation. University of Chicago Press, Chicago, Illinois, USA.

Chazdon, R. L., A. R. Brenes, and B. V. Alvarado. 2005. Effects of climate and stand age on annual tree dynamics in tropical second-growth rain forests. Ecology 86:1808–1815.

Chazdon, R. L., A. Chao, R. K. Colwell, S. Y. Lin, N. Norden, S. G. Letcher, D. B. Clark, B. Finegan, and J. P. Arroyo. 2011. A novel statistical method for classifying habitat generalists and specialists. Ecology 92:1332–1343.

Chazdon, R. L., B. Finegan, R. S. Capers, B. Salgado-Negret, F. Casanoves, V. Boukili, and N. Norden. 2010. Composition and dynamics of functional groups of trees during tropical forest succession in northeastern Costa Rica. Biotropica 42:31–40.

Chazdon, R. L., S. G. Letcher, M. van Breugel, M. Martínez-Ramos, F. Bongers, and B. Finegan. 2007. Rates of change in tree communities of secondary Neotropical forests following major disturbances. Philosophical Transactions of the Royal Society B 362:273–289.

Clark, D. B., and D. A. Clark. 2000. Landscape-scale variation in forest structure and biomass in a tropical rain forest. Forest Ecology and Management 137:185–198.

Denslow, J. S., and S. Guzman. 2000. Variation in stand structure, light and seedling abundance across a tropical moist forest chronosequence, Panama. Journal of Vegetation Science 11:201–212.

Eva, H. D., et al. 2012. Forest cover changes in tropical South and Central America from 1990 to 2005 and related carbon emissions and removals. Remote Sensing 4:1369–1391.

FAO. 2010. Global Forest Resources Assessment 2010. FAO Forestry Paper 163. Food and Agriculture Organization of the United Nations, Rome, Italy.

Feeley, K. J., S. J. Davies, P. S. Ashton, S. Bunyavejchewin, M. N. N. Supardi, A. R. Kassim, S. Tan, and J. Chave. 2007. The role of gap phase processes in the biomass dynamics of tropical forests. Proceedings of the Royal Society B 274:2857–2864.

Feldpausch, T. R., C. D. Prates-Clark, E. C. M. Fernandes, and S. J. Riha. 2007. Secondary forest growth deviation from chronosequence predictions in central Amazonia. Global Change Biology 13:967–979.

Feldpausch, T. R., M. A. Rondon, E. C. M. Fernandes, S. J. Riha, and E. Wandelli. 2004. Carbon and nutrient accumulation in secondary forests regenerating on pastures in central Amazonia. Ecological Applications 14(Supplement):S164–S176.

Finegan, B. 1996. Pattern and process in neotropical secondary rain forests: The first 100 years of succession. Trends in Ecology and Evolution 11:119–124.

Fisher, J. I., G. C. Hurtt, R. Q. Thomas, and J. Q. Chambers. 2008. Clustered disturbances lead to bias in large-scale estimates based on forest sample plots. Ecology Letters 11:554–563.

Gehring, C., M. Denich, and P. L. G. Vlek. 2005. Resilience of secondary forest regrowth after slash-and-burn agriculture in central Amazonia. Journal of Tropical Ecology 21:519–527.

Gómez-Pompa, A., and C. Vázquez-Yanes. 1981. Successional studies of a rain forest in Mexico. Pages 246–266 in D. C. West, H. H. Shugart, and D. B. Botkin, editors. Forest succession. Concepts and application. Springer-Verlag, New York, New York, USA.

Guariguata, M. R., and R. Ostertag. 2001. Neotropical secondary forest succession: changes in structural and functional characteristics. Forest Ecology and Management 148:185–206.

Hughes, R. F., J. B. Kauffman, and V. J. Jaramillo. 1999. Biomass, carbon, and nutrient dynamics of secondary forests in a humid tropical region of Mexico. Ecology 80:1892–1907.

Kauffman, J. B., R. F. Hughes, and C. Heider. 2009. Carbon pool and biomass dynamics associated with deforestation, land use, and agricultural abandonment in the neotropics. Ecological Applications 19:1211–1222.

Lang, G. E., and D. H. Knight. 1983. Tree growth, mortality, recruitment, and canopy gap formation during a 10-year period in a tropical moist forest. Ecology 64:1075–1080.

Letcher, S. G., and R. L. Chazdon. 2009. Rapid recovery of biomass, species richness, and species composition in a forest chronosequence in northeastern Costa Rica. Biotropica 41:608–617.

Lewis, S. L., J. Lloyd, S. Sitch, E. T. A. Mitchard, and W. F. Laurance. 2009. Changing ecology of tropical forests: evidence and drivers. Annual Review of Ecology, Evolution, and Systematics 40:529–549.

Marín-Spiotta, E., D. F. Cusack, R. Ostertag, and W. L. Silver. 2008. Trends in above and belowground carbon with forest regrowth after agricultural abandonment in the Neotropics. Pages 22–72 in R. W. Myster, editor. Post-agricultural succession in the neotropics. Springer, New York, New York, USA.

Marín-Spiotta, E., R. Ostertag, and W. L. Silver. 2007. Long-term patterns in tropical reforestation: plant community composition and aboveground biomass accumulation. Ecological Applications 17:828–839.

Martin, P. A., A. C. Newton, and J. M. Bullock. 2013. Carbon pools recover more quickly than plant biodiversity in tropical secondary forests. Proceedings of the Royal Society B 280:no. 1773 20132236.

Mascaro, J., G. P. Asner, D. H. Dent, S. J. DeWalt, and J. S. Denslow. 2012. Scale-dependence of aboveground carbon accumulation in secondary forests of Panama: A test of the intermediate peak hypothesis. Forest Ecology and Management 276:62–70.

McDade, L., and G. S. Hartshorn. 1994. La Selva Biological Station. Pages 6–14 in L. McDade, H. Hespenheide, and G. S. Hartshorn, editors. La Selva: Ecology and natural history of a neotropical rain forest. University of Chicago Press, Chicago, Illinois, USA.

Milton, K., E. A. Laca, and M. W. Demment. 1994. Successional patterns of mortality and growth of large trees in a Panamanian lowland forest. Journal of Ecology 82:79–87.

Nakagawa, S., and H. Schielzeth. 2013. A general and simple method for obtaining R^2 from generalized linear mixed-effects models. Methods in Ecology and Evolution 4:133–142.

Norden, N., R. L. Chazdon, A. Chao, Y. H. Jiang, and B. Vilchez-Alvarado. 2009. Resilience of tropical rain forests: tree community reassembly in secondary forests. Ecology Letters 12:385–394.

Norden, N., S. G. Letcher, V. Boukili, N. G. Swenson, and R. Chazdon. 2012. Demographic drivers of successional changes in phylogenetic structure across life-history stages in plant communities. Ecology 93(Supplement):S70–S82.

Oliver, C. D., and B. C. Larson. 1996. Forest stand dynamics. Update edition. Wiley, New York, New York, USA.

Pan, Y. D., et al. 2011. A large and persistent carbon sink in the world's forests. Science 333:988–993.

Peet, R. K., and N. L. Christensen. 1987. Competition and tree death. BioScience 37:586–595.

Peña-Claros, M. 2003. Changes in forest structure and species composition during secondary forest succession in the Bolivian Amazon. Biotropica 35:450–461.

Phillips, O. L., S. L. Lewis, T. R. Baker, K. J. Chao, and N. Higuchi. 2008. The changing Amazon forest. Philosophical Transactions of the Royal Society B 363:1819–1827.

Pickett, S. T. A. 1989. Space-for-time substitution as an alternative to long-term studies. Pages 110–135 in G. E. Likens, editor. Long-term studies in ecology. Springer-Verlag, New York, New York, USA.

Plourde, B. T., V. K. Boukili, and R. L. Chazdon. 2014. Radial changes in wood specific gravity of tropical trees: inter- and intra-specific variation during secondary succession. Functional Ecology, in press. http://dx.doi.org/10.1111/1365-2435.12305

R Development Core Team. 2013. R version 3.0.1. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Rich, P. M. 1987. Mechanical structure of the stem of arborescent palms. Botanical Gazette 148:42–50.

Rutishauser, E., F. Wagner, B. Herault, E. A. Nicolini, and L. Blanc. 2010. Contrasting above-ground biomass balance in a neotropical rain forest. Journal of Vegetation Science 21:672–682.

Saldarriaga, J. G., D. C. West, M. L. Tharp, and C. Uhl. 1988. Long-term chronosequence of forest succession in the upper Rio Negro of Colombia and Venezuela. Journal of Ecology 76:938–958.

Silver, W. L., R. Ostertag, and A. E. Lugo. 2000. The potential for carbon sequestration through reforestation of abandoned tropical agricultural and pasture lands. Restoration Ecology 8:394–407.

Uriarte, M., C. D. Canham, J. Thompson, and J. K. Zimmerman. 2004. A neighborhood analysis of tree growth and survival in a hurricane-driven tropical forest. Ecological Monographs 74:591–614.

Valencia, R., R. Condit, H. C. Muller-Landau, C. Hernandez, and H. Navarrete. 2009. Dissecting biomass dynamics in a large Amazonian forest plot. Journal of Tropical Ecology 25:473–482.

van Breugel, M., F. Bongers, and M. Martínez-Ramos. 2007. Species dynamics during early secondary forest succession: recruitment, mortality and species turnover. Biotropica 39:610–619.

van Breugel, M., M. Martínez-Ramos, and F. Bongers. 2006. Community dynamics during early secondary succession in Mexican tropical rain forests. Journal of Tropical Ecology 22:663–674.

van Breugel, M., J. Ransijn, D. Craven, F. Bongers, and J. S. Hall. 2011. Estimating carbon stock in secondary forests: decisions and uncertainties associated with allometric biomass models. Forest Ecology and Management 262:1648–1657.

Walker, L. R., D. A. Wardle, R. D. Bardgett, and B. D. Clarkson. 2010. The use of chronosequences in studies of ecological succession and soil development. Journal of Ecology 98:725–736.

Wright, S. J., et al. 2010. Functional traits and the growth–mortality trade-off in tropical trees. Ecology 91:3664–3674.

Supplemental Material

Ecological Archives

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