



Floristic and functional affiliations of woody plants with climate in western Amazonia

Nathalie Butt^{1*}, Yadvinder Malhi¹, Oliver Phillips² and Mark New³

¹Environmental Change Institute, Oxford University Centre for the Environment, Oxford, UK, ²Earth and Biosphere Institute, School of Geography, University of Leeds, Leeds, UK, and ³Oxford University Centre for the Environment, Oxford, UK

ABSTRACT

Aim To test whether a direct relationship exists between the relative abundance of woody plant genera and precipitation regime along the north–south climate gradient of the western Amazon.

Location Lowland rain forests in the western Amazon.

Methods Floristic data on 91 woody plant genera, from 39 0.1-ha plots across the western Amazon, and precipitation data from a 0.5° global data set were used to test for correlations between plant relative abundance (defined as percentage number of stems \geq 2.5 cm diameter at breast height for each woody plant genus per plot) and derived dry-season variables. Moisture preference was then assessed in terms of pioneer and shade-tolerant life-history strategy.

Results There were significant associations between the distribution of plant relative abundances and seasonal precipitation variables in 34% of genera analysed. Significant differences were identified in size-class distribution between dry affiliates and generalists. Dry affiliates were not dominant in any size class in any plot type, whereas climate generalists dominated most of the size classes in the dry plots and the mid-range size classes in the wet plots. Dry-affiliate genera were a minority, even in dry forests. Wet-affiliate genera were correlated with shade tolerance, whereas genera with no rainfall affiliation were often pioneers.

Main conclusions The results suggest that moisture variable seasonality influences community composition in a manner that can be related to the life-history trade-off between shade tolerance and pioneer ranking. One possible reason for higher diversity in wetter forests is that high rainfall amplifies the niche space available to shade-tolerant plants. Determining which plant groups are constrained by which environmental variables can contribute to our understanding of how forest composition may be changing now, and how it may change under future climate: if shade-tolerant trees are also drought-intolerant, community structure in wet forests may be more vulnerable to future increases in moisture stress.

Keywords

Amazon forest, community composition, dry-season intensity, precipitation gradient, relative abundance, shade tolerance.

*Correspondence: Nathalie Butt, Environmental Change Institute, Oxford University Centre for the Environment, South Parks Road, Oxford OX1 3QY, UK.
E-mail: nathalie.butt@eci.ox.ac.uk

INTRODUCTION

In the Amazon region, relationships between climate and biota have been established at the biome level, but species distributions are not well mapped, let alone properly understood (Terborgh & Andresen, 1998; Phillips *et al.*, 2003a; Tuomisto

et al., 2003; Killeen *et al.*, 2007). Recent modelling work has suggested that Amazonian plant diversity has been markedly underestimated (Hopkins, 2007). Many possible underlying processes could determine plant distributions across the Amazon Basin, for example soil type or distance dependence (Clinebell *et al.*, 1995; Terborgh *et al.*, 1996; Givnish, 1999;

Hubbell, 2001; Pitman *et al.*, 2001, 2002; ter Steege & Hammond, 2001). Species richness (Gentry, 1988b) and tree α diversity and density (ter Steege *et al.*, 2003) have each been related to rainfall seasonality, as have gradients in tree composition and function (ter Steege *et al.*, 2006), but our understanding of the underlying ecosystem biotic and abiotic processes remains incomplete.

Niche theory (Hutchinson, 1957) does not clearly explain existing patterns of species ranges and their constraining environmental variables. While the neutral theory of biodiversity and biogeography (Hubbell, 2001) invokes stochastic processes such as dispersal limitation as the mechanisms determining distributions, partitioning along environmental gradients is clearly also important for plant community composition (Silvertown, 2004). Tuomisto *et al.* (2003) showed that differences in floristic composition between Amazonian sites in a landscape are driven more by environmental than dispersal factors. Condit *et al.* (2002) also argued that beta-diversity patterns in the western Amazon could not be explained solely by the neutral theory, rather that distribution can be thought of as being constrained by both a plant's dispersal capacity and its ability to survive, which are determined by the biotic and abiotic environment.

Precipitation has long been indicated as a major environmental determinant in floristic assemblages (Schimper, 1898; Bailey & Sinnott, 1916; Beard, 1944; Holdridge, 1947; Grubb & Whitmore, 1966; Pyke *et al.*, 2001). Gentry (1988b) identified dry-season length as the key control of vascular plant diversity in Amazonia, and later work (Clinebell *et al.*, 1995; ter Steege *et al.*, 2003) confirmed this observation. The link between α diversity and stem number (ter Steege *et al.*, 2003), and stem number and precipitation (Losos and CTFS Working Group, 2004) is well known. An analysis by Losos and CTFS Working Group (2004) found that, for mid-storey trees (between 20 and 60 cm d.b.h.), tree density is strongly correlated with seasonality. Malhi *et al.* (2002b) demonstrated a correlation between dry-season intensity and forest basal area and stem density, indicating a definite and important relationship between tree abundance and rainfall regime. Total precipitation and precipitation seasonality are thus strongly implicated in both the diversity and the physical structure of tropical forest communities.

Shade tolerance has been discussed as a mechanism in species coexistence (Wright, 2002) and is associated with plant abundance (Duivenvoorden *et al.*, 2002). These studies found that where water is not limiting, shade-tolerant species have a competitive advantage (Wright, 2002). Conversely, where water supply is limited and limiting (through root competition for water, for instance), biomass production is restricted, more sunlight reaches the ground, and shade tolerance offers less competitive advantage. This fundamental trade-off may underpin forest structure and function, community composition, and therefore plant distributions across the tropics. Consistently high moisture levels could enhance shade tolerance within the local species pool and promote understorey

diversity (Givnish, 1999; ter Steege *et al.*, 2003). Pitman *et al.* (2002) linked consistent water availability to increases in understorey species persistence and stem densities, and Gentry & Emmons (1987) showed a negative correlation between understorey species diversity and rainfall, which becomes stronger with increasing dry-season stress.

Here, using previously collated Gentry floristic plot data and improved climate data, we aim to elucidate and quantify the relationships between the relative abundance of woody plant genera and rainfall along a north–south precipitation gradient in the western Amazon and investigate how the composition of diverse plant communities is related to rainfall. We focus on the frequency of each woody plant genus per plot: we use 'relative abundance' as shorthand throughout. We then establish which groups of trees and woody plants are most constrained by precipitation seasonality. Our aims are to: (1) derive rainfall affiliations for the more abundant genera in western Amazonia; (2) explore the relationship with size-class distribution and precipitation regimes; and (3) explore the pioneer and shade-tolerance characteristics of rainfall-dependent groups with regard to community composition. We test the hypotheses that wet affiliation is linked to shade tolerance and dry affiliation to pioneer life history, and that larger trees are more drought tolerant due to a larger water capacity and greater exposure. As an adjunct to the third aim, we consider whether the difference in plant densities between wet and dry forest plots introduces a methodological bias in our determination of rainfall affiliations.

MATERIALS AND METHODS

Study region

We define western Amazonia as the area between latitudes 1° N and 20° S, and longitudes 62° W and 79° W, and the study region is located within this area (Fig. 1). This region

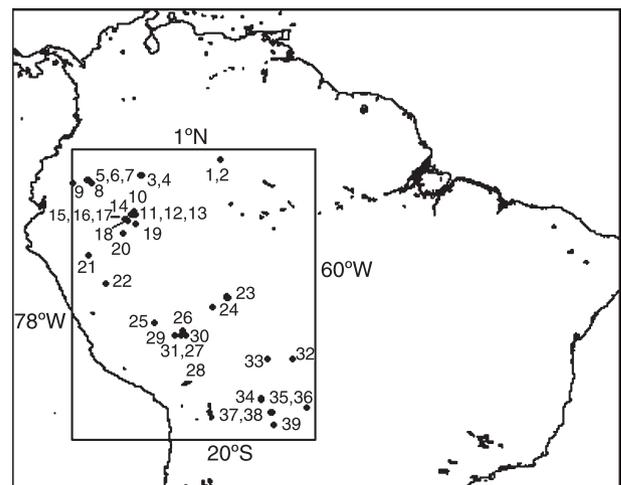


Figure 1 Distribution across the western Amazon of Gentry and Yasuni plots used in the analysis, in the marked area. Numbers correspond to plot numbers in Appendix S1.

includes the most species-rich forests in the world (Gentry, 1988a) and has a well-documented gradient in precipitation regime and seasonality, and directly comparable floristic plot data are available. The mean annual precipitation across the Amazonian tropical rain forest region is *c.* 2200 mm (Malhi & Wright, 2004), although this varies temporally, especially in El Niño years (Müller, 1982; Barry & Chorley, 2003). Changes in solar radiation through the year influence rainfall patterns: seasonality of rainfall in Amazonia is primarily a result of convective rains that migrate north–south according to the angle of insolation, in synchrony with the intertropical convergence zone over the Atlantic.

A standard indicator for the dry season in the lowland tropics is when precipitation is below 100 mm per month (ter Steege *et al.*, 2003) as transpiration of a wet tropical forest is typically *c.* 100 mm per month (Malhi *et al.*, 2002b); dry-season length is frequently defined in terms of the number of months per year that fit this criterion (Fig. 2a). However, dry-season intensity is also likely to be important for plant growth and survival. As the < 100-mm measure is very coarse, a more informative way of looking at seasonality is to look at the total rainfall over the three driest months (Fig. 2b). Eastern Amazonia has long but relatively weak dry seasons, the far north and south-east have the most intense, and north-west Amazonia normally has no dry season. The north–south gradient in western Amazonia is clear, with some complications caused by wet zones in close proximity to the Andes.

The dry season begins slowly in the north and is irregular in length, centred on January, while in southern Amazonia the onset is sudden and regular, with peak intensity centred on July–August (Marengo *et al.*, 2001). Across the region, there is a seasonal migration of the dry season shifting from south to north (Fig. 2c).

Floristic data

We used the Gentry plot data set from the SALVIAS database (<http://www.salvias.net/pages/index.html>). All stems ≥ 2.5 cm d.b.h. were sampled in ten 2×50 -m 0.01-ha transects. This is the 0.1-ha technique, developed by Gentry (1982) and commonly referred to as ‘Gentry plots’, which samples a larger proportion of the flora than the 1-ha plot protocol (a one-off census in a 1-ha area of all stems > 10 cm d.b.h.) due to the inclusion of smaller stem sizes (Phillips & Miller, 2002; Phillips *et al.*, 2003b). Vouchers of plants were collected and identified at the Missouri Botanic Garden. The analysis used 39 plots below 1000-m elevation (lowland) and west of 62° W. Floristic data for four of the plots, in Yasuni, Ecuador, were provided by M.J. Macia. A measure of relative abundance (percentage frequency of each tree genus per plot) was calculated to enable comparisons in the representation of each genus across plots and varying precipitation regimes (see Appendix S1 in Supplementary Material for data on each plot), and to account for the differences in plant numbers between plots. Although not strictly lowland forest, three plots in the very dry south-east

of the region were included as part of the precipitation gradient and to provide information on the plant distribution continuum. Figure 1 gives the location and distribution

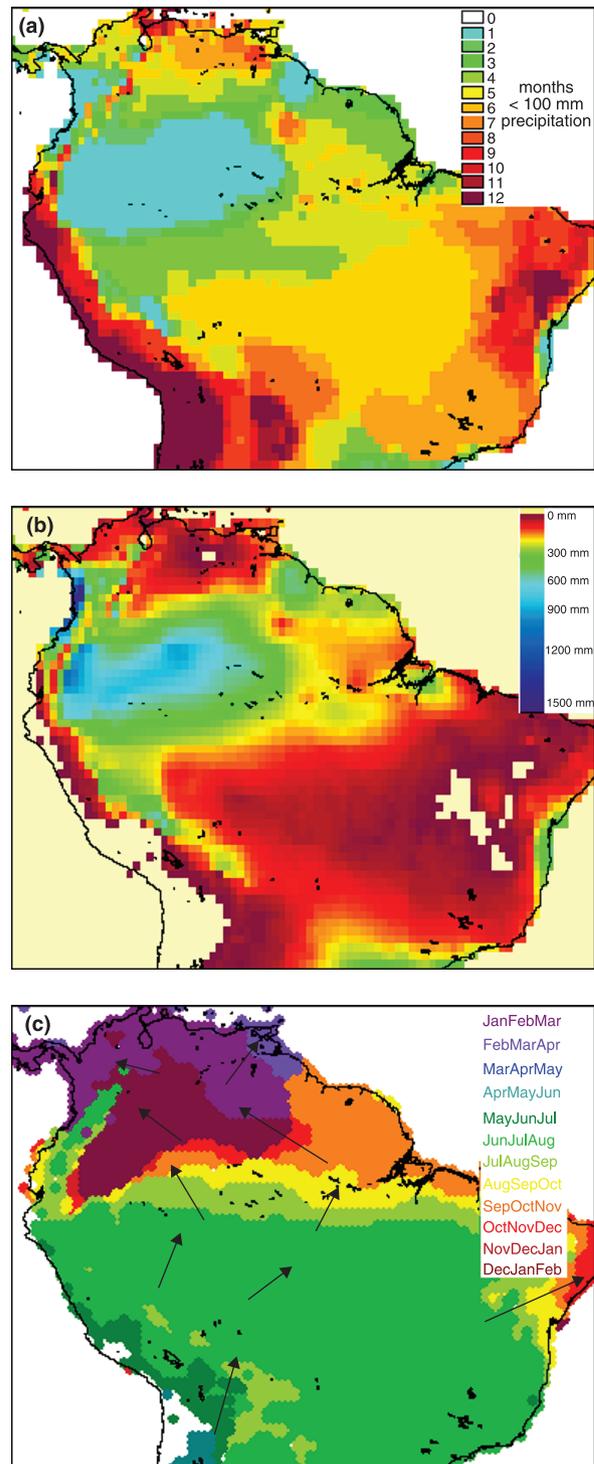


Figure 2 (a) Dry-season length expressed as number of months receiving 100 mm precipitation or less, on average. (b) Dry quarter rainfall (mm) per 0.5° pixel, derived from the Climate Research Unit (New *et al.*, 1999) global data set, 1961–1998. (c) Timing of dry season (driest 3 months) across the region; arrows indicate direction of temporal shift.

of the plots used in the analysis across the western Amazon, ranging from Bolivia in the south to Venezuela in the north. The north–south rainfall gradient in western Amazonia is complicated by local orographic effects at the base of the Andes that make interpolated precipitation estimates unreliable. For this reason, data from plots very near the Andes were excluded from the analysis.

Species diversity ranged from 32 to 276 species per 0.1-ha sample (Gentry, 1982) so that most species were too rare (e.g. fewer than one individual per sample unit) to include in the analysis. Even in relatively well-sampled regions (e.g. south-eastern Peru), rare species in the area are very likely to be missed. Moreover, many more trees were accurately identified to genus than to species – about a third of all trees recorded were not identified to species level (and in the Gentry data set many were identified only to morphospecies). Therefore we used genus-level plant distribution data for plants of diameter > 2.5 cm d.b.h. As many Amazonian congeneric tree species are ecologically similar (cf. ter Steege & Hammond, 2001; Baker *et al.*, 2004; Laurance *et al.*, 2004), we anticipate that relatively little ecological precision was lost by conducting the analysis at genus rather than species level.

Methodology and statistical analysis

Climate data were obtained from the Climate Research Unit's (UEA, Norwich, UK) 0.5° global data set (New *et al.*, 1999). These data cover the period 1961–98, and were assembled from station time-series data. The data were interpolated using thin-plate splines to provide gridded fields. Accuracy was evaluated through cross-validation and comparison with other climatologies (New *et al.*, 1999). Agreement is reasonable in lowland Amazonia, but decreases in close proximity to the Andes due to steep spatial gradients. From this monthly data set, precipitation data were used to derive a measure of dry-season intensity for rainfall and rainfall-related variables. For each (half-degree) pixel, the sum of the minimum 3-months' precipitation was calculated and then used as a dry-season (intensity) measure, although in the far north of the region the dry season is nominal as monthly precipitation rarely falls < 150 mm per month in the driest 3 months. The mean interpolation error for these 0.5° data across the Amazon region was estimated (through cross-validation) to be 20 mm (or 20%), but smaller in lowland areas (New *et al.*, 2000). For several plots in southern Peru close to the Andes (25–29, 31), local rainfall data were used as they were considered to be more accurate (O. Phillips, personal observation). To increase the scope of the analysis, two other precipitation-related variables were included: soil water content (SWC) and potential evapotranspiration minus precipitation (PET – *p*). PET (from the Climate Research Unit) was calculated from temperature, sunshine/radiation, wind and humidity data using the Penman–Monteith equation. The SWC estimates were obtained from the Sheffield dynamic vegetation global model (DVGGM); the internal soil hydrology model uses FAO soil map data to define soil parameter values (Woodward & Lomas, 2004). The data set created for the analysis

represented the average monthly climate (1961–98) and accounted for seasonal variation across the year, not variability between years.

Relative abundance, derived from the percentage number of stems ≥ 2.5 cm d.b.h., was determined for each woody plant genus for each plot; size-class distributions were also calculated. For the present purpose we analysed only genera that occurred in one or more plots (91 genera), with over 1% abundance (this represents only 12% of a total *c.* 700 identified genera, but 59% of 20,000 recorded stems in these plots). There was no significant difference between using absolute and relative abundance in the correlation analysis (see below), but relative abundance allowed for cross-plot comparisons. For each genus, we correlated each moisture variable (dry quarter precipitation, PET – *p*, SWC) with the relative abundance of that genus across all sites. For each genus, the correlation coefficients (Kendall's τ) derived against each moisture variable were averaged to produce a rainfall seasonality ranking.

Kendall's τ -tests, which assess the significance or strength of the measured correlation (Kanji, 1999), were used to explore the nature of the relationship between precipitation and abundance. This nonparametric bivariate correlation makes no assumption of linearity or distribution of the values, and is especially statistically robust in the case of small data sets. Bonferroni's correction for multiple comparisons was applied to give $P < 0.05$ and $P < 0.01$ equivalents (Grafen & Hails, 2002). The 91 genera were then each initially classified into one of two categories: no correlation with moisture, or correlation with one, two or three moisture variables. Those with a significant correlation were then allocated to one of seven categories according to variables with which they were correlated (Appendix S2). Stem density differences among wet and dry plots were evaluated using *t*-tests. Plots were 'dry', 'intermediate' or 'wet' according to mean dry quarter rainfall (0–150 mm, strongly seasonal; 150–300 mm, moderate dry season; > 300 mm, no dry season, respectively). These rainfall amounts are ecologically significant as cut-offs for different forest zones as the evapotranspiration of a wet rainforest is in the order of 300 mm over 3 months: rainfall < 300 mm indicates some water stress, and < 150 mm indicates severe water stress. Available soil water in the top 1 m of rainfall soil is typically 100–150 mm, hence rainfall < 300 mm results in moisture depletion in the top metre of soil and < 150 mm depletion below the top 1 m (Malhi *et al.*, 2002b).

A Pioneer index was used to rank genera according to the extent to which they are perceived to be pioneers. This index approach, adapted from an ethnobotanical technique (cf. Phillips & Gentry, 1993), reflects the degree of consensus among botanists familiar with the taxa, in this case three botanists (O. Phillips, Rodolfo Vasquez, Abel Monteagudo) and collector's label comments in herbarium reference material. Each taxon was judged by each botanist on one or more independent occasions, as a 'non-pioneer' (0) or a 'pioneer' (1), and the average calculated for that taxon–expert combination. Each taxon's consensus score was the sum of these average values divided by the number of experts consulted, so that the index

had a potential range of zero to unity. For our analysed genera, scores ranged from 0 to 0.622 (Appendix S2). These values were then compared with the rainfall regime affiliation score.

The distribution of the plots was such that two or more sometimes fell within the same pixel (of climatological data), giving rise to concerns about possible spatial autocorrelation. These concerns were explored by aggregating the genera abundance data of these plots to the 0.5° grid level (to correspond with the resolution of the climate data) – the analysis gave very similar results to the 39-plot analysis, but because there were fewer plots (23), information was lost. Aggregated results are also given in the Results section, but our discussion will focus on the 39-plot analysis.

RESULTS

The range of densities was consistent with other findings for Amazonia from a largely independent data set assembled by the RAINFOR project. For example, for trees larger than 10 cm d.b.h., tree density varies between around 350 and 1200 ha⁻² for this data set, and between 350 and 950 ha⁻¹ (basal area *c.* 20–40 m² ha⁻¹) in the RAINFOR data (Phillips *et al.*, 1994; Malhi *et al.*, 2002a).

Climate affiliations

For two-thirds (60) of the genera analysed, no significant correlation was found between relative abundance and precipitation or precipitation-related variables (Table 1). Thirty-one genera (34%) did show a correlation with one, two or all three of the moisture variables. Rainfall seasonality rankings are given in Appendix S3. Of the 31 genera with a significant correlation, 23 (70%) were associated with all three moisture regime variables (dry quarter precipitation, PET – *p* and SWC), and

Table 1 Summary of correlations (Kendall's τ) between generic relative abundance (percentage frequency of each genus per plot for woody plant genera > 2.5 cm d.b.h. across 39 western Amazonian plots) and climate variables.

	Number (%)
All genera	
Significant correlation	31 (34) ($P < 0.05/P < 0.01$)
No significant correlation	60 (66)
Correlated genera	
All three variables	23 (70)
Dry quarter, PET – <i>p</i>	4 (13)
SWC	2 (6)
PET – <i>p</i> , SWC	1 (3)
PET – <i>p</i>	1 (3)

Overall breakdown (of the 91 genera analysed) and (below) breakdown of the correlation between those affiliated with seasonal rainfall by precipitation variable.

Dry quarter, summed rainfall of the three driest months; PET – *p*, potential evapotranspiration minus precipitation; SWC, soil water content.

four (13%) with dry quarter precipitation and PET – *p*. Each genus was associated with wetter or drier conditions according to the correlation coefficients (Appendix S2). Table 2 gives the wet/dry/generalist associations for all 91 genera. Of those with a significant correlation with precipitation/precipitation-related variables, four genera (13%) were correlated with drier conditions and the remaining 27 genera (87%) with wetter conditions. Five other genera were correlated only with annual rainfall, in a separate analysis (Appendix S2).

The aggregated plots analysis ($n = 23$, using aggregation to the 0.5° grid) showed some changes in the results for a few genera: *Bauhinia*, *Capparis*, *Coussarea*, *Paullinia*, *Serjania*, *Strychnos*, *Swartzia* and *Talisia* were generalists, while *Iriartea*, *Rinorea* and *Trigynaea* were wet affiliates. Overall, using the aggregated data set, 3% of genera were dry-affiliated, 26% were wet-affiliated and 70% were generalists.

One family had genera associated only with drier conditions: Capparaceae (*Capparis*). *Acacia* was the only genus from Fabaceae (10 genera), and *Arrabidaea* the only genus from Bignoniaceae (five genera) to be affiliated with drier conditions. Of the 91 genera, all genera analysed in the Myristicaceae (three), Rubiaceae (three) and Sterculiaceae (two) were affiliated with wetter conditions. Arecaceae and Moraceae both had several genera with generalist affiliation (seven and five, respectively), and for Moraceae only one was affiliated with wetter conditions (*Perebea*). Only Fabaceae had genera in all three categories (generalist, wet and dry). Of these 91 abundant genera, 15 comprised only liana species. One of these liana genera (*Arrabidaea*) was associated with drier conditions, two with wetter conditions (*Paullinia* and *Strychnos*), and the other 10 (*Adenocalymna*, *Callichlamys*, *Cissus*, *Clytostoma*, *Combretum*, *Cydista*, *Dalbergia*, *Doliocarpus*, *Forsteronia* and *Salacia*) appeared to be climate generalists.

Are there more wet-affiliated genera simply because there are more plants in wet plots? An analysis to test the results for 'wet' and 'dry' genera (using *t*-tests) showed that there are significant differences between the proportions of 'wet'- and 'dry'-affiliated plants across the rainfall gradient. These were calculated as the fraction of all recorded genera in the plots (including those not used in the analysis): dry-affiliated plants comprised 8% of the total in dry plots, 4% in intermediate plots and 2% in wet plots; wet-affiliated plants made up 6% of the total in dry plots, 12% in intermediate plots and 21% in wet plots. A comparison across plots showed that, for both dry and wet affiliates, the differences in relative abundance were greatest between dry and wet plots ($P < 0.001$ and $P < 0.02$ respectively). The differences in relative abundance of dry affiliates between wet and intermediate plots, and of wet affiliates between dry and intermediate plots, were also significant ($P < 0.001$ and $P < 0.04$, respectively). These significant differences in stem numbers between plots indicate that wet affiliates outnumbered dry affiliates, independently of stem density. It also demonstrates that the genera used in the analyses were a representative sample of the overall plot floristic compositions – the proportional relationships hold across all plots, including those not used in the analysis.

Table 2 Climate variable seasonality correlations (Kendall's τ) by genera

'Dry' affiliation: **Acacia* (Fabaceae); **Arrabidaea* (Bignoniaceae); **Aspidosperma* (Apocynaceae); **Capparis* (Capparaceae)

'Wet' affiliation: *Aniba* (Lauraceae); **Bauhinia* (Fabaceae); *Coussarea* (Rubiaceae); **Cyathea* (Pteridophyta); **Duguetia* (Annonaceae); **Endlicheria* (Lauraceae); **Eschweilera* (Lecythidaceae); **Faramea* (Rubiaceae); **Guarea* (Meliaceae); **Gutteria* (Annonaceae); **Inga* (Fabaceae); **Iryanthera* (Myristicaceae); **Licania* (Chrysobalanaceae); **Mabea* (Euphorbiaceae); **Machaerium* (Fabaceae); **Miconia* (Melastomataceae); **Otoba* (Myristicaceae); **Paullinia* (Sapindaceae); **Perebea* (Moraceae); **Protium* (Burseraceae); **Psychotria* (Rubiaceae); **Sterculia* (Sterculiaceae); **Strychnos* (Loganiaceae); *Swartzia* (Fabaceae); **Talisia* (Sapindaceae); **Theobroma* (Sterculiaceae); **Virola* (Myristicaceae)

'None'/'Generalist' affiliation: *Adenocalymna* (Bignoniaceae); *Allophylus* (Sapindaceae); *Apeiba* (Tiliaceae); *Astrocaryum* (Arecaceae); *Bactris* (Arecaceae); *Brosimum* (Moraceae); *Callichlamys* (Bignoniaceae); *Caraiipa* (Clusiaceae); *Carpotroche* (Flacourtiaceae); *Casearia* (Flacourtiaceae); *Cecropia* (Cecropiaceae); *Celtis* (Ulmaceae); *Cissus* (Vitaceae); *Clusia* (Clusiaceae); *Clytostoma* (Bignoniaceae); *Coccoloba* (Polygonaceae); *Combretum* (Combretaceae); *Cordia* (Boraginaceae); *Cydista* (Bignoniaceae); *Dalbergia* (Fabaceae); *Doliocarpus* (Dilleniaceae); *Erythroxylum* (Erythroxylaceae); *Eugenia* (Myrtaceae); *Euterpe* (Arecaceae); *Ficus* (Moraceae); *Forsteronia* (Apocynaceae); *Geonoma* (Arecaceae); *Hippocratea* (Hippocrateaceae); *Hirtella* (Chrysobalanaceae); *Iriarte* (Arecaceae); *Leonia* (Violaceae); *Lonchocarpus* (Fabaceae); *Mouriri* (Melastomataceae); *Naucleopsis* (Moraceae); *Neea* (Nyctaginaceae); *Ocotea* (Lauraceae); *Oenocarpus* (Arecaceae); *Piper* (Piperaceae); *Pithecellobium* (Fabaceae); *Pourouma* (Cecropiaceae); *Pouteria* (Sapotaceae); *Pseudolmedia* (Moraceae); *Quararibea* (Bombacaceae); *Rinorea* (Violaceae); *Salacia* (Hippocrateaceae); *Scheelea* (Arecaceae); *Sclerolobium* (Fabaceae); *Serjania* (Sapindaceae); *Siparuna* (Monimiaceae); *Sloanea* (Elaeocarpaceae); *Socratea* (Arecaceae); *Sorocea* (Moraceae); *Tachigali* (Fabaceae); *Tapirira* (Anacardiaceae); *Tetragastris* (Burseraceae); *Trichilia* (Meliaceae); *Trigynaea* (Annonaceae); *Unonopsis* (Annonaceae); *Xylopia* (Annonaceae); *Zanthoxylum* (Rutaceae).

*Genera with significant ($P < 0.05/P < 0.01$) correlations between relative abundance (percentage frequency of each woody plant genus per plot) and all three moisture variables: dry quarter precipitation, potential evapotranspiration minus precipitation, and soil water content.

Relationship between size-class distribution and precipitation regimes

A comparison of basal area and stem number by affiliation and rainfall category was carried out for all woody plant genera ($n = 91$) across dry, intermediate and wet plots (Fig. 3a,b). ANOVA results gave significant differences between 'dry' and

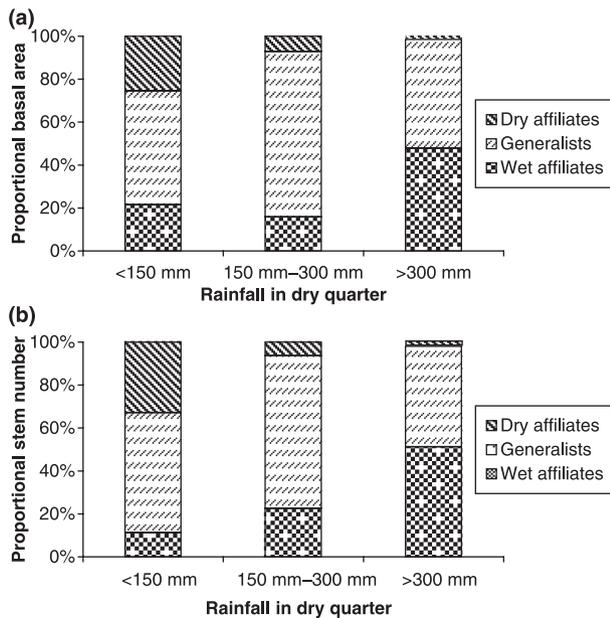


Figure 3 Proportional basal areas (a) and proportional stem numbers (b) of 91 analysed genera in each of three rainfall affiliation categories across the precipitation range (< 150, 150–300, > 300 mm). Affiliations are given in Table 2.

'generalist' groups for both basal area and stem number across all plots ($P = 0.027$ and $P = 0.01$ respectively). In the dry plots, genera in the 'wet' plants had greater proportional basal area (20%) than stem number; (10%) – these plants were larger than average for the plot; for the 'dry' genera the opposite was true; the proportional number of individuals was greater than basal area (30% for stems; 25% for basal area). Overall, for numbers of individuals by tree and liana type across stem diameter categories (Fig. 4), generalists were most numerous in dry and intermediate plots, and wet affiliates were most numerous in the wet plots. Contributions to total basal area were spread more irregularly across classes, with the groups between 20 and 30 cm d.b.h. having the largest overall basal area contribution in the intermediate plots, and those between 10 and 20 cm d.b.h. contributing most in the dry and wet plots. Lianas made a trivial contribution to basal area, and were represented only in the smaller size classes. There were no trees > 70 cm d.b.h. in the dry plots, and no wet-affiliated genera > 60 cm d.b.h. in the intermediate plots. The importance of the contribution made by small stems to forest composition can be seen clearly in how individuals were allocated to size class: 80% of all stems ($n > 10,600$) in the analysis (91 genera, 39 plots) are < 10 cm d.b.h.; 92.4% < 20 cm d.b.h.; 96.7% < 30 cm, and 98.5% < 40 cm d.b.h.

To summarize the key discoveries of this analysis: (1) given our definition and classifications, we would predict that the dry affiliates would dominate dry plots. However, the analysis showed that climate generalists dominated here, especially in the medium-sized classes, and the dry affiliates were not dominant in any size class. (2) In the wet plots, dry affiliates were represented only in the smallest size classes, and wet affiliates were partially dominant in small size classes. There

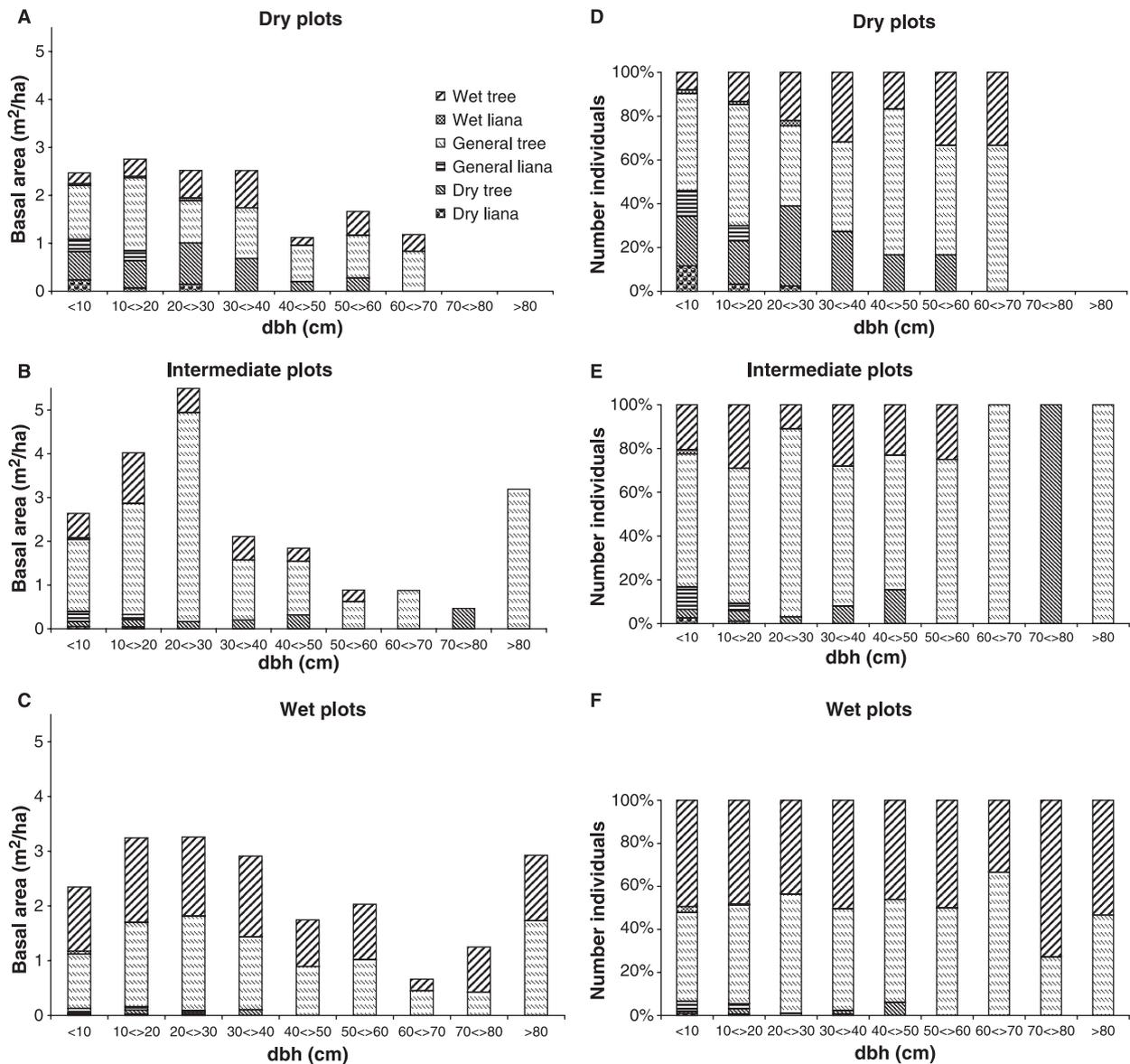


Figure 4 Basal area (m² ha⁻¹) (a–c) and number of individuals (proportional) (d–f) in each stem-diameter category by woody plant type, for dry (< 150 mm dry quarter rainfall), intermediate (150–300 mm rainfall) and wet (> 300 mm rainfall) plots.

were significantly more wet affiliates in the smallest size classes in the wet plots than in the dry and intermediate plots. More surprisingly, generalists dominated the mid-size ranges in the wet plots. The smallest size classes in all three plot types were most functionally similar, in that they were the most mixed (the dry plots were the most varied of all).

Pioneer and shade-tolerance characteristics of rainfall-dependent groups

Analysis of the relationship between the Pioneer index and the predominantly arboreal genera, grouped by moisture preference, showed that the plants in the climate generalist group had a greater average pioneer rating than those in the wet-affiliate group (0.15 and 0.1, respectively; the ‘dry’ group

was 0.12, overall average 0.13). Mann–Whitney tests indicated that the only statistically significant difference between these groups was between wet-affiliate and climate generalist ($P = 0.017$) (probably the number of ‘dry’ genera in this particular analysis was too small to give meaningful statistical outputs). Climate generalists were more likely to be pioneers; the wet-affiliated genera had significantly lower pioneer scores than the other two groups.

Phylogenetic context

The genera analysed were situated on an evolutionary axis (see cladogram based on Angiosperm Phylogeny Website, Fig. 5) and found to spread across a wide range of angiosperm groups. At a higher taxonomic level, all our studied genera can be

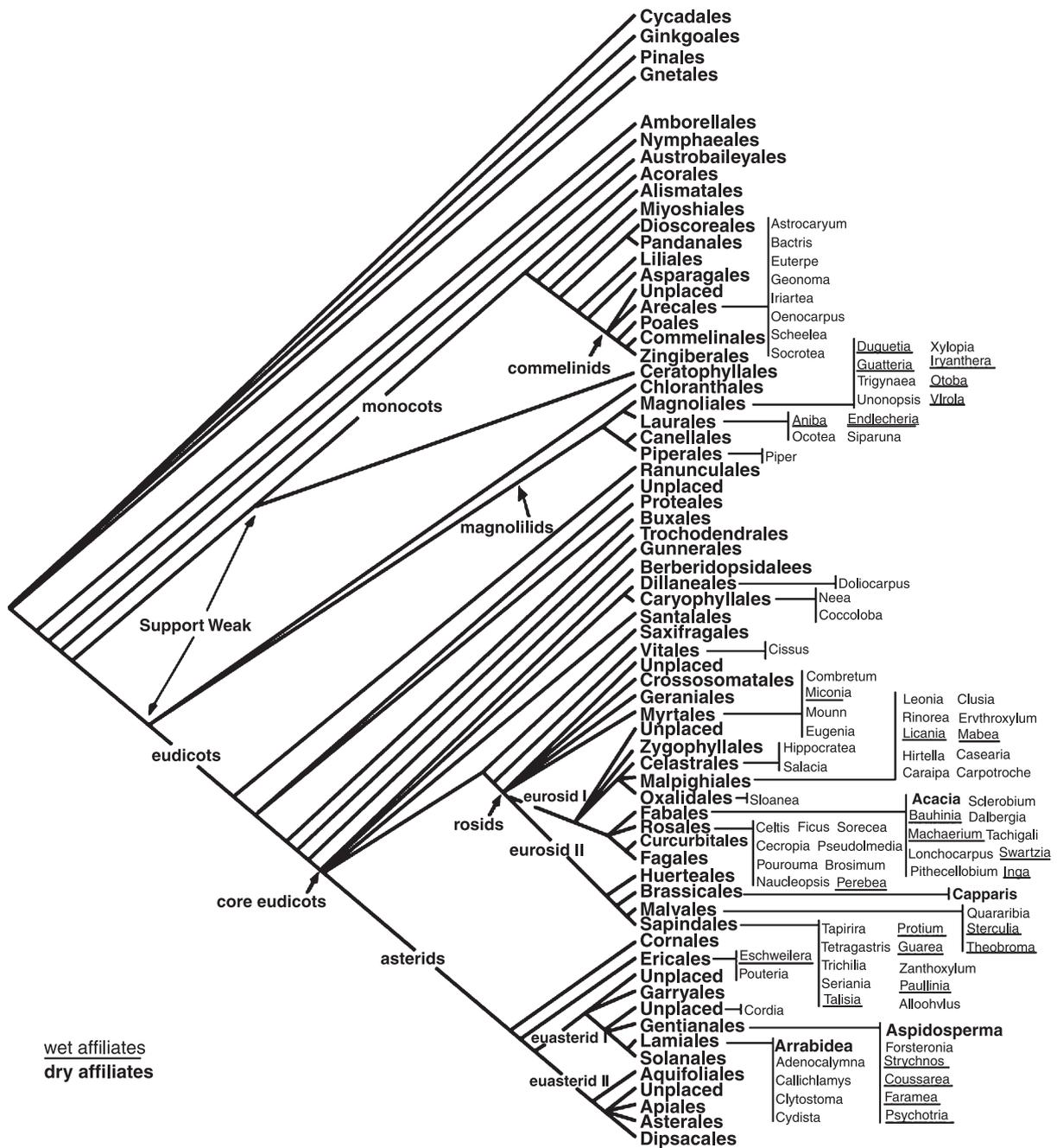


Figure 5 Cladogram based on Angiosperm Phylogeny Website (<http://www.mobot.org/mobot/research/APweb/welcome.html>), illustrating evolutionary relationships between the families of genera analysed (affiliations as in Table 2). Dry affiliation appears to be a more recently derived trait in the core eudicots.

grouped into monocots, Magnoliids and the two core eudicot groups: Rosids and Asterids. Wet affiliates were found in all groups except the monocots; dry affiliates were found only in the core eudicots, reflecting their widely known diversification in dry regions (Soltis & Soltis, 2004). The eudicots arose during the Mesozoic era in the middle of the Cretaceous period, *c.* 100 Ma (Willis & McElwain, 2002; Stevens, 2006). The earliest group represented here, the monocots, are all generalists; wet or dry affiliation does not appear to be a phylogenetically conservative attribute, but rather to be more

recently evolved. Within core eudicot families, both wet and dry affiliation can occur, and wet affiliation evolved earlier. In general, rainfall affiliations are diverse at all scales – shifts between dry and wet affiliation occurring across levels in many groups.

DISCUSSION

The analysis has shown, for the most abundant genera, a significant relationship between the variation in precipitation

regime along the north–south gradient and relative abundance of 31 of 91 genera of Amazonian woody plants. We concluded that for these 31 genera, especially the 23 significantly correlated with all three moisture variables (Table 1), precipitation may be a strong limiting factor on their distribution and abundance, reflecting the importance of partitioning along environmental gradients in community composition (Silver-town, 2004; ter Steege *et al.*, 2006).

In terms of rainfall affiliations, of the 31 genera associated with precipitation, four may be considered to be drought-tolerant/drought-adapted, with greater abundance in drier areas, whereas the other 27 were drought-intolerant (Table 2; Appendix S3). It is possible that successful ‘dry’ genera are able to manage water stress to colonize drier soils and out-compete other plants in the drier south-west. The much higher number of wet- than dry-affiliated plants could be a function of the fact that wet forests have greater floristic diversity than dry forests (Clinebell *et al.*, 1995), partly due to high rainfall amplifying the niche space available to shade-tolerant taxa. Consistent with this observation, the original plot data had, on average, 62 genera in dry plots, 93 in intermediate plots, and 123 in wet plots.

All 33 genera with significant correlations between abundance and rainfall seasonality also had a significant correlation with annual precipitation, and five additional genera were correlated only with annual precipitation: *Apeiba*, *Bactris*, *Hippocratea*, *Iriarteia* and *Trigynaea*. Although precipitation was an important variable in terms of abundance distribution for these five, they were not necessarily sensitive to rainfall seasonality. Of the genera that showed no dry-season sensitivity, several are widespread across the western Amazon (e.g. *Ficus*, *Iriarteia*, *Piper*). Environmental variables other than dry-season intensity apparently limit the distribution of these plants; a landscape-scale study (Phillips *et al.*, 2003a) showed that, in the south of western Amazonia, these genera are strongly associated with more fertile soils, and western Amazonia as a whole has pockets of relatively fertile soils throughout the region (Sombroek, 2000).

The analysis of the relationship between size-class distribution and precipitation regimes showed that dry-affiliate and generalist groups differed significantly in both stem numbers and basal area. While generalists accounted for between 45% and 80% of basal area and stem number, and dominated both dry and intermediate plots, dry affiliates accounted for only 30% of the stand in dry plots. These data suggest two possibilities: that the niche for dry affiliates is smaller than for wet affiliates or generalists, which is supported by the fact that wetter forests have greater floristic diversity, and/or that dry affiliation is a more expensive life strategy, takes more energy, or is a more specialized attribute.

The hypotheses we tested were that wet affiliation is linked to shade tolerance and dry affiliation to pioneer life history, and that larger trees are more drought-tolerant. The first hypothesis was supported, with a strong relationship demonstrated between wet affiliation and shade tolerance, while we found no association between dry affiliation and pioneer life strategy. We found no support for the hypothesis that larger trees are

more drought-tolerant – even in the drier plots, the generalist and wet-affiliated trees dominated the larger size classes.

In terms of community composition, plants without affiliation to either dry or wet conditions were more likely to be pioneers, while the 28 genera associated with wetter conditions were shade-tolerant rather than pioneers, including Annonaceae, Burseraceae, Meliaceae, Moraceae, Rubiaceae (Condit *et al.*, 1996), *Eschweilera* and most of the Myristicaceae (Mabberley, 1992). The increase in relative abundance of shade-tolerant taxa lends support to the hypothesis that shade tolerance controls abundance in climatologically and geographically similar areas (Condit *et al.*, 2002; Duivenvoorden *et al.*, 2002). If, as our analysis suggests, shade-tolerant trees also tend to be drought-intolerant trees, then the community structure in these wet forests may be less resilient to future increases in moisture stress than would otherwise be expected.

Our results also suggest that measures of seasonal moisture availability are more critical for woody plant abundance than total dry-season rainfall alone (Table 1), which reflects earlier findings (Gentry, 1988b; Clinebell *et al.*, 1995; ter Steege *et al.*, 2003) that diversity is determined by dry-season length. The available data have allowed investigation of climate–abundance relationships for almost 60% of all recorded genera in the plots. As rarer taxa tend to be proportionally more numerous in wetter, higher-density forests, our analysis may have underestimated the importance of wet affiliation among taxa – there may be an even greater abundance of wet affiliates than our results suggest. In tropical West Africa, by contrast, the abundance of dry affiliates may be much greater, possibly as a result of a historically drier climate (Parmentier *et al.*, 2007). It is also worth noting that if dry affiliation is a derived attribute, genus-level aggregation may result in an underestimation of the number of dry affiliates. Another data issue to consider for future work is the exclusion of unidentified stems from the analysis; these may include stems of the analysed genera as well as of the non-analysed remainder, which may, in turn, result in an underestimation of the number of stems of some genera in some cases.

Precipitation (and precipitation-related variables such as soil water content) is clearly a significant factor in species composition, but not the only one. Our results strongly support the hypothesis of a direct relationship between moisture variables and distribution of genera abundance, and thereby community composition (niche theory), but are not inconsistent with other environmental or historical factors having controlling roles at other spatial scales. Similarly, in central tropical West Africa, dispersal is the most powerful driver of landscape-scale tree community composition, while at the regional scale, environmental factors are most constraining (Parmentier *et al.*, 2005).

It is unclear how the Amazon hydrological system will respond to climate change, but as the timing of plant production is directly linked to seasonality (Mulkey *et al.*, 1996; Huete *et al.*, 2006), changes in seasonality will further affect plant community interactions (*sensu* Pyke *et al.*, 2001). Over the past three decades there has been a drying trend in

northern Amazonia (Marengo, 2004), and the climate models suggest about a 20% overall probability of significant dry-season intensification in the western Amazon, and a 10% probability of severe drought (Malhi *et al.*, 2008). The threat of drying is much greater in eastern and south-eastern Amazonia. Changes in community composition, as at the last glacial–interglacial transition (Mayle *et al.*, 2008), may result from this predicted drying, and in a future paper we will use the ranking built here to look at evidence of shifts in abundance of wet- and dry-affiliated climate functional groups over recent decades.

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SUPPLEMENTARY MATERIAL

The following supplementary material is available for this article online:

Appendix S1 Name, location and climatic moisture variables data for each plot.

Appendix S2 Results of statistical analyses on the relative abundance of western Amazon genera.

Appendix S3 Rainfall seasonality ranking for genera in the western Amazon.

This material is available as part of the online article from: <http://www.blackwell-synergy.com/doi/abs/10.1111/j.1365-2699.2008.01878.x>.

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BIOSKETCHES

Nathalie Butt is a doctoral student in the Oxford University Centre for the Environment, working on tropical climatology and biodiversity. She previously worked on modelling the impacts of climate change on species distributions at UK and European scales.

Yadvinder Malhi is Professor of Ecosystem Science at the Oxford University Centre for the Environment. His research focuses on interactions between tropical ecosystems and the global atmosphere, their role in global carbon, energy and water cycles, and how the ecology of natural ecosystems may be shifting in response to global atmospheric change.

Oliver Phillips is Professor of Tropical Ecology at the Earth and Biosphere Institute and School of Geography, University of Leeds. His research centres on the ecology, conservation and sustainable development of tropical forests, especially Amazonia, and an understanding of where, how and why the ecology of these forests may be changing.

Mark New is a Reader in Climate Science at the Oxford University Centre for the Environment. His research focuses on observed climate change and variability, climate prediction and hydrological responses to climate change.

Editor: Mark Bush