

Environmental factors predict community functional composition in Amazonian forests

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Summary

1. The consequences of biodiversity loss for ecosystem services largely depend on the functional identities of extirpated species. However, poor descriptions of spatial patterns of community functional composition across landscapes hamper accurate predictions, particularly in highly diverse tropical regions. Therefore, understanding how community functional composition varies across environmental gradients remains an important challenge.

2. We sampled 15 functional traits in 800 Neotropical tree species across 13 forest plots representative of the broad climatic and soil gradients encompassed by three widespread lowland forest habitats (terra firme forests on clay-rich soils, seasonally flooded forests and white-sand forests) at opposite ends of Amazonia (Peru and French Guiana). We combined univariate and multivariate approaches to test the magnitude and predictability of environmental filtering on community leaf and wood functional composition.

3. Directional shifts in community functional composition correlated with environmental changes across the 13 plots, with denser leaves, stems and roots in forests occurring in environments with limited water and soil-nutrient availability. Critically, these relationships allowed us to accurately predict the functional composition of 61 additional forest plots from environmental data alone.

4. *Synthesis.* Environmental filtering consistently shapes the functional composition of highly diverse tropical forests at large scales across the terra firme, seasonally flooded and white-sand forests of lowland Amazonia. Environmental factors drive and allow the prediction of variation in community functional composition among habitat types in Amazonian forests.

Key-words: Amazonian landscape, climatic and soil gradients, determinants of plant community diversity and structure, environmental filtering, functional traits, tree communities, tropical forests

Introduction

A pressing challenge facing ecologists is to understand the processes controlling species distributions across environmental gradients. Functional traits provide an important tool in this respect, as they reflect trade-offs that determine species performance in a given environment and consequently species abundances along environmental gradients (Engelbrecht *et al.* 2007; Cornwell & Ackerly 2009; Swenson *et al.* 2012). The quantification of functional traits for co-occurring species also provides the opportunity to distinguish the signatures of deterministic and stochastic assembly processes in communities (e.g. Kraft, Valencia & Ackerly 2008; Cornwell & Ackerly

2009; Ingram & Shurin 2009). Several recent studies have specifically used functional traits to demonstrate the importance of environmental filtering in determining the assembly of species-rich tropical forests (ter Steege *et al.* 2006; Engelbrecht *et al.* 2007; Kraft, Valencia & Ackerly 2008; Swenson & Enquist 2009; Paine *et al.* 2011; Katabuchi *et al.* 2012). However, these studies included only a few functional traits (ter Steege *et al.* 2006) or species (Engelbrecht *et al.* 2007), or covered relatively small areas (Kraft, Valencia & Ackerly 2008; Katabuchi *et al.* 2012) or limited habitat ranges (Paine *et al.* 2011). Thus, the extent to which the environmental filtering results in predictable changes in community functional composition along broad environmental gradients at large scales remains unclear, particularly in highly diverse tropical forests (Malhi *et al.* 2008; Asner, Loarie & Heyder 2010). A

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better understanding of this issue is critical to improve predictions of the response of community functional composition and associated ecosystem functioning to global change (Lavergne *et al.* 2010; Reu *et al.* 2011).

Recent investigations into woody plant strategies in Amazonian rain forests have identified two orthogonal axes of functional trade-offs: the ‘leaf economics spectrum’, opposing leaves with high specific leaf area (SLA) and nutrient concentrations against thick, tough and dense leaves with high C : N ratio (*sensu* Wright *et al.* 2004), and the ‘wood economics spectrum’, opposing dense wood against wood with high water content and thick bark (Baraloto *et al.* 2010b). Woody plants can optimize their survival and growth across environmental gradients by investing differentially in leaf and wood tissues. For instance, SLA relates to resource acquisition, to water regulation (Reich, Walters & Ellsworth 1997; Wright *et al.* 2004), and to defence against herbivores and pathogens (Agrawal & Fishbein 2006), whereas wood density relates to hydraulic conductivity from roots to stems and to defence against both physical hazards and natural enemies (Chave *et al.* 2009). Thus, integrating leaf and wood trait axes to define functional strategies provides a measure of ‘whole-plant’ response to environmental changes for woody plants (Fortunel, Fine & Baraloto 2012).

Here, we investigate changes in leaf and wood strategies across broad environmental gradients in lowland Amazonian forests to test the magnitude and the predictability of environmental filtering on community assembly. We combine univariate and multivariate approaches to study whether environmental filters have convergent or divergent effects on leaf and wood strategies. We focus on the three most common lowland forest habitats of tropical South America: terra firme forests on clay-rich soils, seasonally flooded forests and

white-sand forests that cover, respectively, around 90%, 7% and 3% of lowland Amazonian forests, respectively (ter Steege *et al.* 2000). These habitats span broad gradients of resource availability (*i.e.* light, soil nitrogen and phosphorus), herbivory, drought and flooding (Baraloto *et al.* 2011). We measured 15 leaf and wood traits in 800 tree species in 13 forest plots that represent the range of environmental variation found in a network of 74 forest plots covering 180 000 km² of terra firme, seasonally flooded and white-sand forests in French Guiana and Peru (Fig. 1). These two regions cover the gradient of soil fertility, seasonality and forest structure found in lowland Amazonian forests (Baraloto *et al.* 2011) and therefore allow to test the generality of environmental filtering among habitats across the Amazonian landscape.

If environmental conditions strongly filter species among the three studied habitats, we expect directional shifts in mean trait values among habitats and reductions in the range and variance of traits at the community level (ter Steege *et al.* 2006; Engelbrecht *et al.* 2007; Kraft, Valencia & Ackerly 2008). We can test for deviations from a purely stochastic model of community assembly by comparing the values of these statistics in observed communities against those expected under a null model of community assembly that does not include environmental filtering. We further test hypotheses related to the differences among habitats. Amazonian terra firme forests have relatively poor soils compared with soils outside the Amazon basin (Huston 2012; Quesada *et al.* 2012), but are more fertile than white-sand forests. Terra firme forests experience neither extreme drought nor flooding and exhibit a high density of large stems (Baraloto *et al.* 2011), generating strong competition among plant species for light and nutrients, as seen in temperate vegetation (Tilman 1990; Craine 2005). Thus, we predict shifts towards lower wood

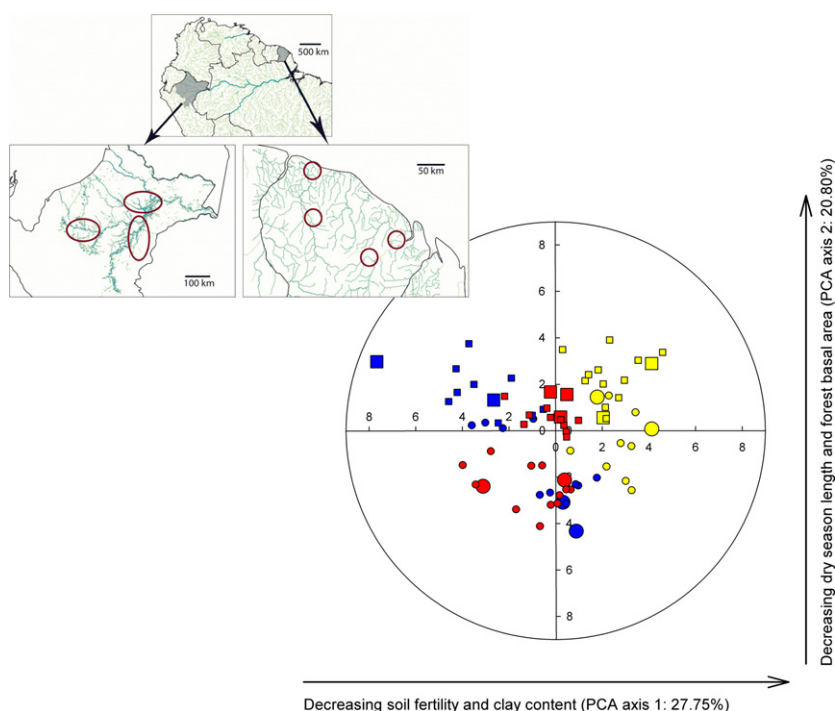


Fig. 1. Position of the 74 plots in multivariate space following principal components analysis (PCA), defined by soil fertility and texture (PCA axis 1) and climate and forest structure (PCA axis 2). The first three axes of the PCA account for 62.75% of the total variation among plots. Details on environmental factors can be found in Baraloto *et al.* (2011). Squares indicate Peruvian plots, circles indicate French Guianan plots. Colours indicate habitat type (blue: seasonally flooded, red: terra firme, yellow: white sand). Larger symbols indicate the 13 plots where traits were measured; smaller symbols indicate the other 61 plots of the network. The inset shows a map of the Amazon region, illustrating the seven studied zones that cover 180 000 km² in Peru and French Guiana. Within each zone, 2–6 plots were established in each of the three habitat types.

density and greater SLA (Muller-Landau 2004; Wright *et al.* 2006; Liu *et al.* 2012). Seasonally flooded forests have relatively fertile soils compared with terra firme forests (Baraloto *et al.* 2011) and a year-round high water availability which favours greater hydraulic conductivity from roots to stems and does not constrain foliar transpiration (Parolin 2001). However, flooding can drastically change nutrient availability as well as oxygen levels and reduce plant growth (Parolin *et al.* 2004). Thus, we expect shifts towards even lower wood density and greater SLA in seasonally flooded forests compared with terra firme forests (Kraft, Valencia & Ackerly 2008). Seasonally flooded forests in the Amazon basin include varzea (whitewater-flooded forest with relatively rich soils) and igapo (blackwater-flooded forests with relatively poor soils); thus, we expect shifts in trait values to be greater in varzea than in igapo. Finally, white-sand forests are characterized by infertile soils supporting a low density of large stems (Baraloto *et al.* 2011). The herbivory costs to plants are greater in white-sand forests because the low soil resource availability makes tissue replacement more difficult (Fine *et al.* 2006), and frequent droughts increase the risk of cavitation (Chave *et al.* 2009). Thus, in white-sand forests, we predict shifts towards greater wood density and lower SLA.

Finally, if environmental filtering drives consistent shifts in community functional composition, we can test whether the relationships between environmental factors and community functional composition can be used to attempt a predictive landscape-scale analysis. Previous studies found that plant functional types responded predictably to changes in environmental conditions, such as soil resources or climate (e.g. Chapin *et al.* 1996; Berry & Roderick 2002), but plant functional types determined in one ecosystem often failed when applied in other ecosystems (Keith *et al.* 2007; Harrison *et al.* 2010). Using plant functional traits to address this issue represents a more promising approach (Suding & Goldstein 2008; Ordonez *et al.* 2009; Webb *et al.* 2010), though predicting community functional composition via trait-based environmental filtering remains an important challenge (Lebrija-Trejos *et al.* 2010; Laughlin *et al.* 2011; Liu *et al.* 2012). In this contribution, we examine whether abiotic and biotic environmental factors can predict community functional composition in lowland Amazonian forests. Specifically, we test (i) whether functional similarity between communities decreases with increasing environmental dissimilarity between plots in both studied regions (Swenson, Anglada-Cordero & Barone 2010); and (ii) whether community functional composition can be accurately predicted from environmental descriptions in the 61 additional forest plots of our network, in the absence of data on species taxonomy or traits.

Materials and methods

DATA COLLECTION

We established a network of 74 plots in French Guiana and Loreto, Peru, located in terra firme clay, seasonally flooded and white-sand forests (Fig. 1). Seasonally flooded forests in French Guiana and at Porvenir in Peru are igapo (blackwater-flooded forests with relatively

poor soils), whereas seasonally flooded forests at Jenaro Herrera in Peru are varzea (whitewater-flooded forest with relatively rich soils). Our plot sample method represents a further modification of the Phillips *et al.* (2003) modified Gentry plots: our protocol aggregates 10 10 × 50 m transects within a 2-ha area (Baraloto *et al.* 2011, 2013). In these, 74 plots we recorded (i) botanical identity for all trees > 2.5 cm diameter at 1.3 m height (DBH), standardizing taxonomy across regions with project-specific vouchers referenced to the Missouri Botanical Gardens herbarium; and (ii) environmental factors describing climate (mean annual rainfall and dry season length), soil (texture and chemistry) and forest structure (mean basal area, height, DBH and density of stems in three classes: 2.5–10 cm DBH, 10–30 cm DBH and > 30 cm DBH) (Baraloto *et al.* 2011). In our study, climate data were determined at fine spatial and temporal scales allowing precise calculation of the dry season index, which global data bases such as WorldClim (www.worldclim.org) could not provide (Wagner *et al.* 2011). Forest structure factors were taken here as proxies of the environmental conditions because they may indicate some community processes such as competition for resources. For instance, a high mean basal area or DBH is associated with a high competition for light (Coates, Lilles & Astrup 2013). A principal component analysis (PCA) on all 21 environmental factors across the 74 plots defined a first gradient (PCA axis 1) of decreasing soil fertility and clay content and a second gradient (PCA axis 2) of decreasing dry season length and forest basal area and diameter at breast height (Fig. 1).

We selected 13 plots representative of the gradients of environmental conditions and floristic composition found in the network (Fig. 1), and measured 15 leaf and wood traits (Table 1) on one individual per species in each plot (Baraloto *et al.* 2010a), representing 1080 individuals and 800 species (see Tables S1 and S2 in Supporting Information). For each species in each plot, we chose the stem nearest to 5 cm DBH, to standardize trait measures for the majority of taxa to understorey light conditions and the small tree stage. Hence, we did not investigate ontogenetic effects on plant functional traits. Palm species were excluded from this study because of the unfeasibility to measure stem wood specific gravity (WSG), that is, the density of wood relative to the density of water (Williamson & Wiemann 2010). The 15 leaf and wood traits defined two orthogonal axes of functional trade-offs: a first axis defined by leaf traits, corresponding to a 'leaf economics spectrum', and a second axis defined by covarying stem and woody root traits, corresponding to a 'wood economics spectrum' (see Fig. 3 in Fortunel, Fine & Baraloto 2012).

DATA ANALYSES

Our first analysis tested the extent to which community functional composition is filtered among habitats. To answer this, we separated plots from French Guiana and Peru to run both univariate and multivariate approaches, considering a regional pool of species from within each country. First, we used univariate tests on each trait considered alone, taking the community mean, range and variance for each of 15 traits in each of 13 plots. Because range is sensitive to the two extreme trait values in the community, we calculated range as the difference between the 10th and 90th percentiles of trait values in the community. To disentangle the effect of differences in abundance between common and rare species, we calculated the trait statistics (i) using species presence-absence and (ii) by weighting by species abundances in the corresponding community (Cingolani *et al.* 2007; Lavorel *et al.* 2008). We chose to weight by species abundances rather than their basal area because our focus was to study the effect of environmental filtering on community composition rather than ecosystem-level processes. To evaluate the magnitude of environmental filtering on indi-

Table 1. List of the 15 measured traits, as well as their assignment to leaf or wood group and their corresponding ecological strategy

Trait	Abbreviation	Unit	Mean	Range	Group	Strategy	References
Laminar thickness	Lthick	mm	0.21	[0.07, 0.85]	Leaf	Resource capture and defence	Niinemets (1999)
Laminar toughness	Ltough	N	1.46	[0.29, 5]	Leaf	Resource capture and defence	Agrawal & Fishbein (2006); Onoda <i>et al.</i> (2011)
Leaf tissue density	LTD	g cm ⁻³	0.42	[0.064, 2.12]	Leaf	Resource capture and defence	Niinemets (1999); Kitajima & Poorter (2010)
Specific leaf area	SLA	m ² kg ⁻¹	13.76	[1.98, 50.95]	Leaf	Resource capture and defence	Reich, Walters & Ellsworth (1997); Wright <i>et al.</i> (2004)
Leaf area	LA	cm ²	103.48	[0.11, 1537.36]	Leaf	Resource capture	Wright <i>et al.</i> (2007)
Foliar carbon	LCC	cg g ⁻¹	47.34	[33.89, 67.67]	Leaf	Resource capture and defence	Chaturvedi, Raghubanshi & Singh (2011)
Foliar nitrogen	LNC	cg g ⁻¹	2.15	[0.73, 8.04]	Leaf	Resource capture	Reich, Walters & Ellsworth (1997)
Foliar phosphorus	LPC	µg g ⁻¹	0.08	[0.004, 0.33]	Leaf	Resource capture	Chaturvedi, Raghubanshi & Singh (2011)
Foliar potassium	LKC	µg g ⁻¹	0.69	[0.11, 3.60]	Leaf	Resource capture	Wright <i>et al.</i> (2005)
Foliar C : N ratio	LC.N	g g ⁻¹	24.76	[5.96, 66.68]	Leaf	Resource capture and defence	Agrawal & Fishbein (2006)
Foliar ¹³ C composition	L13C	‰	-33.78	[-38.25, -28.66]	Leaf	Resource capture	Farquhar, Ehleringer & Hubick (1989)
Laminar total chlorophyll	LChl	µg mm ⁻²	67.81	[13.20, 132.17]	Leaf	Resource capture	Chaturvedi, Raghubanshi & Singh (2011)
Trunk bark thickness	Bark thick	mm	0.03	[-2.14, 5.94]	Wood	Transport, structure and defence	Paine <i>et al.</i> (2010); Brandão <i>et al.</i> (2012)
Stem wood specific gravity	Stem WSG	No unit	0.59	[0.21, 1.12]	Wood	Transport, structure and defence	Chave <i>et al.</i> (2009)
Root wood specific gravity	Root WSG	No unit	0.58	[0.19, 0.92]	Wood	Transport, structure and defence	Chave <i>et al.</i> (2009)

Values for trunk bark thickness are the residuals of a linear regression between trunk bark thickness and diameter at breast height for all 1079 individuals.

vidual traits, we compared the observed statistics of each trait in each plot to its predicted distribution under the null hypothesis of no association between habitat and traits. We generated the null expectation for each plot by creating 999 random communities with an equal number of individuals drawn from the regional species pool (French Guiana or Peru, respectively), irrespective of their traits, weighing by species local abundances when included in the community statistics (Kraft, Valencia & Ackerly 2008). We tested the strength and direction of habitat filtering by comparing the observed statistics with the 95% confidence interval of the random communities.

To account for the multidimensional nature of plant strategies (Baraloto *et al.* 2010b), we developed a multitrait approach that takes into account the correlations among functional traits. Our approach builds upon the technique of convex hull volumes, which are multivariate ranges typically used to test for the effects of habitat filtering (Cornwell, Schwilck & Ackerly 2006). By definition, ranges and convex hulls are very sensitive to outliers, and they provide no information about the distribution of values between the extremes. Here, we improve upon the convex hull approach using a kernel density estimate to calculate the density of trait values in multivariate space. For each of the 13 plots, we constructed a two-dimensional binned kernel density using two axes of trait variation: SLA and stem wood specific gravity (Stem WSG). These traits were selected because of their interpretability and their strong correlations with the leaf and wood economics spectra, respectively (Poorter *et al.* 2008; Baraloto *et al.* 2010b; Wright *et al.* 2010). We refer to these multivariate descriptors of functional composition as 'trait clouds'. Similar to the univariate approach described above, we calculated trait clouds using (i) species relative abundances and (ii) species presence-absence. We used the trait cloud overlaps as an index of the functional similarity between two plots in each region. Trait cloud overlap, as an index of similarity between two communities, is a measure between two groups, hence the use of pairwise comparisons in the subsequent analyses. To test for shifts in trait clouds between habitats due to environmental filtering, we compared the observed trait cloud overlaps between plot pairs in each region to their predicted distributions under the null hypothesis. The null expectation for each plot pair in each region was generated in the same way as specified for the univariate tests. If the observed overlap was less than the fifth percentile of expected overlaps, we concluded that there was significant multivariate environmental filtering.

To test the correlations between functional and environmental dissimilarity, we performed Mantel tests for correlations between dissimilarity matrices of plot pairs in French Guiana and Peru, respectively. Functional dissimilarity between plot pairs was calculated by subtracting the observed pairwise trait cloud overlap, with and without species abundances, from the maximum trait cloud overlap (maximum trait cloud overlap = 1). Environmental dissimilarity was calculated as the Euclidean distance between plot pairs on the first three axes of the PCA on all environmental factors describing climate, soil and forest structure across the network of 74 plots in French Guiana and Peru (Fig. 1). To illustrate the correlations between functional and environmental dissimilarities, we used ordinary least square (OLS) regressions (Warton *et al.* 2006) between trait cloud overlap, with and without species abundances, and environmental dissimilarity between plot pairs in each region. For the OLS regression parameters, we tested whether the slope and the elevation differed from zero.

Our second analysis tested the extent to which quantitative environmental factors in isolation can predict community functional composition. To achieve this aim, we pooled data from both regions to run models that could be used for any site in Amazonia. We per-

formed stepwise regressions between each of the 15 community mean traits and five key environmental factors (mean annual rainfall, dry season length, soil sand content, soil C : N ratio and stand mean DBH) for the 13 studied plots. We used AICc, the small-sample-size-corrected version of Akaike Information Criterion (Kadane & Lazar 2004), to select the best linear model in order to test for significant effects of environmental factors on community mean traits. We then used the model-averaged estimates of the best linear models selected by AICc (Burnham & Anderson 2004) to predict community mean traits in the 61 other plots from their environmental factors alone. To evaluate the validity of our predictions, we calculated the community functional composition we expect in the 61 plots using species relative abundance in each of the 61 plots and assuming that species traits in those plots were similar to those determined in the 13 plots. When a species occurring in one of the 61 plots was not represented by the species measured in the 13 studied plots (18% of species in the data set), we used the trait means from the closest taxonomic level (genus or family). We tested the accuracy of our predictive framework using standard major axis (SMA) regressions between the 'predicted' and 'calculated' community mean traits, with and without species abundances. For the SMA regression parameters, we tested whether the slope differed from one and whether the elevation differed from zero.

All analyses were conducted in the R 2.15.3 statistical platform (R Development Core Team 2011), using packages *ade4* (Dray & Dufour 2007), *KernSmooth* (Wand 1994), *glmulti* (Calcagno & de Mazancourt 2010), *smatr* (Warton *et al.* 2006) and *vegan* (Oksanen *et al.* 2012).

Results

At the community level, leaf trait values were similar in both regions, with the sole exception that mean leaf phosphorus content was lower in French Guiana than in Peru ($F = 18.66$, d.f. = 1, $P < 0.01$). Trees tended to have thicker bark and denser wood in French Guiana than in Peru (bark thickness: $F = 16.89$, d.f. = 1, $P < 0.01$, stem WSG: $F = 4.19$, d.f. = 1, $P = 0.065$, root WSG: $F = 4.39$, d.f. = 1, $P = 0.060$). Most traits showed strong signatures of environmental filtering in each of the three habitats in both regions, in that observed trait means, ranges and variances tended to differ from the expected values produced by the null models (Fig. 2 and see Table S3 for complete results).

Community-weighted mean (CWM) stem WSG was greater than expected in white-sand forests, whereas it was lower than expected in terra firme and seasonally flooded forests (Fig. 2). CWM root WSG generally showed the same pattern among habitats as CWM stem WSG (Table S3), because stem and root wood densities were strongly correlated ($R = 0.47$, $P < 0.0001$). Observed CWM values of leaf traits linked with resource acquisition (SLA, leaf area, leaf nitrogen, phosphorus and potassium contents) were lower than expected in white-sand forests, whereas they were greater than expected in terra firme and seasonally flooded forests (Fig. 2 and Table S3). Conversely, CWM values for leaf traits pertaining to resource conservation and plant defence (leaf thickness, toughness, carbon content and C : N ratio) were greater than expected in white-sand forests, and lower than expected in terra firme and seasonally flooded forests (Table S3). CWM values of trunk

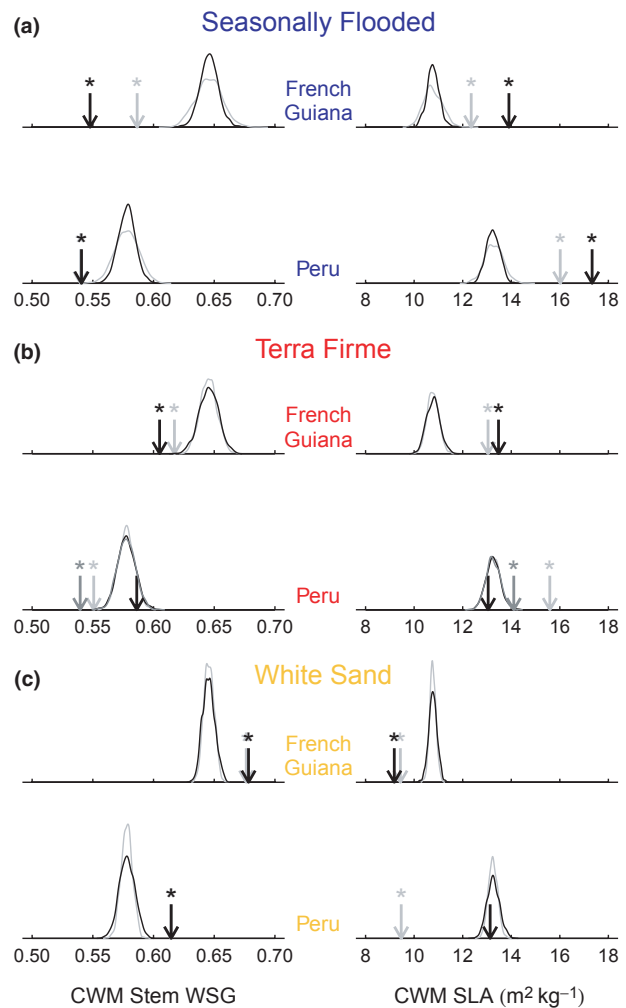


Fig. 2. Environmental filtering on community-weighted mean (CWM) traits defining the two axes of tropical tree vegetative strategy: stem wood specific gravity (Stem WSG) for the wood economics spectrum and specific leaf area for the leaf economics spectrum. For each of the 13 studied plots, the observed CWM trait (arrow) is plotted along its null model (line whose colour matches the corresponding arrow). To emphasize the filtering among habitats, the observed plot value and its null model are plotted for (a) seasonally flooded ($n = 4$), (b) terra firme ($n = 5$) and (c) white-sand ($n = 4$) plots in French Guiana and Peru. Note that some arrows may overlap. Stars indicate significant deviation from the null expectation. Complete results for all 15 CWM traits are given in Table S3.

bark thickness, leaf tissue density, ^{13}C composition and chlorophyll content deviated from the null expectation in most habitats, but showed no consistent pattern across habitat types. Community-unweighted mean traits (based on presence-absence) showed generally similar patterns, though less often detected: patterns of environmental filtering were detected in 82.2% of the cases for community-unweighted means vs. in 99.6% of the cases for CWM traits (Table S3).

Observed ranges and variances of most community traits differed from the null expectation in all three habitats (Table S3). In particular, the ranges of community wood traits (e.g. root WSG) and leaf traits pertaining to the resource acquisition-conservation trade-off (e.g. leaf C : N ratio) were lower

overall than expected (Table S3). The ranges of community-weighted traits were reduced in most habitats, while the ranges of community-unweighted traits were generally greater than expected across habitats. The variances of community wood traits (e.g. stem and root specific wood gravity) and leaf traits pertaining to the resource acquisition-conservation trade-off (e.g. SLA, leaf C : N ratio) were in general lower than expected (Table S3). However, the variances of other community traits such as leaf nutrient contents generally showed no clear pattern across habitats. The reduction in variance of community traits across habitats was stronger overall when species abundance was taken into account.

Trait clouds, integrating either species relative abundances or species presence-absence, shifted significantly among the three habitats in both French Guiana and Peru (Fig. 3, see Figs S1 and S2 for complete results), further confirming the effect of environmental filtering on whole-plant functional strategy. Trait clouds showed less overlap between habitats than predicted by the null model in both regions, the pattern being more pronounced when trait clouds integrated species abundances (Figs 3, S1 and S2). With their sturdier leaves and denser wood, white-sand forests were significantly distinct from terra firme and seasonally flooded forests (Figs 3, S1 and S2). In addition, seasonally flooded forests had less dense wood than both terra firme and white-sand forests (Figs 3, S1 and S2). Although seasonally flooded forests in Peru included varzea and igapo forests, the trait clouds in

both forest types showed similar overlaps with terra firme and white-sand forests (Fig. S2).

Together, climate, soil and stand factors represented important factors driving the environmental dissimilarity between plot pairs among and within habitats in both French Guiana and Peru (Figs 4 and S3). Whether functional dissimilarity integrated species abundances or not, Mantel tests consistently showed that functional and environmental dissimilarity matrices between plot pairs were significantly correlated in French Guiana and less so in Peru (Figs 4 and S3). The SMA regressions illustrated that functional dissimilarity between plot pairs decreased with increasing environmental dissimilarity in both regions (Figs 4 and S3), suggesting that community functional composition can be quantitatively explained by environmental factors.

Whereas the best linear models relating community functional composition to five key environmental factors varied among the 15 community mean traits, we found that most community mean traits were best explained when combining climate, soil and forest structure factors (see Table S4). For instance, community mean leaf carbon content was best explained with a combination of dry season length, soil sand content and plot mean stem diameter at breast height. Similarly, community mean leaf nitrogen content was best explained by soil C : N ratio and plot mean stem diameter at breast height. CWM SLA was best explained by soil chemistry, while community-unweighted mean SLA was best

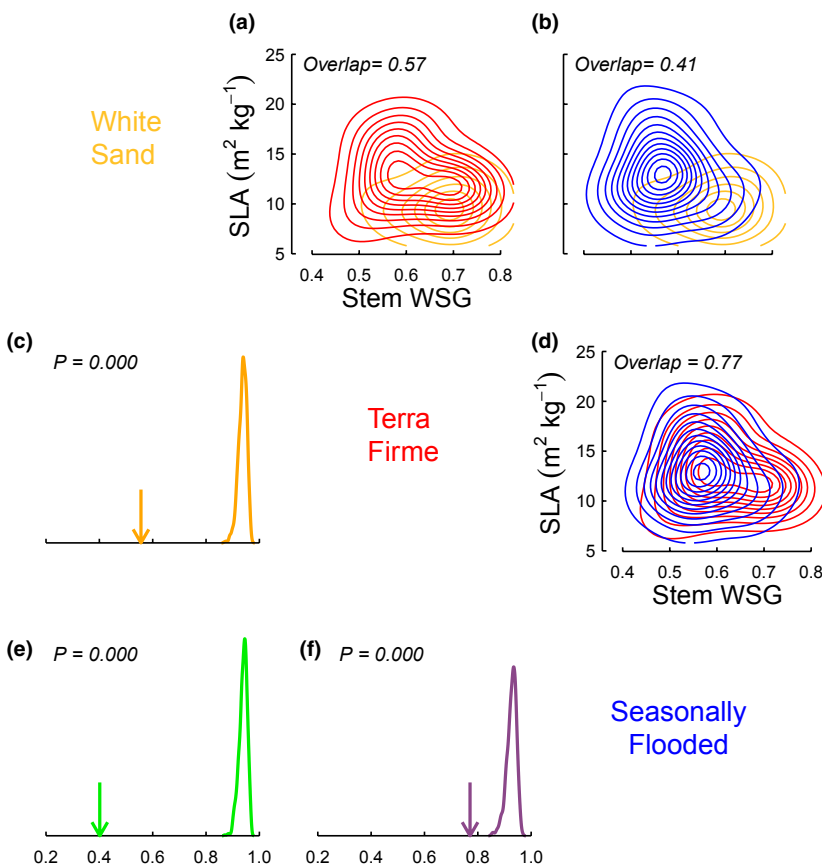


Fig. 3. Bivariate differences in community trait clouds between habitats. Trait clouds were built in wood (Stem WSG) and leaf (specific leaf area) dimensions, integrating species abundances. Above the diagonal (a, b, d): Trait cloud overlap between habitats. Overlaps are given in the top-left corner for one plot per habitat in French Guiana. Colours indicate habitats as in Fig. 1. Below the diagonal (c, e, f): Trait cloud differentiation between habitats. Observed overlaps between plot pairs (arrows) are plotted along the distribution of overlaps between plot pairs in 999 simulations for terra firme (TF), seasonally flooded (SF) and white-sand (WS) plots. Test significances are given in the top-left corner for each plot pair. Colours indicate habitat comparisons (violet: SF-TF, green: SF-WS, orange: TF-WS). Complete results for all plot pairs in each region are given in Fig. S1.

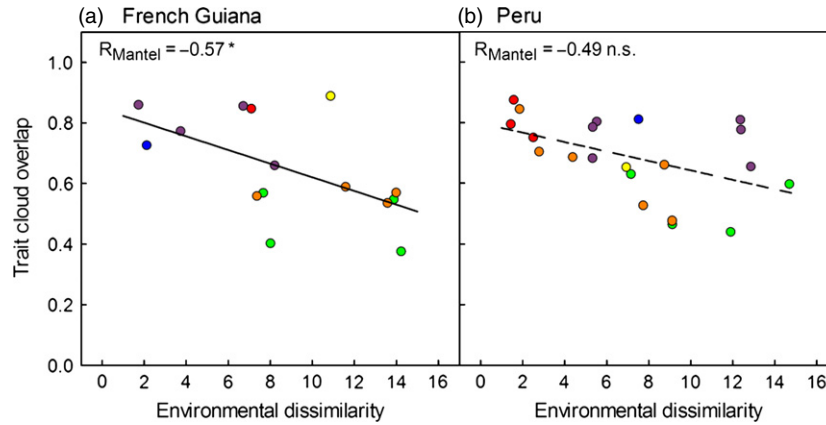


Fig. 4. Functional and environmental dissimilarities between plot pairs in (a) French Guiana ($n = 6$ plots and 15 plot pairs) and (b) Peru ($n = 7$ plots and 21 plot pairs). The Mantel tests between functional and environmental dissimilarities among plot pairs are indicated ($*P < 0.05$, n.s.: not significant). To illustrate these relationships, standard major axis regressions are drawn in solid line when the Mantel test is significant, in dashed line otherwise. Colours indicate habitat comparisons (blue: SF-SF, red: TF-TF, yellow: WS-WS, violet: SF-TF, green: SF-WS, orange: TF-WS). See Fig. 3 for habitat abbreviations.

explained by mean annual rainfall, soil sand content and plot mean stem diameter at breast height. Community mean stem WSG was best explained with a combination of mean annual rainfall, dry season length and plot mean stem diameter at breast height.

Using the model-averaged estimates of the best linear models relating the five environmental factors and each of the 15 community mean traits in the 13 plots (Table S5), we predicted the 15 community mean traits in the 61 other plots in the network for which traits were not measured, but for which environmental factors were available. Most of these 'predicted' community mean traits correlated well with the 'calculated' community mean traits that we estimated by combining the species abundance data we collected in the 61 additional plots and the species traits we measured in the 13 intensively studied plots (e.g. bark thickness, stem and root wood specific gravities, leaf thickness and toughness, SLA, leaf carbon, nitrogen, phosphorus and potassium contents, leaf C : N ratio

and leaf 13C composition; Fig. 5 and see Fig. S4 for complete results). CWMs yielded slightly more accurate and less biased predictions than community-unweighted mean traits did (Fig. S4).

Discussion

STRONG ENVIRONMENTAL FILTERING ACROSS HABITATS IN LOWLAND AMAZONIAN FORESTS

Environmental filtering consistently shapes the functional composition of highly diverse tropical forests at large scales across the terra firme, seasonally flooded and white-sand forests of lowland Amazonia (Figs 2, 3, S1 and S2, Table S3). Combining univariate and multivariate approaches, we show that environmental filters have convergent effects on leaf and wood strategies: white-sand forests had denser wood and sturdier leaves with lower nutrient contents than terra firme and

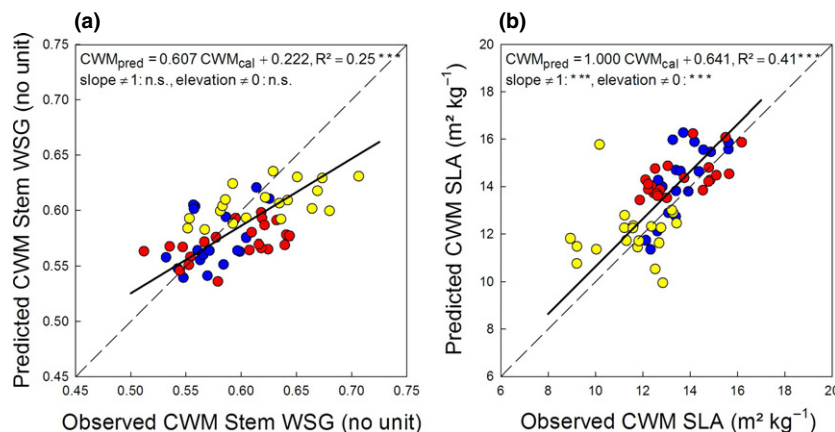


Fig. 5. Calculated and predicted community-weighted mean (CWM) traits in 61 plots for (a) stem wood specific gravity (Stem WSG) and (b) specific leaf area. The dashed and solid lines indicate the 1 : 1 slope and standard major axis (SMA) regressions, respectively. SMA equations and R^2 are given with significance tests. The tests on SMA regression parameters indicate whether the slope differs from 1 and whether the intercept differs from 0 ($***P < 0.0001$). Colours indicate habitat type (blue: seasonally flooded, red: terra firme, yellow: white sand).

seasonally flooded forests, whereas terra firme forests exhibited denser wood than seasonally flooded forests. Environmental filtering also reduced the range and variance of key community wood and leaf traits (e.g. stem and root wood specific gravities, SLA, leaf C : N ratio) in the three habitats, further confirming the importance of niche-based processes in lowland Amazonian forests. Although environmental filtering directionally affected the mean of most other community leaf traits, it did not consistently reduce their range and variance. Our results suggest that environmental filtering acts particularly upon key wood and leaf traits, re-emphasizing their contributions to the global spectra of leaf and wood economics (Wright *et al.* 2004; Baraloto *et al.* 2010b).

The effect of environmental filtering on community trait statistics was generally stronger when integrating species abundances (Table S3). In particular, the effect of environmental filtering on the mean and variance of community traits was detected more often when accounting for species abundances. Environmental filtering more consistently reduced the range of community traits when including species relative abundance, but increased it when including species presence–absence. Thus, environmental filtering determines species relative abundance more strongly than species presence–absence, which further suggests the significant role of environmental filters on species recruitment and establishment in the local communities (Keddy 1992; Belyea & Lancaster 1999).

Although French Guianan forests have less fertile soils, longer dry seasons and greater above-ground biomass than Peruvian forests (Baraloto *et al.* 2011), environmental filtering acted similarly on community functional composition among the three habitats in both regions. Even though seasonally flooded forests in Peru included both varzea forests with relatively rich soils and igapo forests with relatively poor soils, the signature of environmental filtering was similar in both seasonally forest types. Interestingly, environmental filtering on community functional composition was independent of the relative area that each habitat covers in the Amazon basin: environmental filtering was strong in rare and extreme habitats (i.e. seasonally flooded and white-sand forests) as well as in the most common habitat (i.e. terra firme forests). Our study thus extends on previous research showing the importance of environmental filtering in tropical forests (ter Steege *et al.* 2006; Engelbrecht *et al.* 2007; Kraft, Valencia & Ackerly 2008; Paine *et al.* 2011; Katabuchi *et al.* 2012) to demonstrate that environmental gradients underlie directional shifts in community functional composition across lowland Amazonian forests.

Contrasting environmental conditions in terms of climate, soil and forest structure favour different ecological strategies for both leaf and wood axes among habitats. The poor soils and frequent drought stress of white-sand forests favour species with resource conservation strategies (*sensu* Grime 1974), whereas the fertile soils and high water availability of terra firme and seasonally flooded forests support species with rapid growth strategies. The pattern was more pronounced in seasonally flooded forests in accordance with its more frequent disturbance and thus more rapid forest turnover (Ferry

et al. 2010). The least ‘stressful’ abiotic conditions of terra firme forests also strongly filtered community functional composition, as found in previous studies (Muller-Landau 2004; Wright *et al.* 2006; Liu *et al.* 2012). We interpret this result as an indication of the potential importance of the interplay between abiotic filters and biotic filters in community assembly (Belyea & Lancaster 1999; Lortie *et al.* 2004): species establishing in a local environment must not only tolerate the local abiotic conditions but also cope with negative interactions with other plant species (e.g. competition) as well as with other organisms (e.g. herbivory, attack by soil pathogens). We found in earlier work that terra firme forests exhibit a high density of large stems, resulting in greater above-ground biomass than found in seasonally flooded or white-sand forests (Baraloto *et al.* 2011). This result suggests that individual trees establishing in terra firme forests are probably filtered by the strong competition with large established stems for resources, both above-ground for light and below-ground for nutrients (Tilman 1990; Craine 2005). Similarly, the environmental filtering observed in white-sand forests may be magnified by natural enemies (Fine, Mesones & Coley 2004; Smith & Sibly 2008). The higher costs of herbivory in these forests can indeed select for species with functional strategies favouring defence (Fine *et al.* 2006).

PREDICTING COMMUNITY FUNCTIONAL COMPOSITION ACROSS ENVIRONMENTAL GRADIENTS IN LOWLAND AMAZONIAN FORESTS

An important goal for ecologists is to predict spatial distributions of community functional composition, for which we need a precise description of spatial environmental variation. In this study, we described abiotic (climate and soil) and biotic (forest structure) environmental factors in a network of lowland Amazonian forests. In both studied regions across Amazonia, the multivariate distance between plot pairs calculated from climate, soil and stand factors captured quantitative environmental dissimilarities that go beyond the qualitative description of habitat types. In particular, plots from habitats that we categorized as the same habitat type appeared sometimes more environmentally dissimilar than plots from different habitats. For example, environmental dissimilarity was sometimes greater among white-sand plots than between white-sand and terra firme plots (Figs 4 and S3). Quantifying these environmental variables allows a better understanding of how community functional composition changes across broad environmental gradients (Swenson, Anglada-Cordero & Barone 2010). In fact, we found that community functional dissimilarity correlated with environmental dissimilarity in 13 intensively studied plots across both studied regions (Figs 4 and S3).

Furthermore, five key environmental factors describing variation in climate, soil and forest structure explained an important proportion of the spatial variation in community functional composition: linear combinations of these environmental factors correlated well with community functional composition in the 13 intensively studied plots (Table S4). In particular, decreasing soil fertility and increasing soil sand

content, describing the first environmental axis (Fig. 1), are associated with decreasing SLA and leaf nitrogen content, but with increasing leaf toughness and C : N ratio. Hence, poorer soils relate to leaf traits associated with resource conservation strategies (Wright *et al.* 2004; Chaturvedi, Raghubanshi & Singh 2011; Onoda *et al.* 2011), including leaf defence against herbivores and pathogens (Agrawal & Fishbein 2006; Fine *et al.* 2006). Decreasing dry season length and forest mean diameter at breast height, describing the second environmental axis (Fig. 1), correlates with decreasing leaf toughness and leaf carbon isotopic descriptors that are linked to plant water use (Farquhar, Ehleringer & Hubick 1989), but with increasing community mean bark thickness, stem WSG, leaf area and C : N ratio. A longer dry season thus simultaneously filters for wood traits related to resource conservation, and conversely for leaf traits related to resource acquisition (Table S4), suggesting that tropical trees can invest differentially in wood and leaf tissues to optimize their performance across environmental gradients. The functional significance of bark thickness in tropical forests is still unclear (Paine *et al.* 2010), but our results suggest that bark thickness could be related to climatic parameters. Additionally, changes in leaf area could also be affected by climate, because smaller leaves could better avoid overheating by limiting the surface irradiated by the sun. Hence, community functional composition shifts according to quantitative changes in environmental factors (Fyllas *et al.* 2009; Ordonez *et al.* 2009): less fertile soils, drier climate and smaller diameter stands shift community functional composition towards species with greater leaf and wood tissue densities, and thus slower growth, but higher survival through greater resource conservation and investment in defence. Such variations in community functional composition may in turn translate into differences in ecosystem processes, such as carbon storage (de Deyn, Cornelissen & Bardgett 2008).

Moreover, the relationships we derived between environmental factors and community mean traits allowed us to accurately predict 12 of the 15 community mean traits in 61 additional forest plots in our data set using environmental data alone (Figs 5 and S4). Community mean wood and leaf traits (e.g. trunk bark thickness, stem and root wood specific gravities, SLA, leaf thickness and toughness, and leaf nutrient contents) overall showed small deviations between predicted and calculated values. Predictions of community mean root WSG were underestimated when including species abundances, whereas predictions were improved when accounting for species presence-absence. However, predicted community mean leaf tissue density, leaf area and leaf chlorophyll content were generally underestimated in comparison with their calculated values. This deviation between predicted and calculated values could be due to the variability of these particular traits along environmental gradients or to the fact that our environmental descriptors did not capture the factors influencing these particular traits. Although we could not satisfactorily predict three community mean traits, we accurately predicted 12 community mean traits that are linked to the resource acquisition-conservation trade-off, and especially the

community mean traits that showed inconsistent patterns across habitats (namely trunk bark thickness, leaf ^{13}C composition and leaf chlorophyll content).

IMPLICATIONS FOR PREDICTING THE RESPONSE OF TROPICAL FORESTS TO GLOBAL CHANGES

Community functional composition of Amazonian forests can thus be predicted from environmental factors that are relatively easy to determine in the field, or that can be extracted from existing environmental maps and remote sensing methods (Landsberg 2003; Asner & Alencar 2010). For instance, soil factors such as chemical, physical and morphological characteristics could be extracted from geological or pedological maps (Quesada *et al.* 2011), whereas climate factors such as rainfall or dry season length, and forest structure factors such as forest type and structure could be obtained by remote sensing (Anderson *et al.* 2009; Asner & Alencar 2010; Ryan *et al.* 2012). In this way, our study provides a framework to predict the functional composition of the vast tracts of tropical forests where detailed ecological studies have not been conducted. Finally, as our framework integrates quantitative climate, soil and stand factors, direct extensions of our models could be integrated to predict the degree to which climate and land use changes would shift community functional composition. Extrapolation from our study may thus prove valuable across the many tropical forests that represent major contributors to global biodiversity and biogeochemical cycling, but that face threats from land use and climate change (Malhi *et al.* 2008; Asner, Loarie & Heyder 2010).

To conclude, we report predictable directional shifts in community functional composition across Amazonian forests, with consistent environmental filtering for denser leaf, stem and root tissues in dry and poor soil environments. Our results underline the importance of environmental filtering to community functional composition in these hyperdiverse forests and provide a robust predictive framework for modelling the impacts of global changes on tree functional diversity.

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Supporting Information

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

Table S1. Individual and species sampling in each plot in each habitat in French Guiana and Peru.

Table S2. List of the 800 studied species ordered alphabetically by family based on APG3 classification.

Table S3. Effect of environmental filtering on community-weighted and community-unweighted mean, range and variance for 15 leaf and wood traits in the 13 studied plots.

Table S4. Estimates of the best linear model between observed community-weighted and community-unweighted mean traits and environmental data across 13 plots.

Table S5. Model-averaged estimates of the best linear models between observed community-weighted and community-unweighted mean traits and environmental data across 13 plots.

Figure S1. Environmental filtering on community trait clouds integrating species abundances and built in leaf and wood dimensions.

Figure S2. Environmental filtering on community trait clouds integrating species presence-absence and built in leaf and wood dimensions.

Figure S3. Community-unweighted functional dissimilarity and environmental dissimilarity between plot pairs in French Guiana and Peru.

Figure S4. Calculation vs. prediction of community-weighted and community-unweighted mean traits in 61 plots.