

Seasonal drought limits tree species across the Neotropics

Adriane Esquivel-Muelbert, Timothy R. Baker, Kyle G. Dexter, Simon L. Lewis, Hans ter Steege, Gabriela Lopez-Gonzalez, Abel Monteagudo Mendoza, Roel Brien, Ted R. Feldpausch, Nigel Pitman, Alfonso Alonso, Geertje van der Heijden, Marielos Peña-Claros, Manuel Ahuite, Miguel Alexiades, Esteban Álvarez Dávila, Alejandro Araujo Murakami, Luzmila Arroyo, Milton Aulestia, Henrik Balslev, Jorcely Barroso, Rene Boot, Angela Cano, Victor Chama Moscoso, James A. Comiskey, Fernando Cornejo, Francisco Dallmeier, Douglas C. Daly, Nallarett Dávila, Joost F. Duivenvoorden, Alvaro Javier Duque Montoya, Terry Erwin, Anthony Di Fiore, Todd Fredericksen, Alfredo Fuentes, Roosevelt García-Villacorta, Therany Gonzales, Juan Ernesto Guevara Andino, Euridice N. Honorio Coronado, Isau Huamantupa-Chuquimaco, Timothy J. Killeen, Yadvinder Malhi, Casimiro Mendoza, Hugo Mogollón, Peter Møller Jørgensen, Juan Carlos Montero, Bonifacio Mostacedo, William Nauray, David Neill, Percy Núñez Vargas, Sonia Palacios, Walter Palacios Cuenca, Nadir Carolina Pallqui Camacho, Julie Peacock, Juan Fernando Phillips, Georgia Pickavance, Carlos Alberto Quesada, Hirma Ramírez-Angulo, Zorayda Restrepo, Carlos Reynel Rodríguez, Marcos Ríos Paredes, Rodrigo Sierra, Marcos Silveira, Pablo Stevenson, Juliana Stropp, John Terborgh, Milton Tirado, Marisol Toledo, Armando Torres-Lezama, María Natalia Umaña, Ligia Estela Urrego, Rodolfo Vasquez Martinez, Luis Valenzuela Gamarra, César I. A. Vela, Emilio Vilanova Torre, Vincent Vos, Patricio von Hildebrand, Corine Vriesendorp, Ophelia Wang, Kenneth R. Young, Charles Eugene Zartman and Oliver L. Phillips

A. Esquivel-Muelbert (adriane.esquivel@gmail.com), T. R. Baker, S. L. Lewis, G. Lopez Gonzales, R. Brien, J. Peacock, G. Pickavance and O. L. Phillips, School of Geography, University of Leeds, Leeds, UK. SLL also at: Dept of Geography, Univ. College London, London, UK. – K. Dexter and R. García-Villacorta, Royal Botanic Garden of Edinburgh, Edinburgh, UK. KD also at: School of Geosciences, Univ. of Edinburgh, Edinburgh, UK. RGV also at: Inst. of Molecular Plant Sciences, Univ. of Edinburgh, UK. – H. ter Steege, Naturalis Biodiversity Center, Leiden, the Netherlands. – A. Monteagudo, V. Chama Moscoso, R. Vasquez Martinez and L. V. Gamarra, Jardín Botánico de Missouri, Oxapampa, Perú. – T. R. Feldpausch, Geography, College of Life and Environmental Sciences, Univ. of Exeter, UK. – N. Pitman and C. Vriesendorp, The Field Museum, Chicago, IL, USA. – J. Terborgh and NP, Center for Tropical Conservation, Nicholas School of the Environment, Duke Univ., Durham, NC, USA. – A. Alonso and F. Dallmeier, Smithsonian Conservation Biology Inst., National Zoological Park, Washington, DC, USA. – G. van der Heijden, School of Geography, Univ. of Nottingham, Nottingham, UK. – M. Peña-Claros, T. Fredericksen and M. Toledo, Inst. Boliviano de Investigación Forestal, Santa Cruz, Bolivia. MP also at: Forest Ecology and Forest Management Group, Wageningen Univ., Wageningen, the Netherlands. – M. Ahuite, Univ. Nacional de la Amazonia Peruana, Iquitos, Perú. – M. Alexiades, School of Anthropology and Conservation, Univ. of Kent, Canterbury, Kent, UK. – F-E. Álvarez Dávila and Z. Restrepo, Fundación Con Vida, Medellín, Colombia. – A. A. Murakami and L. Arroyo, Museo de Historia Natural Noel Kempff Mercado, Santa Cruz, Bolivia. – M. Aulestia, Herbario Nacional del Ecuador, Quito, Ecuador. – H. Balslev, Univ. of Aarhus, Aarhus, Denmark. – J. Barroso and M. Silveira, Univ. Federal do Acre, Rio Branco, Brazil. – R. Boot, Tropenbos International, Wageningen, the Netherlands. – A. Cano and P. Stevenson, Laboratorio de Ecología de Bosques Tropicales y Primatología, Univ. de Los Andes, Bogotá, Colombia. – J. A. Comiskey, National Park Service, Fredericksburg, VA, USA. – F. Cornejo, Andes to Amazon Biodiversity Program, Madre de Dios, Perú. – D. C. Daly, New York Botanical Garden, Bronx, New York, NY, USA. – N. Dávila, Univ. de Campinas, São Paulo, Brazil. – J. F. Duivenvoorden, Inst. of Biodiversity and Ecosystem Dynamics, Univ. of Amsterdam, Amsterdam, the Netherlands. – A. J. Duque Montoya and L. E. Urrego, Univ. Nacional de Colombia, Medellín, Colombia. – T. Erwin, Smithsonian Inst., Washington DC, USA. – A. Di Fiore, Dept of Anthropology, Univ. of Texas at Austin, Austin, TX, USA. – A. Fuentes and P. M. Jørgensen, Missouri Botanical Garden, St. Louis, MO, USA, and Museo Ecuatoriano de Ciencias Naturales, Quito, Ecuador. – T. Gonzales, ACEER Foundation, Puerto Maldonado, Perú. – J. E. Guevara Andino, Dept of Integrative Biology, Univ. of California, Berkeley, CA, USA. – E. N. Honorio, Coronado, Inst. de Investigaciones de la Amazonia Peruana, Iquitos, Perú. – I. Huamantupa-Chuquimaco, Herbario CUZ, Univ. Nacional San Antonio Abad del Cusco, Perú. – T. J. Killeen, AGTECA – Amazonica, Santa Cruz, Bolivia. – Y. Malhi, Environmental Change Inst., Oxford Univ. Centre for the Environment, Oxford, UK. – C. Mendoza, Forest Management in Bolivia, Sacta, Bolivia – Endangered Species Coalition, Silver Spring, MD, USA. – J. C. Montero, Inst. of Silviculture, Univ. of Freiburg, Freiburg, Germany. – B. Mostacedo, Univ. Autónoma Gabriel René Moreno, Facultad de Ciencias Agrícolas, Santa Cruz, Bolivia. – W. Nauray, P. Núñez Vargas and N. C. Pallqui Camacho, Univ. de San Antonio Abad del Cusco, Perú. – D. Neill, Universidad Estatal Amazónica, Puyo, Pastaza, Ecuador. – M. Mogollón, Community Foodworks, Washington, DC, USA. – S. Palacios, Herbario de la Facultad de Ciencias Forestales, Univ. Nacional Agraria La Molina, Lima, Perú. – W. Palacios Cuenca, Escuela

de Ingeniería Forestal, Univ. Técnica del Norte, Ecuador. – M. R. Paredes, Servicios de Biodiversidad EIRL Iquitos, Peru. – J. F. Phillips and P. von Hildebrand, Fundación Puerto Rastrojo, Bogotá, Colombia. – C. A. Quesada and C. E. Zartman, Inst. Nacional de Pesquisas da Amazônia, Petrópolis, Manaus, Brazil. – H. Ramírez-Angulo, A. Torres-Lezama and E. Vilanova Torre, Univ. de Los Andes, Mérida, Venezuela. – C. Reynel Rodríguez, Univ. Nacional Agraria La Molina (UNALM), Perú. – R. Sierra, Univ. of Texas, Austin, Texas, USA. – J. Stropp, Inst. of Biological and Health Sciences, Federal Univ. of Alagoas, Maceió, AL, Brazil. – M. Tirado, Geoinformática y Sistemas, Cia. Ltda. (GeoIS), Quito, Ecuador. – M. N. Umaña (<http://orcid.org/0000-0001-5876-7720>), Dept of Biology, Univ. of Maryland, MD, USA. – C. I. A. Vela, Facultad de Ciencias Forestales y Medio Ambiente, Univ. Nacional de San Antonio Abad del Cusco, Puerto Maldonado, Madre de Dios, Perú. – V. Vos, Univ. Autónoma del Beni Riberaltá, Beni, Bolivia. – O. Wang, Northern Arizona Univ., Flagstaff, AZ, USA. – K. R. Young, Geography and the Environment, Univ. of Texas, Austin, TX, USA.

Within the tropics, the species richness of tree communities is strongly and positively associated with precipitation. Previous research has suggested that this macroecological pattern is driven by the negative effect of water-stress on the physiological processes of most tree species. This implies that the range limits of taxa are defined by their ability to occur under dry conditions, and thus in terms of species distributions predicts a nested pattern of taxa distribution from wet to dry areas. However, this ‘dry-tolerance’ hypothesis has yet to be adequately tested at large spatial and taxonomic scales. Here, using a dataset of 531 inventory plots of closed canopy forest distributed across the western Neotropics we investigated how precipitation, evaluated both as mean annual precipitation and as the maximum climatological water deficit, influences the distribution of tropical tree species, genera and families. We find that the distributions of tree taxa are indeed nested along precipitation gradients in the western Neotropics. Taxa tolerant to seasonal drought are disproportionately widespread across the precipitation gradient, with most reaching even the wettest climates sampled; however, most taxa analysed are restricted to wet areas. Our results suggest that the ‘dry tolerance’ hypothesis has broad applicability in the world’s most species-rich forests. In addition, the large number of species restricted to wetter conditions strongly indicates that an increased frequency of drought could severely threaten biodiversity in this region. Overall, this study establishes a baseline for exploring how tropical forest tree composition may change in response to current and future environmental changes in this region.

A central challenge for ecologists and biogeographers is to understand how climate controls large-scale patterns of diversity and species composition. Climate-related gradients in diversity observed by some of the earliest tropical biogeographers, including the global latitudinal diversity gradient itself (von Humboldt 1808, Wallace 1878), are often attributed to the physiological limitations of taxa imposed by climate conditions (Dobzhansky 1950). This idea is expressed in the ‘physiological tolerance hypothesis’ (Janzen 1967, Currie et al. 2004), which posits that species richness varies according to the tolerances of individual species to different climatic conditions. Thus, species able to withstand extreme conditions are expected to be widely distributed over climatic gradients, while intolerant species would be constrained to less physiologically challenging locations and have narrower geographical ranges. An implicit assumption of this hypothesis is that species’ realized niches tend to reflect their fundamental niches, and a key implication of the hypothesis is that past, present, and future distributions of species will tend to track changes in climate (Boucher-Lalonde et al. 2014).

Within the tropics tree diversity varies considerably, possibly as a consequence of variation in water supply (ter Steege et al. 2003). Water-stress is indeed one of the most important physiological challenges for tropical tree species (Engelbrecht et al. 2007, Brenes-Arguedas et al. 2011), and precipitation gradients correlate with patterns of species richness at macroecological scales (Clinebell et al. 1995, ter Steege et al. 2003). In particular, tree communities in wetter tropical forests tend to have a greater number of species than in drier forests (Gentry 1988, Clinebell et al. 1995, ter Steege et al. 2003). If this pattern were driven by variation among species in the degree of physiological tolerance to dry conditions, then we would predict that all tropical tree species could occur in wet areas whilst communities at the

dry extremes would be made up of a less diverse, drought-tolerant subset. Thus, we would expect a nested pattern of species’ occurrences over precipitation gradients, characterised by widespread dry-tolerant species and small-ranged species restricted to wet environments. In this paper we refer to this scenario as the dry tolerance hypothesis (Fig. 1a).

Alternatively, nestedness may not be the predominant pattern for tropical tree metacommunities over precipitation gradients. Multiple studies have documented substantial turnover in floristic composition over precipitation gradients in tropical forests (Pitman et al. 2002, Engelbrecht et al. 2007, Quesada et al. 2012, Condit et al. 2013). This pattern could be driven by a trade-off between shade-tolerance and drought-tolerance (Markesteyn et al. 2011, Brenes-Arguedas et al. 2013). Whilst drought-tolerant species tend to have a higher capacity for water conductance and CO₂ assimilation under water-limiting conditions, they grow more slowly in the scarce understory light of wet forests where shade-tolerant species have a competitive advantage (Brenes-Arguedas et al. 2011, 2013, Gaviria and Engelbrecht 2015). Drought-tolerant species are also apparently more vulnerable to pest damage in moist areas (Baltzer and Davies 2012, Spear et al. 2015). Thus, in less physiologically stressful environments, tropical tree species’ occurrences could be limited by stronger biotic interactions, both with competitors and natural enemies (MacArthur 1972, Normand et al. 2009). In a scenario in which both wet and dry limitations to species distributions are equally important, we would expect progressive turnover of species’ identities along precipitation gradients (cf. Fig. 1b), rather than the nested pattern described above.

Both nested and turnover patterns have to some extent been documented in the tropics. A nested pattern has been detected in the Thai-Malay peninsula where widespread species, occurring across both seasonal and aseasonal regions,

(a)	Sites							(b)	Sites						
	wet			dry					wet			dry			
	A	B	C	D	E	Occurrence			A	B	C	D	E	Occurrence	
1	1	1	1	1	1	5	1			1	1	1	3		
2	1	1	1	1	1	5	2			1	1	1	3		
3	1	1	1	1		4	3			1	1		2		
4	1	1	1	1		4	4		1	1			2		
5	1	1	1			3	5	1	1				2		
6	1	1	1			3	6	1	1				2		
7	1	1				2	7	1	1				2		
8	1	1				2	8	1	1				2		
9	1					1	9	1					1		
10	1					1	10	1					1		
Richness	10	8	6	4	2		Richness	6	5	4	3	2			

Figure 1. Two conceptual models of how species' distributions may be arrayed along a precipitation gradient, with presence/absence matrices where rows represent taxa and columns represent communities, ordered from wet to dry. (a) Nested pattern expected by the dry tolerance hypothesis. Nestedness (sensu Leibold and Mikkelsen 2002) is represented by gradual disappearance of taxa along the precipitation gradient from wet to dry. (b) Turnover of taxa along the precipitation gradient. This pattern is characterized by the substitution of taxa from site to site, resulting in communities at opposite sides of the precipitation gradient being completely different in composition (Leibold and Mikkelsen 2002).

are more resistant to drought than species restricted to aseasonal areas (Baltzer et al. 2008). Across the Isthmus of Panama, Engelbrecht et al. (2007) found a direct influence of drought sensitivity on species' distributions, whilst light requirements did not significantly limit where species occur, which is consistent with the mechanisms underlying a nested pattern of species distributions. Also in Panama, another experimental study found that pest pressure was similar for species regardless of their distribution along a precipitation gradient (Brenes-Arguedas et al. 2009), indicating that the distributions of taxa that occur in drier forests may not be constrained by pest pressure. However, recent data from the same area show that drought-tolerant species are more likely to die than drought-intolerant taxa when attacked by herbivores or pathogens (Spear et al. 2015). Furthermore, when comparing two sites, an aseasonal (Yasuní; ca 3200 mm yr⁻¹ rainfall) and seasonal (Manu; ca 2300 mm yr⁻¹) forest in lowland western Amazonia, Pitman et al. (2002) reported that a similar proportion of species were unique to each site (Yasuní, 300 exclusive species out of 1017; Manu, 200 out of 693). The presence of a similar and large proportion of species restricted to each site is consistent with species distributions showing a pattern of turnover among sites. While there is thus evidence of both nestedness and turnover in tropical tree species distributions, a comprehensive investigation at large scale is lacking.

There are various approaches to estimate the tolerance of taxa to water-stress. For example, experimental studies of drought imposed on trees provide the clearest indicator of sensitivity to water-stress and provide insight into the ecophysiological mechanisms involved. Yet in the tropics, these are inevitably constrained to a minor proportion of tropical diversity, limited by tiny sample sizes (Nepstad et al. 2007, da Costa et al. 2010) and practical challenges of achieving any spatial replication and of integrating effects across multiple life stages (Brenes-Arguedas et al. 2013). By contrast, observational approaches, which

consist of mapping species' distributions across precipitation gradients, could potentially indicate the sensitivity of thousands of species to dry or wet conditions (Slatyer et al. 2013). Fixed-area inventories of local communities from many locations, offer a particular advantage for this kind of study as they avoid the bias towards more charismatic or accessible taxa that affects ad hoc plant collection records (Nelson et al. 1990, Sastre and Lobo 2009). Inventory-based attempts to classify tropical tree taxa by their affiliations to precipitation regimes have already advanced the understanding of species precipitation niches (Butt et al. 2008, Fauset et al. 2012, Condit et al. 2013), but have been fairly limited in terms of spatial scale, number of sample sites and taxa. In this paper we apply this inventory-based approach to investigate the macroecological patterns of trees across the world's most species-rich tropical forests, those of the western Neotropics, an area of 3.5 million km² that encompasses Central America and western South America. Because species richness in this region is so high, meaning that individual species' identifications are often challenging, we also explore whether analyses at the genus – or family – level offers a practical alternative for assessing the impacts of water-stress on floristic composition.

We selected the western Neotropics as our study area for two reasons. First, there is substantial variability in climate at small spatial scales relative to that of the entire region, meaning that associations between precipitation and floristic composition are less likely to be the result of dispersal limitation and potential concomitant spatial autocorrelation in species' distributions. The Andean Cordilleras block atmospheric moisture flow locally, maintaining some areas with very low precipitation levels, whilst enhancing orographic rainfall in adjacent localities (Lenters and Cook 1995). As a result, there are wetter patches surrounded by drier areas across the region, such as the wet zones in central Bolivia and in south east Peru (Fig. 2). The inverse is also observed, such as the patches of drier forests south of Tarapoto in central

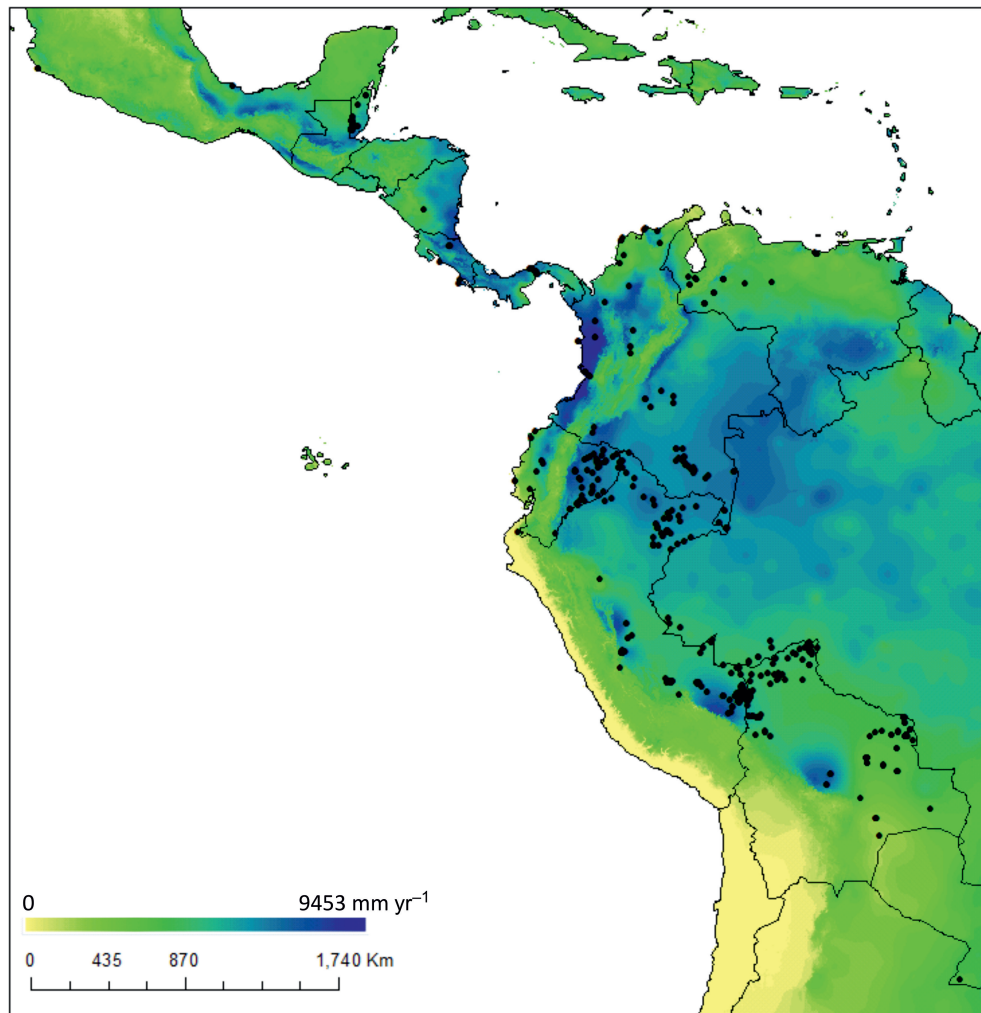


Figure 2. Mean annual precipitation in the western Neotropics and distribution of the 531 forest inventory plots (black dots) analysed in this study. Precipitation data come from WorldClim (Hijmans et al. 2005). Note the spatial complexity of precipitation patterns within the study area.

Peru. There is also a general tendency for precipitation to decline away from the equator in both northward and southward directions (Fig. 2). Secondly, the western Neotropics is a cohesive phylogeographic unit. Western Amazonian forests are floristically more similar to forests in Central America than to those in the eastern Amazon, despite the greater distances involved and the presence of the world's second highest mountain range dividing Central America from southern Peru (Gentry 1990). This floristic similarity between the western Amazon and Central American forests is thought to be because: 1) the Andes are young (~ 25 Ma) so represent a recent phytogeographic barrier (Gentry 1982, 1990), and 2) the soils of moist forests in western Amazonia and Central America are similar, being young, relatively fertile, and often poorly structured, largely as a consequence of the Andean uplift and associated Central American orogeny (Gentry 1982, Quesada et al. 2010).

Here, we use a unique, extensive forest plot dataset to investigate how precipitation influences the distribution of tree taxa, at different taxonomic levels, across the western Neotropics. Using 531 tree plots that include 2570 species, we examine the climatic macroecology of the region's tropical

trees. Specifically, we 1) test the dry tolerance hypothesis, which posits that tolerance to dry extremes explains taxa geographic ranges within closed-canopy forests (Fig. 1a); and 2) quantify the affiliations of taxa to precipitation using available data, in order to assess individual taxon-climate sensitivities and predict how tropical trees may respond to potential future climatic changes.

Methods

Precipitation in the western Neotropics

To investigate the effects of water-stress on the distribution of tropical forest taxa we used the maximum climatological water deficit (CWD) (Chave et al. 2014). This metric represents the sum of water deficit values (i.e. the difference between precipitation and evapotranspiration) over consecutive months when evapotranspiration is greater than precipitation. CWD values were extracted at a 2.5 arc-minute resolution layer, based on interpolations of precipitation measurements from weather stations between

1960 and 1990 and evapotranspiration calculated using the same data (New et al. 2002) (Supplementary material Appendix 1). Additionally, we used mean annual precipitation (MAP) from the WorldClim database (Hijmans et al. 2005) to quantify total annual precipitation. MAP values are derived from interpolations of weather station data with monthly records between ca 1950 and 2000 at a resolution equivalent to ca 1 km². Although these datasets have different grain sizes, the underlying data used in both interpolations have the same spatial scale (Hijmans et al. 2005, Chave et al. 2014).

Vegetation data set

We used data from 531 floristic inventories from three plot networks: ATDN (ter Steege et al. 2003, 2013), RAINFOR (Malhi et al. 2002) and Gentry and Phillips plots (Gentry 1988, Phillips and Miller 2002, Phillips et al. 2003), distributed throughout the western Neotropics (Supplementary material Appendix 2). Plot areas varied from 0.1 to 5.0 ha. We included all trees with a diameter (D) ≥ 10 cm. Our analysis was restricted to lowland terra firme forests below 1000 m a.s.l., excluding all lianas. The RAINFOR and Phillips datasets were downloaded from ForestPlots.net (Lopez-Gonzalez et al. 2009, 2011) and the Alwyn H. Gentry Forest Transect Data Set from <www.mobot.org/mobot/research/gentry/welcome.shtml>.

The plots in our dataset provide a largely representative sample of actual precipitation values across all western neotropical lowland forests (Supplementary material Appendix 3). However, the dataset only includes 18 plots in very wet environments (above 3500 mm yr⁻¹, Supplementary material Appendix 3, Fig. A3.2), which are largely confined to small pockets on both flanks of the Andes. As this sample (3% of all plots) is insufficient to accurately determine species' occurrences and ranges in the wettest forests, we restricted our precipitation and taxa distribution analyses (see below) to the 513 plots with MAP ≤ 3500 mm yr⁻¹.

Analyses

Precipitation and diversity

If water supply broadly limits species' distributions, then community-level diversity should also be controlled by precipitation regime. However, variation in local diversity is nevertheless expected as a consequence of other factors (ter Steege et al. 2003). For example, even under wet precipitation regimes, local edaphic conditions such as extremely porous soils could lead to water stress and lower diversity. Therefore, we fitted a quantile regression (Koenker and Bassett 1978), describing the role of precipitation in controlling the upper bound of diversity. Diversity was quantified using Fisher's α because this metric is relatively insensitive to variable stem numbers among plots. In addition, to assess whether the correlation between diversity and precipitation is robust to the potential influence of spatial autocorrelation we applied a Partial Mantel test (Fortin and Payette 2002), computing the relationship between the Euclidian distances of diversity and precipitation, whilst controlling for the effect of geographic distances. Lastly, we also used Kendall's τ non-parametric correlation coefficient to assess the relationship

between diversity and precipitation. We restricted all diversity analyses to the 116 1-ha plots that had at least 80% of trees identified to species level.

Metacommunity structure

We used the approach of Leibold and Mikkelsen (2002) to test whether the distribution of taxa along the precipitation gradient follows a turnover or nested pattern. Our analysis was performed by first sorting the plots within the community matrix by their precipitation regimes. Then we assessed turnover by counting the number of times a taxon replaces another between two climatologically adjacent sites and comparing this value to the average number of replacements found when randomly sorting the matrix 1000 times. More replacements than expected by chance indicate a turnover structure, whilst fewer imply that the metacommunity follows a nested pattern (Presley et al. 2010) as predicted by the dry tolerance hypothesis. This analysis was conducted applying the function 'Turnover' from the R package 'metacom' (Dallas 2014).

Precipitation and taxa distribution

To explore the influence of precipitation on taxa distributions firstly, we simply plotted taxa precipitation ranges, i.e. the range of precipitation conditions in which each taxon occurs, to visually inspect the variation of precipitation ranges among taxa. According to the dry tolerance hypothesis, for each taxon the precipitation range size should be positively associated with the driest condition at which it is found, i.e. the more tolerant to dry conditions the taxon is, the larger its climatic span should be. However, the predicted pattern could also arise artefactually if taxa that occur under extreme regimes have on average bigger ranges regardless of whether they are associated to dry or wet conditions. We therefore, secondly, used Kendall's τ coefficient of correlation to explore analytically the relationship between taxon precipitation range and both the driest and wettest CWD values at which each taxon occurs. If the dry tolerance hypothesis holds we expect precipitation range size to be negatively correlated with the driest precipitation condition where each taxon occurs and not correlated with wettest precipitation where each taxon is found.

Thirdly, we compared taxa discovery curves, which represent the cumulative percentage of taxa from the whole metacommunity that occur in each plot when following opposite environmental sampling directions, i.e. from wet to dry and from dry to wet. The dry tolerance hypothesis predicts that wet to dry discovery curves should be steeper initially than dry to wet curves, as wet areas are expected to have more narrow-ranged taxa.

Finally, we examined the loss of taxa from extremely wet and from extremely dry plots over the precipitation gradient. We tested whether tree taxa found at the driest conditions within our sample can tolerate a larger range of precipitation conditions than taxa in the wettest plots. We thus generated taxa loss curves to describe the decay of taxa along the precipitation gradient within the 10% driest plots and the 10% wettest plots.

We compared discovery and loss curves in different directions of the precipitation gradient (i.e. from wet to dry and from dry to wet) against each other and against null models of no influence of precipitation on taxa discovery or loss.

These null models represented the mean and confidence intervals from 1000 taxa discovery and loss curves produced by randomly shuffling the precipitation values attributed to each plot. Taxa recorded in 10 plots or fewer are likely to be under-sampled within the metacommunity and were excluded from the analyses regarding metacommunity structure and taxa distribution.

Taxa precipitation affiliation

To describe the preferred precipitation conditions for each taxon we generated an index of precipitation affiliation, or precipitation centre of gravity (PCG). We adopted a similar approach to that used to estimate the elevation centre of gravity by Chen et al. (2009) (see also Feeley et al. 2011), which consisted of calculating the mean of precipitation of locations where each taxon occurs in, weighted by the taxon's relative abundance in each community (Eq. 1).

$$PCG = \frac{\sum_1^n P \times Ra}{\sum_1^n Ra} \quad (1)$$

where: n = number of plots; P = precipitation; Ra = relative abundance based on number of individuals.

The resulting taxon-level PCG values are in units of millimetres per year, the same scale as the precipitation variables: CWD or MAP. We tested the null hypothesis of no influence of precipitation on the distribution of each taxon by calculating the probability of an observed PCG value being higher than a PCG generated by randomly shuffling the precipitation records among the communities, following Manly (1997) (Supplementary material Appendix 4). We also generated an alternative estimator of precipitation affiliation for each taxon by correlating its plot-specific relative abundance and precipitation values using Kendall's τ coefficient of correlation (following Butt et al. 2008). Here, a negative correlation indicates affiliation to dry conditions, whilst a positive correlation indicates affiliation to wet conditions (Supplementary material Appendix 6).

PCG values were calculated for each taxon recorded in at least three localities (1818 species, 544 genera and 104 families), and Kendall's τ values were calculated for each taxon recorded in at least 20 localities (525 species, 327 genera and 78 families). We also calculated the proportions of significantly dry- and wet-affiliated taxa. To verify that these

proportions were not merely a consequence of the number of taxa assessed, we compared our observed proportions to 999 proportions calculated from random metacommunity structures where taxa abundances were shuffled among plots (Supplementary material Appendix 5).

Each analysis was repeated at family, genus and species levels. All analyses were performed for CWD, and precipitation affiliations were also calculated for MAP. Analyses were carried out in R ver. 3.1.1 (R Core Team).

Results

In the western Neotropics, diversity was negatively related to water-stress at all taxonomic levels, being strongly limited by more extreme negative values of maximum climatological water deficit (CWD) (Fig. 3). This result remained after accounting for possible spatial autocorrelation (Partial Mantel test significant at $\alpha = 0.05$ for all taxonomic levels: $r = 0.31$ for species; $r = 0.38$ for genera; $r = 0.37$ for families). The large increase in diversity towards the wettest areas was most evident at the species level (around 200-fold), but was also strong at genus (ca 70-fold) and family levels (ca 16-fold) (Fig. 3).

For all our analyses of taxa distributions it was evident that they follow a nested pattern along the water-deficit gradient, as predicted by the dry tolerance hypothesis. Thus, firstly, when investigating metacommunity structure, among any given pair of sites, the number of times a taxon replaced another was significantly lower than expected by chance at all taxonomic levels (Table 1). Secondly, compared to all taxa, those able to tolerate the dry extremes were clearly distributed over a wider range of precipitation regimes (Fig. 4a–c). This was confirmed by precipitation ranges being very strongly and negatively correlated to the driest condition where each taxon occurs (Kendall's $\tau = -0.93$ for species, -0.96 for genera and -0.99 for families, one-tailed p -values < 0.001) and not correlated to the wettest condition of occurrence (Kendall's $\tau = 0.01$ for species, 0.05 for genera and -0.01 for families, p -values > 0.05).

Thirdly, nested patterns were evident in most taxa discovery curves, with the floristic composition of dry plots being a subset of wet plots (Fig. 4d–f). At species and genus levels, the wet–dry cumulative discovery curves

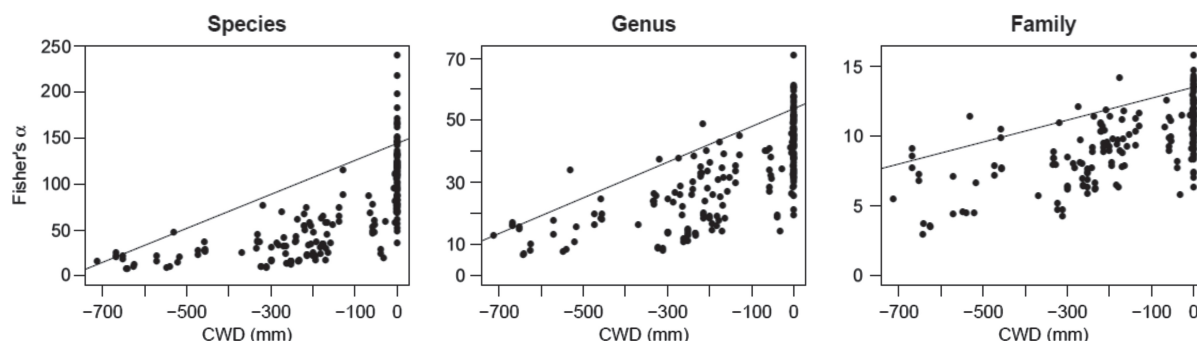


Figure 3. Tree alpha diversity (evaluated with Fisher's alpha parameter) as a function of precipitation, represented by maximum climatological water-deficit (CWD) for 1 ha plots across the western Neotropics. Solid curves represent the 90% upper quantile regression. Note that more negative values of CWD limit alpha diversity and that the diversity vs CWD correlation is stronger for finer taxonomic levels – Kendall's $\tau = 0.66$ for species, 0.60 for genus and 0.51 for family level, p -values < 0.001 .

Table 1. Observed and expected turnover of taxa along the precipitation gradient. Turnover was measured by the number of times a taxon replaces another between two sites. Expected values represent the average turnover when randomly sorting the matrix 1000 times. P-values test the null hypothesis that replacement of taxa along the precipitation gradient does not differ from random expectations considering $\alpha = 0.05$. Note that observed taxa turnover is significantly lower than the expected, which indicates that the distributions of taxa follows a nested pattern along the precipitation gradient (Leibold and Mikkelsen 2002, Presley et al. 2010).

	Observed turnover	Expected turnover	p
Families	0	755 226	0.01
Genera	2061	3 529 527	<0.01
Species	0	25 592 113	<0.01

were steeper than the dry–wet curves, indicating more taxa restricted to wet conditions. However, this distinction in the shape of the discovery curves between the directions of the precipitation gradient (wet–dry vs dry–wet) was much less evident at the family level (Fig. 4f). Finally, the loss curve analysis also showed that plots at the wet extremes of the precipitation gradient have many more taxa restricted to wet conditions than expected by chance (Fig. 4g–i). Extreme dry plots also had a much greater proportion of species with wide precipitation ranges than the wettest plots, with at least 80% of their species persisting until all but the very wettest forests are reached (Fig. 4g – red curve). Again, these patterns were most clearly evident for species and genera.

For the 1818 species, 544 genera and 104 families assessed across the western Neotropics, we found a large proportion of taxa with significant values for rainfall affiliation (Table 2a, Supplementary material Appendix 9, Table A9.1, A9.2 and A9.3). Affiliations to wet conditions were substantially more common than affiliations to dry conditions at all taxonomic levels (Table 2b) (Supplementary material Appendix 5). Anacardiaceae and Rutaceae are examples of the 10 most dry-affiliated families registered in 10 or more localities and Lecythidaceae, Myrsinaceae and Solanaceae are amongst the most wet affiliated families (see Supplementary material Appendix 7, Table A7.1 and A7.2 for the most wet and dry affiliated taxa). Lastly, the observed patterns persisted when repeating the analyses excluding those species possibly affiliated to locally enhanced water supply (Supplementary material Appendix 8).

Discussion

Our results demonstrate the influence of precipitation gradients on the patterns of diversity and composition for families, genera and species of Neotropical trees. We confirm that community diversity is much higher in wet than in drier forests, being as much as 200-fold greater at the species level (Fig. 3). Additionally, our analyses indicate that the diversity decline towards more seasonal forests is a consequence of increasingly drier conditions limiting species distributions. To our knowledge this is the first time that the influence of precipitation affiliation has been quantified at the level of individual Amazon tree species.

Water-stress during the dry season, represented here by the climatological water-deficit (CWD), limits tree species distributions across the western Neotropics (Fig. 4). In areas with a very negative CWD, forest composition is a subset of those communities that do not suffer water-stress (Fig. 4). These findings are consistent with results from studies at much smaller scales (Engelbrecht et al. 2007, Baltzer et al. 2008). The physiological challenges in dry areas require species to have specific characteristics in order to recruit and persist. For example, certain species have the capacity to maintain turgor pressure and living tissues under more negative water potentials at the seedling stage, which allow them to obtain water from dry soils (Baltzer et al. 2008, Brenes-Arguedas et al. 2013). At the wet extreme of the gradient, more favourable conditions may allow a wider range of functional strategies to coexist (Spasojevic et al. 2014). Consistent with this, most taxa in our data set occur in the wet areas, with only a small proportion restricted to dry conditions (Fig. 4). Furthermore, our results indicate that other factors such as pests and pathogens (Spear et al. 2015) or tolerance to shaded environments (Brenes-Arguedas et al. 2013), are much less important in determining the distribution of taxa. In some cases these may restrict the abundance of dry affiliated taxa but generally appear not to limit their occurrence. Geomorphology and dispersal limitation can impact species' distributions, and these drivers likely account for some of the unexplained variation in the relationship between diversity and precipitation shown here (Higgins et al. 2011, Dexter et al. 2012). The scarcity of plots from the very wettest forests (Supplementary material Appendix 3, Fig. A3.2) may also have limited our ability to fully document patterns of species turnover. Nevertheless, our analysis shows that more than 90% of the species occurring in the driest 10% of the neotropical forest samples are also registered in at least one forest with zero mean annual CWD (Fig. 4g). It could be argued that such widespread taxa may not necessarily tolerate dry conditions, but instead be sustained by locally enhanced water supply due to particular conditions such as the presence of streams. However, our results were robust even after excluding taxa potentially affiliated to such local water availability (Supplementary material Appendix 8). Thus, our findings, together with those from Asian and Central American tropical forests (Baltzer et al. 2008, Brenes-Arguedas et al. 2009), suggest that the limitation of most tree species' distributions by water-stress may represent a general macroecological rule across the tropics. This has obvious parallels to the well-known pattern for temperate forest tree species, for which frost tolerance substantially governs species' geographical ranges (Pither 2003, Morin and Lechowicz 2013).

Affiliations to specific precipitation regimes are strongest at the species level, but climate sensitivity can still be clearly detected with genus-level analyses (Fig. 4d–i). The stronger relationship between species and precipitation when compared to other taxonomic levels could be a consequence of a relatively stronger influence of climate on recent diversification. In particular, massive changes in precipitation regimes took place in the Neogene and Quaternary due to Andean uplift and glacial cycles (Hoorn et al. 2010). During this period, global fluctuations in climate and atmospheric CO₂ concentrations, which affect water-use efficiency (Brienen

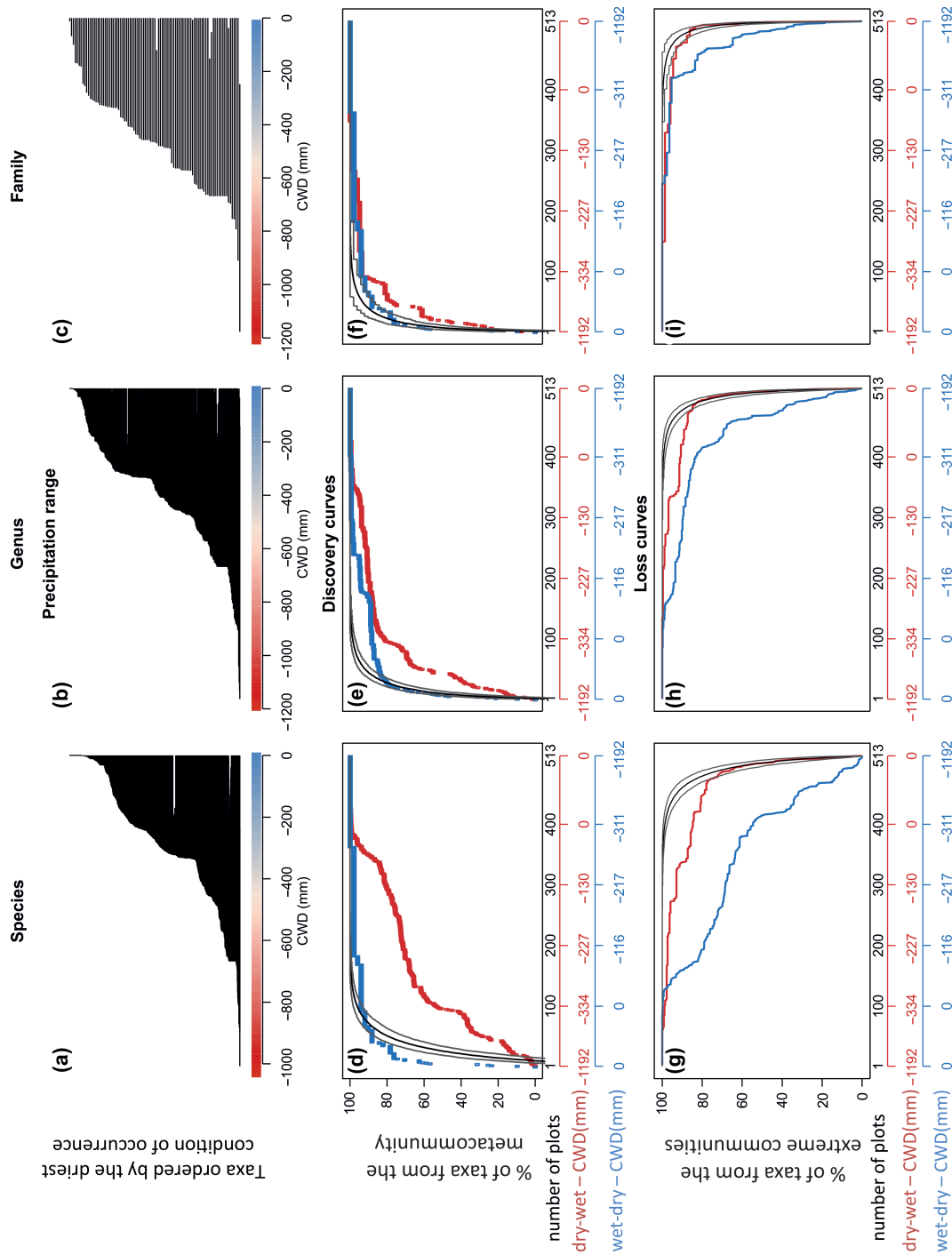


Figure 4. The influence of precipitation on the distribution of taxa in western Neotropics. (a–c) Range of water-deficit conditions (black horizontal lines) over which each (a) species, (b) genus, and (c) family occurs. The x-axes express the water-deficit gradient in mm of maximum climatological water-deficit (CWD) from dry (red) to wet (blue), while taxa are stacked and ordered along y-axes by the most negative value of CWD of occurrence. (d–f) Discovery curves showing the cumulative percentage (y-axes) of (d) species, (e) genera, and (f) families from the whole region found in each plot when moving along the CWD gradient (x-axes). (g–i) Loss curves giving the percentage of (g) species, (h) genera, and (i) families from the 10% of plots under the most extreme precipitation regimes that drop out when moving to the opposite extreme of the gradient. In (d–i) the x-axes show the number of plots, ordered from wet to dry (blue axes and blue curves) and from dry to wet (red axes and red curves). Black and grey curves represent respectively, the mean and 95% confidence limits of loss and discovery curves generated by shuffling values of precipitation within the plots 1000 times. Taxa restricted to 10 or fewer localities were excluded from analyses. Note that of the taxa from the 10% driest communities, 86% of species, 91% of genera and 96% of families are also recorded in plots with zero CWD.

Table 2a. Number of taxa significantly affiliated to wet or dry precipitation regimes, based on their precipitation centre of gravity (PCG) and Kendall's τ coefficient of correlation between relative abundance and precipitation. Taxa with significant PCG are more dry or wet-affiliated than expected by chance, at $\alpha < 0.05$. Significant values of Kendall's τ indicate that the probability of observing a correlation between relative abundance and precipitation by chance is lower than 5%. Affiliation was calculated for two precipitation variables: maximum climatological water deficit (CWD) and mean annual precipitation (MAP). Values in brackets show the proportions of significant values of precipitation affiliations in relation to the total number of taxa in the analyses. We tested the influence of the sample size on the proportion of significant values by comparing the observed proportion against 1000 random proportions generated by shuffling precipitation values across communities. The null hypothesis that proportions are an artefact of the number of taxa analysed was rejected considering $\alpha = 0.001$ in all cases (see Supplementary material Appendix 5 for details).

	Total	Significant PCG		Total	Significant Kendall's τ	
		CWD	MAP		CWD	MAP
Species	1818	1065 (58%)	615 (34%)	525	426 (81%)	398 (76%)
Genera	544	291 (53%)	236 (43%)	327	259 (79%)	242 (74%)
Families	104	60 (58%)	46 (44%)	78	60 (77%)	59 (76%)

Table 2b. As in Table 2a, but giving a breakdown by affiliations to wet and dry conditions. As for Table 2a the influence of the sample size on the proportion of significant values was assessed by comparing the observed proportion against 1000 random proportions generated by shuffling precipitation values across communities (see Supplementary material Appendix 5 for details). P-values test the null hypothesis that proportions are an artefact of the number of taxa.

	Maximum climatological water deficit (mm) (CWD)		Mean annual precipitation (mm) (MAP)	
	dry	wet	dry	wet
Significant PCG				
Species	112 (6%)*	953 (52%)*	153 (8%)*	462 (25%)*
Genera	67 (12%)*	224 (41%)*	94 (17%)*	142 (26%)*
Families	13 (12%)*	47 (45%)*	18 (17%)*	28 (27%)*
Significant Kendall's τ				
Species	59 (11%)*	367 (70%)*	52 (10%)*	346 (66%)*
Genera	49 (15%)*	210 (64%)*	48 (15%)*	194 (59%)*
Families	6 (8%)*	54 (69%)*	8 (10%)*	51 (65%)*

* $p < 0.05$.

et al. 2011), are thought to have influenced speciation (cf. Richardson et al. 2001, Erkens et al. 2007, although see Hoorn et al. 2010). Climate sensitivity was also clearly evident at the genus level (Fig. 4), which has relevant practical implications for tropical community and ecosystem ecology. Because of the challenges of achieving sufficient sample size and accurate identification in hyperdiverse tropical forests (Martinez and Phillips 2000), ecosystem process and community ecological studies in this ecosystem often rely on the simplifying assumption that the genus-level represents a sufficiently functionally-coherent unit to address the question at hand (Harley et al. 2004, Laurance et al. 2004, Butt et al. 2014). Our results suggests that analysis at the genus-level could be used to assess, for instance, the impacts of climate change on diversity, but that nevertheless such impacts would be underestimated without a species-level analysis.

In addition to the physiological tolerance to dry conditions, other, underlying geographical and evolutionary processes could conceivably drive the patterns we observe in this study. These are, notably, 1) a greater extent of wet areas (Terborgh 1973, Fine 2001), 2) greater stability of wet areas through time leading to lower extinction rates (Klopper 1959, Jansson 2003, Jablonski et al. 2006), and 3) faster rates of speciation in wet forests (Rohde 1992, Allen et al. 2002, Jablonski et al. 2006). The first alternative (Rosenzweig 1992) requires that species–area relationships govern the climate-diversity associations that we find. Within our region, the areas that do not suffer water-stress (i.e. CWD = 0) are where the great majority of the species (90%) can be found (Fig. 4), yet they occupy a relatively small area (25% of

the western Neotropics and 31% of plots). Thus, the area hypothesis appears unlikely to be driving the precipitation–diversity relationship.

The other two alternative hypotheses could more plausibly be contributing to the patterns observed here. Climate stability is indeed associated with diversity throughout the Neotropics (Morueta-Holme et al. 2013). In contrast with most of the Amazon basin, the lowland forests close to the Andes and in Central America apparently had relatively stable climates, with only moderate changes during the Quaternary/Neogene (Hoorn et al. 2010), which could have reduced extinction rates (Klopper 1959, Jablonski et al. 2006). The diversity gradient may also be a consequence of more diverse areas having higher diversification rates (Rohde 1992, Jansson 2003, Jablonski et al. 2006). While both lower extinction rates and higher speciation rates in wet forest might contribute to explaining the climate-diversity gradient, their influence does not invalidate the idea that wet-affiliated species are drought-intolerant. Indeed, the mechanisms that might have favoured lower extinction rates in wetter forests are related to the inability of many taxa to survive environmental fluctuations such as droughts. Experiments showing that seedlings of species from wet tropical environments have higher mortality under water-stress than dry-distributed taxa (Engelbrecht et al. 2007, Baltzer et al. 2008, Poorter and Markesteijn 2008) indicate that water stress can have direct impacts on species survival and distribution. As ever, untangling ecological and historical explanations of patterns of diversity is difficult with data solely on species distributions (Ricklefs 2004).

Implications for climate change responses

Understanding how floristic composition is distributed along precipitation gradients is critical to better predict outcomes for the rich biodiversity of the region in the face of climatic changes. The observed small precipitation ranges of wet-affiliated taxa (Fig. 4a–c) together with the rareness of extremely wet areas (Supplementary material Appendix 3, Fig. A3.2) indicate high potential vulnerability to changes in climate. So far, while total precipitation has recently increased in Amazonia (Gloor et al. 2013), much of Amazonia and Central America have also seen an increase in drought frequency, and more generally in the frequency of extreme dry and wet events (Malhi and Wright 2004, Aguilar et al. 2005, Li et al. 2008, Marengo et al. 2011). These neotropical trends toward similar or greater annual precipitation, but a greater frequency and intensity of dry events, are expected to continue, albeit with important regional differences (IPCC 2013). While elevated atmospheric CO₂ concentrations may alleviate physiological impacts of water-stress on plants by increasing water-use efficiency (Brienen et al. 2011, van der Sleen et al. 2015), warming will have the opposite impact. Temperatures have increased markedly in Amazonia since 1970 (Jiménez-Muñoz et al. 2013) and this trend is highly likely to continue (IPCC 2013) so that plants will experience increased water-stress throughout the Basin (Malhi et al. 2009) with thermally-enhanced dry season water-stress challenging trees even in wetter environments. The restriction of most tree taxa in the western Neotropics to wetter areas indicates widespread low tolerance to dry conditions and low capacity to acclimate to them. Together with the anticipated climate changes this suggests that floristic composition may change substantially, potentially with the loss of many wet forest specialists and compensatory gains by the fewer, more climatologically-generalist dry tolerant species. While research is clearly needed to track and analyse ecological monitoring sites to examine where and how tropical forest composition responds to anthropogenic climate changes, protecting the remaining ever-wet forests and coherent up-slope migration routes will be essential if most neotropical diversity is to survive into the next century.

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Supplementary material (Appendix ECOG-01904 at <www.ecography.org/appendix/ecog-01904>). Appendix 1–9.