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Background: Climate change is driving ecosystem shifts, which has implications for tropical forest system function and productivity.

Aim: To investigate Amazon forest dynamics and test for compositional changes between 1985 and 2005 across different plant groups.

Methods: Tree census data from 46 long-term RAINFOR forest plots in Amazonia for three climate-functional groups were used: dry-affiliate, climate-generalist and wet affiliate. Membership of each group was ascribed at genus level from the distribution of individuals across a wet–dry gradient in Amazonia, and then used to determine whether the proportions of these functional groups have changed over time, and the direction of any change.

Results: In total, 91 genera, representing 59% of the stems and 18% of genera in the plots, were analysed. Wet-affiliates tended to move from a state of net basal area gain towards dynamic equilibrium, defined as where gain $\approx$ loss, governed by an increase in loss rather than a decrease in growth and mainly driven by plots in north-west Amazonia, the wettest part of the region. Dry-affiliates remained in a state of strong net basal area gain across western Amazonia and showed a strong increase in stem recruitment. Wet-affiliates and climate-generalists showed increases in stem mortality, and climate-generalists showed increased stem recruitment, resulting in overall equilibrium of stem numbers.

Conclusions: While there were no significant shifts in most genera, the results suggest an overall shift in climate-functional forest composition in western Amazonia away from wet-affiliates, and potential for increased forest persistence under projected drier conditions in the future.

Keywords: climate trends; forest composition; moisture affiliation; moisture seasonality; tropical forest

Introduction

A number of studies worldwide have shown that climate change elicits forest ecosystem responses such as changes in phenology, forest composition and productivity (Nemani et al. 2003; Parmesan and Yohe 2003; IPCC 2007). The tropics host the most diverse and productive forest systems on Earth (Beer et al. 2010) yet, until the end of the twentieth century, they were relatively poorly studied, for reasons of remoteness and inaccessibility. While research on the impacts of climate change has typically focused elsewhere, changes in ecosystem structure and function are also very likely to be occurring in the tropics where climate-driven changes may affect the role forests play as carbon sinks (Lewis et al. 2004a, 2009). Analysis of long-term Amazon plot data, part of the RAINFOR project (Malhi et al. 2002), has shown that old growth forests have increased in biomass in recent years (Baker et al. 2004), and that Amazonian forests generally have become more, productive and dynamic in terms of rates of stem recruitment, mortality and turnover (Phillips et al. 1998, 2004; Baker et al. 2004; Lewis et al. 2004b). Such changes in structure

have included an Amazon-wide increase in stem recruitment and mortality (Phillips et al. 2004), and a Neotropical increase in above-ground woody biomass (Phillips et al. 1998, 2002; Baker et al. 2004), albeit perhaps temporarily reversed by an intense drought in 2005 (Phillips et al. 2009).

There have been few studies of trends in functional composition in old-growth tropical forests, although Phillips et al. (2002) have shown that large lianas in intact western Amazon forests have recently increased in relative dominance, a pattern that may extend across the Neotropics (Wright et al. 2004; Schnitzer and Bongers 2011) and Laurance et al. (2004) found increasing rates of growth in most relatively abundant tree genera in a central Amazonian landscape, and a general increase in rates of tree mortality and recruitment. The results suggested that numbers of faster-growing old-growth genera (primarily canopy trees) increased, while slower-growing understory genera decreased. Pan-tropical analyses by Chave et al. (2008) and Lewis et al. (2009) also showed a significant increase in biomass across 10 and 156 forest plots respectively.

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Changes in climate variables such as temperature, precipitation, solar radiation and diffuse fraction of solar radiation, more important for sub-canopy species (cf. Nemani et al. 2003), are possible drivers of this observed accelerated growth, as is the increase of atmospheric CO_2 concentration (Curtis and Wang 1998; Norby et al. 1999; Cramer et al. 2001). While water use efficiency (WUE) is predicted to increase with rising atmospheric CO_2 concentrations (Farquhar 1997; Winter et al. 2001), rising temperatures may increase transpiration rates and water stress (Malhi et al. 2009), and across the region there was a long-term trend of temperature increase of 0.26 °C decade^{-1} (Malhi and Wright 2004). With plant moisture availability the strongest of several environmental and biophysical variables in terms of forest structure (Toledo et al. 2011a), precipitation seasonality is an important factor in plant species richness and diversity and the composition of plant assemblages (Gentry 1988; ter Steege et al. 2003; Butt et al. 2008). Although changes in interannual and seasonal precipitation amounts were insignificant across the region overall (Malhi and Wright 2004), there has been a trend of increasing dry season length (Marengo et al. 2011), a significant decrease in dry season cloud fraction and cloud-related diffuse radiation, of about 8% (Butt et al. 2009), and an increasing trend of incoming short-wave solar radiation (Hashimoto et al. 2010). While it has not been established whether other climatic or environmental variables may be influencing tropical biodiversity and productivity, these three factors may act to increase seasonal water stress even in the absence of changes in the rainfall regime.

From the perspective of plot dynamics, this paper sets out to investigate temporal trends in forest community composition across Amazonian old-growth forests utilising a large and unique database. While earlier studies examined shifts in species in relation to drought (Condit 1998;

Enquist and Enquist 2011; Feeley et al. 2011), they were focussed on single sites or smaller areas; possible trends in relation to water availability have not been previously investigated across a large number of sites. The aim of the work is to establish if there have been any shifts or trends in proportions and dynamics of wet-affiliate, dry-affiliate and climate-generalist tree genera on a decadal level, and to quantify the magnitude of any change. Moisture affiliation is related to drought and shade tolerance, and productivity is a function of the potential trade-off between drought tolerance and growth, which may also be determined by CO_2 concentration. We therefore expect that, in response to environmental trends: 1) increasing seasonality would favour more drought-tolerant plant groups; and that 2) increasing ambient CO_2 concentrations might favour more drought-sensitive plant groups by improving water use efficiency.

Materials and methods

Floristic data

Floristic data were extracted from the RAINFOR database (www.forestplots.net; Lopez-Gonzalez et al. 2011) in November 2006. The RAINFOR census plots are located across the Amazon region and the data vary greatly in temporal range. Measurement details and methodology have been previously described (e.g. Phillips et al. 2002). For this analysis we selected plot censuses which spanned at least 10 years, with at least two census intervals. In total, 46 plots below 1000 m a.s.l. were used in the analysis. The plots were allocated to one of three regions: south-west and north-west, at either end of the north–south moisture gradient (north→south = wetter→drier) across western Amazonia, and east-central Amazonia (Figure 1), which are characterised by different climates. Mean monthly
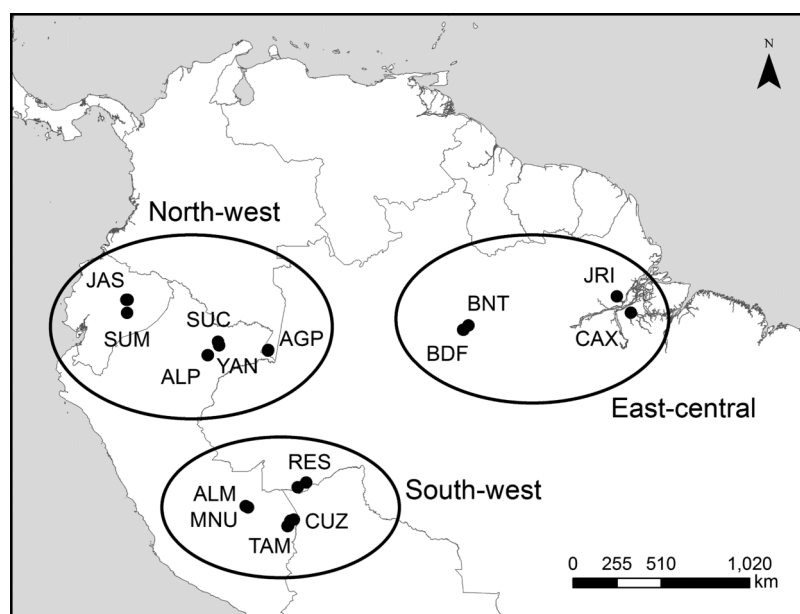

Figure 1.   Distribution of the RAINFOR census plots in Amazonia used in this analysis.

dry quarter rainfall over the period covering the census monthly data (1985–2005), was 202 mm for the north-west region, 74 mm for the east-central region and 36 mm for the south-west (University of Delaware (UDEL) and Climate Research Unit, University of East Anglia (CRU) long-term data).

As the temporal range of the plot censuses varied so greatly, the investigation focused on the 20-year period from 1985 until 2005, ending immediately prior to the Amazon drought of 2005 (Phillips et al. 2009). Overall, 24 plots had 15 or more years of census data. The number of plots per region was as follows: for the east-central region, $n = 17$; for the north-west region, $n = 11$, and for the south-west region, $n = 18$. Plot details are given in Appendix 1.

Climate functional groups

We previously investigated generic affiliations with the precipitation gradient in western Amazonia (Butt et al. 2008), quantifying the relationship between moisture seasonality and plant abundance for nearly 100 common woody plant genera using all woody stems $\geq$ 2.5 cm dbh in 39 plots (0.1 ha) below 1000 m elevation (lowland), and west of 62° W, of the Gentry sample plot dataset (http://www.salvias.net/pages/index.html) (Appendix 2). Of the 91 genera analysed, there were significant correlations for a third of the genera with either wetter (designated as 'wet-affiliates') or drier conditions (designated as 'dry-affiliates'), and two-thirds, with no moisture seasonality affiliation, were designated as 'climate-generalists'. In the current analysis, the climate functional groups represent about 60% of individuals and 18% of genera in the plots analysed.

Here we use data for stems $\geq$ 10 cm dbh from the RAINFOR dataset and first divide the genera into the three climate functional groups; the remainder (those genera not previously tested) were grouped as 'unknown' (430 genera). Relative abundances were calculated using the data for all stems, including the 'unknown' group as well as the three functional groups.

We used plots with at least two census intervals and standardised the dataset to analyse three censuses with two census intervals of about the same length to avoid possible census interval effects confounding the results. The average date of the first, mid and final censuses was 1988, 1994 and 2003. The first census interval, on average, was 6.4 ± 1.9 years (standard deviation; range 4–11 years); the second was 8.1 ± 2.5 years (range 4–13 years). The regions varied from each other only slightly in this respect, with a first census interval of 5.9 years for the north-west, 6.1 years for the south-west, and 7.1 years for east-central. The second census interval was 8.5 years for the north-west and east-central regions, and 7.6 years for the south-west region. The mean plot size was 1.4 ± 0.2 ha (range 0.4–9 ha).

We examined net changes, between ~1985 and ~2005, for each of the three climate functional groups (wet-affiliate, climate-generalists and dry-affiliates). We

calculated basal area (BA) and stem density at each census, BA growth and mortality rates, and stem recruitment and mortality rates, for both census intervals, and used Wilcoxon two-sample tests (as the rates were not normally distributed) to establish the significance of the differences over time. The calculations were as follows (cf. Lewis et al. 2004b):

$$\text{Mortality } \lambda = \left[\ln n_0 - \ln(n_0 - D_t)\right]/t \qquad 1$$

$\lambda \times 100$ gives percent per annum, where λ is the mortality coefficient, n_0 is the total BA or number of stems at the start of the interval, D_t is the BA or stem loss during the interval, and t is the interval (in years).

$$\text{Recruitment } \mu = \left[\ln n_t - \ln(n_0 - D_t)\right]/t \qquad 2$$

$\ln n_t$ is the value for BA or stems at the end of the interval. These calculations allowed us to compare mortality and growth/recruitment for BA and stem density across the climate functional groups, overall, and by region. We used a log-linear analysis in order to retain normal distributions in the analysis.

We assessed whether the climate functional groups, overall and by region, are in (or close to) dynamic equilibrium, defined as where the level of gain is similar to that of loss, and examine changes between intervals. We determined these measures for all woody plants overall, by climate functional group, and by region, and considered whether the changes over time were driven by mortality or growth. Within a plot, changes in BA correlate strongly with changes in biomass (Malhi et al. 2006), and hence the BA dynamics can be taken to be broadly indicative of changes in biomass dynamics, neglecting net changes in tree allometry and wood density.

Results

Distribution and abundance of the climate functional groups

The 'dry' group (four genera) was present in 41 of the 46 plots at the beginning of the period of study. The plots where it was not present were primarily in the north-west, the wettest Amazonian region. The 'wet' (27 genera) and 'generalist' (60 genera) groups were present in all plots. The dominant genera in the wet-affiliate group were: *Eschweilera* and *Protium* (>15% each of classified wet-affiliate stems); *Pouteria* and *Iriartea* each contributed more than 10% of stems to the generalist group; in the dry-affiliate group *Aspidosperma* overwhelmingly dominated, with around 90% of classified stems. The relative abundance, in terms of proportional BA and individuals, of the three climate functional groups varied by region with the climate-generalists dominating in the south-west region and the wet-affiliates dominating in the north-west and east-central regions (Table 1).

In terms of stem numbers, but not BA, the dry-affiliates were more abundant in the south-west and east-central

Table 1(a).   Relative abundance (%) by region, by climate functional group as a proportion of all stems, including the 'unknown' group.

	Climate functional group			
	Wet	Generalist	Dry	Unknown
South-west				
% BA	12	41	1	45
% stems	17	48	1	34
East-central				
% BA	26	19	2	52
% stems	35	24	1	40
North-west				
% BA	30	24	2	43
% stems	32	28	0.3	39

Table 1(b).   Absolute stem numbers by region and by climate functional group, including the 'unknown' group.

	Wet	Generalist	Dry	Unknown
All regions				
Census 1	9684	11589	237	13456
Census 2	9689	11674	231	13415
Census 3	9411	11537	235	14386
South-west				
Census 1	2150	6206	127	4551
Census 2	2144	6372	122	4494
Census 3	2113	6505	128	4648
East-central				
Census 1	6008	4081	94	7035
Census 2	5962	3999	93	7071
Census 3	5682	3778	90	7816
North-west				
Census 1	1526	1302	16	1870
Census 2	1583	1303	16	1850
Census 3	1616	1254	17	1922

regions, more than twice as abundant as in the north-west. However, the dry-affiliate group as defined in our analysis comprised less than 2% of stems or BA in any of the regions (Table 1(a), and Table 1(b) for absolute stem numbers).

Temporal trends in climate functional group growth and mortality

We present statistically significant results in the figures, and all results in Table 2 (Wilcoxon analyses at $P < 0.05$). Overall, there was a clear relationship between climate functional group and dynamism, with wet-affiliates being the most dynamic, and dry-affiliates the least dynamic. In terms of net changes between intervals, wet-affiliates moved from experiencing strong net gain in BA in the first interval towards dynamic equilibrium (not significantly different from the one-one line), in the second as BA loss rates increased. Wet-affiliates maintained high dynamism overall (Figure 2(a)). Climate-generalists maintained a slight net BA gain while dry-affiliates remained in a strong dynamic disequilibrium (significantly different from the one-one line) of net BA gain. Analysis of stem dynamics

by climate functional group indicates that the wet-affiliate and climate-generalist groups showed increases in stem mortality ($P < 0.05$, $_z1.645$ $P = 0.2$, $_z0.842$ respectively) (Figure 2(b)), and both groups shifted slightly away from dynamic equilibrium (from $P = 0.7$, $_z-0.524$ to $P < 0.05$, $_z1.645$ for wet-affiliates; $P = 0.5$, $_z-0.01$ to $P < 0.05$, $_z1.645$ for climate-generalists): the first interval was not significantly different from dynamic equilibrium. Dry-affiliates, the least dynamic group of the three, showed a strong increase in recruitment and weaker decrease in mortality ($P < 0.08$, $_z1.405$, $P = 0.7$, $_z-0.524$ respectively), and moved from a state of net stem loss to net stem gain.

Temporal trends in climate functional group growth and mortality by region

All groups in the north-west plots gained in BA in the first interval (Table 2, Figure 3(a)). Wet-affiliates and climate-generalists all showed a significant ($P < 0.05$, $_z1.645$ and $P < 0.01$, $_z2.326$) increase in BA loss, and climate-generalists also showed a significant increase in BA gain ($P < 0.05$, $_z1.645$). The most marked change was that wet-affiliate and climate-generalist groups showed a significant increase in stem mortality ($P < 0.05$, $_z1.645$ and $P < 0.01$, $_z2.326$, respectively), causing an overall increase in stem mortality ($P < 0.05$, $_z1.645$) (Table 2, Figure 3(b)).

Dry-affiliates showed a significant increase in stem recruitment in the south-west ($P < 0.01$, $_z2.326$) and moved from net stem loss to net stem gain (Figure 4). This large increase in dry-affiliate stem recruitment was not driven by one plot but is seen in most plots. There was no significant change in dry-affiliate BA.

As the dry-affiliate group is dominated by a single genus *Aspidosperma* (~90% of all dry-affiliate individuals), analyses were performed to investigate whether this genus alone was driving the dynamics of the dry-affiliate group. There were 24 species of *Aspidosperma* distributed across the plot network in the north-west and south-west, which indicates a potentially high level of intra-generic ecophysiological variability. For the north-west plots, *Aspidosperma* was the sole driver of changes in stem mortality (and thus BA loss) and stem recruitment in the dry-affiliate group. However, there was a larger difference (increase) in BA gain between the two census intervals when *Aspidosperma* was excluded from the analysis, i.e. the increase in growth over time was more pronounced in the other dry genera than in *Aspidosperma* (Figure 5(a)). In the other region where dry-affiliates other than *Aspidosperma* were recorded, the south-west, BA gain and stem recruitment were both higher between intervals when *Aspidosperma* was excluded, while stem mortality increased rather than decreased (but not significantly) (Figure 5(b) and Table 3). Hence exclusion of *Aspidosperma* enhances the trends in the dry-affiliates rather than suppressing them. Further investigation of the other dry-affiliates indicated that the trends reported overall for dry-affiliates were consistent across plots and genera: no single genus or plot was driving the results.

Table 2. Mean and standard error values for plant climate functional group basal area loss and growth and stem mortality and recruitment, for all groups and all regions, for the two intervals. Significant changes between interval highlighted; *, $P < 0.05$; **, $P < 0.01$ significant change (Wilcoxon test statistic).

Wet affiliate	Basal area loss		Std error		Basal area growth		Std error	
	Interval 1	Interval 2	Interval 1	Interval 2	Interval 1	Interval 2	Interval 1	Interval 2
North-west	*1.66	*3.28	0.28	0.43	2.69	2.93	0.21	0.16
East-central	1.46	1.37	0.36	0.13	1.41	1.55	0.1	0.07
South-west	2.62	2.76	0.41	0.34	3.04	2.93	0.15	0.19

Wet affiliate	Stem mortality		Std error		Stem recruitment		Std error	
	Interval 1	Interval 2	Interval 1	Interval 2	Interval 1	Interval 2	Interval 1	Interval 2
North-west	*1.61	*2.44	0.24	0.22	2.22	2.48	0.31	0.34
East-central	1.57	1.32	0.34	0.09	1.23	0.77	0.17	0.13
South-west	2.61	2.73	0.28	0.23	2.59	2.48	0.23	0.3

Climate generalist	Basal area loss		Std error		Basal area growth		Std error	
	Interval 1	Interval 2	Interval 1	Interval 2	Interval 1	Interval 2	Interval 1	Interval 2
North-west	**1.66	**3.05	0.39	0.28	*2.40	*2.95	0.2	0.32
East-central	1.86	1.32	0.39	0.17	1.43	1.52	0.09	0.13
South-west	2.18	2.11	0.29	0.16	2.41	2.48	0.13	0.14

Climate generalist	Stem mortality		Std error		Stem recruitment		Std error	
	Interval 1	Interval 2	Interval 1	Interval 2	Interval 1	Interval 2	Interval 1	Interval 2
North-west	**1.87	**2.85	0.21	0.22	*1.81	*2.40	0.24	0.23
East-central	1.77	1.38	0.37	0.11	1.08	0.83	0.15	0.17
South-west	1.83	2.11	0.1	0.11	2.15	2.18	0.23	0.19

Dry affiliate	Basal area loss		Std error		Basal area growth		Std error	
	Interval 1	Interval 2	Interval 1	Interval 2	Interval 1	Interval 2	Interval 1	Interval 2
North-west	0.02	0.01	0.02	0.01	1.4	2.22	0.43	0.58
East-central	0.69	1.11	0.4	0.74	0.97	1.12	0.16	0.22
South-west	0.94	1.06	0.62	0.52	1.77	1.97	0.37	0.41

Dry affiliate	Stem mortality		Std error		Stem recruitment		Std error	
	Interval 1	Interval 2	Interval 1	Interval 2	Interval 1	Interval 2	Interval 1	Interval 2
North-west	0.6	0.4	0.6	0.4	0.6	0.47	0.6	0.47
East-central	1.07	0.53	0.69	0.1	0.68	0.16	0.4	0.1
South-west	1.51	0.44	0.26	0.98	*0.44	*2.29	0.26	0.65

Discussion

Our analysis demonstrates the forest change that occurred in Amazonia between 1985 and 2005: wet affiliates showed a relative decrease in both BA and stem number overall, while generalists and dry affiliates showed relative increases in these two metrics. Recent findings from an analysis of species composition in plots in Costa Rica, on Barro Colorado Island, and across a Panama-wide precipitation gradient, also indicated an increase in the representation of drought-tolerant taxa in forest community composition, which may suggest widespread shifts in similar directions (Enquist and Enquist 2011; Feeley et al. 2011).

Although overall most genera did not show significant changes, the pronounced increase in BA loss and stem mortality for wet-affiliates would suggest a potential slowing of growth rates for this group, which could be an indication of climate sensitivity or long-term successional processes. These changes, combined with an increase in all four measures of dynamism for climate-generalists in the north-west

broadly reflects earlier findings (Lewis et al. 2004b; Phillips et al. 2004), that forests in the west of the region have been changing more rapidly than those in the east. Wet-affiliate BA gain decreased in the south-west, while stand-level analyses showed no significant change in stem numbers. If this group is decreasing in gain and increasing in loss (in the north-west), a shift in community composition could be suggested. It is difficult to isolate this as a marked trend, although it is supported by the strong relative increase in dry-affiliate numbers in the region.

Our climate analyses showed no significant changes in precipitation seasonality in the north-west and southwest, which suggests that any changes in forest composition with regard to our climate functional groups are unlikely to be driven by changes in rainfall regime alone in this region. However, while interannual precipitation trends were insignificant in the three regions (Malhi and Wright 2004), the increasing dry season length combined with the changes in dry season cloud fraction and cloud-related diffuse radiation, temperature and incoming
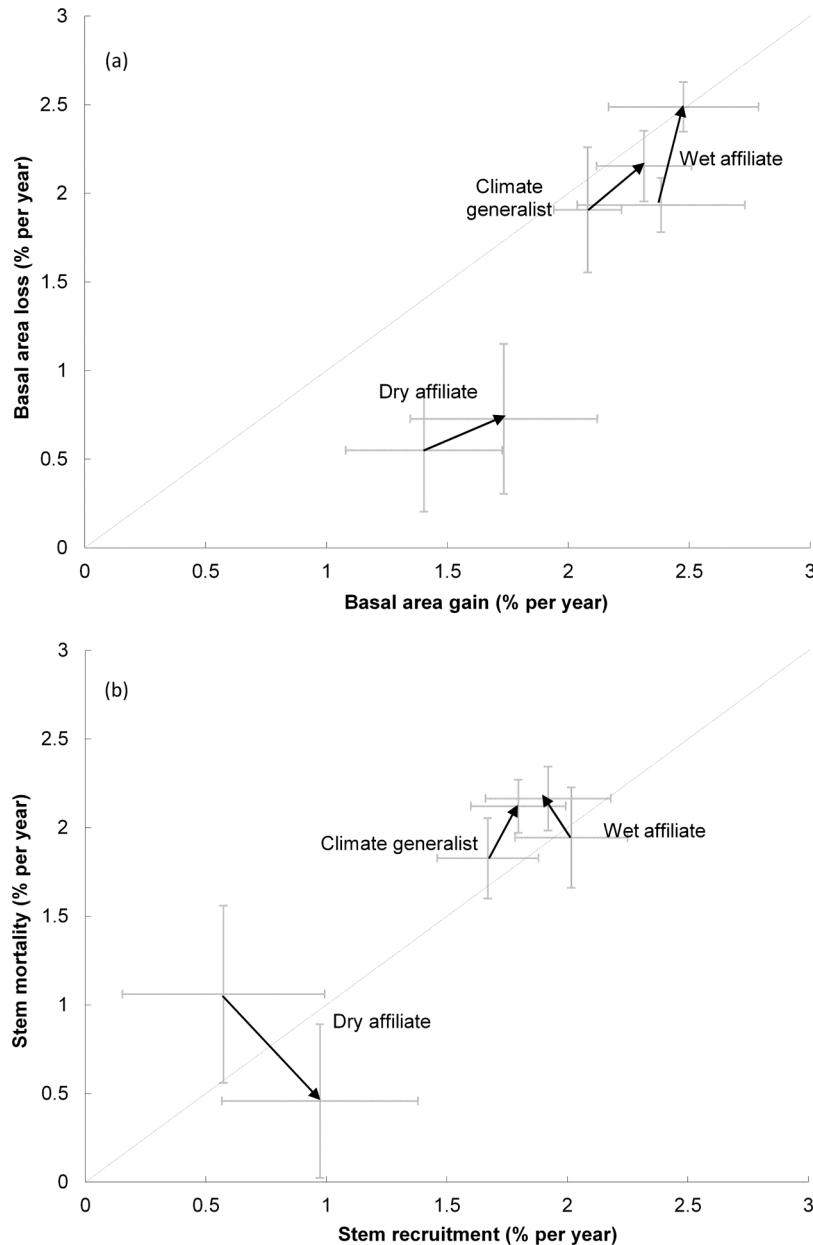
Figure 2.   Direction and magnitude of changes in (a) basal area loss and gain and (b) stem mortality and recruitment between Interval 1 and Interval 2 for all plots, mean plot %, by climate functional group. Standard error bars (95% confidence limits). The rates of change for each of the three functional groups and across each region separately are shown in gain vs. loss plots to illustrate both absolute magnitude and changes in parameters. For basal area, 'gain' here includes recruitment and growth, while stem gain is recruitment only; 'loss' for basal area and stems is mortality. Net change is the difference between gain and loss. In these figures, points close to the 1:1 line are in dynamic equilibrium (gain ≈ loss); *P* values give the significance of difference from the 1:1 line. Points below the line indicate greater gain than loss, and points above the line greater loss than gain. Distance from the origin is an indicator of overall dynamism and turnover (but not equal to turnover *sensu strictu*). The error bars represent standard error.

short-wave solar radiation (Malhi and Wright 2004; Butt et al. 2009; Hashimoto et al. 2010; Arias et al. 2011; Marengo et al. 2011), may increase transpiration and hence seasonal water stress even with no change in precipitation seasonality. They may thus be responsible for the increase in dry-affiliate stem recruitment in the south-west, while wet-affiliates and climate-generalist groups may be becoming more vulnerable to moisture stress induced by higher dry season transpiration rates (Malhi et al. 2009). In addition, temperature increase may drive increases in

nutrient availability through more rapid decay and mineralisation of litter, and the more dynamic species or groups (including drier groups) are able to respond rapidly (Lewis et al. 2004a; 2009).

A drought classification and subsequent analysis of forest dynamics derived from trees in plots across the same (as above) Panama moisture gradient, using a similar method to our work, concluded that species distribution and forest composition was driven by seasonal and spatial variation in moisture availability, especially in drier
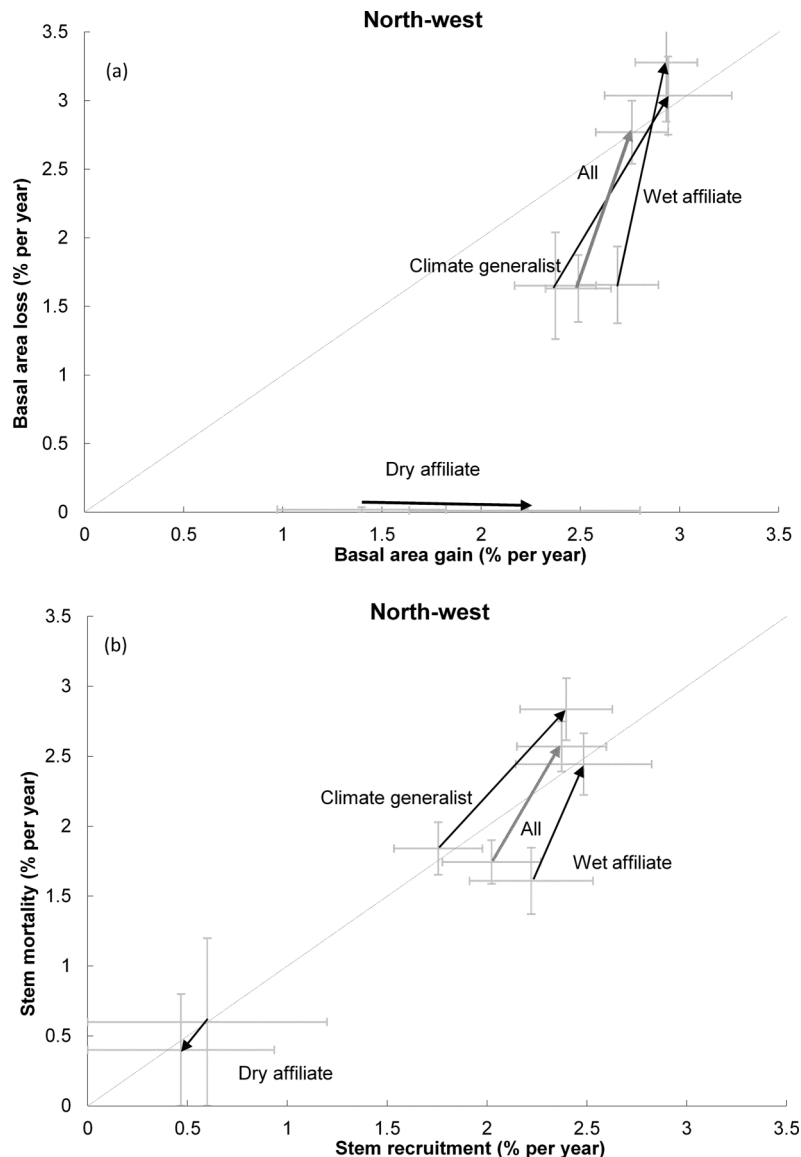
Figure 3.   Gain/loss diagram for (a) basal area gains and losses, and (b) stem recruitment and mortality, for all climate-functional groups, for the north-west region. The total for all climate-functional group stems, 'all' (the three functional groups combined) is included (grey line). Wet-affiliates and climate-generalists all showed a significant ($P < 0.05$, $_z1.645$ and $P < 0.01$, $_z2.326$) increase in basal area loss, which brought them into dynamic equilibrium in the second interval (gain ~ loss). Climate-generalists also showed a significant increase in basal area gain ($P < 0.05$, $_z1.645$). Wet-affiliates moved from a state of net stem gain ($P < 0.07$, $_z1.484$) into dynamic equilibrium ($P < 0.9$, $_z-1.315$), while a significant increase ($P < 0.01$, $_z2.326$) in climate-generalist dynamism moved this group into disequilibrium (net stem loss). Wet-affiliate and climate-generalist groups showed a significant increase in stem mortality ($P < 0.05$, $_z1.645$ and $P < 0.01$, $_z2.326$, respectively), causing an overall increase in stem mortality ($P < 0.05$, $_z1.645$). The dry-affiliate group, a very small component of trees in these plots, has extremely low dynamism and was in equilibrium.

years, when moisture stress increased (Engelbrecht et al. 2007; Comita and Engelbrecht 2009). This suggests that changes in moisture seasonality would drive shifts in forest composition; an increase in seasonality would therefore support our first hypothesis, that drought-tolerant groups would be favoured by these changes. Drought-intolerant genera, while increasing in mortality, showed no decrease in growth, suggesting that the rising CO_2 concentrations (from 346 ppmv in 1985 to 380 ppmv in 2005 – Carbon Dioxide Research Group, Mauna Loa) have counteracted any negative impacts of moisture stress for this group.

There are indications of some changes in stand-level stem numbers and BA for the different climate-functional groups. Wet-affiliates, or drought-intolerant plants, also tend to be shade tolerant (Butt et al. 2008), and the fact that they showed significant increases in both BA loss and stem loss, but no significant gains in either BA or stem recruitment, in the wetter north-west could suggest that forests are beginning to shift towards more generalist communities. If the climate functional groups are also associated with shade tolerance and temperature sensitivity, these factors could be driving such a shift. The
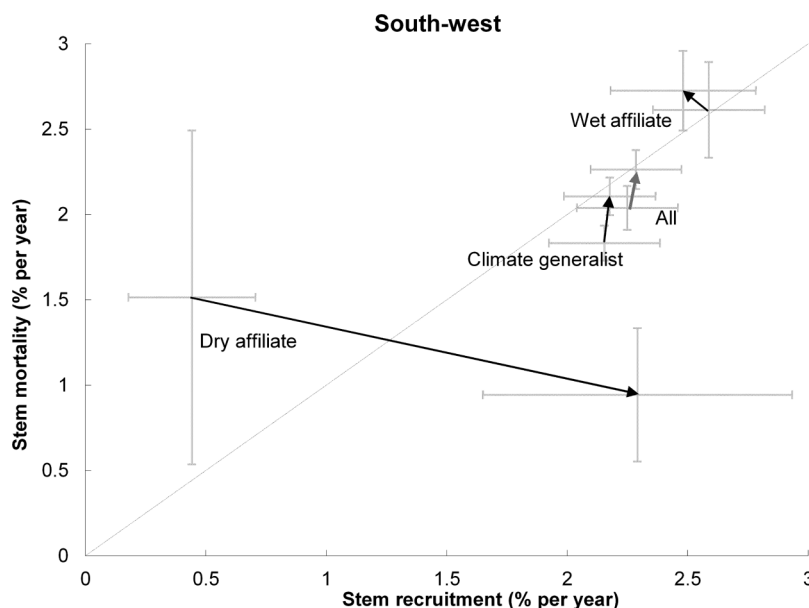
Figure 4. Gain/loss diagram for stem gains and losses, for all climate-functional groups, for the south-west region. The regional total for each climate-functional group stems, 'all' (all three functional groups combined, for each region) is included (grey line). Climate-generalists and wet-affiliates started in stem equilibrium and remained there in the second interval. Dry-affiliates showed a significant increase in stem recruitment ($P < 0.01$) and moved from net stem loss to net stem gain.

parallel increase in dry-affiliates could also support such a shift. The clear link between climate sensitivity, as defined here by moisture seasonality affiliation and dynamism, is ecologically interesting; currently, dry-affiliate plants are the least dynamic of the climate-functional groups, but if forest conditions become drier there may be further increases in dry-affiliates and dry-affiliate dynamism. Such shifts away from wetter communities and towards more generalist and drier communities could have positive consequences for forest persistence under future climate drying conditions, and further implications for forest productivity and carbon sequestration (Toledo et al. 2011b).

In addition to possible climate drivers of changes in composition and dynamics, forests may be recovering from previous disturbances and at different stages of recovery/succession, thus exhibiting shifts in dynamism (Wright 2005; Lewis et al. 2009; Feeley et al. 2011); however, the approach we used in this paper, of many plots spread over a large geographic region, should reduce the relative importance of disturbance events at stand level. Other related factors which may influence the estimation of changes in composition include lag-times: (i) between seedling recruitment and growing to 10 cm dbh, which may be very long and stochastic; (ii) for dying, and (iii) for recovery after drought events. Although our analysis considers changes prior to the extreme droughts of 2005 and 2010 (Lewis et al. 2011), it is possible that earlier droughts influenced growth rates, maybe even sufficiently to cause a directional change in composition.

We note that the dry-affiliate functional group as defined here accounts for only a very small fraction ($<2\%$) of stem numbers or BA in the plots, and hence does not indicate a large impact on overall community dynamics or a strong shift in overall community composition, but rather a

shift related to water status. It is possible, however, that the group represents part of a wider spectrum of dry-favouring genera that remain unclassified into functional group, or allocated as climate-generalists, in which case there may already have been substantial overall shifts in community composition in either direction along the wet–dry affiliation spectrum.

Finally, it should be noted that the period analysed in this paper (overall, 20 years split in two) is still relatively short for identifying long-term trends. Nevertheless, parts of Amazonia experienced two strong droughts after the period of this study, in 2005 (Aragao et al. 2007) and 2010 (Lewis et al. 2011), which may sharpen the tendency towards increasing abundance of dry-affiliates. The present analysis provides initial clues to functional compositional changes occurring in Amazonian forests; these will need to be tested with longer-term, and more trait-based, analyses of functional groups.

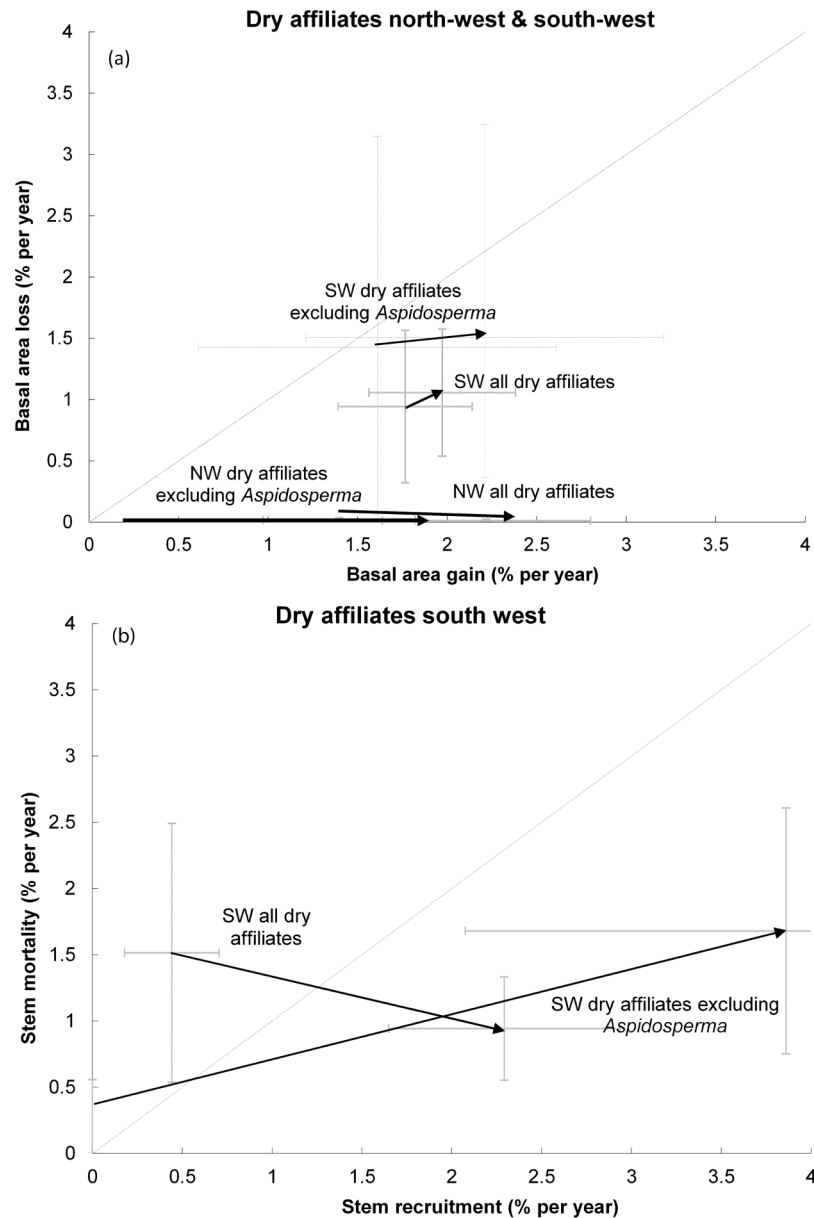**Dry affiliates north-west & south-west**

Dry affiliates south west

Figure 5. Comparison of changes between census intervals for the dry-affiliate group, including and excluding *Aspidosperma*, for (a) basal area gain and loss, and (b) stem recruitment and mortality. (East-central is not included as the dry-affiliate group comprised only *Aspidosperma* in this region; there were no dry-affiliate-excluding *Aspidosperma* stem changes in the north-west).

Table 3. Comparison of changes for the dry-affiliate group by including vs. excluding *Aspidosperma*.

	% annual change between intervals	
	All dry-affiliates	Excluding *Aspidosperma*
North-west		
BA gain	0.82	1.86
BA loss	0.01	0
Stem recruitment	−0.13	0
Stem mortality	−0.20	0
South-west		
BA gain	0.21	0.61
BA loss	0.11	0.08
Stem recruitment	−0.95	−1.86
Stem mortality	−0.19	0

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Appendix 1. Plot and census information

Plots sited very closely together and 0.25 ha or less were combined; 12 plots became three in the east-central region.

Plot	Plot name	Latitude	Longitude	Plot area (ha)	Census 1	Census 2	Census 3
ALM-01	Altos de Maizal	−11.8	−71.47	2	1994	1999	2004
ALP-11	Allpahuayo A poorly drained	−3.95	−73.43	0.44	1990	1996	2005
ALP-12	Allpahuayo A, very well drained	−3.95	−73.44	0.4	1990	1996	2005
ALP-21	Allpahuayo B, sandy	−3.95	−73.44	0.48	1990	1996	2005
ALP-22	Allpahuayo B, clayed	−3.95	−73.44	0.44	1990	1996	2005
BDF-03	BDFFP, 1101 Gaviao	−2.4	−59.9	1	1987	1991	2003
BDF-04	BDFFP, 1102 Gaviao	−2.4	−59.9	1	1987	1991	2003
BDF-05	BDFFP, 1103 Gaviao	−2.4	−59.9	1	1987	1991	2003
BDF-06	BDFFP, 1201 Gaviao	−2.4	−59.9	3	1986	1992	2003
BDF-07	BDFFP, 1105 Gaviao	−2.4	−59.9	1	1988	1999	2004
BDF-08	BDFFP, 1109 Gaviao	−2.4	−59.9	1	1988	1999	2004
BDF-09	BDFFP, 1113 Florestal	−2.4	−59.9	1	1987	1992	2002
BDF-10	BDFFP, 1301 Florestal 1 = plot 1301.1 and 1301.3	−2.4	−59.9	2	1988	1997	2002
BDF-11	BDFFP, 1301 Florestal 2 = plots 1301.4,5,6	−2.4	−59.9	3	1988	1997	2002
BDF-12	BDFFP, 1301 Florestal 3 = plots 1301.7,8	−2.4	−59.9	2	1988	1997	2002
BDF-13	BDFFP, 3402 Cabo Frio	−2.4	−59.9	9	1985	1991	2003
BDF-14	BDFFP, 3304 Porto Alegre	−2.4	−59.9	1	1987	1992	2003
BNT-01	Bionte 1	−2.63	−60.17	1	1986	1995	2005
BNT-02	Bionte 02	−2.63	−60.17	1	1986	1995	2004
BNT-04	Bionte 4	−2.63	−60.15	1	1986	1995	2005
CAX-01	Caxiuana 1	−1.74	−51.46	1	1994	1999	2004
CUZ-01	Cuzco Amazonico, CUZAM1E	−12.58	−69.15	1	1989	1994	2003
CUZ-02	Cuzco Amazonico, CUZAM1U	−12.58	−69.15	1	1989	1994	2003
CUZ-03	Cuzco Amazonico, CUZAM2E	−12.50	−68.96	1	1989	1994	2003
CUZ-04	Cuzco Amazonico, CUZAM2U	−12.56	−69.13	1	1989	1994	2003
JAS-02	Jatun Sacha 2	−1.07	−77.6	1	1987	1994	2002
JAS-03	Jatun Sacha 3	−1.07	−77.67	1	1988	1994	2002
JAS-05	Jatun Sacha 5	−1.07	−77.67	1	1989	1994	2002
JRI-01	Jari 1	−0.89	−52.19	1	1985	1990	1996
MNU-01	Manu, alluvial Cocha Cashu Trail 3, M1	−11.87	−71.35	1	1990	1995	2000
MNU-03	Manu, terra firme terrace, M3	−11.88	−71.35	2	1991	1996	2001
MNU-04	Manu, terra firme ravine, M4	−11.88	−71.35	2	1991	1996	2001
MNU-05	Manu, alluvial Cocha Cashu Trail 12	−11.87	−71.35	2	1989	1994	1999
MNU-06	Manu, alluvial Cocha Cashu Trail 2 & 31	−11.87	−71.35	2.25	1989	1994	2004
RES-03	Porongaba 1	−10.82	−68.77	1	1991	1999	2003
RES-04	Porongaba 2	−10.80	−68.77	1	1991	1999	2003
SUC-01	Sucusari A	−3.25	−72.91	1	1992	1996	2005
SUC-02	Sucusari B	−3.25	−72.90	1	1992	1996	2005
SUM-01	Sumaco	−1.75	−77.63	1	1989	1996	2002
TAM-01	Tambopata plot zero	−12.84	−69.29	1	1987	1994	2003
TAM-02	Tambopata plot one	−12.83	−69.29	1	1987	1994	2003
TAM-04	Tambopata plot two swamp edge clay	−12.84	−69.28	0.42	1985	1990	2003
TAM-05	Tambopata plot three	−12.83	−69.27	1	1986	1994	2005
TAM-06	Tambopata plot four	−12.84	−69.30	1	1991	1998	2005
TAM-07	Tambopata plot six	−12.83	−69.26	1	1985	1994	2003
YAN-01	Yanamono A	−3.44	−72.85	1	1989	1996	2005

Appendix 2

The Gentry dataset of 0.1 ha floristic samples was used (http://www.salvias.net/pages/index.html) for all woody stems ≥2.5 cm dbh. 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, including additional data for four 0.1 ha plots in Yasuní, Ecuador, provided by MJ 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, and to account for the differences in plant numbers between plots. Species diversity was such that most species were too rare (e.g. fewer than one individual per sample unit) to include in the analysis. As many more trees were accurately identified to genus than to species (about 30% of all trees recorded were not identified to species level, and many identified only to morphospecies), genus-level plant distribution data were used. Climate data were obtained from the Climate Research Unit (CRU) 0.5-degree global dataset (New et al. 1999). From this monthly dataset, 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 precipitation in the driest three months was calculated and then used as a dry season (intensity) measure. Two other precipitation-related variables were also included: soil water content (SWC) and potential evapotranspiration minus precipitation (PET - p). The SWC estimates were obtained from the Sheffield dynamic vegetation global model (Woodward and Lomas 2004), and PET (from CRU) was calculated from temperature, sunshine/radiation, wind and humidity data using the Penman–Monteith equation. The dataset created for the analysis represented the average monthly climate (1961–98). Relative abundance was determined for each woody plant genus for each plot and only genera that occurred in one or more plots (91 genera), with over 1% abundance analysed (representing 59% of 20,000 recorded stems in these plots). For each genus, each moisture variable (dry quarter precipitation, PET - p, SWC) was correlated with the relative abundance of that genus across all sites and correlation coefficients (Kendall's t) averaged to produce a rainfall seasonality ranking. The 91 genera were then each initially classified as one of two categories: no correlation with moisture, or correlation with one, two or three moisture variables, and, of those correlated with the moisture variables, each genus was then associated with wetter or drier conditions, according to the correlation coefficients (Table A1). The results gave significant correlations for a third of these genera with either wetter (designated as 'wet-affiliates') or drier conditions (designated as 'dry-affiliates'): two-thirds, with no moisture seasonality affiliation, were designated as 'climate-generalists'. 12% of genera and 60% of individuals were thus classified – the remainder was unclassified because of low abundances (see Butt et al. 2008). In the current analysis, the climate functional groups represent about 60% of individuals and >20% of genera in the plots used (the rest were unclassified, 'unknown' and were not included in all subsequent analyses).

Table A1. Rainfall seasonality ranking for woody genera in the western Amazon. The rankings, derived from Kendall's t coefficients, range approximately between 0.5 (strongly wet-affiliated) and −0.4 (strongly dry-affiliated). Generally values between around 0.2 and −0.2 indicate no significant correlation with rainfall. (The asterisked genera are those with a statistically significant correlation; $P < 0.05$ or $P < 0.01$ equivalents after the application of Bonferroni's correction for multiple comparisons). Source: Butt et al. (2008).

Genus	t	Genus	t	Genus	t
*Acacia	−0.395	*Cissus	0.105	*Miconia	0.228
*Arrabidaea	−0.380	*Tapirira	0.107	*Eugenia	0.229
*Capparis	−0.359	*Socratea	0.118	*Paullinia	0.241
*Aspidosperma	−0.357	*Tachigali	0.125	*Pithecellobium	0.243
*Serjania	−0.277	*Caraipa	0.128	*Coussarea	0.267
*Hippocratea	−0.273	*Geonoma	0.138	*Strychnos	0.282
*Cydista	−0.223	*Sorocea	0.138	*Talisia	0.289
*Hirtella	−0.149	*Unonopsis	0.142	*Theobroma	0.290
*Combretum	−0.121	*Clusia	0.145	*Iryanthera	0.295
*Forsteronia	−0.120	*Pourouma	0.146	*Licania	0.306
*Clytostoma	−0.097	*Brosimum	0.150	*Aniba	0.312
*Sclerolobium	−0.083	*Dalbergia	0.164	*Eschweilera	0.314
*Zanthoxylum	−0.083	*Cecropia	0.171	*Swartzia	0.330
*Adenocalymna	−0.080	*Doliocarpus	0.171	*Virola	0.341
*Oenocarpus	−0.075	*Rinorea	0.175	*Duguetia	0.344
*Cordia	−0.057	*Tetragastris	0.183	*Perebea	0.347
*Piper	−0.035	*Leonia	0.183	*Mabea	0.349
*Lonchocarpus	−0.033	*Casearia	0.185	*Protium	0.352
*Euterpe	−0.025	*Salacia	0.187	*Endlicheria	0.353
*Xylopia	−0.019	*Naucleopsis	0.200	*Guatteria	0.358
*Celtis	−0.018	*Trigynaea	0.201	*Bauhinia	0.361
*Neea	0.028	*Sloanea	0.201	*Otoba	0.371
*Allophylus	0.039	*Ficus	0.203	*Cyathea	0.378
*Siparuna	0.043	*Apeiba	0.205	*Faramea	0.381
*Scheelea	0.053	*Astrocaryum	0.208	*Inga	0.391
*Quararibea	0.053	*Carpotroche	0.208	*Guarea	0.424
*Coccoloba	0.071	*Trichilia	0.215	*Psychotria	0.454
*Mouriri	0.078	*Callichlamys	0.216	*Sterculia	0.473
*Pseudolmedia	0.086	*Pouteria	0.219	*Machaerium	0.482
*Erythroxylum	0.096	*Bactris	0.222		
*Ocotea	0.104	*Iriartea	0.227		