van der Sande, M.T., Arets, E.J.M.M, Peña-Claros, M., Hoosbeek, M.R., Cáceres-Siani, Y., van der Hout, P., Poorter, L. (2018):
Soil fertility and species traits, but not diversity, drive productivity and biomass stocks in a Guyanese tropical rainforest
Funct. Ecol. **32** (2), 461 – 474

http://dx.doi.org/10.1111/1365-2435.12968

Article type : Research Article

Section: Community Ecology
Editor: Rebecca Ostertag

Title: Soil fertility and species traits, but not diversity, drive productivity and biomass stocks in a Guyanese tropical rainforest

Running headline: Drivers of productivity, biomass and soil organic matter

Authors:

Masha T. van der Sande[1,2,3,4*], Eric J. M. M. Arets[2], Marielos Peña-Claros[1], Marcel R. Hoosbeek[5], Yasmani Cáceres-Siani[6], Peter van der Hout[7], Lourens Poorter[1]

[1] Forest Ecology and Forest Management Group, Wageningen University and Research, PO Box 47, 6700 AA Wageningen, The Netherlands

[2] Wageningen Environmental Research (Alterra), Wageningen University and Research, PO Box 47, 6700 AA Wageningen, The Netherlands

[3] Department of Community Ecology, Helmholtz Centre for Environmental Research- UFZ, Theodor-Lieser-Straße 4, 06120 Halle (Saale), Germany

[4] German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Deutscher Platz 5e, 04103 Leipzig, Germany

[5] Department of Soil Quality, Wageningen University, PO Box 47, 6700 AA Wageningen, The Netherlands

[6] Rurrenabaque, Beni, Bolivia

[7] Van der Hout Forestry Consulting, Rotterdam, the Netherlands

[*] Corresponding author:

Masha van der Sande

Phone no.: +49 341 9733117

Email: masha.vandersande@idiv.de

Summary:

- Tropical forests store and sequester large amounts of carbon in above- and belowground plant biomass and soil organic matter (SOM), but how these are driven by abiotic and biotic factors remains poorly understood.
- Here, we test the effects of abiotic factors (light variation, caused by logging disturbance, and soil fertility) and biotic factors (species richness and functional trait composition) on biomass stocks (aboveground biomass, fine root biomass), SOM and productivity in a relatively monodominant Guyanese tropical rainforest. This forest grows on nutrient-poor soils and has few species that contribute most to total abundance. We therefore expected strong effects of soil fertility and species' traits that determine resource acquisition and conservation, but not of diversity. We evaluated 6 years of data for 30 0.4-ha plots and tested hypotheses using structural equation models.
- Disturbance increased productivity but decreased aboveground biomass stocks. Soil phosphorus (P) enhanced aboveground biomass and productivity, whereas soil nitrogen reduced fine root biomass. In contrast to expectations, trait values representing acquisitive strategies (e.g., high leaf nutrient concentration) increased biomass stocks, possibly because they indicate higher nutrient absorption and thus higher biomass build-up. However, under harsh conditions where biomass increase is slow, acquisitive trait values may increase respiration and vulnerability to hazards and therefore increase biomass loss. As expected, species richness did not affect productivity.
- We conclude that light availability (through disturbance) and soil fertility – especially P – strongly limit forest biomass productivity and stocks in this Guyanese forest. Low P availability may cause strong environmental filtering, which in turn results in a small set of

dominant species. As a result, community trait composition but not species richness determines productivity and stocks of biomass and SOM in tropical forest on poor soils.

Key words:

biodiversity-ecosystem functioning, diversity, fine root biomass, functional traits, logging disturbance, mass-ratio hypothesis, niche complementarity, soil organic matter

Introduction

Tropical forests store about 25% of global terrestrial carbon and account for 34% of terrestrial gross primary productivity (Beer *et al.* 2010) and they are therefore important for the global carbon cycle and climate change mitigation. Logged forests cover about a quarter of the world's tropical forest area and although they store less biomass per hectare, they sequester more carbon per unit time than mature forests (Rutishauser *et al.* 2015). The factors driving carbon fluxes and pools are less studied and understood particularly for relatively mono-dominant tropical forests on nutrient-poor soils.

Forest carbon is composed of different stocks, such as above- and belowground living biomass, and soil organic matter (SOM) (Malhi *et al.* 2009). Most studies focus only on the drivers of aboveground biomass (e.g., Poorter et al. 2015), but a third of the biomass is found in belowground roots (Robinson 2007). Moreover, SOM in the first meter of soil represents a significant part of the total carbon pool (Malhi, Baldocchi & Jarvis 1999; Robinson 2007). Here, we evaluate how abiotic and biotic factors directly and indirectly affect aboveground biomass productivity and stocks of aboveground biomass, fine roots, and SOM for an experimentally logged tropical rainforest in Guyana (see conceptual model, Fig. 1). Few studies have simultaneously evaluated the effects of a combination of abiotic and biotic drivers on carbon stocks and fluxes in tropical forests (e.g. Poorter *et al.* 2015; van der Sande *et al.* 2017), and none have done so for nutrient-poor, mono-dominant forests.

Abiotic effects on biomass productivity and stocks – Disturbances such as logging or natural treefall gaps result in heterogeneity in forest structure and, hence, light availability. Logging directly reduces above- and belowground biomass stocks, but the increased light levels reaching the lower tree strata may increase ecosystem productivity (Fig. 1a) (Peña-Claros *et al.* 2008). Moreover, logging may temporarily increase soil fertility due to increased litter input, and increase species diversity due to establishment of light-demanding species. Soil conditions also vary at small spatial scales due to heterogeneity within soil types and topography. Soil fertility should positively affect biomass productivity especially in forests growing on very poor soils (Baker *et al.* 2009), such as the old and leached nutrient-poor soils of the Guiana shield (van Kekem, Pulles & Khan 1996).

Biotic effects on biomass productivity and stocks – The diversity and composition of the tree community can affect biomass productivity and stocks (Fig. 1a) (Hooper *et al.* 2005). For example, high species richness can increase the chance of including a very productive species (sampling effect, Loreau 1998), and can increase niche complementarity or facilitation among species (Tilman 1999), and hence, enhance resource use efficiency and stand productivity. We expect, however, that such diversity effects are weak when conditions are harsh and few species with well-adapted strategies are abundant, as in this nutrient-poor Guyanese.

The relationship between biodiversity and ecosystem functioning is well studied for temperate systems (e.g., Tilman *et al.* 2001; Vilà *et al.* 2013). For tropical forests, however, evidence is still rare and comprises positive effects (e.g. Chisholm *et al.* 2013; Sullivan *et al.* 2017; van der Sande *et al.* 2017a) as well as no or negative effects (e.g. Potvin *et al.* 2011; van der Sande *et al.* 2017b) of species diversity on biomass productivity and stocks. This lack of consensus may be caused by many variables that simultaneously influence productivity and stocks. Here, we apply structural equation modelling to tease apart the independent contributions of abiotic and biotic factors (Fig 1).

The lack of consensus regarding diversity effects may also partly be caused by the fact that species richness does not provide information on the functional traits of the species. Morphological or physiological plant traits represent species' strategies to acquire and use resources, and thus determine their growth, reproduction and survival (Poorter & Bongers 2006). Trait diversity instead of species richness may thus better predict ecosystem functioning (Hooper *et al.* 2005). Furthermore, Grime's mass-ratio hypothesis (Grime 1998) predicts that the dominant trait values in a community (i.e., the community-average trait values weighted by species' basal area, here called the 'trait composition') are better predictors for biomass stocks and productivity than diversity.

Abiotic and biotic effects on soil organic matter – Abiotic and biotic factors are also important drivers of SOM stocks (Fig. 1b). SOM stocks refer to all carbon in non-living organic stocks, including decomposing litter, and are mainly balanced by carbon input through litter production and carbon output through decomposition. Litter production is determined by the turnover rate of living biomass and should thus relate to gross productivity of the forest. Decomposition depends on environmental conditions, litter quality, and the decomposer community (Cornwell *et al.* 2008). Logging disturbance initially increases litter input and activity of the microbial community, but the more open vegetation leads to higher temperatures and lower humidity, which may slow down decomposition and as a result increase SOM stocks (van Dam 2001). Years after disturbance, however, the activity of the microbial community should have stabilized and the canopy should have closed, resulting in weaker effects of microbial activity, temperature and moisture on SOM. Soil fertility may indirectly affect SOM through increasing productivity and thus litter production (De Deyn, Cornelissen & Bardgett 2008). High litter quality, such as high concentrations of nitrogen and phosphorus, increases palatability for decomposers and decomposition rates (Wardle, Bonner & Barker 2002) and should therefore reduce SOM stocks.

Conceptual framework; abiotic and biotic effects on productivity and stocks of biomass and soil organic matter – We ask three questions. First, how does logging influence other abiotic factors (soil fertility), biotic factors (species richness and trait composition), productivity, biomass, and soil organic matter? Second, how do these abiotic and biotic factors affect aboveground productivity and aboveground and fine root biomass stocks (Fig. 1)? We expect that productivity is positively affected by logging disturbance, soil fertility, species richness and an acquisitive trait composition (e.g., relatively high leaf nutrient concentration). Aboveground and fine root biomass stocks would, however, decrease with disturbance because of biomass removal, and with an acquisitive trait composition because of increased tissue turnover and decreased residence time of the biomass. Third, how do disturbance, litter quantity and litter quality affect SOM? We expect that logging disturbance should have little long-term effects on SOM because too much time has passed since the disturbance took place (a time difference of 19 year) and microbial activity and the microclimate should have readjusted (Cleveland *et al.* 2014). SOM should increase with litter quantity because this represents organic matter input, and decrease with litter quality because more palatable leaves speed up decomposition.

Materials and Methods

Research site

This study was based on the permanent sample plots at Pibiri creek in Central Guyana (see below for plot description), located 50 km south of Mabura Hill (5°13’ N58°38’ W). This site receives on average 2772 mm rainfall per year (van Dam 2001). The relatively dry periods are from September to November and from March to April, although monthly rainfall is always higher than 100 mm. Mean annual temperature is 25.9 °C (ter Steege et al. 1996). The plots are positioned up to 1.5 km apart on brown sand ferralsols (van Kekem *et al.* 1996; van der Hout 1999) with very low phosphorus availability (Quesada *et al.* 2010). The forest is a mixed Greenheart-Morabukea forest with an average canopy height of 30-40 m, and is classified as a moist tropical forest. It has a few very dominant species, with the 5 most abundant ones accounting for 50% of the total biomass (> 5 cm DBH) (Appendix S1).

Permanent sample plots and sampling design

In 1993, 15 permanent sample plots of 140x140 m were set up at Pibiri Creek as part of the Tropenbos Guyana Programme (van der Hout 1999) and are currently managed by the Guyana Forestry Commission. The central 1 ha (100x100 m) was subdivided into 25 20x20 m subplots, and in each subplot one 10x10 m subplot was established in the South-West corner in which trees larger than 5 cm DBH were measured and identified (composing 0.25 ha per plot).

In 1994, the plots were experimentally logged, resulting in five different treatments (3 repetitions per treatment): control (no logging), logging of 4 trees ha^{-1}, 8 trees ha^{-1}, or 16 trees ha^{-1}, and one silvicultural treatment with logging of 8 trees ha^{-1}, followed by post-harvest liberation thinning (van der Hout 1999). The logging treatments caused a reduction in basal area between 1.5-35% (Appendix S2). The plots were completely re-measured in 1995, 1997 and 2000.

For this study, we used a plot size of 0.4 ha to quantify and match biomass and soil variables as well as possible, as biomass stocks and productivity are most accurately measured in large plots (e.g., 1 ha) while soil heterogeneity is best captured in small plots (e.g., 0.1 ha). Consequently, we split each 1 ha plot into 2 subplots of 100x40 m separated by a buffer zone of 100x20 m, making a total of 30 plots.

Aboveground biomass productivity and stocks

To determine aboveground productivity and aboveground living biomass stocks, we used the post-logging censuses of 1995 and 2000. Because we aimed to evaluate natural processes, we excluded all trees from the dataset that died as a delayed result of logging and silviculture activities. All trees between 5-20 cm DBH, which were measured on a subsample of ¼ of the 0.4-ha plot, were considered four times to scale this diameter group to the whole plot. Per tree and per census, we calculated living aboveground biomass (AGB) using the equation from Chave *et al.* (2014):

$$AGB = exp[-1.803-0.976*(E)+0.976*ln(WD)+2.673*ln(DBH)-0.0299*(ln(DBH))\^{}2], \qquad \text{(Eq. 1)}$$

where E is a measure of environmental stress of the site, which depends on temperature seasonality and water deficit and has a value of -0.1092452 at the Pibiri site (extracted from http://chave.ups-tlse.fr/pantropical_allometry/readlayers.r with the *retrieve_raster* function in R). DBH is the diameter at breast height (cm) and WD is the wood density (g cm^{-3}), which was based on local wood density if available (see explanation under *Wood sampling*), and otherwise on wood density data obtained from the Global Wood Density Database from DRYAD (Chave *et al.* 2009). Biomass stock per 0.4-ha plot was calculated by summing the biomass of all live trees in 1995, summing the biomass for all live trees in 2000, and averaging these two values per plot to obtain a value that better represents the census period. Average biomass stock per 0.4 ha was multiplied by 2.5 to express per ha.

To calculate productivity (Mg ha^{-1} yr^{-1}) between 1995 and 2000, we summed the growth of all trees that were present in both censuses, and the growth of trees that were newly recruited in 2000. To calculate the growth of recruits between 1995 and 2000, we subtracted the biomass of that individual with a DBH of 5 cm from its biomass in 2000. Hence, we assumed that recruits grew from 5 cm at the start of the census interval until the diameter that was measured at the end of the interval. Assuming that recruits started growing from 5 cm DBH slightly underestimates growth, because in reality most recruits will have reached the diameter limit later. However, it still yields more accurate recruitment estimations than assuming that recruits started growing from 0 cm at the start of the census interval, which strongly overestimates growth (Talbot *et al.* 2014). All growth values per tree were summed per 0.4-ha plot, divided by the time in between the two census periods for the 0.4-ha plots (on average 5.65 years) to obtain annual productivity, and multiplied by 2.5 to obtain annual productivity per hectare. Hence, with productivity we refer to aboveground biomass growth by trees that recruit and trees that survive, and do not include mortality and belowground productivity.

Fine root biomass, soil organic matter, soil fertility, and litter

The plots are located on relatively flat surfaces in between drainage tributaries, and thus spatial variation in soil conditions should be small. For that reason, per 0.4-ha plot we used two sampling points more than 60 m apart: one towards the north and one towards the south end. Per sampling point, soil samples were taken between 0-5 cm for bulk density, root biomass and concentrations of carbon, nitrogen (N_{soil}), total phosphorus (P_{soil}), and the ratios between carbon and nitrogen ($C{:}N_{soil}$) and nitrogen and phosphorus ($N{:}P_{soil}$, Table 1). Fine root biomass was collected at 0-5 cm and 15-20 cm depth in three sample points per plot (i.e., the two points mentioned earlier and an intermediate one). More details about the collection of fine root biomass, soil organic matter, soil fertility and litter can be found in Appendix S3.

Soil organic matter was averaged per plot and scaled to Mg ha^{-1} in the 10 cm topsoil, and fine root biomass was scaled to Mg ha^{-1} in the 20 cm topsoil (using an exponential function, see Appendix S3), in order to compare values with aboveground productivity and biomass stocks (also in Mg ha^{-1}). At the two sampling points per plot, fragmented litter mass was determined and scaled to Mg ha^{-1}. Only fragmented litter was included due to the relatively low quantity and high spatial variability of the freshest litter. Compared to fresh litter, nutrients in this fragmented litter may already partly have mineralized, and we may therefore expect weaker effects of litter nutrient concentrations on soil organic matter. The variation in soil conditions between our samples was in the range found for other published results in tropical forests and should therefore well represent the average soil conditions in the plots (for more details, see Appendix S4).

We are aware that we have not sampled the full soil and litter heterogeneity, and therefore that the relations of soil and litter variables with biomass stocks and productivity may be more conservative and that the chance to find significant effects may be lower.

Logging disturbance

Logging disturbance was determined in two ways: 1) by using the pre-defined logging treatments (which was set up using a categorical design) and 2) by calculating a continuous disturbance variable. The continuous relative logging disturbance (in %) was computed per 0.4-ha subplot, based on the basal area of all trees that were logged or died during the census interval due to logging or post-logging activities, divided by the total basal area of the subplot before harvesting. We used a continuous variable because logging disturbance depends on the distribution and density of commercial species and is therefore not evenly distributed in space and varies strongly within treatments (Appendix S2).

Logging disturbance took place in 1994 and the aboveground data (i.e., biomass productivity and stocks, species richness and trait composition) were collected in 1995–2000, but belowground data (i.e., root data, litter data, SOM, and soil fertility) could not be collected during this time and were collected in 2013. Hence, time-lag may affect some of the relations between below- and aboveground data, and between disturbance and belowground data. Shortly after disturbance (e.g., 1-5 years, which is the timeframe of the aboveground data), differences among plots may have been large, whereas during later years of recovery, plots may again have become more similar. Hence, we may find strong variation among plots in their aboveground variables (1995–2000), but less variation among plots in belowground variables (2013). Our relations between below- and aboveground variables and between disturbance and belowground variables may therefore be conservative.

Leaf and stem traits

We used six leaf traits that we expected to be good predictors for productivity and above- and belowground biomass stocks (Table 2). Leaf traits were determined for the 33 most abundant tree species, composing on average 78% of the basal area (>5 cm DBH) in the 30 0.4-ha plots over the two census years. For 5 individuals per species, between 7 and 17cm DBH, we sampled 5 healthy and young but mature leaves growing at the outer side of the crown (thus in relatively high light conditions, but mostly in the understory). All leaf traits were measured according to standard protocols (Pérez-Harguindeguy *et al.* 2013). See Appendix S5 for a detailed description of trait collection and measurements.

Besides leaf traits, we measured wood density and wood dry matter content to also define the species' functional strategy in terms of their stem characteristics, as leaf and stem economics spectra can vary independently for large rainforest trees. Wood density and stem dry matter content increase wood defence and should therefore decrease productivity, but they enhance tree longevity and therefore biomass stocks (Baker *et al.* 2004).

We took wood samples for 25 of the 33 species using an increment borer, because wood of the remaining 8 species was too tough to sample and was therefore excluded. For three individuals per species, we took one wood core at breast height, from the outer sapwood until the pith. We aimed to select individuals that were between 20 and 40 cm in diameter, to include possible radial gradients in wood density (Woodcock & Shier 2002). However, for some species that did not grow this big or that had too tough wood at large sizes, we sampled trees of around 12-20 cm in diameter. Wood density was calculated as the wood dry mass divided by the wood fresh volume (Appendix S5).

Diversity and trait composition

We calculated two diversity indices: rarefied species richness and functional trait dispersion. We used rarefied species richness to account for variation in stem number among plots that could affect species richness (Gotelli & Colwell 2001), and because it is often used in biodiversity-ecosystem function research. Rarefied richness (hereafter referred to as ‘species richness’) was calculated as the number of species per 100 randomly drawn stems for all live individuals per 0.4-ha plot and per census, using the *rarefy* function from the *vegan* package in R (Oksanen *et al.* 2015).

Functional trait dispersion (Fdis) is a multivariate trait diversity measure weighted by species basal area, and based on the mean distance in the multidimensional trait space of all individual species to the centroid of all species (Pakeman 2014). Fdis would be a better indicator than species richness of the niche space occupied by the community. We chose this measure because other (unweighted) multivariate trait measures are more sensitive for an underestimation of diversity when trait values are missing for part of the species.

For trait composition, we calculated the community weighted mean (CWM) for all leaf and stem traits (i.e., the trait value of an average tree in the community), by multiplying each species’ trait value by its relative dominance in the plot (in terms of basal area), and summing all species occurring in the subplot for which traits were measured. Hence, for each subplot at each census, we used the formula:

$$\mathrm{CWM} = \sum_{i=1}^{S} wi * xi$$

where w_i is the relative basal area of species i, x_i is the trait value of species i, and S is the total number of species. Diversity and all trait composition variables were calculated per subplot and per census, and were then averaged between the two census years to obtain one value per subplot.

Adaptation or plasticity in trait values can result in strong differences in species’ trait values across sites, and we therefore calculated trait composition based on locally collected trait data. Note that we used mean trait values per species. Hence, differences in CWM trait values among plots are only due to differences in species composition, not due to intraspecific differences caused by acclimation to local environmental conditions. We did not include intraspecific trait variation, because interspecific differences generally explain most variation in trait values (78%; Rozendaal *et al.*, 2006), and sapling traits and adult traits are strongly correlated (Poorter 2008). Moreover, we collected traits in 2013, and used species composition of 1995-2000 to calculate CWM traits values. We thus assume that species ranking in average trait values remains constant over time. Correlations between community-weighted mean leaf and stem traits can be found in Appendix S6.

Statistical analyses

Since our study site was originally designed as a logging experiment with different treatment intensities, we first evaluated differences among logging treatments in abiotic and biotic factors, productivity, aboveground and fine root biomass, and SOM. We tested for differences among treatments using linear mixed models with 1-ha plots as random effect. Logging treatments cause heterogeneous effects, depending on the size and type of trees logged and the initial biomass in the plot. As a result, the actual disturbance intensities overlap among treatments (Appendix S2), and we therefore use logging intensity as a continuous variable for further analyses.

Our main aim was to evaluate the effects of abiotic factors (logging disturbance and soil fertility) and biotic factors (diversity and trait composition) on productivity and stocks of biomass and SOM (i.e., the ‘response variables’), as shown in Fig. 1. One could think of many variables and interactions between variables to affect the response variable. For example, biotic conditions could affect soil fertility. However, soil fertility is probably more strongly determined by the parent material and the topographic position. To limit the number of possible models and the number of explanatory factors per model, we only evaluated the framework corresponding to our *a priori*, as simple as possible hypotheses (see Fig. 1). To test this framework, we used structural equation modelling (SEM), which is based on regression analyses, allows to test multivariate and hierarchical relations, and can be used for testing causality between variables (Shipley 2004).

For each response variable, multiple models with different combinations of variables representing the abiotic and biotic factors were possible; we had one variable to represent disturbance, but two for diversity and multiple for soil fertility and trait composition. For diversity, we used species richness for the initial SEMs, because richness is most often used in biodiversity research. For soil fertility and trait composition, we first performed all subsets regression analyses to select one or two variables for each with the highest relative importance value (see Appendix S7). We then tested a maximum of four SEMs per response variable (two soil fertility variables x two trait composition variables), from which we selected one SEM with the combination of variables that resulted in the highest explained variation (R^2) of the response variable. To test for effects of trait diversity instead of species diversity, we replaced species richness by functional trait dispersion (Fdis) in the final SEMs. To compare these results with the more often used linear regressions, we tested how all explanatory variables in the final SEMs were related to the four response variables (thus ignoring indirect effects), using linear mixed models with 1-ha plots as random effect. For more details on model selection and refinement, see Appendix S7.

All analyses were performed in R 2.15.2. Linear mixed models were evaluated using the *lme* function from the *nlme* package. Difference between logging treatments were evaluated using the *Anova* function from the *car* package. Structural equation modelling was performed using the *sem* function of the *lavaan* package. We corrected for nesting of 0.4-ha plots within the larger 1-ha plots by using the *svydesign* function of the *survey* package and the *lavaan.survey* function of the *lavaan.survey* package.

Results

Logging disturbance treatments caused significant differences in aboveground biomass shortly after logging (ANOVA, P=0.005), with lower biomass in the most intense logging treatment (8 harvested trees/ha plus thinning) compared to the control and least intense logging treatment (4 harvested trees/ha; Tukey posthoc tests, P<0.05) (Appendix S8). Other variables (e.g. aboveground productivity shortly after logging and root biomass 19 years after logging) did not differ between treatments, except for higher N_{litter} in the least intense logging treatment (4 harvested trees/ha) compared to the second least intense treatment (8 harvested trees/ha) (ANOVA, P=0.024).

Aboveground biomass productivity and stocks of biomass and soil organic matter (SOM) varied strongly among plots, with an average aboveground productivity of 6 ± 1.5 Mg ha^{-1} yr^{-1} (average ± standard error), an average aboveground biomass of 367 ± 90 Mg ha^{-1}, an average belowground fine root biomass (in the top 20 cm of the soil) of 17 ± 4 Mg ha^{-1}, and an average SOM (in the top 10 cm of the soil) of 66 ± 14 Mg ha^{-1} (Table 3).

Our main aim was to evaluate the effects of abiotic and biotic factors on productivity and stocks of biomass and SOM (Fig. 1). For aboveground productivity, P_{soil} was the only selected soil variable, and SLA and P_{leaf} were selected as leaf variables in the SEM. The two possible structural equation models (SEMs) were accepted, but the SEM including SLA was selected because it gave a higher R^2 for productivity (Appendix S10). This SEM showed a negative effect of SLA (β=-0.35) on productivity and positive effects of P_{soil} (β=0.51) and disturbance (β=0.34) on productivity (Fig. 2a, Table 4).

For aboveground biomass stocks, only P_{soil} and P_{leaf} were evaluated in the SEM, and showed positive effects of P_{soil} (β=0.27) and P_{leaf} (β=0.47) and a negative effect of disturbance (β=-0.73) on aboveground biomass stocks (Fig. 2b, Table 4).

For fine root biomass, only N_{soil} and $C{:}N_{leaf}$ were evaluated in the best SEM and showed a positive effect of N_{soil} (β=0.39), but negative effects of $C{:}N_{leaf}$ (β=-0.44) and species richness (β=-0.38) on fine root biomass stocks (Fig. 2c, Table 4). All these three models showed a positive effect of soil fertility on species richness and a negative effect of disturbance on species richness.

For SOM, N_{litter} was included in the SEM and was the only variable that tended to reduce SOM (β=-0.37, P=0.063, Fig. 2d, Table 4). Replacing species richness for functional trait dispersion (Fdis) in the final SEMs (Appendix S11) and using linear regressions instead of SEMs (Appendix S12) gave largely similar results. For all relationships used in the SEMs, a bivariate scatterplot is shown in Fig. 3.

Discussion

We first evaluated how logging treatments affected abiotic and biotic factors and response variables, and found very little effects. We then evaluated how abiotic and biotic factors drive productivity, biomass stocks, and SOM using structural equation models (Fig. 1). Our results indicate that logging disturbance, soil fertility and mass-ratio, rather than species or trait diversity, determine productivity and biomass in this tropical rainforest.

Logging disturbance increases productivity but decreases aboveground biomass stocks

We found very little effect of logging treatments (it only reduced aboveground biomass), because logging disturbance depends on the distribution of commercial species and varies therefore strongly within treatments (Appendix S2). Logging disturbance as a continuous variable did reduce aboveground biomass and increase aboveground biomass productivity shortly after logging (1-6 years) but it did not reduce fine root biomass, which was measured longer (19 years) after logging (Fig. 2 and 3e,f). Possibly, roots of the remaining trees quickly expanded after disturbance to acquire more nutrients, which resulted in a fast recovery of fine root biomass. Hence, disturbance effects on fine root biomass may only be visible up to a few years after disturbance. Despite strong reduction in aboveground biomass, disturbance increased biomass productivity (Fig. 2 and 3a), as is often found for logged or secondary tropical forests (e.g. Poorter *et al.* 2016). This indicates that, as expected, disturbance increases the availability of light and other resources, and in this way promotes growth of the remaining trees so strongly that these overcompensate for the loss in growth from removed trees.

Soil fertility – especially P – shapes productivity and biomass stocks

Soils on the Guiana shield are old and leached, and as a result nutrient-poor. We therefore expected that soil fertility would strongly determine productivity and biomass stocks. Soil fertility indeed increased productivity and biomass stocks (Fig. 2 and 3b, f , j), indicating that this forest is limited by soil nutrients at the 0.4-ha scale. Soil data were collected 13 years later than data on biomass productivity and stocks, and therefore the strong effects of soil fertility on biomass stocks and productivity indicate that the differences among plots (though not necessarily the absolute values of soil nutrients in the plots) persist over time. Average productivity among undisturbed plots (4.9 Mg ha^{-1} yr^{-1}) was lower than the average productivity of Neotropical forests (around 5.5 Mg ha^{-1} yr^{-1}; Brienen *et al.*, 2015), which also supports the idea that soil fertility limits productivity (Quesada *et al.* 2012) on the nutrient-poor soils in Guyana. Soil fertility effects may be weaker for larger plots where small-scale heterogeneity is averaged out, and it is therefore of paramount importance to define the relevant scale for the ecological question at hand. Other studies also show positive effects of soil fertility on productivity and aboveground biomass across Neotropical forests (Malhi *et al.* 2004; Aragão *et al.*

2009; Baraloto *et al.* 2011) and on fine root biomass in temperate forests (Valverde-Barrantes *et al.* 2015).

Both nitrogen (N) and phosphorus (P) are important for plant growth. The old and leached soils in Guyana are particularly limited in phosphorus (P_{soil}), as visible from low P_{soil} in our forest (0.0014%) and other Eastern Amazonian forests (Quesada *et al.* 2010). N_2-fixing tree species are relatively abundant in Guyanese forests, and N_{soil} may therefore be readily available. N_2-fixing species also produce more N-requiring phosphatases, which help to mineralize organic P, and N_2-fixing species have greater proportions of their root length colonized by mycorrhizal fungi that help to absorb P (Nasto *et al.* 2014). N stimulates root biomass (Fig. 2c) and may in this way facilitate P uptake especially in P-poor sites. In line with this idea, the proportion of trees belonging to genera that have ectomycorrhizal associations is higher in Guyana compared to the rest of the Amazon (ter Steege *et al.* 2006). In sum, P is likely the most limiting element in this forest (for a more extensive discussion on N vs. P limitation, see Appendix S13).

Soil fertility increases, but disturbance decreases diversity

Species richness often shows a hump-backed relationship with disturbance (i.e., the 'intermediate disturbance hypothesis'; Connell 1978), although this relation is generally weak for wet tropical forests (Bongers *et al.* 2009). We found a marginally significant, negative effect of logging disturbance on species richness (Fig. 2a-c). Perhaps, an increase in species diversity as a result of increased light availability and stronger differences may emerge over longer timescales (cf. de Avila *et al.* 2015). Alternatively, recruitment of pioneer species, which are normally favoured by increased light availability, is inhibited by the low nutrient availability in this forest, and by the low abundance of pioneer species in the surrounding landscape (ter Steege & Hammond 2001).

At high soil fertility, the most competitive species should outcompete other species and thus diversity would be low (Huston 1979). Contrary to this hypothesis, we found that soil fertility increased species richness. Even the most fertile plot in this forest is still relatively nutrient poor. Possibly, an increase in soil fertility provides the opportunity also for non-N_2-fixing species to establish, and therefore has a positive effect on species richness.

Diversity has no or negative effect on productivity and biomass stocks

We expected that species richness would lead to facilitation and niche complementarity (or to reduced negative plant-soil feedback; Mangan *et al.*, 2010), which would increase productivity, and hence accumulated (above- and belowground) biomass. However, this effect could be weak for this forest, where soil fertility and growth rates are low and relatively few species are very abundant (Appendix S1). We found that species richness did not significantly affect aboveground productivity and biomass stocks, and it even decreased fine root biomass stocks (Fig. 2 and 3c, g, k). This negative effect on fine root biomass stocks may be caused by relatively few species that can cope well with low nutrient availability and produce high amounts of fine root biomass. This idea is supported by the positive effect of soil fertility on species richness, indicating that more species are able to occur when soil conditions are less limiting. Also for functional trait dispersion (Fdis), which should better reflect the variation in species' strategies and niche separation, we found no positive effects on productivity and stocks, and even a negative effect on aboveground biomass stocks (Appendix S11), indicating that a narrow range in trait values (i.e., tall species with dense wood) rather than diversity in trait values increases biomass stocks (Conti & Díaz 2013; Finegan *et al.* 2015). A positive effect of diversity could be present at large spatial scales (e.g., regional and continental) where variation in species richness is greater (Chisholm *et al.* 2013; Poorter *et al.* 2015; van der Sande *et al.* 2017b), or in systems where diversity is lower and less redundancy may occur, such as in temperate forests.

Mass-ratio drives productivity and stocks of biomass and soil organic matter

Trait composition, i.e. the traits of an average tree in the forest, should reflect abiotic and biotic conditions and ultimately drive the biomass stocks and growth of the forest, as predicted by the mass-ratio hypothesis (Grime 1998). Trait values representing 'acquisitive' strategies (e.g., high leaf nutrient concentrations) increase resource-use efficiency and should result in higher productivity. We indeed found that trait composition affected all four response variables (Fig. 2 and 3c,g,k,o). Surprisingly, however, productivity *decreased* with community weighted mean (CWM) specific leaf area (SLA), indicating that forests with low abundance of acquisitive species attained higher productivity (Fig. 2 and 3d). This is contrary to our expectations, to other studies that show positive effects of CWM SLA or other acquisitive trait values on productivity (Baker *et al.* 2009; Finegan *et al.* 2015), and to current trait paradigms (Reich 2014). Compared to other Amazonian forests, this forest in Guyana is nutrient poor (Quesada *et al.* 2010), composed of a small number of dominant species, and possesses on average very conservative trait values (ter Steege & Hammond 2001). Such conservative trait values allow trees to retain scarce (soil) resources and enhance nutrient residence time in plants (Zhang *et al.* 2015), reduce respiration (Poorter & Bongers 2006), and protect plants better against physical and biotic hazards, thus enhancing carbon gain and plant survival and therefore also stand productivity. In tropical dry forests, conservative trait composition also increased productivity (Prado-Junior *et al.* 2016). Hence, whereas current trait paradigms may hold for most tropical forests, these relations may be contrary – with conservative traits enhancing productivity – for tropical forests growing under limiting resource availability (nutrients, water, light). Additionally, these trait paradigms might hold across large regions with very wide variation in site conditions and traits, but not within sites (Funk & Cornwell 2013).

Acquisitive trait values should increase biomass turnover and reduce biomass residence time and, hence, decrease biomass stocks (Reich 2014). Surprisingly, we found that acquisitive trait increased biomass stocks; P_{leaf} increased aboveground biomass stocks and $C{:}N_{leaf}$ decreased fine root biomass stocks. These findings are in agreement with some studies (Conti & Díaz 2013; Loiola, Scherer-lorenzen & Antônio 2015) but in contrast with others (Falster *et al.* 2011). It could be that, with limiting (soil) resources and an overall conservative trait composition, relatively acquisitive trait values (e.g. high nutrient concentrations) indicate increased availability and/or uptake of nutrients, which may lead to increased build-up of biomass rather than increased biomass turnover. The importance of P_{leaf} for aboveground biomass stocks and of $C{:}N_{leaf}$ for fine root biomass stocks is in line with the findings for the soil nutrients, and indicate that P may mainly limit aboveground biomass processes because it is the most limiting element, whereas N may limit belowground biomass processes because it is needed for P uptake by the roots.

High litter nutrient concentrations decrease soil organic matter

We hypothesized that logging disturbance would not affect soil organic matter (SOM) because logging happened 19 years before the collection of SOM data, and therefore the forest canopy should have closed and the microbial community should have recovered. SOM stock was indeed not significantly explained by logging disturbance. SOM was neither affected by the litter quantity that can potentially reach the soil as SOM, but tended to decrease with litter quality (Fig. 2 and 3o), which is in line with the mass-ratio hypothesis. Litter N had a negative effect on SOM because litter with high N is easily decomposed (Cleveland *et al.* 2014), resulting in a reduction of litter and organic matter in the soil (Wardle *et al.* 2002). Hence, SOM is mainly determined by decomposition rates that are in turn driven by litter quality, as predicted by the mass-ratio hypothesis.

Conclusions – mechanisms driving forest productivity and stocks of biomass and soil organic matter

Logging disturbance decreased aboveground biomass and increased aboveground biomass productivity, but did not affect fine root biomass. Soils on the Guiana shield are highly weathered and nutrient poor, and the forests are relatively mono-dominant with a conservative trait composition. P_{soil} strongly increased aboveground productivity and aboveground biomass stocks, indicating that P is the most limiting element in this forest. High leaf nutrient concentration increased biomass stocks, possibly because it indicates higher availability of soil nutrients and thus increases biomass build-up. However, acquisitive trait values decreased productivity, possibly because conservative trait values result in less respiration and biomass loss under harsh conditions. Species and trait diversity did not increase productivity and biomass stocks. Hence, we found evidence for the mass-ratio hypothesis but not for diversity effects. All these results indicate that this forest is severely constrained by P availability, which may limit the number and type of species that are abundant. Hence, disturbance, soil fertility and species traits, but not species or trait diversity, drive productivity and stocks of biomass and SOM in this Guyanese tropical rainforest.

Authors' Contributions

M.S., E.A., M.P.C., M.H. and L.P. designed the research; M.S. and Y.C.S. performed the research; P.H. contributed data; M.S. analyzed the data; M.S., E.A., M.P.C., M.H. and L.P. wrote the paper, and all others discussed the results and provided comments.

Acknowledgements:

The research leading to these results has received partial funding from the European Union Seventh Framework Programme (FP7/2007-2013) under grant agreement n° 283093 – The Role Of Biodiversity In climate change mitigatioN (ROBIN). This research is part of the strategic research program KBIV (KB-14) “Sustainable spatial development of ecosystems, landscapes, seas and regions”, funded by the Dutch Ministry of Economic Affairs and carried out by Wageningen University & Research centre (project code KB-14-003-030). We are grateful to the Guyana Forestry Commission for logistical support and support of the fieldwork, and to the Environmental Protection Agency for providing the fieldwork permits. Specifically, we thank Benedict Harry, Karlon Warde, and Rehaaz Mohamed for assistance in the field. We furthermore thank Jemberu Biru and Tereza Němcová for help with data collection Eef Velthorst for doing all chemical analyses of soil, root and litter in the laboratory at Wageningen University, the Netherlands, and the editor and two reviewers for helpful comments on the manuscript.

Data accessibility:

Data associated with this paper have been deposited in Data Archiving and Networked Services (DANS): https://doi.org/10.17026/dans-xaw-ju8s.

References:

Aerts, R. (1997) Climate, leaf litter chemistry and leaf litter decomposition in terrestrial ecosystems: a triangular relationship. *Oikos*, **79**, 439–449.

Aragão, L.E.O.C., Malhi, Y., Metcalfe, D.B., Silva-Espejo, J.E., Jiménez, E., et al. (2009) Above- and below-ground net primary productivity across ten Amazonian forests on contrasting soils. *Biogeosciences*, **6**, 2759–2778.

de Avila, A.L., Ruschel, A.R., de Carvalho, J.O.P., Mazzei, L., Silva, J.N.M., et al. (2015) Medium-term dynamics of tree species composition in response to silvicultural intervention intensities in a tropical rain forest. *Biological Conservation*, **191**, 577–586.

Baker, T.R., Phillips, O.L., Laurance, W.F., Pitman, N.C.A., Almeida, S., et al. (2009) Do species traits determine patterns of wood production in Amazonian forests? *Biogeosciences*, **6**, 297–307.

Baker, T.R., Phillips, O.L., Mahli, Y.R., Almeida, S., Arroyo, L., et al. (2004) Variation in wood density determines spatial patterns in Amazonian forest biomass. *Global Change Biology*, **10**, 545–562.

Baraloto, C., Rabaud, S., Molto, Q., Blanc, L., Fortunel, C., et al. (2011) Disentangling stand and environmental correlates of aboveground biomass in Amazonian forests. *Global Change Biology*, **17**, 2677–2688.

Beer, C., Reichstein, M., Tomelleri, E., Ciais, P., Jung, M., et al. (2010) Terrestrial gross carbon dioxide uptake: global distribution and covariation with climate. *Science*, **329**, 834–838.

Bongers, F., Poorter, L., Hawthorne, W.D. & Sheil, D. (2009) The intermediate disturbance hypothesis applies to tropical forests, but disturbance contributes little to tree diversity. *Ecology Letters*, **12**, 798–805.

Brienen, R.J.W., Phillips, O.L., Feldpausch, T.R., Gloor, E., Baker, T.R., Lloyd, J., Zagt, R.J., et al. (2015) Long-term decline of the Amazon carbon sink. *Nature*, **519**, 344–348.

Chave, J., Coomes, D., Jansen, S., Lewis, S.L., Swenson, N.G. & Zanne, A.E. (2009) Towards a worldwide wood economics spectrum. *Ecology letters*, **12**, 351–66.

Chave, J., Réjou-Méchain, M., Búrquez, A., Chidumayo, E., Colgan, M.S., et al. (2014) Improved allometric models to estimate the aboveground biomass of tropical trees. *Global Change Biology*, **20**, 3177–3190.

Chisholm, R.A., Muller-Landau, H.C., Abdul Rahman, K., Bebber, D.P., Bin, Y., Bohlman, S.A., Zimmerman, J.K., et al. (2013) Scale-dependent relationships between tree species richness and ecosystem function in forests. *Journal of Ecology*, **101**, 1214–1224.

Cleveland, C.C., Reed, S.C., Keller, A.B., Nemergut, D.R., O'Neill, S.P., Ostertag, R. & Vitousek, P.M. (2014) Litter quality versus soil microbial community controls over decomposition: A quantitative analysis. *Oecologia*, **174**, 283–294.

Connell, J.H. (1978) Diversity in tropical rain forests and coral reefs. *Science*, **199**, 1302–1310.

Conti, G. & Díaz, S. (2013) Plant functional diversity and carbon storage – an empirical test in semi-arid forest ecosystems. *Journal of Ecology*, **101**, 18–28.

Cornwell, W.K., Cornelissen, J.H.C., Amatangelo, K., Dorrepaal, E., Eviner, V.T., et al. (2008) Plant species traits are the predominant control on litter decomposition rates within biomes worldwide. *Ecology letters*, **11**, 1065–71.

van Dam, O. (2001) *Forest Filled with Gaps. Effects of Gap Size on Water and Nutrient Cycling in Tropoical Rain Forest. A Study in Guyana*. PhD thesis, Utrecht University, Utrecht.

De Deyn, G.B., Cornelissen, J.H.C. & Bardgett, R.D. (2008) Plant functional traits and soil carbon sequestration in contrasting biomes. *Ecology letters*, **11**, 516–31.

Falster, D.S., Brännström, Å., Dieckmann, U. & Westoby, M. (2011) Influence of four major plant traits on average height, leaf-area cover, net primary productivity, and biomass density in single-species forests: a theoretical investigation. *Journal of Ecology*, **99**, 148–164.

Finegan, B., Peña-Claros, M., de Oliveira, A., Ascarrunz, N., Bret-Harte, M.S., et al. (2015) Does functional trait diversity predict above-ground biomass and productivity of tropical forests? Testing three alternative hypotheses (ed C Canham). *Journal of Ecology*, **103**, 191–201.

Funk, J.L. & Cornwell, W.K. (2013) Leaf traits within communities: context may affect the mapping of traits to function. *Ecology*, **94**, 1893–1897.

Gotelli, N.J. & Colwell, R.K. (2001) Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. *Ecology Letters*, **4 Abstract**, 379–391.

Grime, J.P. (1973) Competitive exclusion in herbaceous vegetation. *Nature*, **242**, 344–347.

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

Hooper, D.U., Chapin III, F.S., Ewel, J.J., Hector, A., Inchausti, P., et al. (2005) Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecological Monographs*, **75**, 3–35.

van der Hout, P. (1999) *Reduced Impact Logging in the Tropical Rain Forest of Guyana: Ecological, Economical and Silvicultural Consequences*. PhD thesis, Utrecht University, Utrecht.

Huston, M. (1979) A general hypothesis of species diversity. *The American Naturalist*, **130**, 81–101.

van Kekem, A.J., Pulles, J.H.. & Khan, Z. (1996) *Soils of the Rainforest in Central Guyana. Tropenbos Guyana Series Vol. 2. Georgetown, Guyana.*

Loiola, P.P., Scherer-lorenzen, M. & Antônio, M. (2015) The role of environmental filters and functional traits in predicting the root biomass and productivity in savannas and tropical seasonal forests. *Forest Ecology and Management*, **342**, 49–55.

Loreau, M. (1998) Separating sampling and other effects in biodiversity experiments. *Oikos*, **3**, 600–602.

Malhi, Y., Aragão, L.E.O.C., Metcalfe, D.B., Paiva, R., Quesada, C.A., et al. (2009) Comprehensive assessment of carbon productivity, allocation and storage in three Amazonian forests. *Global Change Biology*, **15**, 1255–1274.

Malhi, Y., Baker, T.R., Phillips, O.L., Almeida, S., Alvarez, E., et al. (2004) The above-ground coarse wood productivity of 104 Neotropical forest plots. *Global Change Biology*, **10**, 563–591.

Malhi, Y., Baldocchi, D.D. & Jarvis, P.G. (1999) The carbon balance of tropical, temperate and boreal forests. *Plant, Cell and Environment*, **22**, 715–740.

Mangan, S.A., Schnitzer, S.A., Herre, E.A., Mack, K.M.L., Valencia, M.C., Sanchez, E.I. & Bever, J.D. (2010) Negative plant-soil feedback predicts tree-species relative abundance in a tropical forest. *Nature*, **466**, 752–5.

Marklein, A.R. & Houlton, B.Z. (2012) Nitrogen inputs accelerate phosphorus cycling rates across a wide variety of terrestrial ecosystems. *New Phytologist*, **193**, 696–704.

Melillo, J.M., Aber, J.D. & Muratore, J.F. (1982) Nitrogen and lignin control of hardwood leaf litter decomposition dynamics. *Ecology*, **63**, 621–626.

Nasto, M.K., Alvarez-Clare, S., Lekberg, Y., Sullivan, B.W., Townsend, A.R. & Cleveland, C.C. (2014) Interactions among nitrogen fixation and soil phosphorus acquisition strategies in lowland tropical rain forests (ed N Johnson). *Ecology Letters*, **17**, 1282–1289.

Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., et al. (2015) vegan: Community Ecology Package. R package version 2.2-1. http://CRAN.R-project.org/package=vegan

Pakeman, R.J. (2014) Functional trait metrics are sensitive to the completeness of the species' trait data? (ed J Oksanen). *Methods in Ecology and Evolution*, **5**, 9–15.

Parton, W., Silver, W.L., Burke, I.C., Grassens, L., Harmon, M.E., et al. (2007) Global-scale similarities in nitrogen release patterns during long-term decomposition. *Science*, **315**, 361–364.

Peña-Claros, M., Fredericksen, T.S., Alarcón, a., Blate, G.M., Choque, U., et al. (2008) Beyond reduced-impact logging: Silvicultural treatments to increase growth rates of tropical trees. *Forest Ecology and Management*, **256**, 1458–1467.

Pérez-Harguindeguy, N., Díaz, S., Garnier, E., Lavorel, S., Poorter, H., et al. (2013) New handbook for standardised measurement of plant functional traits worldwide. *Australian Joural of Botany*, **61**, 167–234.

Poorter, L. (2008) The relationships of wood-, gas- and water fractions of tree stems to performance and life history variation in tropical trees. *Annals of botany*, **102**, 367–75.

Poorter, L. & Bongers, F. (2006) Leaf traits are good predictors of plant performance across 53 rain forest species. *Ecology*, **87**, 1733–1743.

Poorter, L., Bongers, F., Aide, T.M., Almeyda Zambrano, A.M., Balvanera, P., Becknell, J.M., Rozendaal, D.M.A., et al. (2016) Biomass resilience of Neotropical secondary forests. *Nature*, **530**, 211–214.

Poorter, L., van der Sande, M.T., Thompson, J., Arets, E.J.M.M., Alarcón, A., et al. (2015) Diversity enhances carbon storage in tropical forests. *Global Ecology and Biogeography*, **24**, 1314–1328.

Potvin, C., Mancilla, L., Buchmann, N., Monteza, J., Moore, T., et al. (2011) An ecosystem approach to biodiversity effects: Carbon pools in a tropical tree plantation. *Forest Ecology and Management*, **261**, 1614–1624.

Prado-Junior, J.A., Schiavini, I., Vale, V.S., Arantes, C.S., van der Sande, M.T., Lohbeck, M. & Poorter, L. (2016) Conservative species drive biomass productivity in tropical dry forests. *Journal of Ecology*, **104**, 817–827.

Quesada, C.A., Lloyd, J., Schwarz, M., Patiño, S., Baker, T.R., et al. (2010) Variations in chemical and physical properties of Amazon forest soils in relation to their genesis. *Biogeosciences*, **7**, 1515–1541.

Quesada, C.A., Phillips, O.L., Schwarz, M., Czimczik, C.I., Baker, T.R., et al. (2012) Basin-wide variations in Amazon forest structure and function are mediated by both soils and climate. *Biogeosciences*, **9**, 2203–2246.

Reich, P.B. (2014) The world-wide “fast – slow” plant economics spectrum: a traits manifesto. *Journal of Ecology*, **102**, 275–301.

Robinson, D. (2007) Implications of a large global root biomass for carbon sink estimates and for soil carbon dynamics. *Proceedings of the Royal Society B: Biological Sciences*, **274**, 2753–2759.

Rozendaal, D.M.A., Hurtado, V.H. & Poorter, L. (2006) Plasticity in leaf traits of 38 tropical tree species in response to light; relationships with light demand and adult stature. *Functional Ecology*, **20**, 207–216.

Rutishauser, E., Hérault, B., Baraloto, C., Blanc, L., Descroix, L., et al. (2015) Rapid tree carbon stock recovery in managed Amazonian forests. *current Biology*, **25**, 1–2.

van der Sande, M.T., Peña-Claros, M., Ascarrunz, N., Arets, E.J.M.M., Licona, J.C., Toledo, M. & Poorter, L. (2017a) Abiotic and biotic drivers of biomass change in a Neotropical forest. *Journal of Ecology*, In press.

van der Sande, M.T., Poorter, L., Kooistra, L., Balvanera, P., Thonicke, K., et al. (2017b) Biodiversity in species, traits and structure determines carbon stocks and uptake in tropical forests. *Biotropica*.

Shipley, B. (2004) *Cause and Correlation in Biology. A User's Guide to Path Analysis, Structural Equations and Causal Inference*. Cambridge University Press, Cambridge.

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

ter Steege, H., Pitman, N.C.A., Phillips, O.L., Chave, J., Sabatier, D., et al. (2006) Continental-scale patterns of canopy tree composition and function across Amazonia. *Nature*, **443**, 444–7.

Sullivan, M.J.P., Talbot, J., Lewis, S.L., Phillips, O.L., Qie, L., et al. (2017) Diversity and carbon storage across the tropical forest biome. *Scientific Reports*, **7**, 1–12.

Talbot, J., Lewis, S.L., Lopez-Gonzalez, G., Brienen, R.J.W., Monteagudo, A., et al. (2014) Methods to estimate aboveground wood productivity from long-term forest inventory plots. *Forest Ecology and Management*, **320**, 30–38.

Tilman, D. (1999) The ecological consequences of changes in biodiversity: a search for general principles. *Ecology*, **80**, 1455–1474.

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**, 843–5.

Valverde-Barrantes, O.J., Smemo, K.A., Feinstein, L.M., Kershner, M.W. & Blackwood, C.B. (2015) Aggregated and complementary: symmetric proliferation, overyielding, and mass effects explain fine-root biomass in soil patches in a diverse temperate deciduous forest landscape. *New Phytologist*, **205**, 731–742.

Vilà, M., Carrillo-Gavilán, A., Vayreda, J., Bugmann, H., Fridman, J., et al. (2013) Disentangling biodiversity and climatic determinants of wood production (ed LA Newsom). *PLoS ONE*, **8**, e53530.

Violle, C., Navas, M.-L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I. & Garnier, E. (2007) Let the concept of trait be functional! *Oikos*, **116**, 882–892.

Wardle, D.A., Bonner, K.I. & Barker, G.M. (2002) Linkages between plant litter decomposition, litter quality, and vegetation responses to herbivory. *Functional Ecology*, **16**, 585–595.

Woodcock, D.W. & Shier, A.D. (2002) Wood specific gravity and its radial variations: the many ways to make a tree. *Trees*, **16**, 437–443.

Zhang, J.-L., Zhang, S.-B., Chen, Y.-J., Zhang, Y.-P. & Poorter, L. (2015) Nutrient resorption is associated with leaf vein density and growth performance of dipterocarp tree species. *Journal of Ecology*, **103**, 541–549.

Tables:

Table 1: All abiotic variables (soil fertility variables and logging disturbance) with abbreviation, description, units (the variables expressed in % are mass-based), what it indicates, and the average (Avg), minimum value (Min) and maximum value (Max) across the 0.4-ha plots.

Abbreviation	**Variable description**	**Units**	**Indicator of:**	**Avg**	**Min**	**Max**
N_{soil}	Soil nitrogen content	%	Soil fertility	0.193	0.077	0.179
P_{soil}	Soil phosphorus content	%	Soil fertility	0.003	0.001	0.008
$N{:}P_{soil}$	Soil nitrogen: phosphorus ratio		Soil fertility, nutrient limitation	47.686	16.680	86.250
$C{:}N_{soil}$	Soil carbon : nitrogen ratio		Soil fertility, nutrient limitation	13.075	10.419	16.455
Disturbance	Relative basal area removed due to logging	%	Light availability	10.4	0.0	35.0

Table 2: All biotic variables (trait composition indices and species richness) with abbreviation, description, units (the variables expressed in % are mass-based), what it indicates, and the average (Avg), minimum value (Min) and maximum value (Max) across the 0.4-ha plots.

Abbreviation	**Variable description**	**Units**	**Indicator of:**	**Avg**	**Min**	**Max**
SLA	Specific leaf area	cm^2 g^{-1}	Light interception efficiency	127.55	119.44	140.07
N_{leaf}	Leaf nitrogen content	%	Photosynthetic capacity	1.78	1.64	1.94
P_{leaf}	Leaf phosphorus content	%	Growth capacity	0.05	0.04	0.05
$C:N_{leaf}$	Leaf carbon : nitrogen ratio		Relative nutrient limitation	27.86	25.87	29.74
$N:P_{leaf}$	Leaf nitrogen : phosphorus ratio		Relative nutrient limitation	37.74	34.21	40.58
FPs	Specific force to punch	N cm^{-2}	Leaf defence	263.37	243.17	284.42
WD	Wood density	g cm^{-3}	Volume growth, wood defence	0.89	0.83	0.95
WDMC	Wood dry matter content	g g^{-1}	Wood defence	0.74	0.71	0.76
Richness	Rarefied species richness per 100 stems	# ha^{-1}	Niche complementarity	29.0	21.01	38.2

Table 3: The four response variables (aboveground productivity, aboveground biomass, fine root biomass, and soil organic matter) with description, units, average (Avg), minimum value (Min) and maximum value (Max) across the 0.4-ha plots.

Response variable	**Description**	**Units**	**Avg**	**Min**	**Max**
Aboveground productivity	Gross biomass increase	Mg ha^{-1} y^{-1}	6.3	3.7	11.1
Aboveground biomass	Stem and crown biomass	Mg ha^{-1}	367.4	235.1	566.1
Fine root biomass	Root biomass in top 20 cm of the soil	Mg ha^{-1}	17.3	8.9	30.4
Soil organic matter	Soil organic matter in top 10 cm of the soil	Mg ha^{-1}	66.3	38.9	108.1

Table 4: Results for the four structural equation models (SEMs) of aboveground productivity, aboveground biomass, fine root biomass, and soil organic matter (see also Fig. 2), to evaluate the effects of various abiotic and biotic factors. The regression coefficients (Coeff), standardized regression coefficients (Std. coeff), Z-values and P-values are given for all regressions (i.e., all arrows in Fig. 2), and the R^2 of the endogenous variables (i.e., variables that are affected by other variables: productivity and stocks of biomass and soil organic matter, species richness, and trait composition)). All four models were accepted (P = 0.89, 0.94, 0.62, 1.00; and χ^2= 0.02, 0.01, 0.25, 0.10 for productivity, aboveground biomass, fine root biomass, and soil organic matter, respectively; Appendix S10). For trait abbreviations, see Table 1.

SEM response variable	SEM predictor variable	Coeff	Std. coeff	Z-value	P-value
Aboveground biomass productivity					
Productivity	Disturbance	0.01	0.34	2.41	0.016
	P_{soil}	0.29	0.51	2.68	0.007
	Richness	-0.01	-0.10	-0.49	0.627
	SLA	-0.02	-0.35	-2.01	0.044
Richness	Disturbance	-0.13	-0.38	-1.90	0.057
	P_{soil}	2.95	0.35	2.46	0.014
SLA	Disturbance	0.01	0.02	0.10	0.917
	P_{soil}	2.03	0.19	1.30	0.194
R^2 Productivity		0.46			
R^2 Richness		0.24			
R^2 SLA		0.04			
Aboveground biomass					
Aboveground biomass	Disturbance	-0.02	-0.73	-7.20	<0.001
	P_{soil}	0.15	0.27	2.61	0.009
	Richness	-0.01	-0.12	-1.53	0.126

	P_{leaf}	0.06	0.47	4.66	<0.001
Richness	Disturbance	-0.13	-0.38	-1.90	0.057
	P_{soil}	2.95	0.35	2.46	0.014
P_{leaf}	Disturbance	<0.01	0.01	0.05	0.961
	P_{soil}	0.57	0.12	0.58	0.560
R^2 Aboveground biomass		0.73			
R^2 Richness		0.24			
R^2 P_{leaf}		0.02			
Fine root biomass					
Fine root biomass	Disturbance	<0.01	-0.07	-0.39	0.698
	N_{soil}	4.25	0.39	2.02	0.044
	Richness	-0.03	-0.38	-2.39	0.017
	C: N_{soil}	-0.12	-0.44	-3.46	0.001
Richness	Disturbance	-0.11	-0.31	-2.44	0.015
	N_{soil}	75.06	0.51	3.01	0.003
C: N_{soil}	Disturbance	0.03	0.28	2.06	0.039
	N_{soil}	-5.87	-0.15	-1.21	0.227
R^2 Fine root biomass		0.34			
R^2 Richness		0.38			
R^2 C:N_{leaf}		0.11			
Soil organic matter					
Soil organic matter	Disturbance	<0.01	0.11	0.67	0.503
	Litter quantity	0.01	0.13	0.59	0.555
	N_{litter}	-0.04	-0.37	-1.86	0.063
Litter quantity	Productivity	-0.23	-0.17	-1.24	0.214
N_{litter}	Productivity	-0.12	-0.09	-0.42	0.674

R^2 Soil organic matter	0.16
R^2 Litter quantity	0.03
R^2 N_{litter}	0.01

Figure decriptions:

Figure 1: Expected direct and indirect effects of disturbance, soil fertility, species richness and trait composition on productivity and above- and belowground living biomass (*a*), and the direct and indirect effects of disturbance, aboveground productivity, leaf litter quantity and leaf litter quality on soil organic matter (*b*). Expected positive (+) and negative (-) effects are given. The expected effect of disturbance is negative for above- and belowground biomass but positive for productivity. Disturbance and soil fertility favour species with acquisitive trait composition (e.g., high specific leaf area, low wood density), and an acquisitive trait composition increases productivity but decreases biomass stocks. High litter quality means that nutrient concentrations are high, which increases decomposition rates and thus decreases soil organic matter stocks. Litter quality may depend on the trait composition of the standing vegetation, but to keep the model simple (given the limited amount of replicates we had available) we did not include the relationship between trait composition and litter quality in the analysis.

Figure 2: Structural equation models for aboveground biomass productivity (*a*), aboveground biomass (*b*), fine root biomass (*c*), and soil organic matter (*d*). For aboveground biomass productivity, aboveground biomass and fine root biomass, direct and indirect effects of disturbance, soil fertility, rarefied species richness (per 100 stems), and trait composition (i.e., a community weighted mean stem or leaf trait) were evaluated. For soil organic matter, direct and indirect effects of litter quantity, litter quality, disturbance and productivity were evaluated. All four models were accepted (Appendix S10). For all relations that were significant (continuous black lines), the beta coefficient and significance level are given (* = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$), and for all non-significant relations (grey, dotted lines), no statistics are shown. R^2 values show the explained variance of the

ultimate response variables. The variables between brackets for soil fertility and trait composition are the variables that were selected to best predict productivity, biomass, or soil organic matter. For more statistics of the structural equation models, see Table 3.

Figure 3: Bivariate relations of disturbance (a, e, i), soil fertility (b, f, j) and litter quantity in the case of soil organic matter (n), trait composition (c, g, k, o) and rarefied species richness per 0.4 ha plot (d, h, l) with aboveground biomass productivity (a-d), aboveground biomass (e-h), and fine root productivity (i-l), and soil organic matter (m-o). Each dot is one 0.4 ha plot. 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. SLA = specific leaf area; P_{soil} and N_{soil} = soil phosphorus and nitrogen concentration, respectively; P_{leaf} and $C:N_{leaf}$ = leaf phosphorus concentration and leaf carbon : nitrogen ratio, respectively. Note that the y-axes are in ln-scale.

Appendices

S1: Accumulative relative biomass abundance of the species in this forest

S2: Harvest intensity per treatment.

S3: Collection and calculation of soil organic matter, fine root biomass, nutrient concentrations, and litter variables.

S4: Variation in soil conditions in our study compared to other studies

S5: Details of leaf and stem trait collection

S6: Spearman's correlations between productivity, biomass stocks and soil organic matter, between soil variables, and between community-weighted mean trait values.

S7: Selection and refinement of structural equation models.

S8: Results of ANOVAs to test the effect of logging treatment on soil fertility, biotic factors, and response variables

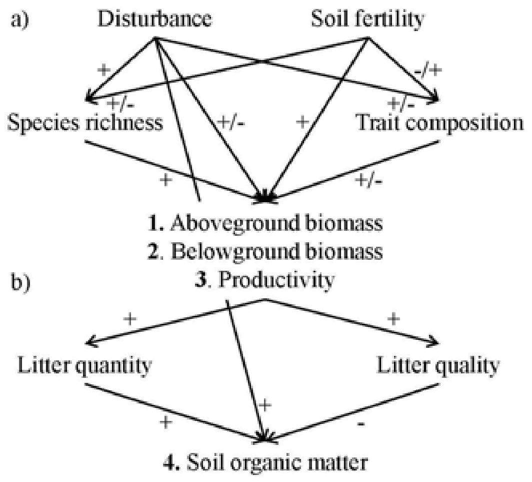
S9: Results of all subsets regression analyses for aboveground productivity, aboveground biomass, fine root biomass, and soil organic matter (i.e., the response variable), followed by averaging of all possible models.

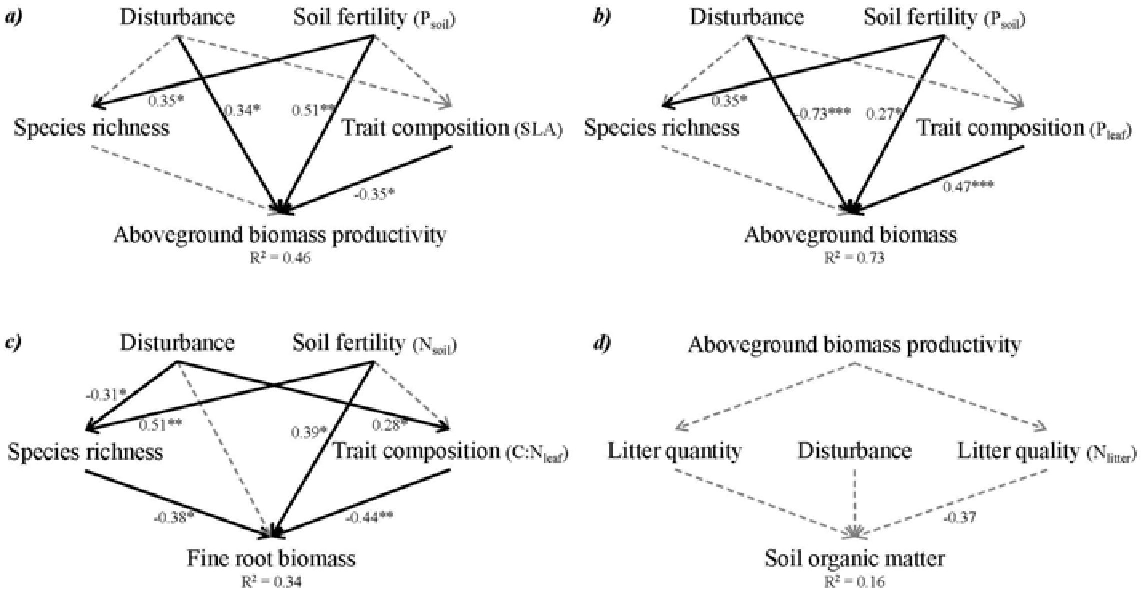
S10: Statistics showing the model fit of structural equation models (SEMs) for productivity, aboveground biomass, fine root biomass, and soil organic matter.

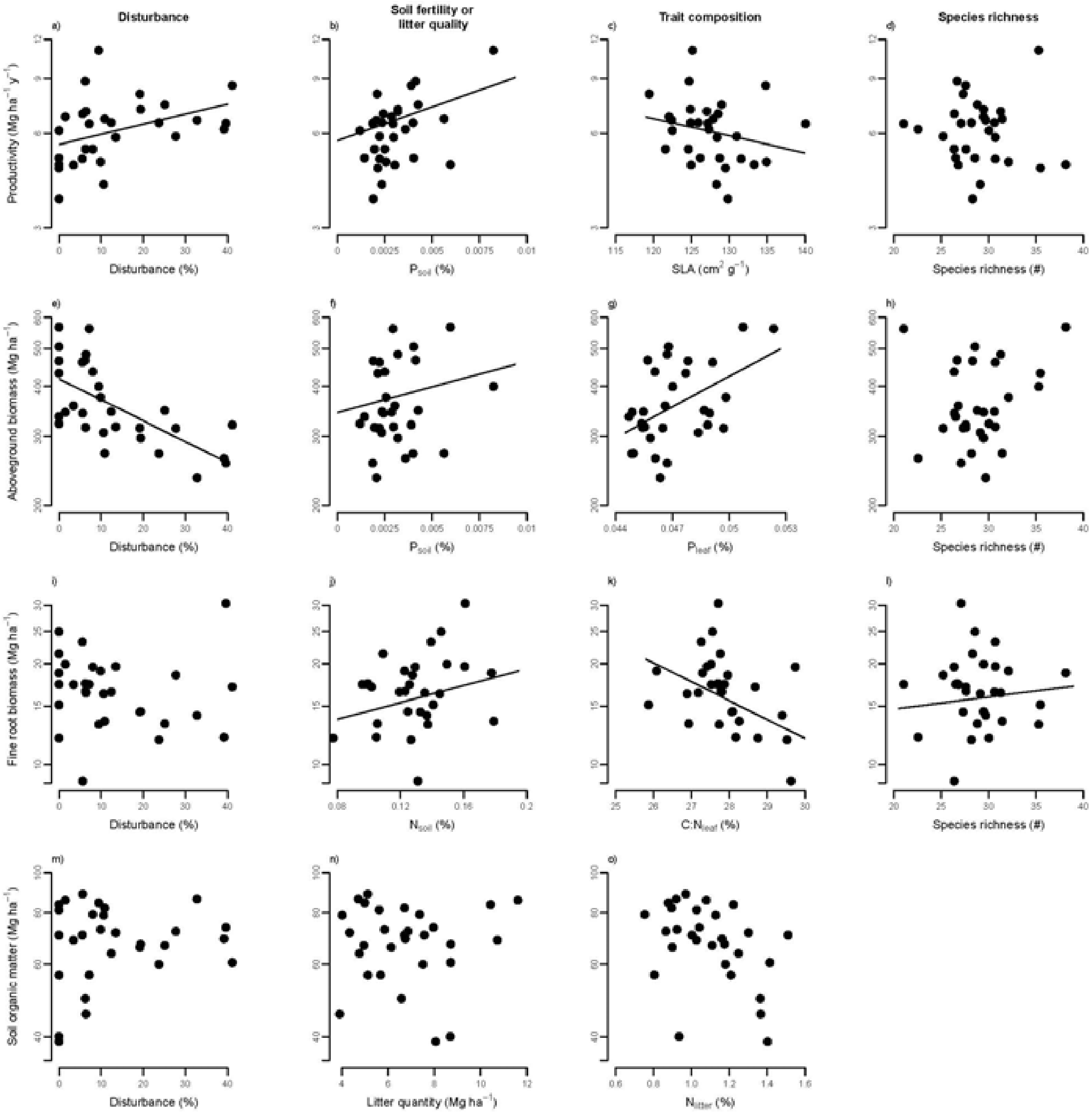
S11: Results from structural equation models with species richness replaced by functional trait dispersion (Fdis).

S12: Results from linear mixed models (with 0.4-ha plots nested in 1-ha plots) for the variables used in the 'best' structural equation models (Fig. 2).

S13: Extensive discussion on the relative importance of nitrogen vs. phosphorus limitation




a)
Disturbance
Soil fertility (P_{soil})
0.35*
0.34*
0.51**
Species richness
Trait composition (SLA)
-0.35*
Aboveground biomass productivity
$R^2 = 0.46$
b)
Disturbance
Soil fertility (P_{soil})
0.35*
-0.73***
0.27*
Species richness
Trait composition (P_{leaf})
0.47***
Aboveground biomass
$R^2 = 0.73$
c)
Disturbance
Soil fertility (N_{soil})
-0.31*
0.51**
0.39*
0.28*
Species richness
Trait composition ($C:N_{leaf}$)
-0.38*
-0.44**
Fine root biomass
$R^2 = 0.34$
d)
Aboveground biomass productivity
Litter quantity
Disturbance
Litter quality (N_{litter})
-0.37
Soil organic matter
$R^2 = 0.16$


Disturbance
Soil fertility or litter quality
Trait composition
Species richness
a)
b)
c)
d)
e)
f)
g)
h)
i)
j)
k)
l)
m)
n)
o)
Productivity (Mg ha^{-1} y^{-1})
Aboveground biomass (Mg ha^{-1})
Fine root biomass (Mg ha^{-1})
Soil organic matter (Mg ha^{-1})
12
9
6
3
600
500
400
300
200
30
25
20
15
10
100
80
60
40
Disturbance (%)
0
10
20
30
40
P$_{soil}$ (%)
0
0.0025
0.005
0.0075
0.01
SLA (cm^2 g^{-1})
115
120
125
130
135
140
Species richness (#)
20
25
30
35
40
P$_{leaf}$ (%)
0.044
0.047
0.05
0.053
N$_{soil}$ (%)
0.08
0.12
0.16
0.2
C:N$_{leaf}$ (%)
25
26
27
28
29
30
Litter quantity (Mg ha^{-1})
4
6
8
10
12
N$_{litter}$ (%)
0.6
0.8
1.0
1.2
1.4
1.6