
1 Responses of leaf traits to climatic gradients: adaptive 2 variation *versus* compositional shifts

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4 T.-T. Meng^{1,2,3}, H. Wang^{4,5}, S. P. Harrison^{5,6}, I. C. Prentice^{4,5,7}, J. Ni^{3,8,9}, G. Wang³

5 [1] {Beijing Enterprises Water Group Limited, Beijing, China}

6 [2] {Beijing Beihuaqingchuang Environmental Science and Technology Co., Ltd., Beijing,
7 China}

8 [3] {State Key Laboratory of Vegetation and Environmental Change, Institute of Botany,
9 Chinese Academy of Science, Beijing, China}

10 [4] {State Key Laboratory of Soil Erosion and Dryland Farming on the Loess Plateau,
11 College of Forestry, Northwest Agriculture & Forestry University, Yangling 712100, China}

12 [5] {Department of Biological Sciences, Macquarie University, Sydney, Australia}

13 [6] {Centre for Past Climate Change and School of Archaeology, Geography and
14 Environmental Science (SAGES), University of Reading, Whiteknights, Reading, UK}

15 [7] {AXA Chair in Biosphere and Climate Impacts, Grand Challenges in Ecosystems and the
16 Environment and Grantham Institute – Climate Change and the Environment, Department of
17 Life Sciences, Imperial College London, Silwood Park Campus, Ascot, UK}

18 [8] {State Key Laboratory of Environmental Geochemistry, Institute of Geochemistry,
19 Chinese Academy of Science, Guiyang, China}

20 [9] {Alfred Wegener Institute for Polar and Marine Research, Potsdam, Germany}

21 Correspondence to: H. Wang (wanghan_sci@yahoo.com)

22 23 **Abstract**

24 Dynamic global vegetation models (DGVMs) typically rely on plant functional types (PFTs),
25 which are assigned distinct environmental tolerances and replace one another progressively
26 along environmental gradients. Fixed values of traits are assigned to each PFT; modelled trait
27 variation along gradients is thus driven by PFT replacement. But empirical studies have

1 revealed “universal” scaling relationships (quantitative trait variations with climate that are
2 similar within and between species, PFTs and communities); and continuous, adaptive trait
3 variation has been proposed to replace PFTs as the basis for next-generation DGVMs.

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

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

20 Although the adaptive nature of many of these trait-climate relationships is understood
21 qualitatively, a key challenge for modelling is to predict them quantitatively. Models must
22 take into account that community-level responses to climatic gradients can be influenced by
23 shifts in PFT composition, such as the replacement of deciduous by evergreen trees, which
24 may run either parallel or counter to trait variation within PFTs. The importance of PFT shifts
25 varies among traits, being important for biophysical traits but less so for physiological and
26 chemical traits. Finally, models should take account of the diversity of trait values that is
27 found in all sites and PFTs, representing the “pool” of variation that is locally available for
28 the natural adaptation of ecosystem function to environmental change.

29

1 **1 Introduction**

2 The plant functional type (PFT) concept has been important in the development of dynamic
3 global vegetation models (DGVMs), which combine vegetation dynamics (changes in
4 vegetation composition, expressed as abundances of PFTs) at the grid-cell scale with
5 hydrological and biogeochemical processes driven by the physical environment and
6 modulated by PFT characteristics (Prentice et al., 2007; Prentice and Cowling, 2013). PFT
7 classifications vary among models but nearly all include distinctions of life form (at least,
8 woody versus herbaceous plants), leaf habit (evergreen or deciduous) and leaf form (broad or
9 needle-leaves). Some models also distinguish climatic tolerance classes, related primarily to
10 different overwintering mechanisms for woody plants (Harrison et al., 2010), and most
11 distinguish C₄ plants. Usually a fixed set of properties (parameter values) is assigned to each
12 PFT. This expedient simplifies modelling, but it is a potential weakness because it disregards
13 continuous adaptive variation within PFTs; the fact that trait variation within PFTs often
14 exceeds trait differences between PFTs; and the possibility that such variation is “universal” –
15 that is, manifested similarly within and between species, PFTs and communities. Neglect of
16 continuous adaptive variation in models could lead to underestimation of the potential for
17 vegetation to adapt to environmental change and generally incorrect assessments of the
18 response of vegetation to climate (Kleidon et al., 2007; Scheiter and Higgins, 2009) and
19 vegetation feedbacks to climate (Alton et al., 2011).

20 Numerous observational studies have documented continuous relationships between
21 quantitative plant traits and climate (e.g. Werger and Ellenbroek, 1978; Díaz et al., 1998;
22 Fonseca et al., 2000; Niinemets, 2001; Wright and Westoby, 2002; Wright et al., 2004, 2005a,
23 b; Swenson & Enquist, 2007; Reich et al., 2007; Cornwell and Ackerly, 2009; Meng et al.,
24 2009; Ordoñez et al., 2009, 2010; Albert et al., 2010; Prentice et al., 2011; Zhang et al.,
25 2012). Analyses of trait-environment relationships have been motivated partly by the
26 objective of improving the representation of plant structural and functional diversity in
27 DGVMs (Woodward and Cramer, 1996; Díaz and Cabido, 1997; Lavorel et al., 2007; Kattge
28 et al., 2011). In a new strand of DGVM development, modelling quantitative trait values
29 rather than PFT abundances is the central objective (Kleidon et al., 2009; van Bodegom et al.,
30 2012, 2014; Scheiter et al., 2013; Fyllas et al., 2014). Trait-based modelling can take better
31 advantage of the wealth of georeferenced data now available on plant functional traits (Kattge
32 *et al.*, 2011) as well as providing a more realistic representation of functional diversity and

1 competition in plant communities (Scheiter et al., 2013) On the other hand, trait-environment
2 relationships have been shown to differ between PFTs in some cases (e.g. Barboni et al.,
3 2004; He et al., 2006; Meng et al., 2009), implying that not all such relationships are
4 universal; some adaptive trait variation might depend on the values of other traits, including
5 those conventionally used to define PFTs. Moreover there are systematic leaf-trait differences
6 between PFTs and in some studies these have been found to account for a substantial fraction
7 of the total climatically related variation in leaf traits (e.g. Reich et al., 2007; Ordoñez et al.,
8 2009, 2010; He et al., 2010). Thus, observational studies have reached somewhat varying
9 conclusions about the utility of PFT distinctions in predicting adaptive trait variation along
10 environmental gradients.

11 In this work we address the following questions that are important for modelling, and not
12 definitively resolved based on the current literature. (1) To what extent are quantitative trait-
13 environment relationships universal? Alternatively, (2) are there systematic differences in the
14 trait-environment relationships shown by different PFTs? (3) To what extent are variations in
15 traits along environmental gradients accounted for by variation within PFTs, as opposed to
16 successive replacements of one PFT by another? (4) What fractions of total trait variation are
17 linked to climate, and/or to PFT membership, as opposed to being unexplained by either
18 climate or PFTs? We address these questions with an analysis of variations in leaf traits in
19 plant communities sampled on long gradients of temperature and moisture availability in
20 China (Fig. 1). The data set consists of >11,000 quantitative leaf trait determinations on all of
21 the species present at 80 sites (1549 species-site combinations; between 1 and 59 (median 16)
22 species sampled per site), with a wide geographic and climatic spread as shown in Fig. 1. We
23 consider biophysical traits (leaf area: LA, specific leaf area: SLA and leaf dry matter content:
24 LDMC), field-measured chlorophyll fluorescence traits (the ratio of variable fluorescence to
25 maximal fluorescence: F_v/F_m and the quantum yield of PhotoSystem II: QY), and chemical
26 traits: carbon content by mass (C_{mass}), and nitrogen (N), phosphorus (P) and potassium (K)
27 contents, expressed on both an area and a mass basis. Thus we consider 12 traits in all.
28 Although area-based nutrient contents are simply derived from mass-based nutrient contents
29 and SLA, we analyse them separately because their functional significance is different – for
30 example, leaf N comprises a photosynthetic component that is expected to be proportional to
31 LA and a structural component inversely proportional to SLA (Niinemets and Tenhunen
32 1997). LA, SLA, LDMC and N were measured at all sites; the other traits were measured at
33 the 47 sites in eastern China, which cover most of the climatic range of the full data set,

1 except for the driest climates in the west. Adopting a conventional PFT classification, we
2 analyse variations of each trait with bioclimatic temperature and moisture indices (Harrison et
3 al., 2010) within and across PFTs.

5 **2 Materials and methods**

6 **2.1 Sampling sites**

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

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

24 **2.2 Chlorophyll fluorescence measurements**

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

1 **2.3 Foliage sampling and analysis**

2 At least 10 g of leaves were collected for each species, except for a few species with very
3 small leaves at the driest sites, where at least 2 g of leaves were collected. Sunlit leaves of tree
4 species were obtained with long-handled twig shears. The samples were subdivided for the
5 measurement of specific leaf area (SLA), leaf dry matter content (LDMC) and C, N, P and K
6 contents. The measurements used are averages of three replicates. Leaf area (LA) was
7 determined by scanning three replicate sets of five leaves (or more in the case of small leaves,
8 to make up a total area $\geq 20 \text{ cm}^2$ per replicate) with a laser scanner. Areas were measured
9 using Photoshop on the scanned images. Leaf fresh weight was measured in the field. Dry
10 weight was obtained after air-drying for several days and then oven-drying at 75°C for 48
11 hours. Leaf C was measured by the potassium dichromate volumetry method (e.g. Slepetiene
12 et al., 2008) and leaf N by the microkjeldahl method (e.g. Bremner, 1960). Leaf P was
13 analyzed colorimetrically (Shimadzu UV-2550). Leaf K was measured by Flame Atomic
14 Emission Spectrophotometry (PE 5100 PC).

15 **2.4 Climate data and analysis**

16 Mean monthly values of temperature, precipitation and fractional sunshine hours were
17 obtained from 1814 meteorological stations (China Meteorological Administration,
18 unpublished) and interpolated to a 10-km grid using ANUSPLIN 4.36 (Hutchinson and
19 Hancock, 2006) with the help of a digital elevation model (Farr et al., 2007). Mean annual
20 temperature (MAT) and precipitation (MAP), mean winter (P_{DJF}) and summer (P_{JJA})
21 precipitation and of precipitation seasonality and timing (defined as in Prentice et al., 2011)
22 were calculated for each site. Bioclimatic variables were derived as in Gallego-Sala et al.
23 (2010): mean temperature of the coldest month (MTCO) and warmest month (MTWA),
24 growing degree days above 0°C (GDD_0), photosynthetically active radiation during the
25 growing season (PAR_0), annual equilibrium evapotranspiration (EET), Moisture Index ($MI =$
26 MAP/EET), annual actual evapotranspiration (AET) and the Cramer-Prentice α index of
27 plant-available soil moisture ($\alpha = AET/EET$) (Cramer and Prentice, 1988). Available water
28 holding capacity (AWHC) values for the calculation of α were assigned following Prentice et
29 al. (2011), using sand, silt and clay fractions digitized from Shi et al. (2004).

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

4 **2.5 Plant functional types (PFTs)**

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

21 **2.6 Generalized linear models**

22 Generalized linear models (GLMs: Nelder and Wedderburn, 1972; Nelder and Baker, 2006)
23 were used to quantify the relationships of trait values to climate variables (α and GDD_0), to
24 avoid spurious bivariate relationships that can arise when (as here) the predictor variables are
25 not perfectly independent and to allow the inclusion of qualitative variables (PFTs) as
26 predictors in some analyses. The unit of analysis was the species-site combination, i.e. a
27 species sampled at a site. All trait measurements were transformed to natural logarithms (\ln)
28 to reduce skewness and linearize their relationships to the climate variables. This
29 transformation has the property that regression coefficients represent fractional changes,
30 which can be compared among traits measured in different units. The coefficients are
31 expressed per unit of α (in other words, the change in \ln trait value across the global range of
32 α from 0 to 1) and per $10^4 GDD_0$ (equivalent to the change in \ln trait value across the global

1 range from 0 to around 10^4 GDD₀), so that their values are broadly comparable in magnitude
2 between climate variables as well as between traits.

3 We carried out three GLM analyses for each trait: (1) With climate variables (α and GDD₀)
4 only as predictors, equivalent to ordinary least-squares multiple regression; (2) with climate
5 variables and PFTs as predictors; (3) with PFTs and PFT-climate interactions as predictors.
6 Analysis (1) measures the partial effect of each climate variable on the observed trait values.
7 Analysis (2) measures the average partial effect of each climate variable on trait values *within*
8 PFTs, allowing that the PFTs might have consistently lower or higher trait values. Analysis
9 (3) estimates the partial effect of each climate variable on trait values within *each* PFT (the
10 PFT-climate interaction). These three analyses are needed to answer the following questions
11 in sequence: (1) What is the overall (community-level) response of trait values to climate? (2)
12 To what extent is this response caused by similar trait variations *within* each PFT, *versus*
13 shifts in the occurrence and abundance of PFTs with innately different trait values? (3) Do
14 trait values of some PFTs respond to climate differently from others?

15 A significance criterion of $P < 0.01$ was adopted for all regression coefficients in all three
16 analyses. This is stringent enough to minimize the chance of ‘false positives’ in analyses (2)
17 and (3). In the description of Results, “significant” always implies $P < 0.01$ or better.
18 Significant differences between trait values for different PFTs (assessed at a common
19 environmental value) were inferred from significant coefficients for the relevant factors
20 (PFTs) in analysis (2), while significant differences between the trait-environment slopes for
21 different PFTs were inferred from significant PFT-environment interactions in analysis (3).
22 All GLM results are presented as partial residual plots, using the *visreg* package in R. Partial
23 residual plots are the multiple-regression analogue of simple x - y plots in ordinary regression.
24 In plots showing the relationship of each trait to α , the y -axis values of the data points are
25 adjusted so as to remove the fitted effect of GDD₀. Similarly, in plots showing the
26 relationship of each trait to GDD₀, the y -axis values of the data points are adjusted so as to
27 remove the fitted effect of α .

28 **2.7 Multivariate analysis and variance partitioning**

29 As a complement to single-trait analyses, we performed redundancy analysis (the constrained
30 equivalent of PCA: ter Braak & Prentice 1988) with variance partitioning (Legendre 2008), to
31 quantify the unique and combined contributions of climate and PFT identity to the total

1 variation in all traits. This analysis was performed with the CANOCO package (Leps &
2 Smilauer 2003), based on the sites for which all traits were measured.

3 **3 Results**

4 **3.1 Climate gradients**

5 More than 80% of the geographic variation in the climate of our sampling sites can be
6 summarized by variation on two principal axes (Table 1). Each principal axis is defined as a
7 linear combination of variables, and each variable is assigned a “loading” which represents
8 the contribution of that variable to the combination. The first principal axis explains 60% of
9 total variation and is primarily related to temperature. MAT, GDD₀, MTCO, MAP, MI, P_{DJF}
10 and P_{JJA} have the largest positive loadings. The positive loadings for precipitation variables
11 reflects the general tendency for absolute amounts of precipitation to increase with
12 temperature. The second axis explains a further 25% of total variation and is related to
13 moisture *versus* aridity. MI, α , and P_{JJA} have large positive loadings while PAR₀ and MTWA
14 have large negative loadings. The similar behaviour of PAR₀ and MTWA reflects an
15 increasing period without clouds, and thus also higher temperatures in summer, as moisture
16 availability decreases. A third axis relating to the seasonality of precipitation accounts for
17 only 9% of total variation. A closely similar pattern emerged from the analysis of climate data
18 for the whole country (Table S3). This similarity confirms that the pattern of variation in
19 climate across the sites reflects the general pattern of climate gradients across China, and that
20 these gradients can be summarized using two variables, representing temperature and plant
21 moisture availability respectively.

22 For all further analysis we used the variables GDD₀ and α . GDD₀ was preferred to MAT as
23 MAT values in climates with a long, cold winter, as in northern China, show the influence of
24 conditions unrelated to those prevailing at the time of growth. The pattern of variation of
25 GDD₀ and α across China is shown, with the site locations, in Fig. 1. Fig. 1 also shows the
26 frequency of different GDD₀- α combinations among grid cells in the whole country (grey
27 scale), and the site positions in this climate space. Significant regions of climate space not
28 sampled correspond to low GDD₀ at high α (far northeast China) and low α (Tibetan plateau),
29 and high GDD₀ 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 broadly overlap with groups (1) and (3). (3) Dwarf shrubs, grasses, forbs and geophytes favour still 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 *versus* 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.

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

10 **3.4 Trait-climate relationships: temperature effects**

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

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

29 Relationships to GDD_0 fitted separately within PFTs (Fig. S4) showed fewer significant
30 slopes, and less consistency among PFTs, than the corresponding relationships to α .
31 Individually significant ($P < 0.01$) PFT responses of SLA to GDD_0 could be increasing or
32 decreasing (-0.57 to $+1.3$). Slopes of LDMC are negative (-1.6 to -3.0), with forbs and

1 grasses showing the steepest declines. Area- and mass-based nutrients show few significant
2 differences among PFTs in their responses to either GDD_0 ; however forbs show an increase in
3 N_{mass} and more steeply increasing P_{mass} with GDD_0 compared to other PFTs, and evergreen
4 needleleaf trees show a steeper increase in P_{area} .

5 **3.5 Climate, PFT and residual contributions to total trait variance**

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

19

20 **4 Discussion**

21 **4.1 Adaptive significance of trait responses to moisture availability**

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

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

5 The reduction in QY with aridity points to drought-induced photoinhibition at the arid end of
6 the gradient. Dry climates are characterized by high N_{area} , consistent with a high
7 photosynthetic capacity (compensating for low $c_i:c_a$) as mentioned above. High K_{area} in dry
8 climates is consistent with the role of K in maintaining leaf function under water-limited
9 conditions (Sardans and Peñuelas, 2015; Lloyd et al., 2015). The regulation of leaf P is less
10 well understood, but the trend towards higher P_{area} in dry climates is consistent with a
11 relatively conservative N:P ratio within PFTs. Reduced mass-based N and P in arid climates
12 are consistent with the increased allocation of carbon to leaf structural components in leaves
13 with low SLA.

14 **4.2 Adaptive significance of trait responses to growing-season warmth**

15 The observed tendency towards lower community-level SLA with increasing temperature
16 may be linked to the well-known relationship between SLA and leaf longevity (Wright et al.,
17 2004; Poorter et al., 2009). However, temperature-related trends in SLA within PFTs are
18 mostly non-significant. The overall trend to lower SLA with increasing temperature is mainly
19 driven by the shift from deciduous to evergreen PFTs, which is to be expected given the clear
20 advantage for evergreens in a subtropical climate that favours year-round photosynthesis and
21 growth. Leaves also become more dense (higher LDMC) towards the warm end of the
22 gradient, but within PFTs, the only significant responses are for leaves to become *less* dense
23 with increasing temperature. The community-level response of LDMC is thus driven by PFT
24 replacement, with evergreen broad leaves characterized by high LDMC.

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

30 The decline of both N_{area} and N_{mass} with temperature (after PFT differences have been
31 considered) is consistent with the declining N requirement to achieve a given catalytic activity

1 of photosynthetic proteins as temperature increases (Reich and Oleksyn, 2004). The reasons
2 for declining K_{area} and K_{mass} with temperature are unclear; possibly low temperatures in
3 winter, towards the cold end of the gradient, create a K requirement similar to that caused by
4 drought. The observed increases in both P_{area} and P_{mass} with temperature are opposite to the
5 general tendency of leaf N to increase allometrically with leaf P (e.g. Reich et al., 2010).
6 These trends might reflect an increase in non-photosynthetic electron transport processes that
7 require a large supply of inorganic phosphate.

8 **4.3 Trait variation within and between PFTs**

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

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

1 4.4 Implications for modelling

2 It is reasonable to expect that the performance of vegetation models would be improved by
3 representing the values of phenotypically or genotypically plastic traits as state variables,
4 rather than parameters (Prentice et al., 2007). This ‘adaptive’ approach has been adopted
5 explicitly in some recently developed models, e.g. Schymanski et al. (2009) and Scheiter et al.
6 (2013). In the LPJ family of models descended from Sitch et al. (2003), leaf-level
7 photosynthetic capacity (V_{cmax}) is allowed to vary adaptively within PFTs, based on an
8 optimality hypothesis that predicts realistic responses of N_{area} to light, temperature and CO_2
9 (Dewar, 1996; Haxeltine and Prentice, 1996). Most of the LPJ-family models have treated
10 SLA as a PFT-specific parameter and thus do not allow for covariation of SLA with N_{area} , as
11 has been demonstrated to occur, here and in other contexts (e.g. Lloyd et al., 2010; Prentice et
12 al., 2011). This deficiency has recently been corrected in an LPJ version by Sakschewski et al.
13 (2015). But the adaptive approach embedded in LPJ is unusual among “first-generation”
14 DGVMs, which generally treat leaf traits as fixed PFT properties.

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

30 Fixed, PFT-specific values in models could be replaced by adaptive functions of
31 environmental variables: thus reducing the multiplicity of uncertain parameters, while
32 simultaneously increasing the realism of next-generation DGVMs (Prentice et al., 2014b). To

1 do so, however, requires that these functions be well specified and robust. Although some
2 progress has been made in developing trait-based models based on statistical trait-
3 environment relationships, process-based model development requires these responses to be
4 quantitatively predictable, based on explicit hypotheses about the adaptive significance of
5 traits.

6 Practical considerations, including the problem of access with equipment at some of the forest
7 reserve sites, prevented us from including measurements of photosynthetic rates in this trait
8 data set. Chlorophyll fluorescence measurements give different information from CO₂
9 fixation measurements. Although N_{area} has often been found to be correlated with
10 carboxylation capacity (V_{cmax}), a key quantity for DGVMs, the correlation is far from perfect
11 because of the large and variable structural component of leaf N (Niinemets and Tenhunen,
12 1997) and other significant components unrelated to photosynthesis, including nucleic acids
13 and defence compounds. However, there are encouraging indications that V_{cmax} too may be
14 broadly predictable as a function of environmental variables (Ali et al., 2015; Fisher et al.,
15 2015). The theory behind the adaptive representation of photosynthetic capacity in the LPJ
16 family of models (Haxeltine and Prentice, 1996) makes predictions about the relationship
17 between V_{cmax} and environment, which could be tested given a sufficiently wide-ranging set
18 of measurements. Quantifying the predictability of key photosynthetic parameters will thus
19 also be important for developing next-generation DGVMs, and is a high priority for our future
20 research.

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

1

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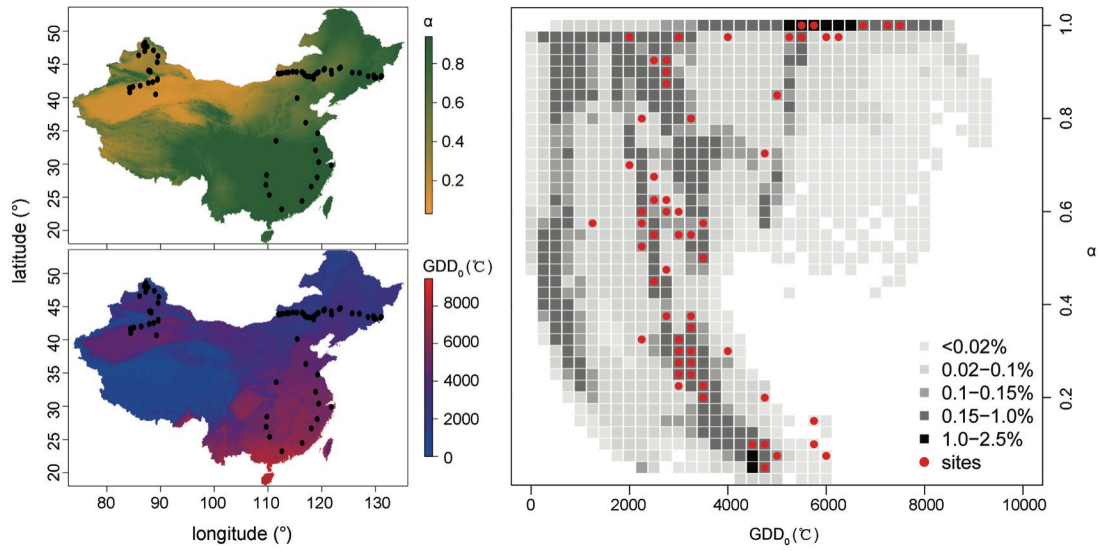
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1 Figures

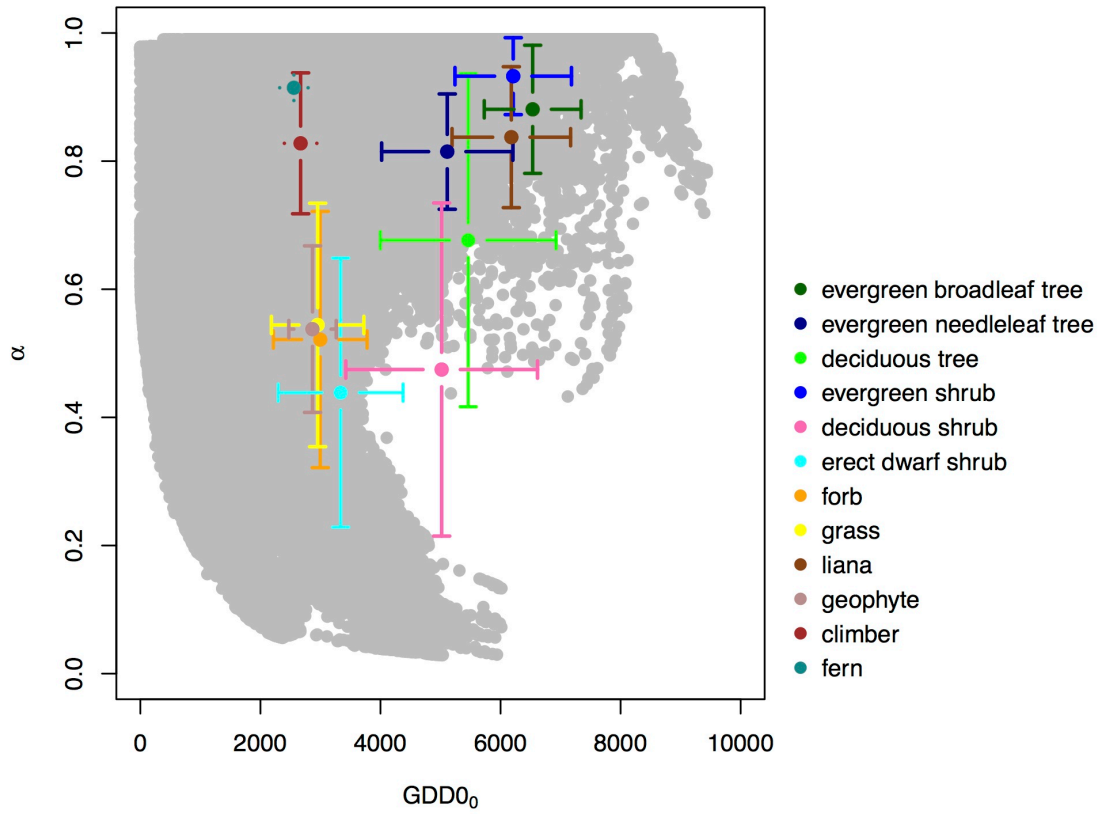
2 Figure 1: Left: Geographic variation in the mean Cramer-Prentice moisture index (α) and
3 annual growing degree days above 0°C (GDD₀) in China. Right: frequency distribution of 10-
4 km grid cells (grey squares) and location of sampling sites (red circles) in climate space.



5

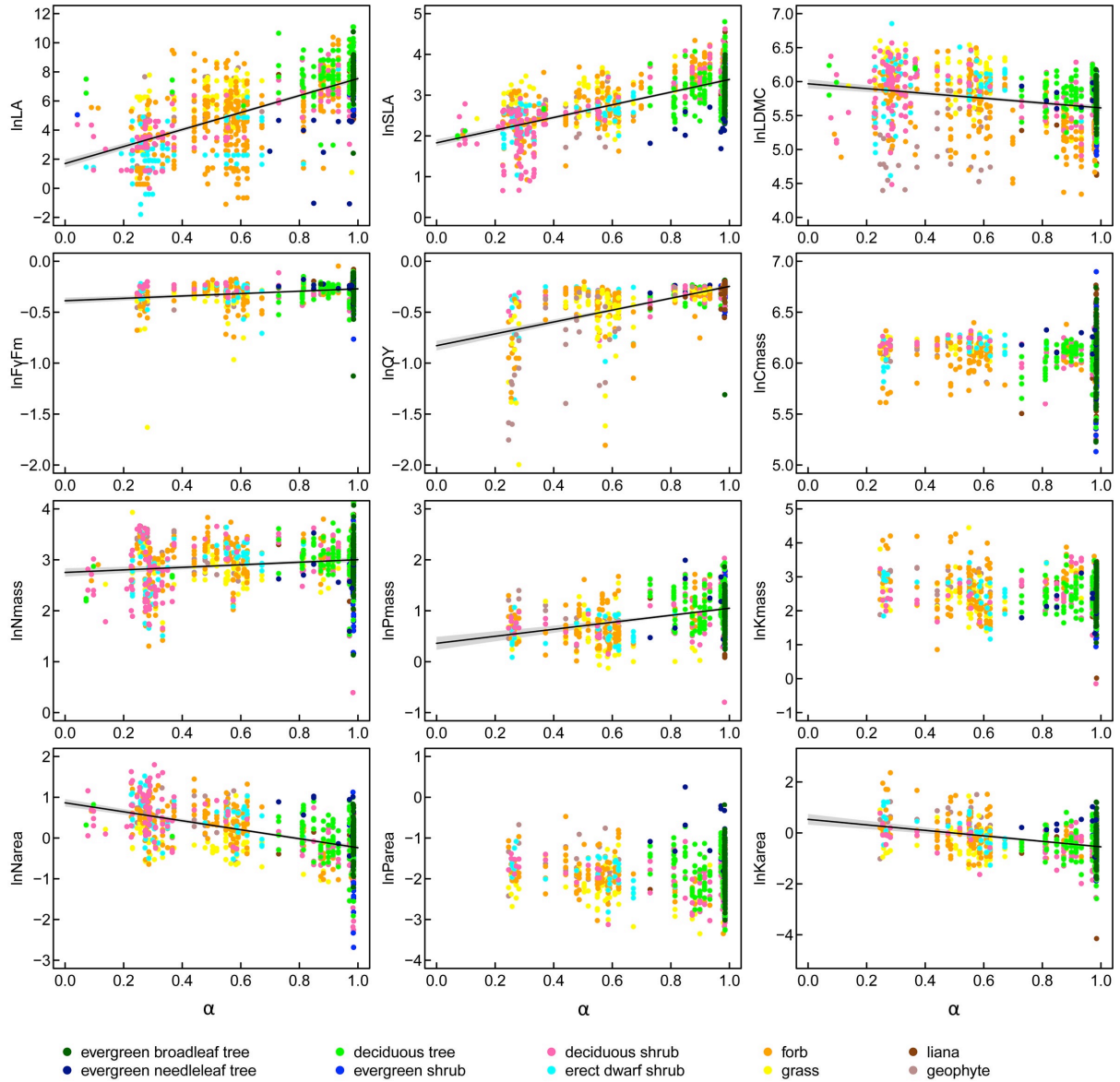
6

1 Figure 2: Optima and tolerances of PFTs in climate space, based on data from the sampling
2 sites. The grey dots represent the climates of all grid cells in China.



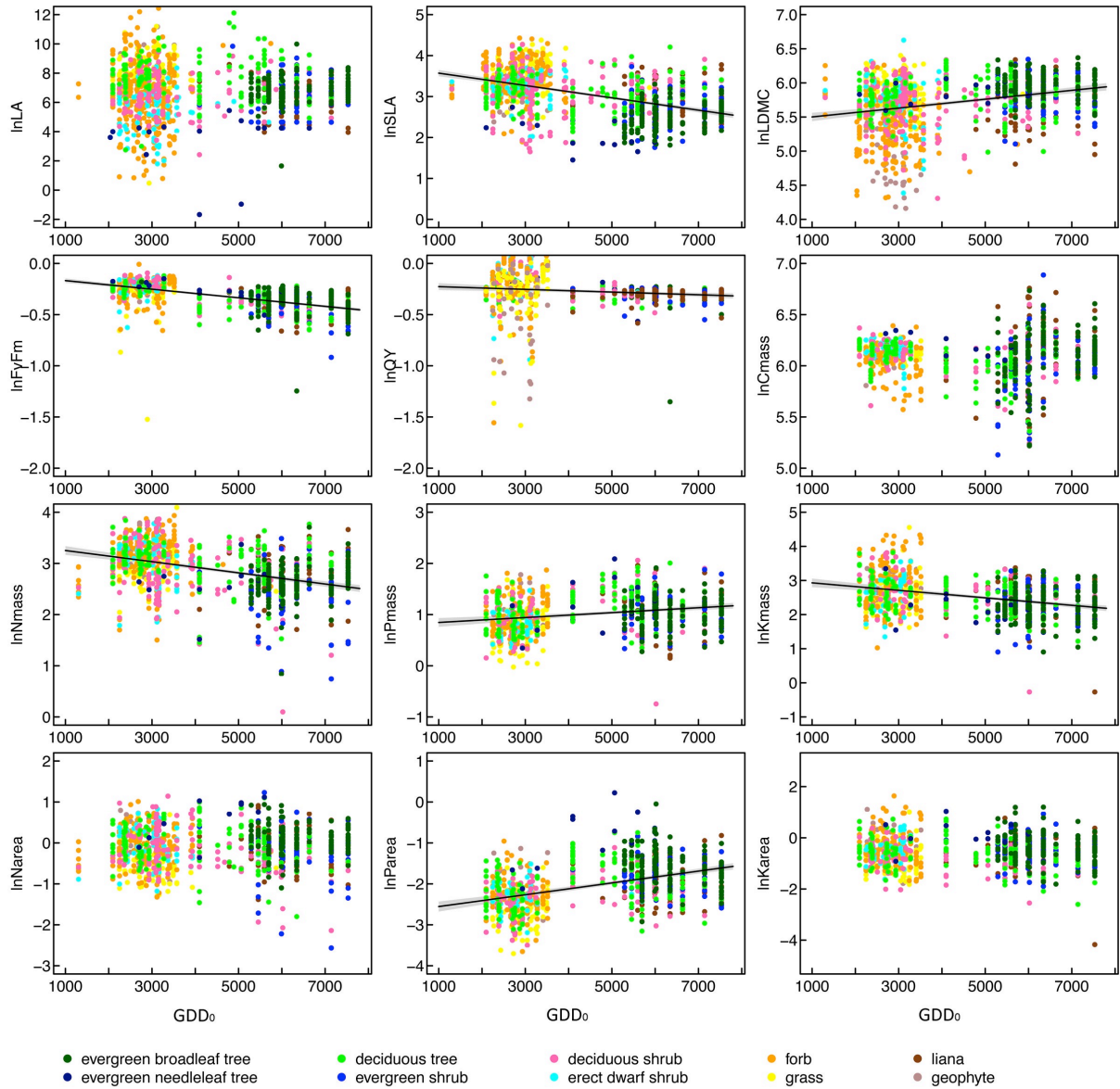
3

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



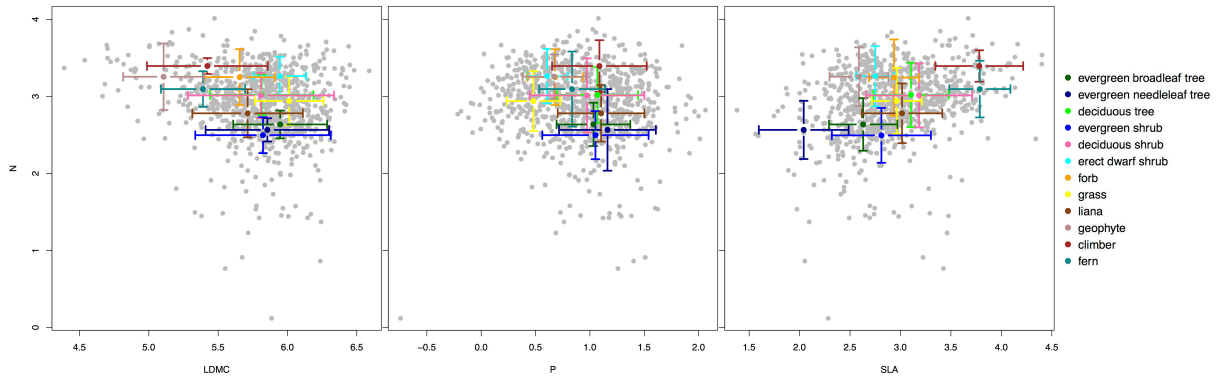
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1 Figure 4: Partial residual plots for the relationships between leaf traits and growing degree
 2 days (GDD₀), from the GLM analysis summarized in Table 2. Each point denotes a species-
 3 site combination; PFTs are indicated by colours. Only significant regression slopes (P < 0.01)
 4 are shown.



5

1 Figure 5: Illustrative plots showing means and standard deviations of trait values within PFTs
2 for $\ln N_{\text{area}}$ combined with LDMC, $\ln P_{\text{area}}$ and SLA.



1 **Tables**

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

	PC 1	PC 2	PC 3 ⁶
MAT	0.870	-0.462	0.12 8 ⁷
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%

1 Table 2: Regression coefficients for the GLM with only climate variables as predictors.
 2 Values in **bold** are significant at $P < 0.01$.
 3

	intercept		alpha		GDD0	
	slope	\pm sd error	slope	\pm sd error	slope	\pm 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

4
5

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

4

	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
<i>All</i>	<i>40.1</i>	<i>33.6</i>	<i>21.1</i>

5