Research article

Deriving Plant Functional Types for Amazonian forests for use in vegetation dynamics models

Nikolaos M. Fyllas [a,*], Carlos A. Quesada [a,b], Jon Lloyd [a,c]

[a] Ecology and Global Change, School of Geography, University of Leeds, Woodhouse Lane, LS2 9JT Leeds, UK
[b] Institito Nacional de Pesquisas da Amazônia, Manaus, Brazil
[c] School of Earth and Environmental Sciences, James Cook University, Cairns, Australia

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ABSTRACT

Recent advances in our understanding of the linkages between plant physiological and morphological traits suggest a new means by which to define Plant Functional Types (Φ) for use in conceptual and mathematical models of vegetation dynamics. In this study we used data from the RAINFOR-network database, aiming to numerically derive Φ for tropical forest trees by jointly analysing an Amazon-wide dataset of (409) species abundance, species functional traits (10) and site edaphic and climatic conditions across 53 plots. We followed a stepwise procedure of numerical Φ definition with increasing complexity, starting from a simple PCA on species functional traits. We subsequently applied a three-table (RLQ) multivariate ordination method in two ways: with and without spatial autocorrelation between plots being taken into account. In all cases the environmental contribution to trait variation had been partialled out. Thus our results link species-specific "inherent" trait values with associated species abundances along environmental gradients. Our final classification of Amazonian tree species based on foliar dry leaf mass per area (M_A), leaf concentrations of C, N, P, Ca, K, Mg, carbon isotopic discrimination (Δ), branch xylem density (ρ_X) and maximum tree height (H_{max}) yielded four discrete Φ. These Φ were found to represent distinct life-history strategies and can be aligned with previous empirical definitions of tropical tree guilds. In particular, two ecological dimensions are identified: (1) a leaf deployment dimension which co-varies with soil fertility and (2) a stem deployment dimension which co-varies with soil texture. By analysing diameter growth rates of the same trees used to define the four Φ we found each Φ to have a different overall growth pattern. Furthermore, from a Basin-wide forest survey, differences in the relative abundance of the four Φ were related to stand level basal area growth and/or turnover rate variations. These new derived Φ should enhance our ability to better understand and model the dynamics of the Amazon forest, with the general procedure for plant functional trait definition described here potentially applicable to many other ecosystems.

Introduction

The classification of plant species into different physiognomic forms goes all the way back to Theophrastus (370–285 BC) who, writing the first scientific book about higher plants, *Historia Plantarum*, divided them into tree, shrub, under-shrub and herb. Theophrastus also subdivided these categories through the use of genetically dependent characters of systematic value such as leaf form, longevity, the annual versus perennial habit and many more (Morton, 1981; Pavord, 2009). More sophisticated classification schemes emerged in the early 20th century (Warming, 1909; Du Rietz, 1931; Raunkiær, 1934), but it is only in the last two decades that the categorisation of plants as "Plant Functional Types" (Φ) has assumed a pivotal role in ecological research (Smith et al., 1997; Lavorel and Garnier, 2002; Lavorel et al., 2007) having played a central role in vegetation and earth-system modelling since some of the earliest conceptions (Prentice et al., 1992; Box, 1996; Prentice et al., 2007). There is, however, now a clear need to increase Φ diversity or abandon their inelastic description to provide better representations of ecosystem responses to both climatic and disturbance gradients (Lavorel et al., 2007) as befits our rapidly increasing understanding of the importance of trait diversity and plasticity; within the one vegetation type – or even within individual species (Fyllas et al., 2009; Albert et al., 2010; Baraloto et al., 2010; Hulshof and Swenson, 2010; Messier et al., 2010; Kattge et al., 2011).

* Corresponding author.
  E-mail address: n.fyllas@leeds.ac.uk (N.M. Fyllas).

The concept of expressing the wealth of plant taxa with a finite number of groups already has a long history in tropical forest research with different tree species categorised into "guilds" in terms of their shade tolerance (gap dependent or independent) and/or pattern of resource allocation (growth *vs.* survival trade-off); such classifications generally being based on empirical information of a species performance along temporal and spatial gradients (Denslow, 1987; Swaine and Whitmore, 1988; Turner, 2001). Other studies have attempted to quantitatively define Φ for tropical ecosystems using sets of morphological, demographic and/or growth data (Lieberman et al., 1985; Vanclay, 1991; Condit et al., 1996; Nascimento et al., 2005). In general Φ definitions used in local/regional scale vegetation models (Huth and Ditzer, 2000; Kohler et al., 2000; Phillips et al., 2002) include more "guilds" compared to global scale ones, but usually lack the generality required for larger scale research objectives (Picard and Franc, 2003). Furthermore, the way key processes are simulated in stand-level tropical forest models are inevitably empirical because the appropriate values for the process-based drivers are unknown. For example, carbon gain is often estimated through a simple light saturation type curve (Chave, 1999; Huth and Ditzer, 2000; Sato, 2009), or an empirical optimum growth curve (Gourlet-Fleury and Houllier, 2000; Phillips et al., 2003). On the other hand, despite usually defining their Φ in a way little more advanced than Theophrastus, most global vegetation models are of a relatively sophisticated process based design, for example usually using the detailed Farquhar et al. (1980) photosynthesis model with the relevant parameters generally dependent on simulated foliar physiological properties such as nitrogen and/or leaf mass per unit area.

Ultimately, the way that tropical Φ are defined will depend on the research objectives and the ecological processes that are required to be represented in the conceptual framework used. Nevertheless, with the identification of "major axes of plant specialization" (Westoby et al., 2002; Diaz et al., 2004) and with datasets of a geographic coverage sufficient to capture the environmental heterogeneity of tropical forest now available (Fyllas et al., 2009; Quesada et al., 2010) it should be possible to come up with Φ definitions applicable for both local and global scale modelling schemes and here we present one procedure to do this.

Our approach is based on the notion that integrated dimensions of plant physiological variation can be considered to reflect adaptations to environmental conditions (Westoby and Wright, 2006), but that for any set of environmental conditions there is no one combination of traits that necessarily constitute the only viable approach. The study here relates to three integrated dimensions, namely the leaf mass per area (M_A) – leaf lifespan ($M_A - L_L$) continuum; the trade-off between maximum height (H_{max}) and shade tolerance and the interplay between xylem hydraulics, wood density and leaf size. The $M_A - L_L$ dimension or "leaf economic spectrum" represents a continuum of carbon and nutrient investment strategy at the leaf level (Reich et al., 1997). At the fast return end, species are generally characterised by a short L_L, low M_A and high nutrient concentrations (dry weight basis). Such plants exhibit higher gas exchange rates (Reich et al., 1994; Raaimakers et al., 1995; Domingues et al., 2010) and higher growth but lower survival rates (Reich et al., 1992; Poorter and Bongers, 2006) at least at the seedling/sapling stage; although a recent study in mature tropical forests showed that M_A was an ambiguous predictor of diameter increment (Poorter et al., 2008). The other end of the spectrum, and characterised by a higher M_A and lower nutrient concentrations, are species being considered to follow a more conservative resource use strategy. Leaf

chemical defence should also be related to this ecological axis with species that follow a conservative lifestyle investing resources (C, tannins, phenolics) for better defence of their photosynthetic tissue (Specht and Rundel, 1990; Fine et al., 2004; Read et al., 2008).

Focusing on the second ecological dimension of H_{max}, taller plants have the advantage of potentially harvesting more light during their lifetime compared with shorter ones (Poorter et al., 2005) and also to reduce light availability of their smaller competitors below (Poorter et al., 2008). However smaller statured species tend to be more shade tolerant and present higher survival rates under low light availability (Poorter, 2007).

In terms of the third dimension considered here, we were interested to see if branch xylem density, ρ_X (Patiño et al., 2009), and carbon isotope discrimination, Δ, integrate into a whole-plant hydraulics/water transport/water use efficiency spectrum, this potentially aiding species classification. Photosynthetic $^{13}C/^{12}C$ discrimination is an indicator of the relative magnitudes of photosynthetic capacity versus stomatal conductance (Farquhar et al., 1989) with its genetic variation within tropical trees correlating negatively with a range of physiological and structural characteristics (Fyllas et al., 2009; Lloyd et al., 2010; Patiño et al., 2011).

Existing dynamic global vegetation models (DGVMs) have already started to incorporate such trait linkages. For example in the "LPJ" model, Sitch et al. (2003) used the $M_A - L_L$ relationship of Reich et al. (1997) to characterise deciduous versus evergreen Φ. Moorcroft et al. (2001) used equations from the leaf economic spectrum, to derive M_A and leaf [N] from leaf life span, also specifying a functional relationship between L_L, and H_{max} and wood density (ρ_W) for their four defined Φ. It should be noted that the accuracy of these parameterisations could affect the reliability of simulations (Wright et al., 2005), and thus "optimum" functional descriptions should be pursued. Tree diversity in tropical forests remains, however, poorly represented: For example by one broadleaved Φ in TRIFFID (Cox et al., 2000) and two broadleaved groups in LPJ (Sitch et al., 2003). Refining the way functional diversity is represented especially in the highly significant tropical forest ecosystem may be of critical importance in improving model predictions of future vegetation change, especially in relation to potential increases in both the frequency and intensities of soil water deficits in currently moist tropical regions (Ostle et al., 2009).

With the implementation of a "continuum" approach of trait variation within DGVMs still under development (Scheiter and Higgins, 2009) the development of new numerical Φ definition procedures should constitute an important step forward in global vegetation modelling. Here we derive plant functional groups (Lavorel and Garnier, 2002) based on traits that are directly related to physiological processes, focussing on the way groups of species (defined by a specific set of functional traits) ordinate along the environmental gradients which exist within the Amazon Basin. The basic idea was to identify the trait groupings (with species taken as the inherent source of variability) that were best associated with the observed differences in species abundances as affected by variations in soils and climate. Differences in the functional characteristics of the derived Φ are then considered in relation to, and as possible extensions of, previously published classification schemes (Turner, 2001; Poorter et al., 2006). We also modelled the potential growth curve for each Φ (Uriarte et al., 2004) in order to explore trait-associated variations in life-history strategies and ontogenetic growth changes, especially in relation to soil fertility. Finally, stand-level variations in the relative abundances of the four Φ, were related to integrated stand level properties such as mean turnover time and basal area growth rate.

Materials and methods

We use an eigenanalysis that maximises the covariance of a linear combination of the variables of an environmental table and linear combinations of the variables of a species trait table weighted by a species abundance table (Ribera et al., 2001). This type of analysis is called *RLQ* (Dolédec et al., 1996), and it has been used to link species traits with habitat characteristics (Ribera et al., 2001; Hausner et al., 2003; Choler, 2005), to match forest data sets from different spatial samples (Dray et al., 2002), and to explore patterns of plant invasions based on a suite of functional traits (Thuiller et al., 2006). Species scores on the *RLQ* axes are clustered to identify an "optimum" number of groups. The derived Plant Functional Types are subsequently tested against an independent pioneer index, tree-level diameter growth data and stand-level aboveground growth and turnover rates data.

Data

For the purpose of this study three data tables, *viz. R* (environmental), *L* (link-species abundance) and *Q* (species traits) were compiled using data from the RAINFOR and ForestPlots.net databases (Peacock et al., 2007; Lopez-Gonzalez et al., 2011). The *R* table combined climatic data (mean annual temperature [T_A], total annual precipitation [P_A] and precipitation during the three driest months [P_D]) from the Worldclim dataset (http://www.worldclim.org) with a set of soil chemical and physical data for 0–0.3 m depth, collected and analysed as described in Quesada et al. (2010). The soil variables of interest were pH, total reserve bases (Σ_{RB}: a good indication of the extent of soil weathering), total [C] and [N], total extractable P obtained through a sequential extraction method (Quesada et al., 2010), exchangeable concentrations of soil Ca, Mg, K, Na, Al, as well as sand and clay fractions. For each site, maximum soil available water was estimated using data obtained during soil sampling and root density observation (in increasing increments to 4 m depth: Quesada et al., 2011) with laboratory measured soil textures from pit samples used to estimate soil water holding capacity using the tropical soil pedotransfer functions of Hodnett and Tomasella (2002). Calculations were done for each sampled layer and then integrated across the observed rooting depth.

The *L* table quantified the per plot species abundance, using as an indicator the established basal area per hectare, in 53 permanent RAINFOR plots across the Amazonian basin (Lopez-Gonzalez et al., 2011). The *Q* table contained a set of structural and foliar traits. The structural traits of interest were branch xylem density, ρ_X (Patiño et al., 2009), and species-specific maximum height, H_{max} (Baker et al., 2009; Patiño et al., 2011). Foliar traits (Fyllas et al., 2009) included: leaf mass per area (M_A) and leaf level [N], [C], [P], [Ca], [K] and [Mg] concentrations (dry-weight basis). Foliar $^{13}C/^{12}C$ discrimination Δ, was estimated from measurements of foliar $\delta^{13}C$ (Fyllas et al., 2009; Lloyd et al., 2010) using an assumed value for the isotopic composition of source air equal to −8.0‰ (Farquhar et al., 1989), and subsequently transformed to a stomatal limitation index, ø, according to:

$$\varnothing = 1 - \sqrt{\frac{(\Delta - a)/(b - a) - d}{[c_i/c_a]_{max}}}, \tag{1}$$

which utilises the well-known relationship between Δ and the ratio of intercellular to ambient CO_2 concentrations, c_i/c_a (Farquhar et al., 1989). Eq. (1) assumes that at current day c_a, photosynthesis can be considered a roughly linear function of c_i and with a maximum practical c_i/c_a (indicating minimal stomatal limitation) of 0.8,

with $a = 4.4‰$, $b = 30‰$ and d taken as 0.2 and is discussed further in Patiño et al. (2011).

Numerical techniques

In a previous study we have shown that plot-level contributions to trait variation along a wide geographical gradient in Amazonia, are in most cases spatially patterned but with these patterns also predictable from a set of key soil and climate variables (Fyllas et al., 2009). Here, the plot-level contribution to trait variation was excluded by using an estimate of the intrinsic value for each trait, given from the summation of intercept + family + genus + species terms of the multilevel models (intercept + family/genus/species + plot) as fitted in Fyllas et al. (2009) and Patiño et al. (2009). Thus, for the traits of interest, a matrix (denoted Q^+) was constructed which theoretically excludes the contribution of climatic and soil patterns on trait variation. Variables in Q^+ were retained in a $\log_{10}$ transformed format, apart from ρ_X for which the raw data was already approximately normally distributed (Patiño et al., 2009). It was also found that raw H_{max} were similarly close to normally distributed (see also Patiño et al., 2011) and so similarly with no transformation applied to this estimate. We also assumed that our H_{max} estimates (from Baker et al., 2009) reflect a species-specific height potential and with no partialling out of environmental effects being required.

The *R* matrix consists of environmental data in 53 RAINFOR plots distributed across Amazonia, over which both climatic (Sombroek, 2000; Malhi and Wright, 2004) and soil gradients (Sombroek, 2001; Quesada et al., 2011) have been documented. We attempted to account for spatial patterns in the matrix of environmental variables (*R*) by constructing a new matrix (*R**), where the spatial autocorrelation had been removed using PCNM (principal coordinates of neighbour matrices) analysis (Borcard and Legendre, 2002; Dray et al., 2006). The PCNM method initially creates a set of spatial explanatory variables (ф) obtained through a principal coordinate analysis based on site coordinates, after which an appropriate selection method is used to reduce those spatial variables to a smaller set where each ф contributes significantly to the explanation of the response data (Borcard et al., 2004). Here we derived the full set of 18 ф from the coordinates of the RAINFOR plots (package spacemakeR) using a forward selection method (package packfor) to identify the smaller set significantly contributing to the explanation of the original environmental variables matrix. The reduced set contained eight ф. Finally a redundancy analysis (RDA) of *R* was conducted, using the eight selected ф as the covariance matrix with residuals of this RDA providing an estimate of the environmental variability not accounted for by the ф. It is thus denoted the space-free environmental variability (*R**) matrix.

Using a complete set of 409 fully functionally described species, Plant Functional Types were derived for Amazonian forests using (1) the clustering of species scores following a principal component analysis (using matrix Q^+, PCA), (2) a normal three-table ordination (using matrix *R*, denoted as *RLQ*-n) and, (3) a three-table ordination where spatial autocorrelation has been removed (using matrix *R**, denoted as *RLQ*-s). The stepwise procedure followed for the latter two cases is illustrated in Fig. 1. The *RLQ* procedure we used is a form of co-inertial analysis (Dray et al., 2003) and relates species traits to the environmental conditions where the species are most abundant. This is achieved through the joint analysis of the *R* (environmental), *L* (link – species performance) and *Q* (species traits) tables as detailed elsewhere (Dolédec et al., 1996). A stepwise procedure is usually followed when implementing any *RLQ* analysis. This consists first of separate ordinations of the *R*, *L* and *Q* tables, and then a simultaneous ordination of these three tables (Ribera et al., 2001). In our case we first conducted a correspondence analysis
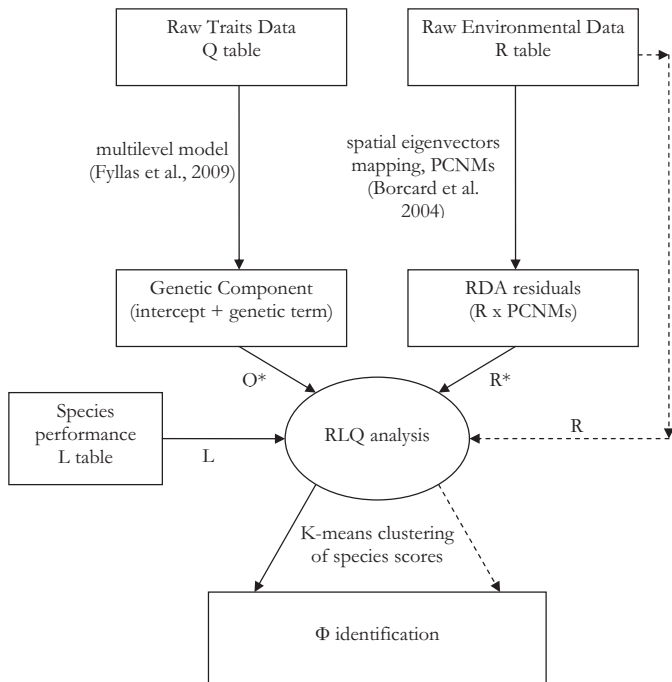
Fig. 1. Schematic representation of the implemented numerical technique. For the right side of the figure (R table pathway) solid lines indicate the case of removing spatial autocorrelation, while the broken lines indicate the case where spatial auto-correlation is not taken into account (bypassing the spatial eigenvectors and RDA procedures).

Table 1
Correlation between the variables and the first three axes of the PCA on the genetic traits matrix Q^*. The highest correlations (>0.60) are indicated with boldface.

Eigenvalue	3.060	1.848	1.273
Proportion of variance	0.306	0.185	0.127
M_A	−0.525	0.320	0.549
[C]	−0.563	−0.543	0.002
[N]	0.452	**−0.744**	-0.089
[P]	**0.612**	**−0.642**	0.027
[Ca]	**0.719**	0.404	0.176
[K]	**0.802**	0.134	0.029
[Mg]	**0.740**	0.397	0.050
ρ_x	−0.334	0.115	−0.261
l	0.220	−0.351	**0.640**
H_{max}	−0.151	−0.095	**0.671**

to identify potential differences in trait interrelationships among the derived Φ (package smatr). For the same trees from which trait data had been obtained for the analysis above, diameter at breast height (D) increment between 1997 and 2001 was estimated from repeated census measurements (Baker et al., 2009) and with an average diameter growth rate, dD/dt, subsequently calculated. With each individual already assigned to one of the derived Φ, and assuming that potential diameter growth (g) of each tree is a unique function of tree size and Φ, the observed growth rate for each tree was then modelled using a log-normal function as proposed by Zeide (1993); see also (Uriarte et al., 2004) viz.

$$g = g_m e^{-0.5((\log D/D_o)/D_b)^2} \tag{2}$$

where g_m is the maximum potential growth rate (mm a^{-1}) at the peak of the log-normal growth curve, D_0 is the value of D associated with the maximum growth rate, and D_b determines the breadth of the function. For this analysis all individuals exhibiting growth >−5 mm and <50 mm per year were used.

Finally, Kendall's τ (a robust nonparametric measure of association) was used to explore the relationship between stand level Φ abundance (expressed as the proportion of stems for each Φ per plot) and two key stand level variables, viz. aboveground basal area growth rate (ΔB) and turnover rate (φ). The former (m^2 ha^{-1} a^{-1}) is the sum of the increments in cross-sectional stem area from all trees in each plot, measured at breast height (1.3 m) or 0.5 m above buttresses if present. Turnover rates were calculated as the average of stem recruitment and mortality rates. All analyses were performed with the R statistical platform (R Development Core Team, 2010) employing the packages mentioned above.

Results

Defining Φ for Amazonian tree species

Principal components analysis of the Q^* matrix (PCA)

The first three PCA axes of the functional trait matrix Q^+ accounted for 0.62 of the total variance (Table 1). In brief, the first axis was positively related to leaf cation concentrations (Ca, K and Mg) and negatively to M_A and leaf [C]. The second axis was strongly negatively associated with foliar [N] and [P], this being similar to the "leaf economic spectrum" of Wright et al. (2004). The third axis was mainly associated with H_{max}, the stomatal limitation index (ø) and M_A. These first three axes are very similar in structure and weightings to those identified through a common principal components analysis on a subset of the same data matrix (fewer plots but with additional structural traits) by Patiño et al. (2011) and to which the reader is referred for an extensive discussion of the various trait contributions above axes of variation and their significance.

Using these first three PCA axes, application of the Calinski–Harabasz pseudo-F index identified an optimum of
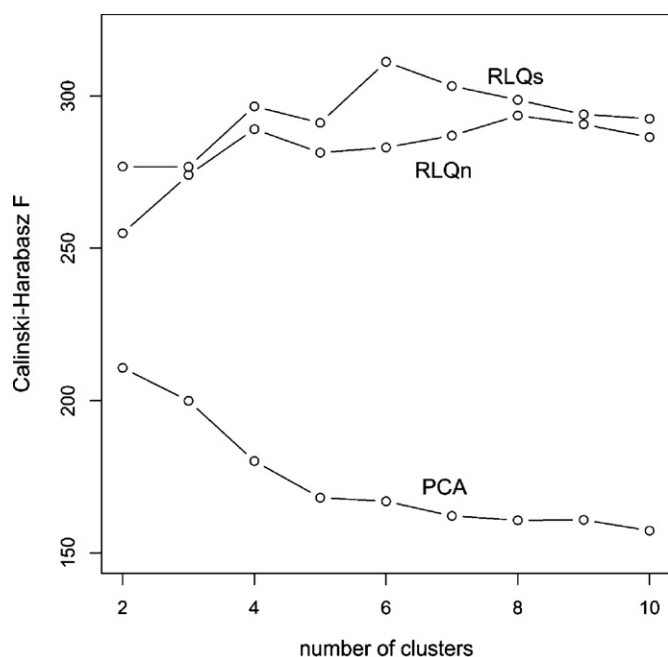
(CA) of the species abundance (L) table, providing the maximal correlation between sites and species scores. Those results were then compared with the RLQ ordination, while the species and site scores of the CA served as links between the R and Q^+ tables (Hausner et al., 2003). The R and Q^+ matrices were analysed with a PCA on the correlation table with row weights from the respective CA site and species scores. All multivariate analyses were implemented with the ade4 package available within R (Dray et al., 2007).

Plant functional groups (Φ) were defined using a K-means clustering algorithm (package cluster). In the PCA case, species scores on the first three orthogonal axes were used, while in both RLQ cases only the first two axes were used. The best number of Φ in each case was informed by considering the Calinski–Harabasz pseudo-F index (package vegan) and the need to pursue relatively simple and usable interpretations of our results. In both RLQ-based classifications the first ordination axis contained most of the information with a relatively small species regrouping taking place when considering the second axis. There was, however, an appreciable effect of spatial autocorrelation in the allocation of some species to the various Φ. We thus only retained for the final analysis those species which partitioned into the same groups for both the RLQ-n and RLQ-s classification.

As an additional metric for exploring our Φ definitions we used the independent pioneer index (Π) of Phillips, Vasquez-Martınez and Monteagudo (Malhado et al., 2009) to rank genera according to the extent to which they are perceived to be pioneers. To calculate the index each taxon had been judged independently by each botanist and given a value between zero ("non-pioneer") and one ("pioneer"). A mean species Π close to zero indicates a non-pioneer species while a mean Π closer to 1 indicates a species with more "pioneer" type characteristics.

Differences between Φ mean trait values were explored with analyses of variance followed by a Tukey post hoc test. Additionally standardised major axis (SMA) regressions were applied in order

Fig. 2. Calisnky–Harabasz pseudo F for a number of clusters ranging from 2 to 10 using the species scores of the PCA, RLQn and RLQs ordination.

only two Φ (Fig. 2). The first group brings together species with potentially high gas exchange rates (as indicated by low M_A and high leaf [N] and [P]: Domingues et al., 2010) with low investments in carbon rich compounds, *viz.* a low leaf [C], a low ρ_X and high leaf cation concentrations (Fig. S1.1). All of these characteristics may be considered indicative of species with an early successional (fast growth) strategy (Turner, 2001) and the second group thus have the generally opposing characteristics of late successional type species. Consistent with this notion, the mean pioneer index (Π) of the first group $\pm$ standard error (S.E.) was 0.18 ± 0.02 with $\Pi = 0.11 \pm 0.01$ for the second group.

"Normal" RLQ ordination of the R, L, Q* matrices (RLQ-n)

A detailed presentation of the *RLQ*-n based classification can be found in SI2 and results are summarised only briefly here. The first five axes of the CA on species abundance accounted for 0.27 of the total variance, with a maximal correlation of 0.82 between sites and species scores. The PCA of the *R* table identified three environmental gradients; the first related with soil fertility and the second and third related with climatic and soil textural parameters (Table SI2.1). Similar to the simple PCA of Table 1, the Q^+-PCA (weighted here with CA species scores) yielded three ecological dimensions, again related with leaf construction, leaf economics and plant water use strategies (Table SI2.2). The simultaneous ordination of the *R*, *L*, Q^+ triplet then indicated a significant link between environmental variables and functional traits, with the first two *RLQ* axes accounting for 0.89 and 0.05 of the total variance respectively (Table SI2.3). The first *RLQ* axis (RLQ_1), suggests a gradient of soil fertility with soil Σ_{RB}, total extractable phosphorus and exchangeable Ca, Mg and K all positively related (Table SI2.4). The second axis, RLQ_2, reflected an environmental gradient with drier sites (defined in terms of incoming precipitation) but also corresponding with soils which have a high sand content and an associated lower water holding capacity. Of note, Table SI2.5 shows that RLQ_1 also aggregated the leaf construction and leaf economic dimensions found in the Q^+-PCA (Table 1). This suggests a correspondence of species dependent leaf physiological characteristics and soil nutrient status along Amazonia. In terms of tree trait

characteristics, RLQ_2 was also strongly related to H_{max} suggesting that potentially taller species are more likely to occur in the warmer and/or moister areas of the Basin.

The Calinski pseudo-*F* peaked equivocally at both four and eight groups for the *RLQ*-n case (Fig. 2) and consistent with the *RLQ*-s described later (and for which a six group case is more extensively considered) we investigate here only the lesser case of four Φ. This division gives our Φ_1 as relatively small statured tree species with a potential for high photosynthetic rates (lowest M_A – high leaf nutrients), these also tending to be found on fertile relatively dry sites (Fig SI2.1) with Φ_3 the taller, fast lifestyle "equivalent" of Φ_1 mainly abundant in moister locations. At the other end of the spectrum Φ_4 groups together with taller tree species with low photosynthetic rates (lowest M_A – low leaf nutrients) these with a tendency to be found on relatively infertile and wet sites; with Φ_2 being the conservative counterpart of Φ_1 *viz.* smaller statured species of a low photosynthetic potential. They tend to be found on infertile plots in relatively dry areas.

"Spatial RLQ" ordination of the R*, L, Q+ matrices (RLQ-s)

A detailed presentation of the *RLQ*-s based classification can be found in SI3 with differences to the *RLQ*-n case above arising from the contribution of the "space-free" R^* matrix to the ordination of the R^*, *L*, Q^+ triplet. This separate ordination of table R^* yielded a better differentiation of the climatic and the edaphic variables than for *R*, with the first PCA axis reflecting a soil fertility gradient mainly controlled by the soil chemical properties, the second PCA axis reflecting a precipitation gradient, and the third axis summarising a soil texture gradient. The simultaneous ordination of tables R^*, *L*, Q^+ again indicated a significant link between environmental variables and functional traits, with the first two *RLQ* axes again accounting for 0.89 and 0.05 of the total variance respectively (Table SI3.3). As for the "non-spatial" case, the first axis, RLQ_1, was positively associated with soil pH and exchangeable [Ca], [Mg] and [K] and total extractable phosphorus, indicating a soil fertility gradient (Table SI3.4). The importance of climatic variables was, however, not maintained in RLQ_2 as compared with the *RLQ*-n case. Here, a second texture gradient running from sandy soils of high plant available phosphorus and [C] to clay soils of high exchangeable [K] emerged as the major environmental correlate of this axis. In terms of species traits, RLQ_1 was again related with leaf nutrients and cations concentrations with higher elemental concentrations found on richer soils (Table SI3.5) and RLQ_2 related mainly to a maximum height – xylem density dimension.

Again using the Calinski pseudo-*F* to help identify the optimum number of clusters (Fig. 2) we chose to select only four groups. This was even though a slightly higher *F* value was obtained for the more complex case of six Φ and for which the interested reader is referred to a description and discussion in SI6.

Each of the four Φ in the final *RLQ*-n analysis had a similar species composition as compared to the *RLQ*-n case, something that was expected as most of the variation was explained in both cases by the first *RLQ* axis. Thus, Φ_1 again yielded a small H_{max} and also with the lowest M_A and highest leaf [N] and [P] of any group; being mostly found in fertile environments with high soil pH, total extractable P, and exchangeable cations concentrations (Fig. SI3.1). The low fertility counterpart of Φ_1 was again Φ_2 which was more abundant on sandy soils. Of the four groups identified, Φ_3 follows the least conservative strategy presenting the group-wide lowest xylem density (ρ_X) with higher leaf cation concentrations and also characterised by a high ø. This group was also more abundant on fertile clay soils. Finally, Φ_4 brings together tall tree species with low leaf nutrient concentrations and specific leaf area, again being mostly abundant on relatively infertile soils.
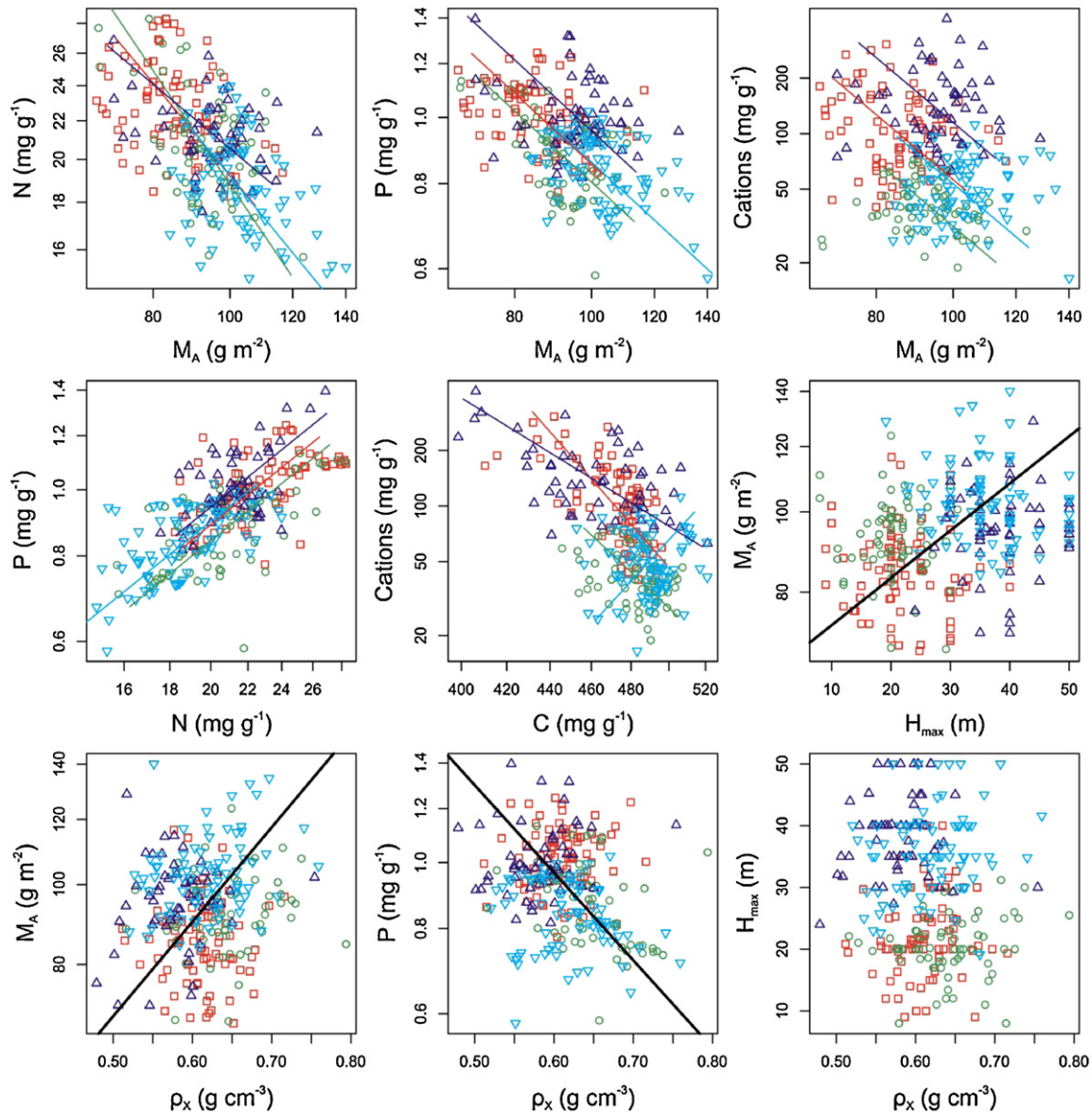
Fig. 3. Bivariate relationships for important trait pairs. Red squares for the genetic trait component of species classified at Φ_1, green circles for Φ_2 species, blue triangles for Φ_3 species and cyan triangles for Φ_4 species. Lines illustrate the standardised major axis (SMA) regression. Please see SI5 for intercept and slope estimates of the SMA line fits. Separate lines indicate cases where significant differences in either the slope or the intercept between Φ-specific SMA lines have been identified. A single line indicates cases where a common line can be used for all groups. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of the article.)

An optimum Φ definition combining the RLQ-n and the RLQ-s based classifications

The primary strategies identified by the "non-spatial" and the "spatial" *RLQ* ordinations were similar, with most of the variation explained through the first axis, summarising similar patterns in soil fertility and species dependent leaf physiological properties. In the case of the species dependent properties, even though the second *RLQ* axis could be similarly related through variations in tree hydraulic architecture for both analyses, the environmental correlates of this second axis varied. In the *RLQ*-n case variation was mostly driven by annual and dry season precipitation, but for the *RLQ*-s case it was driven mostly by soil texture. Despite this difference, when comparing the two cases there was a similar range of trait values for each group with 0.68 of the study species having the same classification for both the *RLQ*-n and the *RLQ*-s cases. We thus used the trait values of these 276

commonly partitioned species to characterise our four Plant Functional Types and to provide the mean trait values for our best Φ definition. These are summarised in Table 2 with the species listed by Φ-classification in Table S1.1. This shows Φ_1 to have the group-wide lowest M_A and high [N] and [P] suggesting a potential to achieve high photosynthetic rates. Both Φ_1 and Φ_2 had a low H_{max} with Φ_2 having the group wide highest leaf [C] and highest ρ_X. It thus has substantial structural carbon investments suggestive of a conservative life style. By contrast, Φ_3 has the lowest leaf [C] and ρ_X and with high [N] and [P] and cations, also yielding the lowest ø. Finally Φ_4 had the group-wide highest M_A and low [N] and [P] suggesting a low photosynthetic potential. Thus, in many ways, Φ_1 and Φ_2 can be considered the smaller stature equivalents of Φ_3 and Φ_4, respectively.

Differences in within group trait interrelationships were then assessed with standardised major axis regression (Fig. 3 and

Table 2
Mean trait intrinsic values for the optimum Φ definition. In all cases ANOVAs were significant for the overall difference between the four groups. Different letters denote significance difference in the mean trait value based on a Tukey HSD post hoc test.

	Φ_1	Φ_2	Φ_3	Φ_4	Min.	Max.	$F_{274,3}$	p
M_A (g/m^2)	85.4a	93.5b	95.9b	103.2c	67.9	140.1	38.8	<0.001
[C] (mg/g)	471.4b	483.2c	462.8a	488.5c	398.7	521.2	25.4	<0.001
[N] (mg/g)	22.89c	20.80b	21.34b	18.80a	14.91	28.31	40.1	<0.001
[P] (mg/g)	1.02b	0.88a	1.01b	0.84a	0.58	1.40	50.8	<0.001
[Ca] (mg/g)	6.42b	4.80a	7.25b	4.95a	2.66	13.43	48.6	<0.001
[K] (mg/g)	6.33b	4.89a	6.96c	5.09a	2.78	10.05	69.0	<0.001
[Mg] (mg/g)	2.69c	1.83a	2.89c	2.04b	1.29	4.31	77.6	<0.001
ρ_X (g/cm^3)	0.611b	0.642c	0.582a	0.618b	0.479	0.794	16.9	<0.001
∅	0.178a	0.174a	0.187b	0.174a	0.144	0.219	15.1	<0.001
H_{max} (m)	22.4a	20.5a	38.5b	35.9b	8.0	50.0	139.5	<0.001

Table SI5.1). Slightly different scaling relationships were detected for the [N] $\leftrightarrow$ M_A scaling with the intercept of the SMA line fit being statistically different for the [P] $\leftrightarrow$ M_A, [cations] $\leftrightarrow$ M_A, and pairs. Specifically, although slopes were similar for all four groups, Φ_3 had a noticeably higher intercept than the other groups for both the P $\leftrightarrow$ M_A and [cations] $\leftrightarrow$ M_A linkages and with Φ_2 having the lowest intercept. In terms of [P] $\leftrightarrow$ [N], Φ_3 again had the highest intercept and Φ_2 the lowest and with, as for [P] $\leftrightarrow$ M_A and [cations] $\leftrightarrow$ M_A, with Φ_1 and Φ_4 intermediate and tending to fall on the same line, but with Φ_4 shifted towards higher M_A, lower [cations] and lower [P]. Differences between the four groups were more ambiguous for [N] $\leftrightarrow$ M_A, though with the Φ_1/Φ_4 shift apparent. For [cations] $\leftrightarrow$ [C], although some trade-off is apparent for Φ_1 and Φ_3, no relationship is evident for Φ_2 and Φ_4 with these two groups limited to a domain of relatively low [cations] and relatively high [C]. Less well defined, but still statistically significant relationships were observed for the $M_A - H_{max}$, $M_A - \rho_X$ and the [P] $- \rho_X$ pairs with no differences between the various Φ discernable.

Our Φ classification does not allocate species randomly in terms of the pioneer index estimates of Phillips and colleagues (Malhado et al., 2009). The potentially fast resource capture Φ_1 strategy has a mean ($\pm$S.E.) Π of 0.17 ± 0.02 compared with the database mean of 0.15 with the potentially taller Φ_3 (but otherwise with more or less the same trait characteristics as Φ_1) having the highest overall Π of 0.25 ± 0.03. These values contrast with $\Pi = 0.05 \pm 0.01$ for Φ_2, with the taller but similarly low [N] and [P] grouping of Φ_4 having $\Pi = 0.10 \pm 0.02$.

Growth patterns

Using the model of Eq. (2), Φ-specific potential growth curves are presented in Fig. 4, with fitted parameters listed in Table SI4.1. Overall, Φ_1 yielded a higher potential growth $g_m \approx 5.4$ mm a^{-1} at a diameter of $D_o \approx 27$ cm, compared to its theoretically more conservative Φ_2 counterpart with a $g_m \approx 4.4$ mm a^{-1} at a diameter of $D_o \approx 34$ cm. Similarly Φ_3 showed a continuously increasing growth up to a size of $D_o \approx 36$ cm, achieving a higher $g_m \approx 6.3$ mm a^{-1}. This compares with the slower growing Φ_4 which achieved its $g_m \approx 4.3$ mm a^{-1} at the biggest size of $D_o \approx 50$ cm. Thus Fig. 4 suggests that Φ_1 and Φ_3, both of which have traits that are expected to be associated with a rapid growth rate, indeed have a greater g_m than the more conservatively aligned Φ_2 and Φ_4. Nevertheless, soon after this maximum growth rate is reached both these groups show a rapid decline in growth, especially the shorter Φ_1. This contrasts the more conservatively aligned Φ_2 and Φ_4 who, although showing less of an increase in growth rate, as D increases from 10 cm to 30 cm, also show no significant decline in g at higher D. At

the highest D, the higher H_{max} grouping of Φ_3 and Φ_4 have higher growth rates than their more vertically constrained counterparts.

Functional composition and stand-level properties

The relationship between the proportions of Φ in each plot (stem basis) with both aboveground basal area growth (ΔB) and stem turnover rates (φ) is shown in Fig. 5. Several significant correlations were apparent. For example, although the relative abundance of Φ_1 did not show any strong relationship with ΔB, it was positively correlated with to stand-level φ. On the other hand, higher Φ_3 stem abundance was associated with an increase in ΔB but not φ. The proportion of Φ_4 stems was negatively related with both stand-level properties, with this functional group being most abundant in stands with low stem ΔB as well as low φ. Different to the other three groupings, the relative abundance of Φ_2 did not show any significant relationships to either ΔB or φ.

Discussion

Plant Functional Types can be used at a range of scales ranging from the stand level ($\sim$1 ha) to the planet, with data-driven Φ definitions based on plant physiological and structural proper-
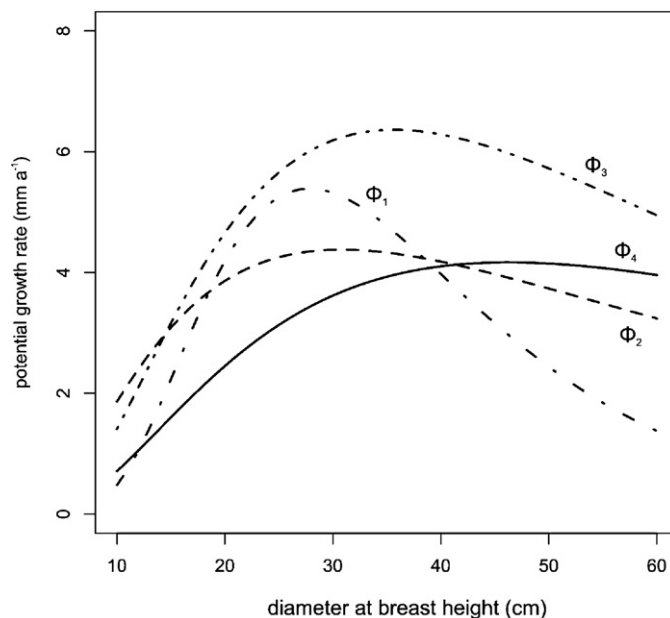

Fig. 4. Potential diameter growth per Φ as inferred from the non-linear model described in Eq. (2) (see text for details) and parameter estimates summarised in Table SI4.1. Individual level annual growth rates estimated as the mean difference between diameter at breast height between 2001 and 1997 censuses.
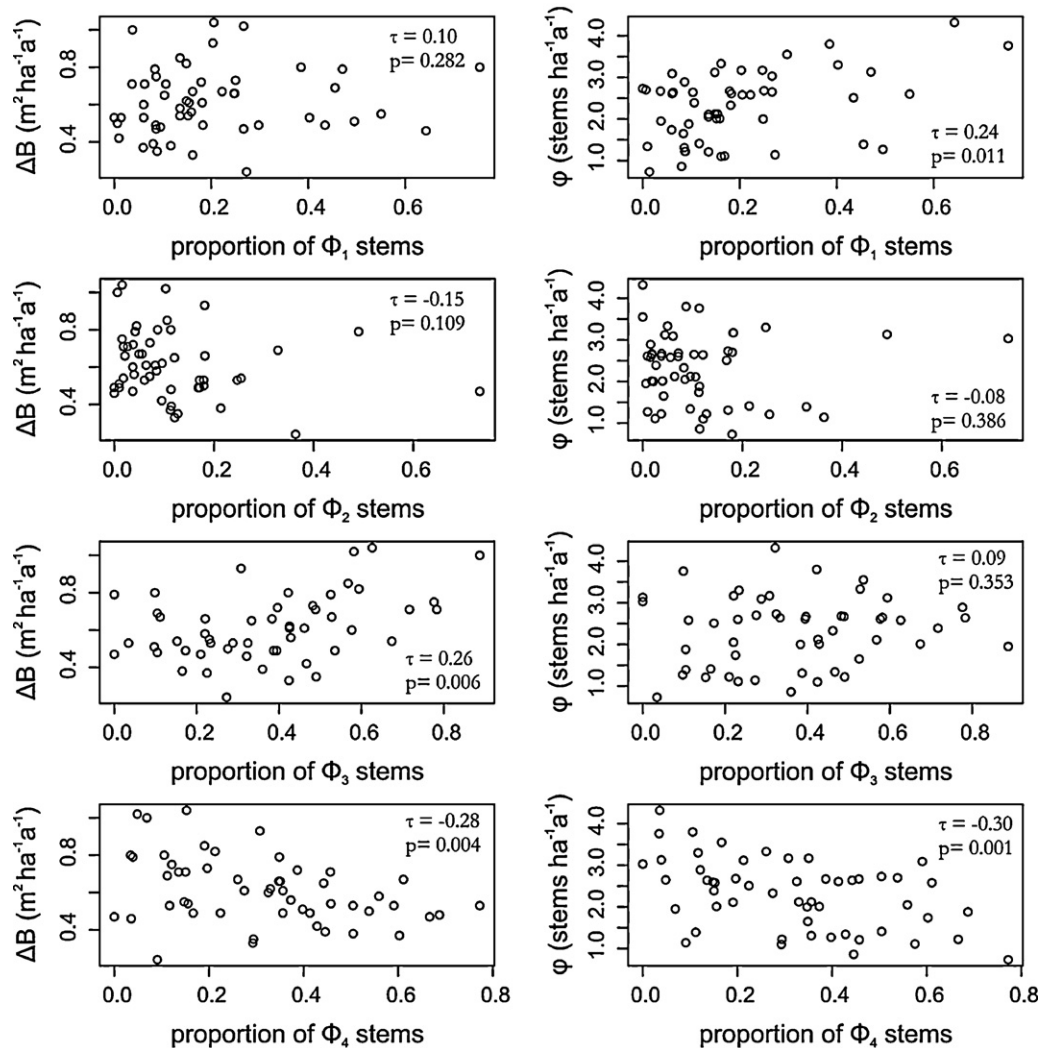
Fig. 5. Correlations between stand functional composition as portion of total stems per Φ and two stand level properties, aboveground basal area growth (ΔB) on the left and turnover rate (φ) on the right. Kendall's τ and significance level are provided within each figure.

ties, as developed here, with a potential to yield better simulations of the relevant vegetation processes. In addition, the characteristic variability of traits within any one Φ are also quantified by our procedure, along with the relevant covariances. This should allow future vegetation models to incorporate variability within a given Φ; consistent with the concept of a traits continua as has recently been implemented in dynamic global vegetation models (Scheiter and Higgins, 2009).

The proposed numerical framework

Numerical classification frameworks have previously been used to identify groups of species with similar behaviour (Lavorel and Garnier, 2002) at both the global and the regional scale (see for example, Pillar and Sosinski, 2003; Diaz et al., 2004). As has been done here, most of these schemes have generally involved a multivariate analysis of the functional traits of interest followed by a grouping of species based on their traits scores or performance along environmental and disturbance gradients (Condit et al., 1996; Diaz and Cabido, 1997; Nascimento et al., 2005). Nevertheless, with only a few exceptions such as Thuiller et al. (2006) and Bernhardt-Römermann et al. (2008), these numerical Φ definitions have not explicitly provided for a direct link between a taxon's functional traits, and its relative abundance as influenced by edaphic and environmental variables. The *RLQ* analysis applied here does, however, identify such relationships and further test their significance by the use of the linkage table *L* (Dolédec et al., 1996; Choler, 2005); this in our case being a basin-wide species/plot basal area table. The derived Φ therefore provides not only a classification of Amazon forest trees with similar characteristics, but also brings together groups of species with similar patterns of abundance along environmental gradients. This has an advantage for many modelling applications, as simulating changes in plant distribution in response to spatial and/or temporal variability in the environment is often the research question to which Φ are being applied in the first place. We also note that our results indicate that inherent differences in tree physiological and structural characteristics are currently interacting with soils and climate to influence tree species distributions across the Amazon Basin. This is because, as well as being a simple ordination technique, *RLQ* analysis provides one means to solve the 4th-corner problem (Legendre et al., 1997; Dray and Legendre, 2008) with the potential to answer questions directly applicable to niche theory *viz.* a quantification of the extent to which the biological characteristics of a species determines its relative locations in an ecosystem (Legendre and Legendre, 1998).

Ecological dimensions and Plant Functional Types for Amazonian trees

Principal components ordination of the traits table (Table 1) revealed three main axes of variation for Amazonian trees and using a similar dataset but a slightly different approach to differentiate between species associated with low versus high fertility soils, Patiño et al. (2011) obtained similar results which they also discuss in some detail. In brief, the first axis reflects an under-appreciated dimension of the leaf economic spectrum (Poorter and de Jong, 1999), this being a continuum of strategies for leaf construction, ranging from the use of relatively cheap components (minerals) to more expensive carbon based constituents such as lignin; the latter strategy also being associated with increased carbon based defences and other factors associated with long leaf durability such as a high M_A (see also Fyllas et al., 2009). Species at the positive end of this axis probably gamble on cheap and quick foliage development, this giving them advantages over short time periods but with a high risk of large-scale foliar damage due to herbivory and/or other forms of structural damage. The second dimension reflects the classic leaf economic spectrum as identified by Wright et al. (2004); identifying a trade-off between M_A and leaf concentrations of the two basic nutrients directly related to photosynthesis, namely N and P (Field and Mooney, 1986; Rao and Pessarakli, 1997; Domingues et al., 2010). As shown by Patiño et al. (2011) the third PCA axis may be related more to whole-plant hydraulics and/or light acquisition, with H_{max}, M_A and ø having strong loadings on this dimension and suggesting that taller trees are, on average, more constrained in terms of water use compared with smaller ones (Nabeshima and Hiura, 2004; Lloyd et al., 2010; Patiño et al., 2011). Less significant ecological dimensions identified by the analysis of our dataset and details of how all physiological and structural traits studied here vary in a sample bivariate manner are illustrated in Fyllas et al. (2009) and Patiño et al. (2011).

In both the "spatial" and "non-spatial" *RLQ* analyses the first two leaf dimensions of the PCA were aggregated onto the first *RLQ* axis; this then summarising most of the variation in the dataset (Table SI2.3 and 3.3). This RLQ_1 axis aggregated the leaf development and leaf economics dimension, discussed above, aligning species along a basin wide fertility gradient (Quesada et al., 2010) running from infertile soils dominated by species of a high M_A and intrinsically low nutrient concentrations to fertile soils where the species present tend to have low M_A and higher intrinsic nutrient concentrations. Thus, inherently higher nutrient leaf concentrations (accompanied with lower M_A and [C]) are characteristic of species which are more abundant on the more fertile soils characterised by a high pH, high plant phosphorus availability and high exchangeable cations concentrations. This is consistent with the results of Fyllas et al. (2009) who found that species located on more fertile soils tend to have inherently higher nutrient concentrations and a lower M_A than those generally found on less fertile soils, as indicated by a shift along the same axes of several simple bivariate relationships.

In both *RLQ* ordinations the second axis was more related to traits associated with variations in tree hydraulic properties, also being associated with variations in precipitation and/or the soil water holding capacity. Although accounting for only a small amount of the total variance the way in which functional traits and environmental variables are related along this axis points to an important water availability dimension involving both stem and leaf traits. In the *RLQ*-n case, moister sites were also associated with finer textured soils which in general also support higher water availability and taller trees. When spatial autocorrelation between the 53 plots was removed (i.e. the *RLQ*-s case), RLQ_2 was mainly related to soil texture and to a smaller extent to dry season

precipitation. Although a slightly different result, this again highlights water availability dimension linked with a higher species dependent maximum height, but with a lower xylem density. Our analysis does not, however, include many plots in the forest/savanna transition zone at the drier southern Amazon forest periphery, many of which are dominated by seasonally deciduous species not found in the contiguous forest region (Killeen et al., 2005) and whose structural and physiological characteristics await quantification.

Even so, as most of the variation in our analysis was found along a soil fertility axis, our optimum Φ identification combining both *RLQ* analyses should provide robust plant functional definitions applicable to much of the Amazon Basin with the four Φ identified showing contrasting patterns in terms of resource allocation and life history strategy (Table 2). In general Φ_1 encompasses relatively small statured tree species with a potential for high photosynthetic rates (Reich et al., 1992), mainly being found on fertile soils and investing their resources towards rapid growth rates to provide the best position in a developing canopy or gap. This rapid investment return strategy is also suggested by the early peak in maximum growth rates observed for this group (Fig. 4). Φ_2 illustrates another relatively small-statured group, but here with mid-range M_A, low leaf [N] and [P], it also being the group with the highest ρ_X (Table 2), with member species apparently configured for medium rate gas exchange but with a strong selective pressure to protect their leaves by investing greater (high [C]) amounts of carbon based components (Bryant et al., 1983; Fine et al., 2006). We therefore interpret Φ_2 to represent a grouping of species with a relatively conservative life history strategy, this also being reflected in the growth rate curve (Fig. 4). Specifically, Φ_2 have a relatively constant potential growth rate that only outperforms Φ_1 after a diameter of approximately 40 cm. The Φ_3 illustrate the least conservative resource allocation strategy in terms of both foliage and architecture, having the lowest leaf [C] and lowest ρ_X. We thus interpret this group as containing species that gamble on cheap foliage development, using minerals of cheap construction cost (Poorter and de Jong, 1999) and avoiding investment into expensive carbon rich components for protecting their photosynthetic tissue (Coley et al., 1985). It differs from Φ_1 most obviously in terms of being characterised by a greater H_{max}. The acquisition of resources by this pioneer group should be allocated on the basis of a rapid foliar and stem expansion, this providing a competitive advantage in terms of vertical positioning for light resources at least in the short term. This strategy seems to agree with the highest potential diameter growth rates achieved by Φ_3 compared to the other three groups. Finally, Φ_4 with the highest genetically constrained M_A in addition to low leaf [N] and [P], might be expected to achieve the lowest gas exchange rates (Poorter and de Jong, 1999). This long term resource turnover strategy clearly yields a maximum growth at relatively bigger size classes (Fig. 4).

Although not specifically taken into account in this analysis a set of additional characters should co-vary with our plant functional classification. For example, leaf longevity has been shown to be positively related with M_A in a number of studies (Reich et al., 1992; Santiago and Wright, 2007; Shiodera et al., 2008). The extent to which other plant dimensions such as seed size, leaf area and leaf area; sapwood area ratio integrate with the traits used in our classification is considered in Patiño et al. (2011).

Comparison with other classification schemes

Functional classifications of tropical tree species have traditionally used two plant dimensions, with growth potential and adult size being the assumed main axes of ecological specialization (Davies et al., 1998; Turner, 2001; Nascimento et al., 2005).
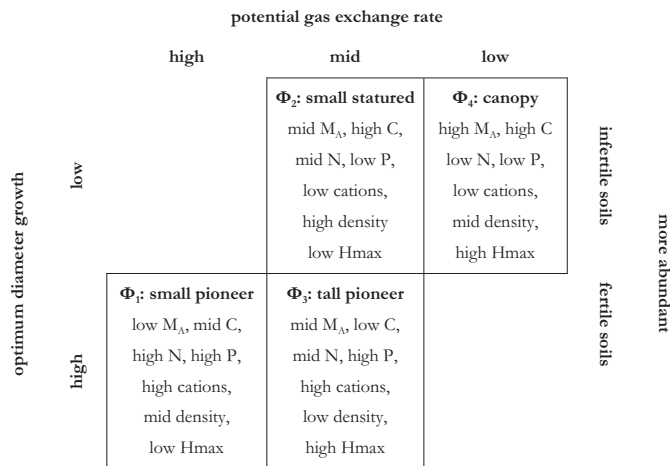
potential gas exchange rate

	high	mid	low	
low		Φ_2: small statured mid M_A, high C, mid N, low P, low cations, high density low Hmax	Φ_4: canopy high M_A, high C low N, low P, low cations, mid density, high Hmax	infertile soils
high	Φ_1: small pioneer low M_A, mid C, high N, high P, high cations, mid density, low Hmax	Φ_3: tall pioneer mid M_A, low C, mid N, high P, high cations, low density, high Hmax		fertile soils

(left axis: optimum diameter growth; right axis: more abundant)

Fig. 6. Schematic representation of the derived Φ, by extending the functional classification of Turner (2001).

For example, in his concluding synthesis chapter, Turner (2001) argues on the basis of accumulated evidence for there being four discrete groups of tropical tree species; *viz.* small pioneers, large pioneers, understorey species and canopy species. In this scheme small and large pioneers are considered to exhibit fast growth rates while understorey and canopy species have lower growth potentials Additionally the four groups are identified on the basis of their adult size with small pioneers and understorey species of a lesser stature and also with a shorter life cycle (see also Poorter et al., 2006).

Our four Φ can be considered partially coincident with Turner's classification (Fig. 6). Here Φ_2 equates with small statured (understory) species, Φ_3 with large pioneers and Φ_4 with Turner's canopy species. Less clear is Φ_1, though they may equate in part with Turner's small pioneer species. It should be noted, however, that Φ_1 may not be a solid group of pioneer species. But rather a guild of small statured trees usually found on high fertility soils with high initial potential growth rates but with a limited ability to maintain these growth rates (Fig. 4). This group, which bears some similarities to the "short and short lived" pioneer group of Ackerly (1996) is relatively rare in low-fertility forests of Amazonia which suggests they may be at a distinct growth or survival disadvantage when occurring on such soils. Considering their physiological and structural properties (Table 2) along with their mean growth rate trajectories (Fig. 4), this group might be anticipated to perform best in more dynamic forests where there are ample opportunities for gap colonisation and rapid growth to and beyond reproductive maturity. After which they would be prone to being shaded out by longer lived and eventually taller competitors. Occasionally members of this group are found in appreciable amounts on poorer soils, but when so, these are the most infertile stands with "white sand" Φ_1 species such as members of the genus *Eperua* sometimes present in large numbers in these low stature slow growing forests. Perhaps smaller trees are at an advantage where soil resources are severely or there are some other characteristics of these species that puts them at a relative advantage in such situations: For example an ability to obtain nitrogen through either nodulation or non-nodulating bacterial interactions (Villadas et al., 2007) or the ability to produce heavy and toxic seeds on these infertile soils (ter Steege et al., 2010).

Relatively high assimilation rates might also reasonably be anticipated for the large pioneer group, Φ_3. This functional group seems to follow the least conservative strategy, this being reflected in both the development of unprotected leaves (lowest [C]) and risk of xylem cavitation (lowest ρ_X). The latter, along with the characteristic tall H_{max} imposing additional hydraulic constraints might also be the reason for relatively high ø observed (Lloyd et al., 2010). Despite this apparent tradeoff, the main advantage for Φ_3 species may be that they can rapidly achieve a large adult stature with associated high rates of insolation interception at a young age combined with a high photosynthetic potential enabling them to sustain their growth rates at high D (Fig. 4). The smaller statured Φ_2 species should exhibit mid rates of carbon assimilation, which is then conservatively invested in well protected foliage (high [C]) and dense wood (high ρ_X). On the other hand the potentially taller Φ_4 canopy species are configured for slower gas exchange rates that are allocated in a long-term payback strategy. This notion is well supported by their ability to maintain sustained growth rates over their entire life cycle (Fig. 4). Thus, the two-way classification scheme of Turner (2001) is well supported by our analysis. And our four identified sets of leaf and structural characters could be readily incorporated into it, providing a physiological characterisation of the distinct life-history strategies identified (Fig. 6).

Poorter et al. (2006) also enhanced Turner's two-way classification, by considering a set of architectural and shade tolerance characteristics with their "short-lived pioneers", "long-lived pioneers", "shade-tolerants" and "partial shade-tolerants", descriptions partially coinciding with our Φ_1, Φ_3, Φ_3 and Φ_4, respectively. In agreement with their 54 Bolivian species dataset, short-lived pioneers and shade tolerants illustrate lower adult stature compared to long-lived pioneers and canopy species (Table 2). However, their shade tolerant group had a much lower H_{max} compared to those derived here (Φ_2). This may be a consequence of the design of our study, where only individuals with leaves exposed to sunlight for at least some of the day were sampled Thus our dataset could contain a bias towards larger individuals. Alternatively, this could be due to the contrasts in the geographic range between the two datasets with the Bolivian study sampling only from one site on the southern fringe of the Amazon basin. Leaf life-spans were found to be higher for Poorter et al. (2006) shade tolerant groups compared with both pioneer types, this also being in accordance with our descending mean M_A values from Φ_4 to Φ_1. The higher M_A displayed by our canopy functional group (Φ_4) is also in accordance with positive height effects on M_A both within and between Amazon forest trees (Lloyd et al., 2010).

Although we chose to undertake our main analysis with a grouping of four Φ, the Calinski grouping of six Φ also provided a reasonable functional group derivation for the *RLQ*-s case (Fig. 2). The Φ derived in this case "divide" the canopy to three levels (low, mid and tall statured groups), being located at the same time along a soil texture axis (SI6). This added vertical dimension produces a Φ partitioning with strong similarities to the "guild" type approach of individual based models as applied to tropical forests. For example, for a simulation of lowland Malaysian dipterocarp forest dynamics, Huth and Ditzer (2000) classified all species into five functional groups based solely on potential height, then assigning shade-tolerance characteristics to each H_{max} grouping. Taking data from French Guiana, Chave (1999) delineates four H_{max} categories and within each of these height groupings there are three shade tolerance groups. For an East Kalimantan forest Phillips et al. (2002) used H_{max} and phylogenetic information to define their ten groups. In general, both the number of Φ and the criteria used to define them will depend on the research objectives for which the grouping is used. For example, stand-level growth models require a high number of Φ in order to represent important ecological processes like forest succession or responses to partial logging (Chave, 1999; Huth and Ditzer, 2000; Phillips et al., 2003), with species-dependent characteristics such as seed size and dispersal mode for realistic simulations. On the other hand, continental-to-global scale

simulations require an understanding of the way that plant functional strategies are driven by environmental gradients, even though it is well acknowledged that processes such as dispersal must eventually be included (Thuiller et al., 2008) and with some demographic processes now being included in new generation DGVMs (Fisher et al., 2010).

Our four Φ vary substantially in the nature of many trait interrelationships (Fig. 3) although exactly how these differences will pan out as being contributing factors for larger scale differences of forest dynamism and carbon fluxes across Amazonia remains to be determined. It is, however, clear that although there may be some case for arguing the existence of a single plant or leaf "economic spectrum" (Wright et al., 2004) even when examined within the same biome/regional grouping, there are significant differences in the way that traits covary and that these are not independent of the environment in which a particular species is found. Fig. 3 also illustrates the importance of cations in delineating the four Φ, especially in terms of the different relationships with M_A, these differences most likely reflecting foliar construction costs/longevity tradeoffs, with the somewhat ambiguous nature of the cation *vs.* [C] relationships probably attributable to some highly reduced compounds (e.g. lipids) being actively involved in metabolism, but with other carbon-rich compounds such as lignin having a much more structural role (Patiño et al., 2011).

Stand level properties regulated by species functional composition?

An analysis of stand level properties in relation to the relative Φ abundance (Fig. 5) showed above-ground growth rates, to be positively correlated with the proportion of the total stem population consisting of Φ_3 species and for ΔB to decline as the Φ_4 species increase in abundance. This suggests that at least some part of the higher forest productivity on the more fertile soils of Amazonia may be attributed to a greater proportion of species with functional attributes associated with higher growth rates being present (and *vice versa*). Nevertheless, such relationships could also be attributable to different Φ tending to associate with different soil types with variations in soil fertility and climate actually being the prime drivers of variations in ΔB (Quesada et al., 2009).

Correlations with the relative abundance of the Φ_1 and Φ_4 were also found for stand level turnover rates. Although this could be due to well-known growth/mortality tradeoffs (Chao et al., 2008; Baker et al., 2009), the relationship between Φ abundance and φ could likewise be indirect. For example, Φ_1 abundances may be favored where disturbance rates are high due to adverse soil physical conditions and the slower growing/low turnover Φ_4 favoured on less fertile but characteristically deeper soils (Quesada et al., 2009; Chao et al., 2009). Indeed, this is something that would be expected in terms of the growth strategy of Φ_1 as evidenced by the early peak in maximum growth rates (Fig. 4 and Table 2) and the longer-term increase in G over time for Φ_4.

Limitations of our approach

Our general procedure and Φ definitions are based on the assumption that different tree functional configurations are associated with different life strategies which then translate into different growth and mortality rates and that, under the normal competitive conditions of natural environments, these are also reflected in differential species distributions. We have also assumed that the foliar and structural traits we have measured are those critical in explaining why some species are more abundant in some environments than others. Thus, if neutral rather than niche dependent processes were to dominate, then our entire analysis would

be invalid. However neutral processes are probably not dominant at the Basin-wide scale investigated here as our permutation test indicated a very significant link between environmental variables and the species dependent foliar traits; this remaining significant even after the removal of spatial autocorrelation effects ($p < 0.001$; SI1).

But in any such analysis, the traits chosen to partition the species must necessarily be subjective and finite in number. Thus, some traits that could be important in accounting for differences in the distributions of different genera (for example maximum rooting depth or seed size) may have been overlooked in our classification. Similarly, the choice of environmental and/or edaphic drivers will affect how the various species segregate into the various Φ.

One approach to minimise this problem may be the tailoring of the Φ classification criteria with those of the model drivers to which the classification is to be applied. For example, both our *RLQ*-s and *RLQ*-n analyses suggest an important role of soil fertility in accounting for Amazon forest tree distributions. Thus, if the Φ we have derived here were to be applied to a model not explicitly including variations in soil fertility as well as a means by which soil fertility can modulate plant function then there would probably be little difference in model predictions as opposed to the usual single tropical forest Φ.

One second issue is in how to determine the number of Φ to be employed; the question as to "when enough is enough" being a common to many classification and ordination studies (Legendre and Legendre, 1998; Dray, 2008; Guidi et al., 2009). Again, we suggest this be guided by the requirements of the model in which the various Φ are to be applied, the final number of Φ being guided (but not forced) by the use of statistical metrics such as the Calinski–Harabasz pseudo-F index as done here (Fig. 2); as well as the investigator's already known requirements. For example as already discussed, the number of tropical forest Φ likely to be required for an individually-based forest-stand growth simulator operating over a small area (1–100 ha) is likely to be considerably greater than the number of tropical forest Φ required for a realistic simulation of global scale biome shifts in response to climate change.

Conclusions

This study has developed and tested a numerical method to identify Plant Functional Types for Amazonian tropical forest. The numerically derived Φ agree in broad terms with several previous classifications and can easily be implemented in both small and large scale vegetation dynamics models providing for each set of Φ-specific physiological and structural parameters frequently required for such simulations. These are also of interest for biochemical models of larger scale photosynthetic carbon fluxes (Mercado et al., 2009, 2011) with associated measures of potential growth rate and wood density of interest in smaller scale models like forest gap dynamics simulators. We expect that the Φ defined in this study could provide a first basis for better simulations of large-scale tropical forest dynamics, thus extending litter decomposition and soil carbon dynamics which should also vary with the functional composition of tropical forest stands (Santiago, 2007; Coq et al., 2010).

Each of the Φ is not necessarily defined only by its mean trait characteristics. But rather each group can be considered a population of similar but different species with the underlying statistical distributions of traits (including covariances) known and quantifiable. This means they are potentially malleable into forms for the more sophisticated models of the future where trait plasticity

and/or defined continua of trait characteristics within a given Φ will likely be required.

The general procedure we have developed should be generally applicable to any ecological system of interest as long as species abundances and the traits of interest have been sampled across a sufficiently wide range of environments and with the parameters employed in the ordination also of direct relevance to any model to which the Φ are to be applied.

Acknowledgments

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.ppees.2011.11.001.

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