



Which is a better predictor of plant traits: temperature or precipitation?

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Abstract

Question: Are plant traits more closely correlated with mean annual temperature, or with mean annual precipitation?

Location: Global.

Methods: We quantified the strength of the relationships between temperature and precipitation and 21 plant traits from 447,961 species-site combinations worldwide. We used meta-analysis to provide an overall answer to our question.

Results: Mean annual temperature was significantly more strongly correlated with plant traits than was mean annual precipitation.

Conclusions: Our study provides support for some of the assumptions of classical vegetation theory, and points to many interesting directions for future research. The relatively low R^2 values for precipitation might reflect the weak link between mean annual precipitation and the availability of water to plants.

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Introduction

Our planet supports an astonishing array of plant communities, ranging from arctic tundra through to lush tropical rain forests, boreal forests, tropical savannas, deserts, temperate grasslands and tropical dry forests. Understanding the factors that underlie the dramatic differences in community structure and composition, and the ecological strategies employed by the plants and animals that inhabit these communities, has long been a goal of ecologists and vegetation scientists (Schimper & Fisher 1902; Fischer 1960; MacArthur 1972; Schemske et al. 2009).

Our main aim in this research was to provide a quantitative test of the relative importance of mean annual temperature and mean annual precipitation in shaping plant functional traits. Addressing this question will both improve our basic understanding of the factors that shape plant ecological strategies and the distribution of different

vegetation types. Although many studies have included both rainfall and temperature variables (Reich et al. 1997; Niinemets 2001; Wright et al. 2004; Ordoñez et al. 2010a; Silva et al. 2010; Sack & Scoffoni 2013), ours is the most comprehensive quantification to date.

Precipitation and temperature have been two of the most commonly considered variables in studies of how the climate shapes plant community distribution and diversity at the global scale (Whittaker 1970; MacArthur 1972; Clarke & Gaston 2006). Both ecological (Walter 1994) and evolutionary (Donoghue 2008) theory suggest that temperature and precipitation are major determinants of plant traits at a global scale. Temperature affects leaf energy balance (i.e. the balance of radiative heating and evaporative cooling, and boundary layer conductance; Lambers 1998; Harrison et al. 2010), metabolic rate (in a wide range of taxa, including plants; Gillooly et al. 2001) and plant growth rate (Went 1953; Rawson 1992), and exposure to either very high or very low temperatures can damage

plants (Went 1953). Many ecological traits are known to be correlated with temperature, including leaf nutrient content, leaf mass per unit area and leaf life span (Reich & Oleksyn 2004; Wright et al. 2004), seed mass (Murray et al. 2004) and wood density (Swenson & Enquist 2007). There are also strong relationships between plant traits and mean annual precipitation, both within and across biomes, particularly for traits related to drought tolerance, such as leaf venation architecture, osmotic potential, xylem structure and hydraulic physiology (Maherali et al. 2004; Choat et al. 2007; Blackman et al. 2010; Freschet et al. 2011; Bartlett et al. 2012; Sack & Scoffoni 2013).

Of course, mean annual temperature and mean annual precipitation are not the only factors that affect plant growth and reproduction, and they do not work independently: the effects of temperature might be partly mediated by its effect on evaporative demand and thereby water availability. If our aim were to build a model that explained the maximum amount of variation in plant traits, then we would include factors such as climate extremes, irradiance, potential evapotranspiration, climatic variability, soil properties and interactions between variables. We aim to address many such questions using these variables in the near future with our unprecedented trait database. For now, even though variables like potential evapotranspiration or related measures of aridity would likely have been strongly correlated with plant traits, the fact that they combine precipitation and temperature means they would not help to address our question, which is whether mean annual temperature or mean annual precipitation is most strongly related to plant traits.

Methods

Twenty-one traits were selected to capture information about various aspects of plant ecological strategy (traits are listed in Table 1). Seed mass, seed dispersal syndrome and possession of clonal structures capture information about a species' reproductive strategy (Grime & Jeffrey 1965; Grime et al. 1981; Grubb & Burslem 1998; Leishman et al. 2000; Aarssen & Jordan 2001; Wright et al. 2010). Specific leaf area, evergreen/deciduous phenology, photosynthetic pathway, leaf area, whether leaves are simple or compound, leaf life span and leaf nitrogen, phosphorus and carbon concentration all influence various aspects of a species' carbon budget, growth rate and survival (Givnish 1978; Niinemets & Kull 1994; Niinemets 1998; Poorter & De Jong 1999; Reich et al. 1999, 2003; Diaz et al. 2004; Wright et al. 2004, 2010). Presence of spines, specific leaf area and presence of hairs on leaves can contribute to species' defence against damage from both biotic and abiotic factors (Grubb 1992; McIntyre et al. 1999; Díaz et al. 2001; Hanley et al. 2007). Finally, plant life span, maxi-

mum plant height, ability to fix atmospheric nitrogen and growth form capture crucial information about resource acquisition, competitive ability and life-history strategy (Falster & Westoby 2005; Pérez-Harguindeguy et al. 2013). Ultimately, these strategies (and underlying traits) relate to stress tolerance and to regimes of resource availability and disturbance (Chapin et al. 1993; McIntyre et al. 1999; Weiher et al. 1999; Pérez-Harguindeguy et al. 2013).

Data for most traits were taken from the TRY database (Kattge et al. 2011), supplemented with data for plant height and seed mass from previous global compilations. A list of included TRY data sets is provided in Appendix S1, and the original publications associated with the data used are: Shipley (1995); Cornelissen (1996); Bahn et al. (1999); Hickler (1999); Medlyn et al. (1999); Medlyn & Jarvis (1999); Niinemets (1999); Pyankov et al. (1999); Fonseca et al. (2000); Medlyn et al. (2001); Niinemets (2001); Shipley & Vu (2002); Anand et al. (2003); Cornelissen et al. (2003); McDonald et al. (2003); Ogaya & Penuelas (2003); Pillar & Sosinski (2003); Quested et al. (2003); Cornelissen et al. (2004); Diaz et al. (2004); Wright et al. (2004); Bakker et al. (2005); Louault et al. (2005); Overbeck (2005); Bakker et al. (2006); Cavender-Bares et al. (2006); Cornwell et al. (2006); Kazakou et al. (2006); Ogaya & Penuelas (2006); Preston et al. (2006); Wright et al. (2006); Ackerly & Cornwell (2007); Blanco et al. (2007); Duarte et al. (2007); Garnier et al. (2007); Moles et al. (2007); Müller et al. (2007); Ogaya & Penuelas (2007); Overbeck & Pfadenhauer (2007); Swaine (2007); Wright et al. (2007); Cornwell et al. (2008); Kleyer et al. (2008); Kurokawa & Nakashizuka (2008); Ogaya & Penuelas (2008); Pakeman et al. (2008); Reich et al. (2008); Royal Botanic Gardens Kew (2008); Sardans et al. (2008a,b); Shiodera et al. (2008); van Bodegom et al. (2008); Baker et al. (2009); Cornwell & Ackerly (2009); Craine et al. (2009); Fortunel et al. (2009); Fyllas et al. (2009); Kattge et al. (2009); Moles et al. (2009); Pakeman et al. (2009); Patiño et al. (2009); Poorter et al. (2009); Poorter (2009); Reich et al. (2009); Freschet et al. (2010a, b); Laughlin et al. (2010); Messier et al. (2010); Ordoñez et al. (2010a,b); Penuelas et al. (2010a,b); Willis et al. (2010); Wright et al. (2010); Onoda et al. (2011); and Gutiérrez & Huth (2012).

Because many traits vary across species' ranges (Frenne et al. 2013), we only used data from these databases if they were associated with geospatial information (i.e. we did not apply mean trait values across the distribution of the species for continuous traits). We also included data for four additional binary traits; woody vs herbaceous growth form (a global data set from Zanne et al. 2013) and presence of clonal reproductive structures, hairs and spines (data only for Australian species, taken from the Flora of

Table 1. Relationships between plant traits, mean annual temperature (°C) and mean annual precipitation (mm). The higher R^2 for each trait is highlighted in bold. We have included the direction of relationships between each climate variable and each continuous and binary trait, and summarized the results for categorical variables. A positive slope in a logistic regression (for binary variables) indicates that as temperature or precipitation increases, the state of the binary is more likely to be 1 [yes] (see Appendix S3 for a visual representation of these relationships). Sample sizes (n) are the number of species–site combinations, and in parentheses, the number of sites. The sample size sometimes differs slightly between temperature and precipitation analyses because of small differences in the coverage of climate data that met our quality control criteria between the CRUTEM and GPCC data sets.

Trait	Mean annual temperature				Mean annual precipitation			
	R^2	Direction of relationship	n	P	R^2	Direction of relationship	n	P
Plant height (m)	0.245	+	14 535 (481)	<0.001	0.206	+	14 492 (480)	<0.001
Leaf area (mm ²)	0.184	+	7168 (312)	<0.001	0.147	+	7168 (312)	<0.001
Seed mass (mg)	0.172	+	10 154 (1296)	<0.001	0.080	+	10 154 (1296)	<0.001
Leaf life span (months)	0.170	+	753 (55)	<0.001	0.287	+	753 (55)	<0.001
Spinescence (yes/no)	0.133	–	408 551 (38 281)	0.987	0.004	–	408 543 (38 280)	0.99
Plant life span (years)	0.098	–	729 (317)	0.100	0.174	+	729 (317)	<0.001
Leaf P_{mass} (mg·g ⁻¹)	0.069	–	5117 (822)	<0.001	0.027	–	5118 (823)	<0.001
Specific leaf area (m ² ·kg ⁻¹)	0.058	–	10 792 (722)	<0.001	0.001	+	10 792 (722)	<0.001
Leaf C_{mass} (mg·g ⁻¹)	0.051	+	3351 (400)	<0.001	0.136	–	3351 (400)	<0.001
Woody/herbaceous	0.042	+	315 271 (37 442)	<0.001	0.002	–	315 233 (37 442)	<0.001
Ability to fix N (yes/no)	0.012	+	446 696 (41 612)	<0.001	0.029	–	446 654 (41 612)	<0.001
Presence of clonal structures (yes/no)	0.035	–	413 037 (39 495)	<0.001	0.022	+	413 029 (39 494)	<0.001
Dispersal syndrome (wind, unassisted, water, animal)	0.028	Animal > (unassisted, wind, water)	4381 (461)	<0.001	0.016	Animal > wind > unassisted; water ns different to any	4381 (461)	<0.001
Evergreen/deciduous	0.020	+	100 725 (23 695)	<0.001	0.00005	+	100 719 (23 694)	0.0947
Leaf N_{mass} (mg·g ⁻¹)	0.016	–	125 70 (1425)	<0.001	0.001	+	12 571 (1423)	0.522
Leaf C_{area} (g·m ⁻²)	0.013	–	1996 (272)	0.360	0.0005	–	1996 (272)	0.039
Leaf N_{area} (g·m ⁻²)	0.011	–	4871 (434)	0.045	0.0004	–	4871 (434)	0.104
Presence of hairs on mature leaves (yes/no)	0.006	+	362 108 (37 808)	0.916	0.003	–	362 101 (37 807)	<0.001
Photosynthesis (C ₃ /C ₄ /CAM)	0.006	(C ₃ , CAM) < C ₄	10 872 (1920)	<0.001	0.011	C ₃ > (C ₄ , CAM)	10 874 (1921)	<0.001
Leaf P_{area} (g·m ⁻²)	0.005	–	2356 (214)	0.005	0.011	–	2356 (214)	<0.001
Compound leaves (yes/no)	0.002	+	143 179 (28 144)	0.727	0.0001	–	143 153 (28 143)	0.568

Australia Online 2013), combined with distribution data from the Atlas of Living Australia (<http://www.ala.org.au/>). The data set includes angiosperms, gymnosperms, ferns and fern allies and bryophytes. Nomenclature was standardized and the data were extensively error checked before analysis (details in Appendix S2).

The replicates in the analyses were species–site combinations, where ‘sites’ were defined as 0.1° grid squares. Where we had multiple observations for the same trait for a species within the same 0.1° grid square, we used the geometric mean to calculate a single species–site combination, with the exception of plant height, for which we used the maximum value. The final data set included 447 961 species–site combinations, including 25 354 species and 41 672 sites (Fig. 1).

Data for mean annual temperature were taken from the CRUTEM database (Jones et al. 2012) and data for mean annual precipitation were taken from GPCC

(Schneider et al. 2011). CRUTEM is on a 5° × 5° grid, and GPCC a 2.5° × 2.5° grid, created by gridding and weighting algorithms that use all appropriate stations within each grid cell. These two data sets are widely used in the climate science community. Stations are required to meet rigorous quality control checks to be used in the gridding procedure. Note that the number and spatial distribution of stations employed differs between the two products. These resolutions were chosen to avoid problems with the interpolation algorithms used to generate higher resolution data sets, and to improve the coverage of our data set, which is particularly important in tropical regions. While temperature and precipitation vary within grid squares (especially in mountainous areas where there are rain shadows and altitudinal temperature gradients), we suspect the overall effect is small relative to the global patterns studied here. Climate data were extracted for a 60-yr period

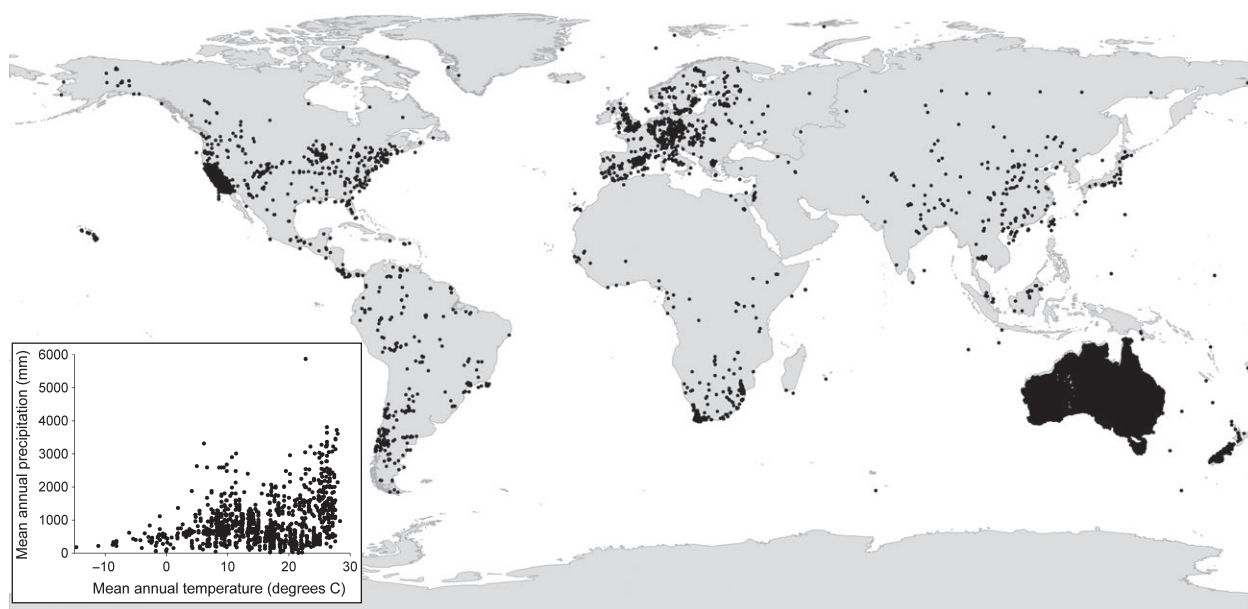


Fig. 1. World map showing distribution of the sites included in this study. The inset shows the spread of mean annual temperature and mean annual precipitation spanned by these sites. The unusually high coverage across Australia is only for three categorical traits: presence/absence of clonal structures, hairs on leaves and spinescence. Excluding these three traits from analyses did not qualitatively affect our results.

spanning 1951–2010. Each observational data set was masked to omit ocean data, which are not relevant to this study. Due to the coarse resolution of the observational grids, and the fact that some land areas may not be covered by suitable observational data, search radii were used. If a specific species' location did not fall in a land-based grid box, then a 1000-km search radius was fitted to find the nearest grid box with appropriate data. If no data-filled grid box was found using a 1000-km radius, then relationships between that specific site and observational data set could not be obtained. Due to the different compositions and resolutions of the climate data sets, not all statistics could be retrieved for each species location.

For continuous traits, we ran separate linear mixed-effects models (Venables & Ripley 2002) for temperature and precipitation, with each model including a fixed effect for temperature or precipitation, a random effect for site and a random effect for species. All continuous traits were \log_{10} transformed before analysis. For binary traits, we ran separate random effects logistic regressions for temperature and precipitation, with each model including fixed effects terms for temperature or precipitation, and random effects for site and species (except for the N-fixation regressions, which failed to optimise when a random effect for species was included and were thus run only with a random effect for site). We included these random effects to account for the non-independence of species occurring at the same site, and of multiple records of the same species at different

sites. Our inclusion of random effects did not qualitatively affect the results. Models were fitted using restricted maximum likelihood using the *lme4* package in R v 2.14.2 (R Foundation for Statistical Computing, Vienna, Austria). The R^2 -values for mixed models were calculated following Moles et al. (2011b); using sequential reduction in the residual sum of squares on addition of each term, adding the fixed-effects term to the model before the random-effects terms. We have focused on R^2 -values rather than P -values, because we are interested in the strength of the correlations rather than their significance (and because even extremely weak relationships can be statistically significant with very large sample sizes), but P -values are presented in Table 1 for completeness.

We used meta-analysis to obtain an overall quantification of the relative strength of the correlation between plant traits, precipitation and temperature. A log response ratio, calculated as $\ln(R^2 \text{ for mean annual temperature} / R^2 \text{ for mean annual precipitation})$ was calculated for each plant trait, and the meta-analysis was performed in Meta-win (Rosenberg et al. 2000). If temperature and precipitation were equally strongly (or weakly) correlated with a plant trait, then the log response ratio would be zero ($\ln(x/x) = 0$), so the meta-analysis asks whether the mean effect size is different to zero.

Relationships between climatic variables and plant traits are not always linear (Porter & Semenov 2005; Poorter et al. 2010). We therefore performed additional non-linear analyses on our continuous traits (the best performing of

which were most often quadratic relationships). We selected the highest R^2 -value for each trait–climate relationship, and used these in a second ‘best fit’ meta-analysis.

Results

Fifteen of the 21 traits included in this study were more closely related to mean annual temperature than to mean annual precipitation (Table 1, Appendix S3). A chi-squared test confirms that 15/21 is greater than would be expected by chance alone ($\chi^2 = 3.857$, $df = 1$, $P < 0.05$). The six traits that were more closely correlated with rainfall were: plant life span, leaf life span, leaf C_{mass} , ability to fix nitrogen, photosynthetic pathway and leaf P_{area} (Table 1).

Meta-analysis confirmed that, overall, temperature was significantly and substantially more strongly correlated with plant traits than was precipitation (mean effect size = 1.35, 95% confidence intervals = 0.90–1.81).

The R^2 -values of the relationships between traits and climate variables were all below 0.29 (Table 1). The main reason for these weak correlations is that a substantial proportion of the variation in each trait lies at the within-site level, and thus cannot be explained by differences in climate between sites. For instance, models including a random effect for site but not for species show that 34% of the variation in maximum plant height, 43% of the variation in leaf area and 54% of the variation in seed mass lies at the within site level. A high level of within-site variation is normal for global-scale analyses of plant traits (e.g. Freschet et al. 2011).

The R^2 -value of most correlations was higher for non-linear models than for linear models. However, meta-analysis using the best-fit (highest) R^2 -value for each relationship did not change the overall outcome of our study – temperature was still significantly more strongly correlated with plant traits than was precipitation (meta-analysis, mean effect size = 1.11, 95% confidence intervals 0.65–1.57).

Some traits showed very weak relationships with temperature, precipitation or both (Table 1), and we wondered whether our inclusion of low R^2 -values might have influenced our results. We therefore performed an additional meta-analysis that did not include effect sizes based on R^2 -values < 0.001 . Temperature was still significantly more strongly correlated with plant traits than was precipitation (meta-analysis, mean effect size = 0.76, 95% confidence intervals = 0.24–1.27).

Finally, we asked whether the inclusion of three binary traits (possession of clonal reproduction, hairs and spines) that were dominated by data from Australia might have influenced our findings. Excluding these traits from the meta-analysis did not qualitatively affect our results (mean effect size = 1.32, 95% confidence intervals = 0.82–1.82).

Discussion

We have quantified the relative importance of two of the most intensively studied drivers of plant form and function worldwide, and demonstrated that temperature is more strongly correlated with plant traits than is precipitation. Our results are consistent with several previous studies (Reich & Oleksyn 2004; Swenson & Enquist 2007; van Ommen Kloeke et al. 2012), but are based on a far larger primary data set.

Mean annual precipitation was relatively poorly correlated with most of the plant traits investigated here. Mean annual precipitation is often interpreted as an indicator of water availability (Qian et al. 2013). However, the link between precipitation and access to water is often quite weak, as is apparent if we consider the vegetation in different areas of the world with similar levels of precipitation (e.g. Fig. 2). At the same mean annual precipitation, the availability of water to plants depends on a suite of factors, including the seasonal distribution of rainfall, hydrology, soil depth, soil type (including soil moisture-holding capacity and the soil moisture characteristic curve), access to groundwater and on temperature, which determines both whether the precipitation falls as rain or snow and the

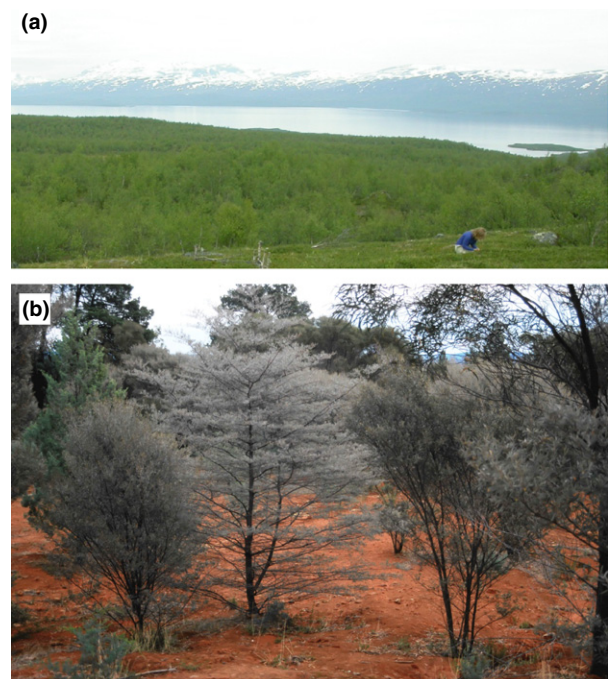


Fig. 2. Ecosystems with similar levels of annual precipitation: (a) Abisko, northern Sweden, which has a mean annual precipitation of 300 mm-yr⁻¹, and (b) Round Hill, western New South Wales, Australia, which has a mean annual precipitation of 389 mm-yr⁻¹ (photos taken by Angela Moles and Ian Wright).

level of evaporative demand (Gardner 1965; Stephenson 1998; Decker et al. 2013). Global variation in any or all of these factors will work to weaken the relationship between mean annual precipitation and plant traits.

The idea that mean annual precipitation may be a poor proxy of the availability of water for plants is certainly not new. Indices of aridity, evapotranspiration and water availability have been used in many ecological studies (Reich et al. 1999; Wright et al. 2004; Poorter et al. 2010; Douma et al. 2012; van Ommen Kloeke et al. 2012), and the combined use of temperature and precipitation to understand the distribution of different vegetation types goes back many decades (e.g. in the Köppen–Geiger climate classification system, originally formulated in 1884, and in Holdridge's life zones, Holdridge 1947). Several plant traits, particularly those related to drought tolerance, show stronger relationships with climate variables that combine rainfall and temperature data, such as potential evapotranspiration and aridity indices (Bartlett et al. 2012; Griffiths et al. 2013). Despite this, many ecologists still rely quite heavily on mean annual precipitation data. Of the 30 papers published in *Global Ecology and Biogeography* between June and October 2013 that included climate variables and were not focused on aquatic systems, the most commonly included variables were mean annual temperature (17 studies) and mean annual precipitation (17 studies). Twenty-eight of these 30 studies included at least one measure of temperature, 24 included at least one measure of precipitation, but only eight included a measure of soil water availability. Precipitation data are certainly easier to obtain than are data for water availability, but ecologists might need to reconsider whether precipitation really is a good enough proxy for their purposes (Hickler et al. 2009; Bartholomeus et al. 2011, 2012).

Even though precipitation is less strongly correlated with plant traits than is temperature, it can still play a key role in shaping plant growth. For instance, the sensitivity of atmospheric carbon dioxide growth rate to inter-annual variability in temperature is higher when tropical land regions experience drier conditions, suggesting that the sensitivity of atmospheric carbon dioxide growth rate to inter-annual temperature variation is regulated by moisture despite the weak direct correlation with tropical precipitation (Wang et al. 2014).

Mean annual temperature was more strongly correlated with plant traits than was mean annual precipitation. However, mean annual temperature is not a perfect variable either. In many parts of the world, particularly at high latitudes, extreme variation in temperature between warm summers and freezing winters means that the ecosystems may spend relatively little time at their mean temperature. The temperature during the times of the year when plants are not growing may have less impact on

plant traits than temperatures during the growing season (Moles et al. 2009). Local factors, such as the aspect of slopes, microclimatic variation and abrupt differences in elevation, are also expected to lead global analyses such as ours to underestimate the true importance of temperature for plants. The different ecological strategies of plants may also act to weaken the overall relationship between traits and temperature. For instance, some species respond to short growing seasons (which are often associated with low mean annual temperatures) through a stress-avoidance strategy (e.g. deciduous species with short-lived leaves and high photosynthetic capacities), while other species take a stress-tolerance strategy (e.g. evergreen species such as the conifers in boreal forests). These different strategies could act to weaken the overall relationship between traits and mean annual temperature (as found in Wright et al. 2005; Kikuzawa et al. 2013).

Given the imperfections of both mean annual temperature and mean annual precipitation, the potential for unmeasured factors to weaken relationships, and the fact that one-third to one half of the global variation in many plant traits lies at the within-site level (and thus cannot be explained by broad climate variables), the R^2 -values for the correlations between mean annual precipitation and mean annual temperature are actually surprisingly high for many traits (Table 1).

Our analysis shows strong differences among traits in their association with mean annual temperature and mean annual precipitation at a global scale. Some traits (e.g. plant height, leaf area and leaf life span) have relatively strong correlations with both temperature and precipitation. Other traits, including possession of compound leaves and presence of hairs on leaves, have R^2 -values <0.01 in both analyses. This suggests a stronger control of climate on some traits compared to others. Some traits differ substantially in the strength of their relationship with temperature vs precipitation. For example, photosynthetic pathway, which is related to drought tolerance, was more strongly related to precipitation than to temperature (Table 1). Similarly strong correlations with mean annual precipitation have been previously shown for stem xylem hydraulic vulnerability (Maherali et al. 2004), for leaf osmotic potential at full turgor and turgor loss point (Bartlett et al. 2012), and for leaf major and minor vein density (Sack & Scoffoni 2013).

Our demonstration that temperature is more strongly correlated with plant traits than is precipitation has relevance to several theories about global patterns in diversity, species' distribution and abundance, traits of plants and animals and plant–animal interactions. Many of these ideas are underpinned by the idea that the climate in tropical ecosystems is more benign and more stable. For instance, one of the leading hypotheses about the latitudi-

nal gradient in biodiversity began from ideas in MacArthur's classic book *Geographical Ecology* (1972). This theory postulates that the greater climatic stability and lower seasonality of tropical systems leads to higher population stability. This stability enables populations to specialize and exploit narrower niches, which allows for a higher diversity of co-existing species in tropical ecosystems. Another widely held idea is that the stable, more amenable climate of the tropics leads to populations of animals and plants that interact year-round without being set back by harsh winters. According to theory, this allows for more intense interactions between plants and animals (such as increased herbivory and seed predation), which in turn leads to higher rates of specialization in tropical systems, and higher levels of defences against predators (Schemske et al. 2009; but see Moles et al. 2011a; Onoda et al. 2011; Schleuning et al. 2012). Although the increased stability of tropical climates is very widely accepted, the data only partially support this idea. While tropical ecosystems are not exposed to harsh winters, many tropical ecosystems (both savannas and forests) experience substantial seasonality in the form of dry and wet seasons. As noted by MacArthur (p. 201; MacArthur 1972) and quantified by Vázquez & Stevens (2004), the tropics have substantially lower variability in temperature, but substantially higher variability in precipitation than do temperate and high-latitude regions. Vázquez & Stevens (2004) concluded that unless we are prepared to argue that precipitation is less important than temperature, we must abandon the idea that the tropics are more climatically stable than are ecosystems at higher latitudes.

Our study provides the first general evidence that precipitation is in fact less closely related to a range of crucial plant traits than is temperature, thus providing some support for traditional theories about how latitudinal gradients shape biology (MacArthur 1972; Schemske et al. 2009). To fully resolve this issue, we would need to quantify the relative importance of the seasonality in temperature and precipitation in shaping plant traits. This is beyond the scope of the present study, but we will use our data set to address this question in the near future.

An interesting possibility is that the high levels of precipitation seasonality in the tropics (Vázquez & Stevens 2004) might not always translate into high variability in water availability for tropical plants. Many plant species have surprisingly deep root systems, with the current record held by the 68-m deep roots of *Boscia albitrunca* (Burch.) Gilg & Benedict, a tree growing in the Kalahari (Canadell et al. 1996). Deep roots allow many plants to access groundwater, and thus maintain photosynthesis and green canopies even through sustained dry periods (Nepstad et al. 1994; Decker et al. 2013). Quantifying the actual variability in water avail-

ability to plants across the latitudinal gradient is a very important goal for the future, but a global quantification of a variable so heavily impacted by local processes is currently constrained by the lack of available data sets at the requisite level of detail.

The increasing availability of global-scale data sets for a wide range of plant traits, combined with our ever-improving knowledge of global scale patterns in environmental factors (including vegetation, climate and soil properties) and exponential growth in analytical power, means that we are at an exciting point in ecology. Many of our most influential theories were put forward in the 1960s and 1970s (MacArthur & Wilson 1963; Janzen 1970; Pianka 1970; MacArthur 1972; Connell 1978), often before the data necessary to test their predictions were available. Now is the time to determine which of the theories that underpin present-day ecology are consistent with empirical data, and which need attention.

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References

- Aarssen, L.W. & Jordan, C.Y. 2001. Between-species patterns of covariation in plant size, seed size and fecundity in monocarpic herbs. *Ecoscience* 8: 471–477.
- Ackerly, D.D. & Cornwell, W.K. 2007. A trait-based approach to community assembly: partitioning of species trait values into within- and among-community components. *Ecology Letters* 10: 135–145.
- Anand, M., Ma, K. & Okonski, A. 2003. Characterising biocomplexity and soil microbial dynamics along a smelter-damaged landscape gradient. *The Science of the Total Environment* 311: 247–259.
- Bahn, M., Wohlfahrt, G., Haubner, E., Horak, I., Michaeler, W., Rottmar, K., Tappeiner, U. & Cernusca, A. 1999. Leaf photosynthesis, nitrogen contents and specific leaf area of 30 grassland species in differently managed mountain ecosystems in the Eastern Alps. In: Cernusca, A., Tappeiner, U. & Bayfield, N. (eds.) *Land-use changes in European mountain ecosystems. ECOMONT- concept and results*, pp. 247–255. Blackwell, Berlin, DE.
- Baker, T.R., Phillips, O.L., Laurance, W.F., Pitman, N., Almeida, S., Arroyo, L., DiFiore, A., Erwin, T., Higuchi, N. & Killeen, T. 2009. Do species traits determine patterns of wood production in Amazonian forests? *Biogeosciences* 6: 297–307.
- Bakker, C., Rodenburg, J. & Bodegom, P.M. 2005. Effects of Ca- and Fe-rich seepage on P availability and plant performance in calcareous dune soils. *Plant and Soil* 275: 111–122.
- Bakker, C., Bodegom, P.M., Nelissen, H.J.M., Ernst, W.H.O. & Aerts, R. 2006. Plant responses to rising water tables and nutrient management in calcareous dune slacks. *Plant Ecology* 185: 19–28.
- Bartholomeus, R.P., Witte, J.P.M., van Bodegom, P.M., van Dam, J.C. & Aerts, R. 2011. Climate change threatens endangered plant species by stronger and interacting water-related stresses. *Journal of Geophysical Research* 116: G04023.
- Bartholomeus, R.P., Witte, J.P.M., Bodegom, P.M., Dam, J.C., Becker, P. & Aerts, R. 2012. Process-based proxy of oxygen stress surpasses indirect ones in predicting vegetation characteristics. *Ecohydrology* 5: 746–758.
- Bartlett, M.K., Scoffoni, C. & Sack, L. 2012. The determinants of leaf turgor loss point and prediction of drought tolerance of species and biomes: a global meta-analysis. *Ecology Letters* 15: 393–405.
- Blackman, C.J., Brodribb, T.J. & Jordan, G.J. 2010. Leaf hydraulic vulnerability is related to conduit dimensions and drought resistance across a diverse range of woody angiosperms. *New Phytologist* 188: 1113–1123.
- Blanco, C.C., Sosinski, E.E., dos Santos, B.R.C., da Silva, M.A. & Pillar, V.D. 2007. On the overlap between effect and response plant functional types linked to grazing. *Community Ecology* 8: 57–65.
- Canadell, J., Jackson, R.B., Ehleringer, J.R., Mooney, H.A., Sala, O.E. & Schulze, E.D. 1996. Maximum rooting depth of vegetation types at the global scale. *Oecologia* 108: 583–595.
- Cavender-Bares, J., Keen, A. & Miles, B. 2006. Phylogenetic structure of floridian plant communities depends on taxonomic and spatial scale. *Ecology* 87: S109–S122.
- Chapin, F.S. III, Autumn, K. & Pugnaire, F. 1993. Evolution of suites of traits in response to environmental stress. *The American Naturalist* 142: S78–S92.
- Choat, B., Sack, L. & Holbrook, N.M. 2007. Diversity of hydraulic traits in nine *Cordia* species growing in tropical forests with contrasting precipitation. *New Phytologist* 175: 686–698.
- Clarke, A. & Gaston, K.J. 2006. Climate, energy and diversity. *Proceedings of the Royal Society B: Biological Sciences* 273: 2257–2266.
- Connell, J.H. 1978. Diversity in tropical rainforests and coral reefs. *Science* 199: 1302–1310.
- Cornelissen, J.H.C. 1996. An experimental comparison of leaf decomposition rates in a wide range of temperate plant species and types. *Journal of Ecology* 84: 573–582.
- Cornelissen, J., Cerabolini, B., Castro-Díez, P., Villar-Salvador, P., Montserrat-Martí, G., Puyravaud, J., Maestro, M., Werger, M. & Aerts, R. 2003. Functional traits of woody plants: correspondence of species rankings between field adults and laboratory-grown seedlings? *Journal of Vegetation Science* 14: 311–322.
- Cornelissen, J., Queded, H., Gwynn-Jones, D., Van Logtestijn, R., De Beus, M., Kondratyuk, A., Callaghan, T. & Aerts, R. 2004. Leaf digestibility and litter decomposability are related in a wide range of subarctic plant species and types. *Functional Ecology* 18: 779–786.
- Cornwell, W.K. & Ackerly, D.D. 2009. Community assembly and shifts in plant trait distributions across an environmental gradient in coastal California. *Ecological Monographs* 79: 109–126.
- Cornwell, W.K., Schwilk, D.W. & Ackerly, D.D. 2006. A trait-based test for habitat filtering: Convex Hull Volume. *Ecology* 87: 1465–1471.
- Cornwell, W.K., Cornelissen, J.H.C., Amatangelo, K., Dorrepaal, E., Eviner, V.T., Godoy, O., Hobbie, S.E., Hoorens, B., Kurokawa, H., (...) & Westoby, M. 2008. Plant species traits are the predominant control on litter decomposition rates within biomes worldwide. *Ecology Letters* 11: 1065–1071.
- Craine, J.M., Elmore, A.J., Aida, M.P.M., Bustamante, M., Dawson, T.E., Hobbie, E.A., Kahmen, A., Mack, M.C., McLaughlan, K.K., (...) & Wright, I.J. 2009. Global patterns of foliar nitrogen isotopes and their relationships with climate, mycorrhizal fungi, foliar nutrient concentrations, and nitrogen availability. *New Phytologist* 183: 980–992.
- Decker, M., Pitman, A.J. & Evans, J.P. 2013. Groundwater constraints on simulated transpiration variability over South-

- eastern Australian Forests. *Journal of Hydrometeorology* 14: 543–559.
- Díaz, S., Hodgson, J., Thompson, K., Cabido, M., Cornelissen, J., Jalili, A., Montserrat-Martí, G., Grime, J., Zarrinkamar, F. & Asri, Y. 2004. The plant traits that drive ecosystems: evidence from three continents. *Journal of Vegetation Science* 15: 295–304.
- Díaz, S., Noy-Meir, I. & Cabido, M. 2001. Can grazing response of herbaceous plants be predicted from simple vegetative traits? *Journal of Applied Ecology* 38: 497–508.
- Donoghue, M.J. 2008. A phylogenetic perspective on the distribution of plant diversity. *Proceedings of the National Academy of Sciences of the United States of America* 105: 11549–11555.
- Douma, J.C., Bardin, V., Bartholomeus, R.P. & Bodegom, P.M. 2012. Quantifying the functional responses of vegetation to drought and oxygen stress in temperate ecosystems. *Functional Ecology* 26: 1355–1365.
- Duarte, L.d.S., Carlucci, M.B., Hartz, S.M. & Pillar, V.D. 2007. Plant dispersal strategies and the colonization of *Araucaria* forest patches in a grassland–forest mosaic. *Journal of Vegetation Science* 18: 847–858.
- Falster, D.S. & Westoby, M. 2005. Alternative height strategies among 45 dicot rain forest species from tropical Queensland, Australia. *Journal of Ecology* 93: 521–535.
- Fischer, A.G. 1960. Latitudinal variations in organic diversity. *Evolution* 14: 64–81.
- Flora of Australia Online 2013. Australian Biological Resources Study, Canberra. <http://www.environment.gov.au/biodiversity/abrs/online-resources/flora/main/index.html>
- Fonseca, C.R., Overton, J.M., Collins, B. & Westoby, M. 2000. Shifts in trait-combinations along rainfall and phosphorus gradients. *Journal of Ecology* 88: 964–977.
- Fortunel, C., Garnier, E., Joffre, R., Kazakou, E., Quested, H., Grigulis, K., Lavorel, S., Ansquer, P., Castro, H. & Cruz, P. 2009. Leaf traits capture the effects of land use changes and climate on litter decomposability of grasslands across Europe. *Ecology* 90: 598–611.
- Frenne, P., Graae, B.J., Rodríguez-Sánchez, F., Kolb, A., Chabrerie, O., Decocq, G., Kort, H., Schrijver, A., Diekmann, M. & Eriksson, O. 2013. Latitudinal gradients as natural laboratories to infer species' responses to temperature. *Journal of Ecology* 101: 784–795.
- Freschet, G.T., Cornelissen, J.H.C., Van Logtestijn, R.S.P. & Aerts, R. 2010a. Evidence of the 'plant economics spectrum' in a subarctic flora. *Journal of Ecology* 98: 362–373.
- Freschet, G.T., Cornelissen, J.H.C., van Logtestijn, R.S.P. & Aerts, R. 2010b. Substantial nutrient resorption from leaves, stems and roots in a subarctic flora: what is the link with other resource economics traits? *New Phytologist* 186: 879–889.
- Freschet, G.T., Dias, A.T., Ackerly, D.D., Aerts, R., van Bodegom, P.M., Cornwell, W.K., Dong, M., Kurokawa, H., Liu, G. & Onipchenko, V.G. 2011. Global to community scale differences in the prevalence of convergent over divergent leaf trait distributions in plant assemblages. *Global Ecology and Biogeography* 20: 755–765.
- Fyllas, N.M., Patino, S., Baker, T., Nardoto, G., Martinelli, L., Quesada, C., Paiva, R., Schwarz, M., Horna, V. & Mercado, L. 2009. Basin-wide variations in foliar properties of Amazonian forest: phylogeny, soils and climate. *Biogeosciences* 6: 2677–2708.
- Gardner, W. 1965. Dynamic aspects of soil-water availability to plants. *Annual Review of Plant Physiology* 16: 323–342.
- Garnier, E., Lavorel, S., Ansquer, P., Castro, H., Cruz, P., Dolezal, J., Eriksson, O., Fortunel, C., Freitas, H. & Golodets, C. 2007. Assessing the effects of land-use change on plant traits, communities and ecosystem functioning in grasslands: a standardized methodology and lessons from an application to 11 European Sites. *Annals of Botany* 99: 967–985.
- Gillooly, J.F., Brown, J.H., West, G.B., Savage, V.M. & Charnov, E.L. 2001. Effects of size and temperature on metabolic rate. *Science* 293: 2248–2251.
- Givnish, T.J. 1978. On the adaptive significance of compound leaves, with particular reference to tropical trees. In: Tomlinson, P.B. & Zimmerman, M.H. (eds.) *Tropical Trees as Living Systems*, pp. 351–380. Cambridge University Press, Cambridge, UK.
- Griffiths, H., Weller, G., Toy, L.F. & Dennis, R.J. 2013. You're so vein: bundle sheath physiology, phylogeny and evolution in C3 and C4 plants. *Plant, Cell & Environment* 36: 249–261.
- Grime, J.P. & Jeffrey, D.W. 1965. Seedling establishment in vertical gradients of sunlight. *Journal of Ecology* 53: 621–642.
- Grime, J., Mason, G., Curtis, A., Rodman, J. & Band, S. 1981. A comparative study of germination characteristics in a local flora. *Journal of Ecology* 69: 1017–1059.
- Grubb, P.J. 1992. A positive distrust in simplicity—lessons from plant defences and from competition among plants and among animals. *Journal of Ecology* 80: 585–610.
- Grubb, P.J. & Burslem, D.F. 1998. Mineral nutrient concentrations as a function of seed size within seed crops: implications for competition among seedlings and defence against herbivory. *Journal of Tropical Ecology* 14: 177–185.
- Gutiérrez, A.G. & Huth, A. 2012. Successional stages of primary temperate rainforests of Chiloé Island, Chile. *Perspectives in Plant Ecology, Evolution and Systematics* 14: 243–256.
- Hanley, M.E., Lamont, B.B., Fairbanks, M.M. & Rafferty, C.M. 2007. Plant structural traits and their role in anti-herbivore defence. *Perspectives in Plant Ecology Evolution and Systematics* 8: 157–178.
- Harrison, S.P., Prentice, I.C., Barboni, D., Kohfeld, K.E., Ni, J. & Sutra, J.P. 2010. Ecophysiological and bioclimatic foundations for a global plant functional classification. *Journal of Vegetation Science* 21: 300–317.
- Hickler, T. 1999. *Plant functional types and community characteristics along environmental gradients on Öland's Great Alvar (Sweden)*. Masters Thesis, University of Lund, SE.

- Hickler, T., Fronzek, S., Araujo, M.B., Schweiger, O., Thuiller, W. & Sykes, M.T. 2009. An ecosystem model-based estimate of changes in water availability differs from water proxies that are commonly used in species distribution models. *Global Ecology and Biogeography* 18: 304–313.
- Holdridge, L. 1947. Determination of world plant formations from simple climatic data. *Science* 105: 267–268.
- Janzen, D.H. 1970. Herbivores and the number of tree species in tropical forests. *The American Naturalist* 104: 501–528.
- Jones, P.D., Lister, D.H., Osborn, T.J., Harpham, C., Salmon, M. & Morice, C.P. 2012. Hemispheric and large-scale land-surface air temperature variations: an extensive revision and an update to 2010. *Journal of Geophysical Research-Atmospheres* 117: D05127.
- Kattge, J., Knorr, W., Raddatz, T. & Wirth, C. 2009. Quantifying photosynthetic capacity and its relationship to leaf nitrogen content for global-scale terrestrial biosphere models. *Global Change Biology* 15: 976–991.
- Kattge, J., Diaz, S., Lavorel, S., Prentice, C., Leadley, P., Bonisch, G., Garnier, E., Westoby, M., Reich, P.B., (...) & Wirth, C. 2011. TRY – a global database of plant traits. *Global Change Biology* 17: 2905–2935.
- Kazakou, E., Vile, D., Shipley, B., Gallet, C. & Garnier, E. 2006. Co-variations in litter decomposition, leaf traits and plant growth in species from a Mediterranean old-field succession. *Functional Ecology* 20: 21–30.
- Kikuzawa, K., Onoda, Y., Wright, I.J. & Reich, P.B. 2013. Mechanisms underlying global temperature-related patterns in leaf longevity. *Global Ecology and Biogeography* 22: 982–993.
- Kleyer, M., Bekker, R.M., Knevel, I.C., Bakker, J.P., Thompson, K., Sonnenschein, M., Poschod, P., van Groenendael, J.M., Klimes, L., (...) & Peco, B.. 2008. The LEDA Traitbase: a database of life-history traits of the Northwest European flora. *Journal of Ecology* 96: 1266–1274.
- Kurokawa, H. & Nakashizuka, T. 2008. Leaf herbivory and decomposability in a Malaysian tropical rainforest. *Ecology* 89: 2645–2656.
- Lambers, H. 1998. Leaf energy budgets: Effects of radiation and temperature. In: Lambers, H., Chapin, F.S. & Pons, T.L. (eds.) *Plant Physiological Ecology*, pp. 210–228. Springer-Verlag, New York, NY, US.
- Laughlin, D.C., Leppert, J.J., Moore, M.M. & Sieg, C.H. 2010. A multi-trait test of the leaf-height-seed plant strategy scheme with 133 species from a pine forest flora. *Functional Ecology* 24: 493–501.
- Leishman, M.R., Wright, I.J., Moles, A.T. & Westoby, M. 2000. The evolutionary ecology of seed size. In: Fenner, M. (ed.) *Seeds - The Ecology of Regeneration in Plant Communities*, pp. 31–57. CAB International, Wallingford, UK.
- Louault, F., Pillar, V.D., Aufrère, J., Garnier, E. & Soussana, J.F. 2005. Plant traits and functional types in response to reduced disturbance in a semi-natural grassland. *Journal of Vegetation Science* 16: 151–160.
- MacArthur, R.H. 1972. *Geographical ecology: patterns in the distribution of species*. Princeton University Press, Princeton, NJ, US.
- MacArthur, R.H. & Wilson, E.O. 1963. An equilibrium theory of insular zoogeography. *Evolution* 17: 373–387.
- Maherali, H., Pockman, W.T. & Jackson, R.B. 2004. Adaptive variation in the vulnerability of woody plants to xylem cavitation. *Ecology* 85: 2184–2199.
- McDonald, P.G., Fonseca, C.R., Overton, J.M. & Westoby, M. 2003. Leaf-size divergence along rainfall and soil-nutrient gradients: is the method of size reduction common among clades? *Functional Ecology* 17: 50–57.
- McIntyre, S., Lavorel, S., Landsberg, J. & Forbes, T. 1999. Disturbance response in vegetation – towards a global perspective on functional traits. *Journal of Vegetation Science* 10: 621–630.
- Medlyn, B.E. & Jarvis, P.G. 1999. Design and use of a database of model parameters from elevated [CO₂] experiments. *Ecological Modelling* 124: 69–83.
- Medlyn, B., Badeck, F.W., De Pury, D., Barton, C., Broadmeadow, M., Ceulemans, R., De Angelis, P., Forstreuter, M., Jach, M. & Kellomäki, S. 1999. Effects of elevated [CO₂] on photosynthesis in European forest species: a meta-analysis of model parameters. *Plant, Cell & Environment* 22: 1475–1495.
- Medlyn, B., Barton, C., Broadmeadow, M., Ceulemans, R., De Angelis, P., Forstreuter, M., Freeman, M., Jackson, S., Kellomäki, S. & Laitat, E. 2001. Stomatal conductance of forest species after long-term exposure to elevated CO₂ concentration: a synthesis. *New Phytologist* 149: 247–264.
- Messier, J., McGill, B.J. & Lechowicz, M.J. 2010. How do traits vary across ecological scales? A case for trait-based ecology. *Ecology Letters* 13: 838–848.
- Moles, A.T., Ackerly, D.D., Tweddle, J.C., Dickie, J.B., Smith, R., Leishman, M.R., Mayfield, M.M., Pitman, A.J., Wood, J.T. & Westoby, M. 2007. Global patterns in seed size. *Global Ecology and Biogeography* 16: 109–116.
- Moles, A.T., Warton, D.I., Warman, L., Swenson, N.G., Laffan, S.W., Zanne, A.E., Pitman, A., Hemmings, F.A. & Leishman, M.R. 2009. Global patterns in plant height. *Journal of Ecology* 97: 923–932.
- Moles, A.T., Bonser, S.P., Poore, A.G.B., Wallis, I.R. & Foley, W.J. 2011a. Assessing the evidence for latitudinal gradients in plant defence and herbivory. *Functional Ecology* 25: 380–388.
- Moles, A.T., Wallis, I.R., Foley, W.J., Warton, D.I., Stegen, J.C., Bisigato, A.J., Cella-Pizarro, L., Clark, C.J., Cohen, P.S., (...) & Prior, L.D. 2011b. Putting plant resistance traits on the map: a test of the idea that plants are better defended at lower latitudes. *New Phytologist* 191: 777–788.
- Müller, S., Overbeck, G., Pfadenhauer, J. & Pillar, V. 2007. Plant functional types of woody species related to fire disturbance in forest-grassland ecotones. *Plant Ecology* 189: 1–14.
- Murray, B.R., Brown, A.H.D., Dickman, C.R. & Crowther, M.S. 2004. Geographical gradients in seed mass in relation to climate. *Journal of Biogeography* 31: 379–388.

- Nepstad, D.C., Decarvalho, C.R., Davidson, E.A., Jipp, P.H., Lefebvre, P.A., Negreiros, G.H., Dasilva, E.D., Stone, T.A., Trumbore, S.E. & Vieira, S. 1994. The role of deep roots in the hydrological and carbon cycles of Amazonian forests and pastures. *Nature* 372: 666–669.
- Niinemets, Ü. 1998. Are compound-leaved woody species inherently shade-intolerant? An analysis of species ecological requirements and foliar support costs. *Plant Ecology* 134: 1–11.
- Niinemets, Ü. 1999. Components of leaf dry mass per area – thickness and density – alter leaf photosynthetic capacity in reverse directions in woody plants. *New Phytologist* 144: 35–47.
- Niinemets, Ü. 2001. Global-scale climatic controls of leaf dry mass per area, density, and thickness in trees and shrubs. *Ecology* 82: 453–469.
- Niinemets, Ü. & Kull, K. 1994. Leaf weight per area and leaf size of 85 Estonian woody species in relation to shade tolerance and light availability. *Forest Ecology and Management* 70: 1–10.
- Ogaya, R. & Penuelas, J. 2006. Contrasting foliar responses to drought in *Quercus ilex* and *Phillyrea latifolia*. *Biologia Plantarum* 50: 373–382.
- Ogaya, R. & Penuelas, J. 2003. Comparative field study of *Quercus ilex* and *Phillyrea latifolia*: photosynthetic response to experimental drought conditions. *Environmental and Experimental Botany* 50: 137–148.
- Ogaya, R. & Penuelas, J. 2007. Tree growth, mortality, and above-ground biomass accumulation in a holm oak forest under a five-year experimental field drought. *Plant Ecology* 189: 291–299.
- Ogaya, R. & Penuelas, J. 2008. Changes in leaf $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ for three Mediterranean tree species in relation to soil water availability. *Acta Oecologica* 34: 331–338.
- Onoda, Y., Westoby, M., Adler, P.B., Choong, A.M., Clissold, F.J., Cornelissen, J.H., Díaz, S., Dominy, N.J., Elgart, A. & Enrico, L. 2011. Global patterns of leaf mechanical properties. *Ecology Letters* 14: 301–312.
- Ordoñez, J.C., Van Bodegom, P.M., Witte, J.-P.M., Bartholomeus, R.P., Van Dobben, H.F. & Aerts, R. 2010a. Leaf habit and woodiness regulate different leaf economy traits at a given nutrient supply. *Ecology* 91: 3218–3228.
- Ordoñez, J.C., van Bodegom, P.M., Witte, J.P.M., Bartholomeus, R.P., van Hal, J.R. & Aerts, R. 2010b. Plant strategies in relation to resource supply in mesic to wet environments: does theory mirror nature? *The American Naturalist* 175: 225–239.
- Overbeck, G.E. 2005. *Effect of fire on vegetation dynamics and plant types in subtropical grassland in southern Brazil*. PhD Thesis, Technische Universität München, Freising, DE.
- Overbeck, G.E. & Pfadenhauer, J. 2007. Adaptive strategies in burned subtropical grassland in southern Brazil. *Flora* 202: 27–49.
- Pakeman, R.J., Garnier, E., Lavorel, S., Ansquer, P., Castro, H., Cruz, P., Doležal, J., Eriksson, O., Freitas, H. & Golodets, C. 2008. Impact of abundance weighting on the response of seed traits to climate and land use. *Journal of Ecology* 96: 355–366.
- Pakeman, R.J., Lepš, J., Kleyer, M., Lavorel, S. & Garnier, E. 2009. Relative climatic, edaphic and management controls of plant functional trait signatures. *Journal of Vegetation Science* 20: 148–159.
- Patiño, S., Lloyd, J., Paiva, R., Baker, T., Quesada, C., Mercado, L., Schmerler, J., Schwarz, M., Santos, A. & Aguilar, A. 2009. Branch xylem density variations across the Amazon Basin. *Biogeosciences* 6: 545–568.
- Penuelas, J., Sardans, J., Llusià, J., Owen, S.M., Carnicer, J., Giambelluca, T.W., Rezende, E.L., Waite, M. & Niinemets, Ü. 2010a. Faster returns on ‘leaf economics’ and different biogeochemical niche in invasive compared with native plant species. *Global Change Biology* 16: 2171–2185.
- Penuelas, J., Sardans, J., Llusià, J., Owen, S.M., Silva, J. & Niinemets, Ü. 2010b. Higher allocation to low cost chemical defenses in invasive species of Hawaii. *Journal of Chemical Ecology* 36: 1255–1270.
- Pérez-Harguindeguy, N., Díaz, S., Garnier, E., Lavorel, S., Poorter, H., Jaureguiberry, P., Bret-Harte, M., Cornwell, W., Craine, J. & Gurvich, D. 2013. New handbook for standardised measurement of plant functional traits worldwide. *Australian Journal of Botany* 61: 167–234.
- Pianka, E.R. 1970. On r- and K-selection. *The American Naturalist* 104: 492–597.
- Pillar, V.D. & Sosinski, E.E. 2003. An improved method for searching plant functional types by numerical analysis. *Journal of Vegetation Science* 14: 323–332.
- Poorter, L. 2009. Leaf traits show different relationships with shade tolerance in moist versus dry tropical forests. *New Phytologist* 181: 890–900.
- Poorter, H. & De Jong, R. 1999. A comparison of specific leaf area, chemical composition and leaf construction costs of field plants from 15 habitats differing in productivity. *New Phytologist* 143: 163–176.
- Poorter, H., Niinemets, Ü., Poorter, L., Wright, I.J. & Villar, R. 2009. Causes and consequences of variation in leaf mass per area (LMA): a meta-analysis. *New Phytologist* 182: 565–588.
- Poorter, H., Niinemets, Ü., Walter, A., Fiorani, F. & Schurr, U. 2010. A method to construct dose–response curves for a wide range of environmental factors and plant traits by means of a meta-analysis of phenotypic data. *Journal of Experimental Botany* 61: 2043–2055.
- Porter, J.R. & Semenov, M.A. 2005. Crop responses to climatic variation. *Philosophical Transactions of the Royal Society B: Biological Sciences* 360: 2021–2035.
- Preston, K.A., Cornwell, W.K. & DeNoyer, J.L. 2006. Wood density and vessel traits as distinct correlates of ecological

- strategy in 51 California coast range angiosperms. *New Phytologist* 170: 807–818.
- Pyanikov, V.I., Kondratchuk, A.V. & Shipley, B. 1999. Leaf structure and specific leaf mass: the alpine desert plants of the Eastern Pamirs, Tadjikistan. *New Phytologist* 143: 131–142.
- Qian, H., Swenson, N.G. & Zhang, J. 2013. Phylogenetic beta diversity of angiosperms in North America. *Global Ecology and Biogeography* 22: 1152–1161.
- Quested, H.M., Cornelissen, J.H.C., Press, M.C., Callaghan, T.V., Aerts, R., Trosien, F., Riemann, P., Gwynn-Jones, D., Kondratchuk, A. & Jonasson, S.E. 2003. Decomposition of subarctic plants with differing nitrogen economies: a functional role for hemiparasites. *Ecology* 84: 3209–3221.
- Rawson, H. 1992. Plant responses to temperature under conditions of elevated CO₂. *Australian Journal of Botany* 40: 473–490.
- Reich, P.B. & Oleksyn, J. 2004. Global patterns of plant leaf N and P in relation to temperature and latitude. *Proceedings of the National Academy of Sciences of the United States of America* 101: 11001–11006.
- Reich, P.B., Walters, M.B. & Ellsworth, D.S. 1997. From tropics to tundra: global convergence in plant functioning. *Proceedings of the National Academy of Sciences of the United States of America* 94: 13730–13734.
- Reich, P.B., Ellsworth, D.S., Walters, M.B., Vose, J.M., Gresham, C., Volin, J.C. & Bowman, W.D. 1999. Generality of leaf trait relationships: a test across six biomes. *Ecology* 80: 1955–1969.
- Reich, P.B., Wright, I.J., Cavender-Bares, J., Craine, J.M., Oleksyn, J., Westoby, M. & Walters, M.B. 2003. The evolution of plant functional variation: traits, spectra and strategies. *International Journal of Plant Sciences* 164: S143–S164.
- Reich, P.B., Tjoelker, M.G., Pregitzer, K.S., Wright, I.J., Oleksyn, J. & Machado, J.-L. 2008. Scaling of respiration to nitrogen in leaves, stems and roots of higher land plants. *Ecology Letters* 11: 793–801.
- Reich, P., Oleksyn, J. & Wright, I. 2009. Leaf phosphorus influences the photosynthesis–nitrogen relation: a cross-biome analysis of 314 species. *Oecologia* 160: 207–212.
- Rosenberg, M.S., Adams, D.C. & Gurevitch, J. 2000. *MetaWin: Statistical software for meta-analysis. Version 2*. Sinauer Associates, Sunderland, MA, US.
- Royal Botanic Gardens Kew 2008. Seed Information Database (SID). Version 7.1. Available from: <http://data.kew.org/sid/>.
- Sack, L. & Scoffoni, C. 2013. Leaf venation: structure, function, development, evolution, ecology and applications in the past, present and future. *New Phytologist* 198: 983–1000.
- Sardans, J., Penuelas, J. & Ogaya, R. 2008a. Drought-induced changes in C and N stoichiometry in a *Quercus ilex* Mediterranean forest. *Forest Science* 54: 513–522.
- Sardans, J., Penuelas, J., Prieto, P. & Estiarte, M. 2008b. Changes in Ca, Fe, Mg, Mo, Na, and S content in a Mediterranean shrubland under warming and drought. *Journal of Geophysical Research: Biogeosciences* 113: G03039.
- Schemske, D.W., Mittelbach, G.G., Cornell, H.V., Sobel, J.M. & Roy, K. 2009. Is there a latitudinal gradient in the importance of biotic interactions? *Annual Review of Ecology, Evolution and Systematics* 40: 245–269.
- Schimper, A.F.W. & Fisher, W.R. 1902. *Plant-geography upon a physiological basis*. Clarendon Press, Oxford, UK.
- Schleuning, M., Fründ, J., Klein, A.-M., Abrahamczyk, S., Alarcón, R., Albrecht, M., Andersson, G.K., Bazarian, S., Böhning-Gaese, K. & Bommarco, R. 2012. Specialization of mutualistic interaction networks decreases toward tropical latitudes. *Current Biology* 22: 1925–1931.
- Schneider, U., Becker, A., Finger, P., Meyer-Christoffer, A., Rudolf, B. & Ziese, M. 2011. GPCC full data reanalysis version 6.0 at 2.5°: monthly land-surface precipitation from rain-gauges built on GTS-based and historic data. doi:10.5676/DWD_GPCC/FD_M_V6_100. http://ftp-anon.dwd.de/pub/data/gpcc/html/fulldata_v6_doi_download.html
- Shiodera, S., Rahajoe, J.S. & Kohyama, T. 2008. Variation in longevity and traits of leaves among co-occurring understorey plants in a tropical montane forest. *Journal of Tropical Ecology* 24: 121–133.
- Shipley, B. 1995. Structured interspecific determinants of specific leaf area in 34 species of herbaceous angiosperms. *Functional Ecology* 9: 312–319.
- Shipley, B. & Vu, T.-T. 2002. Dry matter content as a measure of dry matter concentration in plants and their parts. *New Phytologist* 153: 359–364.
- Silva, L.C., Anand, M. & Leithead, M.D. 2010. Recent widespread tree growth decline despite increasing atmospheric CO₂. *PLoS ONE* 5: e11543.
- Stephenson, N.L. 1998. Actual evapotranspiration and deficit: biologically meaningful correlates of vegetation distribution across spatial scales. *Journal of Biogeography* 25: 855–870.
- Swaine, E.K. 2007. *Ecological and evolutionary drivers of plant community assembly in a Bornean rain forest*. PhD Thesis, University of Aberdeen, Aberdeen, UK.
- Swenson, N.G. & Enquist, B.J. 2007. Ecological and evolutionary determinants of a key plant functional trait: wood density and its community-wide variation across latitude and elevation. *American Journal of Botany* 94: 451–459.
- van Bodegom, P.M., Sorrell, B.K., Oosthoek, A., Bakker, C. & Aerts, R. 2008. Separating the effects of partial submergence and soil oxygen demand on plant physiology. *Ecology* 89: 193–204.
- van Ommen Kloeke, A., Douma, J., Ordoñez, J., Reich, P. & Van Bodegom, P. 2012. Global quantification of contrasting leaf life span strategies for deciduous and evergreen species in response to environmental conditions. *Global Ecology and Biogeography* 21: 224–235.
- Vázquez, D.P. & Stevens, R.D. 2004. The latitudinal gradient in niche breadth: concepts and evidence. *The American Naturalist* 164: E1–E19.
- Venables, W.N. & Ripley, B.D. 2002. *Modern applied statistics with S*. Springer, New York, NY, US.

- Walter, H. 1994. *Vegetation of the earth and ecological systems of the geo-biosphere*. Springer, Berlin, DE.
- Wang, X., Piao, S., Ciais, P., Friedlingstein, P., Myneni, R.B., Cox, P., Heimann, M., Miller, J., Peng, S. & Wang, T. 2014. A two-fold increase of carbon cycle sensitivity to tropical temperature variations. *Nature* 506: 212–215.
- Weiher, E., van der Werf, A., Thompson, K., Roderick, M., Garnier, E. & Eriksson, O. 1999. Challenging Theophrastus: a common core list of plant traits for functional ecology. *Journal of Vegetation Science* 10: 609–620.
- Went, F. 1953. The effect of temperature on plant growth. *Annual Review of Plant Physiology* 4: 347–362.
- Whittaker, R.H. 1970. *Communities and ecosystems*. Macmillan, New York, NY, US.
- Willis, C.G., Halina, M., Lehman, C., Reich, P.B., Keen, A., McCarthy, S. & Cavender-Bares, J. 2010. Phylogenetic community structure in Minnesota oak savanna is influenced by spatial extent and environmental variation. *Ecography* 33: 565–577.
- Wright, I.J., Reich, P.B., Westoby, M., Ackerly, D.D., Baruch, Z., Bongers, F., Cavender-Bares, J., Chapin, F.S., Cornelissen, J.H.C., (...) & Villar, R. 2004. The world-wide leaf economics spectrum. *Nature* 428: 821–827.
- Wright, I.J., Reich, P.B., Cornelissen, J.H.C., Falster, D.S., Groom, P.K., Hikosaka, K., Lee, W., Lusk, C.H., Niinemets, U., (...) & Westoby, M. 2005. Modulation of leaf economic traits and trait relationships by climate. *Global Ecology and Biogeography* 14: 411–421.
- Wright, I.J., Reich, P.B., Atkin, O.K., Lusk, C.H., Tjoelker, M.G. & Westoby, M. 2006. Irradiance, temperature and rainfall influence leaf dark respiration in woody plants: evidence from comparisons across 20 sites. *New Phytologist* 169: 309–319.
- Wright, I.J., Ackerly, D.D., Bongers, F., Harms, K.E., Ibarra-Manriquez, G., Martinez-Ramos, M., Mazer, S.J., Muller-Landau, H.C., Paz, H. & Pitman, N.C. 2007. Relationships among ecologically important dimensions of plant trait variation in seven Neotropical forests. *Annals of Botany* 99: 1003–1015.
- Wright, S.J., Kitajima, K., Kraft, N.J., Reich, P.B., Wright, I.J., Bunker, D.E., Condit, R., Dalling, J.W., Davies, S.J. & Díaz, S. 2010. Functional traits and the growth–mortality trade-off in tropical trees. *Ecology* 91: 3664–3674.
- Zanne, A.E., Tank, D.C., Cornwell, W.K., Eastman, J.M., Smith, S.A., FitzJohn, R.G., McGlenn, D.J., O’Meara, B.C., Moles, A.T., (...) & Beaulieu, J.M. 2013. Three keys to the radiation of angiosperms into freezing environments. *Nature* 506: 89–92.

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. List of TRY data sets used.

Appendix S2. Error checking procedures.

Appendix S3. Figures showing raw data and relationships between each trait and each climate variable.