Abiotic and biotic drivers of biomass change in a Neotropical forest

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Abstract

1. Tropical forests play an important role in the global carbon cycle, but the drivers of net forest biomass change (i.e., net carbon sequestration) are poorly understood. Here, we evaluate how abiotic factors (soil conditions and disturbance) and biotic factors (forest structure, diversity and community trait composition) shape three important demographic processes (biomass recruitment, growth, and mortality) and how these underlie net biomass change.

2. To test this, we evaluated 9 years of biomass dynamics using 48 1-ha plots in a Bolivian tropical moist forest, and measured for the most abundant species eight functional traits that are important for plant carbon gain and loss. Demographic processes were related to the abiotic and biotic factors using structural equation models.

3. Variation in net biomass change across plots was mostly due to stand-level mortality, but mortality itself could not be predicted at this scale. Contrary to expectations, we found that species richness and trait composition – which is an indicator for the mass-ratio theory – had little effect on the demographic processes. Biomass recruitment (i.e., the biomass growth by recruiting trees) increased with higher resource availability (i.e., water and light) and with high species richness, probably because of increased resource use efficiency. Biomass growth of larger, established trees

increased with higher sand content, which may facilitate root growth of larger trees to deeper soil layers.

4. In sum, diversity and mass-ratio are of limited importance for the productivity of this forest. Instead, in this moist tropical forest with a marked dry season, demographic processes are most strongly determined by soil texture, soil water availability and forest structure. Only by simultaneously evaluating multiple abiotic and biotic drivers of demographic processes, better insights can be gained into mechanisms playing a role in the carbon sequestration potential of tropical forests and natural systems in general.

Introduction

Tropical forests play an important role in global carbon storage (Saatchi *et al.* 2011) and sequestration (Malhi 2012), and hence, in climate change mitigation strategies (e.g., Reduced Emissions from Deforestation and forest Degradation; REDD+). Yet, it is still poorly understood what factors are driving net forest biomass change and, thus, net carbon sequestration (Malhi 2012). At the stand-level, net biomass change is the result of three underlying demographic processes of biomass change; recruitment, growth and mortality. These demographic processes should be analysed individually to understand net biomass change, as each process may be driven by different biotic factors (e.g., the diversity and trait composition of the forest) and abiotic factors (e.g., soil properties and light availability) (see the conceptual framework in Fig. 1).

To explain biotic effects on demographic processes, several theories have been put forward: a group of diversity theories and the mass-ratio theory (Grime 1998). Diversity effects can have multiple underlying mechanisms. According to the niche differentiation theory (Tilman 1999), high diversity increases the overall resource use efficiency of a community, leading to increased growth rates. Diversity could also increase overall growth rates due to facilitation among species (Hooper *et al.* 2005) or due to weaker effects of species-specific pathogens (Schnitzer *et al.* 2011). A positive effect of species diversity on productivity (i.e., growth) was found for herbaceous communities (Tilman *et al.* 2001) and forest ecosystems (Balvanera *et al.* 2006; Paquette & Messier 2011). However, rather than the number of species, the identity of species and their traits are thought to provide a more direct and mechanistic link with forest processes (Violle *et al.* 2007). Variation in plant traits positively affected productivity in grasslands (Tilman et al. 1997) and temperate forests (Butterfield & Suding 2013), but its effect may be different for diverse tropical forests where trait redundancy between species may not further enhance forest growth (Walker 1992).

Grime's (1998) mass-ratio theory predicts that ecosystem processes are driven by the characteristics of the most dominant species in the community, which in turn partly depend on local abiotic conditions. The trait values of the most abundant species are reflected in the 'trait composition', i.e., average basal-area weighted leaf and stem trait values of the community. Few studies have simultaneously evaluated the relative importance of taxonomic diversity (i.e., species diversity), trait diversity and trait composition on demographic processes in natural communities. Mokany et al. (2008) found in temperate grasslands that trait composition is a stronger driver of productivity than taxonomic diversity. Similarly, Finegan et al. (2015) found across three tropical forests that trait composition, and not trait diversity, determined productivity, whereas Lohbeck et al. (2015) found that during secondary forest

succession, neither trait composition nor trait diversity, but aboveground biomass had a positive effect on productivity. Hence, the relative importance of taxonomic and trait effects in natural systems remains poorly understood and may depend on various factors, such as local abiotic or biotic conditions. Here, we evaluate the independent and causal effects of diversity and trait composition using a structural equation modelling approach.

Abiotic factors are strong drivers of demographic processes as they determine resource availability for plant growth and survival (Fig. 1). For example, soil conditions are key drivers of tropical forest growth across the Amazon (Quesada et al. 2012) and locally (Paoli, Curran & Zak 2005), and disturbance, e.g. due to natural tree falls or logging, can increase light availability and therefore the opportunity for higher rates of recruitment and growth (Peña-Claros *et al.* 2008). Abiotic factors can also have an indirect effect on demographic processes, via their effects on biotic factors (Fig. 1). Across the Neotropics, trait composition reflects differences in climate and soil fertility (van der Sande *et al.* 2016). At a more local scale in African forests, sandy soils, compared to clayey soils, had a higher abundance of species with high wood density that are more drought tolerant and better survive on sandy and resource-limited soils (Fayolle *et al.* 2012). In our study forest, disturbance due to logging treatments changed the trait composition of demographic groups towards more acquisitive trait values (e.g., high specific leaf area and low wood density) that are typical of pioneer species that benefit from higher light-levels (Carreño-Rocabado *et al.* 2012). Moreover, disturbance alters the forest structure (e.g., decreases plot basal area), which may in turn result in a change in species diversity (Armesto & Pickett 1985). Consequently, forest structure can determine demographic processes directly, but also indirectly via its effects on the diversity and trait composition of different demographic groups (Vilà *et al.* 2013). These studies show that abiotic factors can affect the biotic factors, but they did not evaluate how the biotic factors in

turn affect demographic processes (but see Vilà et al. 2013). To our knowledge, there is only one study that combined effects of abiotic and biotic factors on demographic processes that underlie net biomass change in forest systems (Prado-Junior *et al.* 2016).

We address two questions. First, how are demographic processes (biomass growth by recruits (i.e., recruitment), by survivors (i.e., growth) and biomass mortality) driven by abiotic factors (soil conditions and disturbance due to logging) and biotic factors (forest structure, taxonomic and trait diversity, and trait composition)? We expect that i) biomass recruitment and growth increase with light availability and, hence, with an open forest structure and disturbance. Mortality of small trees would decrease with resource availability and conservative trait values (Poorter & Bongers 2006), but mortality of larger trees that mainly determine total biomass mortality would depend more on individual senescence or stochastic winds and therefore not strongly on the abiotic and biotic factors we measured; ii) biomass recruitment and growth increase when their demographic group has high species or trait richness (as predicted by diversity theories) and an acquisitive trait composition (as predicted by mass-ratio theory); and iii) trait composition has a stronger effect on demographic processes than diversity because the bulk of these processes are determined by the dominant species. Secondly we ask: how do these demographic processes contribute to variation in net biomass change? We expect that variation in mortality most strongly contributes to variation in net biomass change because mortality would have highest absolute biomass values due to the presence of large trees, followed by growth and recruitment. We tested these hypotheses using long-term data of 48 1-ha forest plots in a tropical moist forest in Bolivia with strong gradients in demographic processes and abiotic and biotic variables.

Materials and Methods

Research site and plots

Research was carried out in the moist, semi-deciduous forest of La Chonta, Santa Cruz, Bolivia (15°47'S, 62°55'W). Mean annual rainfall is 1580 mm, with a dry season from April until September when precipitation is <100 mm, and mean annual temperature is 24.3 °C. The forest is located on ultisols, with sandy-loam soils that are neutral in pH and rich in nutrients (Peña-Claros *et al.* 2012), and topography is homogeneous (Peña-Claros *et al.* 2008). On average, the forest has 367 stems (>10 cm DBH), 59 species per ha, and a canopy height of 25 m (Peña-Claros *et al.* 2012).

For this study, we used 48 one-hectare (100 x 100 m) permanent sample plots of the Long-Term Silvicultural Research Program (LTSRP) managed by Instituto Boliviano de Investigación Forestal (IBIF), in which all trees larger than 10 cm in diameter at breast height (DBH) were first recorded between September 2000 and December 2001. Plots were established in areas with similar vegetation type and topography (Peña-Claros *et al.* 2008). After the initial census, four treatments were applied, each on 12 plots using a randomized block design. The treatments varied in the intensity of logging and silvicultural practices applied, from an unlogged control treatment to an intensive silvicultural treatment with post-logging activities such as girdling to liberate trees from overtopping non-commercial trees (see Peña-Claros et al. 2008 for more details on treatments). Due to the heterogeneous nature of forests and logging activities, the actual intensity of logging varied strongly within treatments and overlapped among treatments (Peña-Claros *et al.* 2008). We therefore here consider logging intensity as a continuous variable. The most recent census was done for 16 plots in 2009, for 16 plots in 2010, and for 16 plots in 2011 (each time for four plots per treatment).

Demographic processes

We calculated three demographic processes: biomass recruitment by recruiting trees, biomass growth by surviving trees, and biomass mortality by dying trees (in Mg ha^{-1} yr^{-1}). Henceforth, these will be referred to as *recruitment, growth, and mortality*, respectively. Hence, our demographic processes refer to the annual rate of biomass increase and loss rather than to changes in abundance. We calculated demographic processes between the pre-logging census and the last post-logging census. We used a long census interval of 8-10 years to reduce the effect of stochastic variation in biomass dynamics. Palms were excluded from the analyses because they do not have radial growth and thus their growth is hard to estimate, and because they have outlying trait values that would affect the relation between trait composition and demographic processes. Since we focus on natural demographic processes, we excluded all trees that were logged or that died due to logging activities (e.g., due to damage caused by logging operations or due to post-logging silvicultural treatments). Hence, all mortality should represent natural mortality. We also excluded trees that died due to fire that took place in 2004 in 4 of the plots. These excluded trees were also excluded for calculations of other variables (i.e., forest structure, diversity and trait composition), but used to calculate the disturbance intensity (see 'Disturbance').

For each tree and each of the two census years, we calculated the aboveground biomass using the equation from Chave et al. (2014):

$$Biomass = exp(-1.803-0.976*(E)+0.976*log(WD)+2.673*log(DBH)-0.0299*(log(DBH))^2)$$

where DBH is the diameter at breast height (in cm) and WD is the wood density (in g cm^{-3}, see explanation in Appendix S1). *E* is a measure of environmental stress experienced at the site, which depends on temperature seasonality and water deficit. We calculated the *E*-value

(see Chave et al. 2014) for 26 sites across Bolivia for which we had accurate rainfall data (using data from Toledo 2010), and predicted the *E*-value of La Chonta based on the relation between locally available annual rainfall and the *E*-value for these surrounding Bolivian sites ($E_{predicted}= 0.776 - 0.000356 *$ precipitation; $R^2 = 0.79$). This resulted in the *E*-value 0.25 for La Chonta.

Recruitment, growth, mortality, and net biomass change

Recruitment (Mg ha^{-1} yr^{-1}) was based on recruited trees after the first census. Per individual, biomass recruitment was calculated as its biomass in the last census minus its biomass for a DBH of 10 cm. In this way, we assumed that the recruits were 10 cm DBH just after the initial census, and calculate growth based on the increase in diameter from 10 cm until its measured diameter in the last census. This may slightly underestimate biomass recruitment, as most trees may have reached the 10 cm limit later during the census interval, but it should yield more accurate estimations than assuming that recruits were 0 cm DBH (which would lead to stronger overestimations of growth), and similar estimations as using the tree's growth rate during other censuses to predict when it reached the 10 cm limit (Talbot *et al.* 2014). Total annual recruitment per plot was calculated by summing the recruitment per plot and dividing this by the census length.

   Growth (Mg ha^{-1} yr^{-1}) was based on the growth of trees that were present at the first census and survived until the last census. It was calculated by subtracting the biomass of a tree in the last census from the biomass of the same tree in the first census. By summing all growth values per plot and dividing it by the census length (in years), we obtained annual growth per hectare.

Mortality (Mg ha^{-1} yr^{-1}) was based on trees that died between the first and last census. It was calculated as the biomass of the tree in the initial census when it was still alive, minus its biomass for a DBH of 10 cm, to be able to compare biomass loss (i.e., mortality) with biomass gain (i.e., recruitment and growth) (Talbot *et al.* 2014). Annual mortality was obtained by summing mortality per plot and dividing this by the census length. Net biomass change was calculated per plot by summing recruitment and growth, and subtracting mortality.

Soil

For each plot, soil variables were collected in 2005 from the top 30 cm of the soil at 20 fixed locations distributed in each plot systematically. Collection was done after logging (which occurred in 2001) but samples were taken from areas that were not affected by logging, to represent pre-logging variation in soil conditions among plots. All samples were pooled per plot and brought to the Soil Laboratory of the Centro de Investigación Agricola Tropical (CIAT), Santa Cruz, Bolivia, for analyses of the following soil nutrients and conditions: calcium, magnesium, potassium, sodium, cation exchange capacity as the sum of all exchangeable cations and acidity (all in cmol kg^{-1}), total available phosphorus (mg kg^{-1}) using the Olson method, total nitrogen using the micro-Kjeldahl method (%), pH, and soil texture (sand content and clay content) (for more explanation, see Toledo 2010). Dry season soil water potential per plot (MPa), a measure for minimum soil water availability, was obtained from L. Markesteijn (unpublished data). Soil water potential was measured during the peak of the dry season (July 2007) (Markesteijn *et al.* 2010). One sample per plot was taken from the first 10 cm of the soil, and soil water potential was determined using the filter paper method (for a more extensive description, see Markesteijn et al. 2010). Note that soil water potential

was based on only one sample per plot, which may result in less accurate differences among plots and therefore in more conservative relationships with demographic processes.

Disturbance

We developed a continuous measure for disturbance, based on the basal area of all trees that died due to fire or logging (i.e., that were logged or died due to (post-)logging activities between the first and last census) relative to the total initial basal area of that plot, in %. The disturbed plots ranged from 0.1 % - 40.3 % in basal area loss.

Forest structure

We wanted to evaluate the effect of forest structure, as a measure of biotic competition for resources and space, on the diversity and trait composition of the demographic groups (i.e., the recruits, survivors and trees that died) and on demographic processes (Fig. 1). We therefore calculated several structural variables (based on trees >10 cm DBH), per plot and per census (all after disturbance), that would indicate abiotic competition for light and other resources: total plot basal area (m^2 ha^{-1}), tree density (ha^{-1}), average diameter at breast height (cm), and the basal area of "large trees" (all trees > 60 cm DBH; m^2 ha^{-1}). The values of the two censuses per plot were averaged to obtain one value per plot that would better represent the whole monitoring period.

Diversity

Diversity theories such as niche differentiation predict that diversity increases resource use efficiency and reduces competition, and as a result increases the overall productivity of the forest stand. We used taxonomic richness and functional trait richness to evaluate diversity in functioning among species. Although it is highly debated what processes (e.g., competition)

determine diversity (Mayfield & Levine 2010), our main interest is in understanding how diversity contributes to demographic processes and ultimately to net biomass change, and we will therefore not go into deep discussion of what causes variation in diversity. The indices were calculated based on all trees belonging to each specific demographic group (i.e., recruitment, growth and mortality), and calculated per plot and per census. We described taxonomic richness using rarefied species richness, calculated as the number of species found in a random sample of 50 individuals (as this number of individuals is found in all demographic groups per plot). We used rarefied richness to prevent that differences in stem number among plots would determine differences in species richness. Functional trait richness (Frich) was described as the amount of multivariate trait space occupied by species in the plot (Mason *et al.* 2005; Mouillot *et al.* 2005), and was based on all traits (Table 1). Values for taxonomic richness and trait richness of the initial and final census were averaged to obtain values that would better represent the whole census interval. Taxonomic richness was obtained using the *vegan* package (Oksanen *et al.* 2014), and trait richness using the *dbFD* function of the *FD* package in R (Laliberté, Legendre & Shipley 2015). Taxonomic and trait richness are hereafter collectively called 'diversity'.

Trait composition

Trait collection

We selected six leaf traits and two stem traits that are important components of the leaf- and stem economics spectra (Baraloto *et al.* 2010) and that are important for demographic processes (Table 1). Specific leaf area (SLA) and leaf mass fraction of the metamer (LMF_m) indicate the light interception efficiency per leaf investment and metamer investment, respectively, and leaf nitrogen (N_{mass}) and phosphorus (P_{mass}) concentration and chlorophyll content (Chl) are important for photosynthetic capacity and growth capacity. All these traits

would therefore increase the rate of the demographic processes. On the other hand, high specific force to punch (FPs; a measure for leaf toughness) and wood density (WD) are part of the shade-tolerant traits that increase survival (i.e., reduce mortality) but reduce growth. Maximum diameter (DBH_{max}) is a measure for tree longevity and life-history strategy, with high values indicating species that can benefit from high light levels in the upper canopy and have the capacity to grow fast.

All traits were determined for 161 tree species that together made up on average 97.5% of the basal area across the 48 permanent sample plots in the first and last census year. The community mean trait values weighted by species' basal area can be accurately determined if it is based on the species that together compose at least 80% of the abundance (Pakeman & Quested 2007), but a higher coverage is needed to accurately determine trait diversity (Pakeman 2014). Traits were measured on individuals between 10 and 20 cm DBH that were exposed to direct sunlight or high lateral light levels. See Appendix S1 for a more detailed description of trait data collection.

Trait composition indices

Grime's (1998) mass ratio theory states that ecosystem processes are driven by the characteristics of the most dominant species in the community. We calculated the trait composition (or average trait values) of the stand as the sum of the trait values of all species multiplied by their relative basal area, which is also known as the community-weighted mean (CWM, Pla et al. 2012). We used species' basal area rather than tree abundance because basal area scales better with biomass than abundance (Poorter *et al.* 2015), and hence, with biomass-driven demographic processes. For these calculations only the species were used for which trait data were available, which together made up 93-100% of the basal area in the plots

(averaged for the two census years). We calculated the CWM values based on the subset of trees belonging to the specific demographic group (i.e., trees that recruited, trees that survived, and trees that died), since their traits drive their biomass dynamics. The CWM values were calculated per plot and per census for each of the 8 traits, and values of the initial and final census per plot were averaged to represent the average trait composition of the community during the monitoring period. Note that diversity and trait composition are indices rather than direct measurements for different diversity theories and mass-ratio.

Statistical analyses

We evaluated how demographic processes that underlie net biomass change were affected by abiotic factors (soil conditions, disturbance) and biotic factors (forest structure, trait composition, and diversity). To do so, we wanted to develop one structural equation model (SEM) for each of the three demographic processes (Fig. 1). This SEM approach allows to take the direct and indirect effects and (cor)relations among variables into account, and has the additional advantage that it can test whether the overall model is "correct" (i.e., statistically accepted) and provides an accurate description of the data.

SEM can be performed in different ways. On the one extreme is the confirmatory approach, which is based on using a-priori knowledge and hypotheses to set up the model structure and its variables. On the other extreme is the exploratory approach, which explores different model structures and combinations of variables. The first approach can be useful for testing well-established theories or hypotheses, whereas the second approach can be useful when the exact relationships among variables and most relevant variables are unknown. Here, we use a partially confirmatory model (Appendix S2): the model structure is fixed because we know that abiotic conditions and biotic conditions can determine ecosystem processes, but we

have multiple candidate variables for the abiotic and biotic conditions because we did not have strong a priori hypotheses of which of these variables would be better predictors of demographic processes. We also performed a fully confirmatory model based on our expectations of which abiotic and biotic variables may matter most (see Appendix S3 for a description of the setup of the model, the results and interpretation).

For the partially confirmatory approach (which is further used in the main text), we had multiple candidate variables to use for soil conditions, forest structure, trait composition and diversity. Furthermore, the demographic processes may be driven by different aspects of abiotic and biotic factors (e.g., light availability for understory, recruiting trees and water availability for larger surviving trees). We therefore used multiple regression analyses to pre-select a maximum of two variables per abiotic and biotic factor, which led to maximum 2 * 2 * 2 * 2 = 16 possible SEMs per demographic process. In total we had 16 SEMs for biomass recruitment and growth and 8 SEMs for mortality (for which only one variable for forest structure was pre-selected). From these 8 or 16 SEMs per process, we selected the 'best' as the one that was accepted and had the highest R^2 for the demographic process. For more details on model selection, see Appendix S2. We had no a-priori hypothesis for a relationship between diversity and trait composition, as diversity is mainly determined by the presence of rare species while the trait composition is mainly determined by the most dominant species. Soil variables and disturbance were generally only weakly correlated (Appendix S4) and we therefore did not include this correlation in the SEMs. Recruitment and mortality were ln-transformed to meet the assumptions of equal variances and normal distribution of the residuals.

The relative contributions of the three demographic processes to the variation in net biomass change (N) were evaluated using the following three equations for growth (G), recruitment (R) and mortality (M): relative contribution of G = [var(G)+cov(R,G)-cov(G,M)]/var(N), relative contribution of R = [var(R)+cov(R,G)-cov(R,M)]/var(N), and relative contribution of M = [var(M)-cov(R,M)-cov(G,M)]/var(N). These calculations were done on the untransformed variables.

We performed all analyses in R 2.15.2. Linear models were evaluated using the lm function, and structural equation modelling was performed using the *sem* function of the *lavaan* package (Rosseel 2012).

Results

Across all plots, average net biomass change was 1.68 Mg ha^{-1} yr^{-1} ± 0.30 (average ± standard error), recruitment was 0.78 Mg ha^{-1} yr^{-1} ± 0.05, growth of surviving trees was 3.78 Mg ha^{-1} yr^{-1} ± 0.20, and mortality was 2.88 Mg ha^{-1} yr^{-1} ± 0.22.

The structural equation model for recruitment showed a strong negative effect of plot basal area (i.e., forest structure) on biomass recruitment. Disturbance increased recruitment directly, and also indirectly by reducing the basal area and thus reducing the negative effect of basal area on recruitment (Fig. 2a, Appendix S5a). High taxonomic richness was associated with an increased recruitment, whereas high sand content decreased recruitment (Fig. 3*a*, *d*, *g*, *j*, *m*).

The model for growth showed that plot basal area (i.e., forest structure) had a strong positive effect on growth (Fig. 2b, Appendix S5b), whereas soil water potential had a negative effect on growth, indicating that plots on wetter soils had slower biomass growth. Disturbance had an indirect negative effect on growth by decreasing the basal area of the growing stand (Fig. 2*b*, Fig. 3*b*, *e*, *h*, *k*, *n*). None of the abiotic or biotic variables had a significant effect on mortality (Fig. 2c, Fig. 3*c*, *f*, *i*, *l*, *o*, Appendix S5c).

In the selected SEM for each of the three demographic processes, disturbance negatively affected forest structure. Other abiotic factors did not consistently relate to biotic factors. We only found a negative effect of disturbance on community-weighted mean (CWM) leaf toughness (i.e., trait composition) of recruiting trees (because disturbance may increase the abundance of light-demanding species that generally have low leaf toughness) and a negative effect of tree density (i.e., forest structure) on rarefied taxonomic richness of trees that died during the monitoring period.

Mortality had the strongest relative contribution to cross-plot variation in net biomass change (0.56), followed by growth (0.42) and recruitment (0.02; Fig. 2*c*, Fig. 4).

Discussion

We evaluated how abiotic and biotic factors drive three stand-level demographic processes, and how these underlie net biomass change. We show that mortality most strongly predicted net biomass change but was unpredictable itself. Diversity (i.e., taxonomic and trait diversity) and mass-ratio (i.e., community-average trait values) had little effect on recruitment and growth. Plot basal area (i.e., forest structure) increased growth but decreased recruitment, and soil water availability increased recruitment but decreased growth. These results indicate that vegetation quantity and abiotic conditions matter most for ecosystem processes in this seasonally moist Amazonian tropical forest.

Dense forests increase growth but decrease recruitment

We hypothesized that biomass recruitment and growth would be most strongly affected by the direct effect of disturbance. Recruits face more light limitation than survivors, which would be reflected by a stronger positive effect of disturbance and a negative effect of stand basal area on recruitment growth. We found that stand basal area was the most important driver for

both processes, with a negative effect on recruitment and a positive effect on growth (Fig. 2*a* vs. *b*, Fig. 3*c* vs. *h*). Plot basal area is mainly composed of the basal area of surviving trees. Therefore, a higher initial basal area of surviving trees resulted in higher growth rates, especially since many of these trees are large and contribute most to growth (Stephenson *et al.* 2014). For recruiting trees in lower canopy layers, however, high plot basal area decreased growth probably because of low light availability (Poorter 1999). Similarly, disturbance had no effect on growth but increased recruitment due to more light availability. Canopy trees are less limited by light and do not benefit from increased light levels due to disturbance, which mostly increases light levels in lower canopy layers (IBIF, unpublished data). Disturbance can, however, also impact other abiotic variables, for example through soil compaction or changing of soil variables such as soil water availability (although the correlations between disturbance and soil variables were generally weak, Appendix S4). Soil compaction and reduced soil water availability may, in turn, reduce the biomass growth of recruiting trees.

Water availability increases recruitment but decreases growth of larger trees

For a wide range of ecosystems, soil fertility is an important driver of productivity and demographic processes (e.g. van der Sande *et al.* in review), partly via its effect on species composition (Waide *et al.* 1999). Our confirmatory structural equation model, however, showed no significant effect of soil phosphorous on demographic processes (Appendix S3). In this seasonally dry tropical forest, water availability is more important for recruitment and growth than soil fertility, and it affects these two demographic processes in contrasting ways (Fig. 2*a* vs. *b*, Fig. 3*b* vs. *g*). Soil sand content had a negative effect on recruitment, indicating that a community of recruits grows slower on drier soils. In contrast, survivors grow faster on soils that are drier in the dry season (as indicated by the negative effect of minimum soil water potential on growth). Recruits root less deeply than surviving trees and may therefore

experience a negative effect of decreased water holding capacity of the upper soil layers and thus more water stress during the dry season (Markesteijn *et al.* 2010).

The finding that drier soils increase growth of survivors is in contrast with studies showing that species increase their growth with increasing soil water availability (Baker, Burslem & Swaine 2003; Sterck *et al.* 2011). A high soil water potential in the dry season indicates that microsites are likely waterlogged and anoxic in the wet season when the forest receives most of its annual precipitation, thus hampering growth especially for large trees with deep roots that suffer more from waterlogged conditions (Ferry *et al.* 2010; Aubry-Kientz *et al.* 2015). However, van der Sande *et al.* (2015) showed for our study site that growth of large canopy trees was most strongly driven by their (water transporting) sapwood area, indicating that large trees can be strongly limited by water supply. Large trees have a high evaporative demand and probably rely on deep groundwater especially during the dry season (Nepstad *et al.* 1994). When we replaced soil water potential by sand content in the structural equation model, we found that sand content had a positive effect on growth. Sandy soils likely facilitate the growth of roots to deeper soil layers, thus allowing access to groundwater in drier periods.

Interestingly, soil conditions were important for recruitment and growth but they did not affect diversity and trait composition, although some effects of soil conditions on forest structure and total diversity were found earlier for the same site (Peña-Claros *et al.* 2012). This is in contrast with studies showing that soil texture affects the trait composition of African forests (Fayolle *et al.* 2012) and soil fertility affects trait composition across the Amazon basin (Fyllas *et al.* 2009), and with studies showing that soil fertility affects species richness positively in a Guyanese tropical rainforest (van der Sande *et al.* in review) but negatively in Costa Rican forests (Huston 1980). This suggests that the effects of soil conditions and disturbance on diversity and trait composition are site-specific and depend on the length of the soil gradient considered, and the amount of species turnover observed. The

lack of soil effects on biotic factors could also be caused by the way we selected the structural equation models (Appendix S2): we used variables for soil conditions, trait composition and diversity that best explained the demographic process in which we were interested, but it could be that other soil variables had a stronger effect on our intermediate variables, trait composition and diversity.

What drives recruitment and growth? Diversity theory vs. mass-ratio theory

We evaluated the role of two (groups of) theories on growth and recruitment: diversity theory due to mechanisms such as niche differentiation (Tilman 1999), facilitation (Hooper *et al.* 2005) and reduced effects of species-specific pathogens (Schnitzer *et al.* 2011), which predict that high diversity leads to facilitation, reduced competition and/or high resource use efficiency and increased growth and recruitment, and the *mass-ratio theory* (Grime 1998), which predicts that growth and recruitment are driven by the traits of an average tree in the forest. Taxonomic richness was important for recruitment but not for growth, and trait composition was not important for either of the two processes (Appendix S5, Fig. 2*a*, *b*). Diversity effects are thus more important than mass-ratio for recruits, probably because they experience strong competition for light, and therefore higher taxonomic diversity may decrease competition and increase the growth of the recruiting community. Hence, recruitment depends strongly on light availability and light use efficiency – through high disturbance, low plot basal area, and high taxonomic diversity – and less on its own trait composition. In contrast, growth does not depend on diversity nor traits.

Several studies find a positive effect of diversity or trait composition on forest productivity (Paquette & Messier 2011; Barrufol *et al.* 2013; Vilà *et al.* 2013; Chamagne *et al.* 2017), but few have simultaneously evaluated the role of the two theories. The few studies that evaluated both theories for tropical forests partly agree with our results. For a secondary forest in

Mexico (Lohbeck *et al.* 2015), biomass instead of trait composition or trait diversity was important for growth, which is in agreement with our results for growth. However, in contrast with our results, across three Neotropical mature forests (Finegan *et al.* 2015), trait composition but not trait diversity affected growth and only biomass affected recruitment, and for a tropical rainforest in Guyana (van der Sande *et al.* in review), trait composition but not taxonomic richness determined productivity. These studies and our study differ in various aspects, such as forest type and environmental conditions, diversity and trait composition indices used, sample size, and percentage of species for which traits were known. So far, results on the relative importance of both theories for tropical forests are not conclusive. Experimental grassland studies have advanced our knowledge on how diversity and trait composition could affect productivity and ecosystem functioning (e.g., Tilman et al. 1997), but more studies are needed in natural and more complex systems at various spatial scales, to unravel mechanisms of various processes, under varying conditions and across a spectrum of species diversity. Possibly, the effect of diversity is most important at local scales (e.g., our study) where interspecific interactions take place, in forests where environmental filtering is less important than interspecific competition, and for recruits because they experience strong interspecific competition for resources. Mass-ratio effects, on the other hand, may be important at regional scales (e.g., Finegan et al. 2015) where variation in trait composition is stronger and better represent functional differences among forests, and in forests where environmental filtering and thus the selection for specific traits is strong (e.g. van der Sande *et al.* in review).

Taxonomic richness outperforms trait richness

Taxonomic richness was selected as the best 'diversity' variable in two of the three SEMs, and it had a significant positive effect on recruitment. Taxonomic diversity was, surprisingly, a better predictor for recruitment than trait diversity (also called functional diversity or

variety, e.g. Mason et al. 2005, Finegan et al. 2015), which should be more mechanistically linked to recruitment. Taxonomic richness and trait richness were significantly positively correlated ($r = 0.57$, n = 48 plots, P < 0.001, for recruiting trees in the plot), indicating that higher taxonomic richness partly translates into higher richness in the eight traits that we measured. However, taxonomic richness better predicted recruitment, possibly because a high number of species increases the diversity of more traits or a different set of traits than we measured, such as leaf phenology or the ability to fix nitrogen. It could also be that a higher number of tree species leads to a lower concentration of species-specific soil pathogens, which allows species to maintain productivity compared to low diversity stands that suffer from pathogen attack, as has been found in temperate grasslands (Schnitzer *et al.* 2011; de Kroon *et al.* 2012). The positive effect of taxonomic richness may also be explained by only one or a few traits, and may therefore partly be concealed when calculating multivariate trait richness based on more but less relevant traits.

The strongest predictor of net biomass change is unpredictable

We hypothesized that growth and mortality would have a stronger contribution to cross-plot variation in net biomass change than recruitment because of their higher absolute values. We found that natural mortality did indeed most strongly contribute to net biomass change (Fig. 4). Our study is in agreement with other studies showing that mortality is a key driver of variation in aboveground biomass stocks across the Amazon (Delbart *et al.* 2010; Johnson *et al.* 2016). These studies thus indicate that mortality is a crucial process determining forest structure and biomass dynamics, and we should therefore aim to better understand what drives stand-level mortality. We show, however, that mortality was unpredictable and not explained by any of the abiotic or biotic factors included in our model (Fig. 2*c*, Fig. 3*k-o*), apart from a weak positive effect of taxonomic richness (Appendix S5c). We did not measure direct causes

of mortality, but we expected that certain trait values (e.g., high wood density) would lead to lower risk of mortality by causes such as diseases, wind storms and herbivory (Putz *et al.* 1983; Poorter *et al.* 2004). The lack of trait effects on mortality supports our hypothesis that mortality is likely a stochastic process at this scale. Although mortality may be well predictable at the individual scale (Chao *et al.* 2008), species scale (Poorter *et al.* 2008) and across stands at regional scale (Quesada *et al.* 2012), mortality across stands at a local scale may be more stochastic as it can be strongly determined by the death of one large tree, individual tree senescence, or the local effect of strong winds. Hence, at the local scale the strongest predictor of net growth is itself unpredictable by the variables we measured.

Drivers of demographic processes, a matter of scale?

The relative contribution of different drivers on demographic biomass processes may vary with the spatial and organizational scale considered (Chisholm *et al.* 2013). At large spatial scales, climate effects vary strongly and may overrule other effects (e.g., pantropical scales, Phillips et al. 2010, Banin et al. 2014), whereas at regional or local scales, soil conditions may determine demographic processes (Paoli *et al.* 2005; Baribault, Kobe & Finley 2012). We found that soil sand content and soil water potential overruled soil fertility. Possibly, soil fertility is more heterogeneous at larger spatial scales due to variation in parent material (Malhi *et al.* 2004; Baker *et al.* 2009; Toledo *et al.* 2011), or at smaller spatial scales such as smaller plot sizes (van der Sande *et al.* in review) or the projection area of tree crowns, due to plant-soil feedback effects (Ehrenfeld, Ravit & Elgersma 2005; Liu *et al.* 2012), but is relatively homogeneous when compared among averaged samples of 1-ha plots.

Organizational scales such as communities and species represent different units of measurements, and their demographic processes may therefore be predicted by different factors. For example, traits and forest structure may predict the mortality rate of individual trees (Chao *et al.* 2008) or species (King *et al.* 2006b; Iida *et al.* 2014), but for a whole stand, stochastic processes such as the death of one very large tree or the local occurrence of heavy winds may strongly determine variation in biomass loss (Gale & Barfod 1999). Furthermore, recruitment and growth can be well explained by traits at the individual- or species-level (e.g., Poorter and Bongers 2006, van der Sande *et al.* 2015), but not by trait composition at the 1-ha stand-level (this study). Species-level demographic changes in growth are a function of their growing strategy and average environmental conditions experienced, whereas community-level differences in demographic processes are a function of multiple species' strategies, species abundances, and local environmental conditions. These discrepancies between spatial and organizational scales highlight the importance for studies explicitly evaluating the drivers of demographic and other ecological processes at various scales.

Conclusions

We evaluated how three demographic processes underlying net biomass change (recruitment, growth and mortality) are determined by abiotic and biotic factors. Variation in net biomass change, and thus net carbon sequestration, was most strongly determined by stand-level mortality. However, we show that mortality itself at this scale cannot be predicted by the abiotic and biotic factors that we measured. We found little support for the effects of diversity and community-weighted mean traits (as predicted by mass-ratio theory) on demographic processes. Biomass growth of recruits increased with soil water availability and light availability, whereas biomass growth of larger and established trees increased on dry soils (that may experience less waterlogging in the wet season) and on sandy soils that may

facilitate root growth to deeper soil layers. These results highlight that simultaneously testing the role of multiple theories will yield better insights into mechanisms playing a role in the biomass dynamics and the carbon sequestration and mitigation potential of natural systems.

Author's contributions

MvdS, MPC, EA and LP designed the research, MvdS and JCL performed the research, NA and MT contributed data, MvdS analyzed the data, and MvdS, MPC, NA, EA, MT and LP wrote the paper.

suggestions for analyses. The fieldwork would have been impossible without the field assistance of Ricardo Mendez, Angel Mendez, and other field workers, who assisted in collecting leaf and stem traits and in establishing and evaluating the permanent plots for the last 10 years.

Data Accessibility

Data associated with this paper have been deposited in Data Archiving and Networked Services (DANS): http://dx.doi.org/10.17026/dans-xvh-hrzx.

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Tables

Table 1: Overview of the leaf and stem traits that were used to calculate community-weighted mean values per plot (i.e., the trait composition), with abbreviation, variable description, units, indicator description, and literature.

Variable group	Abbreviation	Variable description	Units	Indicator for	Literature
Leaf traits	SLA	Specific leaf area	$cm^2\ g^{-1}$	Light interception efficiency	Poorter and Remkes 1990, Schieving and Poorter 1999
	N_{mass}	Leaf nitrogen concentration	%	Photosynthetic capacity, metabolic rate	Evans 1989, Mercado et al. 2011
	P_{mass}	Leaf phosphorus concentration	%	Photosynthetic capacity, metabolic rate	Mercado et al. 2011
	Chl	Chlorophyll content	$\mu g\ cm^{-2}$	Light harvesting capacity	Evans 1989
	FPs	Specific force to punch	$N\ cm^{-2}$	Leaf defense	Kitajima and Poorter 2010, Onoda et al. 2011

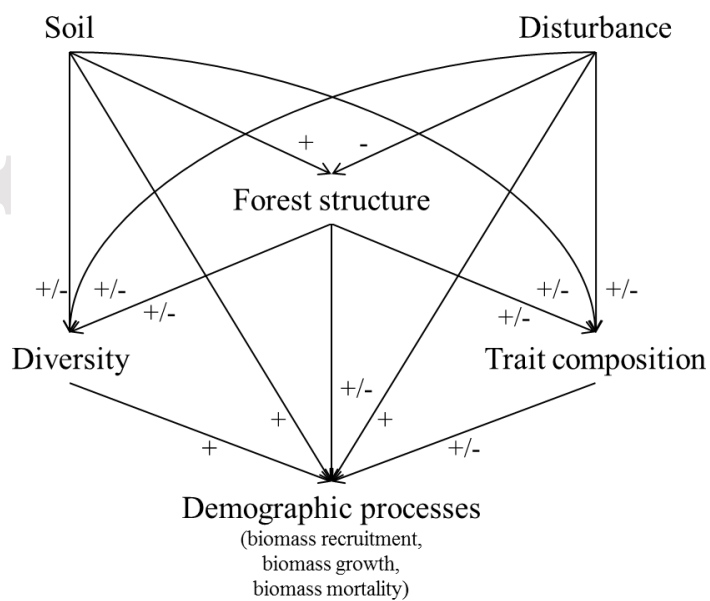|					
	LMFm	Leaf mass fraction of the metamer	$g\ g^{-1}$	Light interception efficiency	Walters and Reich 1999, Lusk 2004
Stem traits	WD	Wood density	$g\ cm^{-3}$	Volume growth, stem defense	Baker et al. 2004, Chao et al. 2008, Chave et al. 2009
	DBH_{max}	Maximum stem diameter at breast height	cm	Tree longevity and life history strategy	Kohyama et al. 2003, King et al. 2006a

Figures

Figure 1: Conceptual framework showing the expected relations of abiotic factors

(disturbance and soil resource availability) and biotic factors (forest structure, diversity and

trait composition) on demographic processes (biomass recruitment, growth, and mortality).

Forest structure (e.g., plot basal area, tree density) is based on all alive trees in the 1-ha plots, whereas diversity and trait composition are based on the individuals of that demographic group only (i.e., recruits, survivors, or trees that died). Hypothesized positive effects are indicated by + signs and hypothesized negative effects are indicated by - signs. The effect of and on trait composition depends on the trait considered; acquisitive trait values (e.g., high specific leaf area and leaf nitrogen concentration) will increase with disturbance and positively affect demographic processes, whereas conservative trait values (e.g., high leaf toughness and wood density) will decrease with disturbance and negatively affect demographic processes. Soil resource availability and disturbance can decrease diversity because of a competitive advantage of few, light-demanding species, or they can increase diversity because of the creation of more niches. Forest structure would decrease recruitment because of light-limitation but would increase growth because of more standing biomass that can grow.
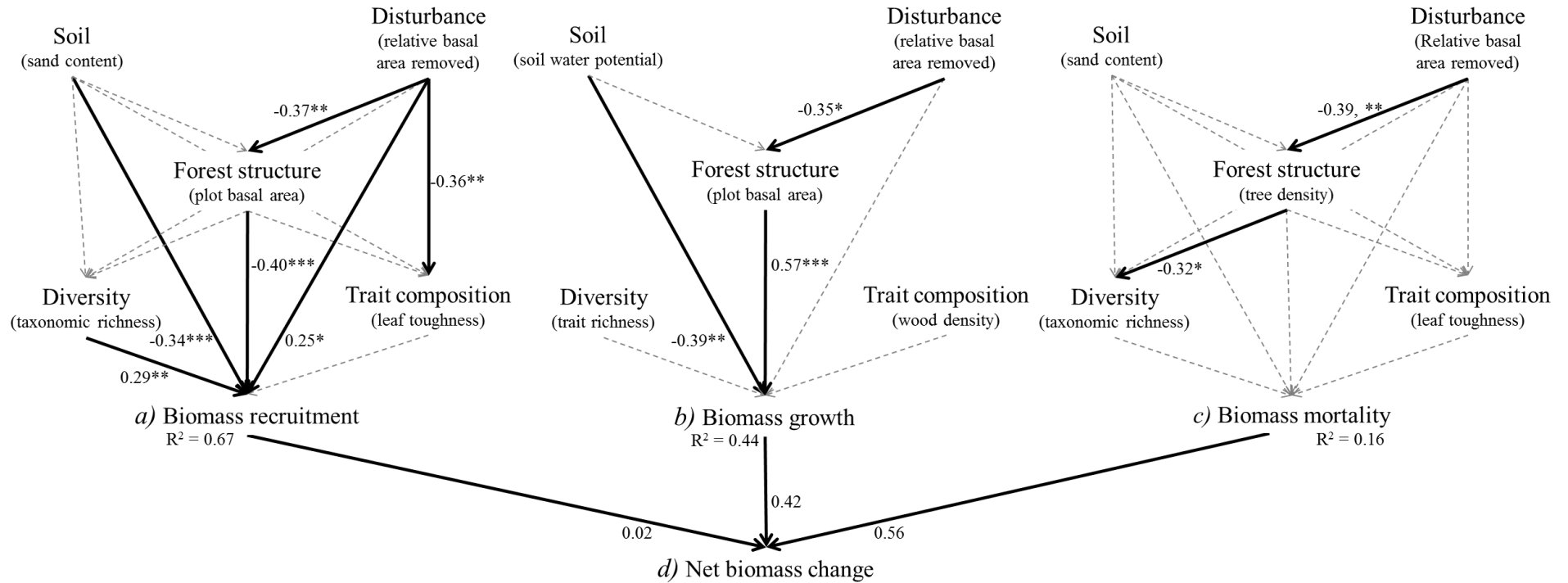
Figure 2: Results for the effects of abiotic factors (soil and disturbance) and biotic factors (forest structure, diversity and trait composition) on three demographic processes (*a*: biomass recruitment, *b*: biomass growth, and *c*: biomass mortality), which underlie net biomass change (*d*). The upper part of the figure (i.e., figures *a*, *b* and *c*) is tested with three separate structural equation models. All three models were accepted (see Appendix S5). The lower part (*d*) could not statistically be tested, but shows the relative contributions of demographic processes to variation in net biomass change across plots. Black arrows show significant effects, dotted grey arrows show non-significant effects, and no arrow means that the relation was not included in the model. For all relations, standardized regression coefficients and significance are given (* < 0.05, ** < 0.01,

*** < 0.001). The variables between brackets were selected as the variable of that abiotic or biotic factor with the strongest effect on the

demographic process. Diversity and trait composition were calculated for each group responsible for the demographic process. Forest structure,

soil, and disturbance were based on the whole plot. Statistics of model *a*, *b* and *c* are in Appendix S5. Details on model building and selection are
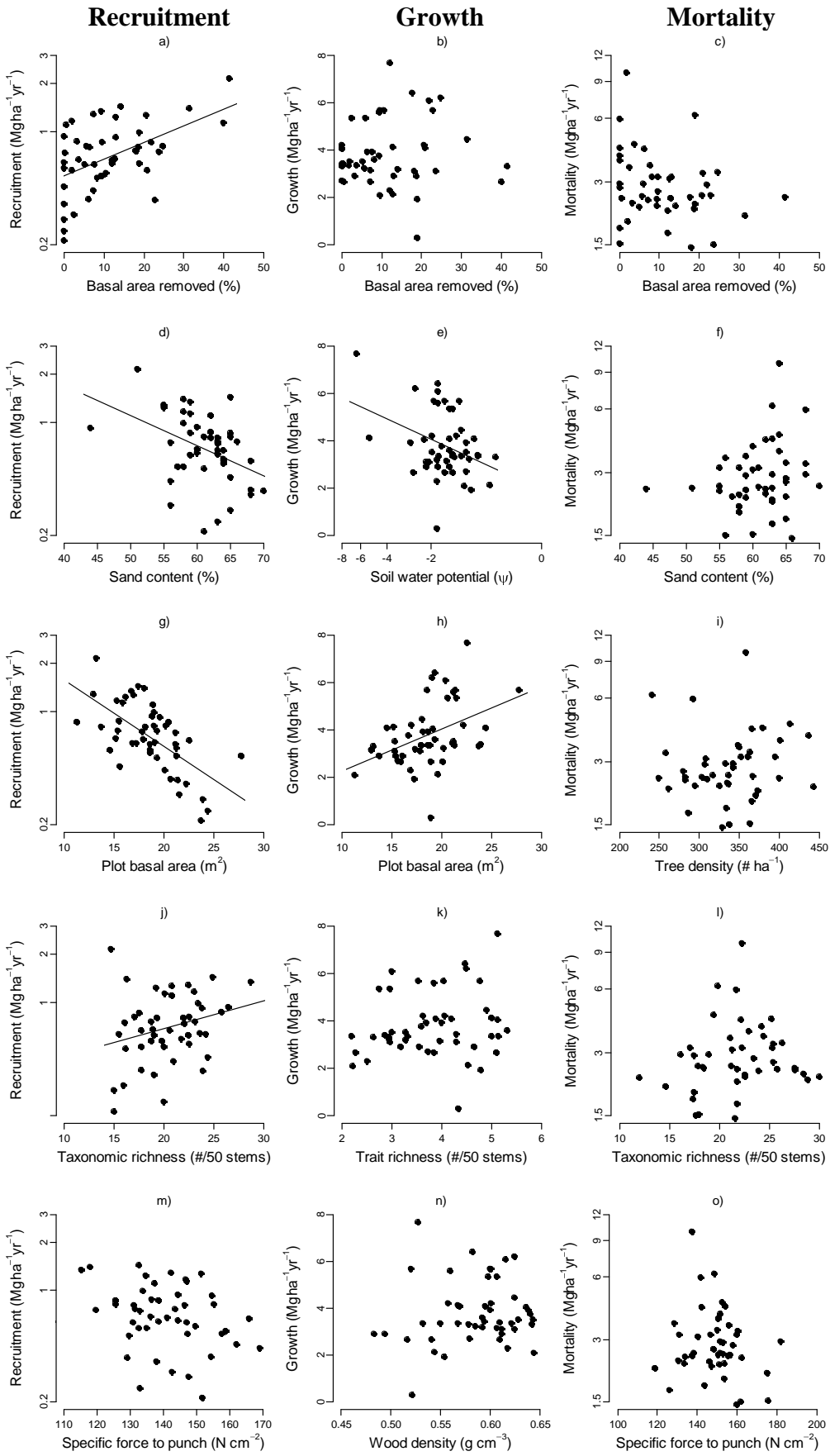
in Appendix S2.

Recruitment   **Growth**   **Mortality**

Figure 3: Bivariate relations of the three demographic processes (recruitment, left column, Fig. *a*, *d*, *g*, *j*, *m*; growth, middle column, Fig. *b*, *e*, *h*, *k*, *n*; and mortality, right column, Fig. *c*, *f*, *I*, *l*, *o*) with the five abiotic and biotic factors in rows (see also Fig. 1 and 2): relative basal area removed (i.e., disturbance, Fig. *a-c*), soil conditions (Fig *d-f*), forest structure (Fig *g-i*), diversity (Fig. *j-l*), and community weighted mean trait composition (Fig. *m-o*) for 48 1-ha plots in the tropical moist forest of La Chonta. See Fig. 2 and Appendix S5 for results of multivariate structural equation models. Regression lines are given for the relations that were significant in the structural equation models (Fig. 2), but are based on simple regressions and meant for illustration purposes only. Note that the axes for recruitment (Fig. *a*, *d*, *g*, *j*, *m*), mortality (Fig. *c*, *f*, *i*, *l*, *o*), and soil water potential (*e*) are in ln-scale.
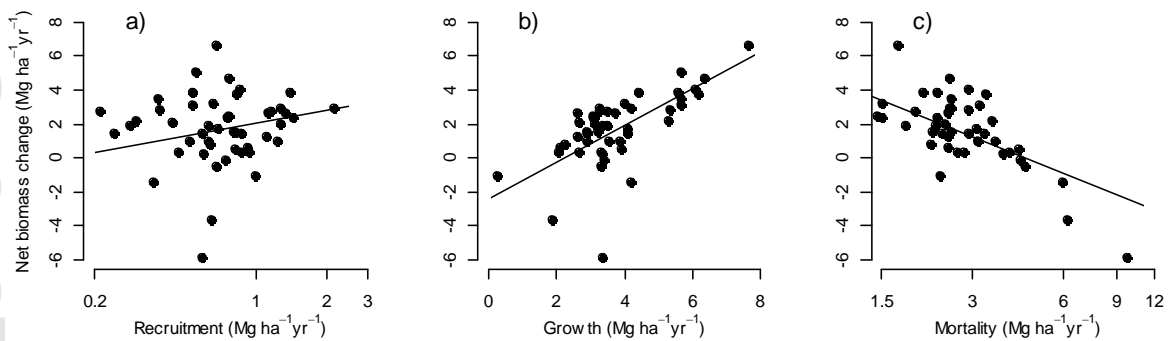

Figure 4: Bivariate relations of net biomass change with recruitment (*a*), growth (*b*), and mortality (*c*) for 48 1-ha plots in the tropical moist forest of La Chonta. Regression lines are based on the multiple regression analysis (by keeping the other predictor variables at their mean), see Appendix S5. Note that the axes for recruitment (*a*) and mortality (*c*) are in ln-scale.