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Responses of leaf traits to climatic gradients: adaptive variation versus compositional shifts

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Abstract. Dynamic global vegetation models (DGVMs) typically rely on plant functional types (PFTs), which are assigned distinct environmental tolerances and replace one another progressively along environmental gradients. Fixed values of traits are assigned to each PFT; modelled trait variation along gradients is thus driven by PFT replacement. But empirical studies have revealed "universal" scaling relationships (quantitative trait variations with climate that are similar within and between species, PFTs and communities); and continuous, adaptive trait variation has been proposed to replace PFTs as the basis for next-generation DGVMs.

Here we analyse quantitative leaf-trait variation on long temperature and moisture gradients in China with a view to understanding the relative importance of PFT replacement vs. continuous adaptive variation within PFTs. Leaf area (LA), specific leaf area (SLA), leaf dry matter content (LDMC) and nitrogen content of dry matter were measured on all species at 80 sites ranging from temperate to tropical climates and from dense forests to deserts. Chlorophyll fluorescence traits and carbon, phosphorus and potassium contents were measured at 47 sites. Generalized linear models were used to relate log-transformed trait values to growing-season temperature and moisture indices, with or without PFT identity as a predictor, and to test for differences in trait responses among PFTs.

Continuous trait variation was found to be ubiquitous. Responses to moisture availability were generally similar within and between PFTs, but biophysical traits (LA, SLA and LDMC) of forbs and grasses responded differently from woody plants. SLA and LDMC responses to temperature were dominated by the prevalence of evergreen PFTs with thick, dense leaves at the warm end of the gradient. Nutrient (N, P and K) responses to climate gradients were generally similar within all PFTs. Area-based nutrients generally declined with moisture; N_{area} and K_{area} declined with temperature, but P_{area} increased with temperature.

Although the adaptive nature of many of these trait-climate relationships is understood qualitatively, a key challenge for

modelling is to predict them quantitatively. Models must take into account that community-level responses to climatic gradients can be influenced by shifts in PFT composition, such as the replacement of deciduous by evergreen trees, which may run either parallel or counter to trait variation within PFTs. The importance of PFT shifts varies among traits, being important for biophysical traits but less so for physiological and chemical traits. Finally, models should take account of the diversity of trait values that is found in all sites and PFTs, representing the "pool" of variation that is locally available for the natural adaptation of ecosystem function to environmental change.

1 Introduction

The plant functional type (PFT) concept has been important in the development of dynamic global vegetation models (DGVMs), which combine vegetation dynamics (changes in vegetation composition, expressed as abundances of PFTs) at the grid-cell scale with hydrological and biogeochemical processes driven by the physical environment and modulated by PFT characteristics (Prentice et al., 2007; Prentice and Cowling, 2013). PFT classifications vary among models but nearly all include distinctions of life form (at least, woody versus herbaceous plants), leaf habit (evergreen or deciduous) and leaf form (broad or needle-leaves). Some models also distinguish climatic tolerance classes, related primarily to different overwintering mechanisms for woody plants (Harrison et al., 2010), and most distinguish C_4 plants. Usually a fixed set of properties (parameter values) is assigned to each PFT. This expedient simplifies modelling, but it is a potential weakness because it disregards continuous adaptive variation within PFTs; the fact that trait variation within PFTs often exceeds trait differences between PFTs; and the possibility that such variation is "universal" – that is, manifested similarly within and between species, PFTs and communities. Neglect of continuous adaptive variation in models could lead to underestimation of the potential for vegetation to adapt to environmental change and generally incorrect assessments of the response of vegetation to climate (Kleidon et al., 2009; Scheiter and Higgins, 2009) and vegetation feedbacks to climate (Alton, 2011).

Numerous observational studies have documented continuous relationships between quantitative plant traits and climate (e.g. Werger and Ellenbroek, 1978; Díaz et al., 1998; Fonseca et al., 2000; Niinemets, 2001; Wright and Westoby, 2002; Wright et al., 2004, 2005a, b; Swenson and Enquist, 2007; Reich et al., 2007; Cornwell and Ackerly, 2009; Meng et al., 2009; Ordoñez et al., 2009, 2010; Albert et al., 2010; Prentice et al., 2011; Zhang et al., 2012). Analyses of trait-environment relationships have been motivated partly by the objective of improving the representation of plant structural and functional diversity in DGVMs (Woodward and Cramer, 1996; Díaz and Cabido, 1997; Lavorel et al., 2007; Kattge et al., 2011). In a new strand of DGVM development, modelling quantitative trait values rather than PFT abundances is the central objective (Kleidon et al., 2009; van Bodegom et al., 2012, 2014; Scheiter et al., 2013; Fyllas et al., 2014). Trait-based modelling can take better advantage of the wealth of georeferenced data now available on plant functional traits (Kattge et al., 2011) as well as providing a more realistic representation of functional diversity and competition in plant communities (Scheiter et al., 2013). On the other hand, trait-environment relationships have been shown to differ between PFTs in some cases (e.g. Barboni et al., 2004; He et al., 2006; Meng et al., 2009), implying that not all such relationships are universal; some adaptive trait variation might depend on the values of other traits, including those conventionally used to define PFTs. Moreover there are systematic leaf-trait differences between PFTs and in some studies these have been found to account for a substantial fraction of the total climatically related variation in leaf traits (e.g. Reich et al., 2007; Ordoñez et al., 2009, 2010; He et al., 2010). Thus, observational studies have reached somewhat varying conclusions about the utility of PFT distinctions in predicting adaptive trait variation along environmental gradients.

In this work we address the following questions that are important for modelling, and not definitively resolved based on the current literature. (1) To what extent are quantitative trait-environment relationships universal? Alternatively, (2) are there systematic differences in the trait-environment relationships shown by different PFTs? (3) To what extent are variations in traits along environmental gradients accounted for by variation within PFTs, as opposed to successive replacements of one PFT by another? (4) What fractions of total trait variation are linked to climate, and/or to PFT membership, as opposed to being unexplained by either climate or PFTs? We address these questions with an analysis of variations in leaf traits in plant communities sampled on long gradients of temperature and moisture availability in China (Fig. 1). The data set consists of > 11 000 quantitative leaf trait determinations on all of the species present at 80 sites (1549 species-site combinations; between 1 and 59 (median 16) species sampled per site), with a wide geographic and climatic spread as shown in Fig. 1. We consider biophysical traits (leaf area: LA, specific leaf area: SLA and leaf dry matter content: LDMC), field-measured chlorophyll fluorescence traits (the ratio of variable fluorescence to maximal fluorescence: F_v / F_m and the quantum yield of PhotoSystem II: QY), and chemical traits: carbon content by mass (C_{mass}), and nitrogen (N), phosphorus (P) and potassium (K) contents, expressed on both an area and a mass basis. Thus we consider 12 traits in all. Although area-based nutrient contents are simply derived from mass-based nutrient contents and SLA, we analyse them separately because their functional significance is different – for example, leaf N comprises a photosynthetic component that is expected to be proportional to LA and a structural component inversely propor-

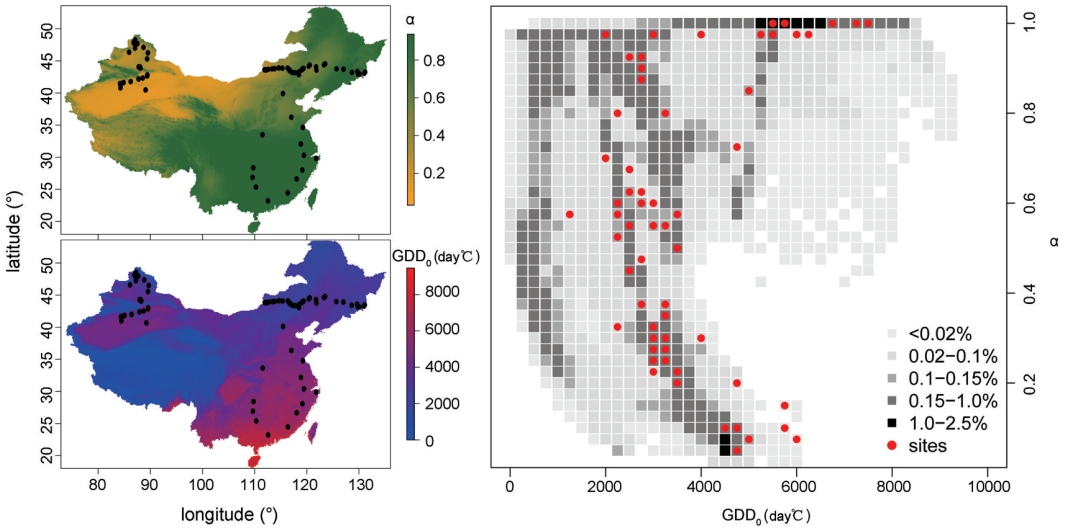

Figure 1. Left: geographic variation in the mean Cramer-Prentice moisture index (α) and annual growing degree days above 0 °C (GDD_0) in China. Right: frequency distribution of 10 km grid cells (grey squares) and location of sampling sites (red circles) in climate space.

tional to SLA (Niinements and Tenhunen 1997). LA, SLA, LDMC and N were measured at all sites; the other traits were measured at the 47 sites in eastern China, which cover most of the climatic range of the full data set, except for the driest climates in the west. Adopting a conventional PFT classification, we analyse variations of each trait with bioclimatic temperature and moisture indices (Harrison et al., 2010) within and across PFTs.

2 Materials and methods

2.1 Sampling sites

The sites (Fig. 1, Table S1 in the Supplement) represent variation along the major gradients in temperature and moisture and include a good sampling of the range of vegetation types present in China. Thirty-three sites in Xinjiang Autonomous Region in western China sample the extreme dry end of the moisture gradient, with annual rainfall between 12 and 468 mm (160 mm on average). Thirty-three sites on the Northeast China Transect (NECT: Ni and Wang, 2004) lie on an aridity gradient from closed forests with annual rainfall > 700 mm in the east, through grasslands to desert with annual rainfall of < 150 mm in the west. Fourteen sites located in forest reserves on the North-South Transect of Eastern China (NSTEC: Gao et al., 2003) have greater annual rainfall and sample a range from temperate climates in the north to warm-temperate/subtropical climates in the south. The NSTEC sites are also differentiated in terms of rainfall, the sites in the east at any given latitude being wetter than those in the west.

Sampling took place during three summer field campaigns, in 2005 (Xinjiang), 2006 (NECT) and 2007 (NSTEC). All sites were occupied by visually homogeneous uncultivated vegetation with minimal signs of disturbance. Species composition and vegetation structure were surveyed at each site. A checklist of vascular species at each site was created and field measurements were made on all the species for which sufficient material could be sampled. Species sampled are listed in Table S2.

2.2 Chlorophyll fluorescence measurements

F_v / F_m and QY were measured using a FluorPen FP100 (Photon Systems Instruments, Czech Republic). F_v / F_m measures the potential rate of photosynthetic electron transport while QY measures the actual rate. QY is correlated with photosynthetic rate, although it also includes the diversion of electrons to non-photosynthetic activities such as the elimination of reactive oxygen species (Cavender-Bares and Bazzaz, 2004).

2.3 Foliage sampling and analysis

At least 10 g of leaves were collected for each species, except for a few species with very small leaves at the driest sites, where at least 2 g of leaves were collected. Sunlit leaves of tree species were obtained with long-handled twig shears. The samples were subdivided for the measurement of specific leaf area (SLA), leaf dry matter content (LDMC) and C, N, P and K contents. The measurements used are averages of three replicates. Leaf area (LA) was determined by scanning three replicate sets of five leaves (or more in the case of small leaves, to make up a total area $\geq 20\,cm^2$ per replicate) with a laser scanner. Areas were measured using Photoshop on the scanned images. Leaf fresh weight was measured in the field. Dry weight was obtained after air-drying for sev-

eral days and then oven-drying at 75 °C for 48 h. Leaf C was measured by the potassium dichromate volumetric method (e.g. Slepetiene et al., 2008) and leaf N by the microkjeldahl method (e.g. Bremner, 1960). Leaf P was analysed colorimetrically (Shimadzu UV-2550). Leaf K was measured by Flame Atomic Emission Spectrophotometry (PE 5100 PC).

2.4 Climate data and analysis

Mean monthly values of temperature, precipitation and fractional sunshine hours were obtained from 1814 meteorological stations (China Meteorological Administration, unpublished) and interpolated to a 10 km grid using ANUSPLIN 4.36 (Hutchinson and Hancock, 2006) with the help of a digital elevation model (Farr et al., 2007). Mean annual temperature (MAT) and precipitation (MAP), mean winter (P_{DJF}) and summer (P_{JJA}) precipitation, and precipitation seasonality (seasonal concentration, which is inversely related to wet season length) and timing (the time of year around which precipitation is concentrated) were calculated for each site, as in Prentice et al. (2011). The seasonality and timing metrics are obtained by representing each month's mean precipitation as a vector with length proportional to precipitation amount, and orientation determined by the month. Seasonality is the length of the resultant of all 12 vectors, and timing is its direction: see Harrison et al. (2003). Bioclimatic variables were derived as in Gallego-Sala et al. (2010): mean temperature of the coldest month (MTCO) and warmest month (MTWA), growing degree days above 0 °C (GDD_0), photosynthetically active radiation during the season when mean daily temperature is above 0 °C (PAR_0), annual equilibrium evapotranspiration (EET), Moisture Index (MI = MAP/EET), annual actual evapotranspiration (AET) and the Cramer-Prentice α index of plant-available soil moisture (α = AET/EET) (Cramer and Prentice, 1988). Available water holding capacity (AWHC) values for the calculation of α were assigned following Prentice et al. (2011), using sand, silt and clay fractions digitised from Shi et al. (2004).

Principal components analysis was performed on standardised climate variables in SPSS. We analysed climate gradients for China as a whole, based on data from 89 623 10 km grid cells, and separately using just the 80 grid cells that included the sampling sites.

2.5 Plant functional types (PFTs)

Plant species were classified as follows: trees (single-stemmed, maximum height > 2 m, subdivided as evergreen broad-leaved, evergreen needle-leaved and deciduous broad-leaved), shrubs (multi-stemmed with maximum height between 50 cm and 2 m, subdivided as evergreen and deciduous), erect dwarf shrubs (multi-stemmed with maximum height < 50 cm), lianas (woody climbing plants with perennial above-ground biomass), climbers (non-woody climbing plants with annual above-ground biomass), forbs, grasses, geophytes and ferns. Climbers and ferns were not included in the statistical analyses, however, as there were too few species of each. The optimum and tolerance of each PFT in terms of α and GDD_0, recommended by Harrison et al. (2010) as useful and globally applicable indices of effective moisture availability and warmth for plants, were calculated non-parametrically as follows (Fig. 2): the range of each variable was divided into bins, and average abundance values were calculated for the sites within each bin. The widths of the bins were selected to yield visually smooth frequency distributions of abundance for each PFT and climate variable. The optimum was calculated as the mean of the climate variable in the bins where the PFT was present, weighted by its average abundance in the bins. The tolerance range was calculated similarly, as the standard deviation of the climate variable weighted by average abundance.

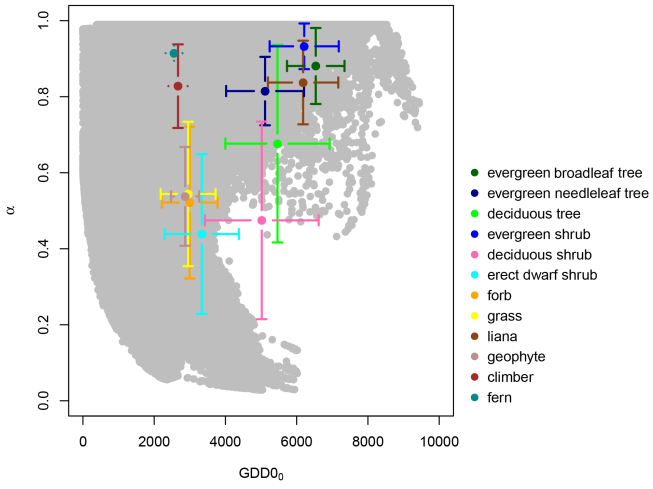

Figure 2. Optima and tolerances of PFTs in climate space of α and GDD_0 (Harrison et al. 2010), based on data from the sampling sites (see Sect. 2.5 for the calculation methods of the optima and tolerances). The grey dots represent the climates of all grid cells in China.

2.6 Generalized linear models

Generalized linear models (GLMs: Nelder and Wedderburn, 1972; Nelder and Baker, 2006) were used to quantify the relationships of trait values to climate variables (α and GDD_0), to avoid spurious bivariate relationships that can arise when (as here) the predictor variables are not perfectly independent and to allow the inclusion of qualitative variables (PFTs) as predictors in some analyses. The unit of analysis was the species-site combination, i.e. a species sampled at a site. All trait measurements were transformed to natural logarithms (ln) to reduce skewness and linearise their relationships to the climate variables. This transformation has the property that regression coefficients represent fractional changes, which can be compared among traits measured in different units. The coefficients are expressed per unit of α (in other words,

the change in ln trait value across the global range of α from 0 to 1) and per 10^4 GDD_0 (equivalent to the change in ln trait value across the global range from 0 to around 10^4 GDD_0), so that their values are broadly comparable in magnitude between climate variables as well as between traits.

We carried out three GLM analyses for each trait: (1) With climate variables (α and GDD_0) only as predictors, equivalent to ordinary least-squares multiple regression; (2) with climate variables and PFTs as predictors; (3) with PFTs and PFT-climate interactions as predictors. Analysis (1) measures the partial effect of each climate variable on the observed trait values. Analysis (2) measures the average partial effect of each climate variable on trait values within PFTs, allowing that the PFTs might have consistently lower or higher trait values. Analysis (3) estimates the partial effect of each climate variable on trait values within each PFT (the PFT-climate interaction). These three analyses are needed to answer the following questions in sequence: (1) What is the overall (community-level) response of trait values to climate? (2) To what extent is this response caused by similar trait variations within each PFT, vs. shifts in the occurrence and abundance of PFTs with innately different trait values? (3) Do trait values of some PFTs respond to climate differently from others?

A significance criterion of $P < 0.01$ was adopted for all regression coefficients in all three analyses. This is stringent enough to minimise the chance of "false positives" in analyses (2) and (3). In the description of Results, "significant" always implies $P < 0.01$ or better. Significant differences between trait values for different PFTs (assessed at a common environmental value) were inferred from significant coefficients for the relevant factors (PFTs) in analysis (2), while significant differences between the trait-environment slopes for different PFTs were inferred from significant PFT-environment interactions in analysis (3). All GLM results are presented as partial residual plots, using the visreg package in R. Partial residual plots are the multiple-regression analogue of simple x-y plots in ordinary regression. In plots showing the relationship of each trait to α, the y axis values of the data points are adjusted so as to remove the fitted effect of GDD_0. Similarly, in plots showing the relationship of each trait to GDD_0, the y axis values of the data points are adjusted so as to remove the fitted effect of α.

2.7 Multivariate analysis and variance partitioning

As a complement to single-trait analyses, we performed redundancy analysis (the constrained equivalent of PCA: ter Braak and Prentice 1988) with variance partitioning (Legendre, 2008), to quantify the unique and combined contributions of climate and PFT identity to the total variation in all traits. This analysis was performed with the CANOCO package (Leps and Smilauer, 2003), based on the sites for which all traits were measured.

3 Results

3.1 Climate gradients

More than 80 % of the geographic variation in the climate of our sampling sites can be summarised by variation on two principal axes (Table 1). Each principal axis is defined as a linear combination of variables, and each variable is assigned a "loading" which represents the contribution of that variable to the combination. The first principal axis explains 60 % of total variation and is primarily related to temperature. MAT, GDD_0, MTCO, MAP, MI, P_{DJF} and P_{JJA} have the largest positive loadings. The positive loadings for precipitation variables reflects the general tendency for absolute amounts of precipitation to increase with temperature. The second axis explains a further 25 % of total variation and is related to moisture vs. aridity. MI, α, and P_{JJA} have large positive loadings while PAR_0 and MTWA have large negative loadings. The similar behaviour of PAR_0 and MTWA reflects an increasing period without clouds, and thus also higher temperatures in summer, as moisture availability decreases. A third axis relating to the seasonality of precipitation accounts for only 9 % of total variation. A closely similar pattern emerged from the analysis of climate data for the whole country (Table S3). This similarity confirms that the pattern of variation in climate across the sites reflects the general pattern of climate gradients across China, and that these gradients can be summarised using two variables, representing temperature and plant moisture availability respectively.

For all further analysis we used the variables GDD_0 and α. GDD_0 was preferred to MAT as MAT values in climates with a long, cold winter, as in northern China, show the influence of conditions unrelated to those prevailing at the time of growth. The pattern of variation of GDD_0 and α across China is shown, with the site locations, in Fig. 1. Figure 1 also shows the frequency of different GDD_0-α combinations among grid cells in the whole country (grey scale), and the site positions in this climate space. Significant regions of climate space not sampled correspond to low GDD_0 at high α (far northeast China) and low α (Tibetan plateau), and high GDD_0 at intermediate α (tropical climates in the extreme south of China).

3.2 Distribution of PFTs in climate space

The PFTs in our data set show distinct patterns of distribution in climate space (Fig. 2), falling broadly into four groups. (1) Evergreen trees, evergreen shrubs and lianas favour the warmest and wettest climates, corresponding to the warm-temperate broad-leaved evergreen forests of southeastern China, with evergreen needle-leaved trees extending into cooler climates in the north. (2) Deciduous trees and deciduous shrubs favour cooler and drier climates, with optima corresponding to the deciduous forests of central eastern China; although these PFTs have a wide tolerance and

Table 1. Principal components of climate data based on the 80 sampling sites. Each component (axis) represents a linear combination of variables. Loadings for variables represent the contribution of each variable to the axis. Values are shown in bold when their magnitude > 0.5.

	PC 1	PC 2	PC 3
MAT	**0.870**	−0.462	0.127
GDD_0	**0.865**	−0.474	0.092
MTCO	**0.946**	−0.219	0.030
MTWA	**0.572**	**−0.727**	0.223
PAR_0	**0.642**	**−0.701**	0.106
MAP	**0.899**	0.427	−0.014
α	**0.603**	**0.753**	0.106
MI	**0.824**	**0.560**	0.000
P_{DJF}	**0.917**	0.200	−0.263
P_{JJA}	**0.747**	**0.599**	0.238
Timing	**−0.833**	−0.021	0.143
Seasonality	−0.314	0.204	**0.900**
Variance explained	59.8 %	25.1 %	8.8 %

broadly overlap with groups (1) and (3). (3) Dwarf shrubs, grasses, forbs and geophytes still favour cooler and drier climates, corresponding to the grasslands, steppes and desert steppes of northern and northwestern China. (4) Ferns and climbers are prominent only in cooler and wetter regions of climate space; they occur more widely but not in any abundance, and they were not sampled elsewhere.

3.3 Trait-climate relationships: moisture effects

Significant ($P < 0.01$) community-level responses to growing-season moisture availability (α) were found for most traits (Fig. 3, Table 2). Dry climates generally favour small, thick, dense leaves (low LA, low SLA, high LDMC). Dry climates are also associated with slightly, or sometimes greatly, reduced potential and actual quantum yield. The steepest overall relationships to α are for LA (5.8), SLA (1.6), and N_{area} and K_{area} (−1.1) and P_{mass} (0.7; Table 2: values in parentheses are slopes of ln trait-values vs. α). The response of N_{mass} to α is slight (0.25) compared to the response of N_{area}.

Inclusion of PFTs as predictors (Fig. S1) shows that there are some significant ($P < 0.01$) differences among PFTs in the typical trait values found at any given α. This is most obvious for biophysical traits – LA, SLA and LDMC – and area-based nutrients. Needle-leaved evergreen trees stand out, having small, thick leaves, and high area-based nutrient contents, relative to other PFTs. The magnitudes of the regression coefficients against α for the different traits in this analysis are similar to those in Fig. 3, but now P_{area} (in common with the other area-based nutrients) shows a significant ($P < 0.01$) negative effect of α. This relationship within PFTs is obscured in Fig. 3 by the abundance of needle-leaved evergreen trees, with their very low SLA and therefore high P_{area} values, towards the wet end of the gradient.

Where significant ($P < 0.01$) trait-PFT interactions in the response to α are found (Fig. S2), the responses are qualitatively (and usually, quantitatively) similar from one PFT to another. Regression coefficients for LA versus α range from 3.8 to 6.1, with deciduous shrubs and forbs showing significantly steeper responses than the rest. Regression coefficients for SLA range from 1.3 to 2.5 with forbs showing the steepest increases. Regression coefficients for LDMC range from −0.35 to −1.5 with forbs showing the steepest decreases. Different PFTs have significantly ($P < 0.01$) different responses of QY to moisture, with geophytes responding most and forbs least. Neither area- nor mass-based nutrients show any significant differences in slopes among PFTs.

3.4 Trait-climate relationships: temperature effects

Significant ($P < 0.01$) overall responses to growing-season warmth (GDD_0) were also found for most traits (Fig. 4, Table 2). Warm climates favour thick and dense leaves (low SLA and high LDMC). Warmer climates also show somewhat reduced potential and actual quantum yield. The steepest overall relationship of any trait to GDD_0 is for SLA (−1.5; Table 2: numbers in parentheses are slopes of ln trait values against $GDD/10^4$). Relatively steep slopes are also shown for N_{mass} (−1.1), P_{area} (1.4) and K_{mass} (−1.1).

Including PFTs as predictors shows some significant ($P < 0.01$) differences among PFTs at any GDD_0 value, similar to those shown for α (Fig. S3). But the effects on the regression coefficients for GDD_0 are more profound. Most importantly, the within-PFT responses of the three biophysical traits – LA, SLA and LDMC – to temperature are non-significant. Thus, the overall responses of SLA and LDMC to GDD_0 shown in Fig. 4 are brought about by PFT replacement, including the dominance of broad-leaved evergreen trees with low SLA and high LDMC at the warm end of the gradient. Within PFTs, N_{area} and K_{area} both decline with temperature, while P_{area} increases. The lack of a significant relationship at the community level between N_{area} and K_{area} and temperature is due to PFT replacement along the gradient – again, most obviously, the prevalence of broad-leaved evergreen trees with high N_{area} and K_{area} at the warm end of the gradient. Similarly, the steep overall declines in N_{mass} and K_{mass} with GDD_0 are mainly due to PFT replacement.

Relationships to GDD_0 fitted separately within PFTs (Fig. S4) showed fewer significant slopes, and less consistency among PFTs, than the corresponding relationships to α. Individually significant ($P < 0.01$) PFT responses of SLA to GDD_0 could be increasing or decreasing (–0.57 to +1.3). Slopes of LDMC are negative (−1.6 to −3.0), with forbs and grasses showing the steepest declines. Area- and mass-based nutrients show few significant differences among PFTs in their responses to either GDD_0; however forbs show an increase in N_{mass} and more steeply increasing P_{mass} with

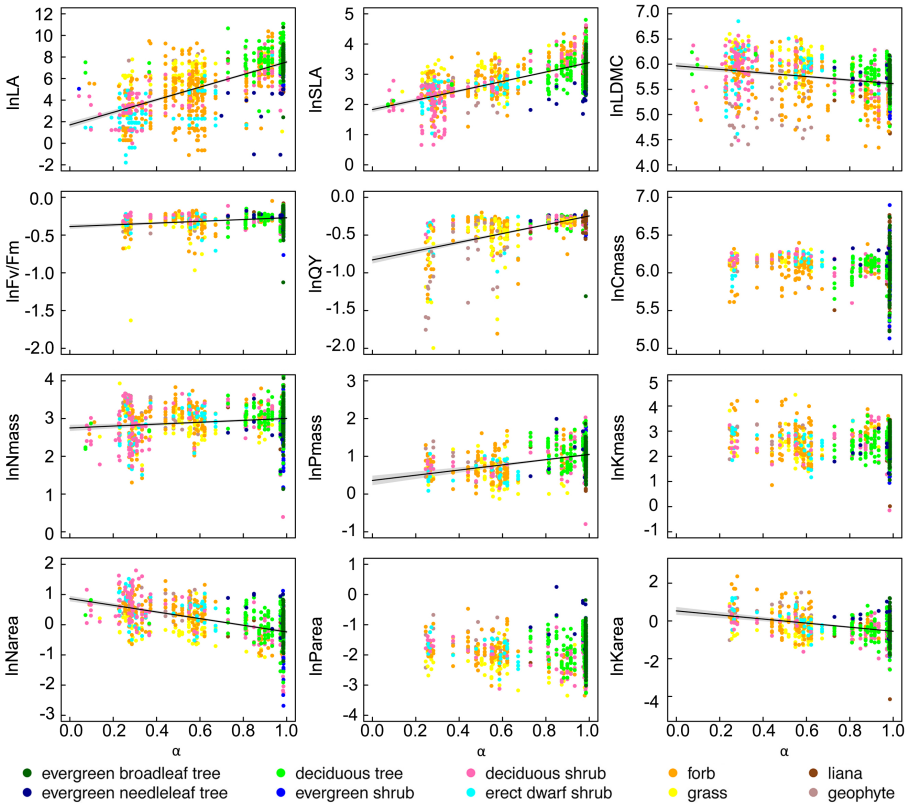

Figure 3. Partial residual plots for the relationships between leaf traits and the Cramer-Prentice moisture index (α), from the GLM analysis summarised in Table 2. Each point denotes a species-site combination; PFTs are indicated by colours. Only significant regression slopes ($P < 0.01$) are shown.

GDD_0 compared to other PFTs, and evergreen needleleaf trees show a steeper increase in P_{area}.

3.5 Climate, PFT and residual contributions to total trait variance

Variance partitioning based on RDA (Table 3) quantifies the total "predictable" fraction of variation for each trait (based on climate and PFT identity), and the fractions uniquely attributable to PFT identity or climate. The difference between the sum of the unique fractions and the total predictable fraction is the "common" fraction, which can be positive or negative and arises because of covariance between the two sets of predictors (Legendre, 2008). The difference between the predictable fraction and 100 % is the residual (unexplained) fraction. Apart from C_{mass} (with low predictability) the predictable fractions of variation for the different traits ranged between 15 % (SLA) and 49 % (LA). Both climate and PFT identity had highly significant ($P < 0.005$, based on a permutation test) unique effects on the ensemble of traits. Variation in LDMC was overwhelmingly dominated by PFT effects and for K_{mass} and P_{area} similar fractions of variation were attributed to PFT and climate effects. For all other traits except C_{mass} the contribution of climate was greater (and in several cases, much greater) than the contribution of PFT identity.

4 Discussion

4.1 Adaptive significance of trait responses to moisture availability

The observed continuous biophysical trait variations with moisture availability are consistent with previous studies (e.g. Reich et al., 1999; Fonseca et al., 2000; Niinemets, 2001; Wright and Westoby, 2002; Wright et al., 2003, 2005a, b; Prentice et al., 2011) and, qualitatively, reasonably well understood. The decrease in LA towards arid climates allows leaves to avoid overheating in environments where soil moisture supplies are inadequate for transpirational cooling to be effective (Campbell and Norman, 1998). High photosynthetic capacity coupled with high CO_2 drawdown, resulting in a low ratio of internal to ambient CO_2 concentration ($c_i : c_a$), is also adaptive in dry environments (Wright et al., 2003; Prentice et al., 2014) because of the high transpirational cost of keeping stomata open under conditions of high atmospheric aridity (vapour pressure deficit). Increased pho-

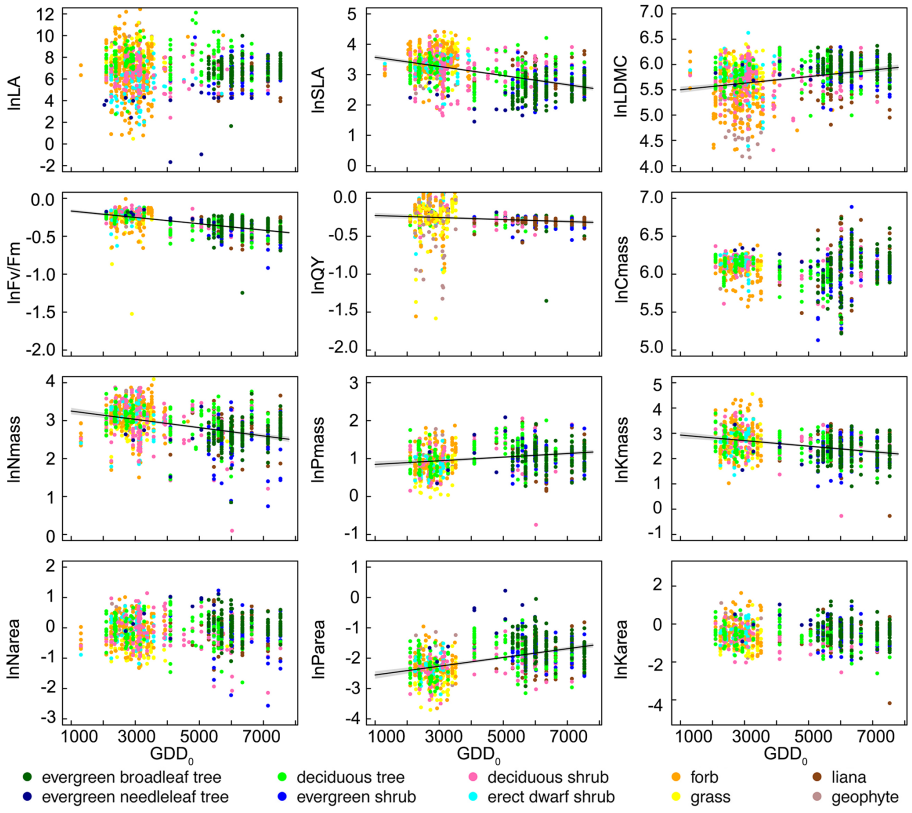

Figure 4. Partial residual plots for the relationships between leaf traits and growing degree days (GDD_0), from the GLM analysis summarized in Table 2. Each point denotes a species-site combination; PFTs are indicated by colours. Only significant regression slopes ($P < 0.01$) are shown.

Table 2. Regression coefficients for the GLM with only α and GDD_0 as predictors. Values in bold are significant at $P < 0.01$.

	intercept		α		GDD_0	
	slope	±sd error	slope	±sd error	slope	±sd error
ln LA	**1.8167**	0.1433	**5.8373**	0.2025	−0.3682	0.3413
ln SLA	**2.3234**	0.0434	**1.5550**	0.0588	**−1.5061**	0.0979
ln LDMC	**5.7544**	0.0347	**−0.3542**	0.0468	**0.6490**	0.0779
ln F_v / F_m	**−0.2400**	0.0136	**0.1168**	0.0196	**−0.4191**	0.0250
ln QY	**−0.7823**	0.0213	**0.5820**	0.0306	**−0.1321**	0.0391
ln C_{mass}	**6.1961**	0.0276	−0.0792	0.0424	−0.0831	0.0547
ln N_{mass}	**3.1357**	0.0419	**0.2511**	0.0605	**−1.0920**	0.1033
ln P_{mass}	**0.1243**	0.0476	**0.6884**	0.0733	**0.4798**	0.0944
ln K_{mass}	**3.2124**	0.0696	−0.1766	0.1072	**−1.0956**	0.1381
ln N_{area}	**0.8419**	0.0462	**−1.1027**	0.0670	0.0638	0.1142
ln P_{area}	**−2.4890**	0.0676	−0.2141	0.1043	**1.4426**	0.1347
ln K_{area}	**0.5975**	0.0767	**−1.0796**	0.1185	−0.1282	0.1530

tosynthetic capacity requires an increase in N_{area} and a reduction in SLA. Low SLA of plants in arid environments may also allow leaves to avoid transient overheating when wind speeds fall (Leigh et al., 2012). The increase in LDMC with aridity is a key adaptation that allows leaves to maintain hydration even at low water potentials that may arise under drought conditions (Bartlett et al., 2012).

The reduction in QY with aridity points to drought-induced photoinhibition at the arid end of the gradient. Dry climates are characterized by high N_{area}, consistent with a high photosynthetic capacity (compensating for low $c_i : c_a$) as mentioned above. High K_{area} in dry climates is consistent with the role of K in maintaining leaf function under water-limited conditions (Sardans and Peñuelas, 2015; Lloyd et al.,

Table 3. Variation (%) in traits accounted for by climate (α and GDD_0) and PFTs together, and the unique contributions (%) of climate and PFTs, based on the first two axes of a redundancy analysis for the sites with data for all traits.

	climate and PFTs	climate	PFTs
ln LA	48.7	23.1	6.4
ln SLA	15.0	12.7	5.8
ln LDMC	25.9	3.9	24.8
ln F_v / F_m	27.7	20.8	1.4
ln QY	36.6	12.4	5.0
ln C_{mass}	3.5	0.6	0.8
ln N_{mass}	29.8	16.4	3.8
ln P_{mass}	29.8	7.3	2.9
ln K_{mass}	20.7	5.3	5.4
ln N_{area}	36.3	27.0	8.9
ln P_{area}	23.2	6.7	8.1
ln K_{area}	18.6	8.1	3.4
All	40.1	33.6	21.1

2015). The regulation of leaf P is less well understood, but the trend towards higher P_{area} in dry climates is consistent with a relatively conservative N : P ratio within PFTs. Reduced mass-based N and P in arid climates are consistent with the increased allocation of carbon to leaf structural components in leaves with low SLA.

4.2 Adaptive significance of trait responses to growing-season warmth

The observed tendency towards lower community-level SLA with increasing temperature may be linked to the well-known relationship between SLA and leaf longevity (Wright et al., 2004; Poorter et al., 2009). However, temperature-related trends in SLA within PFTs are mostly non-significant. The overall trend to lower SLA with increasing temperature is mainly driven by the shift from deciduous to evergreen PFTs, which is to be expected given the clear advantage for evergreens in a subtropical climate that favours year-round photosynthesis and growth. Leaves also become more dense (higher LDMC) towards the warm end of the gradient, but within PFTs, the only significant responses are for leaves to become less dense with increasing temperature. The community-level response of LDMC is thus driven by PFT replacement, with evergreen broad leaves characterized by high LDMC.

Both potential and actual rates of electron transport in woody plants are reduced at the warm end of the temperature gradient. The effect is seen in both deciduous and evergreen woody plants and is likely caused by heat stress resulting in a reduced efficiency of Photosystem II. The decrease in the potential rate implies that electrons are being diverted to protective mechanisms. The decrease in F_v / F_m is steeper than the decrease in QY.

The decline of both N_{area} and N_{mass} with temperature (after PFT differences have been considered) is consistent with the declining N requirement to achieve a given catalytic activity of photosynthetic proteins as temperature increases (Reich and Oleksyn, 2004). The reasons for declining K_{area} and K_{mass} with temperature are unclear; possibly low temperatures in winter, towards the cold end of the gradient, create a K requirement similar to that caused by drought. The observed increases in both P_{area} and P_{mass} with temperature are opposite to the general tendency of leaf N to increase allometrically with leaf P (e.g. Reich et al., 2010). These trends might reflect an increase in non-photosynthetic electron transport processes that require a large supply of inorganic phosphate.

4.3 Trait variation within and between PFTs

Our results add to the growing evidence for extensive trait variability that is not accounted for by PFT differences. Using the global TRY data base, Kattge et al. (2011) found that the largest part of the total variance (as much as 75 %) for several traits (including N_{area} and SLA) was found within rather than between PFTs. Similar observations have been made by van Bodegom et al. (2012) and Wullschleger et al. (2014), while Groenendijk (2011) found that PFTs were not useful predictors of community-level photosynthetic traits. Kattge et al. (2011) also showed (in agreement with our results) that this partitioning varies considerably among traits – with some traits predicted well by PFT identity. Our results extend these previous studies in that they analyse climatically related trait variation. We show contrasts in the responses of different traits to climate, and in their responses to different aspects of climate. In most cases, nutrient traits showed similar responses to climate within PFTs to those shown at the community level; no significant differences were found between the responses within different PFTs, consistent with Zhang et al.'s (2012) findings for multiple element concentrations at the species level.

Variations of biophysical traits with respect to moisture availability are also similar within PFTs and at the community level. However, these same traits show patterns of response to temperature that are dominated by differences among PFTs. The differential responses of leaf N and P contents to moisture availability and temperature require further investigation. Note also that we have not examined trait relationships to soil conditions, especially measures of fertility status, which have been shown to be important in determining photosynthetic and other leaf traits (Ordoñez et al., 2009; Maire et al., 2015). It would be particularly interesting to assess the degree to which leaf chemistry is influenced by nutrient supplies, as opposed to internal stoichiometric regulation. Results presented here suggest that the latter process does at least play an important role, for all three nutrients measured.

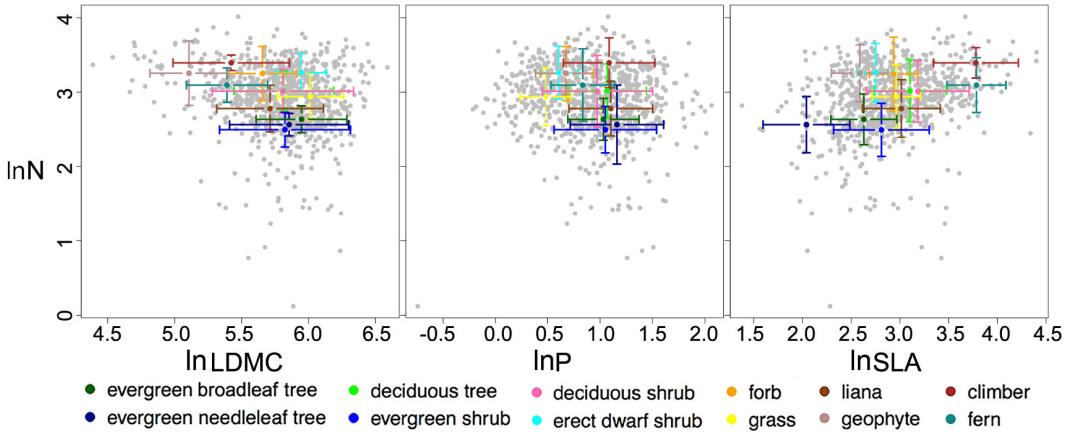

Figure 5. Illustrative plots showing means and standard deviations of trait values within PFTs for ln N_{area} combined with lnLDMC, ln Parea and lnSLA.

4.4 Implications for modelling

It is reasonable to expect that the performance of vegetation models would be improved by representing the values of phenotypically or genotypically plastic traits as state variables, rather than parameters (Prentice et al., 2007). This "adaptive" approach has been adopted explicitly in some recently developed models, e.g. Schymanski et al. (2009) and Scheiter et al. (2013). In the LPJ family of models descended from Sitch et al. (2003), leaf-level photosynthetic capacity (V_{cmax}) is allowed to vary adaptively within PFTs, based on an optimality hypothesis that predicts realistic responses of N_{area} to light, temperature and CO_2 (Dewar, 1996; Haxeltine and Prentice, 1996). Most of the LPJ-family models have treated SLA as a PFT-specific parameter and thus do not allow for covariation of SLA with N_{area}, as has been demonstrated to occur, here and in other contexts (e.g. Lloyd et al., 2010; Prentice et al., 2011). This deficiency has recently been corrected in an LPJ version by Sakschewski et al. (2015). But the adaptive approach embedded in LPJ is unusual among "first-generation" DGVMs, which generally treat leaf traits as fixed PFT properties.

Our findings also indicate that not all trait-environment relationships are "universal". The distinctions between woody and herbaceous, deciduous and evergreen, and angiosperm and gymnosperm plants systematically influence the values of key biophysical traits in ways that would not be predictable from assumed universal relationships. Moreover certain observed overall responses of trait values to climate, including the decline in SLA and increase of LDMC with increasing temperature in our study, appear to be driven principally by PFT replacement rather than by adaptive variation within PFTs. Nonetheless, the prevalence of continuous, consistent trait variation within and between PFTs for many traits and trait-environment relationships supports the conclusion that models should avoid prescribing fixed, PFT-specific values for most quantitative traits (e.g. Wright et al., 2005a). This conclusion is reinforced by examining distributions of PFTs in spaces defined by pairs of traits (Fig. 5). PFTs show considerable overlap in "trait space", even for traits such as LDMC where climate has little direct influence. An additional argument against the imposition of fixed trait values for PFTs is that PFT identity itself can be environmentally plastic; for example, there are species capable of behaving as trees or shrubs depending on growth conditions.

Fixed, PFT-specific values in models could be replaced by adaptive functions of environmental variables: thus reducing the multiplicity of uncertain parameters, while simultaneously increasing the realism of next-generation DGVMs (Prentice et al., 2015). To do so, however, requires that these functions be well specified and robust. Although some progress has been made in developing trait-based models based on statistical trait-environment relationships, process-based model development requires these responses to be quantitatively predictable, based on explicit hypotheses about the adaptive significance of traits.

Practical considerations, including the problem of access with equipment at some of the forest reserve sites, prevented us from including measurements of photosynthetic rates in this trait data set. Chlorophyll fluorescence measurements give different information from CO_2 fixation measurements. Although N_{area} has often been found to be correlated with carboxylation capacity (V_{cmax}), a key quantity for DGVMs, the correlation is far from perfect because of the large and variable structural component of leaf N (Niinemets and Tenhunen, 1997) and other significant components unrelated to photosynthesis, including nucleic acids and defence compounds. However, there are encouraging indications that V_{cmax} too may be broadly predictable as a function of environmental variables (Ali et al., 2015; Fisher et al., 2015). The theory behind the adaptive representation of photosynthetic capacity in the LPJ family of models (Haxeltine and Prentice, 1996) makes predictions about the relationship between

V_{cmax} and environment, which could be tested given a sufficiently wide-ranging set of measurements. Quantifying the predictability of key photosynthetic parameters will thus also be important for developing next-generation DGVMs, and is a high priority for our future research.

Finally we note that within-site variation in traits is large, indeed it is generally as large or larger than the component that can be predicted from site characteristics; consistent with our finding that at least half of the total measured variation in each trait is related neither to PFT identity nor to climate (Table 3). This is an important caveat for modelling because it implies that unless such variation is allowed for, models will underestimate the ability of locally available species, by shifting abundance, to facilitate community-level adaptation to environmental change. In effect, current DGVMs largely ignore the potential stabilising effects of biodiversity on ecosystem function. Taking account of biodiversity in a more realistic way should be possible within a quantitative trait framework by analysing the extent of trait plasticity within species (e.g. Ackerly and Cornwell, 2007). We suggest this as an important research topic, which could capitalise on the growing body of quantitative plant trait data sets based on comprehensive floristic sampling in different environments.

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