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Demographic drivers of functional composition dynamics

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Abstract. Mechanisms of community assembly and ecosystem function are often analyzed using community-weighted mean trait values (CWMs). We present a novel conceptual framework to quantify the contribution of demographic processes (i.e., growth, recruitment, and mortality) to temporal changes in CWMs. We used this framework to analyze mechanisms of secondary succession in wet tropical forests in Mexico. Seed size increased over time, reflecting a trade-off between colonization by small seeds early in succession, to establishment by large seeds later in succession. Specific leaf area (SLA) and leaf phosphorus content decreased over time, reflecting a trade-off between fast growth early in succession vs. high survival late in succession. On average, CWM shifts were driven mainly (70%) by growth of surviving trees that comprise the bulk of standing biomass, then mortality (25%), and weakly by recruitment (5%). Trait shifts of growing and recruiting trees mirrored the CWM trait shifts, and traits of dying trees did not change during succession, indicating that these traits are important for recruitment and growth, but not for mortality, during the first 30 yr of succession. Identifying the demographic drivers of functional composition change links population dynamics to community change, and enhances insights into mechanisms of succession.

Key words: community-weighted mean traits; leaf phosphorus; seed size; specific leaf area; succession; tropical forests; wood density.

Introduction

Researchers often use metrics of community functional composition to analyze the mechanisms of community assembly and ecosystem function (McGill et al. 2006, Kraft and Ackerly 2010, Lohbeck et al. 2013). For instance, community-weighted mean (CWM) trait values (i.e., species' trait values weighted by their relative abundance) are commonly used to characterize functional composition (Shipley et al. 2006). CWM trait values reflect the selective pressures (e.g., abiotic filtering, competition) and historical contingencies (e.g., dispersal limitation) that determine community composition (Shipley et al. 2006, Muscarella and Uriarte 2016). Shifts of CWM values have been used to infer responses to environmental change (van der Sande et al. 2016).

We have little information, however, about how demographic rates (i.e., recruitment, growth, mortality) give rise to shifts in functional composition (Flores et al. 2014, Prado-Junior et al. 2016). For example, a model of succession may predict increasing mortality for species with relatively low values of a certain trait during succession. Empirical studies finding an increase in the CWM trait value would typically claim support for the model. However, the extent to which the CWM shift was driven by high growth or recruitment of species with high trait values vs. high mortality of species with low trait values would remain unknown. This represents a knowledge gap between many current trait-based approaches (which often focus on static patterns) and theory (which often highlights specific demographic mechanisms). A framework to quantify the role of particular processes in driving CWM trait shifts could facilitate more direct tests of theory and provide novel insight to community assembly (Fig. 1).

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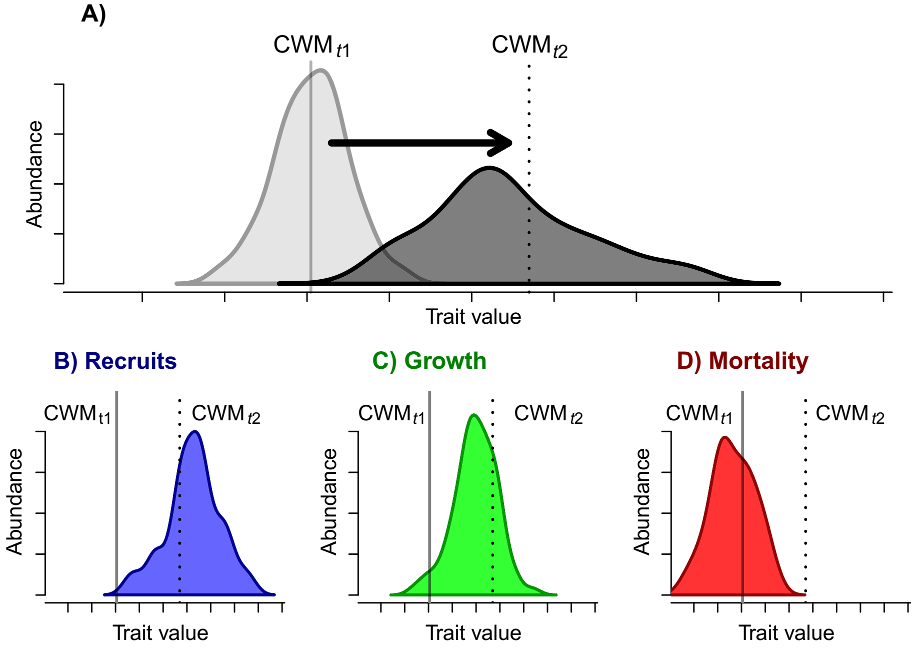

FIG. 1. A conceptual diagram showing the demographic drivers of temporal shifts in community-weighted mean (CWM) trait values. (A) Functional trait-based studies often infer ecological processes by comparing metrics of functional composition (e.g., CWMs) at two time steps (e.g., CWM$_{t_1}$ and CWM$_{t_2}$). The light and dark gray distributions in panel A reflect the relative abundance (measured as, e.g., biomass, basal area, stem abundance) of trait values in a community at two time steps; CWM values at time 1 and 2 are shown with the solid and dotted lines, respectively. In this case, the CWM value increases between the two time steps. The bottom panels show the constituent demographic processes that generate these dynamics (i.e., recruitment of new individuals, growth of surviving individuals, and mortality). In this example, the increase of the abundance metric by (B) recruitment and (C) growth is dominated by species with relatively high trait values. In contrast, species with relatively low trait values dominate the loss of abundance to (D) mortality. The relative contribution of each demographic process to the shift of the CWM trait value depends on the quantity contributed to the change in abundance as well as the trait values of constituent species. Note that *y*-axis scales are relative so the distributions in the three bottom panels do not sum to the top panel distributions. [Color figure can be viewed at wileyonlinelibrary.com]

Models of forest succession have long emphasized trait-mediated differences in performance among species (Chazdon 2008). In mesic forests, initial stages of succession involve colonization by a range of species, followed by disproportionate growth and reproduction of species with acquisitive traits that enable them to rapidly capitalize on abundant resources (Pacala and Rees 1998). As resource availability declines (e.g., understory light availability after canopy closure), species that cannot tolerate low resource levels suffer high mortality and shade-tolerant species dominate the new recruits. Indeed, numerous studies have reported successional shifts in CWM trait values that are at least partially consistent with this model (e.g., Lebrija-Trejos et al. 2010, Lohbeck et al. 2013, Craven et al. 2015, Muscarella et al. 2016). Despite the explicit demographic hypotheses mentioned above, however, changes in CWM values do not reveal the contributions of constituent demographic processes (i.e., recruitment, growth, mortality) in generating community-level patterns.

To date, few studies have directly evaluated how different demographic processes jointly mediate shifts in functional community composition or community functioning (Carreño-Rocabado et al. 2012, Prado-Junior et al. 2016, van der Sande et al. 2016). A larger body of research dealing with the influence of demographic processes on forest structure (e.g., aboveground biomass; AGB) provides a basis for understanding temporal shifts in functional composition. For example, growth of standing trees contributes more strongly to AGB dynamics than stem turnover (i.e., recruitment and mortality) during early tropical forest succession (van Breugel et al. 2006, Chazdon et al. 2007, Lasky et al. 2014, Rozendaal and Chazdon 2015, Rozendaal et al. 2016). The contribution of mortality to AGB dynamics typically increases as early-successional specialists reach maturity. The importance of recruitment for AGB dynamics is small over short timescales (e.g., one year), but is critical for longer-term AGB dynamics.

These studies provide a solid but incomplete foundation for understanding functional composition shifts during succession. For example, mortality contributes relatively little to AGB dynamics during early succession because it is mostly associated with the death of suppressed understory stems (Chazdon et al. 2007), except in cases of sudden massive mortality among the dominant canopy species (van Breugel et al. 2006). However, if species with high mortality rates also have relatively extreme trait values, mortality may contribute more strongly to

CWM trait dynamics than expected (van Breugel et al. 2007). Moreover, CWM traits based on different weighting metrics (e.g., AGB, stem abundance) may show different responses and reflect different underlying processes (Carreño-Rocabado et al. 2012). Ultimately, a complex mix of demographic processes underlies temporal shifts in community functional composition. A framework to quantify the relative strengths of constituent demographic processes in generating community trait patterns will help strengthen links between theory and trait-based ecology.

We introduce a framework for quantitatively partitioning the relative contribution of demographic processes to the temporal dynamics of CWM trait values. We used our approach to understand the demographic drivers of functional composition dynamics during the first three decades of secondary succession of wet tropical forests in Mexico. We asked the following questions:

1. How do the community-weighted mean trait values of recruiting, growing, and dying trees change during succession? During the early phase of succession examined here, we expected that CWM trait values of recruiting trees would shift from values characteristic of pioneer species with strong colonization ability (i.e., small seed size) and fast growth rates (low wood density, high SLA, and leaf P), toward trait values of shade tolerant species (i.e., high wood density and seed size, low SLA, and leaf P). Similarly, we expected that species contributing most strongly to biomass growth would reflect increasingly conservative resource strategies. Finally, we expected that CWM trait values of dying stems would reflect high mortality rates of short-lived pioneers with acquisitive traits.
2. What is the relative contribution of recruitment, growth, and mortality to community-weighted mean trait dynamics during succession? Based on models of biomass dynamics during tropical forest succession, we expected the strongest driver of CWM trait dynamics to be disproportionately high growth of species with acquisitive resource strategies. We expected mortality to have an increasingly important impact on CWM trait dynamics as succession proceeds and larger trees begin to die. We expected recruitment to have a relatively weak effect on CWM trait dynamics except during very early stages when total biomass is small. However, we expected that the contribution of recruitment to trait dynamics would increase as the length of census intervals increased.

METHODS

Study area and tree census plots

Our study is based on data from the Marquéz de Comillas region of Chiapas, Mexico (16°04′ N; 90°45′ W). Mean annual rainfall is ~3,000 mm, with a dry season (<60 mm/month) from February to April. Twenty permanent plots (10 × 50 m) were established between 2000 and 2012 in areas of similar soil and topographic conditions, at elevations of 115–300 m above sea level (van Breugel et al. 2006). All plots are located on old maize fields that were abandoned 0–25 yr prior to plot establishment. In each site, all woody stems with DBH ≥ 1 cm were identified, measured, and tagged. Individual trees have been remeasured at approximately annual intervals for 1–14 yr (Appendix S3: Table S1). We estimated aboveground biomass (AGB) of each stem using an allometric equation based on DBH and wood density (van Breugel et al. 2011). For each interval between two consecutive censuses (i.e., t_0 and t_1), we calculated biomass gained from recruitment ($\mathrm{AGB_R}$) by summing the AGB of stems alive at t_1 and not present at t_0. We calculated biomass gained by growth ($\mathrm{AGB_G}$) for each stem that survived a census interval by subtracting its AGB at t_0 from its AGB at t_1. Finally, we calculated biomass lost to mortality ($\mathrm{AGB_M}$) as the AGB at t_0 of stems alive at t_0 and dead at t_1.

Functional traits

We focused on four traits central to resource uptake and use, competition, and stress tolerance. Traits were measured for 67–83 species (depending on the trait), representing 91% of the total AGB and 89% of the total individuals (see Appendix S1). Briefly, wood density (g/cm^3) reflects a trade-off between hydraulic safety and efficiency (Poorter et al. 2008). Seed volume (mm^3) reflects a trade-off between fecundity and colonization ability on one hand, vs. the ability to establish in the shade on the other hand (Coomes and Grubb 2003). Specific leaf area (SLA, m^2/kg) reflects a trade-off between fast growth by rapid photosynthetic return on carbon investment vs. slow growth by longer nutrient retention (Poorter and Bongers 2006). Leaf P concentration (% dry mass) reflects acquisition strategies for what is thought to be the most limiting nutrient for tropical forest growth and productivity (Walker and Syers 1976). Although we use species mean traits, our approach could incorporate intraspecific variation and is compatible with other relevant methods (e.g., Lepš et al. 2011; see Appendix S2).

Community-weighted mean trait values and statistical analyses

We first calculated a community-weighted mean (CWM) trait value for each plot, *p*, and each census, *c*, based on trait value, *T*, and a weighting factor, *w*, of each species, *i*:

$$\mathrm{CWM}_{pc} = \sum\nolimits_{i=1}^{\mathrm{N}} w_i \times T_i / \sum\nolimits_{i=1}^{\mathrm{N}} w_i \qquad (1)$$

We also separately calculated CWM trait values for the biomass gained by recruitment ($\mathrm{CWM_R}$) and growth ($\mathrm{CWM_G}$), and lost to mortality ($\mathrm{CWM_M}$), during each census interval in each plot (Carreño-Rocabado et al. 2012). We focus on biomass as a weighting factor because it emphasizes the dominant species that drive key ecosystem processes (Lohbeck et al. 2016). Stem abundance, however, also reflects unique aspects of community change and we provide results based on abundance in the Appendix S3. In general, researchers should carefully consider appropriate weighting metrics given their study system and research questions.

To address Question 1, we fit Linear Mixed Models (LMMs) to all CWM values (including the CWM values for each demographic process: $\mathrm{CWM_R}$, $\mathrm{CWM_G}$, $\mathrm{CWM_M}$) as a function of forest age during the census, or at the end of the census interval for demographic process CWMs. These models also included a plot random effect (Bates et al. 2013). We estimated 95% confidence intervals based on 1,000 Markov chain Monte Carlo (MCMC) samples (Gelman et al. 2006). To assess model performance, we quantified marginal and conditional R^2_{GLMM} values (Bartoń 2013). We conducted all analyses in R v. 3.2.3 (R Development Core Team 2016). To address Question 2, we used a novel method to decompose the relative contributions of constituent demographic processes to the dynamics of the CWM trait values. Briefly, the CWM value at t_1 can be decomposed into four components:

$$\mathrm{CWM}_1 = \frac{\sum_{i=1}^{\mathrm{N}}(\mathrm{AGB}_{0_i} \times T_i)}{\sum_{i=1}^{\mathrm{N}}(\mathrm{AGB}_{1_i})} + \frac{\sum_{i=1}^{\mathrm{N}}(\mathrm{AGB}_{\mathrm{R}_i} \times T_i)}{\sum_{i=1}^{\mathrm{N}}(\mathrm{AGB}_{1_i})} + \frac{\sum_{i=1}^{\mathrm{N}}(\mathrm{AGB}_{\mathrm{G}_i} \times T_i)}{\sum_{i=1}^{\mathrm{N}}(\mathrm{AGB}_{1_i})} - \frac{\sum_{i=1}^{\mathrm{N}}(\mathrm{AGB}_{\mathrm{M}_i} \times T_i)}{\sum_{i=1}^{\mathrm{N}}(\mathrm{AGB}_{1_i})} \qquad (2)$$

The four terms represent, respectively, the contribution of AGB-weighted traits at the start of the interval (t_0), the contribution of AGB-weighted traits gained by recruitment, the contribution of AGB-weighted traits gained by growth of surviving trees, and the contribution of AGB-weighted traits lost to mortality. The relative contribution of growth, for example, to the dynamics of the CWM trait value is thus:

$$\frac{\sum_{i=1}^{\mathrm{N}}(\mathrm{AGB}_{\mathrm{G}_i} \times T_i)}{\sum_{i=1}^{\mathrm{N}}(\mathrm{AGB}_{\mathrm{R}_i} \times T_i) + \sum_{i=1}^{\mathrm{N}}(\mathrm{AGB}_{\mathrm{G}_i} \times T_i) + \sum_{i=1}^{\mathrm{N}}(\mathrm{AGB}_{\mathrm{M}_i} \times T_i)} \qquad (3)$$

The relative contributions of recruitment and mortality are calculated by substituting the numerator of Eq. 3 with the corresponding terms for these processes, respectively (see Appendix S2 and Data S1 for more details and simulated examples).

RESULTS

Temporal trends in CWM trait values were partly consistent with an expected shift in dominance from species with resource-acquisitive to resource-conservative functional strategies. Specifically, CWM seed volume increased, both SLA and leaf P decreased, and wood density did not change with forest age (Fig. 2). CWM trait values for separate demographic processes were variable and 4 out of 12 showed significant trends with respect to forest age: changes were most often significant for growth (three out of four cases), followed by recruitment (one of four) and none for mortality. Growth of survivors showed an increase in CWM seed volume and a decline in SLA and leaf P over time, recruits showed an increase of seed volume over time.

Overall, total AGB increased, and total stem density decreased, during succession (Appendix S3: Fig. S1). Based on 1-yr census intervals, growth accounted for the strongest contribution to CWM trait dynamics throughout the study period (70%, on average), followed by mortality (25%), and recruitment (5%) (Fig. 3). The contribution of mortality was highest (>50%) in some plots 8–15 yr after succession started. The contribution of recruitment was highest during the first 3 yr and declined exponentially over time. As expected, recruitment made larger contributions to trait dynamics with longer intervals, but its contribution remained modest compared to growth even with a 12-yr interval (i.e., ~20%; Fig. 4A). When weighting by abundance, mortality contributed slightly more to CWM trait dynamics than recruitment (55% vs. 45%) and there was no trend in their relative importance over time (Appendix S3). Additionally, the contributions of these processes to dynamics of CWM values were not sensitive to the length of the census interval (Fig. 4B). In summary, during the first 30 yr of succession, shifts in AGB-weighted trait values were largely driven by increasing size of surviving individuals rather than by stem turnover (i.e., recruitment and mortality); shifts in abundance-weighted trait values were nearly equally driven by recruitment and mortality.

DISCUSSION

We decomposed dynamics of CWM trait values into relative contributions of constituent demographic processes. Our main findings are that (1) successional changes were especially marked in seed size (reflecting a colonization–establishment trade-off) and SLA (reflecting a growth–survival trade-off), (2) CWM changes were mainly driven by growth of surviving trees, and not by species turnover (although mortality did have a strong contribution to trait changes between 8 and 15 yr, when some short-lived pioneers died), and (3) recruitment had a stronger contribution to AGB-weighted trait dynamics over longer census intervals. We discuss our results in terms of links between models of succession and trait-based ecology.

Two trade-offs (colonization–establishment, growth–survival) govern successional patterns

As predicted, changes in CWM trait values reflected a shift in dominance from acquisitive to more conservative

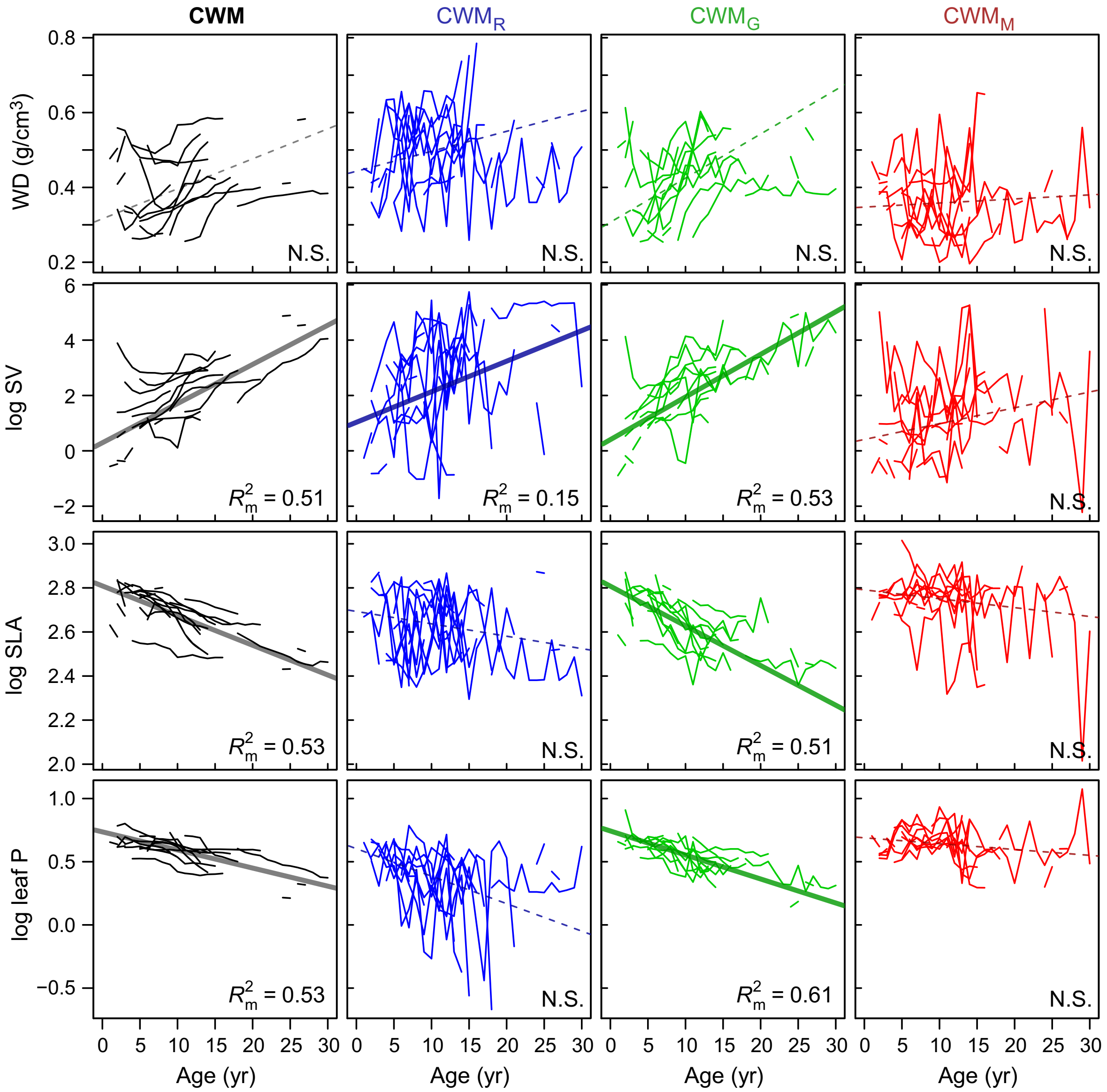

Fig. 2. CWM trait values (weighted by aboveground biomass [AGB]) for wood density (WD), seed volume (SV; mm^3), specific leaf area (SLA; m^2/g), and leaf P during succession (as a percentage of mass) (one trait per row). The left-most column shows changes in CWM values, the other columns show CWM trait values of AGB gained by recruitment (CWM$_R$) and growth of surviving trees (CWM$_G$), and AGB lost to mortality (CWM$_M$), respectively. Each line represents one forest plot; solid regression lines correspond to significant linear mixed models (i.e., where 95% confidence intervals of slope estimates did not overlap zero). Marginal R^2 values are provided for significant relationships. Results for abundance-weighted traits are provided in Appendix S3: Fig. S5. [Color figure can be viewed at wileyonlinelibrary.com]

strategies during succession (Pacala and Rees 1998). Changes were especially marked in seed size, which tended to increase over time. This reflects a trade-off between small seeded species that are able to colonize during early succession vs. large-seeded species that are able to establish in the shaded understory later in succession (Coomes and Grubb 2003). SLA and leaf P decreased over time, reflecting a trade-off between acquisitive species that grow fast early in succession when light availability is high vs. conservative species that have persistent tissues and high survival in the shade (Poorter and Bongers 2006). Leaf P concentrations were highest early in succession, which is consistent with acquisitive strategies, but which is also a bit surprising since soil nutrients are often more depleted early in succession (Wadsworth et al. 1990). Surprisingly, wood density did not vary over time, despite other studies showing that it is tightly linked to shade tolerance (Valladares and Niinemets 2008), the best predictor of the growth performance of trees (Poorter et al. 2008), and of competitive

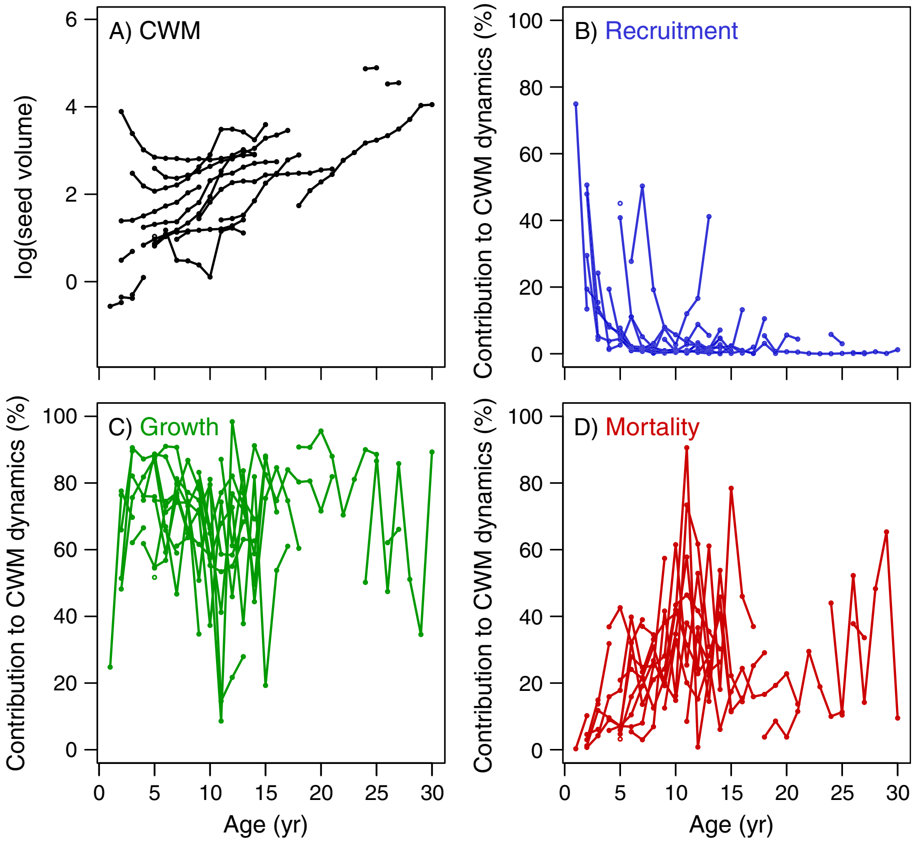

FIG. 3. (A) CWM value of seed volume and proportional contributions of (B) recruitment, (C) increment growth of surviving individuals, and (D) mortality to dynamics of CWM seed volume during 1-yr census intervals. Each line represents a single forest plot through time and points reflect individual censuses. Results for wood density, SLA, and leaf P, as well as results for abundance-weighted traits are provided in Appendix S3. [Color figure can be viewed at wileyonlinelibrary.com]

interactions among neighboring trees (Kunstler et al. 2016). This result is at least partly due to the dominance of a low wood density species (*Vochysia guatemalensis*; wood density = 0.36) in one of the older sites. In addition, some high wood density species (e.g., *Luehea speciosa*; wood density = 0.67) are able to survive (and resprout after) repeated disturbances such as fire, and are present early in succession. In this respect, the absence of the expected CWM wood density pattern might reflect a historical contingency related to land management.

CWM changes are driven by growth of surviving trees, and not by stem turnover

On average, growth of surviving trees contributed most strongly to CWM trait dynamics, followed by mortality and then recruitment. Surviving trees make up the bulk of standing biomass, and their growth drove the observed CWM trait changes. Recruitment contributed most strongly to CWM trait dynamics during the first 3 yr of succession (i.e., stand initiation). Mortality had a stronger contribution to CWM trait values in years 8–15, which coincides with the stand-thinning phase, when some short-lived pioneers (e.g., *Ochroma pyramidale*) have massive die-offs (van Breugel et al. 2007). However, the lack of a change in $\mathrm{CWM_M}$ trait values during succession indicates that, on average, mortality was not strongly mediated by these traits during this period. The overall strongest contribution of growth to CWM trait shifts suggests that trait-driven processes (e.g., competitive interactions) shape growth differences among trees (Lasky et al. 2014, Kunstler et al. 2016), leading to winners that grow disproportionally fast, and losers that remain suppressed in the understory. In sum, successional dynamics of AGB-weighted trait values were driven mainly by the growth of surviving trees, not stem turnover. This is consistent with previous studies of AGB dynamics in early tropical forest succession, which are most strongly driven by growth of surviving trees (van Breugel et al. 2006, Chazdon et al. 2007, Lasky et al. 2014, Rozendaal and Chazdon 2015, Rozendaal et al. 2016).

Several aspects of spatial and temporal scale are critical when interpreting our results. First, the size threshold (1 cm) and census frequency (annual) used here mean that recruiting stems are unlikely to contribute much to AGB-weighted traits. As expected, the contribution of recruitment to AGB-weighted trait dynamics increased with longer census intervals. Interestingly, the contribution

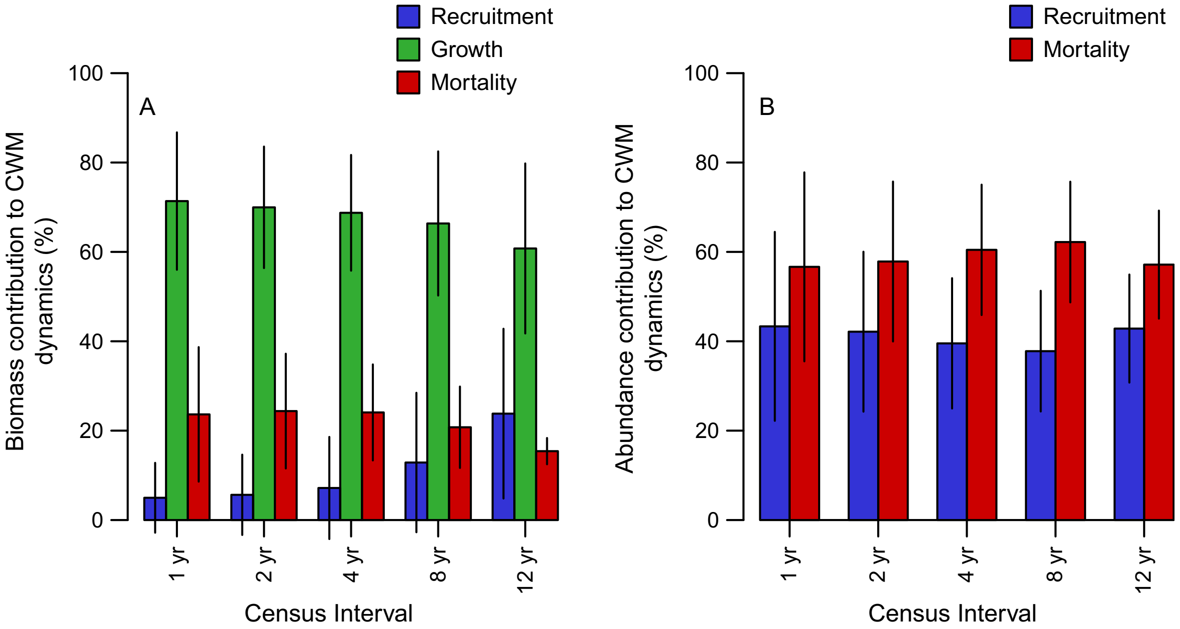

FIG. 4. The average percent contribution of demographic processes to dynamics of (A) biomass- and (B) abundance-weighted wood density for different census interval lengths (results for other traits show similar patterns). Percent contributions are calculated as the average contribution across all plots and all years with censuses that were sufficiently long to include. Vertical bars represent one standard deviation across plots and years. Note that growth is not included in panel B because growth is not partitioned from changes in stem abundance. [Color figure can be viewed at wileyonlinelibrary.com]

of recruitment to abundance-weighted trait dynamics did not change when different census interval lengths were considered. We also note that we focused on the first 30 yr of succession, where most mortality involves small stems suppressed in the understory (Chazdon et al. 2007, Chazdon 2008). Mortality is likely to have a stronger role in driving trait dynamics during later stages of succession when mature trees begin to senesce.

The goals of trait-based ecology include predicting community response to environmental change. We argue that this requires stronger links to underlying demographic processes, and a better understanding of how trait-mediated performance differences scale up to community trait patterns. Our approach provides insight to the demographic processes that lead species with certain traits to become dominant, and subsequently influence ecosystem function (Lohbeck et al. 2016). Future work to understand mechanisms driving trait change during succession could combine our approach with analyses that provide additional insight to trait-environment associations (e.g., the fourth corner approach; Brown et al. 2014), as well as trait-based models of individual-level growth, survival, and recruitment (Lasky et al. 2014). Ultimately, we hope our approach will help in using demography to bridge models of succession and trait-based ecology.

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