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Carbon Accumulation in Neotropical Dry Secondary Forests: The Roles of Forest Age and Tree Dominance and Diversity

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ABSTRACT

Tropical secondary forests are important sinks for atmospheric carbon, yet C uptake and accumulation rates are highly uncertain, and the mechanisms poorly understood. We evaluated the recovery of C stocks in four pools (aboveground biomass, litter, roots and topsoil) during dry forest regrowth by combining a space for time replacement (that is, a chronosequence) with a repeated measurements approach (that is, a resampling). We fit nonlinear models to chronosequence data to test whether forest age could explain differences in C stocks across sites, and to changes in aboveground biomass calculated from resampling over two 3-year periods, to test the predictive potential of forest age. We combined data from both approaches into structural equation models (SEM) to assess forest age and tree community attributes (diversity and dominance) as drivers of C stocks and changes in aboveground biomass. Forest age explained differences across sites in C stocks for aboveground biomass, litter and live roots, but not for the remaining pools. Observed C stock changes in aboveground biomass were poorly predicted by forest age. SEM revealed that aboveground biomass C was consistently and positively related to forest age and to the community weighted mean of maximum tree height ($H_{\max}$ CWM), but not to tree diversity. Observed C stock changes were related only to $H_{\max}$ CWM, although not consistently across the two 3-year periods. Our results highlight that the chronosequence approach can yield reasonable insights into long-term C accumulation trends, but erroneous estimates of C change over specific time periods. They also show that, in addition to age, dominance by tall statured species, but not tree species diversity, plays a significant role in C accumulation.

Key words: carbon cycle; carbon uptake; coarse woody productivity; longitudinal studies; secondary succession; SEM; biomass ratio hypothesis; root biomass.

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Author contributions FM, VJJ and PB conceived the study. FM, RB, MG and IS performed field work. FM and JEKB analyzed data. FM, VJJ and PB wrote the paper, all other authors commented on the manuscript.

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INTRODUCTION

Tropical secondary forests exert an important influence on the terrestrial C balance because they cover large areas of the tropics and accumulate C quickly (Pregitzer and Euskirchen 2004; Wright 2010; Pan and others 2011). During forest recovery, C accumulation in longer lived pools can offset emissions, but estimates of such effect vary widely—ranging from as low as 5 to 100% of total emissions (Pan and others 2011; Achard and others 2014; Grace and others 2014; Chazdon and others 2016). Uncertainty is partially driven by poor characterization of C accumulation during forest recovery (Houghton 2003; Pregitzer and Euskirchen 2004; Anderson-Teixeira and others 2016), constraining model estimates of tropical secondary forest landscapes contribution to the terrestrial C balance (Houghton 2003; Grace and others 2014). This is particularly true for tropical dry forest regions, which despite their wide distribution and severe transformation (Miles and others 2006), have been much less studied than their wetter counterparts (Kauffman and others 2009; Meister and others 2012; Anderson-Teixeira and others 2016).

Forest age is an important driver of C stocks in recovering forests because some portion of net ecosystem production accumulates over time until late in forest development, when C storage asymptotes (Chapin III and others 2011; Yang and others 2011). Chronosequence studies in neotropical dry secondary forests have confirmed such accumulation trends for aboveground biomass (AGB) (Becknell and others 2012; Poorter and others 2016). Stocks in other C pools like root biomass, dead aboveground biomass or soil organic carbon are also expected to be driven by forest age, given the allometric (Niklas 2004; Mokany and others 2006) and/or functional relationships among C pools within the ecosystem (Malhi 2012; Anderson-Teixeira and others 2016). However, evidence of the recovery of these C stocks with forest regrowth in the neotropics is still scarce (Marin-Spiotta and Sharma 2013; Anderson-Teixeira and others 2016), and what limited data exist show no consistent trends of C accumulation in relation to forest age (Saynes and others 2005; Kissing and Powers 2010; Costa and others 2014).

It is possible that forest age is not as relevant a driver of C accumulation as previously considered. Chronosequence studies across the neotropics show that forest age can have a highly variable effect on C accumulation, even when more straight-forward variables such as AGB are measured (Vargas and others 2008; Hernández-Stefanoni and others 2010; Orihuela-Belmonte and others 2013). If forest age was the dominant driver of C stock change during forest recovery, the trajectories identified by multi-year repeated measurement approaches should mirror C recovery trajectories predicted by space-for-time-based chronosequence approaches. Available evidence suggests that site trajectories often deviate from such expectations (Feldpausch and others 2007; Mora and others 2015; Norden and others 2015), maybe in response to additional drivers, such as annual rainfall variability, soil properties or legacies from land use history (Powers and Peréz-Aviles 2012; Zeri and others 2014; Wandelli and Fearnside 2015). Given the large variation across studies and deviations due to selected methodologies, multi-method and multi-year studies are needed that examine how forest age, as well as other possible drivers, influence C accumulation during forest recovery.

Plant community attributes are potential drivers of C recovery after disturbance, with previous results pointing to three main hypotheses. A null hypothesis (H_0), also called the ‘‘vegetation quantity’’ hypothesis, states that the structural development of the plant community (that is, its ‘‘quantity’’) represents the main driver of C accumulation. This hypothesis predicts a declining temporal trend in C accumulation rates because of a negative density-dependence effect of initial biomass (Finegan and others 2015; Lohbeck and others 2015). Alternatively, the ‘‘quality’’ of the plant community may drive ecosystem processes (Lohbeck and others 2015; Lin and others 2016). A first alternative hypothesis (H_1) posits that increases in plant species diversity enhance standing biomass and primary productivity through increased resource use-efficiency (that is, the ‘‘diversity hypothesis’’; Cardinale and others 2011). Tree diversity, assessed as species richness or functional trait diversity, has been positively associated with C stocks and C accumulation rates in aboveground biomass of tropical forests (Chisholm and others 2013; Lasky and others 2014). A second alternative hypothesis (H_2) posits that the dominant species, and therefore their dominant traits, drive ecosystem processes, the so-called biomass ratio hypothesis (Grime 1998). Consistent with this hypothesis, the community weighted mean of several functional traits, including maximum height, wood density and specific leaf area, have been associated with both C stocks and C accumulation rates in the aboveground biomass of tropical secondary forests (Conti and Díaz 2013;

Becknell and Powers 2014; Finegan and others 2015). In tropical dry forest (TDF), plant traits related to desiccation tolerance like specific leaf area, wood density and leaf C isotopic composition (Becknell and Powers 2014; Letcher and others 2015; Pineda-García and others 2016) are likely to drive C accumulation during forest recovery, given the strong restrictions to growth and survival imposed by inter- and intra-seasonal variation in water availability (Lohbeck and others 2013; Letcher and others 2015). Disentangling the role these plant community attributes play to explain C accumulation requires an integrative approach that accounts for the co-variation in forest age, biomass, species diversity, functional diversity and functional traits commonly observed during neotropical dry forest recovery (Becknell and Powers 2014; Prado-Junior and others 2016).

In this study, we assessed C accumulation in four different ecosystem pools (aboveground biomass, standing litter, roots, and soil) during TDF recovery in western Mexico. In contrast to other studies, we used a set of plots differing in forest age (a chronosequence) and measured repeatedly through time (a resampling approach), to test the hypothesis that forest age is a main driver of C accumulation and thus a predictor of C stock changes. By also measuring a set of plant community attributes including species and functional richness and evenness, as well as community weighted means and variances of several functional traits, and then modeling their causal relationships with forest age, C stock in AGB, and C accumulation rates in AGB (Figure 1), we were able to directly test the vegetation quantity (H_0), the vegetation diversity (H_1) and the biomass ratio (H_2) hypotheses to better explain C accumulation in this TDF. Testing these hypotheses allowed us to ask the following questions: (1) To what extent does forest age explain C stocks in these secondary forests? (2) Do chronosequence models adequately predict C stock changes in the aboveground biomass of these forests? (3) Which plant community attributes drive carbon accumulation in the aboveground biomass of these secondary forests?

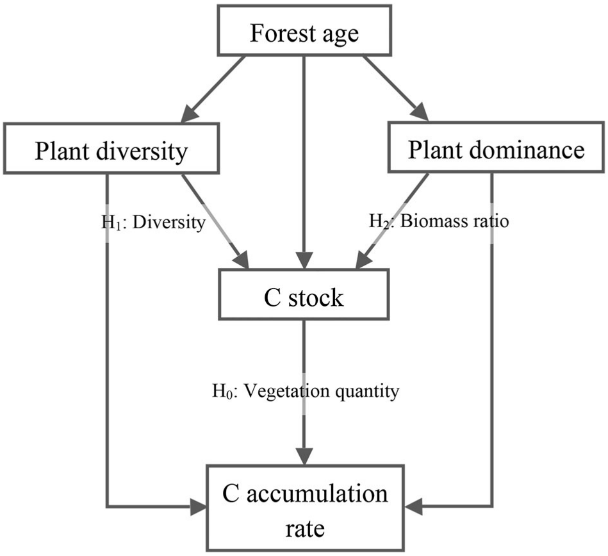

Figure 1. Conceptual model illustrating the hypothesized drivers of C accumulation in the aboveground biomass after forest disturbance. Three main hypotheses are implied by the causal relations between forest age, tree community attributes, C stocks and C accumulation rates (see text for further details). Forest age: time elapsed after land abandonment.

Materials and Methods

Study Area and Site Characteristics

The study was conducted in the Chamela-Cuixmala region, on the Mexican Pacific coast (19°23′–19°30′N, 104°56′–105°04′W, Figure S1). Mean annual temperature is 24.6°C. Mean annual precipitation over the period 1983–2013 is 756 mm, concentrated between June and October (M. Maass *pers. com.*). The predominant land cover is TDF, although some areas have been transformed during the past 40 years to pastures for livestock grazing (Sánchez-Azofeifa and others 2009; Trilleras and others 2015). Twelve sites, nine secondary forests and three old-growth forest, were selected to represent variation in stand age and structure of TDF across the hilly region. All sites were characterized by slopes ranging from 15° to 30°, east to west aspects, and located between 25 and 190 masl. Soils are young, shallow (A and B horizons to 40 cm depth), and poorly developed Regosols (Cotler and others 2002). Distance between sites varied between 0.5 and 26.7 km (Figure S1). Old-growth forest sites were within private lands advocated to TDF conservation since the 1970s (Noguera and others 2002), and the whole region had a very low population density and very localized forest clearance before that (Castillo and others 2005; Tello 2012). They showed no apparent signals of recent disturbance (tree stumps or fire evidence), and were dominated by *Apoplanesia paniculata* and *Caesalpinia eriostachys*. Secondary forests had been abandoned for 0–12 years when permanent plots were established in November 2004, as determined through semi-structured interviews with landowners (Trilleras 2008), after which they were fenced with barbed wire to exclude cattle. They had been cleared by slash and burn and used 1–28 years for agricultural activities, which included 1–3 corn crop rotations, after which they were used as pastures with repeated slashing, burning, planting of exotic grasses and free grazing (Trilleras 2008, Table S1). There was no correlation between forest age and management or physical conditions of sites (Pearson correlation, $P > 0.05$, Table S1). Secondary forests are dominated by resprouter species as *Lonchocarpus mutans*, *Piptadenia constricta* and *C. eriostachys*, as well as *Acacia macracantha*, *Spondias purpurea* and *Cordia elaeagnoides* (Table S1). Compositional similarities to old-growth forest increase as recovering forests age (Mora and others 2015).

Approaches to the Study of C Stocks Recovery

We assessed the recovery of C stocks in four pools during dry forest regrowth after pasture abandonment using a chronosequence approach, that is, a space for time replacement, where sites differing in forest age were sampled once. We focused our assessment on those pools considered highly dynamic during early forest regrowth as a result of biological processes (mainly tree recruitment and growth): aboveground biomass (AGB), litter mass (Litter), root mass (Roots), and topsoil organic carbon (SOC). AGB was further subdivided into woody (AGB_W) and herbaceous (AGB_H) pools. We did not include estimations of coarse woody debris or soil below 10 cm depth. For the aboveground biomass, we also conducted a resampling approach, in which the same sites were measured three times (every 3 years). Resampling allowed the characterization of recovery trajectories and the estimation of ''observed'' C accumulation rates.

AGB_W was defined as the mass in live woody stems of trees and shrubs above the soil surface. AGB_W was estimated from measuring all live woody stems at least 1 cm diameter at breast height (DBH) within a 20 × 50 m plot at each site, following a stratified sampling approach (Figure S2). Measurements were taken in three different years (2004, 2010 and 2010), between September and October. Biomass was estimated with an allometric equation developed for the Chamela TDF including DBH and wood density as predictors (Martínez-Yrízar and others 1992). We used this equation instead of recently published pantropical equations because the latter provide significantly biased estimations for our study region (Chave and others 2014). Tree height was not included as a biomass predictor because the maximum height of the whole plant instead of the height of each individual stem in multi-stemmed trees was measured. Wood density values were obtained from published and unpublished data for the species at Chamela (Barajas-Morales 1985, 1987; Martínez-Yrízar and others 1992; Bojórquez 2014). When site data were not available, species values from other locations or mean genus values were used (Chave and others 2006). For species with no available information, a mean community value was assigned. Lianas and cacti were not included in AGB estimates because of the lack of allometric equations for these life forms in TDF; moreover, they account for only 1.9 and 4.0% of the basal area across all sites, respectively. C stocks in AGB_W were estimated by multiplying biomass by a conversion factor of 0.48 (Jaramillo and others 2003).

AGB_H was quantified by harvesting at ground level all the live material less than 1 cm DBH in three 2 × 0.5 m plots located 2 m away from the 20 × 50 m plot (Figure S2). Biomass was harvested between March and April 2011. Material was oven-dried at 80°C to constant moisture and weighed. C stocks were estimated by multiplying AGB_H by a conversion factor of 0.46 (Jaramillo and others 2003).

Total root mass, including live and dead roots, was estimated by direct harvest. We excavated trenches in the same three 2 × 0.5 m plots used for AGB_H estimation, between March and April 2011 (Figure S2), to a depth of 40 cm, as 80–88% of the root mass is found within this depth (Jaramillo and others 2003). Soil was sieved through a 4 mm mesh to extract roots in the field. Roots were taken to the laboratory, washed and separated in three diameter classes: small (<4 mm), medium (4–20 mm), and coarse (>20 mm). The material was oven-dried at 80°C to constant weight. C stocks in each class were estimated multiplying biomass by mean C concentrations for each diameter class (Jaramillo and others 2003). Total C stock from harvests ($Root_{harv}$) was defined as the sum of these three stocks. Also, allometric equations were used to estimate the biomass of the live roots larger than 2 mm ($Root_{Allom}$). We had no local equations to estimate root mass, so we used an allometric equation relating DBH to the root to shoot ratio ($\text{root:shoot} = 0.2914 - 0.009 \times \ln(\text{DBH})$) derived from equations for both total and aboveground biomass in a Dry Chaco location under very similar latitudinal and climatological conditions (Sato and others 2015). C stocks were estimated multiplying $Root_{Allom}$ by a conversion factor of 0.39 (Jaramillo and others 2003).

Litter, defined as the dead plant material above the surface of the mineral soil layer, was collected in nine 30 × 30 cm microplots at each site in April 2011, date by which most of the plants had shed their leaves. Three microplots were randomly located in the upper, middle and lower positions of the 20 × 50 m plots used for measuring trees (Figure S2). The plant material was sieved through a 0.25 mm mesh to exclude mineral soil particles and then subdivided into three components: leaves, stems (true stems $\leq$ 2.5 cm diameter plus detached petioles or rachises from compound leaves), and reproductive material (inflorescences, flowers, fruits and seeds). The samples were oven-dried at 80°C to constant weight. Litter C stocks were estimated by multiplying biomass by conversion factors of 0.40 for leaves and reproductive material and 0.49 for stems (Jaramillo and others 2003).

Soil organic C (SOC) was defined as the total organic C content in the soil mineral layer to a 10-cm depth. In September 2009, three soil cores 5-cm in diameter were taken with a soil auger at each position (upper, middle and lower) within the 20 × 50 m plot (Figure S2). Independent cores were taken for two sampling depths (0–5 and 5–10 cm). For each position and depth, the three cores were mixed into a composite sample. These were sieved through a 2-mm mesh to remove gravel and pebbles, and organic C concentration was determined with a Shimadzu TOC Autoanalyzer. Dry bulk density was measured for undisturbed soil cores from the same plot positions. Soil samples were sieved, and the fine fraction oven-dried at 80°C for 3 days and weighed. Bulk density was estimated as the ratio between sieved soil mass and the volume of the sample. SOC stocks for each site were estimated by multiplying C concentrations by bulk density for each depth and position and averaging the three values from each site.

Forest Age as Driver of C Stocks

To test the explanatory power of forest age on C stocks, we used a chronosequence approach. We fitted four different nonlinear models to test the association between C stocks and forest age for different pools. All models assume an asymptotic C accumulation during forest regrowth (Sierra and others 2012; Mora and others 2015). Old-growth sites were assigned an age of 100 years, since model parameters did not change in relation to the age assigned to old-growth forests (Mora and others 2015). In the case of aboveground biomass, for which we had measurements from three different years, we used data from 2010 to match the sampling dates of the other pools. The best-fit model for each C pool was selected based on minimization of AICc and confidence intervals for its parameters were derived from fitting the model to one thousand bootstrapped samples. Age needed to reach 50% of the stock levels at the asymptote was also derived from the fitted models. Model fitting was performed with the ''nls'' function in R (R Development Core Team 2016). For those pools lacking a relationship with forest age, bootstrapped *t* tests were performed to compare secondary and old-growth forests using functions ''*t* test'' and ''boot'' (Canty and Ripley 2016).

Predictive Ability of the Chronosequence Model on AGB_W Stock Changes

We tested whether the chronosequence could predict C stock changes in AGB_W by using a combination of chronosequence and resampling approaches. From nonlinear models fitted to data from the chronosequence approach, we derived a model relating the expected changes in AGB_W C stocks ($dAGB_W$) to forest age, following the approach proposed by Mora and others (2015). Using the repeated measurements from the resampling approach, we calculated the observed $dAGB_W$ and modeled their relation to forest age. If nonlinear models fitted to chronosequence data were good predictors of changes during forest recovery, the model relating observed $dAGB_W$ to forest age should fall within the confidence intervals of the model for expected $dAGB_W$ (Mora and others 2015). Observed changes were defined as the difference in C stocks for two subsequent measurement dates ($dAGB_W = AGB_{W t+\Delta t} - AGB_{W t}$) and were calculated for two periods using previous tree measurements on the same plots performed in 2004 and 2007.

Plant Community Attributes as Drivers of C Accumulation

To test the competing hypotheses on how forest age and plant community attributes drive C accumulation in the aboveground biomass, we developed a conceptual model that integrated both chronosequence and resampling approaches (Figure 1). We conceived C accumulation, either already accumulated C (AGB_W) or observed C stock changes ($dAGB_W$), as driven by plant diversity (vegetation diversity hypothesis) and plant dominance (biomass ratio hypothesis). Forest age drives C accumulation either directly (for AGB_W), or indirectly through AGB_W in the case of $dAGB_W$ (vegetation quantity hypothesis). Forest age can also drive C accumulation indirectly through its effect on plant diversity and plant dominance, which commonly change as forest age.

We calculated tree species diversity and tree dominance indicators using species and functional trait data. Diversity was quantified as rarefied species richness (RS_{rich}), functional richness (F_{rich}), and community weighted variances (CWV) of functional traits. Dominance was assessed with Pielou species evenness index (J), functional evenness (F_{eve}), and the community weighted means (CWM) of functional traits. Five traits previously found to be associated with C accumulation in tropical and subtropical secondary forests (Conti and Díaz 2013; Becknell and Powers 2014; Finegan and others 2015) were used to calculate trait-based indicators: maximum height (H_{max}), wood density (WD), specific leaf area (SLA), leaf nitrogen concentration (N_{leaf}), and leaf C isotopic composition ($\Delta_{13}C_{leaf}$). Most of their values were taken from Bhaskar and others (2014a, b). Indicators were calculated using ''vegan'' and ''FD'' packages for R (Oksanen and others 2016; Laliberté and others 2014).

The test of the integrative model required two stages. First, we examined the best indicators of plant diversity and dominance to be included in the model by testing all pairwise relations among indicators and AGB_W across the whole chronosequence or $dAGB_W$ for the 2004–2007 period. To increase the degrees of freedom of those tests, and to account for the within-plot variability in both C accumulation and community attributes, each of the twelve 20 × 50 m plots was subdivided in five 20 × 10 m parallel subplots (Figure S2). We fitted linear mixed effect models with site as a random effect to account for the associated response of subplots (Pinheiro and Bates 2000), using the nlme package in R (Pinheiro and others 2016). Only data for secondary forest sites were included, so we could assume linear relationships among variables, particularly with forest age (total $n = 45$). For both plant diversity and plant dominance, the variable best associated with AGB_W or $dAGB_W$ was included in the model using minimization of AICc as the selection criteria. After indicator selection, we tested our conceptual integrative model by fitting a structural equation model (SEM) using a graph theoretical approach (Grace and others 2012) with

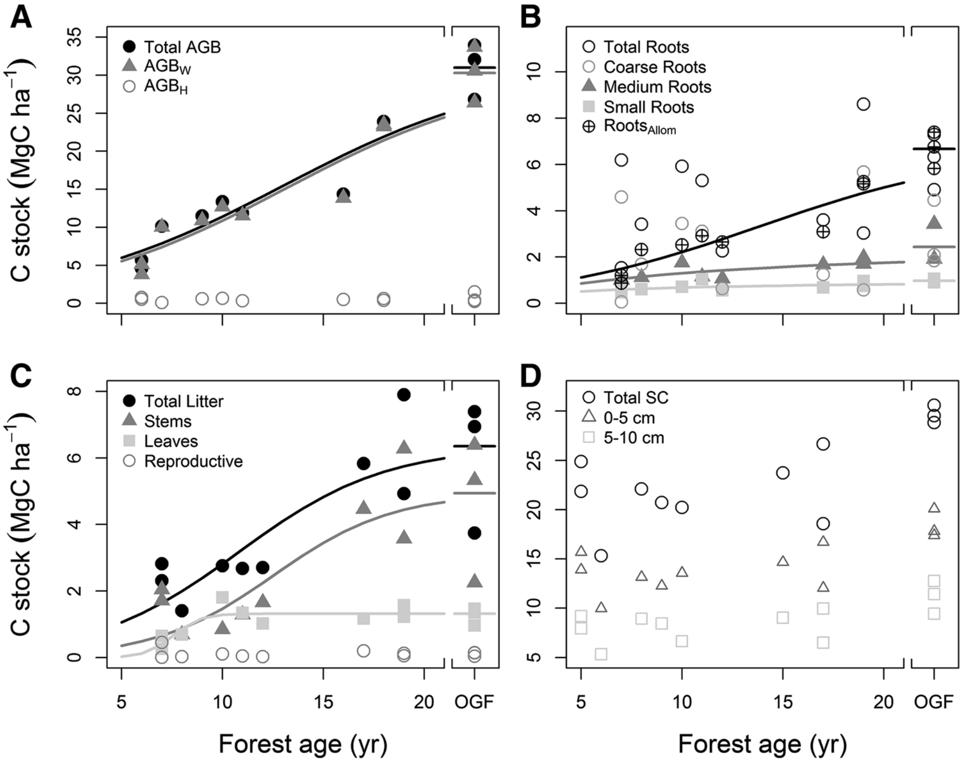

Figure 2. C stocks in relation to forest age in four ecosystems pools: **A** aboveground biomass, **B** roots, **C** litter, and **D** soil. Pools with a significant association with forest age are represented by *filled symbols*, while those not related to forest age are represented by *hollow symbols*. *Lines* represent mean chronosequence trajectories from fitted nonlinear models (see Table 1 for model parameters) for those C pools showing a significant relationship with forest age. *AGB* aboveground biomass, AGB_W woody aboveground biomass, AGB_H herbaceous aboveground biomass, *SOC* soil organic carbon, *OGF* old-growth forest.

mixed effects models to account for the nested structure of the data. We assessed the model for missing paths using a test of d-separation (Shipley 2009), implemented in the ggm package for R (Marchetti and others 2015). Second, we performed a confirmatory analysis of the selected model using 2007–2010 data. The confirmatory test was done using SEM as described above.

RESULTS

Forest Age as a Driver of Carbon Stocks

C in AGB varied between 4.6 Mg C ha^{-1} at the youngest site and 33.9 Mg C ha^{-1} at an old-growth forest (Table S2). Age significantly explained 93% of the variation in AGB, with an expected age of 12 y to attain half the asymptotic stock level of 31.0 Mg C ha^{-1} (Figure 2A; Table 1). Within the AGB pool, C in woody plants showed a significant association with age, while C in herbs showed no significant trend (Table 1; Figure 2A) and did not differ between secondary and old-growth forests ($t = 0.53$; $df = 2.1$, and $P > 0.1$).

Total $Root_{harv}$ C stock ranged from 1.5 to 8.6 Mg C ha^{-1} (Table S2). It was not significantly related to age (Table 1; Figure 2B), nor did it differ between secondary and old-growth forests ($t = 1.72$, $df = 7.0$, $P > 0.05$). C stocks in both small and medium-sized roots were significantly related to age, with 5 and 10.8 years to reach half the expected asymptotic stocks, respectively (Table 1; Figure 2B). Coarse root C showed no trend with age and it did not differ between secondary and old-growth forests ($t = 0.44$, $df = 4.8$, $P > 0.1$). Total C in live roots ($Root_{Allom}$) varied between 0.9 and 7.4 Mg C ha^{-1} (Table S2), and was significantly related to age, with 13.9 years to reach half the expected asymptotic stocks (Table 1; Figure 2B). $Root_{Allom}$ C stock was significantly lower than $Root_{harv}$ C in secondary forests, but not in old-growth forests, with a mean difference between estimates of −1.54 and 0.5 Mg C ha^{-1} for secondary forest and old-growth, respectively ($t = 2.21$; $df = 9.3$, and $P < 0.05$; Figure S3).

Litter C varied between 1.4 and 7.9 Mg C ha^{-1} (Table S2) and age significantly explained 69% of its variation (Table 1; Figure 2C). As many as 10.8 years would be needed to reach half the asymptotic litter C stock value. Both the leaf and stem fractions showed a significant relationship with age (Table 1; Figure 2C). The reproductive fraction showed no trend and was not different

Table 1. Effect of Forest Age on C Stocks in Secondary Tropical Dry Forest

Pool	Model	*a*	*b*	*c*	R^2
Aboveground biomass					
Herbs (<1 cm DBH)	Mic–men	0.7**	3.9		0.05
Trees 1–5 cm DBH	NA				
Trees > 5 cm DBH	Logistic	25.7**	16.4**	3.0**	0.98
Total aboveground	Logistic	31.0**	12.0**	5.6**	0.93
Roots					
<4 mm diam.	Mic–men	1.0**	4.9**		0.52
4–20 mm diam.	Mic–men	2.7**	10.7**		0.61
>20 mm diam.	Mic–men	2.8**	2.1		0.02
Total root	Mic–men	6.5**	5.1		0.18
$Root_{Allom}$ (>2 mm diam.)	Logistic	6.7**	13.9**	5.5**	0.92
Litter					
Leaves	Logistic	1.3**	7.6**	0.7**	0.66
Stems	Logistic	4.9**	12.5**	2.9**	0.63
Reproductive	Mic–men	0.1**	−4.3		0.05
Total litter	Logistic	6.4**	10.8**	3.6**	0.69
Soil					
0–5 cm depth	Mic–men	20.0**	3.3		0.21
5–10 cm depth	Mic–men	15.1**	3.0		0.34
Total soil (0–10 cm)	Mic–men	35.0**	3.2		0.26
Total ecosystem	Mic–men	85.5**	7.7**		0.88

The effect of forest age was tested with four different nonlinear models: Michaelis–Menten (Mic–men; $Stock = at/(b + t)$), asymptotic ($Stock = a + (b - a)e^{-e^{c}t}$), Gompertz ($Stock = ae^{-bc^{t}}$), and logistic ($Stock = (a/(1 + e^{((b-t)/c)}))$). Both secondary and old-growth forests were included during model fitting and model selection was based on minimization of AICc. R^2: coefficient of determination. $^{**}P < 0.01$; $^{*}P < 0.05$. NA: model fitting was not attainable. Parameter b provides an estimation of the time to reach 50% of the maximum (asymptotic) C stock value, which in turn is indicated by parameter a.

between secondary and old-growth forests ($t = -0.13$, $df = 8.8$, $P > 0.1$).

Soil organic C ranged from 15.3 to 30.6 Mg ha^{-1} (Table S2). No pattern was detected in relation to forest age (Table 1; Figure 2D), although mean SOC stocks were significantly higher in old-growth than in secondary forest ($t = 6.5$, $df = 9.9$, $P < 0.01$). No discernible patterns were detected by soil depth with age (Table 1; Figure 2D) and in both cases SOC stocks were greater in old-growth than in secondary forest ($t = 4.6$, $df = 4.9$, $P < 0.01$ at 0–5 cm; $t = 2.9$, $df = 3.2$, $P < 0.01$ at 5–10 cm).

Total C stocks ranged from 30.3 to 76.8 Mg C ha^{-1} (Table S1), with 88% of the variation explained by forest age (Table 1). The relative contribution of each pool to the total stock changed through the chronosequence, with an increasing proportion of C in the aboveground biomass and a decreasing contribution of SOC as forest age increased (Figure S4).

Aboveground Biomass Stock Changes and the Predictive Ability of Forest Age

Observed $dAGB_W$ varied between −1.3 and 7.1 Mg C ha^{-1} 3 y^{-1} (Figure 3; Table S3). It differed significantly between the two periods: $dAGB_W$ 2004–2007 = 1.4; $dAGB_W$ 2007–2010 = 3.1 (paired *t* test: $t = -2.99$, $df = 11$, $P < 0.05$). The difference between secondary and old-growth forests was not significant for the 2004–2007 period (mean $dAGB_W$ secondary forests = 1.6, mean $dAGB_W$ old-growth forest = 0.6, $t = 0.70$, $df = 3.3$, $P > 0.1$), but it was significant for the 2007–2010 period (mean $dAGB_W$ secondary forests = 3.5, mean $dAGB_W$ old-growth forest = 1.8, $t = -2.46$, $df = 9.6$, $P < 0.01$).

A significant relationship was found between observed $dAGB_W$ and forest age in the period 2004–2007, but not during 2007–2010, although it was very loose in both cases (Figure 3; Table 2). The chronosequence showed a very low ability to predict observed $dAGB_W$, since the model relating observed $dAGB_W$ to forest age did not fall within the confidence intervals for predicted $dAGB_W$ in either of the two periods (Figure 3).

Plant Community Attributes as Drivers of C Accumulation

Some indicators of plant diversity such as F_{rich} and $\Delta_{13}C_{leaf}$ CWV showed a positive and significant relation with C stocks in AGB_W (Table 3). In contrast, none of the plant diversity indicators were significantly associated with C stock changes during the period 2004–2007 (Table 3). F_{rich} was included in the SEM as the indicator of plant diversity since it was best associated with AGB_W (Table 3).

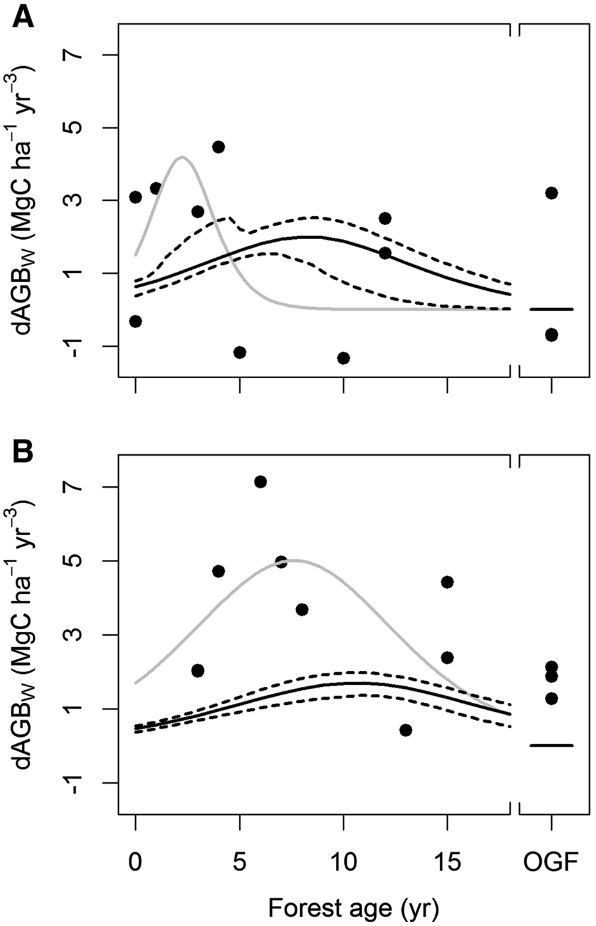

Figure 3. Observed C stock changes in woody aboveground biomass ($dAGB_W$) in relation to forest age. Observed changes were evaluated for two periods: 2004–2007 (**A**), and 2007–2010 (**B**). *Gray continuous lines* represent the model fitted to observed changes. *Black continuous lines* represent mean expected changes from chronosequence models fitted to AGB_W, and *dotted lines* their 95% confidence intervals. *OGF* old-growth forest sites.

Indicators of plant community dominance such as Pielou evenness index (J) showed a negative relation with C stocks in AGB_W, while H_{max} CWM showed a positive relationship with both AGB_W and $dAGB_W$ (Table 3). *L. mutans* and *A. macracantha* among secondary forests, and *A. paniculata*, *Lonchocarpus lanceolatus* and *Thouinia paucidentata* among old-growth forests were the species with the highest weights on H_{max} CWM values; a total of twenty three species were particularly relevant given their high abundance across sites (Table S1).

Table 2. Effect of Forest Age on C Stocks in Aboveground Woody Biomass (AGB_W) of Secondary Tropical Dry Forest and their Observed Change for Two 3-Year Periods ($dAGB_W$)

Response	*a*	*b*	*c*	R^2
AGB_W (2004)	**27.8****	9.7**	**3.4****	0.96
AGB_W (2007)	**28.5****	12.1**	**4.2****	0.97
$dAGB_W$ (2004–2007)	**17.1****	2.2*	**1.0****	0.19
$dAGB_W$ (2007–2010)	**67.1****	7.6 ns	**3.4****	0.16

The effect of forest age was tested by fitting a logistic model to C stocks: $AGB_W = \left(a/\left(1+e^{((b-t)/c)}\right)\right)$*, while its first derivative was fitted to observed C stock changes:* $dABC_T = \left(ae^{((b-t)/c)}/c\right)/\left(1+e^{((b-t)/c)}\right)^2$*. Both secondary and old-growth forests were included during model fitting.* R^2*: coefficient of determination. Parameters in bold correspond to those testing the effect of forest age on the response variable. **P < 0.01; *P < 0.05, ns: non-significant.*

Table 3. Tree Community Attributes Associated with Aboveground Biomass C Stock or Stock Change Rate

Type of community attribute	Response variable	Indicator variable	Coefficient	*df*	*t*	*P*	AICc
Tree diversity	ABC_T	F_{rich}	0.3	21	6.21	<0.01	102.8
		$\Delta_{13}C_{leaf}$ CWV	0.9	21	2.15	<0.05	107.3
	$dABC_T$	*None*					
Tree dominance	ABC_T	H_{max} CWM	0.8	21	4.22	<0.01	98.9
		J	−6.7	21	−2.12	<0.05	103.3
	$dABC_T$	H_{max} CWM	0.1	21	2.50	<0.05	31.8

ABC_T, aboveground biomass C stock; $dABC_T$, aboveground biomass C stock change; F_{rich}, functional richness index; $\Delta_{13}C_{leaf}$, isotopic carbon in leaves; H_{max}, maximum tree height; J, Pielou evenness index; CWM, community weighted mean; CWV, community weighted variance.

All these species were above the third quartile of H_{max} (10.1 m), except *A. paniculata*. H_{max} CWM was included as the indicator of plant community dominance in the SEM model.

Our exploratory model relating forest age, plant diversity (F_{rich}), plant dominance (H_{max} CWM), AGB_W and $dAGB_W$ for the 2004–2007 period was not rejected ($C = 3.35$, $df = 4$, $P = 0.50$; Figure 4A). H_{max} CWM significantly explained variation in AGB_W, while forest age and F_{rich} were only marginally related to AGB_W ($P = 0.054$ and $P = 0.096$, respectively). The three relationships were positive. Both F_{rich} and H_{max} CWM were partially explained by forest age. The total standardized effect size of forest age on ABC_T given by the statistically significant paths was 0.79, with 51% of such effect mediated by H_{max} CWM and F_{rich}. C stock changes during the period 2004–2007 were significantly explained by H_{max} CWM, whereas C stock or F_{rich} had no significant effect on $dAGB_W$ (Figure 4A). The confirmatory model was also supported by the d-separation test ($C = 1.82$, $df = 4$, $P = 0.77$; Figure 4B). However, in this model, the effects of F_{rich} on AGB_W, or that of H_{max} CWM on $dAGB_W$ were not significant (Figure 4B).

DISCUSSION

Forest Age Drives the Recovery of Biomass-Based C Pools

Carbon accumulation during the first 20 years of TDF recovery was restricted to plant biomass pools. As hypothesized, C stocks increased in aboveground woody biomass, litter, and live roots as forests aged. Our aboveground biomass C stock estimations fall within the range of values derivable from recent syntheses of biomass recovery in neotropical dry secondary forests (Becknell and others 2012; Poorter and others 2016). However, our estimate of recovery relative to old-growth forest, reaching half the C stock in 12 years, seems to be among the highest rates of relative recovery across the tropics (Martin and others 2013; Poorter and others 2016). The dominance of resprouting species like *L. mutans* and *P. constricta* (Miller and Kauffman 1998a), as well as fast-growing early successional species like *A. macracantha* and *Mimosa arenosa* (Romero-Duque and others 2007) may explain this rate. In addition, the high proportion of remnant forests in the landscape (Sánchez-Azofeifa and others 2009) could enhance forest regenera-

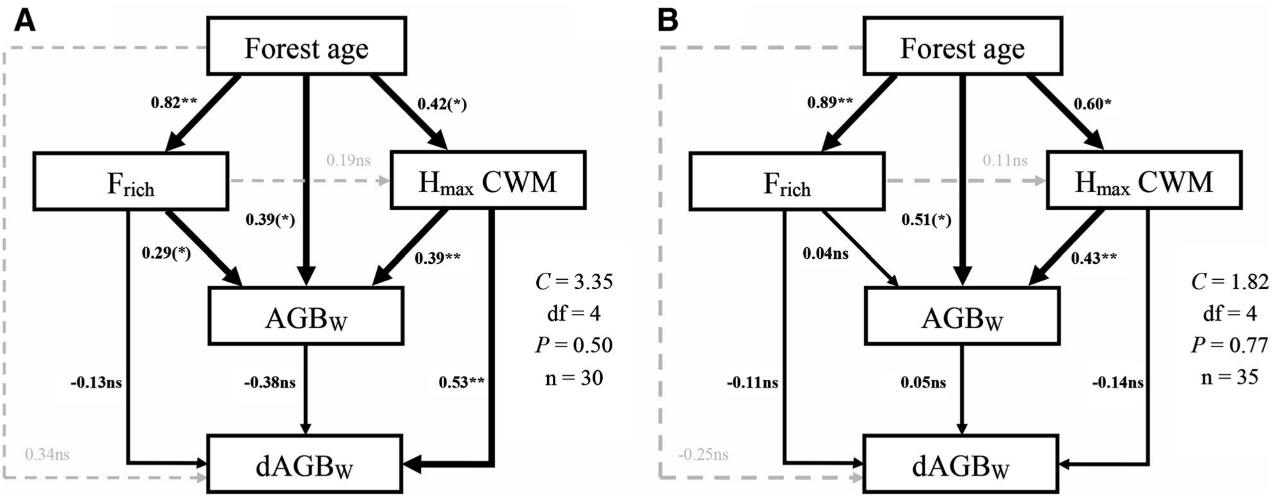

Figure 4. Exploratory (**A**) and confirmatory (**B**) structural equation models testing the causal relationships among forest age, plant diversity, plant dominance and aboveground carbon stocks (AGB_W) and their change through time ($dAGB_W$) in secondary tropical dry forest in the Chamela-Cuixmala region, Western Mexico. The exploratory analysis (**A**) was performed for the 2004–2007 period data, while the confirmatory analysis (**B**) was done on 2007–2010 data. Functional richness (F_{rich}) was included as an indicator of plant diversity and the community weighted mean of maximum tree height (H_{max} CWM) as an indicator of plant community dominance. *Black arrows* are hypothesized causal relationships. *Gray dashed lines* represent associations not assumed to be causal. The test for each model is given on the right. Values on *arrows* are standardized effect sizes. $^{**}P < 0.01$, $^{*}P < 0.05$, $(^{*})P < 0.1$. *ns* non-significant.

tion and C accumulation through increased tree recruitment (Sloan and others 2016; Rozendaal and others 2017).

It is harder to place our litter C stock results into a wider context, as there is very limited information from other secondary TDF with which to compare. To our knowledge, the only other existing chronosequence study (Vargas and others 2008) finds a mean value of 5.3 Mg C ha^{-1} for secondary forests of comparable age, which is higher than our mean value of 3.7 Mg C ha^{-1}. Surprisingly, our estimation is slightly higher than the mean, but within the reported standard deviation for tropical evergreen forests [2.8 ± 2.5 (SD) Mg C ha^{-1}], Anderson-Teixeira and others 2016). The recovery trend found here for litter C matches the increase in litterfall observed for up to 20 years of forest recovery in other secondary TDF (Lawrence 2005; Aryal and others 2015; Moura and others 2016). Canopy closure in Mexican secondary dry forests typically occurs around 10 y following disturbance (Balvanera, pers. com.; Lebrija-Trejos and others 2008), coinciding with the age at which the litter leaf component reaches its asymptote (Figure 2B). Further increases in total litter are therefore driven mainly by increases in the stem component, which are, in turn, associated with an increase in mortality rates over the course of forest recovery (Lebrija-Trejos and others 2010; Rozendaal and others 2017). Our old-growth forest values are comparable to those previously reported in the same region (Jaramillo and others 2003).

The lack of change in coarse roots across our chronosequence may have resulted from our capturing both dead and live root biomass, and suggests that dead root material can strongly influence total belowground biomass. This finding confirms a need to account for dead roots especially in the larger sized root classes (> 20 mm) in mass balance studies (Jaramillo and others 2003; Anderson-Teixeira and others 2016). The persistence of dead coarse roots in these young secondary forests is most probably due to the slower decomposition rates of the coarse root fraction and therefore a longer residence time (Silver and Miya 2001). Alternatively, resprouting, a common regeneration mechanism in young tropical dry forests (Miller and Kauffman 1998b; Lévesque and others 2011), may imply additional coarse root biomass because of live root remnants, not accounted for by the allometric approach (McNicol and others 2015). They also suggest that estimates of live belowground biomass based on the allometric approach (Intergovernmental Panel on Climate Change 2006; Mokany and others 2006) may provide underestimates of root C stocks in secondary forests, affecting inferences about C stock recovery and fluxes from this pool (Kenzo and others 2010; McNicol and others 2015).

The lack of association between SOC and forest age and the lower SOC stock in secondary forests when compared to old-growth forests are concordant with previous studies throughout the tropics (Saynes and others 2005; Don and others 2011; Marin-Spiotta and Sharma 2013). Although previous work in the Chamela region suggests forest conversion to pastures does not necessarily reduces SOC stocks (Jaramillo and others 2003), more recent work also shows a reduction in C concentration with forest conversion, and in SOC stocks as frequency of burns increase (Trilleras and others 2015; Ayala-Orozco and others 2017). Assuming forest conversion to pastures reduce SOC stocks, our results suggest that SOC accumulation is a relatively slow process and therefore the time span of the chronosequence studied may not be sufficient to detect such changes (Marin-Spiotta and Sharma 2013). Alternatively, factors not directly related to forest age or biomass recovery, such as bulk density, may influence SOC in secondary forests (Murty and others 2002; Don and others 2011). C concentration in the top soil layer of the same sites recovers as forest age (Ayala-Orozco and others 2017), but when corrected for bulk density we found no relationship between forest age and SOC stocks. It is possible that the large variation in bulk density across secondary forests obscured the relationship between forest age and SOC stocks.

Chronosequence Models have a Very Low Predictive Ability of C Accumulation During Forest Recovery

Contrary to our initial hypothesis, and despite their high explanatory power, chronosequence models proved to be poor predictors of short-term (3-year period) stock changes in young secondary forests. Similar results have been reported for forest structure, diversity, and biomass (Feldpausch and others 2007; Mora and others 2015; Norden and others 2015). The strong association between C stocks and forest age most probably reflects the long-term effect of multiple drivers of change, while short-term changes may result from stochastic factors like extreme climatic events, driving stocks away from the expected trajectories (Maza-Villalobos and others 2013; Mora and others 2015).

Our results suggest that the chronosequence approach may provide poor estimates of C accumulation rates in the aboveground biomass during forest recovery, at least for tropical dry secondary forests. Based on IPCC guidelines (Intergovernmental Panel on Climate Change 2006), a mean $dAGB_W$ of 5.8 Mg C ha^{-1} 3 y^{-1} would be expected for secondary TDFs occurring in neotropical regions with less than 1000 mm of annual rainfall and under 20-year of recovery. Estimates for similar-aged forests from a global review yield a mean value of 10.8 Mg C ha^{-1} 3 y^{-1} (Bonner and others 2013), although this meta-analysis did not include TDF sensu stricto. In contrast, our observed $dAGB_W$ averaged over the two periods and across the nine secondary forest sites was 2.6 Mg C ha^{-1} 3 y^{-1}. From a larger study of aboveground biomass accumulation calculated from repeated measurements in 5–15 years old trees from neotropical secondary dry forests (DBH ≥ 5 cm), $dAGB_W$ varied between 1.5 and 4.5 Mg C ha^{-1} 3 y^{-1} (Rozendaal and others 2017). These comparisons suggest an extended range of potential C accumulation rates for TDF, particularly toward lower values, for reasons that might relate to differences in methodology, site, species or prior land use across sites (Wandelli and Fearnside 2015; Rozendaal and others 2017).

Carbon Accumulation in Aboveground Biomass is Partially Driven by the Height of the Dominant Species

Our results showing no relationship between AGB_W and $dAGB_W$ did not support the vegetation quantity hypothesis (H_0), in clear contrast with findings from previous studies from tropical wet and dry forests (Finegan and others 2015; Lohbeck and others 2015; Prado-Junior and others 2016). The large variability observed in $dAGB_W$ values across sites and periods suggests the existence of additional, more important drivers of C accumulation. One such driver was the dominance of species with higher H_{max}, allowing the tree community to store more C, and to accumulate it at faster rates. It seems that tall statured species have a functional advantage, perhaps due to lower mortality, which resulted in less severe reductions in C accumulation during the 2004–2007 dry period (Figure S5), whereas during the subsequent wetter period species performed relatively uniformly, as suggested by the exploitative strategy common in tropical dry forest trees (Pineda-García and others 2011), resulting in higher C accumulation rates. Our results therefore provide evidence in favor of the biomass ratio hypothesis (H_2) as an explanation for biomass accumulation, as has been previously reported in both secondary and old-growth tropical forests (Conti and Díaz 2013; Slik and others 2013; Finegan and others 2015). In contrast, carbon accumulation was unrelated to functional richness (F_{rich}), refuting the vegetation diversity hypothesis (H_1). Other studies, with similar integrative approaches, have also found that species diversity per se may not be an important driver of biomass accumulation (Becknell and Powers 2014; Finegan and others 2015; Lohbeck and others 2015).

Contrary to our initial hypothesis, we found plant traits commonly related to desiccation tolerance, like SLA, WD and $\Delta_{13}C_{\mathrm{leaf}}$ to be unrelated to rates of C accumulation, despite the marked differences in rainfall between periods (Figure S5). Similar results were recently reported from other secondary TDF, where biomass accumulation rates were studied (Prado-Junior and others 2016). However, these results contrast those from tropical wet forests (Finegan and others 2015) and those from a chronosequence-based approach in TDF (Becknell and Powers 2014). This suggests that differences across sites and methodologies influence our inferences on the drivers of C accumulation, highlighting the need for other integrative studies to fully disentangle the role of functional traits as drivers of C accumulation during tropical dry forest recovery.

C Accumulation During Forest Recovery in a Context of Increased Land Use Intensity

Our study shows that recovery of C stocks in the biomass-based pools can occur relatively quickly in these neotropical secondary dry forests, along with the recovery of tree diversity and composition (Mora and others 2015). However, an intense management regime, with long periods of land use before abandonment and the concomitant increase in the number of fires, may further reduce soil organic C stocks and the abundance of both resprouts and seedlings (Miller and Kauffman 1998a; Trilleras and others 2015). Under such scenario, C accumulation rates during forest recovery would be reduced, as previously suggested for other tropical locations (Zarin and others 2005; Wandelli and Fearnside 2015). Given the prevalence of such land use intensification process across tropical forest landscapes (van Vliet and others 2012; Rufin and others 2015), further assessments are needed to quantify the magnitude of this effect on the contribution of secondary forests to climate change mitigation.

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