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Basin-wide variations in foliar properties of Amazonian forest: phylogeny, soils and climate

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Abstract

We analysed 1040 individual trees, positioned in sixty three plots across the Amazon Basin for leaf mass per area (M_A), leaf carbon isotope composition (δ^{13}C) and leaf level concentrations of C, N, P, Ca, Mg, K and Al. All trees were identified to the species with the dataset containing 58 families, 236 genera and 508 species, distributed across a wide range of soil types and precipitation regimes. Some foliar characters such as M_A, [C], [N] and [Mg] emerge as highly constrained by the taxonomic affiliation of tree species, but with others such as [P], [K], [Ca] and δ^{13}C also strongly influenced by site growing conditions. By removing the environmental contribution to trait variation, we find that intrinsic values of most trait pairs coordinate, although different species (characterised by different trait suites) are found at discrete locations along a common axis of coordination. Species that tend to occupy higher fertility soils are characterised by a lower M_A and have a higher intrinsic [N], [P], [K], [Mg] and δ^{13}C than their lower fertility counterparts. Despite this consistency, different scaling patterns were observed between low and high fertility sites. Inter-relationships are thus substantially modified by growth environment. Analysing the environmental component of trait variation, we found soil fertility to be the most important predictor, influencing all leaf nutrient concentrations and δ^{13}C composition and reducing M_A. Mean annual temperature was negatively associated with leaf level [N], [P] and [K] concentrations. Total annual precipitation positively influences M_A, [C] and δ^{13}C, but with a negative impact on [Mg]. These results provide a first basis for understanding the relationship between the physiological functioning and distribution of tree species across Amazonia.

1 Introduction

Plants are the central link in the soil-plant-atmosphere continuum, utilising and cycling a range of atmospherically (C, H, O, and N) or geologically (P, Ca, K) derived elements (Jobbagy and Jackson, 2004). Plant growth is usually considered to be either nitrogen-or phosphorus-limited (Aerts and Chapin, 2000), but with less abundant nutrients being also important for discrete ecosystem processes (Hungate et al., 2004; Kaspari et al., 2008). Foliar ratios of leaf level nitrogen, phosphorous, calcium, and potassium concentrations can indicate the nature of nutrient limitation (Koerselman and Meuleman, 1996; Jobbagy and Jackson, 2004). It has been argued, for example, that leaf N:P>12.5 indicate a limitation on ecosystem processes by P availability (Tessier and Raynal, 2003). But different hypotheses have been proposed regarding the main factors controlling the metabolic tissue concentration of the main nutrients related to plant growth (Reich and Oleksyn, 2004), especially N and P (Niklas, 2005). These hypotheses summarize a physiological, temperature or geochemical driven background of N & P cycling and have gained particular interest recently, as foliar C:N:P stoichiometry may be an important factor controlling the growth rate of a wide range of plants (Elser et al., 2000; Kerkhoff et al., 2005; Niklas, 2006). Following on from the now widely accepted suggestion of Vitousek (1984) that tropical forests may generally be P rather than N limited, Reich and Oleksyn (2004) showed that tropical trees typically have higher N:P ratios than are observed at higher latitudes. Nevertheless, Townsend et al. (2007) also showed that for trees growing on the more fertile tropical soils, foliar N:P ratios are generally similar to those observed in the temperate and boreal zones.

The Amazon Basin is highly diverse in terms of climate (Sombroek, 2001; Malhi and Wright, 2004), soil physical and chemical properties (Sombroek, 2000; Quesada et al., 2009a), and species composition (ter Steege et al., 2006). Such complexity hinders any attempt to accurately estimate significant biogeochemical fluxes (Townsend, 2008) or to predict the Amazon carbon balance (Cox et al., 2000). It is also now clear that a large scale gradient in Amazon forest tree dynamics exists, with forests growing on the generally more fertile soils of the western Amazon having lower wood densities (Baker et al., 2004), higher above-ground growth rates (Malhi et al., 2004) and with higher rates of tree turnover (Phillips et al., 2004). But how do key foliar properties vary across evolutionary grouping of trees and relate to these different environmental gradients?

Recent developments in plant functional ecology have highlighted suites of plant traits such as per area leaf mass (M_A) and leaf nutrient concentrations that can serve as predictors of individual plant growth and performance (Reich et al., 1991; Garnier et al., 2004; Poorter and Bongers, 2006). Although a wide variability of these characters has been reported, a global spectrum of coordination has also been proposed (Reich et al., 1997; Wright et al., 2004). One of the major axes of ecological variation is thought to be captured by both leaf longevity and M_A (or its inverse specific leaf area, SLA), with these two traits well correlated at both a global and a tropical scale (Reich et al., 1991, 1997). Species with low M_A tend to have short-lived leaves with high [N] and [P] (dry weight basis) and are usually found at the fast payback end of the "economic spectrum" (Wright et al., 2004). This combination of traits is usually found at species with fast growth rates (Poorter and Bongers, 2006). At the other end of the continuum, species characterised by high M_A, also generally have low leaf [N] and [P] and lower growth rates, thus being considered to represent a more conservative strategy of resource use and turnover (Reich et al., 2003). Wright et al. (2005a) examined the role of potassium within the "leaf economic spectrum", concluding that although associated with M_A, N and P, [K] might be more closely associated with other cations such as calcium and magnesium.

All major cations are considered in this study, including [Al], along with an additional major potential component of the leaf physiological spectrum, viz. the extent of discrimination against the heavier ^{13}C isotope during photosynthetic CO_2 assimilation, Δ. This is indicated by a leaf's carbon isotopic composition, δ^{13}C, and can provide a measure of a plant's water use efficiency, WUE (Farquhar et al., 1989). It has, for example, been proposed that leaves with a high M_A should also have a lower WUE (Lamont et al., 2002).

Here, as well as considering δ^{13}C we also examine the integration into the plant physiological spectrum of leaf carbon content. Although often considered to be relatively invariant, differences in M_A should nevertheless be accompanied by differences in leaf carbon composition. For example, the greater proportion of dry matter invested in cell walls as expected in high M_A plants should also be associated with increased levels of carbon rich structural carbohydrate compounds such as lignin and cellulose (Niinemets, 1997). Although not reporting on the relationships between individual compounds or elements and M_A, when investigating leaf chemical variations for 45 different French Guiana rain forest species, Hättenschwiler et al. (2008) reported considerable variation in foliar carbon contents (from 0.45 to 0.52 of leaf dry weight) with large interspecific variations in different carbon constituent compounds also noted.

Along with the coordination of leaf functional characters, environmental factors, such as climate and/or soil may affect physiological linkages. Modifications of pair-wise relations (Wright et al., 2001) or systematic trends of a functional trait across environmental gradients should indicate trait plasticity and/or adaptive potential (Sultan, 2000). These may have important consequences for individual and community level processes. Evaluating this plasticity is thus a key issue in developing theoretical and computational schemes of the potential vegetation response to changing environmental conditions.

At a global level, Wright et al. (2005b) have shown how some photosynthetic tissue properties and their relationships also vary across climate, but for the selected traits (M_A, leaf longevity, foliar [N] and photosynthetic capacity) climate accounted for only 0.18 of the total variation. Nevertheless, such shifts were considered to be of significant importance for the global leaf economic spectrum. At regional scales and along rainfall and soil phosphorus gradients, significant strategic shifts in leaf properties and functioning have also been identified, with species found at drier sites exhibiting a lower photosynthetic capacity for a given foliar [N] and [P] and higher [N] and [P] concentrations at a given M_A (Fonseca et al., 2000; Wright et al., 2001). Niinemets and Kull (2003) suggested that the strength of the correlation between foliar nutrient concentrations and M_A were controlled by soil nutrient availability, with the strongest associations between M_A and the most limiting nutrient. Similar results were reported for Amazonian species, with weak M_A-[N] relationship in what were considered to be P limited stands (Reich and Walters, 1994). At a pan-tropical scale Townsend et al. (2007) found that leaf N:P ratios vary with soil order, and suggested that species diversity may be an important factor controlling this ratio.

This plasticity of traits and the potential for tree species population to exhibit different trait combinations according to changing soil and climate conditions may be very important for understanding Amazon forest species distributions and how they may respond to global change. Here we analyse nine key leaf traits of 1040 individuals positioned in sixty three plots distributed across the Amazon Basin. The traits reported are M_A, δ^{13}C, and leaf level concentrations of C, N, P, Ca, Mg, K and Al with 508 species sampled across a wide range of Amazon soil types and precipitation regimes.

Different tropical tree species may have markedly different foliar nutrient concentrations (Drechsel and Zech, 1991; Townsend et al., 2007) and, at least at the landscape level, different species tend to be associated with soils of different fertility (Phillips et al., 2003; John et al., 2007). Given that even for the same species, natural variations in soil fertility may also serve to modify foliar seedling nutrient concentrations along with other leaf physiological characteristics such as M_A (Veenendaal et al., 1996; Kanowski, 2001), we were also interested to ascertain whether differences in foliar nutrient concentrations sampled across Amazonia represented directly different levels of soil fertility and/or intrinsic differences in physiological leaf traits of the different species growing in different plots. Likewise, although there may be large scale changes in physiological traits with rainfall or temperature when a range of species are considered (Santiago et al., 2004; Wright et al., 2005b) it is important to know if changes in traits observed at the community level arise solely as a consequence of changes in species composition or whether factors such as dry-season length directly influences physiological properties and their inter-relationships.

The aims of this paper are first to partition variation in foliar properties into genetic and environmental components. Second to identify the extent to which traits are conservative across evolutionary grouping of tree species, and how these traits differ across taxonomic affinities. Third to explore if there is a differentiation in the suite of traits found under different environmental conditions. Finally, we attempt to link environmental components of trait variation with key soil and climate variables.

2 Methods

2.1 Study sites and leaf minerals, xylem density and environmental data

For 63 of the RAINFOR network plots described in detail in Patiño et al. (2009), we utilised foliar nutrient and M_A data from upper canopy sun-exposed leaves from trees reliably identified at the species level, with data collected and analysed as described in detail in Lloyd et al. (2009b). The elements of interest were leaf level concentrations of C, N, P, Ca, Mg, K, all expressed here in $\mathrm{mg\,g^{-1}}$, with leaf mass per unit area, M_A, expressed in units of $\mathrm{g\,m^{-2}}$ and δ^{13}C as per mil (‰). As in Lloyd et al. (2009b) [C] as shown and analysed here has been adjusted for variations in mineral content by subtracting the measured concentrations of the major cations viz. [Ca]+[Mg]+[K]+[Na], allowing variations in [C] to be better interpreted in terms of variations in foliar carbohydrate chemistry, as opposed to variation in [C] simply reflecting differences in mineral concentrations.

Some sample plots included in Patiño et al. (2009) are not included in this analysis. These include ALF-01, MAN-03, SIN-01, SUC-04, ZAR-01,02,03,04). Data from some plots have been aggregated (ex. TAP-01 & TAP-02 & TAP-03→TAP-123, CAX-03 & CAX-03.1→CAX-03) where they were located in close proximity and having all but identical topography, soils and climatic conditions (see supplementary material, Table A1: http://www.biogeosciences-discuss.net/6/3707/2009/bgd-6-3707-2009-supplement.zip).

For each plot, soil chemical and physical data for 0–0.3 m depth, collected and analysed as described in Quesada et al. (2009b) were assembled to allow an initial classification of plots according to soil fertility groups and thus potential differentiation of foliar traits and their relationships between low and high fertility sites Our differentiation into low and high fertility sites, is based on the measured "total reserve bases" Σ_{RB}, from 0.0 to 0.3 m depth as described in Quesada et al. (2009b). As discussed there, Σ_{RB} provides a quantitative estimate of the extent of soil weathering with Σ_{RB}~80 $\mathrm{mmol\,kg^{-1}}$ a natural "breakpoint". Using the World Reference Base for Soil Resources Classification

System (IUSS Working Group WRB, 2006), Σ_{RB}<80 mmol kg^{-1} encompasses nutrient poor soils such as arenosols, podzols, ferrasols along with any dystrophic acrisols, alisols, cambisols gleysols and plinthisols. On the other hand, Σ_{RB}>80 mmol kg^{-1} defines the usually fertile cambisols, along with the more fertile alisols, nitisols, fluvisols lixisols and plinthisols.

Climate, temperature and precipitation datasets were obtained from the free access web site at www.worldclim.org. This set of global climate layers, "WorldClim", includes annual time series with mean monthly data for precipitation, and mean, minimum and maximum temperatures obtained from over 4000 weather stations between 1950 and 2000 (Hijmans et al., 2005). Solar radiation data is from New et al. (2002).

2.2 Statistical analysis

The analysis here focuses on genetic and plot-environmental component of trait variation, as estimated from a multilevel model and discussed below.

Preliminary tests included: analysis of normality (Shapiro-Wilk), and homogeneity of variances (Fligner-Killeen) for each foliar property. This showed [C], [N], [P], [Ca], [Mg] [K] and $M_A$to all not be normally distributed and these parameters were thus $\log_{10}$-transformed prior to analyses. Foliar δ^{13}C was approximately normally distributed, but we $\log_{10}$-transformed the absolute values in order to consistently analyse the full dataset, taking the negative values of the transform and then returning the values to the original sign. One way analysis of variance (ANOVA) was used to explore differences between fertility groups, as well as for differences between families, genera within a family and species within a genus. All analyses were performed with the R statistical platform (R Development Core Team, 2008).

A multilevel model (Snijders and Bosker, 1999; Gelman and Hill, 2006; McMahon and Diez, 2007) was first fitted for each foliar nutrient, M_A and δ^{13}C according to

$$T = \mu + p + f/g/s + \varepsilon, \quad (1)$$

where μ is the overall mean value of each trait (T), p is the plot effect i.e. the effect of the location at which each individual was found (soils and climate), $f/g/s$ represents the genetic structure of the data, i.e. that each individual belongs to a species (s), nested in a genus (g), nested in a family (f), and ε is the error term. All parameters were estimated by the Residual Maximum Likelihood (REML) method with the *lme4* library (Bates, 2008). The multilevel model Eq. (1), in a similar way to taxonomically based nested ANOVAs, can be used to partition the variance from species up to the family level. It is particularly useful for not fully resolved plant supertrees (Kerkhoff et al., 2006; Watanabe et al., 2007). The estimated components of variance can be distinguished into both a {"plot" – "environmental"} and a "genetic" term. Recognising that our study represents an incomplete and, to a large extent, under-represented sampling of the edaphic and climatic variability of Amazonia, as well as only a selection of the many trees species living there, all terms in the multilevel model were treated as random (as opposed to fixed) effects (McCulloch and Searle, 2001). Random effects were quantified through the best linear unbiased predictor (BLUP) method, providing shrunken estimates of the differences between terms and the overall means (Galwey, 2006). The random genetic and the plot effects were then used for further analysis as described below.

In what follows we consider the derived environmental term to represent the combined influences of climate, soil and location. The genetic term (estimated here as the sum of the family, genus and species effects) represents the phylogenetic structure of the dataset. We note that this taxonomically based multilevel model does not use calculated species means across different sites as is sometimes the case (e.g. Wright et al., 2004). But rather, it incorporates the full range of available information, taking into account the observed intra-specific variation in foliage characteristics and allowing for all traits to vary systematically across the different plots sampled, as well as allowing for intra-species variability within the one plot.

Bivariate relationships of foliar properties were first assessed with Pearson's correlation coefficient (r), and with Standardised Major Axis (SMA) line fits (Legendre and Legendre, 1998; Warton et al., 2006) subsequently applied where r was significantly different from zero. SMA regression lines represent the first axis of a principal component analysis (of a correlation matrix) and are often used in plant allometry studies. It is common for variables to be logarithmically transformed with the regression $\log(y)=\log(\beta)+\alpha\log(x)$, this expressing a power law of the form $y=\beta x^{\alpha}$. The slope or scaling exponent α, quantifies the rate of increase of y in relation to x, indicating an isometric ($\alpha\approx1$) or allometric ($\alpha\neq1$) scale. The intercept or elevation β of the regression line expresses the magnitude of y per unit of x (Kerkhoff and Enquist, 2006). SMA regressions were used for both the genetic ($f/g/s$) and the environmental-plot (p) component for high and low fertility plots. When the slopes were not statistically different we tested for differences in elevation and shift across using the R *smatr* library (Warton et al., 2006).

Multiple linear regressions (OLS) were also used to explore the relationship between the plot effect estimates and soil and climate variables. A matrix of soil variables was assembled using data from Quesada et al. (2009b), i.e. total soil C and N concentration, exchangeable Ca, Mg, K, Na and Al, total extractable phosphorus, Σ_{RB}, effective cation exchange capacity, base saturation and the sand and clay fraction. To reduce dimensions in the soil table and avoid multicollinearity we applied principal components analysis (PCA), using the R *ade4* library (Chessel et al., 2004). PCA was applied to the correlation table of the soil matrix to derive the main axes of variation. Multiple regressions for each trait's "plot effect" were then computed on the first three principal components (Legendre and Legendre, 1998) with four climate variables also included; annual mean temperature, total annual precipitation, precipitation during the three driest months of the year and mean annual radiation. Simplification of the full model was explored following a manual stepwise elimination of the less significant terms, based on Akaike's Information Criterion (AIC) to derive the minimum adequate model (Crawley, 2007).

To deal with any spatial autocorrelation of the dataset, we explored the results of the multiple linear regressions through the inspection of correlograms and estimation of the global Moran's I (Legendre and Legendre, 1998). In our case the presence of spatial autocorrelation could simply reflect a patterned functioning of the plot level effects, i.e. nearby plots contributing similarly to the variation observed. Such a spatially structured environmental effect could arise as a consequence of basin-wide gradients in soil age and fertility (Quesada et al., 2009a) and/or precipitation (Malhi and Wright, 2004). Alternatively, spatially structured patterns could arise because of gradients in species or functional group composition (ter Steege et al., 2006). Such compositional patterns, which may be related to historical events, may modulate any plot-level effects directly controlled by environmental factors. These two effects point at exogenous or endogenous forces respectively (Legendre and Legendre, 1993), either of which has the potential to give rise to a violation of the assumption of independently distributed errors. This leads to an overestimation of the relevant degrees of freedom as well as to an overestimation of the importance of the environmental variables included in any such analyses (Lennon, 2000). Interpretation of the macroecological patterns through statistical analyses where spatial autocorrelation is present is an issue of active debate (Lennon, 2000; Diniz-Filho et al., 2003), with recent simulations showing that the existence of autocorrelated residuals does not seriously affect parameter estimates (Hawkins et al., 2007).

To address the above issues, in addition to the non-spatially explicit linear models (OLS), we also fitted two simultaneous autoregressive models (SAR) including a spatial error term at a “fine scale” and at a “medium scale” (Lichstein et al., 2002; Kissling and Carl, 2008). Previous spatial analyses of ecological datasets have revealed that in some cases small neighbourhood distances (first-order) SAR models are able to remove the spatial autocorrelation signal (Jetz and Rahbek, 2002), while other studies suggest that larger neighbourhood (higher-order) SARs should be used (Tognelli and Kelt, 2004). The usual practice to select the neighbourhood size in SAR models is to identify, through the inspection of the OLS residuals, the maximum distance of a significant autocorrelation signal and use this distance as a neighbourhood size (Lichstein et al., 2002; Hawkins et al., 2007). Our data revealed discrete maximum distances of spatial signal for each plot effect (determined from the correlograms of the OLS residuals off each parameter of interest) and we thus used a variant neighbourhood size for the medium scale SARs and a common (50 km) scale for fine scale SARs. We checked the value of the autoregression coefficient (λ) in the SAR models; Specifically, if λ was found to be significantly different from zero after controlling for the environmental effect, then the autoregressive component (i.e. the neighborhood effect) was deemed important. Furthermore, by inspecting the SAR residual correlograms we identified their ability to remove spatial autocorrelation. At the same time we used a Monte Carlo (999) permutation test for the significance of Moran's I for the initial plot effect estimates and the residuals from the OLS and SAR models. In all cases coefficients for ten distance classes of equal widths (200 km) are reported – at this distance all classes have an approximately balanced (more than 100) number of pairs (Legendre and Legendre, 1998). For correlograms the local significance of Moran's I at the j-th class were corrected with a progressive Bonferroni procedure ($a^*=a/j$, with α the original significance level set at α=0.05), while the adjusted significance level for the global Moran's I was 0.005 (0.05/10 reflecting the ten distance classes used) for which more information is available in Legendre and Legendre (1998) and Lichstein et al. (2002). The above were implemented with the R libraries *ncf* (Bjornstad and Falck, 2001) and *spdep* (Bivand, 2006).

Our spatial analysis has not been designed to fully disentangle the scales where different environmental variables control the observed variation of the leaf properties studied. Rather, we have tried to filter the most important environmental predictors and to investigate if the trends identified by the OLS are biased. Our main aim was therefore to determine if the identified important environmental variables from OLS remained significant after accounting for spatial patterns in our models (Lichstein et al., 2002).

Finally as some plot effect versus environmental predictor relationships did not show a simple linear trend and/or normally distributed homoscedatic errors, we used Kendall's τ as a non-parametric measure of association. Though less common than Spearman's ρ, Kendall's τ has slightly better distributional properties and also has the advantage that it can be interpreted in term of probabilities of observing concordant and discordant pairs (Conover, 1980). Specifically, $\tau = \pi_c - \pi_d$, where π_c is the probability of concordant pairs and π_d is the probability of discordant. For example, if $\tau = 0.5$, then 0.75 of the ranked pairs are concordant and 0.25 are discordant. Kendall's τ also has the advantage that it can be generalised to a partial correlation coefficient (Legendre and Legendre, 1998, p. 202). As is discussed in Legendre and Legendre (1998) it is, however, difficult to assess the statistical significance of the partial τ and so here we assess likely significance levels of our calculated partial τ by numerical simulation as described in Maghsoodloo and Laszlo Pallos (1981).

Although not allowing spatial patterns to be taken implicitly into account, this non-parametric approach does allow the inter-relationships between environmental predictors to be explicitly included in the analysis of environmental factors influencing the studied plant physiological properties.

3 Results

3.1 Statistical distribution of measured traits

Trait distributions for the complete dataset divided into the low and high soil fertility groups are shown in Fig. 1, with overall mean values, range and variance of the dataset given in Fig. A1 and mean values for all plots found in Table A1. Figure 1 shows that although M_A did not differ significantly between the two soil fertility groups, significant differences occurred for nutrient and C concentrations and δ^{13}C. Higher [N], [P], [Ca], [Mg], [K] and δ^{13}C were observed for leaves of trees growing on the more fertile soils (statistical distribution shifted to the right), but higher C and [Al] observed for trees on infertile soils (statistical distribution shifted to the left). Mean leaf N:P ratio was 30.5 for the low soil fertility plots, this being significantly higher ($F_{1,789} = 404.5$, $p < 0.001$) than the 19.7 observed on high fertility soils. The natural variations in rain forest soil fertility that occur within the Amazon Basin thus exert large effects on plant nutrient and C concentrations and δ^{13}C, but not for M_A and [C]. Of note is that although [Mg] was still significantly higher for the more fertile soils, the effect of soil fertility on [Mg] was much less than for [Ca] and [K].

3.2 Partitioning of the variance

Through fitting the multilevel model of Eq. (1), a partitioning of the variance to genetic and plot level components was achieved with results presented in Fig. 2. This shows that, not only does the proportion of the variance attributable to the nested taxonomy (genetic) component differ for different traits, but also that the level of genetic variation, particularly at the species level contrasts greatly between traits. For example, for M_A the genetic component accounts for approximately 0.38 of the total variance (with half of this attributable to species effect) and with the variability associated with tree location, the "plot effect", being only 0.15 of the total variance. A little less than half the variance in the dataset is attributable to an error term. The "error term" represents the proportion of the variance in the dataset attributable to intra-species variability as well as measurement error.

In contrast to M_A, the principle source of variation in [P] was the "plot effect" (accounting for 0.47 of the total variance) with only 0.23 of the observed variance attributable to a genetic component and with the species specific component of the variation being less significant. The "plot effect" is similarly very high for [Ca] and [K] (0.42 and 0.47 of the total variance respectively), whilst the lowest plot contribution of 0.1 was observed for [Mg]. Along with M_A, partitioning of the variance to the genetic component was highest for [Mg] (0.48) and [C] (0.40). Also of note is the high proportion of the variance in [Al] attributable at the family level (0.32), consistent with independent phylogenetic analyses (Jansens et al., 2002).

For δ^{13}C, the attributed genetic variation was less than for any of the elements or M_A, but still with an appreciable "plot effect", suggesting that geographic variations in either soil or climate exert significant effects on the extent of photosynthetic $^{13}CO_2$

discrimination across Amazonia.

3.3 Family, genus and species level effects

In our dataset there were significant differences between families for all sampled traits (ANOVA results not shown) with Fig. 3 illustrating mean family effects and their standard error estimates from the multilevel model. This shows that some families like Vochysiaceae, Urticaceae, Sapotaceae, Myristicaceae, Lecythidaceae, Humiriaceae and Clusiaceae are characterised by higher than average M_A, while others like Salicaceae and Annonaceae have unusually low M_A. Although [N] and [P] also tend to be lower in families with high M_A such as Vochysiaceae, Sapotaceae, Humiriaceae and Clusiaceae, these concentrations were also lower for families like Proteaceae, Ochnaceae, Myrtaceae and Chrysobalanaceae which lack a clear M_A trend. Likewise, some families that do not display a markedly lower genetic M_A component (Rutaceae, Meliaceae, Fabaceae and Euphorbiaceae) also have relatively higher [N] and [P].

As an example of within family variation, Fabaceae genus level effects are shown for M_A, [P] and [N] in Fig. 4. For this family, the most abundant within the dataset (160 observations), there were significant genus effects for M_A ($F_{40,111}$=3.832, p<0.001), N ($F_{41,109}$=4.788, p<0.001) and P ($F_{41,108}$=4.095, p<0.001) but with M_A and [N] showing relatively less variability compared to [P]. Nevertheless, genera like *Amerimnon, Dalbergia*, *Inga* and *Tachigalia* all tended to differentiate in both $M_A$and [P] with *Inga* also being notable for it's unusually high [N].

We were also interested to see if there was a difference in the physiological traits examined between the nitrogen fixing and non-nitrogen fixing members of the Fabaceae. We therefore utilised a database summarising published records of the presence or absence of N_2 fixation in the Fabaceae (Patiño et al., 2008) taking a species as a N_2 fixer if the proportion of positive records was greater than 0.9 and as a non-fixer if the proportion of negative records was greater than 0.9. Species with intermediate (conflicting) records of their N_2-fixing status were not included in this analysis (Table 1). This showed that N_2-fixing Fabaceae have significantly higher [N] and [P] than their non-N_2-fixing relatives but with significantly lower [Ca] and no significant differences in M_A. In turn, the non-N_2 fixing Fabaceae have significantly higher [N] and [P] but lower [K] than for the other non-N_2 fixing trees sampled across the Amazon Basin.

For the other widely distributed families, genera within the Malvaceae differed in $M_{A,}$ [N] and [P], with the Euphorbiaceae and Urticaceae showing differences in M_A and [N] only; Moraceae and Myristicaceae in [N] and [P] only; and the Burseraceae and Lecythidaceae giving between-genera variability only for [P]. Moreover, there were no differences in these foliar traits across genera in some families; for example the Chrysobalanaceae and Sapotaceae (results not shown). Generally speaking the highest within family variation was also observed for the more widespread families with the genus level analysis pointing to M_A, [P] and [N] not necessarily always varying in concert with genotype as the sole course of variation. For example, genera within the Moraceae were statistically indistinguishable in terms of M_A, but showed large variations for [P] with *Olmedia* species tending to have significantly higher [P] and *Pseudolmedia* and *Sahaqunia* significantly lower [P] than the family mean estimate.

Within *Eschweilera*, the most extensively sampled genus in our dataset (n=60), significant species-to-species variation were identified in M_A ($F_{14,44}$=2.009, p=0.040), and [P] ($F_{14,43}$=2.591, p=0.008). Species within *Pouteria* (n=44) showed differences in M_A ($F_{18,23}$=2.728, p=0.012), [N] ($F_{18,23}$=4.157, p<0.001) and [P] ($F_{18,23}$=4.217, p<0.001), but within *Inga* (n=38) no species specific differences were identified for either M_A ($F_{21,15}$=1.051, p=0.470), [N] ($F_{19,15}$=1.876, p=0.110) or [P] ($F_{19,15}$=0.796, p=0.685). Other well represented genera such as *Licania* showed significant variation in M_A and [P] only, but other genera for [N] only (*Pourouma*, *Protium*), or in many cases, with no difference at all (e.g. *Pseudolmedia, Virola*).

To illustrate such species effects, we summarize the M_A and [P] estimates from the multilevel model for all *Pouteria* species sampled in Fig. 5. It should be noted that in our analysis all random effect estimates are shrunk towards the overall mean with this shrinkage increasing with decreasing genetic variance and increasing environmental variance (Galwey, 2006). Thus random effect estimates show a greater variability for

M_A and [N] compared with [P], which is realistic considering that only 0.01 of the total variance can be attributed to the species affiliation for [P], compared with the 0.19 for M_A and 0.14 for [N]. Most obvious here is the exceptionally high M_A for *P. gongripii* and *P. tricularis,* the latter also being accompanied by an unusually low [N], as well as very high [N] for *P. glomerata*. Thus within-genera variability is not restricted to specific foliar properties or even to combinations of them.

3.4 Bivariate relationships (raw data)

As is shown in the supplementary material (http://www.biogeosciences-discuss.net/6/3707/2009/bgd-6-3707-2009-supplement.zip), a preliminary analyses of the raw data foliar properties showed significant correlations between most of the examined trait pairs (Supplement Table A2), but with a separation into low and high fertility sites showing differences in elevation and/or shift in all cases (Supplement Table A3). The strongest of these associations are presented in the supplementary material (http://www.biogeosciences-discuss.net/6/3707/2009/bgd-6-3707-2009-supplement.zip), Fig. A2. Interestingly the [P] vs. [N] relationship and all bivariate relationships including [K], showed statistically significant differences in slope, between low and high fertility sites (apart from [K] vs. [N]). We therefore included effects of soil fertility in our analysis on the nature of the bivariate relationships for the genetic component of the overall variation observed.

3.5 Bivariate relationships (genetic component)

The genetic component of the multilevel model (i.e. the family+genus+species) random effects show numerous significant correlations for both low and high fertility soils with this data summarised in Table 2. As is also shown in Fig. 6a and b, using the convention $y \leftrightarrow x$ to denote bivariate relationships, a strong relationship was identified for $[N] \leftrightarrow M_A$ ($r = -0.398$ and -0.409 on low and high fertility soils, respectively) and $[P] \leftrightarrow M_A$ ($r = -0.376$ and -0.435). There was also a reasonably strong relationship between M_A and [K] (Fig. 6c) but this was considerably weaker for [Mg] for both soil types (Table 2, graph not shown). M_A showed a weak correlation with [Ca] for low fertility soils and was stronger associated with [C] only in species found at low soil fertility sites. The genetic components of [C]↔[N] and [C]↔[P] were also marginally significant on low fertility sites.

Very strong correlations were, however, observed between some of the individual nutrients, with [P]↔[N] (r=0.640 and 0.696 on low and high fertility soils respectively) being especially well associated (Fig. 6d). The relationships between [K] and [P] (r=0.392 and 0.504; Fig. 6e), [K] and [Ca] (r=0.459 and 0.453; Fig. 6f) and between [Mg] and [Ca] (r=0.662 and 0.660; Fig. 6g) are also of note, as is the observation that the relationships between [K] and [N] are substantially weaker than for [K]↔[P]. Though not shown in Fig. 6, of interest were the strong negative correlations between [C] and all three of [Ca], [K] and [Mg] as well as the generally strong correlations between the three base cation pairs and with [P].

A comparison of SMA slopes for all M_A↔[nutrient] relationships showed no difference between low and high fertility sites (Table 2). This was also true for between nutrient pairs such as [P]↔[N], [K]↔[P], [Ca]↔[K] and [Ca]↔[Mg]. This suggests that the intrinsic (genetically defined) way M_A is linked with leaf nutrient concentrations, as well as the way by which different nutrients are related to each other is to some degree common for species found across the Amazon and independent of the fertility of the soil where they grow.

As there was no effect of soil fertility on the SMA slopes, for each bivariate relationship exhibiting a common scaling exponent, further tests for difference in elevation and/or shift were then applied (Warton et al., 2006). Although in no case were significant differences in elevation (intercept) identified between SMA regression lines of low and high fertility oriented species, all of the M_A↔[nutrient] and [P]↔[N], [K]↔[P], [Ca]↔[K] pairs presented significant shifts along the M_A axis (Table 2). Thus species found on fertile soils are shifted towards the upper end of the M_A vs. [nutrient] scaling line, tending to have inherently lower M_A and inherently higher leaf nutrient concentrations (Fig. 6a–c). There are 33 species found at both low and high fertility sites, overlapping the two soil groups

For δ^{13}C there was a strong positive relationship with both [N] and [P] only and with soil fertility affecting the elevation of (rather than a shift in) the SMA regressions (Table 2, Fig. 6h and i). This suggests that although there is a general tendency for species with intrinsically higher [N] and [P] to also have an intrinsically lower photosynthetic discrimination against $^{13}CO_2$ Δ, the magnitude of this effect is offset because species on the more fertile soils also have a higher Δ than those typically found under less fertile conditions.

3.6 Bivariate relationships (plot-environmental component)

Very different results were obtained when the correlation and SMA tests were applied to the plot (environmental) component estimated from the taxonomically nested model. Here, to allow a direct comparison with the genetic effects discussed above, we give the equivalent relationships at the plot level in Table 3. But especially as no effects of fertility on the slope or elevation were observed when analysing the genetic component, we use a single line to aid interpretation of the associated graphs of Fig. 7 (the details of which can be found in Table A2). From Table 3, it can be seen that the relationship between M_A and nutrients was significant only for the [C]↔M_A, [N]↔M_A and [Mg]↔M_A pairs in both the low and high fertility plots (Fig. 7a–c). Interestingly although very strong when the source of variation was genetic (Fig. 6), there was no significant [P]↔M_A relationship for either low or high fertility sites (Fig. 7d). This suggests that the often observed relationship between M_A and [P] does not reflect some sort of fundamental physiological imperative. By contrast, slopes for [N]↔M_A were quite similar to that observed for the genetic component (Fig. 6a and Fig. 7b) and correlations between [N] and [P] were either not significant (low fertility sites) or substantially weaker than the respective genetic component (high fertility sites). The overall slope (across all fertility sites) for the [P]↔[N] relationship (Fig. 7e) was 2.69 as compared to 1.17 when genotype was the source of variation (Table A2). Clearly then, although M_A, [N] and [P] are closely linked in a consistent way when examined across different species, the relationships between M_A and [P] and between [N] and [P] can be substantially modified by environment.

Other strong relationships were also evident when examining the plot effects, in particular [K]↔[P] and [Ca]↔[Mg] (Fig. 7f–g). In the former case, the slope of the overall plot effect of 1.54 was quite similar to that observed for the genetic effects (1.40). For the [Ca]↔[Mg] pair, the plot effect slope of 3.55 was substantially greater than that observed for the genetic effect (1.11 and 1.00 for low and high fertility soils respectively). Indeed, generally speaking, slopes for the relationships between individual cations were different for the environmental as opposed to the genetic effects (Table A3). Also of note is the very strong negative [Mg]↔[C] plot effect relationship ($r=-0.738$), the slope of which was slightly less steep than observed for the genetic terms (Fig. 7h).

Though not significant when considered individually for low and high fertility sites (Table 3), the positive relationship between δ^{13}C and [C] was significant when considered overall (see Table A2). At the same time, when environment was the source of variation, δ^{13}C was significantly correlated with [P] with a similar slope to that observed for the genetic terms (Fig. 7i), but it was not significantly associated with [N], although it did show a significant positive correlation with M_A.

3.7 Environmental predictors and spatial autocorrelation

The results from the ordination of the soil variables are illustrated in Table 4 with the first three PCA axes explaining 0.74 of the total variance in the studied soil properties. The first axis which explained 0.45 of the variance was mainly related with variations in exchangeable bases (viz. Ca, K and Mg), total extractable P, total reserve bases (Σ_{RB}) and effective cation exchange capacity, thus reflecting variations in soil fertility (denoted PCAf). The second axis, PCAt, accounted for 0.18 of the variance was mostly associated with variations in exchangeable Al and soil texture, with the third (accounting for 0.11 of the variance) mostly associated with variations in total soil C and N (PCAc). These principal components were used as non-collinear predictor variables, along with mean annual temperature, annual total precipitation, precipitation during the two dry months and incoming solar radiation in a multiple linear regression against the plot level effect as derived from the multilevel model of Eq. (1).

All foliar plot effect estimates had an important spatial pattern as illustrated in the respective maps and tested with the Monte Carlo permutation method at equally distant classes of 200 km, and a global Bonferroni significance level a^* of 0.005 (Fig. B1). This means that spatial autocorrelation needs to be taken into account in any analysis. The results of the non-spatial multiple OLS regression analyses are summarized in the top panel of Table 5, and in the second and third panel we present the results of the SAR models. Correlograms of residuals of all three models are shown in the supplementary material (http://www.biogeosciences-discuss.net/6/3707/2009/bgd-6-3707-2009-supplement.zip, Fig. B2) and the comparative consideration of these models gives some insights to the potential patterns of spatial autocorrelation of each foliar property of interest.

Both the OLS model residuals correlogram (Fig. B2a) and the permutation method (Table 5 – OLS panel – “Moran’s *I*”) did not identify an important autocorrelation signal in the non-spatial regression of M_A, with the OLS accounting for 0.42 of the variation in the plot effect M_A contribution. The fertility PCA axis and total annual precipitation were the most important environmental predictors. As another example we discuss the results for [Ca] plot effect regressions. The OLS indicated the PCA*f* axis, the PCA*t* axis, the PCA*c* axis, annual temperature and solar radiation as important predictors The residuals of the non-spatial model (Fig. B2b – OLS) and the permutation method for the global Moran’s *I* (Table 5) identified a significant spatial signal in the simple OLS. Thus we proceeded by fitting the fine and medium scale SAR models. The fine scale (50 km) SAR model removed the spatial autocorrelation from the residuals as indicated by both the respective correlogram (Fig. B2b – SAR50) and the global Moran’s *I* (Table 5 – SAR50 panel). However, in this model annual temperature and solar radiation lost their significance, while the rest of the predictors retained their significance with a small difference in their coefficient estimates. The medium scale SAR model did not perform better as it was not able to remove the spatial signal from the residuals. We thus accepted the three soil axes identified by both the OLS and SAR50 models as the best predictors for the [Ca] plot-level effects.

A similar comparative consideration was undertaken for the OLS and SAR results for other foliar properties, including δ^{13}C. In summary, plot level nitrogen and magnesium effects showed no spatial signal in the residuals, and thus the OLS model was considered adequate to describe the main environmental predictors. Plot level [N] effects were mainly associated with the mean annual temperature and the soil texture axis with a less important contribution of fertility and dry season precipitation. The plot level [Mg] effect was mainly related with PCA*f* and the third PCA*c* axis, as well as with annual precipitation. These environmental predictors accounted for a high 0.50 and 0.38 of the total plot effect [N] and [Mg] variability, respectively.

On the other hand, leaf [C] variation had a strong spatial pattern which affected the residuals of the OLS (Moran's I=0.394). Nevertheless, the fine scale (50 km) SAR model removed most of this strong spatial signal (Moran's I=0.033) although this was not the case for the medium scale (750 km) SAR model (0.392). Nevertheless, the main environmental predictors of the OLS model, namely soil fertility and dry season precipitation remained important in both SAR models, suggesting their valid influence.

The residuals of the plot effect [P] non-spatial regression presented a spatial signal which was effectively removed by both the fine scale (50 km) and the medium scale (1000 km) SAR models (Fig. B2), and in both cases the autoregression coefficient λ was significantly different from zero (Table 5). Following our comparative approach we thus suggest a significant plot level [P] contribution with the soil fertility axis and a weaker one with total annual precipitation.

Plot level [K] and [Al] effects had autocorrelated residuals when space was not explicitly taken into account. However no spatial signal in the residuals of the fine scale SARs was identified, and the spatial component as expressed through λ was significant in all cases. Following again the comparative consideration of OLS and SAR results we retained as significant the possible associations between PCA*f*, PCA*t* and dry season precipitation with plot [K] effect and annual and dry season precipitation as well as solar radiation with plot [Al] effect. Finally the spatial pattern in the OLS residuals for δ^{13}C was greatly removed by the fine scale SAR model but not from the medium scale model. The plot δ^{13}C effect was mainly related with the soil fertility axis, mean annual temperature and total annual precipitation. Summarizing the above we could suggest that the fine scale SAR models seemed more appropriate to account for the spatial patterns of our dataset, and that soil fertility, precipitation and to a lesser extent annual temperature were the main environmental predictors related with most plot effect contributions.

Nevertheless, it was also the case that some OLS analyses (especially for [P], [Ca], [K], [Al] and δ^{13}C) suggested that data normality and homoscedacity did not always occur. Thus, we also took the approach of using the rank-based Kendall's τ (Legendre and Legendre 1998, p. 199) to evaluate the relationships between plot level trait effects and environmental predictors (i.e. using the first PCA axis from Table 4; PCAf) that retained the strongest significance in the above OLS-SAR comparative analysis. These relationships are illustrated in Fig. 8 along with their associated Kendall's τ and level of significance.

Bearing in mind that any spatial autocorrelation will lead to an overestimate of the level of significance, Fig. 8a thus suggests that the relationship showing the decline between M_A and PCAf, is weak, but that the decrease in [C] plot effect with PCAf (Fig. 8b) and the increasing [N] effect with PCAf (Fig. 8c) are both much more likely to be significant, with the very strong relationship between [P] plot effects and PCAf (Fig. 8d) even more so. Of the cations, the relationships between PCAf and both the [Ca] plot effect (Fig. 8e) and [K] plot effect (Fig. 8f) were both also quite strong, but as is shown in Fig. 8g this was much less the case for the [Mg], after taking into account the likely spatial autocorrelation discussed above, is probably not significantly related to PCAf. Likewise for δ^{13}C the relationship with PCAf was relatively weak.

In a similar manner, Fig. 9 illustrates the strongest relationships found between the various plot effects and climate. Three likely significant plot effects related to mean annual temperature (T_a,) were observed, namely a decline in leaf nitrogen (Fig. 9a), phosphorus (Fig. 9b) and K (Fig. 9c) with increased temperature. Figure 9d–h shows the more important relationships with mean annual precipitation, P_a, with a strong positive relationship observed with M_A (Fig. 9d), [C] (Fig. 9e) and a negative slope for [Mg] (Fig. 9g). Figure 9f and h shows less dramatic though potentially important relationships with precipitation for the [P] and δ^{13}C plot effects, respectively.

Table 6 lists Kendall's partial rank coefficients (τ_P) for the various plot effects examined as related to PCA*f*, PCA*t* (soil texture/pH/aluminum axis), T_a,P_a and mean annual radiation (Q_a). In all cases the co-efficient given is for the one factor after controlling for the other four. Based on our numerical simulations of the partial τ sampling distribution quantiles and the problem of spatial autocorrelation discussed above, we suggest that $\tau_P>0.23$ (approximately relating to the probability of a Type II error, P, being less than 0.01) should be taken as a minimum criterion for statistical significance with $\tau_P>0.31$ almost certainly indicating a meaningful correlative relationship ($P<0.001$). Nevertheless, relationships with $0.17<\tau_P<0.23$ cannot be entirely discounted.

Table 6 shows that very strongly related to PCA*f* were the plot effects for [P], [Ca] and [K], and, with the exception of [Al], the other parameters examined also had close to significant relationships with M_a, [C] declining somewhat with increased soil fertility and δ^{13}C increasing. On the other only the [Ca] plot effect was significantly associated with PCA*t*, although all other cations (including [Al]) did show trends in the same direction, viz. a decline with increasing soil sandiness and/or higher soil pH. Of the climatic parameters, Q_a, showed no meaningful associations, but [N], [P] and [K] were all significantly negatively associated with T_a. There were several strong relationships detected with P_a; in particular an increase in both M_a and [C] with increasing precipitation, but with significant declines in [Mg] and less negative δ^{13}C as P_a increased.

4 Discussion

Suites of plant traits are often used to infer the functioning and performance of different species (Westoby et al., 2002) as well as to identify potential evolutionary pathways of trait variation (Reich et al., 2003; Ackerly, 2003). Among the range of functional characters some traits are regarded as highly conservative while others are considered more plastic. Identifying the variation of different functional traits among and within different evolutionary affinities and exploring the way these key plant functional characteristics vary across environmental gradients should help us to understand the functioning of different ecosystems and their responses to global change.

Analyses of global (Wright et al., 2004) and regional (Fonseca et al., 2000; Wright et al., 2001) datasets have highlighted that a large portion of the variation observed in M_A, [N] and [P] is found between species within a common environment. Studies with both herbaceous (Thompson et al., 1997) and woody (Dauer et al., 2007) species have also demonstrated that this may be the case for cations such as Ca, Mg and K (see also Broadley et al., 2004). Much of the genetically controlled variation in [Ca] and [Mg] seems to be mediated through differences in cation exchange capacities of cell walls (Demarty et al., 1984; White and Broadley, 2003), which are themselves strongly influenced by genetic variations in pectin and galacturonic acid chemistry (Kirkby and Pilbeam, 1984; Sattelmacher, 2001).

Data from nort-west Amazonia presented a thirty-fold variation in leaf longevity and a three-fold variation in M_A and [N] in adjacent communities (Reich et al., 1991). Townsend et al. (2007) highlighted the importance of local-scale species diversity as an important component controlling the variation of foliar N:P ratio. Our results place a special emphasis on this variability, covering considerable tree species diversity across an ecosystem-wide climate and soil gradient. A ten-fold range of variation was identified for M_A, while [N] and [P] presented a six-fold and a seventeen-fold range respectively. At the same time this variability was well retained between all families as well as within most of the widely abundant ones (Figs. 3 and 4). Some properties like M_A, and leaf [C], [N], [Mg] and [Al] seem to be more strongly genetically constrained, with much of their variation attributable to their phylogenetic grouping (Fig. 2). For example approximately 0.07, 0.11 and 0.19 of the total variation in M_A, is apportioned to the family, genus and species component respectively, and only 0.15 is due to the location of an individual. At the other end of the spectrum, traits such as [P], [Ca] and [K] had a much higher level of plasticity, with 0.47, 0.41 and 0.47 of the respective variation being attributed to the site at which the leaf was measured. Thus for these traits the environmental conditions (mainly soil fertility) seem to exert a significant control (Fig. 8).

Across the Amazon basin there are two well-recorded gradients of resource availability, namely a northeast to southwest gradient of soil fertility (Quesada et al., 2009a) and a northwest to southeast gradient in precipitation and dry season length (Sombroek, 2001; Malhi and Wright, 2004). Tree species distributions (ter Steege et al., 2006), diversity (ter Steege et al., 2006) and forest turnover (Phillips et al., 2004) all follow these gradients, with westerns forests being more dynamic and with faster growth rates (Malhi et al., 2004; Phillips et al., 2004). Results here suggest that these gradients are reflected in foliar characteristics as well as other functional properties (Baker et al., 2009). Specifically, species on richer soils tend to have intrinsically lower M_A, and intrinsically higher leaf nutrient concentrations compared with species on poor soils. This was valid when we analysed both the raw dataset (Table A3 and Figs. 1 and A2) and the genetic component of each trait (Table 2 and Fig. 6). Of special interest are the identified shifts across the axis of variation (Table 2), supporting the "habitat tracking" hypothesis (Ackerly, 2003). We suggest specific trait dimensions systematically change along soil fertility gradients.

Our sampling strategy and subsequent analyses were not designed to specifically explore niche separation mechanisms occurring across the RAINFOR plots. Nevertheless, the clear shift in the genetic component of foliar traits associated with rich or poor soils implies that soil fertility exerts a fundamental role in modulating community composition across Amazonia. It seems that potential resourced-based tree niche differentiation processes are accompanied by specific suites of functional foliar properties. However, these correlations could have arisen through a small number of ancient events, and subsequent diversification from common ancestors that colonised rich and poor soils respectively. Alternatively, habitat specialisation may have repeatedly driven diversification in a large range of clades, such as in the Burseraceae (Fine et al., 2005). Distinguishing these hypotheses will require mapping the genetic component of species traits onto their phylogenetic relationships and assessing whether the genetic component of these trait values show overdispersed or clustered distributions (Cavendar-Bares et al., 2006). At the same time due to the unbalanced nature of our data-sampling more than half our sampled species (303) were only measured once. Thus the multilevel estimate of the genetic component may have given rise to biased estimates, driven by the environmental conditions of the site.

Although there have been several previous studies investigating effects of climate and/or soil conditions on foliar trait combinations (e.g. Fonseca et al., 2000; Wright and Westoby, 2002; Wright et al., 2004, 2005a; Townsend et al., 2007) all of these have treated the measured values of the traits examined as being genetically determined, often pooling several values (sometimes even from several different studies) into a single set of values for the one species. We have taken a different approach here, allowing for the traits observed for any given species to vary with location with the REML approach we have used possible due to considerable species overlap across sites. A similar statistical approach has been independently undertaken by Watanabe et al. (2007) in an analysis of evolutionary controls of plant nutrient composition. They fitted a REML model of a similar form, also using random terms only (in their case "site + clade/family/species"), though in their case they were more interested in partialing out any site effects, rather than, as in our case, trying to understand them. A nested variance structure used within a REML context to analyse the genetic variation observed (in our case "family/genus/species") has also previously been recognised by other workers and extensively applied in phylogenetic analyses (Broadley et al., 2004).

Scaling relationships were identified between all $M_A \leftrightarrow$[nutrient] pairs with the only exception being the M_A↔[Al] pair in the analysis of the raw data (Tables A2 and A3). The same was true for the genetic pairs, regardless of the site growing conditions, with the exceptions of M_A↔[Ca] on fertile and M_A↔[Al] on infertile soils (Table 2). Additionally, in most cases for the genetic M_A↔[nutrient] pairs common SMA axes were identified, indicating similar scaling mechanisms regardless of the edaphic conditions. Thus at this level, general axes of leaf traits variation expressing the economic spectrum of fast and slow resource turnover are indeed valid for Amazonian forests.

As discussed in the previous paragraph, there is a clear distinction between traits of species found on fertile and infertile soils. This is illustrated by the significant shifts across axis of variation identified in both the genetic and raw data (Tables 2, A3). Thus species which are found on fertile soils tend to be at the fast return (right hand) side of the M_A↔[nutrient] continuum (Figs. 6, A2). Second, apparent elevation shifts of the SMA for the raw data set (Table A3, difference in elevation) are only related with the environmental contribution of trait variation, as similar differences intercept do not exist for the genetic component. Thus the environment within which a plant is growing affects the M_A↔[nutrient] relationship.

Concentrating first on the genetic component, it is interesting to compare the slopes of the bivariate relationships we have observed with those proposed to operate globally (Wright et al., 2004). Here we note that for the (pooled) genetic component of trait variation we observed [N]↔M_A slopes (with confidence intervals in brackets) of −0.99 (−0.91 to −1.07) slightly steeper than that of Wright et al. (2004), who (taking reciprocal values from the M_A↔[N] slopes, their Table 1) reported a value of −0.78 (−0.76 to −0.81). If we accept that the negative [N]↔ M_A scaling relationship occurs because higher M_A leaves invest a greater proportion of their biomass in structural rather than metabolic compartments (Reich et al., 1999), then this suggests that higher M_A tropical tree species may retain a lesser amount of nitrogen in structural compartments such as cell walls. It is well known that cell wall N contents can vary substantially (Lamport, 1965; Takashima et al., 2004) and although several classes of cell wall protein may also function with an important role in disease resistance (Showalter, 1993; de Bruxelles and Roberts, 2001), an alternative defensive strategy, especially on the most infertile soils (including white sands) where some evidence for N-deficiency exists (Quesada et al., 2009b) may be increased levels of carbon based constitutive defences as shown by Fine et al. (2006). Consistent with this idea is the significant positive [C]↔M_A relationship observed for species found on low fertility soils. This may be accountable for in terms of high M_A leaves having a greater investment in carbon based defensive compounds such as phenols, lignin and tannin, all of which relatively reduced (Poorter and Villars, 1997).

In contrast to [N]↔M_A our genetic scaling slopes for [P]↔M_A, of −1.17 (−1.08 to −1.27) are all but identical to the Wright et al. (2004) global estimate of −1.22 (−1.16 to −1.28) suggesting stronger similarities between Amazon forest trees and other terrestrial plants. The steeper negative slope for the [P]↔M_A relationship as compared to that for [N]↔M_A may be explained by the presence of still appreciable amounts of N, but not P, in structural tissues such as cell walls (Showalter, 1993; Gabriel and Kesselmeir, 1999; White and Hammond, 2008), the proportion of which should generally increase as M_A increases. Also important may be the ability for low P requiring species to exhibit a more conservative use of phosphorus in their metabolically active tissues, for example, through employing organic acids rather than inorganic phosphate to maintain ionic balance in the vacuole, and through substitution of phospholipids in thylakoid and extraplastidic membranes with galactolipids and sulpholipids (Amtmann et al., 2006; White and Hammond, 2008).

Research quantifying relationships between metabolically active tissue properties, for example [N] and [P], and linking these with the way annual growth rate scales with plant mass, has received some attention in recent years, with modellers in this area attempting to provide a modelling framework to predict the way trees accumulate resources (Niklas et al., 2005; Niklas, 2006, 2008). Recent modelling exercises (Kerkhoff et al., 2005, 2006; Kerkhoff and Enquist, 2006) are based on a perceived strong association between leaf [N] and [P], according to a 2/3 (Wright et al., 2004) or 3/4 power law (Niklas et al., 2005). Whilst not necessarily endorsing the generality of such exercises, it is of some interest to see how our observations fit with these conceptual constructs. Our results verify the strong [N]↔[P] relationship, on both fertile and infertile Amazonian soils. This scaling relationship was significant both in the raw data analyses (Tables A2 and A3) and in the analyses of the multilevel effect estimates (Tables 2 and 3, Table A2). The aggregated raw data estimate for the [N]↔[P] scaling exponent is (0.58–0.64), whereas, as was similarly found by Townsend et al. (2007), for low fertility sites the estimated N:P slope (in our case 0.78–0.95) is clearly higher than for low fertility sites (0.63–0.73). Scaling of the genetic component of leaf [N]↔[P] is calculated at (0.76–0.96) and (0.76–0.90) for species found on low and high fertility sites respectively with Table A2 suggesting a value of 0.85 (0.80, 0.91) for the population as a whole. Thus although the raw data analyses, with environmental effects contribution included, seem reasonably close to the 2/3 power law, the analyses of the genetic component clearly show that the 2/3 power law is not adequate for expressing the N:P scaling of Amazonian trees. Indeed, the exponent seems to even be a bit larger than 3/4. The above estimates, in conjunction with the large portion of [P] variance attributed to the plot level (Fig. 2), underline the importance of soil conditions in influencing N:P ratios as is discussed further below.

By removing any plot effects in Table 2, we were able to examine differences between the N_2-fixing and non-N_2-fixing members of the Fabaceae; also comparing this family as a whole to the other families of the Amazon. This result suggests that although [P] and [N] are indeed higher for the N_2-fixing capable members of the Fabaceae, in accordance with the notion that N_2 fixers have a high [P] and a high [N] requiring "lifestyle" (Vitousek et al., 2002), members of the Fabaceae who cannot fix nitrogen also have elevated [N] and [P] compared to the Amazon tree population as a whole. But with [N] and [P] concentrations elevated to a lesser extent than for Fabaceae capable of N_2 fixation. It has recently been suggested that N_2-fixing Fabaceae are abundant in tropical ecosystems through their high [N] status, giving them an ability to exude high level of phosphatase enzymes and hence acquire extra phosphorus (Houlton et al., 2008), But it also seems to be the case that most Fabaceae within Amazonia do not fix nitrogen, even when physiologically capable of doing so (Nardoto et al., 2008). The lower foliar [Ca] for the N_2-fixing Fabaceae may be attributable to the high calcium requirement for *Rhizobia* growth in the nodulating rhizosphere (O'Hara, 2001).

In addition to [N] and [P] we also examined the relationships of [Ca], [K], [Mg] and [Al] with M_A as well as relationships between the various foliar nutrient concentrations, again separating genetic versus environmental effects. Considering genetic effects first: As was reported by Wright et al. (2005a) we found a reasonably strong relationship (r=0.45) between [K] and [P] but our slope of 1.40 was nearly twice as high as their slope of 0.78. This is probably due to the relatively low [P] in Amazon forest leaves (Lloyd et al., 2009), meaning that phosphate ions are less often employed as reserve anions in the vacuole (where they would be balanced by K^+ and other cations) and with a greater proportion of foliar P assigned to the photosynthetic apparatus that is usually the case for what are generally low [P] leaves (White and Hammond, 2008). This would also mean that [K] should also scale with [P] with a higher exponent than is generally observed. Notably the [K]↔[N] genetic relationship was markedly less strong (r=0.178), although our slope of 1.65 was closer to the 1.19 reported in Wright et al. (2005a) than was the case for phosphorus.

The very strong genetic [Ca]↔[Mg] association observed here has also been observed on other studies (Thompson et al., 1997; Broadley et al., 2004) and may be attributable to the chemical similarities between these two divalent cations and a general lack of selectivity during cation uptake by plants (White, 2001; Broadley et al., 2004). It is also likely that these two cations share, to a large extent, the same membrane transporters (Broadley et al., 2008). There were also very strong negative relationships between the concentration of [Ca], [Mg] and [K] with [C], with significant shifts existing between low and high fertility plants. This has been observed before for a range of species (Poorter and de Jong, 1999) and may reflect an underappreciated dimension of the leaf economic spectrum, 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.

Strong genetic based relationships were also seen between δ^{13}C, [N] and, to a stronger extent foliar [P] (Table 2). This suggests that more physiologically active species maintain, on average, a lower partial pressure of CO_2 in their chloroplasts, thus with a higher demand for CO_2 through photosynthesis not being totally balanced by higher stomatal conductances (Farquhar and Sharkey, 1992).

The simple spatial analysis applied, gave us some insights as to the effects of documented soil and climate gradients on the variation of the studied traits. The residuals of the OLS regression for the M_A, [N] and [Mg] plot level effects did not show any spatial autocorrelation (Fig. B2, Table 5), suggesting that at these scales there was no specific fertility oriented pattern in the environmental contribution to the above variables. On the other hand, the residuals of the non-spatial regressions of [P], [Ca] and [K] plot effects on environmental predictors illustrated a significant spatial signal, which was effectively removed by the fine scale (50 km) SAR models. For these three nutrients, the spatial component was important ($\lambda \neq 0$, Table 5) highlighting once more the substantial influence of environmental conditions on trait variation. We note, however, that for the plot level [P] contribution, the medium scale (1000 km) SAR model was equally capable of removing the spatial signal with the spatial component being similarly important. Thus the spatial patterning of environmental contribution to leaf [P] variation may be realized at broader scales. The results of the spatial analysis for [C], δ^{13}C and [Al], presented a similar behavior, with fine scale SAR models removing most of the autocorrelation in the residuals. Although correlograms showed a significant Moran's I for both plot [C] and δ^{13}C effects at the second distance class (Fig. B2), the Monte Carlo permutation did not identify a globally significant spatial signal (Table 5). Thus the comparative consideration of both the spatial and non-spatial regressions identified the most significant environmental factors contributing to trait variation.

By combining the non-spatial and spatially explicit regression models and then using this information to help us interpret the partial Kendall's τ, soil fertility emerges as a key axis of association between leaf level nutrient variation and environmental factors; being positively related with leaf nutrient concentrations and negatively associated with M_A, with leaf [C]. Based on studies with soil nutrients and/or investigations on the effects of variations in soil fertility on tropical tree leaf nutrient concentrations (Montagini, 2000; Webb et al., 2000; Sprecht and Turner, 2006) increased foliar nutrient concentrations for a given species on more fertile soils is not all that surprising. What is more interesting is the coordinated response of M_A and [C]. Clearly for any given species considerable plasticity exists. Leaf structure and physiology can vary together with the wider ranging species investing fewer resources into structural carbon and M_A under high nutrient conditions.

Environmental effects on leaf N concentration were negatively related with annual mean temperature. This result is in agreement with the global scale prediction of leaf nitrogen decreasing with temperature (Reich and Oleskyn, 2004), supporting the "Temperature-Plant Physiology Hypothesis" (Woods et al., 2003) which argues that plants at lower temperatures should show higher concentrations of physiologically relevant compounds in order to compensate for repressed rates of fundamental biochemical processes at lower temperatures. Even after removing the genetic N component of species adapted and established to more fertile environments and accounting for the potential existence of spatial autocorrelation phenomena, the negative effect of temperature on foliar [N] remained highly significant (Table 5) as was also the case for [P] from the partial Kendall's τ analysis (Table 6).

Plot level variation in M_A and leaf [C] both showed a strong positive trend with increasing precipitation, with a significant decline in leaf [Mg] with increasing precipitation also observed. This increase in M_A with increased moisture availability contrasts with the generally accepted pattern for evergreen species where M_A declines with increasing rainfall (Wright et al., 2005b). Nevertheless, it might be explicable on the basis of higher M_A leaves being structurally more robust and thus more resistant to the increased intensities of pathogen and herbivore attack which would be expected in the less seasonal and higher rainfall environments. Consistent with this idea is the increase in [C] also observed with increasing precipitation, pointing to an increased investment of carbon in constitutive compounds, as has been reported, for example to occur for lignin and phenolics (though in this case across different life forms and with a reduction rather than an increase in M_A) in northern Patagonia (Bertiller et al., 2006).

More difficult to explain is the observed decrease in [Mg] with increasing precipitation. Perhaps there are changes in cell wall carbohydrate chemistry associated with increased foliar defences (Vorwerk et al., 2004) and associated with higher precipitation could likely be changes in cell wall structure as mediated, for example, by pectin methylesterase (Pelloux et al., 2007), with the potential for such differences to give rise to substantial changes in cell wall ionic properties and, in particular, foliar magnesium contents (Pilling et al., 2004).

It is also interesting to note that the three foliar properties showing significant changes with precipitation, viz. M_A, [C] and [Mg], were also those for which the overall environmental contribution to the observed variance were all but the lowest and with a substantial genetic contribution to the variation observed (Fig. 2). This suggests that rather than being directly caused by precipitation per se, the "precipitation effect" as calculated might actually reflect phenotypically distinct populations. Such intraspecific variation has been observed before for woody species. For example, in a "common garden" experiment using fifteen distinct populations of red ironbark (*Eucalyptus sideroxylon* subsp. *tricarpa*) in Australia, Warren et al. (2005) found considerable between inter-population variability (i.e. phenotypic plasticity) for both M_A and [N] and with some of this variation attributable to seed-source precipitation regime. Despite the notoriously high biodiversity of Amazon forest (Hubbell et al., 2008) there is no reason why such intra-specific variation should not occur for at least some of the species growing there, as has been shown for different populations of Costa Rican *Cedrela odorata* for example (Gilles et al., 1997; Navarrro et al., 2002).

Taken together our results highlight three important points regarding the biogeochemistry of the Amazon basin, as expressed through a set of key tree foliar properties. There is a substantial variability at most levels of the evolutionary grouping of species.

This variability depends on the studied foliar property: Some key leaf traits are more phylogenetically constrained than others; traits such as foliar [P] showing strong associations with growing conditions. These environmental effects on leaf level nutrient concentrations make the use of general scaling relationships difficult within the Amazon basin, especially if the soil fertility variations are not implicitly taken into account. Nevertheless, the strong genetic correlations between M_A and leaf nutrient concentrations underlines the general existence of the "leaf economic spectrum" across the diverse group of Amazonian tree species studied. Although varying along the same trait coordination axes, Amazonian trees have physiological traits which vary in accordance with the soil conditions most appropriate for their growth. Species are not randomly distributed across the basin. But, rather, they follow distribution patterns based on an association between genetic trait potential and the availability of environmental resources. For plants in general, it has long been argued that this should, indeed, be the case (Lambers and Poorter, 1992).

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References

Ackerly, D. D.: Community assembly, niche conservatism and adaptive evolution in changing environments. Int. J. Plant Sci., 164, S165–S184, 2003.

Aerts, R. and Chapin, F. S.: The mineral nutrition of wild plants revisited: a re-evaluation of processes and patterns. Adv. Ecol. Res., 30, 1–67, 2000.

Amtmann, A., Hammond, J. P., Armengaud, P., and White, P. J.: Nutrient sensing and signalling in plants: Potassium and phosphorus. Adv. Bot. Res., 43, 210–257, 2006.

APG II: An update of the Angiosperm Phylogeny Group classification of the orders and families of flowering plants, APG II. Bot J. Linn. Soc., 141, 399–436, 2003.

Baker, T. R., Phillips, O. L.., Malhi, Y., Almeida, S., Arroyo, L., Di Fiore, A., Erwin, T., Killeen, T. J., Laurance, S. G., Laurance, W. F., Lewis, S. L., Lloyd, J., Monteagudo, A., Neill, D. A., Patiño, S., Pitman, N. C. A., Silva, N. J. M., and Vásquez Martínez, R.: Variation in wood density determines spatial patterns in Amazonian forest biomass, Global Change Biology, 10, 545–562, 2004.

Baker, T. R., Phillips, O. L., Laurance, W. F., Pitman, N. C. A., Almeida, S., Arroyo, L., DiFiore, A., Erwin, T., Higuchi, N., Killeen, T. J., Laurance, S. G., Nascimento, H., Monteagudo, A., Neill, D. A., Silva, J. N. M., Malhi, Y., López Gonzalez, G., Peacock, J., Quesada, C. A., Lewis, S. L., and Lloyd, J.: Do species traits determine patterns of wood production in Amazonian forests?, Biogeosciences Discuss., 5, 3593–3621, 2008, http://www.biogeosciences-discuss.net/5/3593/2008/.

Bates, D. and Sarkar, D.: lme4: Linear Mixed-Effects Models Using S4 Classes, R package version 0.999375-27, 2007.

Bertiller, M. B., Mazzarino, M. J., Carrera, A. L., Diehl, P., Satti, P., Gobbi, M., and Sain, C. L.: Leaf strategies and soil N across a regional humidity gradient in Patagonia, Oecologia, 148, 612–624, 2006.

Bivand, R.: Implementing Spatial Data Analysis Software Tools in R, Geogr. Anal., 38, 23–40, 2006.

Bjornstad, O. N. and Falck, W.: Nonparametric spatial covariance functions: estimation and testing, Environ. Ecol. Stat., 8, 53–70, 2001.

Broadley, M. R., Bowen, H. C., Cotterill, H. L., Hammond, J. P., Meacham, M. C., Mead, A., and White, P. J.: Phylogenetic variation in the shoot mineral concentration of angiosperms, J. Exp. Bot., 55, 321–336, 2004.

Broadley, M. R., Hammond, J. P., King, G. J., Astley, D., Bowen, H. C., Meacham, M. C., Mead, A., Pink, D. A. C., Teakle, G. R., Hayden, R. M., Spracklen, W. P., and White, P. J.: Shoot calcium and magnesium concentrations differ between subtaxa, are highly heritable, and associate with potentially pleiotropic loci in *Brassica oleracea*$^{1[W][OA]}$, Plant Physiol., 146, 1707–1720, 2008.

Cavendar-Bares, J., Keen, A., and Miles, B.: Phylogenetic structure of Floridian plant communities depends on taxonomic and spatial scale, Ecology, 87, 107–122, 2006.

Chessel, D., Dufour, A. B., and Thioulouse, J.: The Ade4 package – I: One-table methods, R News, 4, 5–10, 2004.

Conover, W. J.: Practical Non-Parametric Statistics, 2nd edn. John Wiley and Sons, New York, 492 pp., 1980.

Cox, P. M., Betts, R. A., Jones, C. D., Spall, S. A., and Totterdell, I. J.: Acceleration of global warming due to carbon-cycle feedbacks in a coupled climate model, Nature, 408(6809), 184–187, 2000.

Crawley, M. J.: The R Book, Jon Wiley and Sons, 942 pp., 2007.

Dauer, J. M., Chorover, J., Chadwick, O. A., Oleksyn, J., Tjoelker, M. G., Hobbie, S. E., Reich, P. B., and Eissenstat, D. M.: Controls over leaf and litter calcium concentrations among temperate trees, Biogeochem., 86, 175–187, 2007.

de Bruxelles, G. L. and Roberts, M. R.: Signals regulating multiple responses to wounding and herbivores, Crit. Rev. Plant Sci., 20, 487–521, 2001.

Demarty, M., Morvan, C., and Thellier, M.: Calcium and the cell wall, Plant, Cell Environ., 7, 441–448, 2004.

Diniz-Filho, J. A. F., Bini, L. M., and Hawkins, B. A.: Spatial autocorrelation and red herrings in geographical ecology, Global Ecol. Biogeogr., 12, 53–64, 2003.

Diniz-Filho, J. A. F., Rangel, T. F. L. V. B., and Bini, L. M.: Model selection and information theory in geographical ecology, Global Ecol. Biogeogr., 17(4), 479–488, 2008.

Drechsel, P. and Zech, W.: Foliar nutrient levels of broad leaved tropical trees. A tabular review, Plant Soil, 131, 29–46, 1991.

Elser, J. J., Sterner, R. W., Gorokhova, E., Fagan, W. F., Markow, T. A., Cotner, J. B., Harrison, J. F., Hobbie, S. E., Odell, G. M., and Weider, L. J.: Biological stoichiometry from genes to ecosystems, Ecol. Lett., 3, 540–550, 2000.

Farquhar, G. D. and Sharkey, T. D.: Stomatal conductance and photosynthesis, Ann. Rev. Plant Physiol., 33, 317–345, 1982.

Farquhar, G. D., Ehleringer, J. R., and Hubick, A. T.: Carbon isotope discrimination and photosynthesis, Ann. Rev. Plant Physiol. Plant Mol. Biol., 40, 503–537, 1989.

Fine, P. V. A., Daly, D. C., Munoz, G. V., Mesones, I., and Cameron, K. M.: The contribution of edaphic heterogeneity to the evolution and diversity of Burseraceae trees in the western Amazon, Evolution, 59, 1464–1478, 2005.

Fine, P. V. A., Miller, Z. J., Mesones, I., Irazuzta, S., Appel, H. M., Stgevens, M. H. H., Sääksjärvi, I., Schultz, J. C., and Coley, P. D.: The growth-defence trade-off and habitat specialization by plants in Amazonian forests, Ecology, 87, S150–S162, 2006.

Fonseca, C. R., Overton, J. M. C., Collins, B., and Westoby, M.: Shifts in trait-combinations along rainfall and phosphorus gradients, J. Ecol., 88, 964–977, 2000.

Gabriel, R. and Kesselmeier, J.: Apoplastic solute concentrations of organic acids and mineral nutrients in the leaves of several fagaceae, Plant Cell Physiol., 40, 604–612, 1999.

Galwey, N. W.: Introduction to Mixed Modelling: Beyond Regression and Analysis of Variance, Wiley, Chichester, England, Hoboken, NJ, 376 pp., 2006.

Garnier, E., Cortez, J., Billes, G., Navas, M.-L., Roumet, C., Debussche, M., Laurent, G., Blanchard, A., Aubry, D., Bellmann, A., Neill, C., and Toussaint, J.-P.: Plant functional markers capture ecosystem properties during secondary succession, Ecology (Durham), 85, 2630–2637, 2004.

Gelman, A. and Hill, J.: Data Analysis Using Regression and Multilevel/Hierarchical Models, Cambridge University Press, 648 pp., 2006.

Gillies, A. C. M., Cornelius, J. P., Newton, A. C., Navarro, C., Hernández, M., and Wilson, J.: Genetic variation in Costa Rican populations of the tropical timber species *Cedrela odorata* L., assessed using RAPDs, Mol. Ecol., 6, 1133–1145, 1997.

Hättenschwiler, S., Aeschlimann, B., Coûteaux, M.-M., Roy, J., and Bonal, D.: High variation in foliage and leaf litter chemistry among 45 tree species of a neotropical rainforest community, New Phytol., 179(1), 165–175, 2008.

Hawkins, B. A., Diniz-Filho, J. A. F., Mauricio Bini, L., De Marco, P., and Blackburn, T. M.: Red herrings revisited: spatial autocorrelation and parameter estimation in geographical ecology, Ecography, 30(3), 375–384, 2007.

Hijmans, R. J., Cameron, S. E., Parra, J. L., Jones, P. G., and Jarvis, A.: Very high resolution interpolated climate surfaces for global land areas, Int. J. Climatol., 25, 1965–1978, 2005.

Hobbie, E. A. and Werner, R. A.: Intramolecular, compound-specific, and bulk carbon isotope patterns in C_3 and C_4 plants: a review and synthesis, New Phytol., 161, 371–385, 2004.

Houlton, B. Z., Wang, Y-P., Vitousek, P. M., and Field, C. B.: A unifying framework for dinitrogen fixation in the terrestrial biosphere, Nature, 454, 327–330, 2008.

Hubbell, S. P., He, F., Condit, R., Borda-de-Água, L., Kellner, J., and ter Steege, H.: How many tree species are there in the Amazon and how many of them will go extinct?, P. Natl. Acad. Sci. USA, 105, 11498–11504, 2008.

Hungate, B. A., Stiling, P. D., Dijkstra, P., Johnson, D. W., Ketterer, M. E., Hymus, G. J., Hinkle, C. R., and Drake, B. G.: CO_2 Elicits Long-Term Decline in Nitrogen Fixation, Science, 304(5675), p. 1291, 2004.

IUSS (International Union of Soil Science) Working Group WRB: World Reference Base for Soil Resources 2006, World Soil Resources Report No. 103., FAO, Rome, 132 pp., 2006.

Jansens, S., Broadley, M. R., Robbrecht, E., and Smets, E.: Aluminum Hyperaccumulation in Angiosperms: A Review of Its Phylogenetic Significance, The Botanical Review, 68, 235–269, 2002.

Jetz, W. and Rahbek, C.: Geographic Range Size and Determinants of Avian Species Richness, Science, 297, 1548–1551, 2002.

Jobbagy, E. G. and Jackson, R. B.: The Uplift of Soil Nutrients by Plants: Biogeochemical Consequences Across Scales, Ecology, 85, 2380–2389, 2004.

John, R., Dalling, J. W., Harms, K., Yavitt, J. B., Stallard, R. F., Mirabello, M., Hubbell, S. P., Valencia, R., Navarette, H., Vallejo, M., and Foster, R.: Soil nutrients influence spatial distributions of tropical tree species, P. Natl. Acad. Sci. USA, 104, 864–869, 2007.

Kanowski, J.: Effect of elevated CO_2 on the foliar chemistry of seedlings of two rainforest trees from north-east Australia: Implications for foliar marsupials, Aust. Ecol., 26, 165–172, 2001.

Kaspari, M., Garcia, M. N., Harms, K. E., Santana, M., Wright, S. J., and Yavitt, J. B.: Multiple nutrients limit litterfall and decomposition in a tropical forest, Ecol. Lett., 11(1), 35–43, 2008.

Kerkhoff, A. J. and Enquist, B. J.: Ecosystem allometry: the scaling of nutrient stocks and primary productivity across plant communities, Ecol. Lett., 9, 419–427, 2006.

Kerkhoff, A. J., Enquist, B. J., Elser, J. J., and Fagan, W. F.: Plant allometry, stoichiometry and the temperature-dependence of primary productivity, Global Ecol. Biogeogr., 14, 585–598, 2005.

Kerkhoff, A. J., Fagan, W. F., Elser, J. J., and Enquist, B. J.: Phylogenetic and Growth Form Variation in the Scaling of Nitrogen and Phosphorus in the Seed Plants, Am. Nat., 168, 103–122, 2006.

Kirkby, E. A. and Pilbeam, D. J.: Calcium as a plant nutrient, Plant, Cell Environ., 7, 397–405, 1984.

Kissling, W. D and Carl, G.: Spatial autocorrelation and the selection of simultaneous autoregressive models, Global Ecol. Biogeogr., 17(1), 59–71, 2008.

Koerselman, W. and Meuleman, A. F. M.: The vegetation N:P ratio: A new tool to detect the nature of nutrient limitation, J. Appl. Ecol., 33(6), 1441–1450, 1996.

Lambers, H. and Poorter, H.: Inherent variation in growth rate between higher plants: A search for physiological causes and ecological consequences, Adv. Ecol. Res., 23, 187–261, 1992.

Lamont, B. B., Groom, P. K., and Cowling, R. M.: High leaf mass per area of related species assemblages may reflect low rainfall and carbon isotope discrimination rather than low phosphorus and nitrogen concentrations, Funct. Ecol., 16, 403–412, 2002.

Lamport, D. T. A.: The protein component of primary cell walls, Adv. Bot. Res., 2, 151–218, 1965.

Legendre, P. and Legendre, L.: Numerical Ecology, 2nd English edn, Elsevier, Amsterdam, 853 pp., 1998.

Lennon, J. J.: Red-shifts and red herrings in geographical ecology, Ecography, 23(1), 101–113, 2000.

Lichstein, J. W., Simons, T. R., Shriner, S. A., and Franzreb, K. E.: Spatial autocorrelation and autoregressive models in ecology, Ecol. Monogr., 72(3), 445–463, 2002.

Lloyd, J., Kruijt, B., Hollinger, D. Y., Grace, J., Francey, R. J., Wong, S.-C., Kelliher, F. M., Miranda, A. C., Farquhar, G. D., Gash, J. H. C., Vygodskaya, N. N., Wright, I. R., Miranda, H. S., and Schulze, E.-D.: Vegetation effects on the isotopic composition of atmospheric CO_2 as local and regional scales: Theoretical aspects and a comparison between rainforest in Amazonia and a boreal forest in Siberia, Aust. J. Plant Physiol., 23, 371–399, 1996.

Lloyd, J., Grace, J., Meir, P., and Carswell, F.: Introducing the “Biogeochemistry and Function of Amazon Forest” project, Biogeosciences Discuss., to be submitted, 2009a.

Lloyd, J., Patiño, S., Paiva, R., Nardoto, G. B., Quesada, C. A., Santos, A. J. B., Baker, T. R., Brand, W. A., Hilke, I., Gielmann, H., Raessler, M., Luizão, F. J., Martinelli, L. A., and Mercado, L. M.: Gradients in leaf physiological properties within Amazon forest canopies, Biogeosciences Discuss., to be submitted, 2009b.

Maghsoodloo, S. and Laszlo Pallos, L.: Adymtotic behaviour of Kendall’s partial rank correlation coefficient and additional quantile estimates, J. Stat. Comput. Simul., 13, 41–48, 1981.

Malhi, Y. and Wright, J.: Spatial patterns and recent trends in the climate of tropical rainforest regions, Philos. T. Roy. Soc B., 359(1443), 311–329, 2004.

Malhi, Y., Baker, T. R., Phillips, O. L., Almeida, S., Alvares, E., Arroyo, L., Chave, J., Czimczik, C., Di Fiore, A., Higuchi, N., Killeen, T., Laurance, S. G., Laurance, W. F., Lewis, S., Montoya, L. M. M., Monteagudo, A., Neill, D., Nunes Vargas, P., Panfil, S. N., Patino, S., Pitman, N., Quesada, C. A., Salomao, R., Silva, N., Lezama, A. T., Vasquez Martinez, R., Terborgh, J., Vinceti, B., and Lloyd, J.: The above-ground coarse wood productivity of 104 Neotropical forest plots, Global Change Biol., 10(5), 563–591, 2004.

McCulloch, C. E. and Searle, S. R.: Generalized, Linear and Mixed Models, J. Wiley, New York, 2001.

McMahon, S. M. and Diez, J. M.: Scales of Association: Hierarchical Linear Models and the Measurement of Ecological Systems, Ecol. Lett., 10, 437–452, 2007.

Montagnini, F.: Accumulation in above-ground biomass and soil storage of mineral nutrients in pure and mixed plantations in a humid tropical lowland, For. Ecol. Man., 134, 257–270, 2000.

Nardoto, G. B., Ometto, J. P. H. B., Ehleringer, J. R., Higuchi, N., Bustamante, M. M., Da, C., and Martinelli, L. A.: Understanding the influences of spatial patterns on N availability within the Brazilian Amazon forest, Ecosystems, 11(8), 1234–1246, doi:10.1007/s10021-008-9189-1, 2008.

Navarro, C., Ward, S., and Hernández, M.: The tree *Cedrela odorata* (Meliaceae): A morphologically subdivided species in Costa Rica, Rev. Biol. Trop., 50, 21–29, 2002.

New, M., Lister, D., Hulme, M., and Makin, I.: A high-resolution data set of surface climate over global land areas, Climate Res., 21, 1–25, 2002.

Niinemets, U. and Kull, K.: Leaf structure vs. nutrient relationships vary with soil conditions in temperate shrubs and trees, Acta Oecol., 24, 209–219, 2003.

Niinemets, U.: Distribution patterns of foliar carbon and nitrogen as affected by tree dimensions and relative light conditions in the canopy of *Picea abies*, Trees, 11, 144–154, 1997.

Niklas, K. J., Owens, T., Reich, P. B., and Cobb, E. D.: Nitrogen/phosphorus leaf stoichiometry and the scaling of plant growth, Ecol. Lett., 8(6), 636–642, 2005.

Niklas, K. J.: Carbon/nitrogen/phosphorus allometric relations across species, in: The Ecophysiology of Plant-Phosphorus Interactions, edited by: White, P. J. and Hammond, J. P., Springer Science, p. 9–30, 2008.

Niklas, K. J.: Plant Allometry, Leaf Nitrogen and Phosphorus Stoichiometry, and Interspecific Trends in Annual Growth Rates, Ann. Bot-London, 97, 155–163, 2006.

O'Hara, G. W.: Nutritional constraints on root nodule bacteria affecting symbiotic nitrogen fixation: a review, Aust. J. Exp. Agr., 41, 417–433, 2001.

Paoli, G. D.: Divergent leaf traits among congeneric tropical trees with contrasting habitat associations on Borneo, J. Trop. Ecol., 22, 397–408, 2006.

Patiño, S., Lloyd, J., Paiva, R., Quesada, C. A., Baker, T. R., Santos, A. J. B., Mercado, L. M., Malhi, Y., Phillips, O. L., Aguilar, A., Alvarez, E., Arroyo, L., Bonal, D., Costa, A. C. L., Czimczik, C. I., Gallo, J., Herrera, R., Higuchi, N., Horna, V., Hoyos, E. J., Jimenez, E. M., Killeen, T., Leal, E., Luizão, F., Meir, P., Monteagudo, A., Neill, D., Núñez-Vargas, P., Palomino, W., Peacock, J., Peña-Cruz, A., Peñuela, M. C., Pitman, N., Priante Filho, N., Prieto, A., Panfil, S. N., Rudas, A., Salomão, R., Silva, N., Silveira, M., Soares de Almeida, S., Torres-Lezama, A., Turriago, J. D., Vásquez-Martnez, R., Schwarz, M., Sota, A., Schmerler, J., Vieira, I., Villanueva, B., and Vitzthum, P.: Branch xylem density variations across Amazonia, Biogeosciences Discuss., 5, 2003–2047, 2008a, http://www.biogeosciences-discuss.net/5/2003/2008/.

Patiño, S., Lloyd, J., and Lopez-Gonzalez, G.: Nodulation, in: Functional Traits Database, edited by: Lopez-Gonzalez, G., Baker, T. R., Lewis, S. L., Phillips, O. L., et al., Functional Traits Database, RAINFOR project, University of Leeds, date of extraction: 1 October 2008, 2008b.

Pelloux, J., Rustérucci, C., and Mellerowicz, E. J.: New insights into pectin methylesterase structure and function, Trends in Plant Sci., 12, 267–277, 2007.

Phillips, O. L., Vargas, P. N., Monteagudo, A. L., Cruz, A. P., Chuspe Zans, M.-E., Sanchez, A. P., Yli-Halla, M., and Rose, S.: Habital association among Amazonian tree species: a landscape-scale approach, J. Ecol., 91, 757–775, 2003.

Phillips, O. L., Baker, T., Arroyo, L., Higuchi, N., Killeen, T., Laurance, W. F., Lewis, S. L., Lloyd, J., Malhi, Y., Monteagudo, A., Neill, D., Núñez Vargas, P., Silva, N., Terborgh, J., Vásquez Martínez, R., Alexiades, M., Almeida, S., Brown, S., Chave, J., Comiskey, J. A., Czimczik, C. I., Di Fiore, A., Erwin, T., Kuebler, C., Laurance, S. G., Nascimento, H. E. M., Olivier, J., Palacios, W., Patiño, S., Pitman, N., Quesada, C. A., Saldias, M., Torres Lezama, A., and Vinceti, B.: Patterns and process in Amazon tree turnover, 1976–2001, Phil. Trans. Roy. Soc. B, 359, 437–462, 2004.

Pilling, J., Willmitzer, L., Bücking, H., and Fisahn, J.: Inhibition of a ubiquitously expressed pectin methyl esterase in *Solanum tuberosum* L. affects plant growth, leaf growth polarity, and ion partitioning, Planta, 219, 32–40, 2004.

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

Poorter, L. and De Jong, R.: A comparison of specific leaf area, chemical composition and leaf construction costs of field plants from 15 habitats differing in productivity, New Phytol., 143, 163–176, 1999.

Poorter, L. and Villar, R.: The fate of acquired carbon in plants: Chemical compositoon and construction costs, in: Plant Resource Allocation, edited by: Bazzaz, F. A. and Grace, J., Academic Press, San Diego/London/Boston/New York/Sydney/Tokyo/Toronto., p. 39–72, 1999.

Quesada, C. A., Lloyd, J., Anderson, L. O., Fyllas, N. M., Schwarz, M., and Czimczik, C. I.: Soils of Amazonia with particular reference to the RAINFOR sites, Biogeosciences Discuss., in press, 2009a.

Quesada, C. A., Lloyd, J., Schwarz, M., Martinelli, L., Patino, S., Baker, T. R., Czimczik, C., Fyllas, N. M, Martinelli, L., Nardoto, G. B., Schmerler, J., Santos, A. J. B., Hodnett, M. G., Herrera, R., Luizão, F. J., Arneth, A., Lloyd, G., Dezzeo, N., Hilke, I., Kuhlmann, I., Raessler, M., Moraes Filho, J., Paiva, F., Araujo Filho, R., Chaves, E., Cruz Junior, O., Pimentel, T. P., and Paiva, R.: Chemical and physical properties of Amazonian forest soils in relation to their genesis, Biogeosciences Discuss., in press, 2009b.

Reich, P. B.: Global biogeography of plant chemistry: filling in the blanks, New Phytologist, 168, 263–266, 2005.

Reich, P. B. and Oleksyn, J.: Global patterns of plant leaf N and P in relation to temperature and latitude, Pub. Nat. Acad. Sci. USA, 101, 11001–11006, 2004.

Reich, P. B., Ellsworth, D. S., Walters, M. B., Vose, J. M., Gresham, C., Volin, J. C., and Bowman, W. D.: Generality of leaf trait relationships: A test across six biomes, Ecol., 80, 1955–1969, 1999.

Reich, P. B., Uhl, C., Walters, M. B., and Ellsworth, D. S.: Leaf lifespan as a determinant of leaf structure and function among 23 Amazonian tree species, Oecologia, 86(1), 16–24, 1991.

Reich, P. B., Walters, M. B., and Ellsworth, D. S.: From tropics to tundra: Global convergence in plant functioning, P. Natl. Acad. Sci. USA, 94(25), 13730–13734, 1997.

Reich, P. B., Wright, I. J., Cavender-Bares, J., Craine, M., Oleksyn, J., Westoby, M., and Walters, M. B.: The Evolution of Plant Functional Variation: Traits, Spectra, and Strategies, Int. J. Plant Sci., 164(S3), 143–164, 2003.

Reich, P. B. and Walters, M. B: Photosynthesis-nitrogen relations in Amazonian tree species. 2. Variation in nitrogen vis a vis specific leaf area influences mass- and area-based expressions, Oecologia, 97, 73–81, 1994.

Reich, P. B., Walters, M. B., Ellsworth, D., and Uhl, C.: Photosynthesis-nitrogen relations in Amazonian tree species. I: Patterns among species and communities, Oecologia, 97(1), 62–72, 1994.

Russo, S. E., Brown, P., Tan, S., and Davies, S. J.: Interspecific demographic trade-offs and soil-related habitat associations of tree species along resource gradients, J. Ecol., 96, 192–203, 2008.

Santiago, L. S., Kitajima, K., Wright, S. J., and Mulkey, S. S.: Co-ordinated changes in photosynthesis, water relations and leaf nutritional traits of canopy trees along a precipitation gradient in lowland tropical forest, Oecologia, 139, 495–502, 2004.

Sattelmacher, B.: The apoplast and its significance for plant mineral nutrition, New Phytol., 149, 167–192, 2001.

Showalter, A. M.: Structure and function of plant cell wall proteins, The Plant Cell, 5, 9–23, 1993.

Snijders, T. A. B. and Bosker, R. J.: Multilevel Analysis: An Introduction to Basic and Advanced Multilevel Modeling, SAGE, 266 pp., 1999.

Sombroek, W. G.: Amazonian landforms and soils in relations to biological diversity, Acta Amazonica, 30, 81–100, 2000.

Sombroek, W G.: Spatial and Temporal Patterns of Amazon Rainfall, Ambio, 30(7), 388–396, 2001.

Sprecht, A. and Turner, J.: Foliar nutrient concentrations in mixed-species plantations of subtropical cabinet timber species and their potential as a management tool, For. Ecol. Man., 233, 324–337, 2006.

Sultan, S. E.: Phenotypic plasticity for plant development, function and life history, Trends Plant Sci., 5, 537–542, 2000.

Takashima, T., Hikosaka, K., and Hirose, T.: Photosynthesis or persistence: nitrogen allocation in leaves of evergreen and deciduous *Quercus* species, Plant, Cell Environ., 27, 1047–1054, 2004.

ter Steege, H., Pitman, N. C. A., Phillips, O. L., Chave, J., Sabatier, D., Duque, A., Molino, J.-F., Prévost, M. F., Spichiger, R., Castellanos, H., Hildebrand, P., and Vásquez, R.: Continental-scale patterns of canopy tree composition and function across Amazonia, Nature, 443, 444–447, 2006.

Tessier, J. T. and Raynal, D. J.: Use of nitrogen to phosphorus ratios in plant tissue as an indicator of nutrient limitation and nitrogen saturation, J. Appl. Ecol., 40(3), 523–534, 2003.

Thompson, K., Parkinson, J. A., Band, S. R., and Spencer, R. E.: A comparative study of leaf nutrient concentrations in a regional herbaceous flora, New Phytol., 136, 679–689, 1997.

Tognelli, M. F. and Kelt, D. A.: Analysis of determinants of mammalian species richness in South America using spatial autoregressive models, Ecography, 27, 427–436, 2004.

Townsend, A. R., Asner, G. P., and Cleveland, C. C.: The biogeochemical heterogeneity of tropical forests, Trends Ecol. Evol., 23, 424–431, 2008.

Townsend, A. R., Cleveland, C. C., Asner, G. P., and Bustamante, M. M. C.: Controls over foliar N:P ratios in tropical rain forests, Ecology, 88, 107–118, 2007.

Veenedaal, E. M., Swaine, M. D., Lecha, R. T., Walsh, M. F., Abrese, I. K., and Owusu-Afiyie, K.: Response of West African forest tree seedlings to irradiance and soil fertility, Funct. Ecol., 10, 501–511, 1996.

Vitousek, P. M.: Litterfall, nutrient cycling and nutrient limitation in tropical forest, Ecology 65, 285–298, 1984.

Vitousek, P. M., Cassman, K., Cleveland, C., Crews, T., Field, C. B., Grimm, N. B., Robert, W. H., Marino, R., Martinelli, L., Rastetter, E. B., and Sprent, J. I.: Towards an ecological understanding of biological nitrogen fixation, Biogeochem., 57–58, 1–45, 2002.

Vorwerk, S., Somerville, S., and Somerville, C.: The role of plant cell well polysaccharide compstion in disease resistance, Trends in Plant Sci., 9, 203–209, 2004.

Warren, C. R., Tausz, M., and Adams, M.: Does rainfall explain variation in leaf morphology and physiology among populations of red ironbark (*Eucalyptus sideroxylon* subsp. *tricarpa*) grown in a common garden?, Tree Physiol., 25, 1369–1378, 2005.

Warton, D. I., Wright, I. J., Falster, D. S., and Westoby, M.: Bivariate line-fitting methods for allometry, Biol. Rev., 81, 259–291, 2006.

Watanabe, T., Broadley, M. R., Jansen, S., White, P. J., Takada, J., Satake, K., Takamatsu, T., Tuah, S. J., and Osaki, M.: Evolutionary control of leaf element composition in plants, New Phytol., 174, 516–523, 2007.

Webb, M. J., Reddell, P., Hambleton, A., and Robson, K. E. N.: Growth response of four tropical plantation timber species to increasing phosphorus supply and assessment of phosphorus requirements using foliar analysis, New Forests, 20, 193–211, 2000.

Westoby, M., Falster, D. S., Moles, A. T., Vesk, P. A., and Wright, I. J.: Plant ecological strategies: Some leading dimensions of variation between species, Ann. Rev. Ecol. Syst., 33, 125–159, 2002.

White, P. J.: The pathways of calcium movement to the xylem, J. Exp. Bot. 52, 891–899, 2001.

White, P. J. and Hammond, J. P.: Phosphorus nutrition of terrestrial plants, in: The Ecophysiology of Plant-Phosphorus Interactions, edited by: White, P. J. and Hammond, J. P., Springer Science, p. 51–81, 2008.

White, P. J. and Broadley, M. R.: Calcium in plants, Annals of Bot., 92, 487–511, 2003.

Woods, H. A., Makino, W., Cotner, J. B., Hobbie, S. E., Harrison, J. F., Acharya, K., and Elser, J. J.: Temperature and chemical composition of poikothermic organisms, Funct. Ecol., 17, 237–245, 2003.

Wright, I. J., Reich, P. B., Westoby, M., Ackerly, D. D., Baruch, Z., Bongers, F., Cavender-Bares, J., Chapin, T., Cornelissen, J. H., Diemer, M., Flexas, J., Garnier, E., Groom, P. K., Gulias, J., Hikosaka, K., Lamont, B. B., Lee, T., Lee, W., Lusk, C., Midgley, J. J., Navas,

M. L., Niinemets, U., Oleksyn, J., Osada, N., Poorter, H., Poot, P., Prior, L., Pyankov, V. I., Roumet, C., Thomas, S. C., Tjoelker, M. G., Veneklaas, E. J., and Villar, R.: The worldwide leaf economics spectrum, Nature, 428, 821–827, 2004.

Wright, I. J., Reich, P. B., and Westoby, M.: Strategy shifts in leaf physiology, structure and nutrient content between species of high- and low-rainfall and high- and low-nutrient habitats, Funct. Ecol., 15, 423–434, 2001.

Wright, I. J. and Westoby, M.: Leaves at low versus high rainfall: coordination of structure, lifespan and physiology, New Phytol., 155, 403–416, 2002.

Wright, I. J., Reich, P. B., and Westoby, M.: Strategy shidts in leaf physiology, structure and nutrient content between species of high- and low-rainfall and high- and low-nutrient habitats, Funct. Ecol., 14, 423–434, 2001.

Wright, I. J., Reich, P. B., Cornelissen, J. H. C., Falster, D. S., Groom, P. K., Hikosaka, K., Lee, W., Lusk, C. H., Niinemets, U., Oleksyn, J., Osada, N., Poorter, H., Warton, D. I., and Westoby, M.: Modulation of leaf economic traits and trait relationships by climate, Global Ecol. Biogeogr., 14(5), 411–421, 2005b.

Wright, I. J., Reich, P. B., Cornelissen, J. H. C., Falster, D. S., Garnier, E., Hikosaka, K., Lamont, B. B., Lee, W., Oleksyn, J., Osada, N., Poorter, H., Villar, R., Warton, D. I., and Westoby, M.: Assessing the generality of global leaf trait relationships, New Phytol., 166(2), 485–496, 2005a.

Table 1. Mean genetic values (intercept+genetic effect)±stadard deviation for taxa not belonging to *Fabaceae*, non fixing *Fabaceae* and N-fixing *Fabaceae*. Values followed by different letters within a trait-column indicate significant differences at $p<0.001$ for the three groups.

	LMA ($g\,m^{-2}$)	C ($mg\,g^{-1}$)	N ($mg\,g^{-1}$)	P ($mg\,g^{-1}$)	Ca ($mg\,g^{-1}$)	K ($mg\,g^{-1}$)	Mg ($mg\,g^{-1}$)	Al ($mg\,g^{-1}$)	$\delta^{13}C$ [$^0/_{00}$]
non *Fabaceae*	99.3±14.2a	516.7±9.6a	21.07±1.43c	0.91±0.12c	4.59±0.88a,b	5.78±1.16a	1.95±0.35a	0.042±0.012a	–31.21±0.33
Fabaceae non Fixers	87.9±11.4b	506.7±8.5b	22.53±2.17b	1.01±0.09b	5.40±2.01a	4.95±0.75b	1.89±0.46a,b	0.033±0.006b	–31.16±0.46
Fabaceae N_2-Fixers	84.9±11.0b	508.4±9.1b	25.42±1.81a	1.11±0.09a	4.24±1.01b	5.17±0.63b	1.69±0.26b	0.033±0.008b	–31.2±0.32

Table 2. Pairwise relationships between the genetic components of key foliar properties of species found in low and high fertility plots. The genetic component is computed by summing the Family+Genus+Species effect as estimated from the multilevel model. "Slope" of the SMA, Pearson's *r* correlation coefficient, "sig" the significance of the correlation, and *n* the number of cases used. Boldface indicates significant difference (p<0.05) in slope or elevation and/or shift across the SMA axis. The (−−) sign indicates that the respective test can not be applied. sig: ***<0.001, **<0.01, *<0.05, −< 0.1.

		low fertility					high fertility					sig. of difference in		
Y	X	slope	slope 95%ci	r	sig	n	slope	slope 95%ci	r	sig	n	slope	elevation	shift
C	M_A	0.353	(0.305 0.408)	0.235	**	173	0.391	(0.349 0.438)	0.102	–	301	0.274	0.857	0.002
N	M_A	−1.019	(−0.888 −1.169)	−0.398	***	174	−0.964	(−0.870 −1.069)	−0.409	***	305	0.530	0.806	0.003
P	M_A	−1.191	(−1.036 −1.370)	−0.376	***	173	−1.168	(−1.055 −1.294)	−0.435	***	302	0.824	0.520	0.002
Ca	M_A	−2.298	(−1.980 −2.666)	−0.156	*	173	(−−)	(−−)	−0.082		303	(−−)	(−−)	(−−)
K	M_A	−1.609	(−1.394 −1.858)	−0.294	***	173	−1.711	(−1.537 −1.904)	−0.321	***	303	0.503	0.397	0.001
Mg	M_A	−2.068	(−1.785 −2.397)	−0.197	**	173	−2.209	(−1.974 −2.472)	−0.120	*	303	0.486	0.460	<0.001
Al	M_A	(−−)	(−−)	0.085		173	6.981	(6.240 7.810)	0.130	*	303	(−−)	(−−)	(−−)
δ^{13}C	M_A	0.115	(0.099 0.134)	0.134	–	168	(−−)	(−−)	0.032		305	(−−)	(−−)	(−−)
N	C	2.883	(2.484 3.346)	0.143	–	173	(−−)	(−−)	0.064		302	(−−)	(−−)	(−−)
P	C	3.376	(2.909 3.917)	0.146	–	173	(−−)	(−−)	−0.086		301	(−−)	(−−)	(−−)
Ca	C	−6.510	(−5.670 −7.475)	−0.396	***	173	−5.690	(−5.175 −6.257)	−0.548	***	302	0.115	0.104	<0.001
K	C	−4.559	(−3.962 −5.245)	−0.363	***	173	−4.371	(−3.954 −4.832)	−0.468	***	302	0.632	0.476	0.001
Mg	C	−5.860	(−5.102 −6.731)	−0.390	***	173	−5.654	(−5.113 −6.251)	−0.464	***	302	0.681	0.484	0.001
δ^{13}C	C	0.325	(0.279 0.378)	0.173	*	167	−0.248	(−0.221 −0.277)	−0.047		302	(−−)	(−−)	(−−)
P	N	1.171	(1.043 1.314)	0.640	***	173	1.209	(1.114 1.312)	0.696	***	301	0.655	0.580	0.003
Ca	N	(−−)	(−−)	−0.034		173	(−−)	(−−)	0.091		302	(−−)	(−−)	(−−)
K	N	1.581	(1.362 1.835)	0.130	–	173	1.765	(1.580 1.971)	0.223	***	302	0.245	0.572	<0.001
Mg	N	(−−)	(−−)	−0.045		173	2.283	(2.039 2.555)	0.101	–	302	(−−)	(−−)	(−−)
δ^{13}C	N	0.113	(0.098 0.131)	0.254	***	168	0.101	(0.091 0.113)	0.239	***	305	0.229	0.015	0.107
Ca	P	(−−)	(−−)	0.052		173	1.899	(1.700 2.120)	0.222	***	303	(−−)	(−−)	(−−)
K	P	1.351	(1.176 1.551)	0.392	***	173	1.450	(1.315 1.598)	0.504	***	303	0.412	0.738	<0.001
Mg	P	(−−)	(−−)	0.075		173	1.874	(1.679 2.091)	0.242	***	303	(−−)	(−−)	(−−)
δ^{13}C	P	0.099	(0.085 0.114)	0.347	***	167	0.083	(0.074 0.092)	0.235	***	302	0.059	0.013	0.108
Mg	Ca	0.900	(0.804 1.008)	0.662	***	173	0.993	(0.912 1.081)	0.660	***	304	0.174	0.229	<0.001
δ^{13}C	Ca	(−−)	(−−)	0.096		167	0.043	(0.039 0.049)	0.203	***	303	(−−)	(−−)	(−−)
Ca	K	1.428	(1.249 1.632)	0.459	***	173	1.302	(1.177 1.440)	0.453	***	304	0.279	0.369	<0.001
Mg	K	1.285	(1.132 1.460)	0.534	***	173	1.292	(1.180 1.415)	0.596	***	304	0.946	0.952	<0.001
δ^{13}C	K	(−−)	(−−)	0.123		167	(−−)	(−−)	0.064		303	(−−)	(−−)	(−−)
δ^{13}C	Mg	(−−)	(−−)	0.085		167	0.044	(0.039 0.049)	0.127	*	303	(−−)	(−−)	(−−)

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Table 3. Pairwise relationships between the plot components of key foliar properties, estimated by the multilevel model. "Slope" of the SMA, Pearson's *r* correlation coefficient, "sig" the significance of the correlation, and *n* the number of cases used. Boldface indicates significant difference ($p<0.05$) in slope or elevation and/or shift across the SMA axis. The (−−) sign indicates that the respective test can not be applied. sig: $^{***}<0.001$, $^{**}<0.01$, $^{*}<0.05$, $-<0.1$.

		low fertility					high fertility					sig. of difference in		
Y	X	slope	slope 95%ci	r	sig	n	slope	slope 95%ci	r	sig	n	slope	elevation	shift
C	M_A	0.292	(0.206 0.413)	0.767	***	19	0.408	(0.296 0.563)	0.537	**	33	0.024	(−−)	(−−)
N	M_A	−0.875	(−0.636 −1.204)	−0.732	***	19	−0.939	(−0.645 −1.367)	−0.327	−	34	0.790	0.008	0.103
P	M_A	(−−)	(−−)	−0.104		19	(−−)	(−−)	−0.273		33	(−−)	(−−)	(−−)
Ca	M_A	(−−)	(−−)	−0.241		19	−5.594	(−3.793 −8.250)	−0.474	**	33	(−−)	(−−)	(−−)
K	M_A	(−−)	(−−)	−0.047		19	−3.370	(−2.284 −4.971)	−0.442	*	33	(−−)	(−−)	(−−)
Mg	M_A	−1.638	(−1.081 −2.483)	−0.634	**	19	−1.546	(−1.065 −2.245)	−0.428	*	33	0.686	0.903	0.735
Al	M_A	(−−)	(−−)	0.154		19	(−−)	(−−)	(−−)		33	(−−)	(−−)	(−−)
δ^{13}C	M_A	0.176	(0.104 0.299)	0.671	**	19	(−−)	(−−)	(−−)		31	(−−)	(−−)	(−−)
N	C	−3.025	(−2.047 −4.470)	-0.457	*	19	(−−)	(−−)	(−−)		33	(−−)	(−−)	(−−)
P	C	(−−)	(−−)	0.091		19	(−−)	(−−)	(−−)		33	(−−)	(−−)	(−−)
Ca	C	−14.565	(−9.134 −23.225)	−0.432	−	19	−13.702	(−9.914 −18.940)	−0.680	***	33	0.676	0.001	0.004
K	C	(−−)	(−−)	0.047		19	−8.254	(−5.606 −12.153)	−0.496	**	33	0.001	(−−)	(−−)
Mg	C	−5.615	(−3.923 −8.038)	−0.833	***	19	−3.788	(−2.938 −4.884)	−0.679	***	33	0.037	(−−)	(−−)
δ^{13}C	C	0.603	(0.351 1.036)	0.420	−	19	0.821	(0.560 1.202)	0.306	−	33	0.920	<0.001	0.195
P	N	(−−)	(−−)	0.319		19	3.341	(2.435 4.583)	0.532	**	33	(−−)	(−−)	(−−)
Ca	N	(−−)	(−−)	0.211		19	(−−)	(−−)	0.081		33	(−−)	(−−)	(−−)
K	N	(−−)	(−−)	−0.077		19	3.589	(2.447 5.264)	0.378	*	33	(−−)	(−−)	(−−)
Mg	N	1.856	(1.212 2.842)	0.407	−	19	(−−)	(−−)	0.159		33	(−−)	(−−)	(−−)
δ^{13}C	N	(−−)	(−−)	−0.317		19	0.357	(0.242 0.526)	0.358	*	33	(−−)	(−−)	(−−)
Ca	P	(−−)	(−−)	0.330		19	(−−)	(−−)	0.170		33	(−−)	(−−)	(−−)
K	P	1.659	(1.120 2.458)	0.522	*	19	1.074	(0.804 1.435)	0.532	**	33	0.003	(−−)	(−−)
Mg	P	(−−)	(−−)	0.169		19	(−−)	(−−)	0.076		33	(−−)	(−−)	(−−)
δ^{13}C	P	(−−)	(−−)	0.268		19	(−−)	(−−)	0.232		33	(−−)	(−−)	(−−)
Mg	Ca	0.386	(0.252 0.591)	0.694	***	19	0.276	(0.196 0.390)	0.498	**	33	0.212	<0.001	0.025
δ^{13}C	Ca	(−−)	(−−)	0.113		19	(−−)	(−−)	0.031		33	(−−)	(−−)	(−−)
Ca	K	(−−)	(−−)	0.092		19	1.660	(1.144 2.409)	0.497	***	33	(−−)	(−−)	(−−)
Mg	K	(−−)	(−−)	0.006		19	0.459	(0.312 0.675)	0.477	**	33	(−−)	(−−)	(−−)
δ^{13}C	K	(−−)	(−−)	−0.064		19	(−−)	(−−)	0.116		33	(−−)	(−−)	(−−)
δ^{13}C	Mg	(−−)	(−−)	−0.266		19	(−−)	(−−)	−0.222		33	(−−)	(−−)	(−−)

Table 4. Summary of the Principal Components Analysis for selected soil variables averaged over 0.0–0.3 m depth. Full details on methods used for soil analysis are provided in Quesada et al. (2009a).

Eigenvalue	6.227	2.537	1.597
Proportion of total variance	0.445	0.181	0.114
pH	−0.278	**0.371**	−0.082
Total reserve bases	**−0.328**	−0.072	0.050
Total extractable P[a]	**−0.340**	−0.103	−0.148
Total [N]	−0.290	−0.095	**−0.514**
Total [C]	−0.169	−0.044	**−0.667**
Exchangable [Ca]	**−0.360**	0.162	0.103
Exchangable [Mg]	**−0.367**	0.083	0.202
Exchangable [K]	−0.286	−0.100	0.134
Exchangable [Na]	−0.140	−0.135	−0.022
Exchangable [Al]	0.161	**−0.359**	−0.137
Effective cation exchange capacity	**−0.329**	−0.202	0.109
Base saturation	−0.204	**0.410**	0.237
Fraction sand	0.199	**0.442**	−0.261
Fraction clay	−0.077	**−0.491**	0.187
Axis definition	(in)fertility	texture &Al	C&N

[a] Sum of both inorganic and organic fractions extracted by resin, bicarbonate and NaOH according to a modified Hedley extraction procedure as detailed in Quesada et al. (2009a).

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Table 5. Coefficient estimates from non-spatially multiple linear regressions (OLS), simultaneous autoregressive models at a common fine scale (SAR FS, FS=50 km) and at variant medium scale (SAR MS), for each foliar property on the set of the environmental predictors. FS SARs had a common neighbourhood size of 50 km, while the MS SARs were at 750 km for [C], 1000 km for [P] and δ13C, 1750 km for [Ca] and [K] and 1900 km for [Al]. See text and Fig. B2 for selection of appropriate neighbourhood size. λ gives the autoregression coefficient for each SAR (boldface indicate its significant difference from 0, at p=0.05). Moran's I for each model's residuals tested at a global Bonferroni adjusted level (0.005), with 999 Monte Carlo permutations (bold values indicate the existence of spatial autocorrelation in the residuals). Significance levels for environmental predictors estimates: ***<0.001, **<0.01, *<0.05, −<0.1 and (−−) non significant.

OLS	M_A	C	N	P	Ca	K	Mg	Al	δ^{13}C
Intercept	−9.54E-02 ***	−5.78E-02 **	4.39E-01 ***	−3.09E-01 *	1.63E+00 *	7.34E-01 (−−)	1.16E-01 ***	3.09E+00 *	3.78E-02 (−−)
Fertility PCA*f*	−1.53E-02 **	−5.98E-03 ***	1.02E-02 –	9.07E-02 ***	1.26E-01 ***	7.09E-02 ***	1.79E-02 *		3.11E-03 –
Texture PCA*t*		2.88E-03 (−−)	1.31E-02 **		−4.76E-02 *	−2.50E-02 (−−)			
Soil Carbon PCA*c*	−7.19E-03 (−−)	2.58E-03 (−−)			−7.05E-02 **		−1.79E-02 *		
Temperature			−1.66E-02 ***		−4.41E-02 *	−4.15E-02 **		−1.47E-01 **	−2.60E-03 –
Precipitation	3.88E-05 ***			5.23E-05 *			−4.75E-05 ***	−7.59E-04 **	1.59E-05 *
Dry season precipitation		1.26E-04 ***	−1.24E-04 –			6.61E-04 *		1.09E-02 ***	−9.62E-05 (−−)
Radiation		2.63E-04 *		1.11E-03 –	−2.96E-03 **	1.60E-03 (−−)		8.28E-03 *	
R^2	0.418	0.362	0.498	0.568	0.601	0.488	0.376	0.346	0.305
Moran's I	0.053	**0.394**	−0.049	**0.173**	**0.425**	**0.460**	0.143	**0.477**	**0.469**
SAR FS	M_A	C	N	P	Ca	K	Mg	Al	δ^{13}C
Intercept		−2.73E-02 (−−)		−1.69E-01 (−−)	1.19E+00 –	−4.00E-01 (−−)		1.34E+00 (−−)	6.77E-02 –
Fertility PCA*f*		−4.97E-03 ***		8.26E-02 ***	1.29E-01 ***	6.10E-02 ***			3.40E-03 **
Texture PCA*t*		3.23E-03 *			−4.45E-02 *	−4.38E-02 ***			
Soil Carbon PCA*c*		2.66E-03 (−−)			−6.26E-02 **				
Temperature					−3.48E-02 (−−)	5.68E-03 (−−)		−8.91E-02 –	−3.87E-03 **
Precipitation				5.41E-05 *				−8.40E-04 **	1.68E-05 *
Dry Season Precipitation		8.47E-05 *				1.38E-03 ***		1.21E-02 ***	−9.29E-05 (−−)
Radiation		9.83E-05 (−−)		1.63E-04 (−−)	-1.73E-03 (−−)	4.02E-04 (−−)		1.01E-02 **	
λ		**0.483**		**0.421**	**0.460**	**0.761**		**0.461**	**0.566**
Moran's I		0.033		0.018	0.030	0.023		0.154	−0.010
SAR MS	M_A	C	N	P	Ca	K	Mg	Al	δ^{13}C
Intercept		−5.83E-02 **		−2.42E-01 –	1.71E+00 **	4.14E-01 (−−)		3.54E+00 **	4.45E-02 (−−)
Fertility PCA*f*		−6.01E-03 ***		5.97E-02 ***	1.13E-01 ***	5.87E-02 ***			3.58E-03 *
Texture PCA*t*		2.86E-03 *			−3.87E-02 –	−2.53E-02 –			
Soil Carbon PCA*c*		2.60E-03 (−−)			−6.81E-02 **				
Temperature					−4.50E-02 **	−2.99E-02 *		−2.03E-01 ***	−2.98E-03 *
Precipitation				5.55E-05 ***				−7.94E-04 ***	1.82E-05 **
Dry season precipitation		1.26E-04 ***				5.20E-04 (−−)		1.25E-02 ***	−1.21E-04 *
Radiation		2.66E-04 **		6.51E-04 (−−)	−3.33E-03 ***	1.56E-03 –		1.35E-02 ***	
λ		0.012		**0.832**	**−2.311**	**0.849**		−0.856	−0.622
Moran's I		**0.392**		−0.060	**0.377**	**0.381**		**0.390**	**0.485**

Table 6. Kendall's partial correlation τ for the environmental contribution (plot effect estimate) of each foliar property with the set of environmental predictors. Kendall's τ are estimated as described in Legendre and Legendre (1998, pp. 202). Their significance is computed based on Maghsoodloo and Laszlo Pallos (1981). Bold values indicate a very strong correlation ($p<0.001$) and italics indicate significant correlations at $p<0.01$; see text for details.

	M_A	C	N	P	Ca	K	Mg	Al	δ^{13}C
Fertility PCA*f*	−0.201	*−0.233*	0.204	**0.475**	**0.475**	**0.337**	0.220	0.097	0.203
Texture PCA*t*	0.048	0.103	0.115	0.043	**−0.272**	−0.169	−0.178	−0.149	0.022
Temperature T_a	0.107	0.051	**−0.382**	*−0.256*	−0.081	**−0.408**	0.031	−0.176	−0.133
Precipitation P_a	**0.329**	**0.300**	−0.178	0.171	−0.010	0.113	**−0.306**	0.016	*0.244*
Radiation Q_a	−0.058	0.152	0.018	0.117	−0.140	0.075	0.003	−0.139	0.119

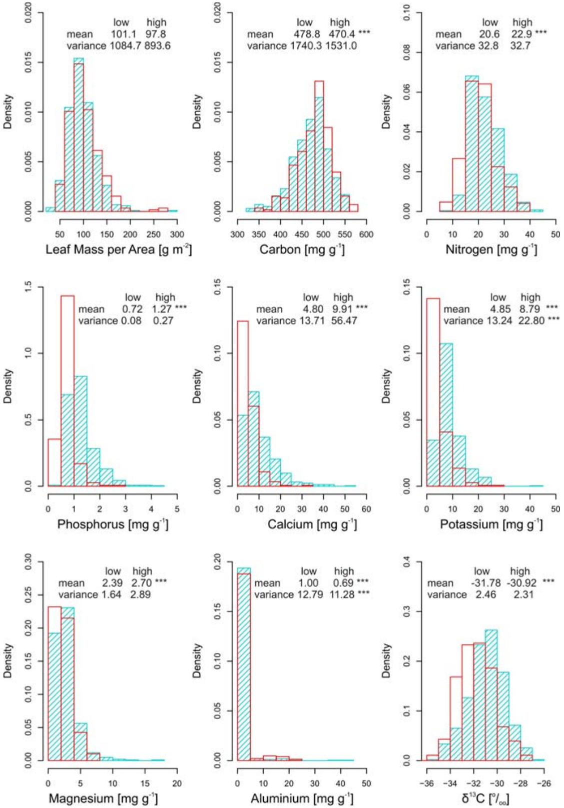

Fig. 1. Probability density histograms of raw data per fertility group. Red bars represent low and blue bars high soil fertility plots, as defined by the quantitative determinations of the level of total reserve bases from 0–30 cm depth (see text). Also given for each histogram are the mean and the variance for each foliar property. Significant differences in mean values and/or variances between the two fertility groups were identified with an one way anova and a Fligner-Killeen test respctivelly. Significance codes: ***<0.001, **<0.01,*<0.05.

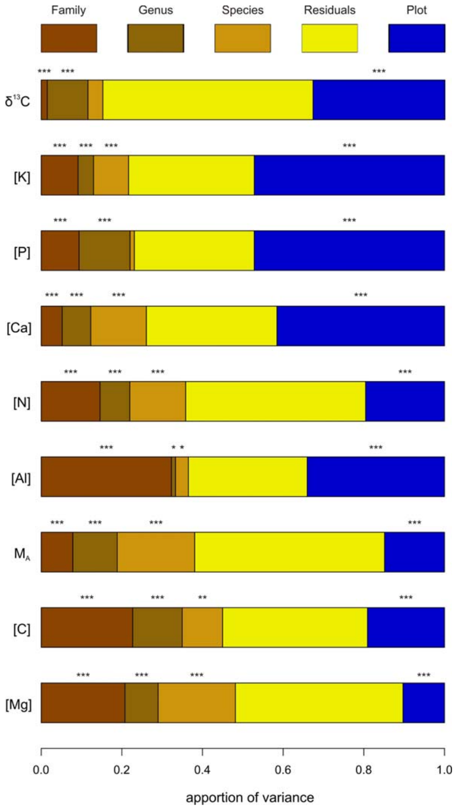

Fig. 2. Partitioning of the total variance for each foliar property into genetic (family/genus/species), environmental (plot) and an error (residual) components. Foliar properties are sorted from less to more phylogenetically constrained. Significance of each variance component was tested with a likelihood ratio test (Faraway, 2004; Galwey, 2006). Significance codes: $^{***}<0.001$, $^{**}<0.01$, $^{*}<0.05$.

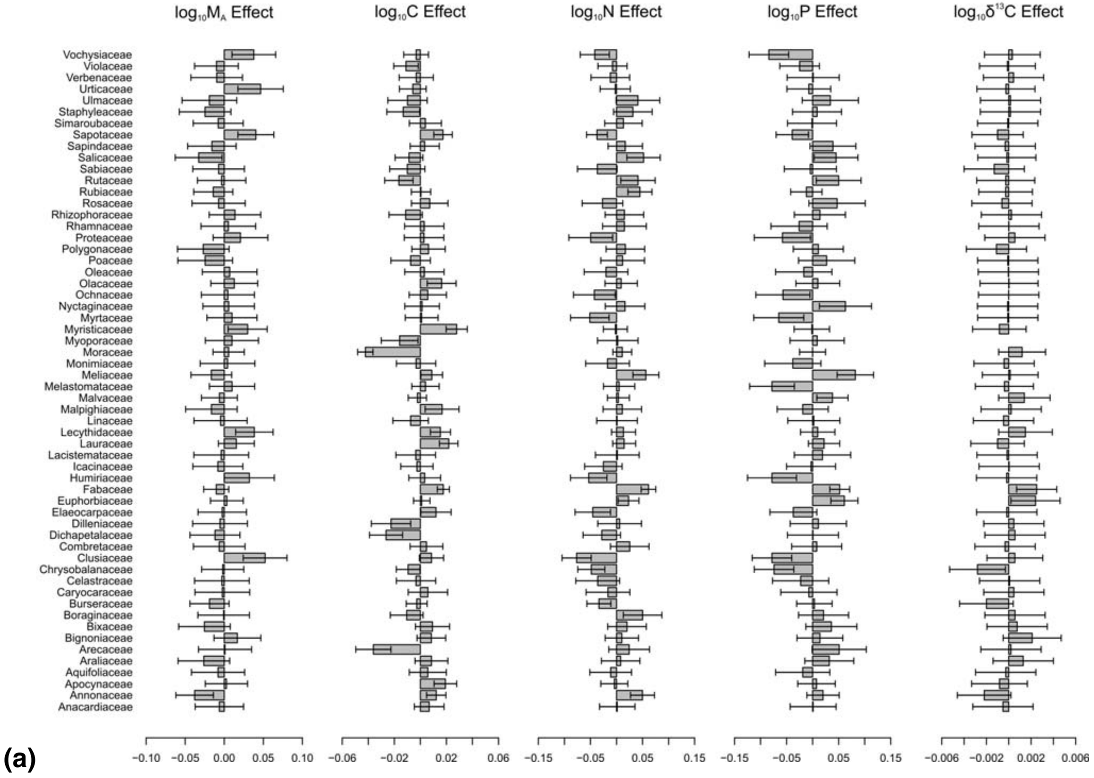

Fig. 3. Family effect±standard error estimates of the fitted multilevel model for leaf mass per unit area (M_A) expressed in g m^{-2}, elemental concentrations (all in mg g^{-1}) and δ^{13}C expressed in [$^0/_{00}$]. Note the $\log_{10}$ scale used for all parameters.

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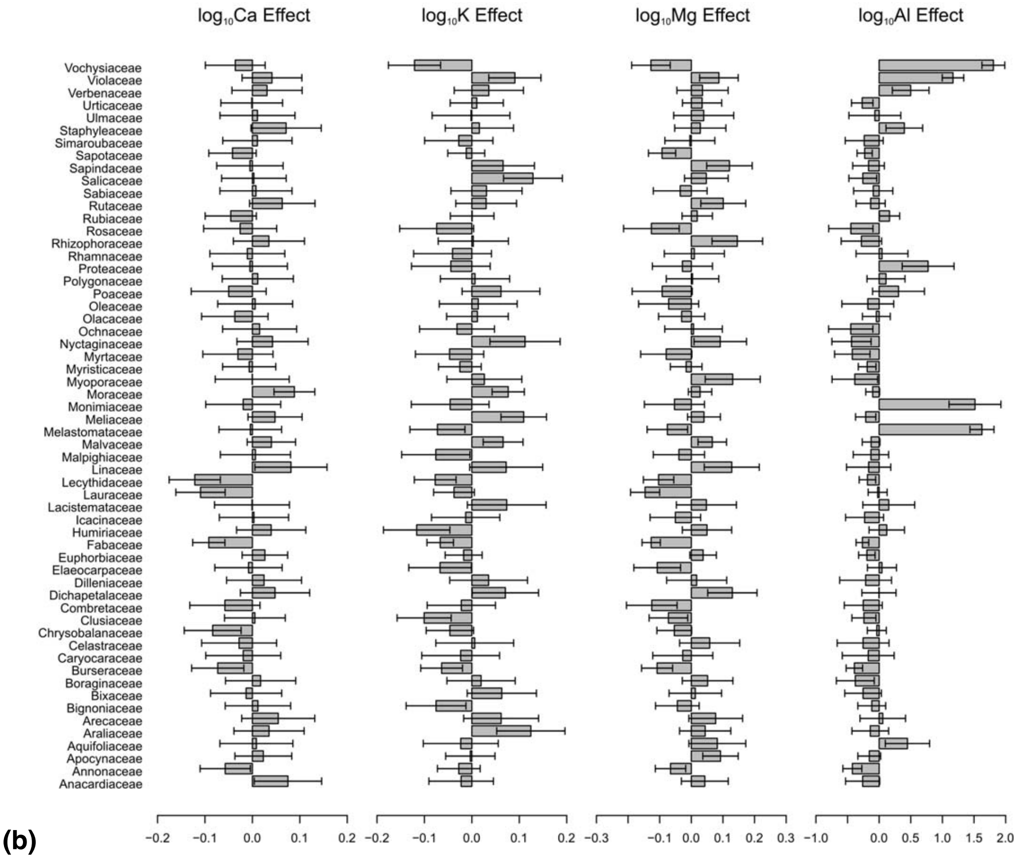

Fig. 3. Continued.

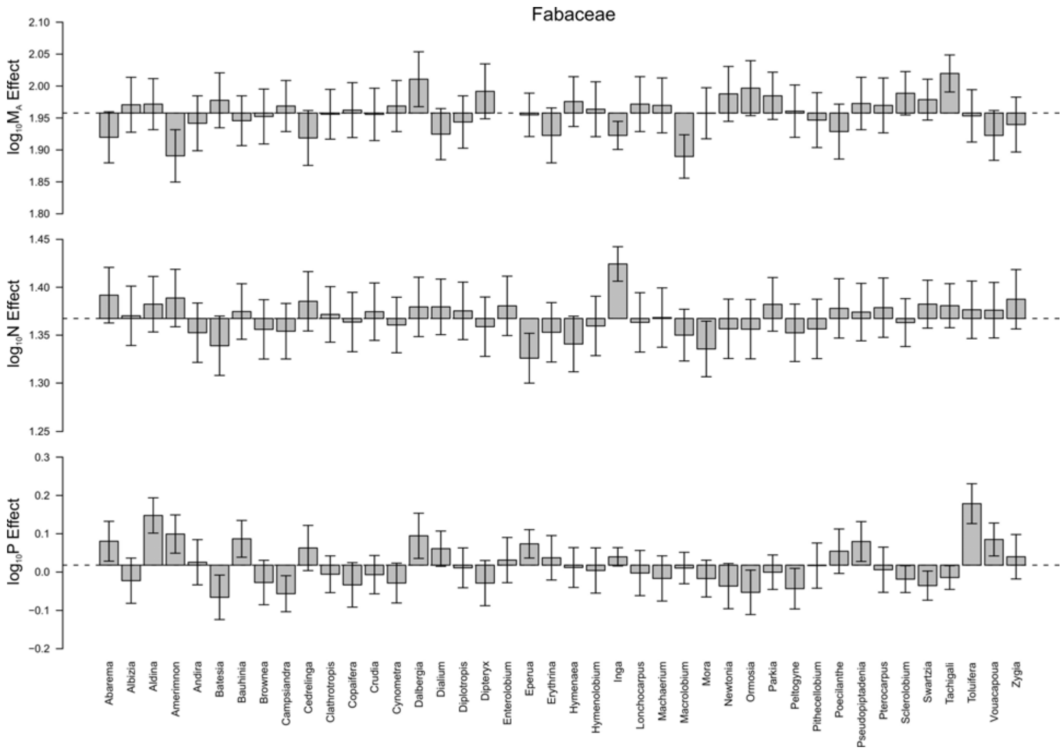

Fig. 4. Genus effect±standard error estimates from the multilevel model for sampled genera within *Fabaceae*. The dotted line illustrates the (mean) family effect for leaf mass per area (M_A) in g m^{-2} and leaf N and leaf P concentrations (mg g^{-1}). Note the log$_{10}$ used scale in all cases.

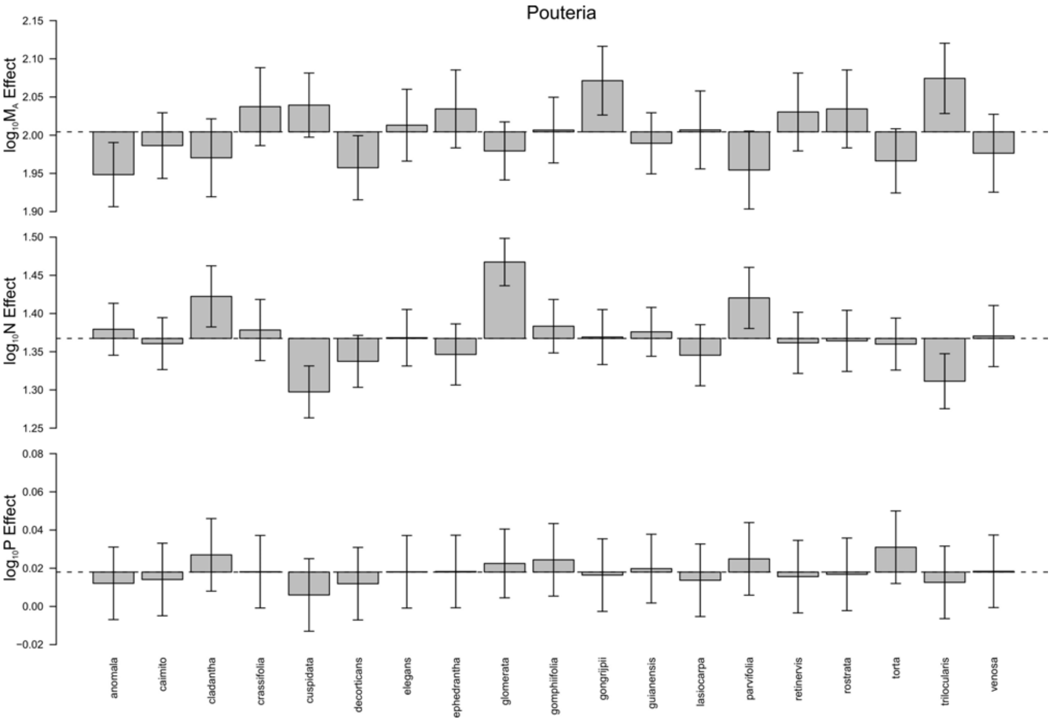

Fig. 5. Species effect±standard error estimates from the multilevel model for species within *Pouteria*. The dotted line illustrates the mean (family+genus) effect for leaf mass per area (M_A) in g m^{-2} and leaf P and leaf N concentrations (mg g^{-1}). Note the log$_{10}$ used scale in all cases.

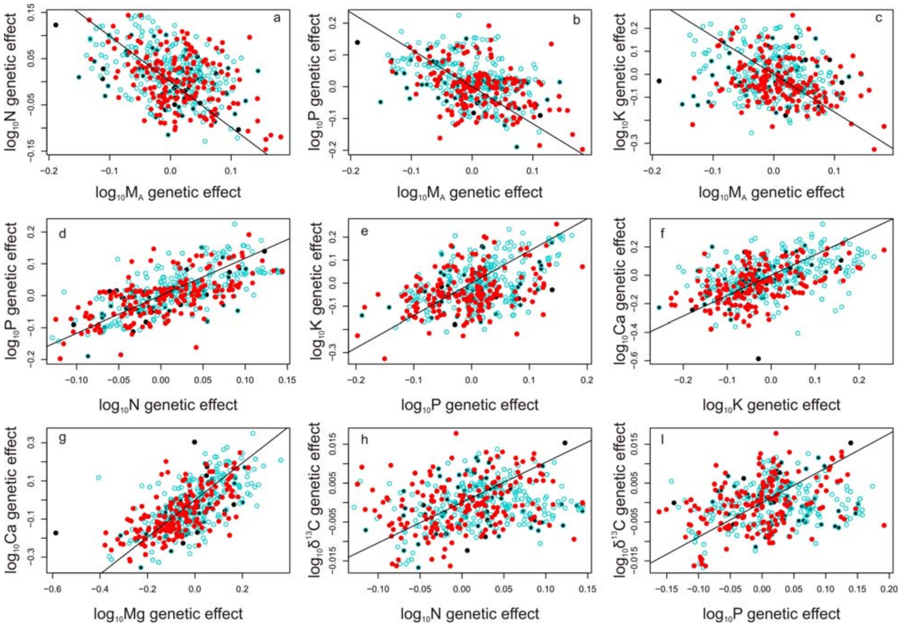

Fig. 6. Standardized Major Axis (SMA) regressions lines between the genetic components of key foliar properties pairs. Red dots indicate species found on low fertility sites and blue circles indicate species found on high fertility sites. Note the overlap for species found on both soil fertility groups (black dots, see text for details). Common slope lines were fit in all cases, note however differences in elevation(intercept) and/or shifts along the SMA axis in Table 2.

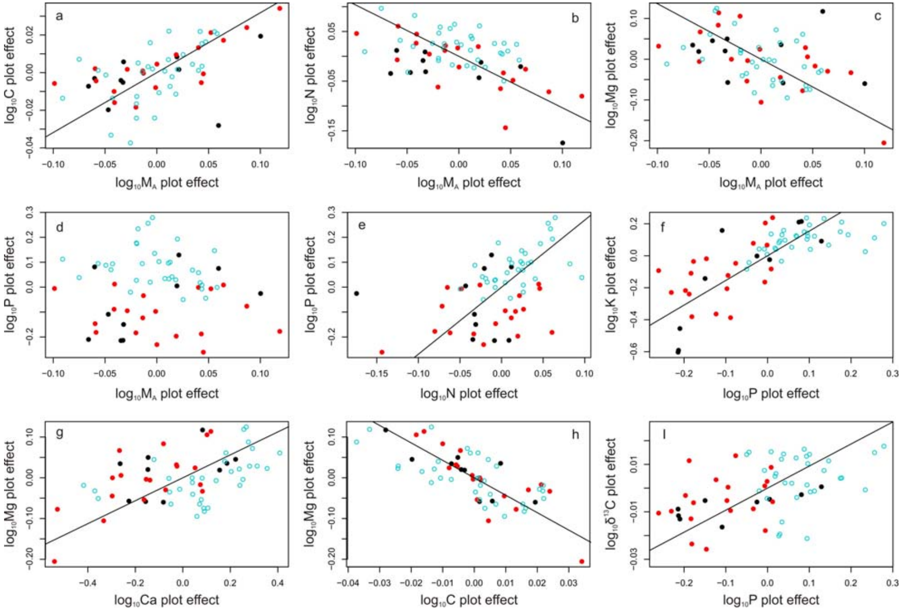

Fig. 7. Standardized Major Axis (SMA) regressions lines between the plot-environmental components for key foliar properties. Red dots indicate low fertility sites, blue circles high fertility sites and black dots the plot effect of sites not classified to any fertility group. Differences in slope, elevation and/or shifts along the SMA axis are summarized in Table 3.

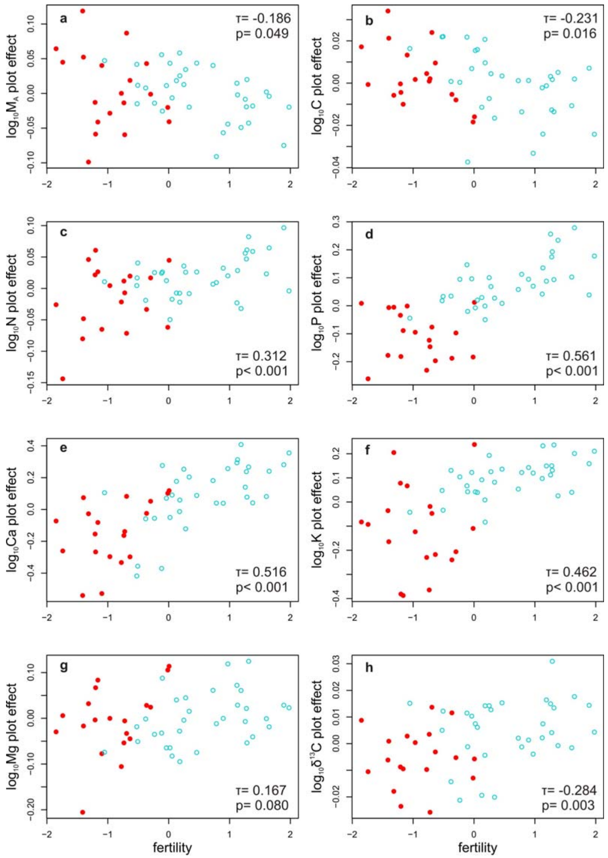

Fig. 8. Relationships between plot level effects and the fertility axis, for key foliar properties. Red dots indicate low fertility plots and blue circles indicate high fertility ones. Full Kendall's τ along with its significance is also given.

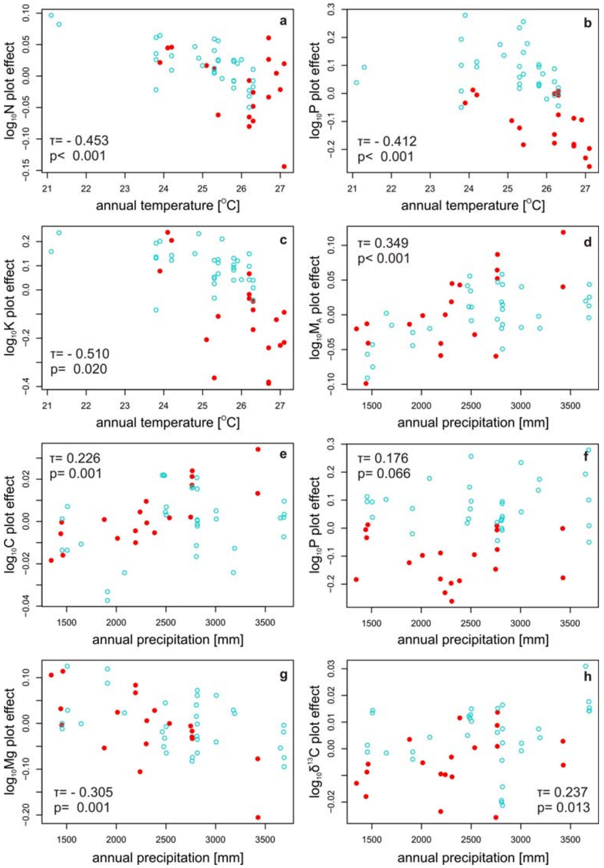

Fig. 9. Relationships between plot level effects and annual temperature and precipitation for key foliar properties. Red dots indicate low fertility plots and blue circles indicate high fertility ones. Full Kendall's τ along with its significance is also given.