

Stand age and soils as drivers of plant functional traits and aboveground biomass in secondary tropical dry forest

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Abstract: The distribution of tropical forest biomass across the landscape is poorly understood, particularly in increasingly common secondary tropical forests. We studied the landscape-scale distribution of edaphic properties, plant community characteristics, and aboveground biomass (AGB) in secondary tropical dry forests in northwest Costa Rica. We used structural equation modeling to examine conceptual models of relationships among these factors, with data from 84 0.1 ha plots. Stand age and soils explained 33%–60% of the variation in community-weighted mean values of foliar traits including specific leaf area, foliar nitrogen, phosphorus, and $\delta^{13}\text{C}$. Aboveground biomass ranged from 1.7 to 409 Mg·ha⁻¹ among plots between 5 and >100 years old. Stand age alone explained 46% of the variation in AGB among plots, while a model including age, soil pH, traits, and forest type explained 58%. Stand age was the most important variable explaining the distribution of AGB and community characteristics in secondary forests. We speculate that plot size, landscape heterogeneity, disturbance history, and stand dynamics contribute to the unexplained variation in AGB across the landscape.

Key words: aboveground biomass, succession, plant functional traits, structural equation modeling, tropical dry forest, secondary forest.

Résumé : La répartition de la biomasse de la forêt tropicale dans le paysage est mal connue, particulièrement dans les forêts tropicales secondaires de plus en plus courantes. Nous avons étudié la répartition à l'échelle du paysage des propriétés édaphiques, des caractéristiques des communautés végétales et de la biomasse aérienne (BA) dans les forêts tropicales secondaires sèches du nord-ouest du Costa Rica. Nous avons utilisé la modélisation par équation structurelle pour examiner des modèles conceptuels des relations entre ces facteurs avec des données provenant de 84 placettes de 0,1 ha. L'âge du peuplement et les sols expliquaient 33%–60% de la variation de la valeur moyenne des traits foliaires pondérée par les communautés incluant la surface foliaire spécifique, la teneur en azote et en phosphore des feuilles et $\delta^{13}\text{C}$. La BA variait de 1,7 à 409 Mg·ha⁻¹ parmi les placettes où l'âge du peuplement se situait entre 5 et >100 ans. L'âge du peuplement seul expliquait 46% de la variation de la BA dans les placettes, tandis qu'un modèle qui incluait l'âge, les caractéristiques et le pH du sol ainsi que le type forestier expliquait 58%. L'âge du peuplement était la plus importante variable pour expliquer la répartition de la BA et les caractéristiques des communautés dans les forêts secondaires. Nous croyons que la dimension de la placette, l'hétérogénéité du paysage, les perturbations passées et la dynamique du peuplement contribuent à la partie inexpliquée de la variation de la BA dans le paysage. [Traduit par la Rédaction]

Mots-clés : biomasse aérienne, succession, traits fonctionnels des plantes, modélisation par équation structurelle, forêt tropicale sèche, forêt secondaire.

Introduction

Tropical forests store more carbon than boreal or temperate forests and are central to our understanding of both the global carbon cycle and the climate system (Bonan 2008). Despite their importance, questions remain about the amount of biomass in tropical forests, the distribution of biomass across the landscape (Mascaro et al. 2011), and the rate of biomass accumulation during secondary succession (Chazdon et al. 2007). As secondary forests (defined here as forests regenerating following anthropogenic disturbance) now comprise 57% of the world's forests (FAO 2010), it is critical to understand the patterns of carbon storage in regenerating tropical forests and how environmental factors, disturbance history, and forest community characteristics affect these processes (Fig. 1).

Carbon in biomass is generally expected to increase logistically as forests recover from disturbance (Chapin et al. 2011), but the

maximum level of biomass reached and the time it takes to reach it can vary across the landscape (Turner 2010). A number of factors may account for this variability, including environmental variables like soil properties (Clark and Clark 2000) or plant community characteristics like tree species diversity (Balvanera and Aguirre 2006) and the functional traits of the tree species present (Baker et al. 2009; Fig. 1). Forest biomass has been shown to vary with tree species diversity (Ruiz-Jaen and Potvin 2010), and tree growth rates have been linked to plant functional traits (Poorter et al. 2008). The effects of environmental variation and disturbance history on forest biomass may be direct or indirect (i.e., mediated by community composition and trait distributions). For example, soil properties may directly affect tree growth and productivity (Baker et al. 2009). Alternatively, soils may affect which species can establish in a location and consequently which functional traits are present (Gourlet-Fleury et al. 2011). Specifically,

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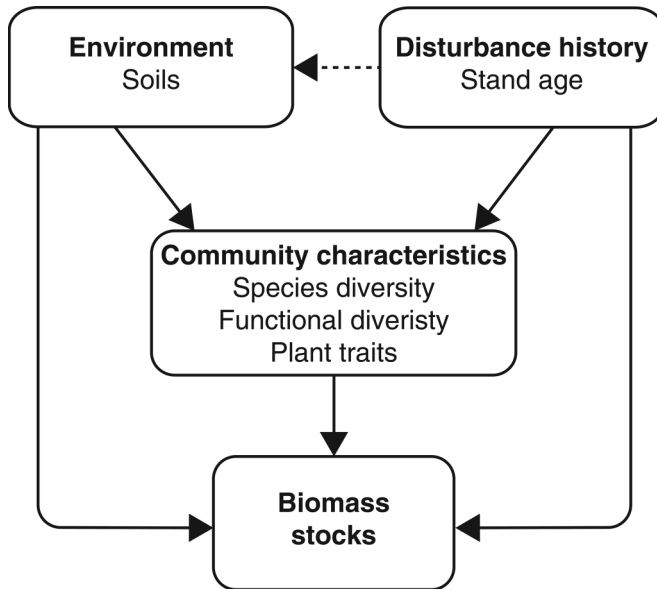
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Fig. 1. Conceptual model of the direct links between soil properties and stand age as drivers of biomass, and the indirect links mediated by plant functional traits, taxonomic, and trait diversity. The line between disturbance history and environment is dashed to indicate that variables like stand age can affect some soil properties but are unlikely to affect others.



soil micro- and macro-nutrients have been found to have strong associations with neotropical tree species distributions (John et al. 2007). Because trait differences may confer different levels of carbon storage (e.g., via differences in wood density), this effect on species composition could lead to an indirect effect of soils on carbon stocks. Similarly, plant communities and their traits are thought to change over the course of succession, as shade-intolerant species with fast growth rates and high resources acquisition rates are replaced by shade-tolerant species with conservative trait syndromes (Bazzaz 1979). Thus, stand age may affect biomass directly as older stands typically contain more larger, older trees, or indirectly as a function of directional change in forest communities and trait distributions (Campetella et al. 2011).

Last, the contribution of species and functional diversity to ecosystem processes like productivity and biomass storage merits discussion as it has been much debated (Tilman 1997; Grime 1998). Understanding which component of diversity, the number of species, or the relative abundance of the traits of those species, is of interest in applying our understanding of processes to ecosystem models or management practices (Mokany et al. 2008). Diversity is thought to affect ecosystem processes if diverse plant communities have more functional roles occupied and make more efficient use of available resources, i.e., niche complementarity (Tilman 1997). Another approach posits that the effects of a species, or rather the traits of a species, correspond to its proportional abundance, the so-called “mass-ratio” theory. In this perspective, the effects on ecosystem processes of many rare but functionally diverse species are relatively small compared to the effects of the dominant species and their traits (Grime 1998). While not mutually exclusive, these two ways of representing diversity suggest alternative pathways through which community variables affect ecosystem processes. Assessing the relative abilities of diversity measures versus traits to explain ecosystem processes is important to our theoretical understanding and to efforts to model or manage forest ecosystems.

Here we examine the relationships among soil variables, plant functional traits, diversity, stand age and biomass, to understand how aspects of the environment and succession affect plant com-

munity characteristics and how all of these factors affect forest biomass, explicitly testing the conceptual model in Fig. 1. A number of caveats accompany our conceptual model. First, we acknowledge that other variables such as seed sources, symbionts, and microclimate also affect regeneration following abandonment from grazing (Holl 1999), but we focused on forest age and soil characteristics as drivers of plant traits and carbon stocks, as previous work has shown these to be strong determinants of forest community composition (Powers et al. 2009). Second, there are possible feedbacks between changes in biomass and species composition that occur during succession and soil properties, which would imply an arrow from “biomass stocks” to “environment” in our conceptual model (Fig. 1). However, in this study we were more interested in the effects of soil heterogeneity on community characteristics and biomass rather than the converse, so we measured soil variables that we expected to be controlled by parent material or other soil forming factors rather than plant communities. In addition to these caveats, we acknowledge the limitations of our empirical approach such as our inability to rigorously document the duration and intensity of prior land-use history and management activities, the potential effects of landscape context and matrix effects on recruitment, and other variables such as site-specific community dynamics that are not well captured in chronosequences.

Our goals were to document how aboveground biomass (AGB), functional traits, and diversity change across succession and soils, and quantify the direct and indirect relationships among stand age, soils, and functional traits as they affect AGB in regenerating tropical dry forests. The traits we focused on included foliar nutrients, specific leaf area, wood density, and the stable isotope of foliar carbon as a measure of water use efficiency. These traits reflect physiological characteristics that are likely to influence photosynthesis (Reich 2012), demographic patterns (Poorter et al. 2008), and growth rates (Poorter et al. 2008), implying a possible link to biomass accumulation. Other studies suggest that some of these traits vary across succession (Lebrija-Trejos et al. 2010, Lohbeck et al. 2012) or environmental gradients such as soil nutrients (Ostertag 2010). Our large dataset enabled us to test the following hypotheses: (i) that the large gradients in edaphic variation among sites contributed to the distribution of plant traits, especially for traits related to biogeochemical cycling (e.g., we predicted that community-weighted mean foliar nutrients would be positively correlated to soil nutrients), (ii) within forest patches that had similar edaphic templates but differed in age, traits that are related to tree growth and plant water relations would change over the course of succession, as species with higher growth rates, higher water use efficiencies, and lower wood densities were replaced by slower growing less drought tolerant species, and (iii) AGB would increase as forests age, but after accounting for stand age the residual variation across the landscape would be explained by combinations of edaphic properties, plant functional traits, and diversity (Fig. 1).

Our approach differs from many studies of succession and secondary forest regeneration that use chronosequences or “space-for-time” substitutions (but see Dupuy et al. 2012). Most studies select a series of plots that are presumably similar in every way except forest age or time since disturbance, and attribute any differences among plots to successional processes. However, in our study landscape, previous studies show that the large gradients in edaphic factors that result from variation in parent materials and other soil forming factors have important effects on tree species distributions and forest composition (Powers et al. 2009). To account for both variation across successional ages and soil variation, we selected a large number of plots distributed among different forest ages and edaphic conditions, and used structural equation modeling to partition variation in aboveground biomass into the direct and indirect effects of forest age, soils, and plant community characteristics (functional traits and diversity).

Methods

Site description

We conducted this study in the tropical dry forest biome located in two national parks in the province of Guanacaste, Costa Rica: Parque Nacional Santa Rosa in the Área de Conservación Guanacaste and Parque Nacional Palo Verde in Área de Conservación Tempisque (about 60 km southeast of Santa Rosa). Santa Rosa has a 30 year mean annual precipitation of 1765 mm (www.investigadoresACG.org), and Palo Verde has a 30 year mean annual precipitation of 1444 mm (www.ots.ac.cr). Both locations experience a five to six month dry season with little measurable precipitation, and annual precipitation totals can vary dramatically among years. The soils of Santa Rosa have developed on an eroding plateau made up of volcanic lava flows and ash deposits that transition into alluvial marine terraces at the lowest elevations (Hartshorn 1983). They are dominated by entisols and vertisols, and are highly variable spatially (Leiva et al. 2009). The soils of Palo Verde developed from alluvial areas along the floodplain and wetlands of the Tempisque River and the eroding limestone hills (Hartshorn 1983). Both parks contain patches of older forest, but are dominated by secondary forests that were previously used for agriculture or pasture land. After the parks were established in the 1970s, forest began to grow back (though anthropogenic fires may have slowed regeneration in some areas), and the current landscape is a heterogeneous mosaic of forests of different ages on different types of soils. Forests contain both evergreen and deciduous tree species, the number and relative abundance of which varies across successional and soil gradients (Powers et al. 2009). In particular, less fertile soils in Santa Rosa support more evergreen canopies that are dominated by a species of live oak (*Quercus oleoides*), while the more fertile soils of Santa Rosa and Palo Verde support more species-rich forests with more deciduous canopies (Powers et al. 2009). Because our previous work has shown that both soil characteristics and species composition vary among these forest cover types (e.g., Palo Verde dry forest, Santa Rosa dry forest, and oak dominated forest at Santa Rosa), we used forest cover type as a dummy variable in the analyses described below.

Forest inventory plots

We measured biomass and sampled soils in 84 20 m × 50 m (0.1 ha) plots, stratified by both forest type and stand age. We acknowledge that our plot size is small, however, secondary forest patches often occur in smaller tracts than in primary forests (Arroyo-Mora et al. 2005). The first 60 of these plots were established on level ground in 2007. Their diversity and structure but not biomass stocks or traits were previously described by Powers et al. (2009). In 2010 we sampled an additional 24 plots arrayed along different topographic positions to investigate whether biomass varied systematically from ridge to slope to valleys. Topographic position was later determined to have no significant effects on biomass and was not included in further analyses, thus both datasets were combined. The 84 plots were distributed among the forest types with 43 in Santa Rosa, 22 in the oak forest, and 19 in Palo Verde (Supplementary data Fig. 1)¹. Stand age estimates were made using a combination of remote sensing observations for younger plots (<20 years old) and expert local knowledge (Powers et al. 2009). Stand age represents the approximate number of years between the previous land use ending and the year our measurements were made. Plots determined to be mature forests were assigned a stand age of 100 for our analysis because TDF biomass accumulation tends to level off well before that age (Becknell et al. 2012), and 100 is well above our next oldest secondary plots (70 years). This assignment of 100 years was shown to have relatively little effect on our results in a sensitivity analy-

sis where we assigned these plots and age of 200 or 300 years (or excluded them) and repeated the analysis (Supplementary data Table 1)¹.

Biomass estimates

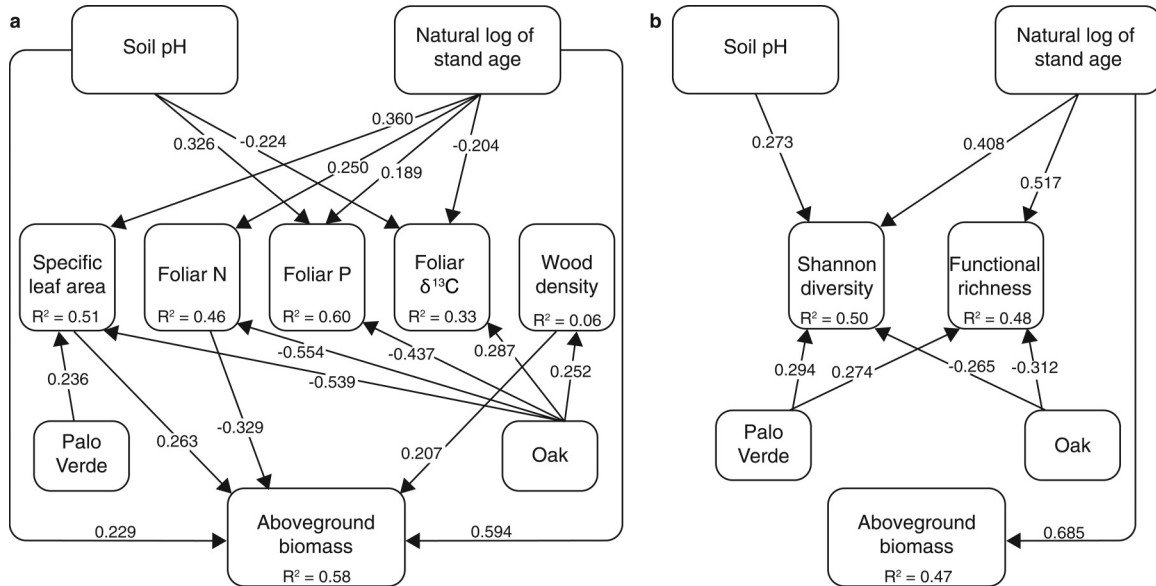
Within each plot we identified the species and measured the diameter at breast height (DBH) of all live trees with trunks ≥10 cm diameter. When necessary, DBH was measured above buttresses or trunk irregularities. In 200 m² subplots we measured the DBH of all trees <10 cm in diameter that were >1.4 m in height, but we did not identify the species of these saplings. For trees ≥10 cm for which we had species-specific wood density, biomass was estimated using an allometric equation designed for secondary forests in Panama, which incorporated both DBH and wood density ($\ln[AGB] = -1.130 + 2.267 \cdot \ln[DBH] + 1.186 \cdot \ln[\text{wood density}]$; van Breugel et al. 2011). Average wood density for each species came from a previous study conducted in the same area (Powers and Tiffin 2010). For trees <10 cm DBH and for species for which we had no wood density data, we calculated biomass using the equation developed in the same system that uses only DBH ($\ln[AGB] = -1.863 + 2.208 \cdot \ln[DBH]$; van Breugel et al. 2011). Although it is desirable to have site-specific allometric equations, deriving site-specific equations for the 146 species identified in our plots was beyond the scope of this study. Our use of the van Breugel secondary tropical forest equations yielded lower total biomass estimates than the mature tropical dry forest equations present in (Chave et al. 2005), due to lower estimates for trees in small diameter classes (results not shown). Biomass of multi-stemmed trees was calculated separately for each stem. Biomass for all trees in each plot was summed to yield plot biomass and expressed as Mg·ha⁻¹. As these secondary forests developed in areas that had previously been grazed or cropped for decades to centuries, coppicing is an unlikely mechanism for regeneration in this landscape. However, leaving remnant trees for shade in pastures is a typical practice, and large (potentially remnant) trees were included in our biomass estimates.

Soil sampling and analysis

Relating forest community characteristics to edaphic variables can be challenging because plant species can also affect soils (Hobbie 1992). We were interested in differences in plant species and their traits along edaphic gradients rather than possible vegetation-caused changes in soil properties during succession, thus we measured total element concentrations because we expected them to vary less across successional gradients than more labile forms of these elements (Powers and Pérez-Aviles 2013). Soil physical and chemical properties for 60 of the 84 plots were measured in 2007 and described in a previous study (Powers et al. 2009). The 24 additional plots sampled in 2010 were analyzed using identical laboratory methods. In each plot, 10 samples were taken from the mineral soil with a punch core sampler to a depth of 10 cm and bulked by plot. Three separate samples were taken at each plot using a volumetric turf sampler to measure bulk density. Soils were analyzed for elemental content after hot nitric acid digestion at the Research Analytical Lab of the University of Minnesota. Here we report data for calcium (Ca), magnesium (Mg), phosphorus (P), and zinc (Zn). Particle size distribution was measured with the hydrometer method. Last, we measured the pH of air dried soils in distilled water at a 1:2.5 soil to solution ratio with an Oakton pH meter. We are confident that measuring soil characteristics in different years did not affect their values, as we remeasured pH on archived soils from 2007 along with the 2010 samples and their values were nearly identical.

¹Supplementary data are available with the article through the journal Web site at <http://nrcresearchpress.com/doi/suppl/10.1139/cjfr-2013-0331>.

Fig. 2. The results of two structural equation models. (a) Represents the trait model, where community characteristics are represented by the CWMs of functional traits. (b) Represents the diversity model, where Shannon diversity and functional richness represent community characteristics. Arrows indicate significant connections in the final, best-fit model. Numbers on lines indicate the standardized coefficients of each model relationship, which represent the relative magnitude of each relationship (non-standardized coefficients are reported in Supplementary data Table 1). Covariance arrows are not shown but listed in the methods. R^2 values in boxes represent the amount of variance in dependent variables explained by the model. Model fit statistics for the trait model were $\chi^2 = 12.159$, p -value = 0.515, RMSEA < 0.001. Fit statistics for the diversity model were $\chi^2 = 7.108$, p -value = 0.418, RMSEA = 0.014.



Community-weighted means of traits and diversity

To evaluate the distribution of functional traits in our forest plots we calculated community-weighted mean values for a set of functional traits from a trait database developed by Powers and Tiffin (2010) that included 87 common species from our study area. For each tree species in the trait database we included wood density, specific leaf area (SLA), foliar N, foliar P, and foliar carbon isotope composition ($\delta^{13}C$, an index of water use efficiency with higher values corresponding to higher water use efficiency). Community-weighted mean (CWM) values for each trait were calculated with the FD package for R (Lavorel et al. 2008). We first calculated the basal area of each tree and then used each species' relative basal area per plot as a measure of proportional abundance in the CWM calculations. Of the 3959 individual trees ≥ 10 cm DBH, 91% were of species represented in the traits database. The percentage of a plot's basal area made up of species not in our trait database ranged from 0% to 50% with an average of 5.9%. In only four plots was this percentage higher than 25%, and in 64 of our 84 plots it was less than 10% (Supplementary data Table 4)¹. Trees belonging to species that did not occur in our trait database were omitted from the CWM calculations, and the remaining trees were rescaled to represent the total basal area for each plot.

In addition, we also considered whether trait diversity contributed to variation in biomass stocks via niche complementarity by calculating functional richness as a measure of trait space that is filled by a particular community (Villéger et al. 2008; calculated in R using the FD package). Functional richness was chosen above other functional diversity indices as it better represents the range of traits that exists in a community rather than the trait's proportional abundance. Functional richness was calculated as the convex hull volume made up of the trait ranges of the species present in each plot (Villéger et al. 2008). We included the SLA, wood density, and foliar N, P, and $\delta^{13}C$ in the functional richness calculation. Last, we calculated the Shannon diversity index as a measure of species diversity as many papers show relationships between this and ecosystem function (Tilman 1997). As species

richness was well correlated to the number of stems per plot ($r = 0.48$, $P < 0.0001$), we preferred the Shannon index as a metric of diversity to raw species counts.

Statistical analysis and structural equation modeling

We performed three sets of statistical analyses. First, we calculated pair-wise Spearman rank correlation coefficients on the soil variables to investigate how these quantitative properties varied among the plots. As all soil variables were well correlated to soil pH, we used pH to represent soil variation in subsequent analyses. Second, we performed standard least-squares regression analyses on AGB, measures of diversity, and CWMs of traits with stand age and soil pH as explanatory variables to investigate the pairwise relationships among these factors. These analyses were conducted using R (R Development Core Team 2012).

Last, we used structural equation modeling (SEM) to assess the direct influence of stand age and soil pH on diversity and plant functional traits and to assess the relative direct and indirect influence of all of these factors on AGB (Fig. 1). SEM allows for analysis of multiple direct and indirect relationships among variables, where some variables are both explanatory and response variables, and has been shown to more effectively deal with such problems compared to using multiple univariate analyses (Grace and Bollen 2005). Using maximum likelihood estimation, parameter values defining the relationships between variables were found that best produce a covariance matrix that is as close as possible to the observed covariance matrix (Grace 2006). We used the natural log of stand age to account for nonlinear relationships.

We started with two initial models, a diversity model and a trait model. The trait model used the CWMs of wood density and four leaf traits: specific leaf area, foliar N, foliar P, and foliar $\delta^{13}C$ (Fig. 2a). The diversity model used functional richness and Shannon diversity as measures of relative influence of the range of functional traits or the number of species in each plot (Fig. 2b). Both models used stand age and soil pH as the primary explanatory variable, with forest type identifying dummy variables for

Table 1. Spearman rank correlation coefficients of soil variables (0–10 cm) collected in 84 0.1 ha plots of regenerating tropical dry forest in Costa Rica.

Variable	Range of values	BD	Clay (%)	Silt (%)	Total P	Total Ca	Total Mg	Total Zn
pH	5.04–6.74	–0.39 (0.0002)	0.26 (0.02)	–0.41 (<.0001)	0.79 (<.0001)	0.84 (<.0001)	0.84 (<.0001)	0.58 (<.0001)
BD (g cm ⁻³)	0.58–1.20	—	0.15 (0.17)	0.10 (0.37)	–0.22 (0.05)	–0.26 (0.01)	–0.28 (0.01)	–0.24 (0.03)
Clay (%)	16.4–45.5	—	—	–0.37 (0.0005)	0.25 (0.02)	0.38 (0.0003)	0.43 (<.0001)	0.26 (0.02)
Silt (%)	17.3–47.8	—	—	—	–0.59 (<.0001)	–0.61 (<.0001)	–0.48 (<.0001)	–0.02 (0.80)
Total P (ppm)	30.3–1272	—	—	—	—	0.90 (<.0001)	0.77 (<.0001)	0.49 (<.0001)
Total Ca (ppm)	1553–29 367	—	—	—	—	—	0.84 (<.0001)	0.46 (<.0001)
Total Mg (ppm)	772–18 196	—	—	—	—	—	—	0.63 (<.0001)
Total Zn (ppm)	18.0–104.2	—	—	—	—	—	—	—

Note: *P*-values are in parentheses.

Palo Verde and Oak areas around Santa Rosa. Dummy variables were given the value 1 if the plot belonged to that group (Palo Verde or Oak) and zero if they did not belong to that group.

For each of these models we began with an initial full model that included all theoretical casual connections between the included variables. Covariance arrows were added to correlated variables without hypothesized causal relationships. The CWMs of functional traits were connected with covariance arrows, as were Shannon diversity with functional richness, and forest type variables with soil pH. We also added covariance connections between stand age and soil, because while we assume stand age has little effect on soil pH over the regeneration time considered in this study, we were unable to locate many older plots in oak forest areas with low soil pH that created a correlation between soil pH and stand age. To find the best-fit model, we iteratively removed non-significant connections between variables, starting with the connection with the highest *p*-value, until no non-significant connections remained. We assessed the overall model fit using the overall *p*-value, χ^2 value, and the root mean square error of approximation (RMSEA). We added each connection back into the model and checked to see if model fit was improved, however neither model fit was improved with the inclusion of non-significant connections. The SEM analyses were conducted using IBM SPSS Amos version 21 (Arbuckle 2010).

Results

Soil variation

As documented previously, edaphic characteristics varied widely across the landscape (Powers et al. 2009). Soil pH ranged by almost two units from 5.04–6.74, and total cations, Zn, and P also varied by 1 to 2 orders of magnitudes (Table 1), suggesting that the large among-plot variation is related to parent material and soil forming factors but not forest dynamics. Most soil variables were strongly correlated in ways that are consistent with our understanding of soil chemistry (e.g., soil pH was positively correlated with total concentrations of Ca and Mg, which were correlated with clay percentage, etc.). These strong correlations suggest that the soil variables are largely redundant; therefore in subsequent analyses we used only soil pH, which has the advantage of being easy to interpret. Last, some of the edaphic variables were significantly correlated with stand age. In particular, pH was positively correlated to stand age ($\rho = 0.43$, $P < 0.0001$) and bulk density was negatively correlated ($\rho = -0.41$, $P < 0.0001$), but other variables like silt percentage were not correlated with stand age ($\rho = -0.07$, $P = 0.53$).

Direct relationships among soils, stand age, biomass, diversity, and traits

Regression analyses were used to investigate the pairwise relationships between the explanatory variables of stand age and soil pH, and the response variables of AGB, diversity, and CWMs of plant functional traits (Figs. 3 and 4). As expected, the regression analyses were broadly consistent with the direction of associations between stand age, pH, and the response variables that are

depicted as direct relationships in structural equation models in Fig. 2. For clarity, each response variable is plotted against stand age or soil pH, along with regression results in Fig. 3 and 4, but we report the results of the two analyses, i.e., regressions and direct effects from SEMs, here together.

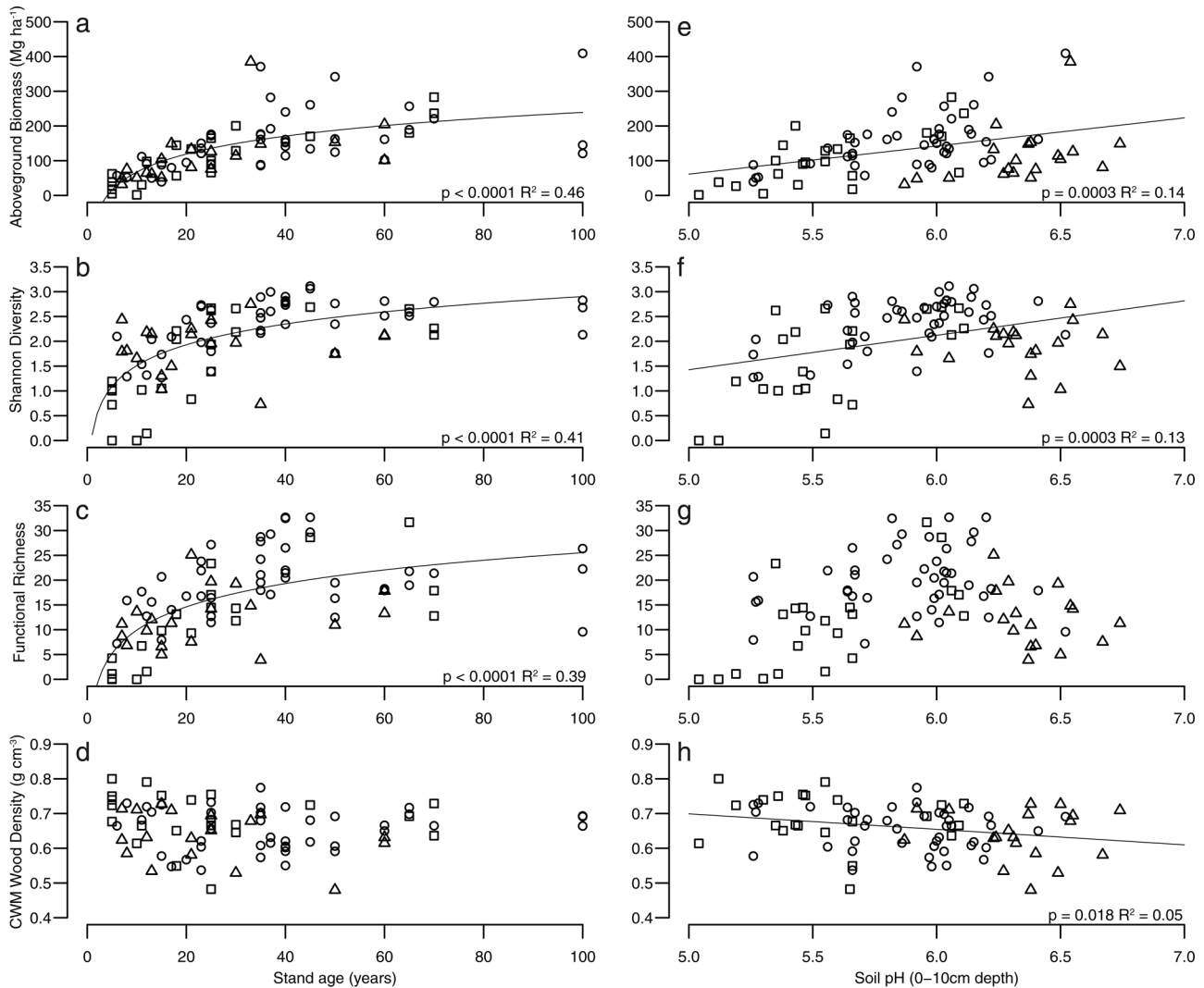
The pattern of AGB accumulation appeared to be a rapid increase in the first 20 years followed by a slower increase in biomass between stand ages of 20 and 100 (Fig. 3). AGB in plots of 50 or greater years of recovery ranged from 101 to 409 Mg·ha⁻¹ with a mean of 200 Mg·ha⁻¹. For any given stand age there was a relatively large range of variation in biomass. Stand age explained 46% of the variation in biomass (Fig. 3a). Soil pH explained 14% of the AGB variation (Fig. 3e) but was not significant when both factors were included in multiple regression (not shown).

For all traits, there was evidence that either or both soil pH and stand age explained variation across the landscape (Figs. 2–4), but the weakest relationships were for CWM-wood density. Our two metrics of diversity, the Shannon index (representing taxonomic diversity) and functional richness (which incorporates trait values), both increased significantly with forest age (Figs. 2b and 3) but were poorly related to soil pH. Similarly, CWM-SLA nearly doubled over the stand age gradient, but was poorly related to soil pH (Figs. 2a, 4a, and 4e). By contrast, traits more related to biogeochemical functioning were better explained by soil pH than stand age (Figs. 2 and 4), with the community weighed mean values of both foliar N and P increasing with soil pH and R^2 values of 0.26 to 0.49, respectively. CWM-foliar $\delta^{13}C$ ranged from –30.77‰ to –28.27‰ among plots, and values decreased consistently with pH and less so with stand age, suggesting increased water use efficiency by vegetation on less fertile soils. Last, the CWM of wood density varied widely among plots from 0.48 to 0.80 g·cm⁻³, but was not significantly related to stand age and only weakly related to pH, contrary to our expectations (Figs. 2, 3d, and 3h). The only variable explaining any variation in wood density in the SEM model was the oak forest type dummy variable. The oak forest type variable had significant effects on all CWM traits, while the Palo Verde dummy variable only affected CWM-SLA (Fig. 2).

Structural equation modeling and direct and indirect effects on biomass

We used SEM to link the variation in aboveground biomass directly to stand age and soil pH and indirectly through the variation in diversity and traits (Fig. 2). To achieve the best-fit models for both the trait model and the diversity model, connections between non-significant parameters were removed. The best-fit diversity model had the connections between AGB and Shannon diversity, functional richness, and soil pH removed, thus, stand age was the only predictor of AGB. The best-fit trait model had the connections between AGB and both CWMs of foliar P and foliar $\delta^{13}C$ removed. The final models for both the trait and diversity models yielded similar measures of fit with the trait model fitting slightly better ($\chi^2 = 12.159$ and 7.108, *p*-value = 0.515 and 0.418, PMSEA < 0.001 and = 0.014 respectively). The trait model explained 58% of the variation in AGB, while the diversity model

Fig. 3. AGB, Shannon diversity, functional richness, and CWM values of wood density plotted as a function of stand age (a–d) and soil pH (e–h) in 84 plots of regenerating tropical dry forest in Costa Rica. Results of linear regression shown with line for significant relationships with the natural log of stand age or soil pH. *P*-values and *R*²-values are shown if *p*-values are less than 0.05. Squares represent oak forest plots, circles represent Santa Rosa plots, and triangles represent Palo Verde plots.



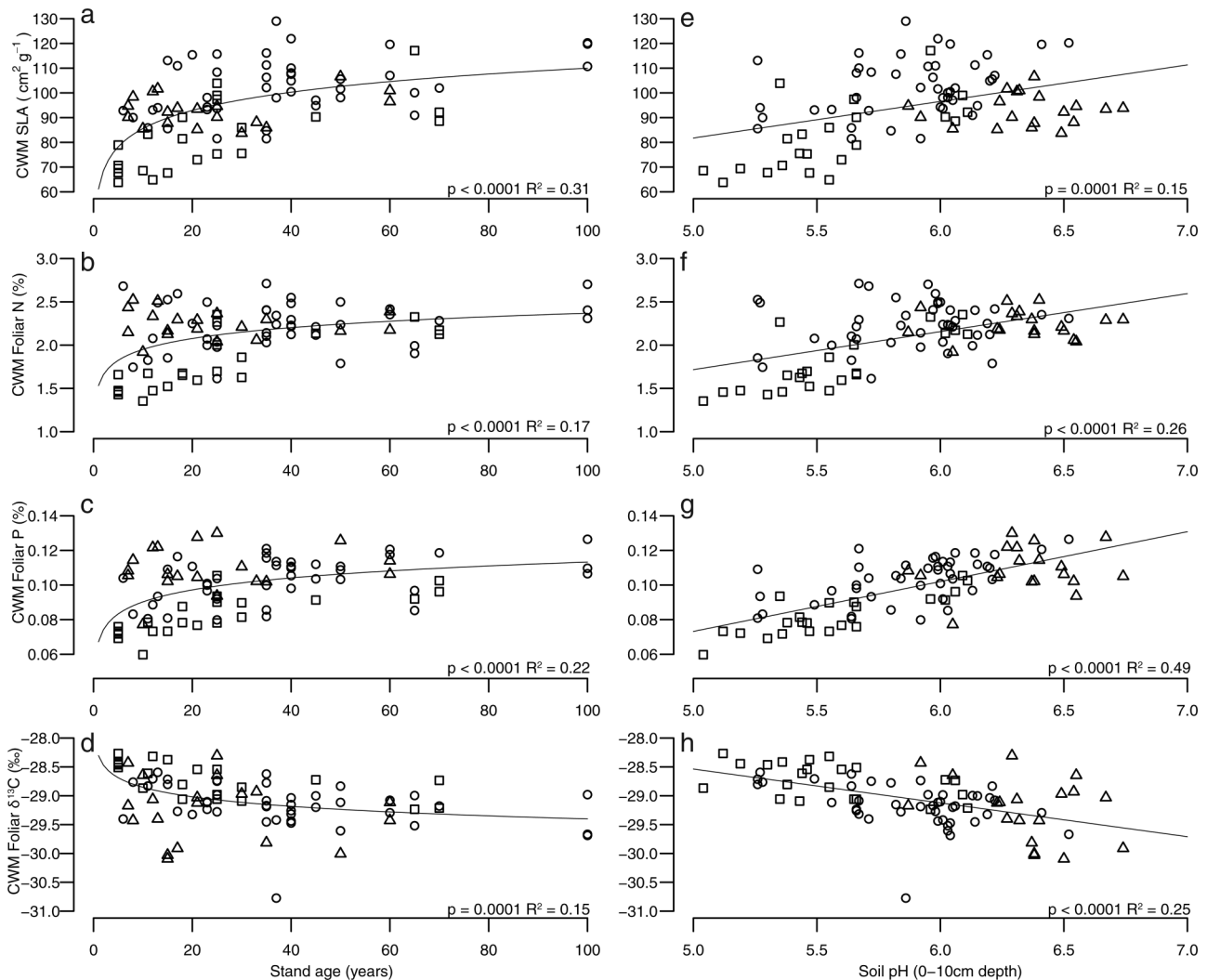
explained 47%. In the diversity model, 50% and 48% of the variation in Shannon diversity and functional richness, respectively, were explained by stand age and soil pH, and forest type. In the trait model, 60% of the variation in foliar P was explained by stand age, soil pH, and oak forest type. Of the other traits 51%, 46%, and 33% of the variation in SLA, foliar N, and foliar $\delta^{13}\text{C}$ were explained by the model, respectively. Only 6% of the variation in wood density was explained, and the oak forest type was the only important factor. Site variables for oak and Palo Verde forests explained some variation in traits and measures of diversity but did not explain variation in AGB. Figure 2 shows the standardized model coefficients along the arrows that connect variables and the *R*² values for response variables under their names. Standardized coefficients can be interpreted as the change in standard deviations in the response variable that would correspond to a change in one standard deviation in the explanatory variable. Significance and non-standardized coefficients are listed in Supplementary data Table 1.¹

Discussion

Tropical landscapes are increasingly dominated by mosaics of forest in various stages of regeneration, and it is important to

understand how ecosystem properties like AGB vary across such mosaics (Becknell et al. 2012). Our goals in this study were to examine patterns of change across succession in AGB, traits, and diversity, and to quantify the direct and indirect influence of stand age and soils on AGB, traits, and diversity. We found that stand age or soil pH was correlated with the distributions of plant functional traits and diversity, but that few of these variables were affected by both drivers (Fig. 2). We also found substantial variation in biomass stocks across the landscape, such that for a given stand age different areas in the landscape support a wide range of biomass levels (Fig. 3a). Despite strong evidence that the distributions of plant functional traits and diversity are driven by edaphic variation and (or) successional state, these community factors explained relatively little variation in AGB after accounting for stand age; stand age alone explained 46% of the variation in AGB (Fig. 3a), the SEM model that included traits explained 58% of variation in AGB, and the SEM model that included diversity explained 47% of variation in AGB. In the trait model, CWMs of SLA, foliar N, and wood density explained additional variation in AGB, while neither diversity metric affected biomass in the diversity model. These results show some support for the hypothesis that a trait model performs better at explaining biomass than

Fig. 4. CWM values of specific leaf area, foliar nitrogen, foliar phosphorus, and foliar $\delta^{13}\text{C}$ plotted as a function of stand age (a–d) and soil pH (e–h) in 84 plots of regenerating tropical dry forest in Costa Rica. Results of linear regression shown with line for significant relationships with the natural log of stand age or soil pH. *P*-values and *R*²-values are shown if *p*-values are less than 0.05. Squares represent oak forest plots, circles represent Santa Rosa plots, and triangles represent Palo Verde plots.



the diversity model, which explained only 1% more variation in AGB than did stand age (Fig. 2b).

Aboveground biomass

AGB ranged widely across our study sites in regenerating tropical dry forest, from 1.6 to 409 $\text{Mg}\cdot\text{ha}^{-1}$, and plots of similar ages often had different AGB levels (Fig. 4). This range is comparable to global values of TDF (Becknell et al. 2012), but the four highest biomass plots were above 300 $\text{Mg}\cdot\text{ha}^{-1}$, which is more typical of wetter forest (Keith et al. 2009). The pattern of biomass appears to saturate around 200–250 $\text{Mg}\cdot\text{ha}^{-1}$, which is typical for forest on the wetter end of the TDF precipitation spectrum (Becknell et al. 2012).

In our trait model, soil pH and stand age both affected AGB directly and indirectly, but the direct effects of stand age were much stronger than that of soil pH or the indirect effects of either factor. Soil pH, which is well correlated with both soil nutrients and texture (Table 1), had relatively little explanatory power over AGB (none in the diversity model; Fig. 2). Similarly, studies of forest structure and biomass across successional gradients in seasonal forests of the Yucatan found that stand age explained much of the variation in biomass and basal area, and that landscape structure and soil properties explained much less variation rela-

tive to stand age (Dupuy et al. 2012). While Clark and Clark (2000) found that in mature rain forests, soil and topography affected forest structural characteristics like stem density but not biomass, other studies in tropical forests have found positive relationships between soil fertility and biomass (Gourlet-Fleury et al. 2011). These contrasting results may represent site-specific differences in which combinations of abiotic and biotic factors control biomass. Clearly, in our study that explicitly focused on recovering forest, successional processes subsume any edaphic-driven effects on biomass. By contrast, in old growth forests where secondary succession is not present, it is possible that traits, topography, edaphic variables, or other factors may become important in determining landscape-scale patterns of AGB.

It is commonly assumed that ecosystem processes are in part controlled by either the number of species present at a site (the diversity-ecosystem function hypothesis) or the traits of the most abundant species (the mass-ratio hypothesis) (Mokany et al. 2008). Collectively, our SEM analyses provided marginal support for our hypothesis that plant functional traits or diversity would explain residual variation in AGB after accounting for effects of stand age and soils; however, the trait model explained more additional variation in AGB than did the diversity. This suggests that these

traits may have some, though perhaps a small amount of, explanatory power over AGB, or that their explanatory power is masked by random variation across our study area and our small plot size. It is also possible that traits other than those used in our study have greater explanatory power. The fact that the final diversity model has no connections between either measure of diversity and AGB suggests that if diversity has any direct effect on biomass, it is masked by the effects of stand age.

Our results show that stand age primarily drives AGB variation, and that there is a small additional contribution from traits and edaphic properties, which collectively explain 58% of the variation in AGB in the study landscape. What explains the remaining variation in biomass among across the landscape? One possibility is that both this unexplained variation and some of the exceptionally high biomass values we recorded can be attributed to the small plot size (0.1 ha) we used. In our fragmented landscape, regenerating forest patches are often small (Arroyo-Mora et al. 2005), and we faced the tradeoffs between plot size and number. There are other biological explanations as well. It is possible that other edaphic or physiological variables that we did not measure, previous land use, unknown recent disturbances, and (or) other forces that affect stand dynamics (such as past dispersal limitation, herbivory, disease, or changing climate patterns) also account for the unexplained variation. Much of our study area was once grazed and may contain remnant shade trees or living fences that impact biomass through their effects on tree recruitment, species composition (wind versus animal dispersed species), and resource availability (Castillo-Núñez et al 2011). Because we could not unambiguously identify remnant trees, they were included in our biomass estimates; it is possible that their presence diminished our ability to attribute variation in biomass across the landscape to particular causes. Forest dynamics are another potentially important source of variation in secondary forests, where there is rapid species turnover during succession. We omitted standing dead and fallen coarse woody debris that increase with stand age in these forests (Kissing and Powers 2010). While all of these factors are likely important to some degree, the use of larger plots would likely decrease this variation more than any other factor (Chave et al. 2004).

Community-wide functional traits and diversity

CWM values of plant functional traits and the indices of taxonomic diversity (Shannon diversity) and functional richness varied with both stand age and soil properties (Fig. 2). However, each of these variables was clearly associated with one dominant control, either soil pH or stand age, with the exception of wood density, which was associated with neither. As our measures of functional traits do not include intra-specific variation, the only mechanism that affects CWM values of traits or functional richness in our dataset is via differences in tree species identities or abundances among plots.

As expected, both the Shannon diversity index and functional richness increased as forests aged. What is more surprising is the increase in the CWM value of SLA with stand age (Fig. 4a). There have been three other studies of variation in SLA across secondary dry forest chronosequences in Mexico, and two found a negative relationship with stand age (Lebrija-Trejos et al. 2010; Lohbeck et al. 2012), while one study found a positive relationship (Alvarez-Anorve et al. 2012). Forest type was also important for SLA, which was the only trait that varied among all of the forest types. These effects are likely attributable to the low SLA values of *Quercus oleoides*, the dominant trees in the oak forest. Oak forests stand out as distinct with respect to other trait means, including wood density. By contrast, there was no indication that trait means differed systematically between the two National Parks (Palo Verde and Santa Rosa). However, our ability to attribute directional change in CWM-SLA to successional gradients versus soil variation is confounded by the fact that the oak stands tend to have poor soils and

thus lower soil fertility (and pH), and older oak forests are rare due to land-use history.

Our SEM trait model explained a large amount of variation (60%) in CWM foliar P, and this was largely due to soil pH (Fig. 4g) and differences between oak forests and other forest types. The correlation between foliar P and soil pH (which was highly correlated with soil nutrients) has at least two possible explanations; that tree species with higher requirements for P are limited to areas with higher nutrient availability, or that soil nutrient concentrations are influenced by the composition of tree species at a site. While we cannot rule out either explanation (and both may be true to some extent), our results support the former because we measured total quantities of soil nutrients assuming that these are a better reflection of parent material and weathering-induced differences among sites (at least for rock derived nutrients). This evidence combined with other studies (Powers et al. 2009; Gourlet-Fleury et al. 2011; Fayolle et al. 2012; Baldeck et al. 2012) suggests that soil gradients may explain trait distributions and potentially aid regional scale predictions of ecosystem function.

Last, wood density deserves special mention, as the CWM of this trait varied by a factor of two across the landscape, but was not associated with either stand age or soils (Figs. 2a, 3d, and 3h). The common paradigm of pioneer species being replaced by shade-tolerant species over succession yields the prediction that fast growing species with low wood density and high nutrient contents should be more abundant in young forests and decrease in abundance as forests age (Bazzaz and Pickett 1980). By contrast, the highest CWM wood density values in our data set were among our youngest plots. This may reflect the fact that in TDF, water resources change as forests age and become cooler, moister environments (Lebrija-Trejos et al. 2011), and high wood density may indicate greater cavitation resistance and drought tolerance. Alternatively, in forests recovering from conversion to pasture, community level wood density may be influenced by the higher wood densities found in some grazing and fire resistant species or early successional legume species that have high wood densities (Powers and Tiffin 2010). For example, in our study area many young forests are dominated by species like *Rehdera trinervis* and the legume *Gliricidia sepium*, which have high wood densities of 0.74 and 0.78 g·cm⁻³, respectively (Powers et al. 2009; Powers and Tiffin 2010). By contrast, Lohbeck et al. (2013) found a negative relationship between wood density and stand age in Mexico. Collectively, our study along with other studies of traits across succession in TDF (Alvarez-Anorve et al. 2012; Lohbeck et al. 2013) suggest that patterns in succession may be more complicated than simple resource-availability driven hypotheses suggest (Bazzaz and Pickett 1980).

Conclusions

Our results paint a complex picture of the variation of both AGB and traits across the secondary tropical dry forest landscape of Costa Rica. We used small plots in a heterogeneous secondary forest landscape and were able to explain 58% of the variation in biomass and up to 60% of the variation in community-level plant traits. These results show marginal support for the hypotheses that traits can be used to explain biomass. However, the contrasting patterns among studies in both AGB and trait variation underscore the need for site-specific understanding of relationships among abiotic and biotic variables across the landscape, and regional or continental syntheses of these patterns. Our results indicate that the processes and factors underlying the distribution of AGB of secondary TDF in Costa Rica are complex and make scaling and regional predictions difficult. However our results also demonstrate the large carbon storage potential of secondary tropical dry forest of this region. Our study shows that, if properly incentivized, this region could continue to restore large areas of

current pastureland to forest and act as a significant carbon sink for decades into the future.

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