**LETTER**

# The relationship between tree biodiversity and biomass dynamics changes with tropical forest succession

Jesse R. Lasky,[1,2]* María Uriarte,[2] Vanessa K. Boukili,[3] David L. Erickson,[4] W. John Kress[4] and Robin L. Chazdon[3]

**Abstract**

Theory predicts shifts in the magnitude and direction of biodiversity effects on ecosystem function (BEF) over succession, but this theory remains largely untested. We studied the relationship between aboveground tree biomass dynamics (Δbiomass) and multiple dimensions of biodiversity over 8–16 years in eight successional rainforests. We tested whether successional changes in diversity–Δbiomass correlations reflect predictions of niche theories. Diversity–Δbiomass correlations were positive early but weak later in succession, suggesting saturation of niche space with increasing diversity. Early in succession, phylogenetic diversity and functional diversity in two leaf traits exhibited the strongest positive correlations with Δbiomass, indicating complementarity or positive selection effects. In mid-successional stands, high biodiversity was associated with greater mortality-driven biomass loss, *i.e.* negative selection effects, suggesting successional niche trade-offs and loss of fast-growing pioneer species. Our results demonstrate that BEF relationships are dynamic across succession, thus successional context is essential to understanding BEF in a given system.

**Keywords**

Disturbance, functional traits, leaf dry matter content, productivity, specific leaf area, tropical rainforest, wood specific gravity.

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## INTRODUCTION

One of the central arguments in support of biodiversity conservation is that biodiversity positively affects ecosystem function (Naeem *et al.* 2012). Theoretical studies of the mechanisms linking biodiversity to ecosystem function (BEF) have often focused on productivity. Theory predicts that diversity is positively correlated with productivity when diversity increases niche complementarity (*e.g.* complementary resource use), known as complementarity effects (Loreau 1998; Chesson *et al.* 2001). Alternatively, selection effects arise when diversity is correlated with species competitive ability (Loreau 1998). Assuming competitive ability is positively correlated with a species' productivity, positive selection effects (causing positive BEF relationships) result when average species competitive ability is greater in high diversity communities. Negative selection effects (causing negative BEF relationships) result if greater diversity is caused by the addition of poor competitors, reducing productivity (Loreau 1998). The mechanisms that drive BEF relationships may change over time (Kinzig & Pacala 2001; Mouquet *et al.* 2002), yet little is known about temporal or successional changes in BEF relationships.

Successional communities are ideal systems for studying dynamic BEF relationships because of rapid changes in species composition and ecosystem function (Letcher & Chazdon 2009). However, few empirical studies have examined BEF relationships in the context of ecological succession, and divergent findings may arise because of differences in the successional stage being investigated (Balvanera *et al.* 2006; Weis *et al.* 2007; Paquette & Messier 2011; Zhang *et al.* 2012). Theory yields multiple predictions of how BEF relationships might change during succession. First, taxonomic and functional diversity are expected to increase with succession (Letcher & Chazdon 2009; Lohbeck *et al.* 2012; Norden *et al.* 2012), but positive BEF effects can saturate at high diversity if additional species are functionally redundant (Tilman *et al.* 1997; Loreau 1998; Chesson *et al.* 2001).

By contrast, the successional niche hypothesis posits that species niches segregate along a trade-off axis between competitive ability and rapid growth when resources are abundant early in succession (e.g. stand initiation) vs. low growth and high mortality later in succession when resources are limiting (e.g. stand thinning) (Pacala & Rees 1998). Under this hypothesis, early in succession competitive ability is characterised by high productivity (i.e. competitive effect) while later in succession competitive ability is characterised by the ability to persist under low resource availability (i.e. competitive response) (Goldberg 1990). As a result, the diversity–productivity relationship is expected to be negative early in succession because early-successional stands dominated by a fast-growing species are more productive than more diverse communities comprised of both early-successional and less productive late-successional species (Kinzig & Pacala 2001).

[1]*Earth Institute, Columbia University, New York, NY, USA*

[2]*Department of Ecology, Evolution and Environmental Biology, Columbia University, New York, NY, USA*

[3]*Department of Ecology and Evolutionary Biology, University of Connecticut, Storrs, CT, USA*

[4]*Department of Botany, National Museum of Natural History, Smithsonian Institution, Washington, DC, USA*

*Correspondence: E-mail: jl3985@columbia.edu*

Later in succession, the theory predicts the reverse: diverse mixtures of early- and late-successional species are more productive than less diverse older stands dominated by slow-growing, late-successional species, causing a positive BEF relationship.

Aboveground biomass (AGB) dynamics are an important component of net primary productivity in tropical forests (Clark *et al.* 2001). Tree AGB dynamics are primarily driven by growth and mortality, which may be related to trade-offs between biomass productivity vs. persistence. The relationship between tree biomass growth and diversity may be similar to predicted diversity effects on productivity (Loreau 1998; Caspersen & Pacala 2001; Kinzig & Pacala 2001). Assuming early-successional species are most productive (Clark *et al.* 2001; Chazdon *et al.* 2010) (Fig. 1), a successional shift from negative to positive BEF effects is expected (Caspersen &

Pacala 2001; Kinzig & Pacala 2001). In contrast, assuming biomass lost to mortality is greatest among early-successional species, a successional shift from positive to negative BEF effects is expected (Fig. 1). We expect diversity effects on total biomass change will follow predictions for productivity. However, high biomass mortality of early-successional species during stand thinning may overwhelm growth effects. Previous studies of BEF effects in forests have been largely conducted in temperate regions (Caspersen & Pacala 2001; Paquette & Messier 2011; Gamfeldt *et al.* 2013) or in low-diversity plantations (Healy *et al.* 2008; Zhang *et al.* 2012), whereas BEF relationships in diverse tropical forests are poorly understood and long-term data are scarce.

Because theory predicts that BEF relationships depend on variation among species in niche and performance across resource gradients, functional diversity may be more closely
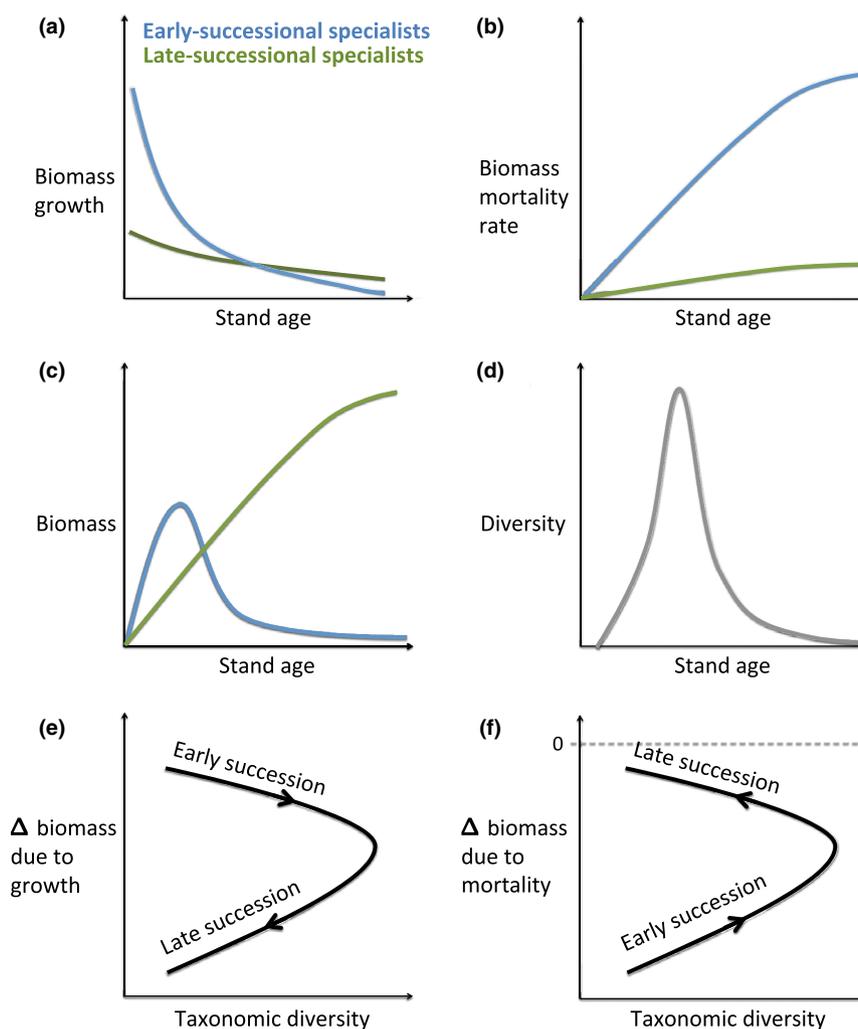


**Figure 1** Qualitative predictions of growth–mortality trade-offs (a–b), biomass (c), diversity (d) and resulting BEF relationships (e–f) based on a successional niche model with only early- and late-successional specialists (*e.g.* two species, Kinzig & Pacala 2001). (a) Biomass growth declines with stand age. Early-successional specialists have higher productivity under abundant resources early, but cannot maintain productivity as stands age. (b) As resources decline with stand age, biomass mortality increases. Increased mortality is higher for early-successional species. (c) As a result, early-successional species biomass peaks early in succession but is supplanted by late-successional species. (d) Under the successional niche hypothesis, the highest diversity occurs in middle-aged stands transitioning from early to late-successional species. (e) Diversity relationship with biomass dynamics (Δbiomass) due to growth shifts from negative to positive across succession. (f) Diversity relationship with Δbiomass due to mortality shifts from positive to negative, due to dominance late in succession by low mortality species.

related to ecosystem function than taxonomic diversity (Flynn *et al.* 2011). Different traits may be associated with niche and competitive ability, thus different axes of functional diversity may reveal distinct relationships with ecosystem function (Ruiz-Jaen & Potvin 2011; Roscher *et al.* 2012). Traits that confer high productivity under abundant resources often differ from those associated with persistence under low resource availability (Goldberg & Landa 1991). Successional changes in the competitive ability conferred by traits may be associated with trade-offs between maximising carbon uptake, minimising construction costs, and maximising leaf life span (Blonder *et al.* 2011). In addition, phylogenetic diversity is often positively correlated with ecosystem function, based on the hypothesis that relevant traits are phylogenetically conserved (Flynn *et al.* 2011). Community functional composition, independent of diversity, also influences ecosystem function (Grime 1998), although here we focus on diversity relationships with ecosystem function.

Here, we utilise a long-term study of community-wide stem dynamics to examine successional changes in the spatial relationship between biodiversity and temporal change in tree AGB (referred to below as Δbiomass). We couple allometric scaling and annual censuses with data on three functional traits and phylogenetic diversity to ask the following questions:

(1) How do the magnitude and sign of diversity–Δbiomass relationships differ across dimensions of biodiversity? We expect functional diversity in leaf functional traits to be associated with variation in resource use niches, and with positive complementarity effects on Δbiomass. In contrast, we expect high wood specific gravity to be associated with a trade-off between productivity during stand initiation (light wood) and biomass persistence later in succession (heavy wood), transitioning from negative to positive selection effects on Δbiomass as succession proceeds.

(2) Does the diversity–Δbiomass relationship change for biomass gained through growth vs. biomass loss to mortality, suggesting trade-offs between productivity vs. persistence? We expect that Δbiomass due to growth vs. Δbiomass due to mortality will show opposite relationships with diversity due to a successional niche trade-off.

(3) How does the diversity–Δbiomass relationship change across succession? We hypothesised that positive diversity–Δbiomass relationships would grow weaker (i.e. less steep slopes) with succession due to functional redundancy at high species diversity. For growth, we expected a successional shift from negative to positive diversity effects due to high productivity of early-successional species. In contrast, for mortality we expected a shift from positive to negative diversity effects due to high mortality of early-successional species.

## METHODS

### Study site

During 1997–2012 (four successional plots) or 2005–2012 (two other successional plots and two old-growth plots) we annually monitored woody vegetation in Sarapiquí County, Heredia Province, in the Caribbean lowlands (50–220 m a.s.l.) of Costa Rica (Chazdon *et al.* 2010; Norden *et al.* 2012) (Table S1). The regional life zone is tropical wet forest with annual temperature and rainfall averaging 26 °C and ~ 3800 mm respectively (Sanford *et al.* 1994). Soils in the plots are derived from weathered basalt and are primarily classified as ultisols (Sollins *et al.* 1994). All successional plots had been cleared and grazed lightly for several years before abandonment and had closed canopies from the initiation of censuses (Chazdon *et al.* 2010).

### Tree censuses

We divided each of the eight 1-ha plots into 100 10 × 10 m quadrats. Each stem ≥ 5 cm diameter at breast height (DBH) was identified to species, tagged, mapped and annually measured for DBH. Across the 1997–2012 study period we monitored 12 113 unique stems belonging to 367 species and 67 families.

### Functional traits

We measured three functional traits that represent leading axes of ecological variation among tropical tree species (Chave *et al.* 2009; Lasky *et al.* 2014), using standardised protocols (Cornelissen *et al.* 2003). We measured functional traits for 215 species, including 200 of 226 tree species that had four or more individuals in any of the annual censuses. Leaf measurements, including leaf dry matter content (LDMC, g/g) and specific leaf area (SLA; mm$^2$/mg), were made on 1–62 individuals per species, totalling 1984 individuals. We collected undamaged, sun-exposed leaves whenever possible. Wood-specific gravity (WSG, unitless) was measured on 1281 individuals of 176 species, using cores collected with an increment borer. We used species mean traits in analyses because we were unable to sufficiently sample intraspecific variation for uncommon species. We log transformed SLA because it was highly right skewed.

### Phylogeny

We constructed a molecular phylogeny to quantify community evolutionary diversity. For 220 species included in the study, leaf tissue samples were collected from one to three individuals. Methods of DNA extraction, PCR and sequencing are reported in detail in Kress *et al.* (2010) and in our Data S1. PCR and sequencing were conducted on each tissue sample for three DNA barcode markers, *rbc*L, *mat*K and *psb*A-*trn*H. The phylogeny was inferred using the CIPRES portal (Miller *et al.* 2010) where we used GARLI (Zwickl 2008), a maximum likelihood phylogenetic reconstruction algorithm, in conjunction with a phylogenetic constraint tree (Kress *et al.* 2010). We converted the molecular phylogeny to a dated chronogram that was then implemented as the phylogeny in our analyses of diversity (Fig. S1).

We tested for phylogenetic signal in the three traits using Blomberg's K and permutations of trait values across the tips of the phylogeny, implemented in the 'picante' package in R (Kembel *et al.* 2010).

## Quantifying biodiversity

AGB dynamics (Δbiomass) and diversity were quantified within each 100-m$^2$ quadrat ($n = 800$). We previously demonstrated significant trait-based species interactions at this spatial scale at our study site (Lasky *et al.* 2014) and other findings indicate that the great majority of tree interactions occur within this spatial scale (Uriarte *et al.* 2004).

Quantitative theories of BEF mechanisms focus on species richness measures of diversity (Loreau 1998; Caspersen & Pacala 2001; Kinzig & Pacala 2001; Mouquet *et al.* 2002). However, Grime (1998) hypothesised that composition and diversity of the most abundant species control ecosystem function. We do not deny the importance of abundant species; we study richness measures of diversity because patterns are more clearly interpreted in light of mechanistic BEF theory. Taxonomic diversity was calculated as species richness of each quadrat. Phylogenetic (PD) and functional (FD) diversity were calculated using analogous approaches. For PD we calculated the total shared branch length along the phylogeny of species occurring in a quadrat (Faith 1992). We calculated FD separately for each trait (FD$_{SLA}$, FD$_{LDMC}$, FD$_{WSG}$) to gain insight into the ecophysiological mechanisms driving BEF relationships. We also calculated a multivariate FD for all three traits combined (FD$_{All\ traits}$). To calculate FD we generated trait dendrograms (analogous to phylogenies) for each trait and for all traits combined, and calculated the total shared branch length of species in a quadrat (Petchey & Gaston 2002).

Tree diversity is sampled in discrete individuals, the number of which can bias measures of diversity (Gotelli & Colwell 2011). Thus, we estimated rarefied diversity of five randomly sampled individuals in each quadrat, resampled each quadrat 100 times and calculated average diversity across resamples. Rarefaction was conducted using the 'vegan' package in R (Oksanen *et al.* 2013). Quadrat observations with fewer than five individuals (8% of observations) were excluded. Rarefied diversity was strongly related to non-rarefied quadrat diversity (each dimension of rarefied vs. non-rarefied diversity, ρ between 0.67 and 0.79). Finally, to test for successional change in biodiversity, we used a linear mixed model to test the effect of stand age on diversity (details below).

## Allometry and aboveground biomass dynamics

We used published allometric scaling equations to estimate AGB for each stem and then calculated temporal Δbiomass in each quadrat. For our 6 second-growth plots, we used the allometric scaling equations of van Breugel *et al.* (2011) developed at lowland secondary rainforests in Panama. For species with known WSG, AGB was calculated as

$$\log(AGB) = -1.13 + 2.267 \log(DBH) + 1.186 \log(WSG) \quad (1)$$

For species with unknown WSG, AGB was calculated as

$$\log(AGB) = -1.863 + 2.208 \log(DBH) \quad (2)$$

The diameter-AGB allometry likely differs between old-growth and second-growth forests due to differences in species composition, crowding conditions and size ranges (van Breugel

*et al.* 2011). Thus, we used separate equations to estimate AGB in our two old-growth forest plots (Brown 1997; Chave *et al.* 2005). For species with known WSG, AGB was calculated as

$$\log(AGB) = \log(WSG) - 1.239 + 1.98 \log(DBH) \\ + 0.207 \log(DBH)^2 - 0.0281 \log(DBH)^3 \quad (3)$$

(Chave *et al.* 2005). For species with unknown WSG, AGB was calculated as

$$\log(AGB) = \log(21.29 - 6.953 DBH + 0.74 DBH^2) \quad (4)$$

(Brown 1997). Because palm allometry is markedly different from other species, we excluded these stems from AGB and subsequent diversity calculations. Canopy palms represent 4.6% of the basal area of stems with DBH $\geq$ 5 cm and likely compose an even lower percentage of AGB because they are unbranched and have lower WSG than dicot trees (Chave *et al.* 2009).

Quadrats differed in their initial AGB, which may feedback into effects on Δbiomass. Thus, we focused on understanding diversity effects on proportional Δbiomass (analogous to relative growth rate), calculated between years $t$ and $t + 5$ as

$$\Delta biomass_t = AGB_{t+5}/AGB_t \quad (5)$$

We selected a 5-year interval because of the slow demography of trees compared to systems more common in BEF studies (e.g. grasslands). In addition, annual observation error in stem diameters is reduced relative to temporal change in diameter at this scale.

To account for potential trade-offs in productivity vs. mortality, we separately analysed Δbiomass due to biomass increases through growth and losses from mortality (Caspersen & Pacala 2001), setting aside recruitment due to its small effect on total Δbiomass. For Δbiomass due to growth, the right side of eqn 5 was restricted to stems alive in both years $t$ and $t + 5$. For Δbiomass due to mortality, we calculated the biomass of surviving stems divided by the total original biomass, *i.e.* the numerator on the right side of eqn 5 was restricted to stems alive in both years $t$ and $t + 5$. As a result, Δbiomass due to mortality was a proportion between zero and unity. To improve normality, we log transformed total Δbiomass and Δbiomass attributable to growth. We arcsin square root transformed Δbiomass attributable to mortality, appropriate for proportional data.

## Statistical model

We used linear regression to evaluate the relationship between biomass change and diversity variation among 100-m$^2$ quadrats, where Δbiomass was the dependent variable, and taxonomic, phylogenetic and functional diversity were covariates of interest. As our study was observational, we cannot exclude the potential role of unmeasured spatiotemporal environmental gradients, such as edaphic conditions and weather. To account for unexplained variation among observations within the same quadrat and observations within the same year, we

used multilevel (mixed-effects) Bayesian inference, allowing us to incorporate quadrat and year as random effects. Next, we focused on proportional biomass change (eqn 5), which allowed us to account for some initial variation among quadrats. Finally, because our study plots were staggered in age, climate effects in any given year would not be confounded with stand age, allowing inference about successional changes in BEF relationships. Year random effects tended to be weak (Table S2), suggesting that our approach is well equipped to evaluate successional changes.

Our full statistical model was as follows:

$$\Delta \text{biomass}_{it} = \beta_0 + \beta_1 \text{diversity}_{it} + \beta_2 \text{stems}_{it} + u_i + v_t + \varepsilon_{it} \quad (6)$$

The parameter $\beta_1$ models the effect of diversity in quadrat $i$ and year $t$, where diversity was taxonomic, phylogenetic or functional. Parameters $u_i$ and $v_t$ were independent and normally distributed random variables representing quadrat and year effects respectively. Irrespective of community composition, a portion of spatial variation in $\Delta$biomass is likely driven by differences in stem density, which when high leads to stand thinning even if species are ecologically equivalent. Thus, we included a parameter, $\beta_2$, to account for effects of stem density of quadrat $i$ in year $t$, stems$_{it}$, which here may be considered a nuisance parameter (Ruiz-Jaen & Potvin 2011). We used diffuse, proper priors and JAGS v.3.3 (http://sourceforge.net/projects/mcmc-jags/) to implement models and sample parameter posterior distributions. Residuals of all models were approximately normally distributed.

To determine how diversity–$\Delta$biomass relationships differ across dimensions of biodiversity (question 1), we tested the BEF relationships ($\beta_1$) for each of the six diversity metrics (species richness, PD, FD$_{SLA}$, FD$_{LDMC}$, FD$_{WSG}$, FD$_{All\ traits}$) in separate regression models. To determine how diversity–$\Delta$biomass relationships change for $\Delta$biomass due to growth vs. mortality (question 2), we tested diversity–$\Delta$biomass relationships ($\beta_1$) in separate regressions where the response variable (eqn 6) was either $\Delta$biomass due to growth or mortality. To determine how diversity–$\Delta$biomass relationships change across succession (question 3), we tested BEF relationships at three different successional stages: early-successional (stand age = 10–23 years), mid-successional (stand age = 24–39 years) and old growth (exact age unknown). For each of the six metrics of biodiversity we tested the BEF relationship separately for each stand-age category across the entire study period. Finally, we conducted a series of regressions to test how each diversity metric changed across stand age category, where age category was an ordinal covariate and quadrat was included as a random effect.

## RESULTS

### Overview: successional change in aboveground biomass and diversity

Total AGB increased across stand-age categories, although we observed extensive variation within and among plots (Fig. 2). Mean tree AGB was 76.36 Mg ha$^{-1}$ (range 44.89–99.72) in early-successional plots, 116.47 Mg ha$^{-1}$ (range 82.53–134.52) in mid-successional plots and 198.30 Mg ha$^{-1}$ (range 192.69–

206.07) in old-growth plots. All dimensions of biodiversity significantly increased with stand-age category with the exception of multivariate trait diversity, which was lowest in mid-successional stands (Table S3, Fig. 2). All three traits showed significant phylogenetic signals, although signals were weak compared to the expectation ($K = 1$) from Brownian motion (LDMC: $K = 0.31$, $z = -3.17$, $P < 0.0001$; SLA: $K = 0.17$, $z = -2.21$, $P = 0.0002$; WSG: $K = 0.31$, $z = -3.10$, $P < 0.0001$, Fig. S1).

### Overview: BEF relationships

Diversity relationships with $\Delta$biomass over 5-year intervals (*i.e.* change in AGB between years $t$ and $t + 5$) were more often significantly positive than significantly negative (Fig. 3, Table S4). Nine of 18 combinations of diversity metric and stand-age category showed positive associations with $\Delta$biomass, six of them significantly so. On the other hand, three combinations of diversity metric and stand-age category showed significant negative relationships with total $\Delta$biomass.

### How do diversity–$\Delta$biomass relationships differ among diversity metrics?

All diversity metrics were positively correlated with 5-year $\Delta$biomass in at least one of the three stand-age categories (Fig. 3). We found the strongest positive relationships with $\Delta$biomass for functional diversity of SLA (FD$_{SLA}$), followed by diversity of LDMC (FD$_{LDMC}$) and phylogenetic diversity (all significantly positive in early-successional stands, Table S4). On the other hand, species richness and functional diversity of SLA and LDMC showed the strongest negative relationships with $\Delta$biomass (all significant in mid-successional stands).

### How do diversity–$\Delta$biomass relationships differ between $\Delta$biomass due to growth vs. mortality?

Diversity relationships with $\Delta$biomass due to growth were more often significantly positive compared to diversity relationships with total $\Delta$biomass (Fig. 4, Table S4). Diversity relationships with $\Delta$biomass due to growth were significantly positive in both early and mid-successional stands for all dimensions of diversity. FD$_{All\ traits}$ in old-growth stands was the only dimension of diversity significantly negatively correlated with $\Delta$biomass due to growth.

Consistent with our expectation of a successional productivity–mortality trade-off, diversity relationships with $\Delta$biomass due to mortality were often significantly negative in mid-successional stands in contrast to diversity relationships with $\Delta$biomass due to growth (Fig. 4, Table S4). Overall, diversity effects on $\Delta$biomass due to mortality were significantly positive for five combinations of diversity metric and successional stage but were also significantly negative for six combinations of diversity metric and successional stage.

### How do biodiversity–$\Delta$biomass relationships change across succession?

For all dimensions of diversity, the correlation of diversity with total $\Delta$biomass became non-significant or negative from early- to mid-successional stands, consistent with saturation of diversity effects and successional niche predictions for
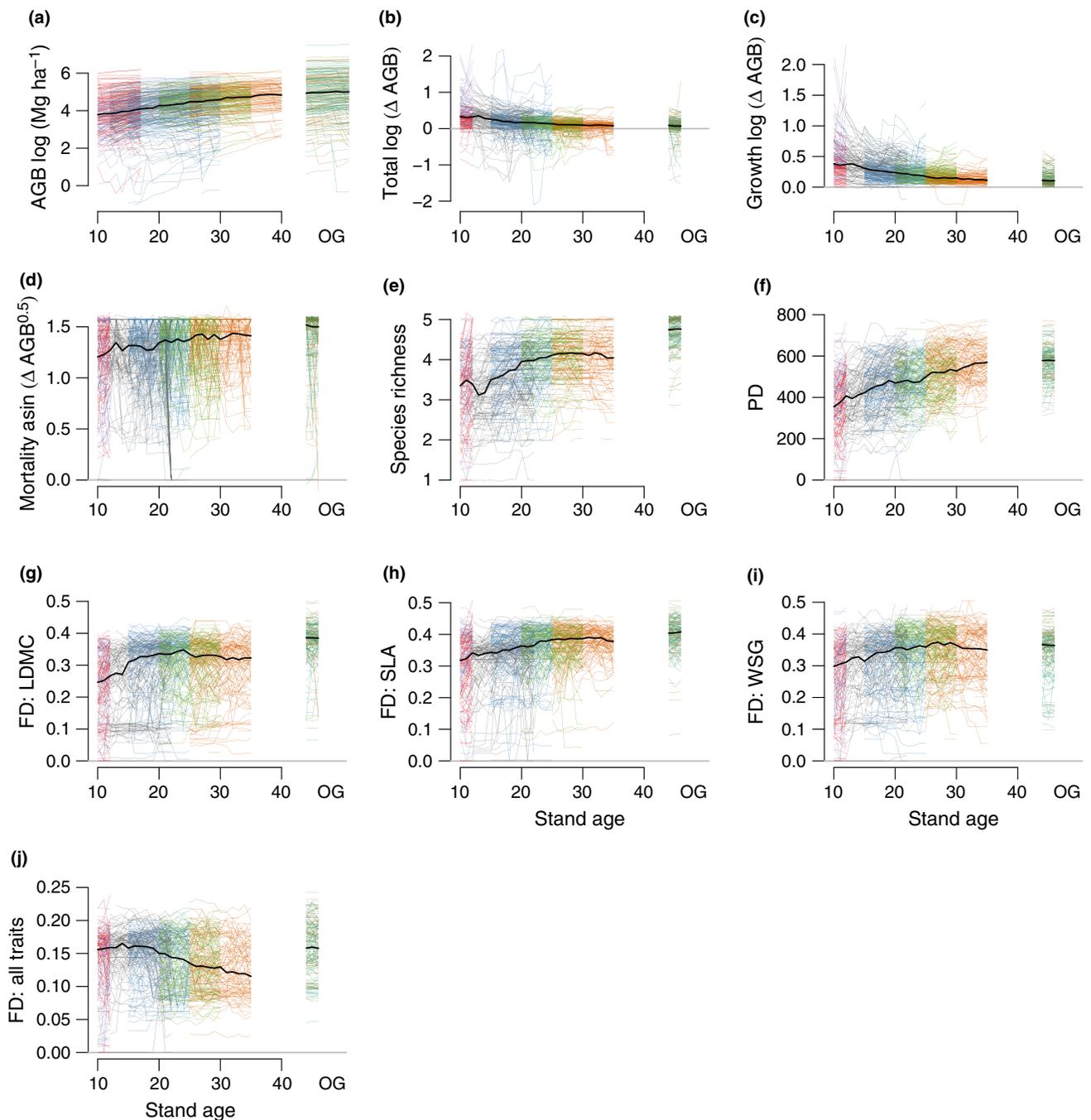
**Figure 2** Change in AGB (a–d) and diversity (e–j) in 100-m² quadrats (represented by coloured lines) within 1-ha study plots (represented by unique colours). Black lines represent the median of quadrat values for each stand age. OG = old growth. (a) Total AGB across 16 annual censuses. (b–f) Variables used in regression of diversity relationships with Δbiomass over 5-year intervals. The final 4 years of data are not shown because 5-year intervals were incomplete. (b) total Δbiomass. (c) Δbiomass due to growth. (d) Δbiomass due to mortality. (e) Rarified quadrat species richness (rarified to five sampled stems). (f) Rarified quadrat phylogenetic diversity (PD, millions of years). (g–j) Rarified quadrat functional diversity (FD); LDMC = leaf dry matter content, SLA = specific leaf area, WSG = wood specific gravity, measured as a proportion of maximum possible. Noise was added to the y-axis values of (d) and (e) for visualisation.

Δbiomass due to mortality (Fig. 3). Diversity of specific leaf area (FD$_{SLA}$) and leaf dry matter content (FD$_{LDMC}$) exhibited the strongest successional changes, where relationships with total Δbiomass shifted from positive (early-successional stands) to negative (mid-successional stands) to positive (old-growth stands) across succession (significant in early- and mid-successional stands).

In general, successional changes in the relationship between diversity and Δbiomass due to mortality were similar to successional changes in the relationship between diversity and total biomass change (i.e. all demographic sources of Δbiomass). The shift from positive to negative diversity relationships from early- to mid-successional stands was most pronounced in Δbiomass due to mortality. By contrast,
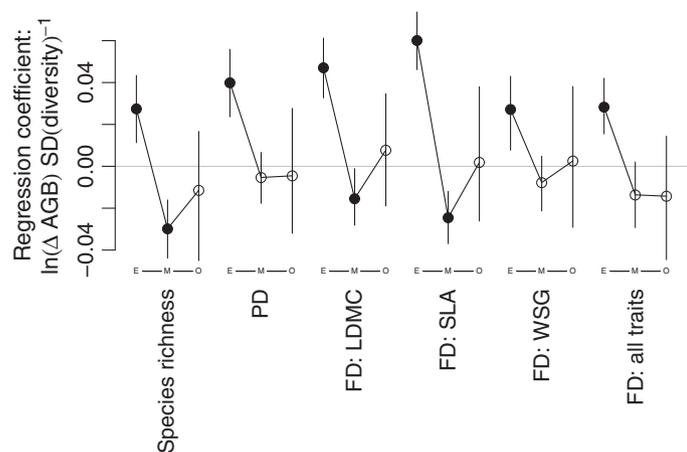
**Figure 3** Standardised regression coefficients determining the relationship between taxonomic (species richness), phylogenetic (PD) or functional diversity (FD) and Δbiomass (log proportional change) over 5-year intervals. Lines connect three circles representing plots categorised as early-successional (E), mid-successional (M) or old-growth (O) stands. Note that some plots aged from early-successional into the mid-successional category during the study. Circles show posterior means and vertical lines represent 95% credibility intervals (CIs). Closed circles represent significant effects (i.e. 95% CIs exclude zero). The y-axis units are log (Δbiomass) per standard deviation change in diversity. For example, early in succession the estimated slope of $FD_{SLA}$ is 0.06 corresponding to a 6.2% increase in Δbiomass for an increase of one SD ($FD_{SLA}$).



**Figure 4** Standardised regression coefficients determining the effect of biodiversity on (a) Δbiomass due to growth and (b) Δbiomass due to mortality. Lines connect three circles representing plots categorised as early-successional (E), mid-successional (M) or old growth (O). Note that some plots aged from early-successional into the mid-successional category during the study. Circles show posterior means and vertical lines represent 95% CIs. Closed circles represent significant effects (i.e. 95% CIs exclude zero). The y-axis units are transformed Δbiomass per standard deviation change in diversity. For example, early in succession the estimated slope of $FD_{All\ traits}$ for growth is 0.03, corresponding to a 3.2% increase in Δbiomass due to growth for an increase of one SD ($FD_{All\ traits}$).

positive diversity relationships with Δbiomass due to growth became weaker with succession, and finally negative in the case of FDAll traits in old-growth stands (Fig. 4). Consistent with predictions of successional niche theory, higher diversity in early-successional stands was associated with lower AGB losses to mortality, whereas higher diversity in mid-successional stands was associated with greater losses of AGB to mortality, with old-growth stands tending to be intermediate. All but one metric of diversity ($FD_{All\ traits}$) had a significantly positive relationship with Δbiomass due to mortality in early succession, a pattern that reversed in mid-successional stands. In mid-successional stands, all dimensions of diversity had significantly negative correlations with Δbiomass due to mortality.

## DISCUSSION

We identified key dimensions of diversity positively associated with aboveground tree biomass dynamics, knowledge that may be important to managing ecosystem function (Naeem *et al.* 2012). Diversity relationships with Δbiomass due to growth were often opposite to those of Δbiomass due to mortality, suggesting interspecific productivity–mortality trade-offs indicative of successional niches. In addition, we found that diversity–Δbiomass relationships weakened or became more negative with succession, suggesting potential saturation of diversity effects. Relationships between biodiversity and ecosystem function have been documented in a variety of systems, although these relationships can be non-linear, non-monotonic, or ambiguous (Balvanera *et al.* 2006; Flynn *et al.* 2011; Zhang
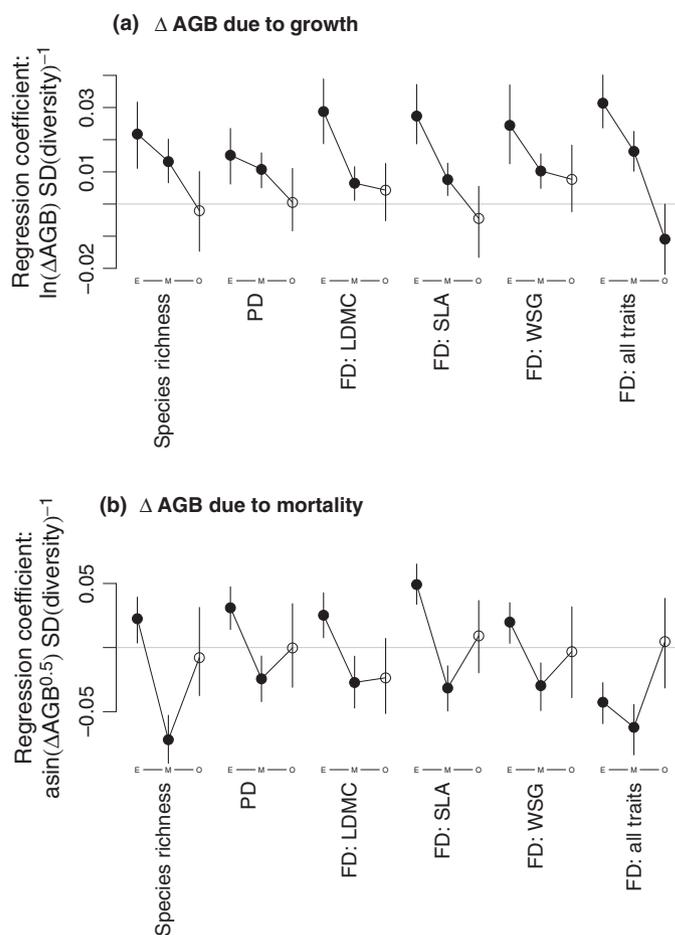
*et al.* 2012). The lack of clarity may partly stem from variation among studies in the mechanisms that drive community diversity, *e.g.* due to the successional stage of study systems (Mouquet *et al.* 2002). The few previous studies of succession and BEF relationships also suggest that positive BEF relationships may be strongest early in succession (Balvanera *et al.* 2006; Weis *et al.* 2007; Ruiz-Jaen & Potvin 2011; Livingston *et al.* 2012; but see Zhang *et al.* 2012). Relative to old-growth forests, successional forests exhibit rapid change in composition and diversity (Chazdon 2008), but few studies of BEF have been conducted along successional gradients.

### Distinct diversity relationships across dimensions of biodiversity

Our results point towards multiple mechanisms driving BEF relationships in successional tropical forests. Here, the

significant positive relationships between phylogenetic and leaf trait diversity and Δbiomass are consistent with our previous findings suggesting that phylogenetic and leaf trait diversity are associated with niche complementarity and increasing diversity over succession (Norden *et al.* 2012; Lasky *et al.* 2014). Results from other tropical forests suggest that these traits are related to key axes of niche variation (Lohbeck *et al.* 2012) and further support the role for niche complementarity in affecting positive diversity–Δbiomass relationships at our site. We found that multivariate trait diversity was distinct: it was negatively associated with Δbiomass due to mortality early in succession, negatively associated with Δbiomass due to growth in old-growth forests, and did not increase across succession. Multivariate functional diversity might diverge from other dimensions of diversity if certain trait combinations affect competitive ability, i.e. trait interactions, and generate negative selection effects.

Species richness, phylogenetic diversity, diversity of leaf dry matter content (LDMC), diversity of SLA and diversity of WSG all exhibited significant shifts from positive to negative mortality relationships during succession (Fig. 4b). The shift in the association of phylogenetic diversity with biomass lost to mortality may have been partly driven by all three functional traits, each of which had a significant phylogenetic signal. Our findings for WSG diversity are consistent with our previous findings that high WSG is associated with competitive dominance by old-growth species over pioneer species (Lasky *et al.* 2014), suggesting that WSG is involved in the trade-off between productivity and mortality. Here, we found weak increases in WSG richness with succession, although we previously showed that abundance-weighted WSG diversity decreases with succession, consistent with a WSG-dominance hypothesis (Lasky *et al.* 2014). Low WSG likely confers greater productivity because it allows rapid growth to the canopy, whereas high WSG confers greater survival through resistance to disease, drought and physical damage (Chave *et al.* 2009). Previous studies finding unimodal or negative relationships between species richness and stand mean WSG in older forests (ter Steege & Hammond 2001; Slik *et al.* 2008) support the hypothesis that WSG is related to successional niche dynamics. In Borneo and Guyana, stands dominated by species with high WSG had lower taxonomic diversity than stands with moderate disturbance, suggesting that intermediate disturbance allows the presence of species with low WSG in addition to more persistent dense-wooded species (ter Steege & Hammond 2001; Slik *et al.* 2008).

The dramatic change in the relationship between leaf trait diversity ($FD_{SLA}$ and $FD_{LDMC}$) and Δbiomass from early- to mid-succession signifies that these traits may be involved in both local niche complementarity and successional niche differences. Previous evidence from our study site (Lasky *et al.* 2014) and others (Roscher *et al.* 2012) suggests that these traits are involved in niche partitioning among neighbours, possibly due to resource partitioning. That diversity in these traits was strongly positively related to Δbiomass due to both growth and survival early in succession is contrary to predictions of successional niche theory (Kinzig & Pacala 2001) and is consistent with the presence of additional mechanisms such

as local niche partitioning. However, SLA is also a key trait associated with a trade-off between construction costs and leaf lifespan, which may drive organismal and species-level trade-offs between biomass productivity vs. persistence (Blonder *et al.* 2011; Roscher *et al.* 2012) In addition, we previously showed that high species LDMC was associated with high survival rates (Lasky *et al.* 2014), indicating that the shift from positive to negative $FD_{LDMC}$–Δbiomass relationships may have been driven by an association between LDMC and successional niche specialisation.

### Distinct biodiversity–Δbiomass relationships for growth vs. mortality

All dimensions of diversity except $FD_{All\ traits}$ showed significantly positive relationships with Δbiomass relationships due to mortality in early succession that became negative in mid-successional stands. The low mortality in high diversity early-successional stands may reflect several mechanisms, for example, niche complementarity and positive selection effects among early-successional species. Greater mortality in highly crowded, higher diversity mid-successional stands is consistent with predictions of successional niche theory, where co-occurrence of pioneers and late-successional species early in succession gives way over time to exclusion of pioneers by late-successional species (Pacala & Rees 1998; Caspersen & Pacala 2001; Kinzig & Pacala 2001; Mouquet *et al.* 2002; Livingston *et al.* 2012).

In contrast to total Δbiomass and Δbiomass due to mortality, diversity relationships with Δbiomass due to growth were always positive in mid-successional stands. If mid-successional diversity is driven by co-occurrence of pioneers, generalists and late-successional species, this positive relationship is consistent with higher productivity by pioneers and the positive BEF relationship predicted later in succession by successional niche models (Caspersen & Pacala 2001; Kinzig & Pacala 2001). Similarly, in Panama, Healy *et al.* (2008) found that diversity effects on biomass growth were more positive than for mortality, and in North America, Caspersen & Pacala (2001) found that greater successional niche diversity was associated with greater biomass growth in both early- and late-successional stands.

The opposing diversity relationships with growth vs. mortality observed in mid-successional stands in our study may have weakened the total Δbiomass–diversity relationship. Although successional niche BEF theory (Caspersen & Pacala 2001) predicts that late-successional species exclude pioneers, it does not predict how diversity is associated with transient biomass dynamics due to pioneer mortality. In our study forests, mid-successional biomass losses to tree mortality occur in large discrete quantities (i.e. through the death of individual trees), suggesting a potential avenue for further development of individual-based successional niche BEF theory. Discrete individual-based models of stand dynamics may be required to further explore this theoretical question (Pacala *et al.* 1996). The contrasting patterns of Δbiomass due to growth vs. mortality highlight the importance of considering competitive effects and responses, growth–mortality trade-offs, and multiple simultaneous BEF mechanisms.

## Successional change in biodiversity–Δbiomass relationships

We demonstrated that BEF relationships often shifted from positive early in succession to weakly negative or not significant in mid-successional and old-growth stands (Fig. 3). This pattern is consistent with increasing diversity across succession, which we observed at our sites (Fig. 2; Norden *et al.* 2012; Lasky *et al.* 2014), and with predicted saturating effects of high biodiversity on ecosystem function (Tilman *et al.* 1997; Loreau 1998). However, our separate analyses of diversity–Δbiomass relationships due to growth vs. mortality suggest that the true cause of successional changes may be more complex, involving stem and species turnover due to internal stand dynamics – a pattern consistent with multiple successional BEF hypotheses. Only one dimension of diversity (multivariate functional diversity of all traits) was significantly associated with AGB dynamics in old-growth forests, suggesting that in these high diversity stands (Fig. 2) positive BEF effects have largely saturated at the scale of our analysis.

## CONCLUSIONS

In summary, our findings support two hypotheses for successional BEF change: (1) an increase in diversity and simultaneous saturation of BEF effects, and (2) the effects of competitive response and effect trade-offs associated with successional niches on AGB dynamics. Our results demonstrate that BEF relationships are dynamic across succession, thus successional context is essential to understanding BEF in a given system. Furthermore, our findings shed light on the drivers of ecosystem change in successional tropical forests, a system of great interest for global biodiversity conservation and carbon cycling (Chazdon 2008). Additional long-term studies are required to understand BEF relationships in forests due to the long lifespan of trees and the possibility that BEF effects accumulate over time (Tilman *et al.* 2001).

## AUTHORSHIP

JRL designed and conducted analyses. MU oversaw analyses. VKB collected trait data. DLE and WJK performed molecular and phylogenetic analyses. RLC designed and collected census data. JRL, MU, VKB and RLC conceived the conceptual framework. All authors contributed to writing the manuscript.

## REFERENCES

Balvanera, P., Pfisterer, A.B., Buchmann, N., He, J.-S., Nakashizuka, T., Raffaelli, D. *et al.* (2006). Quantifying the evidence for biodiversity effects on ecosystem functioning and services. *Ecol. Lett.*, 9, 1146–1156.

Blonder, B., Violle, C., Bentley, L.P. & Enquist, B.J. (2011). Venation networks and the origin of the leaf economics spectrum. *Ecol. Lett.*, 14, 91–100.

van Breugel, M., Ransijn, J., Craven, D., Bongers, F. & Hall, J.S. (2011). Estimating carbon stock in secondary forests: decisions and uncertainties associated with allometric biomass models. *For. Ecol. Manag.*, 262, 1648–1657.

Brown, S. (1997). *Estimating Biomass and Biomass Change of Tropical Forests: A Primer*. Food & Agriculture Org, Rome.

Caspersen, J.P. & Pacala, S.W. (2001). Successional diversity and forest ecosystem function. *Ecol. Res.*, 16, 895–903.

Chave, J., Andalo, C., Brown, S., Cairns, M.A., Chambers, J.Q., Eamus, D. *et al.* (2005). Tree allometry and improved estimation of carbon stocks and balance in tropical forests. *Oecologia*, 145, 87–99.

Chave, J., Coomes, D., Jansen, S., Lewis, S.L., Swenson, N.G. & Zanne, A.E. (2009). Towards a worldwide wood economics spectrum. *Ecol. Lett.*, 12, 351–366.

Chazdon, R.L. (2008). Chance and determinism in tropical forest succession. In: *Tropical Forest Community Ecology* (eds. Carson, W.P. & Schnitzer, S.A.). Wiley-Blackwell, Chichester, UK, pp. 384–408.

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

Chesson, P., Pacala, S. & Neuhauser, C. (2001). Environmental niches and ecosystem functioning. *Funct.* Consequences Biodivers. Princeton University Press, Prince, pp. 213–245.

Clark, D.A., Brown, S., Kicklighter, D.W., Chambers, J.Q., Thomlinson, J.R., Ni, J. *et al.* (2001). Net primary production in tropical forests: an evaluation and synthesis of existing field data. *Ecol. Appl.*, 11, 371–384.

Cornelissen, J.H.C., Lavorel, S., Garnier, E., Díaz, S., Buchmann, N., Gurvich, D.E. *et al.* (2003). A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. *Aust. J. Bot.*, 51, 335–380.

Faith, D.P. (1992). Conservation evaluation and phylogenetic diversity. *Biol. Conserv.*, 61, 1–10.

Flynn, D.F.B., Mirotchnick, N., Jain, M., Palmer, M.I. & Naeem, S. (2011). Functional and phylogenetic diversity as predictors of biodiversity–ecosystem-function relationships. *Ecology*, 92, 1573–1581.

Gamfeldt, L., Snall, T., Bagchi, R., Jonsson, M., Gustafsson, L., Kjellander, P. *et al.* (2013). Higher levels of multiple ecosystem services are found in forests with more tree species. *Nat Commun*, 4, 1340.

Goldberg, D.E. (1990). Components of resource competition in plant communities. In: *Perspectives on Plant Competition* (eds. Grace, J.B. & Tilman, D.). Academic Press, San Diego. 27–49.

Goldberg, D.E. & Landa, K. (1991). Competitive effect and response: hierarchies and correlated traits in the early stages of competition. *J. Ecol.*, 79, 1013–1030.

Gotelli, N.J. & Colwell, R.K. (2011). Estimating species richness. *Biological Diversity: Frontiers in Measurement and Assessment* (eds. Magurran, A.E. & McGill, B.J.). Oxford University Press, Oxford. 39–54.

Grime, J.P. (1998). Benefits of plant diversity to ecosystems: immediate, filter and founder effects. *J. Ecol.*, 86, 902–910.

Healy, C., Gotelli, N.J. & Potvin, C. (2008). Partitioning the effects of biodiversity and environmental heterogeneity for productivity and mortality in a tropical tree plantation. *J. Ecol.*, 96, 903–913.

Kembel, S.W., Cowan, P.D., Helmus, M.R., Cornwell, W.K., Morlon, H., Ackerly, D.D. *et al.* (2010). Picante: R tools for integrating phylogenies and ecology. *Bioinformatics*, 26, 1463–1464.

Kinzig, A.P. & Pacala, S.W. (2001). Successional biodiversity and ecosystem functioning. In: *The functional consequences of biodiversity: empirical progress and theoretical extensions* (eds. Kinzig, A.P., Pacala, S. & Tilman, G.D.), Princeton University Press, Princeton, pp. 175–212.

Kress, W.J., Erickson, D.L., Swenson, N.G., Thompson, J., Uriarte, M. & Zimmerman, J.K. (2010). Advances in the use of DNA barcodes to build a community phylogeny for tropical trees in a Puerto Rican forest dynamics plot. *PLoS ONE*, 5, e15409.

Lasky, J.R., Uriarte, M., Boukili, V. & Chazdon, R.L. (2014). Trait-mediated assembly processes predict successional changes in community diversity of tropical forests. *Proc. Natl Acad. Sci.*, 111, 5616–5621.

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

Livingston, G., Matias, M., Calcagno, V., Barbera, C., Combe, M., Leibold, M.A. *et al.* (2012). Competition-colonization dynamics in experimental bacterial metacommunities. *Nat Commun*, 3, 1234.

Lohbeck, M., Poorter, L., Paz, H., Pla, L., van Breugel, M., Martínez-Ramos, M. *et al.* (2012). Functional diversity changes during tropical forest succession. *Perspect. Plant Ecol. Evol. Syst.*, 14, 89–96.

Loreau, M. (1998). Biodiversity and ecosystem functioning: a mechanistic model. *Proc. Natl Acad. Sci.*, 95, 5632–5636.

Miller, M.A., Pfeiffer, W. & Schwartz, T. (2010). Creating the CIPRES Science Gateway for inference of large phylogenetic trees. In: *Gateway Computing Environments Workshop (GCE), 2010*. IEEE, DOI: 10.1109/GCE.2010.5676129.

Mouquet, N., Moore, J.L. & Loreau, M. (2002). Plant species richness and community productivity: why the mechanism that promotes coexistence matters. *Ecol. Lett.*, 5, 56–65.

Naeem, S., Duffy, J.E. & Zavaleta, E. (2012). The functions of biological diversity in an age of extinction. *Science*, 336, 1401–1406.

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

Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O'Hara, R.B. *et al.* (2013). *vegan: Community Ecology Package*. Available at: http://CRAN.R-project.org/package = vegan.

Pacala, S.W. & Rees, M. (1998). Models suggesting field experiments to test two hypotheses explaining successional diversity. *Am. Nat.*, 152, 729–737.

Pacala, S.W., Canham, C.D., Saponara, J., Silander, J.A., Kobe, R.K. & Ribbens, E. (1996). Forest models defined by field measurements: estimation, error analysis and dynamics. *Ecol. Monogr.*, 66, 1–43.

Paquette, A. & Messier, C. (2011). The effect of biodiversity on tree productivity: from temperate to boreal forests. *Glob. Ecol. Biogeogr.*, 20, 170–180.

Petchey, O.L. & Gaston, K.J. (2002). Functional diversity (FD), species richness and community composition. *Ecol. Lett.*, 5, 402–411.

Roscher, C., Schumacher, J., Gubsch, M., Lipowsky, A., Weigelt, A., Buchmann, N. *et al.* (2012). Using plant functional traits to explain diversity-productivity relationships. *PLoS ONE*, 7, e36760.

Ruiz-Jaen, M.C. & Potvin, C. (2011). Can we predict carbon stocks in tropical ecosystems from tree diversity? Comparing species and functional diversity in a plantation and a natural forest. *New Phytol.*, 189, 978–987.

Sanford, R.L., Paaby, P., Luvall, J.C. & Phillips, E. (1994). Climate, geomorphology, and aquatic systems. *Ecol. Nat. Hist. Neotropical Rain For. U, Chic*, pp. 19–33.

Slik, J.W.F., Bernard, C.S., Breman, F.C., Van Beek, M., Salim, A. & Sheil, D. (2008). Wood density as a conservation tool: quantification of disturbance and identification of conservation-priority areas in tropical forests. *Conserv. Biol.*, 22, 1299–1308.

Sollins, P., Sancho M., F., Mata Ch., R. & Sanford, Jr, R.L. (1994). Soils and Soil Process Research. In: *La Selva: Ecology and Natural History of a Neotropical Rain Forest* (eds McDade, L.A., Bawa, K.S., Hespenheide, H.A. & Hartshorn, G.S.), The University of Chicago Press, Chicago, IL, pp. 34–53.

ter Steege, H. & Hammond, D.S. (2001). Character convergence, diversity, and disturbance in tropical rain forest in Guyana. *Ecology*, 82, 3197–3212.

Tilman, D., Lehman, C.L. & Thomson, K.T. (1997). Plant diversity and ecosystem productivity: theoretical considerations. *Proc. Natl Acad. Sci.*, 94, 1857–1861.

Tilman, D., Reich, P.B., Knops, J., Wedin, D., Mielke, T. & Lehman, C. (2001). Diversity and productivity in a long-term grassland experiment. *Science*, 294, 843–845.

Uriarte, M., Canham, C.D., Thompson, J. & Zimmerman, J.K. (2004). A neighborhood analysis of tree growth and survival in a hurricane-driven tropical forest. *Ecol. Monogr.*, 74, 591–614.

Weis, J.J., Cardinale, B.J., Forshay, K.J. & Ives, A.R. (2007). Effects of species diversity on community biomass production change over the course of succession. *Ecology*, 88, 929–939.

Zhang, Y., Chen, H.Y.H. & Reich, P.B. (2012). Forest productivity increases with evenness, species richness and trait variation: a global meta-analysis. *J. Ecol.*, 100, 742–749.

Zwickl, D.J. (2008). Genetic algorithm approaches for the phylogenetic analysis of large biological sequence datasets under the maximum likelihood criterion. PhD Dissertation. University of Texas at Austin.

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