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# Does functional trait diversity predict above-ground biomass and productivity of tropical forests? Testing three alternative hypotheses

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## Summary

**1.** Tropical forests are globally important, but it is not clear whether biodiversity enhances carbon storage and sequestration in them. We tested this relationship focusing on components of functional trait biodiversity as predictors.

**2.** Data are presented for three rain forests in Bolivia, Brazil and Costa Rica. Initial above-ground biomass and biomass increments of survivors, recruits and survivors + recruits (total) were estimated for trees  $\geq 10$  cm d.b.h. in 62 and 21 1.0-ha plots, respectively. We determined relationships of biomass increments to initial standing biomass ( $AGB_i$ ), biomass-weighted community mean values (CWM) of eight functional traits and four functional trait variety indices (functional richness, functional evenness, functional diversity and functional dispersion).

**3.** The forest continuum sampled ranged from 'slow' stands dominated by trees with tough tissues and high  $AGB_i$ , to 'fast' stands dominated by trees with soft, nutrient-rich leaves, lighter woods and lower  $AGB_i$ .

**4.** We tested whether  $AGB_i$  and biomass increments were related to the CWM trait values of the dominant species in the system (the biomass ratio hypothesis), to the variety of functional trait values (the niche complementarity hypothesis), or in the case of biomass increments, simply to initial standing biomass (the green soup hypothesis).

**5.** CWMs were reasonable bivariate predictors of  $AGB_i$  and biomass increments, with CWM specific leaf area SLA, CWM leaf nitrogen content, CWM force to tear the leaf, CWM maximum adult height  $H_{max}$  and CWM wood specific gravity the most important.  $AGB_i$  was also a reasonable predictor of the three measures of biomass increment. In best-fit multiple regression models, CWM  $H_{max}$  was the most important predictor of initial standing biomass  $AGB_i$ . Only leaf traits were selected in the best models for biomass increment; CWM SLA was the most important predictor, with the expected positive relationship. There were no relationships of functional variety indices to biomass increments, and  $AGB_i$  was the only predictor for biomass increments from recruits.

**6. Synthesis.** We found no support for the niche complementarity hypothesis and support for the green soup hypothesis only for biomass increments of recruits. We have strong support for the biomass ratio hypothesis. CWM  $H_{max}$  is a strong driver of ecosystem biomass and carbon storage and CWM SLA, and other CWM leaf traits are especially important for biomass increments and carbon sequestration.

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**Key-words:** biodiversity, biomass ratio, ecosystem processes, green soup hypothesis, niche complementarity, plant population and community dynamics

## Introduction

Functional trait diversity (FTD) is the value, range, distribution and relative abundance of the functional traits of organisms that make up an ecosystem (Díaz *et al.* 2011). How does FTD affect ecosystem properties, processes and services? Díaz *et al.* (2011) show that depending on the process and the associated service, the key components of FTD might be either the trait values of the most abundant species, the variety or diversity of trait values found in the community or the trait values of particular individual species, which may be rare. Grime (1998) proposed that ecosystem processes are, in fact, determined to a large extent by the trait values of the dominant contributors to the vegetation biomass, which can be synthesized as the community weighted mean (CWM), the expected trait value of an individual randomly selected from the community (Garnier *et al.* 2004; Violle *et al.* 2007; Casanoves *et al.* 2011). This *biomass ratio hypothesis* is analogous to the hypothesis from biodiversity–ecosystem functioning experiments using plant monocultures and mixtures, which postulates that variations in ecosystem productivity are determined by the presence or absence of highly productive species and not by the variety and complementarity of species (Cardinale *et al.* 2007).

What mechanism would underlie a relationship between CWM trait values and ecosystem processes? Traits that are correlated with the growth rate of individual plants (e.g. Pérez-Harguindeguy *et al.* 2013) are also expected to be mechanistically related to primary productivity of the vegetation (Garnier *et al.* 2004). Predictions regarding correlations between CWM trait values and above-ground vegetation biomass (AGB) productivity therefore parallel those for relationships between plant trait values and plant performance. High CWM specific leaf area (SLA) or leaf nitrogen concentration, for example, indicate a community dominated by individuals of fast-growing acquisitive species that are expected to be associated with high productivity. On the other hand, high CWM leaf dry matter content (LDMC) or wood specific gravity (WSG) indicate a community dominated by conservative species and are expected to be associated with low productivity (Garnier *et al.* 2004 and cf. Poorter *et al.* 2008; Wright *et al.* 2010). These predictions have been fulfilled in a growing number of situations. In Mediterranean secondary herbaceous vegetation, for example, primary productivity, litter decomposition rate and total soil carbon and nitrogen were correlated as expected with CWM leaf traits (Garnier *et al.* 2004). In studies of herbaceous communities across a range of land uses in Europe and Israel, CWM LDMC was found to be a valuable predictor of the effects of land use change on nutrient cycling rate (Fortunel *et al.* 2009; see Conti & Díaz 2013 for a study in woody vegetation).

The role of the range or variety of trait values (Functional Variety, FV, Díaz *et al.* 2011) in the determination of ecosystem properties and processes – the *niche complementarity hypothesis* – is less clear than that of CWM trait values. The hypothesis that ecosystem processes and services depend on functional trait variety rather than species richness *per se* has been a major driver of conceptual development in plant functional ecology. Concepts and tools related to functional trait variety have become increasingly available in recent years. Functional variety has been parsed into four relatively independent components: functional richness FRic, evenness FEve, divergence FDiv (Villéger, Mason & Moullot 2008; Mouchet *et al.* 2010) and dispersion FDis (Laliberté & Legendre 2010). These indices quantify the trait hypervolume of the community (FRic, FDis) and the distribution of abundance or biomass of the species in this volume (FEve, FDiv and FDis). Both these functional properties may measure niche complementarity, and therefore enhancement of ecosystem processes by functional trait variety.

Understanding of the effects of FTD as conceived here on ecosystem properties and processes in tropical forests is a work in process. Unweighted mean trait values, for instance, vary with soil fertility and dry season length in Amazonian forests (Baker *et al.* 2009; Fyllas *et al.* 2009). Moreover, Baker *et al.* (2009) found that species functional groups defined on the basis of species WSG and maximum adult height did not differ in their biomass production rates, concluding that soil and climate are the main drivers of variation in biomass production across the Amazon basin. But what might be the effects on biomass storage and dynamics of a wider range of traits known to influence plant and stand productivity, and crucially for the understanding and conservation of biological diversity, what might be the effects of FV?

We present data for three tropical forest sites encompassing a wide range of climate and soil conditions. We estimated above-ground biomass (AGB) and monitored biomass productivity  $\Delta$ AGB for 21 1.0 ha permanent sample plots (PSP) comprising *c.* 10 000 trees. For the dominant species (those forming 60–80% of initial AGB), we measured eight functional traits of known importance for plant growth and survival (Poorter *et al.* 2008; Wright *et al.* 2010), and ecosystem biomass stocks and productivity (e.g., Falster *et al.* 2011; Paquette & Messier 2011). We tested whether variation in  $\Delta$ AGB was driven by FV (the niche complementarity hypothesis), the trait values of the dominant species as measured by CWMs (the biomass ratio hypothesis) or simply by a negative density-dependent effect of AGB, which we call the green soup hypothesis.

We addressed three questions. First, after accounting for site effects, how is  $\Delta$ AGB related to FTD? Regarding the biomass ratio hypothesis, we predicted a positive relationship with  $\Delta$ AGB of CWM SLA, leaf nitrogen concentration, leaf

phosphorous concentration and maximum adult height – high CWM values of these traits would indicate ‘fast’ stands with soft, nutrient-rich leaves and high productivity. Conversely, CWM WSG, LDMC and force to tear were predicted to have negative relationships with  $\Delta\text{AGB}$  – high values of these CWM traits would indicate ‘slow’ stands with low productivity. We also calculated per-plot CWM N:P ratio and determined its relationship with  $\Delta\text{AGB}$  (Koerselman & Meuleman 1996). CWM N:P may indicate the degree to which forest growth is limited by N or P (Cernusak, Winter & Turner 2010), and P is thought to be the most important limiting nutrient in lowland tropical forest productivity (Grubb 1977; Tanner, Vitousek & Cuevas 1998; Wright *et al.* 2004). Ours is one of the first studies to evaluate the relationship between CWM N:P as an ecosystem property and  $\Delta\text{AGB}$  as a process. A final key prediction regarding our first question concerns the niche complementarity hypothesis: that FV would be positively correlated with  $\Delta\text{AGB}$ .

Our second question was what effect does initial biomass  $\text{AGB}_i$  have on  $\Delta\text{AGB}$ ? Highly predictive negative relationships between stand density and rates of forest ecosystem processes are well known (Finegan & Camacho 1999; Guariguata & Ostertag 2001; Peña-Claros *et al.* 2008; Toledo *et al.* 2011). We therefore predicted a negative  $\text{AGB}_i$ – $\Delta\text{AGB}$  relationship in our forest stands.

Finally, our third, main question was what mechanism – biomass ratio hypothesis, niche complementarity or green soup – best explains variation in biomass production?

## Materials and methods

### STUDY SITES

Our analysis used data from long-term ecological research in three tropical forests in Bolivia, Brazil and Costa Rica (Table 1). The Bolivian site was the 100 000 ha forestry concession of Agroindustria Forestal La Chonta, 30 km east of Ascención de Guarayos, Bolivia (from here on, ‘the Bolivian moist forest’). This semi-deciduous tropical moist forest is transitional between Chiquitano dry forest and moist Amazonian forests (Toledo *et al.* 2011). The study site is situated on the southwestern border of the Brazilian Precambrian Shield and has sandy-loam soils that are around neutral in pH and rich in nutrients (Peña-Claros *et al.* 2012).

The Amazonian site is approximately 80 km north of Manaus, Brazil (from here on ‘the Brazilian moist forest’). The site is located within the Biological Dynamics of Forest Fragments Project (BDFFP, Laurance *et al.* 2002). BDFFP maintains long-term studies of vegetation dynamics of old-growth forest without hunting or wood removal. The dominant soil type is yellow latosol (xanthic ferralsol in the FAO/Unesco classification) with fine texture (82% clay). The predominant vegetation is the hyper-diverse *terra firme forest*, a primary non-flooded rain forest.

Data for Costa Rican tropical wet forests are from Corinto, hereafter referred to as the ‘Costa Rican wet forest’. Corinto is located in Pococí Canton, Limón Province. Its topography ranges from flat areas to slopes of 45°. Soils are Inceptisols of volcanic origin, acid, with high aluminium and low base saturation and textures between clay loam and clay and sandy loam. The site is located in Holdridge’s wet tropi-

**Table 1.** Environmental and forest characteristics of the sites included in this study

Country	Bolivia*	Brazil†	Costa Rica‡
Site	La Chonta	Manaus	Corinto
General characteristics			
Forest type	Moist	Moist	Wet
Latitude	15°85' S	2°25' S	10°12' N
Longitude	62°86' W	59°50' W	83°52' W
Mean annual temperature (°C)	23.0	25.2	23.7
Mean annual precipitation (mm year <sup>-1</sup> )	1580	2650	3900
Number months <100 mm precipitation	4	3	0
Altitude (masl)	250	50–100	235–345
Forest characteristics			
Tree density (stems ha <sup>-1</sup> )	367	c. 640	490
Basal area (m <sup>2</sup> ha <sup>-1</sup> )	19.3	30	28.5
Species richness (ha <sup>-1</sup> )	59	>280	90
Canopy height (m)	30–38	30–37	35–40
Number of plots	9 (44)	9	3 (9)

The number of permanent sample plots per site is also given, with the pre-logging plots used for hypothesis testing for  $\text{AGB}_i$  in parentheses for Bolivia and Costa Rica. Forest characteristics are for trees  $\geq 10$  cm d.b.h. Superscripts refer to the source of the site information and plot description: \*Peña-Claros *et al.* (2008, 2012), †De Oliveira & Mori (1999), ‡Carrera, Orozco & Sabogal (1996).

cal forest life-zone and has been classified as *Pentaclethra*-palm forest (Sesnie *et al.* 2009).

Each of these sites is located in landscapes partially affected by human activity. The Bolivian moist forest and Costa Rican wet forest are logging and silviculture experiments, and the Brazilian moist forest is in a landscape partly converted to cattle ranching. Nevertheless the  $\text{AGB}$  data analysed here are from plots in areas free of direct human intervention.

### PERMANENT SAMPLE PLOTS

Standard 1 ha (100 × 100 m) PSP were established at each site in undisturbed primary forest stands. At the initial and final measurements used in this study, all trees  $\geq 10$  cm d.b.h. were individually marked, mapped, measured for d.b.h. using a diameter tape to a precision of  $\pm 1$  mm and identified to species by qualified personnel. Hypothesis testing for  $\text{AGB}_i$  was done using pre-logging data from the Bolivia and Costa Rica sites, giving total  $n = 62$  (see below). For  $\Delta\text{AGB}$ , tests were done with unlogged control plots giving  $n = 21$ . For this study, we analyse annual biomass increment data calculated from an 8- (Bolivia and Costa Rica) and an 11-year period (Brazil).

### Bolivian moist forest

The Bolivian moist forest data are from a logging experiment consisting of twelve 27-ha plots grouped into three blocks (Peña-Claros *et al.* 2008). In this paper, we test hypotheses for initial above-ground biomass  $\text{AGB}_i$  using pre-logging data from 44 plots. For biomass production  $\Delta\text{AGB}$ , we analyse data for trees in 9 unlogged 1-ha control subplots, one from each of 9 of the 27-ha plots. The data used in this study are from the first census (collected in 2001 for block 1 and 2, and in 2002 for block 3) and that carried out 8 years later.

### Brazilian moist forest

These primary moist forest data are from 9 contiguous 1.0-ha plots in a 300 m × 300 m block, established in 1985 on a plateau with clayey soil (Cabo Frio reserve). All trees were measured and species were identified. The data used in this study are from the 1998 and 2009 censuses.

### Costa Rican wet forest

These data are also from a logging experiment in primary forest. For AGB<sub>i</sub> and its predictors, we used measurements from 9 unlogged plots of 180 m × 180 m each consisting of a central PSP of 1 ha (100 m × 100 m) surrounded by a 40 m wide buffer strip. For ΔAGB, we used data from the three unlogged controls located around the logging area in order to facilitate forestry operations.

### FUNCTIONAL TRAITS

We measured eight functional traits for the dominant species that make up a large proportion of the estimated biomass in each individual plot (Grime 1998; Díaz *et al.* 2011). For Costa Rica and Bolivia, this proportion was 70–80% of initial plot AGB. For the hyperdiverse Brazilian moist forest, the mean proportion was 63% (range 59–73%) (see below for biomass estimation calculations). For each plot separately, tree species were ordered on the basis of the percentage of total biomass they represented at the first measurement of the plot. Then, also for each plot separately, the species making up the required percentage of total biomass were identified. Traits were measured for each species found at least once among these dominants. The traits selected are important for plant growth and survival (Poorter *et al.* 2008; Wright *et al.* 2010; Rüger *et al.* 2012), and hence for standing above-ground biomass, biomass productivity and carbon stocks (Pérez-Harguindeguy *et al.* 2013; Table 2). They were as follows: SLA (leaf area per unit leaf mass, cm<sup>2</sup> g<sup>-1</sup>), LDMC (leaf dry

mass per unit leaf fresh mass, mg g<sup>-1</sup>), force to tear ( $F_t$ , N mm<sup>-1</sup>; previously called leaf tensile strength, Pérez-Harguindeguy *et al.* 2013), leaf nitrogen concentration (N, leaf nitrogen mass per unit leaf dry mass, mg g<sup>-1</sup>), leaf phosphorous concentration (P, mg g<sup>-1</sup>), N:P ratio (N:P, unitless), WSG (unitless) and maximum potential tree height ( $H_{max}$ , m). All traits were measured according to standard measurement protocols (Chave 2005; Williamson & Wiemann 2010; Pérez-Harguindeguy *et al.* 2013). Some data from the Global Wood Density Database (Zanne *et al.* 2009) were used for the Brazilian moist forest.

### COMMUNITY WEIGHTED MEAN TRAIT VALUES AND FUNCTIONAL VARIETY INDICES

Community weighted mean trait values and FV indices were calculated per plot for the initial measurements, for the tree species that formed the required percentage of total biomass (palms were excluded, see below). For each trait, the per-plot CWM was calculated using species biomass as percentage of total biomass as the weighting variable. The calculation followed Violle *et al.* (2007, their equation 4).

Because it is desirable to reduce the number of traits relative to the number of species used to measure FV and to use uncorrelated traits as far as possible (Villéger, Mason & Mouillot 2008; Laliberté & Legendre 2010), we quantified per-plot values of FV indices using four traits: a key stem trait, WSG; a key whole plant trait,  $H_{max}$ ; and two key leaf traits, N and SLA. We used four complementary indices to measure FV (see Introduction): functional richness FRic, functional evenness FEve, functional divergence FDiv (Mason *et al.* 2005; Villéger, Mason & Mouillot 2008; Mouchet *et al.* 2010) and functional dispersion FDis (Laliberté & Legendre 2010). As in the case of the CWM, percentage of AGB<sub>i</sub> was used for weighting in the cases of FEve, FDiv and FDis. As recommended by Villéger, Mason & Mouillot (2008), we did not use the N:P ratio in the calculation of indices because it has an obvious relationship with the traits used in

**Table 2.** Descriptive statistics for forest properties and processes, from the 21 unlogged stands used for analysis of biomass change

Forest property/process	<i>n</i>	Mean	Standard error	Minimum	Maximum
Community weighted mean (CWM) specific leaf area (SLA) (cm <sup>2</sup> g <sup>-1</sup> )	21	12.63	0.5	9.84	17.1
CWM Leaf dry matter content (mg g <sup>-1</sup> )	21	407.58	15.2	299	489.83
CWM Force to tear the leaf $F_t$ (N mm <sup>-1</sup> )	21	0.85	0.02	0.71	1.14
CWM Leaf nitrogen content N (mg g <sup>-1</sup> )	21	22.58	0.54	19.58	27.68
CWM Leaf phosphorous content P (mg g <sup>-1</sup> )	21	1.25	0.16	0.5	2.63
CWM Leaf nitrogen:phosphorous ratio N:P	21	26.75	3.07	10.6	43.2
CWM Wood specific gravity WSG	21	0.62	0.03	0.47	0.77
CWM maximum potential height $H_{max}$ (m)	21	33.91	0.86	28.6	40.43
Species used for calculation of functional diversity indices	21	51.24	10.01	5	113
FRic	21	529.9	103.45	23.43	1273.34
FEve	21	0.58	0.02	0.44	0.74
FDiv	21	0.76	0.02	0.61	0.91
FDis	21	8.12	0.25	5.6	10.1
ΔAGB <sub>surv</sub> Mg ha <sup>-1</sup> year <sup>-1</sup>	21	4.11	0.15	3.25	5.47
ΔAGB <sub>rec</sub> Mg ha <sup>-1</sup> year <sup>-1</sup>	21	0.38	0.09	0.08	1.29
ΔAGB <sub>tot</sub> Mg ha <sup>-1</sup> year <sup>-1</sup>	18	4.57	0.25	3.52	7.09
AGB <sub>i</sub> Mg ha <sup>-1</sup>	21	272.79	13.35	165.46	346.9

Biomass properties: AGB<sub>i</sub>, initial above-ground biomass; ΔAGB<sub>rec</sub>, biomass increment due to recruits; ΔAGB<sub>surv</sub>, biomass increment due to trees that survived from the initial to the final measurement of the plots; ΔAGB<sub>tot</sub>, total biomass increment as ΔAGB<sub>rec</sub> + ΔAGB<sub>surv</sub>. Functional variety indices: FRic, functional richness; FEve, functional evenness; FDiv, functional diversity; FDis, functional dispersion.

its calculation. N:P is actually highly correlated with P, but not with N (unpublished data of the authors). Trait values were standardized before the calculation of FV indices. All CWM and functional trait variety calculations were done using F-Diversity software (Casanoves *et al.* 2011, <http://www.FDiversity.nucleodiversus.org/>).

#### ESTIMATION OF TROPICAL FOREST ABOVE-GROUND BIOMASS AND BIOMASS INCREMENTS

Although important in many of our plots, palms were excluded from our study because we have no growth data for them, as palm growth cannot be measured as d.b.h. increment. Plot data were carefully reviewed for anomalous d.b.h. values that could have caused errors or bias in the estimation of above-ground biomass, especially if linked to large trees, as is often the case (Clark & Clark 2000; Chave *et al.* 2003). Large diameter increments were checked on a species-by-species basis. For some species, for example, an annual increment  $\geq 1.0$  cm year<sup>-1</sup> might be considered anomalous, whereas for others, this is the typical mean growth rate (see e.g. Finegan, Camacho & Zamora 1999).

We estimated AGB (Mg ha<sup>-1</sup>) for each measurement of the plots using allometric equations with stem diameter at breast height (d.b.h., 1.3 m or measured above buttresses or other stem deformities) as the predictor variable. We used the Brown (1997) equations rather than biomass equations that require WSG because this is a component of some of our independent variables and is correlated with components of others. We used the Brown (1997) equation for moist forest for our data from Brazil and Bolivia and that for wet forest for the Costa Rica data.

Many sources of error are present in the estimation of biomass using equations and estimated  $\Delta$ AGB between two points in time thus represents the difference between two imperfectly known quantities (Chave *et al.* 2003). However, even if absolute values of AGB are subject to bias, trends over time should not be if the same methods are used (Clark *et al.* 2001; Chave *et al.* 2003). The Brown equation for wet forest that we used is a proven tool (e.g. Clark, Clark & Oberbauer 2013), and 100 of the 169 trees cut to develop it were cut in the same landscape as our Costa Rica plots. The  $R^2$  of this equation is >0.9, and Clark, Clark & Oberbauer (2013) found an  $R^2$  of 0.94 between estimates made using this equation and estimates using the equation from Chave *et al.* (2005) that includes WSG. We believe it to be an accurate equation for the Costa Rica plots. The  $R^2$  of the Brown equation we used for the Brazilian and Bolivian moist forest is 0.97, based on 170 trees from Cambodia, East Kalimantan, Amazonian Brazil and Venezuela (see Brown, Gillespie & Lugo 1989). For 315 trees harvested in moist forest in Central Amazonia, Chambers *et al.* (2001) showed that biomass estimations derived from the Brown equation were accurate and differed only slightly from those of two other equations.

We followed part of the accounting method for biomass increment of dicot trees as proposed by Clark *et al.* (2001) and use the terminology of Chave *et al.* (2003) as follows:

*AGB increment of survivors* ( $\Delta$ AGB<sub>surv</sub>), in Mg ha<sup>-1</sup> year<sup>-1</sup>, is the per-plot annual increment of new biomass produced by the growth of all the trees that survived from  $t_0$  to  $t_1$ .

*AGB increment due to recruits* ( $\Delta$ AGB<sub>rec</sub>), in Mg ha<sup>-1</sup> year<sup>-1</sup>, is the annual increment of biomass obtained from the biomass at  $t_1$  of trees reaching the 10 cm minimum d.b.h. limit during a given growth period. It is calculated as the difference between the estimated biomass of the recruit at  $t_1$  and that of a tree of 10 cm d.b.h. This correction is made because the biomass increment values in this study are for production by trees  $\geq 10$  cm d.b.h. Finally, *total annual AGB increment* ( $\Delta$ AGB<sub>tot</sub>) was estimated as  $\Delta$ AGB<sub>tot</sub> (Mg ha<sup>-1</sup> year<sup>-1</sup>) = ( $\Delta$ AGB<sub>surv</sub> +  $\Delta$ AGB<sub>rec</sub>)/ $t$ .

#### STATISTICAL ANALYSIS

The bivariate relationship between  $\Delta$ AGB and each individual metric of FTD, as well initial above-ground biomass AGB<sub>i</sub>, was analysed with general linear mixed models (GLMM) using Infostat software (Di Rienzo *et al.* 2011). We included site (country) as a random factor in our models, to take into account possible lack of independence between plots within countries. The GLMMs also took into account heterogeneous variances.

To evaluate which predictors – CWM, FV indices or AGB<sub>i</sub> – were the most important for  $\Delta$ AGB<sub>surv</sub>,  $\Delta$ AGB<sub>rec</sub> and  $\Delta$ AGB<sub>tot</sub> in multivariate models, a series of ordinary least squares multiple regression analyses were done using the software package Spatial Analysis in Macroecology version 4.0 (SAM; Rangel, Diniz-Filho & Bini 2010). Regressions were developed for each biomass production response variable starting from 13 potential predictor variables (AGB<sub>i</sub>, eight CWM traits and four FV indices) without interactions, yielding a total of 8191 possible models. For AGB<sub>i</sub>, we used the 12 FTD predictor variables for a total of 4095 possible models. To account for variation amongst countries, sites were always included as dummy variables. The model with the lowest Akaike Information Criterion (AIC) was selected as being the best. Additionally, a modelling averaging approach was developed in SAM used to evaluate which predictor variables contributed consistently across all models evaluated. For this, regression coefficients of each predictor were averaged across all models, weighted by their Akaike Information Criterion weight (AICc-wi), which represents the likelihood of a given model relative to all other models (Wagenmakers & Farrell 2004). An importance value was calculated by adding the AICc-wi values of the models in which the variables were present (Slik *et al.* 2013). Importance values vary between zero (low importance) and one (high importance).

## Results

### ARE BIOMASS AND BIOMASS INCREMENT RELATED TO COMMUNITY FUNCTIONAL PROPERTIES AND/OR STAND DENSITY?

We did a series of bivariate GLMMs to evaluate whether initial stand biomass and the biomass increments of survivors and recruits in 1.0-ha plots were linked to individual community functional properties of the stands. In the case of biomass increments, we also determined whether initial biomass was a predictor. We took into account possible within-site lack of independence by using site as a random factor in the analysis. Descriptive statistics of all predictor and response variables are provided in Table 2.

In bivariate analysis, initial biomass AGB<sub>i</sub> was negatively related to CWM SLA,  $F_t$  and N, and positively to CWM  $H_{max}$  (Table 3, Fig. 1a–c, Appendix S1). This suggests that higher above-ground biomass is associated with higher percentage of biomass of species that are tall when adults, but also of species with conservative leaf trait values – low SLA and N. The negative relationship with CWM force to tear  $F_t$  is unexpected (see below). As a predictor variable, AGB<sub>i</sub> was negatively related to all three measures of biomass increment of survivors, as predicted and suggesting higher biomass increments in lower density stands (Table 3, Fig. 1g). Biomass increment of survivors  $\Delta$ AGB<sub>surv</sub> was significantly positively related with CWM SLA and  $H_{max}$  and negatively with

**Table 3.** Bivariate relationships between initial above-ground biomass  $AGB_i$ , biomass increments  $\Delta AGB$ , and components of functional trait diversity – community weighted mean trait values and functional variety indices – for 1.0-ha plots at three tropical forest sites

Predictor variable	$AGB_i$ ( $n = 62$ )			$\Delta AGB_{surv}$ ( $n = 21$ )			$\Delta AGB_{rec}$ ( $n = 21$ )			$\Delta AGB_{tot}$ ( $n = 21$ )		
	Coefficient	$F$	$P$	Coefficient	$F$	$P$	Coefficient	$F$	$P$	Coefficient	$F$	$P$
Biomass												
AGB	–	–	–	<b>–0.01</b>	<b>21.7</b>	<b>0.0002</b>	<b>–0.005</b>	<b>26.4</b>	<b>&lt;0.001</b>	<b>–0.01</b>	<b>21.9</b>	<b>&lt;0.001</b>
Community weighted mean trait value												
SLA ( $cm^2 g^{-1}$ )	<b>–11.4</b>	<b>6.7</b>	<b>0.01</b>	<b>0.19</b>	<b>7.2</b>	<b>0.02</b>	0.04	0.7	0.43	<b>0.29</b>	<b>23.5</b>	<b>&lt;0.001</b>
LDMC ( $mg g^{-1}$ )	0.2	1.8	0.19	0.0008	0.02	0.89	–0.003	2.2	0.16	0.004	0.7	0.40
$F_t$ ( $N mm^{-1}$ )	<b>–231.8</b>	<b>5.8</b>	<b>0.03</b>	0.72	0.19	0.67	<b>1.3</b>	<b>36.2</b>	<b>&lt;0.0001</b>	3.02	2.5	0.14
N ( $mg g^{-1}$ )	<b>–6.2</b>	<b>5.6</b>	<b>0.02</b>	0.03	0.3	0.58	–0.01	0.04	0.84	–0.02	0.07	0.80
P ( $mg g^{-1}$ )	–38.1	2.2	0.14	0.46	1.1	0.31	<b>0.33</b>	<b>5.4</b>	<b>0.03</b>	0.8	3.6	0.08
N:P	1.51	0.4	0.51	–0.03	1.6	0.22	–0.02	3	0.10	<b>–0.05</b>	<b>11.6</b>	<b>0.003</b>
$H_{max}$ (m)	<b>9.1</b>	<b>24.9</b>	<b>&lt;0.001</b>	<b>0.12</b>	<b>26.5</b>	<b>&lt;0.001</b>	–0.003	0.02	0.88	<b>0.13</b>	<b>17.8</b>	<b>&lt;0.001</b>
WSG	–64.3	1.1	0.3	<b>–3.77</b>	<b>15.4</b>	<b>0.001</b>	–2.2	2.5	0.13	<b>–5.35</b>	<b>22.3</b>	<b>&lt;0.001</b>
Functional variety index												
FRic	–0.04	0.01	0.94	0.0001	0.0001	0.99	–0.003	1.7	0.21	<b>–0.01</b>	<b>15.4</b>	<b>0.001</b>
FEve	–97.7	3.44	0.07	1.76	1.3	0.27	0.09	0.01	0.91	1.65	0.8	0.4
FDiv	–12.3	0.05	0.82	2.19	0.8	0.37	2.5	3.5	0.08	1.95	0.4	0.54
FDIs	9.1	0.21	0.65	–0.66	1	0.34	–0.07	0.2	0.63	–0.83	1.1	0.32

Results of general linear mixed models are presented with forest site as a random factor and community weighted mean trait value or functional variety index as fixed factor. Regression coefficients,  $F$ -values and significance levels are shown; significant coefficients are in bold. See Table 2 for abbreviations and units of biomass increment components and traits.

CWM WSG (Table 3 and Fig. 1d–f), indicating that stands with soft, cheap leaves, softer wood and a higher proportional biomass of tall species have higher productivity. Biomass increment of recruits ( $\Delta AGB_{rec}$ ) was positively related with P and  $F_t$  (Table 3, Appendix S1). This suggests that besides the initial density effect, biomass growth of recruits is higher in stands with higher leaf P, though again the positive relationship with  $F_t$  is unexpected. Total biomass increment  $\Delta AGB_{tot}$  ( $\Delta AGB_{surv} + \Delta AGB_{rec}$ ) was largely made up of the growth of survivors (Table 2), and like  $\Delta AGB_{surv}$  was positively correlated with CWM SLA and CWM  $H_{max}$  and negatively with CWM WSG (Table 3, Fig. 1, Appendix S1). Additionally,  $\Delta AGB_{tot}$  was negatively related to CWM N:P, possibly representing an effect of P limitation (Table 3). The only relationship we found between biomass increment and a FV index was between FRic and  $\Delta AGB_{tot}$ . This relationship was unexpectedly negative (Table 3, Appendix S1). This result could imply that the larger the multivariate functional trait volume occupied in our plot data, the lower the biomass production. However, we believe it to be an artefact of the positive correlation between FRic and species richness (see Discussion). Additional scatter plots of significant GLMMs are provided in Appendix S1.

#### WHICH FTD COMPONENT MATTERS MOST FOR BIOMASS INCREMENTS OF STANDS?

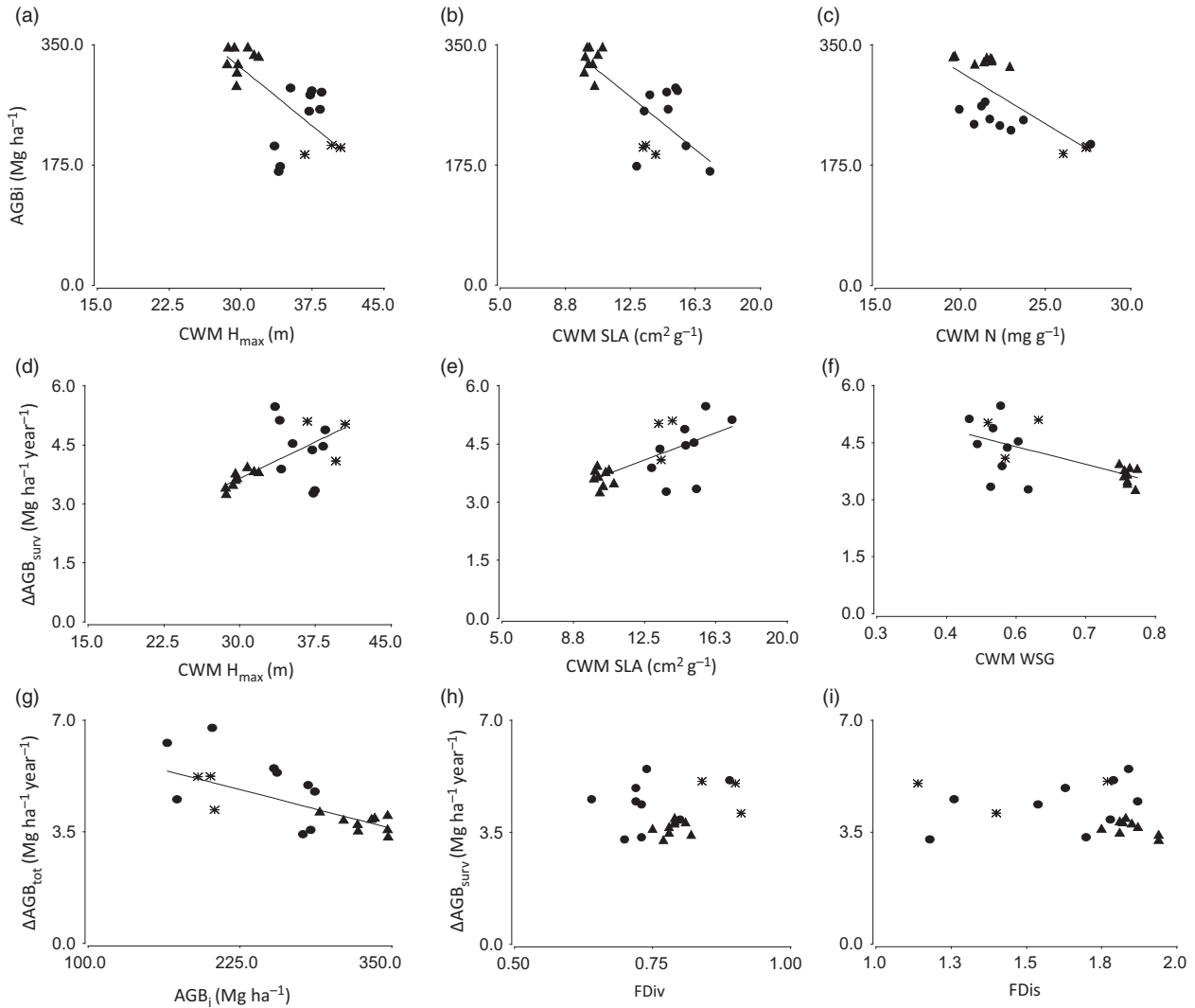
Four series of multiple regression analyses were done. First, we determined the most important predictors of initial above-ground biomass  $AGB_i$ . Then, we tested whether biomass increments  $\Delta AGB$  were primarily driven by CWM traits (testing the biomass ratio hypothesis), FV indices (testing the

niche complementarity hypothesis) or by  $AGB_i$  (testing the green soup hypothesis). We tested all possible combinations of predictor variables, fixing the country effect as dummy variables in all models. We present the best regression model for each biomass response variable (that with the lowest AIC, Table 4) as well as a synthesis across all models (weighted by their AICcwi, Appendix S2).

$R^2$  values for best models were in the range 0.64–0.82 (Table 4).  $AGB_i$  was best predicted by  $H_{max}$ , with a positive relationship (Table 4, Appendix S2). The best model for biomass increments of survivors  $\Delta AGB_{surv}$  showed that it was positively related to CWM SLA and  $F_t$ , although in the synthetic model, the only predictor with a high importance value was CWM SLA.  $AGB_i$  was the only significant predictor for biomass increments of recruits  $\Delta AGB_{rec}$ , both in the best regression model ( $r^2 = 0.64$ ) and in the synthetic model (Table 4, Appendix S2). Total biomass increments  $\Delta AGB_{tot}$  was best modelled with SLA, LDMC,  $F_t$  and P as predictors, all with positive signs. Again, CWM SLA had the highest importance value in the synthetic model (0.89; Appendix S2).

## Discussion

Combining data for three Neotropical forest sites, we found that standing above-ground biomass and three biomass production response variables were related to the CWM values of a few key functional traits, but not to their FV as measured by four complementary indices. Our results therefore support the biomass ratio hypothesis, but do not support the niche complementarity hypothesis.  $AGB_i$  was the most important predictor of  $\Delta AGB_{rec}$ , with a negative relationship and in multiple regression was not related to  $\Delta AGB_{surv}$  or  $\Delta AGB_{tot}$ .



**Fig. 1.** Significant (a–g) and non-significant (h and i) relationships (GLMMs with country as random factor, see also Table 3) between estimates of three biomass response variables and measures of functional trait diversity FTD and initial biomass  $AGB_i$ . Response variables are  $AGB_i$  (top panel, a–c, 62 unlogged plots),  $AGB$  increment due to surviving trees ( $\Delta AGB_{surv}$ , middle panel, d–f, bottom panel, h, i, 21 control plots) and total biomass increment ( $\Delta AGB_{tot}$  bottom panel, g, 21 control plots). FTD measures (see text) are CWM  $H_{max}$  (a, d), CWM SLA (b, e), CWM N (c), CWM WSG (f), and two indices of functional diversity, FDiv (h) and FDis (i). (g) shows the effect on total biomass increment of initial biomass  $AGB_i$ . For  $AGB_i$ , pre-logging and control plots were used ( $N = 62$ ), and for biomass growth only control plots were used ( $n = 21$ ). Symbols represent sites: triangles, Brazilian moist forest; circles, Bolivian moist forest; stars, Costa Rican wet forest.

Thus, the green soup hypothesis was supported mainly for recruits and not for biomass production by trees  $\geq 10$  cm d.b.h. at the beginning of the study.

#### DOES FUNCTIONAL TRAIT DIVERSITY PREDICT ABOVE-GROUND BIOMASS AND BIOMASS PRODUCTION?

Of the eight CWM trait values, four CWM leaf traits were significant predictors of biomass increments  $\Delta AGB$  in bivariate analyses, as well as CWM  $H_{max}$  and CWM WSG. We will deal with leaf traits first. CWM SLA was a significant predictor for  $\Delta AGB_{surv}$  and  $\Delta AGB_{tot}$ , the main components of biomass production estimated by this study, and CWM P was positively related to  $\Delta AGB_{rec}$ . These relationships had the predicted positive signs. These results suggest that as found by Garnier *et al.* (2004) in secondary temperate vegetation, for some traits,

expectations derived from the leaf economic spectrum (Wright *et al.* 2004) will scale up to the level of canopy properties and ecosystem processes. These CWM– $\Delta AGB$  relationships also suggest that tropical forest stands with ‘fast’, productive CWM values such as high SLA and leaf phosphorous tend to have high biomass production and that weighted means of these trait values indeed indicate stand-level carbon gain (Fig. 1e, Table 4, Appendix S2).

Notably, the only relationship we found between biomass response variables and CWM N was the negative one with  $AGB_i$ . Low CWM N in high-biomass stands is consistent with high biomass accumulation in a ‘slow’ forest (Quesada *et al.* 2012). Moreover, many authors consider soil P, not soil N, to be the most likely limiting nutrient for tropical forest productivity (Vitousek & Sanford 1986; Tanner, Vitousek & Cuevas 1998; Mercado *et al.* 2011). The relative importance



**Table 4.** Best models obtained from a series of regression analyses of a response variable on community functional properties

	AGB <sub>i</sub> (n = 62)		ΔAGB <sub>surv</sub> (n = 21)		ΔAGB <sub>rec</sub> (n = 21)		ΔAGB <sub>tot</sub> (n = 21)	
	Coeff.	Beta	Coeff.	Beta	Coeff.	Beta	Coeff.	Beta
Constant	<b>292.81</b>	0.00	<b>-6.91</b>	0.00	<b>2.23</b>	<b>0.00</b>	<b>-38.76</b>	0.00
Site								
Dummy Brazil	<b>240.12</b>	1.57	<b>2.28</b>	1.69	0.07	0.09	0.64	0.34
Dummy CR	25.05	0.16	<b>1.34</b>	0.70	<b>-0.78</b>	-0.70	<b>0.03</b>	0.01
Initial biomass								
AGB <sub>i</sub>	-	-			<b>-0.01</b>	<b>-1.00</b>		
Community weighted mean (CWM)								
SLA			<b>0.49</b>	1.65			<b>0.90</b>	2.16
LDMC	<b>-0.64</b>	-0.64					<b>0.05</b>	3.93
F <sub>t</sub>			<b>4.33</b>	0.69			<b>6.91</b>	0.78
N	<b>-9.56</b>	-0.48						
P							<b>2.86</b>	2.23
H <sub>max</sub>	<b>10.20</b>	0.67						
Model								
R <sup>2</sup>	0.75		0.68		0.64		0.82	
AICc	600.7		10.1		39.3		48.7	

See Table 2 for abbreviations and units of biomass increment components and traits. Response variables were initial above-ground biomass (AGB<sub>i</sub>), annual biomass increment of survivors (ΔAGB<sub>surv</sub>), annual biomass increment of recruits (ΔAGB<sub>rec</sub>) and total annual biomass increment (growth of survivors + growth of recruits, ΔAGB<sub>tot</sub>). As predictor variables, eight CWM functional traits, four functional variety indices, and two dummy variables were used. The dummy variables coding for country (Dummy Brazil, Dummy Costa Rica) were included in each regression model to control for site effects. For the three biomass growth variables, initial biomass AGB<sub>i</sub> was also tested as a predictor. The regression coefficient (Coeff.), standardized regression coefficient (Beta), and coefficient of determination (R<sup>2</sup>) and Akaike Information Criterion (AICc) of the models are given. See Appendix S2 for the contribution to the models of all variables tested. Significant coefficients (P < 0.05) are given in bold.

of CWM N and CWM P in our study is consistent with this expectation, as is the negative bivariate relationship between CWM N:P and ΔAGB<sub>tot</sub>. Finally, CWM force to tear F<sub>t</sub> was negatively related to AGB<sub>i</sub> in bivariate regression, but its relation to the biomass increments of recruits' ΔAGB<sub>rec</sub> was positive. Leaves with high F<sub>t</sub> are considered conservative and are associated with slow litter decomposition and high litter accumulation (Díaz *et al.* 2007; Pérez-Harguindeguy *et al.* 2013). As in the case of leaf nitrogen, the relationship of F<sub>t</sub> to AGB<sub>i</sub> may be consistent with accumulation of high AGB in 'slow' forests. However, this positive relationship of force to tear the leaf to ΔAGB<sub>rec</sub> is unexpected. It may be linked to phylogenetic patterns of leaf anatomy and variation of species composition between our sample plots (Díaz *et al.* 2013), but this point requires further research.

Maximum adult height H<sub>max</sub> represents one of the main axes of species trait variation in tropical forest (Poorter, Bongers & Bongers 2006; Kitajima & Poorter 2010). In bivariate analysis, plots with a high per cent biomass of potentially tall species (high CWM H<sub>max</sub>) tended to have high AGB<sub>i</sub> and ΔAGB (Table 3, Fig. 1e). These relationships underline the potential importance of adult stature for growth and survival in tall, closed-canopy systems (see Thomas & Bazzaz 1999; Poorter, Bongers & Bongers 2006; Poorter *et al.* 2008; Wright *et al.* 2010) and therefore for ecosystem processes and services.

Wood specific gravity is another key trait of woody species. In our bivariate analyses, CWM WSG was, as predicted, strongly negatively related with biomass increments of survivors ΔAGB<sub>surv</sub> and with ΔAGB<sub>tot</sub> (Table 3). Compar-

ative studies consistently show that WSG is the best predictor of individual tree diameter increments of tropical tree species (Poorter *et al.* 2008; Wright *et al.* 2010; Hérault *et al.* 2011; Rüger *et al.* 2012), and our result suggests that this relationship scales up to the community level. However, in our study, neither CWM H<sub>max</sub> nor CWM WSG was retained as predictors of ΔAGB in multiple regression models – CWM leaf traits predominated (see below).

Our results are in line with those of other studies that show that CWM trait values have important consequences for ecosystem properties, processes and services (Garnier *et al.* 2004; Fortunel *et al.* 2009; Conti & Díaz 2013). The study by Mercado *et al.* (2011) suggests that these relationships hold for Amazonian rain forests, but their protocol for sampling traits does not permit the testing of the biomass ratio or niche complementarity hypotheses. We believe that ours is the most comprehensive analysis to date of these relationships in primary tropical forests. An important point remains for future work: palms are an important component of the stand ≥10 cm d.b.h. in some of our forest plots – see Sesnie *et al.* (2009) for Costa Rica, for example. Their influence on ecosystem properties and processes remains to be documented, as both growth data and proven biomass estimation equations are lacking for palms.

We predicted that FV would be positively correlated with biomass increments ΔAGB – the niche complementarity hypothesis. FV may be positively correlated with both standing biomass and biomass productivity in woody vegetation (Paquette & Messier 2011; Conti & Díaz 2013). However, this prediction was not fulfilled. The significant negative

relationship we found (between functional richness FRic and  $\Delta\text{AGB}_{\text{tot}}$ , Table 3) is unexpected. We believe it is due to FRic being, by construction, positively correlated with species richness (Villéger, Mason & Mouillot 2008). We took into account possible within-country lack of independence in our analysis, but FRic values tend to be higher, and  $\Delta\text{AGB}$  lower, in our hyperdiverse (De Oliveira & Mori 1999) Brazilian plots than in the Bolivian and Costa Rican sites (unpublished data of the authors). Overall, we conclude that FV as measured here, for the species that make up most of the biomass, has no positive relationship to AGB or  $\Delta\text{AGB}$ .

$\text{AGB}_i$  was a significant predictor for all three  $\Delta\text{AGB}$  components in bivariate GLMMs. This is our only result in line with the green soup hypothesis that ecosystem properties are simply driven by the amount of vegetation – negative density dependence in this case (Guariguata & Ostertag 2001) – rather than by its taxonomic characteristics or FTD. Our results suggest that negative density dependence is stronger for biomass production by recruits than for survivors. This may occur because many recruits are in shaded microsites and are more sensitive than larger established individuals to competition for light, water and nutrients.

#### WHICH FTD COMPONENT MATTERS MOST?

We proposed the alternative biomass ratio, niche complementarity and green soup hypotheses to explain patterns of biomass production at three tropical forest sites. We used a series of multiple regression analysis to tease apart their relative importance (Table 4, Appendix S2). The green soup hypothesis was the only one supported for  $\Delta\text{AGB}_{\text{rec}}$ . In contrast, for  $\Delta\text{AGB}_{\text{surv}}$  and  $\Delta\text{AGB}_{\text{tot}}$ , the best multiple regression models retained only CWMs of leaf traits – SLA, LDMC,  $F_t$  and P – as predictors. Model  $R^2$  values were in the range 0.64–0.82. For  $\Delta\text{AGB}_{\text{surv}}$  and  $\Delta\text{AGB}_{\text{tot}}$ , the two most important components of biomass productivity estimated by us, strong support is therefore provided for the biomass ratio hypothesis of Grime (1998) – that ecosystem properties are driven by the traits of the dominant species in the plant community.

The strong correlations of CWM leaf traits with stand-level biomass productivity in our study contrast with their being poor predictors of per-species individual tree d.b.h. growth rates in tropical forests. At the individual tree level, species WSG (negative correlation) and  $H_{\text{max}}$  (positive correlation) predominate as predictors of d.b.h. growth (Poorter *et al.* 2008; Wright *et al.* 2010; Hérault *et al.* 2011; Rüger *et al.* 2012). Conversely, our results strongly suggest that at the stand level, weighted means of leaf traits are more important predictors of biomass increments than CWM WSG or  $H_{\text{max}}$ . In line with this result, work in non-tropical biomes has shown that forest stand wood productivity can be predicted principally on the basis of forest canopy properties (e.g. Landsberg & Waring 1997; Smith *et al.* 2002). If tropical forest canopy weighted mean trait values can be measured using remote sensing, then the possibility of estimating spatial and temporal changes in biomass production and carbon storage

may be opened up (e.g. Chambers *et al.* 2001). However, it seems likely that any such work should take into account the possibility that P and not N is the leaf nutrient most correlated with above-ground biomass, as suggested by our empirical study and the modelling approach of Mercado *et al.* (2011). A final point to consider is whether the CWM is a proximate or an ultimate cause of productivity variation, or whether environment is the ultimate cause. Quesada *et al.* (2012) have proposed that soil conditions are the primary determinant of ecosystem properties and that these act in a self-maintaining way – for example, ‘fast’ forests on fertile soils have high stem turnover, which tends to maintain the corresponding trait values. Further work is required to test this model for our plots.

Why have we no evidence for the niche complementarity hypothesis? Studies in both grasslands and forests have found positive effects of species richness on biomass (Tilman, Wedin & Knops 1996; Tilman *et al.* 2001; Cardinale *et al.* 2007; Zhang, Chen & Reich 2012; Gamfeldt *et al.* 2013; Vilà *et al.* 2013), though plot size may affect these results (Chisholm *et al.* 2013). Of course, it is a premise of our study that components of FTD are better predictors of ecosystem properties and processes than species richness (Díaz *et al.* 2011). We measured indices of FV, not species richness, and our plots cover a range of values of the indices (Table 2, Fig. 1). To measure these multivariate FV indices, we chose WSG as a key ‘stem economic spectrum’ trait (Chave *et al.* 2009),  $H_{\text{max}}$  as an independent strategy axis related to tree growth (Poorter *et al.* 2008), and two key ‘leaf economic spectrum’ traits, SLA and N. SLA and N are in principle the most important of the leaf traits we measured, in terms of their relationships to photosynthetic potential and carbon gain (Wright *et al.* 2004). We believe that in the existing FTD framework, we have done adequate tests of our biodiversity–ecosystem function hypotheses. Alternative explanations for the lack of an effect of FV may be that the four indices we measured, or the trait combination we used to measure them, do not adequately represent niche complementarity in the forests studied. Further work is required to test these alternative explanations.

Finally, the result that initial above-ground biomass  $\text{AGB}_i$  was retained by multiple regressions only as a good predictor for the biomass increment of recruits, suggests that in old-growth tropical forests, stand density is an important predictor only of productivity for initially small individuals.  $\Delta\text{AGB}_{\text{rec}}$  is a much smaller component of biomass production than increments of survivors  $\Delta\text{AGB}_{\text{surv}}$ , though its importance may be much greater in disturbed or successional forests. Our study underlines that the factors affecting  $\Delta\text{AGB}_{\text{rec}}$  may be different from those affecting other  $\Delta\text{AGB}$  components, and we recommend the inclusion of  $\text{AGB}_i$  as a predictor in future work.

Understanding of the factors driving biomass and carbon dynamics in tropical forest is critical from both theoretical and practical points of view. Community weighted mean leaf traits (ecosystem properties) were the most important drivers of estimated above-ground woody biomass production (ecosystem processes) in the moist and wet tropical forests we

studied. Given the correspondence of this result with those from studies of leaves in laboratories and forests in other biomes, the way may be open for the characterization of a 'canopy economic spectrum' using CWM trait values. Stand density is likely to contribute to the explanation of patterns of biomass production, however, suggesting that understanding may be improved by taking into account forest structural characteristics alongside CWM leaf traits in a compound model.

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## Data accessibility

Data analysed in this paper are available from the Dryad Digital Repository (Finegan et al. 2014).

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## Supporting Information

Additional Supporting Information may be found in the online version of this article:

**Appendix S1.** Additional scatterplots of significant relationships (GLMMs with country as random factor, see also Table 3) between estimates of three biomass response variables and measures of functional trait diversity FTD and forest structure.

**Appendix S2.** Results of a series of regression analyses of a response variable on community functional properties.