Response to referees and editor

We were happy to read these very positive, thoughtful reviews of our Discussion Paper. We have prepared a revised MS taking the editor's and three referees' comments into account. The comments are reproduced here, in full, with **bold type** used to highlight the key points requiring consideration. Our responses to every comment are given in *italics*.

Anonymous referee #1

General comments

This paper addresses the issue of trait variability within plant functional types in relation to climate. The authors argue that most traits vary in relation to climatic gradients but that change occurs sometimes through trait change within PFTs, and sometimes through shifts in the occurrence and abundance of PFTs with innately different trait values. These ideas are not new and have been suggested and shown in various earlier papers, but the authors present an impressive dataset that is in my opinion more reliable than those upon which earlier analyses have been based. Other tests of trait-environment relationships at similar spatial scales often rely on data collated from multiple studies and environmental data of poorer quality than that used in this manuscript.

The manuscript is very well written and a pleasure to read. The research questions are clearly stated and clearly addressed by the data and analyses. I have few major criticisms, and most of my comments are merely suggestions that I believe would improve the quality and readability of the manuscript and do not point to major flaws in the methodology or interpretation.

There is **only one major issue** that I would like to see addressed in the manuscript before publication. My problem with most studies investigating trait-environment relationships is that despite identifying statistically significant relationships among environmental predictors and trait means, the ability to predict trait values from environmental forcing alone is often quite poor. That is, after accounting for the variance explained by the environmental predictors, and differences among PFTs, most of the trait variability still remains (there is overlap in the traits values observed at either extreme of the environmental gradient and in almost all PFTs). Given that vegetation models are attempting to simulate vegetation and biogeochemistry with these same environmental forcings alone – which account for so little of the observed trait variation – I think it is important to acknowledge limits to the predictability of the vegetation traits we actually observe when using only macroclimate and a few simple soil variables to force models and discuss other potential sources of variation (e.g. microclimatic variation, disturbance, heterogeneity, evolutionary constraint). Specifically I would like to see a **paragraph highlighting these issues** and some attempt at **variance partitioning** in the analyses that highlights the proportion of trait variation explained by climate, PFTs, and unexplained variation.

These points are very well taken. We have added a new paragraph at the end of the Discussion that covers this topic (plus a new sentence at the end of the Abstract). We have also taken the opportunity to present a variance-partitioning analysis, which we think is a significant enhancement to the manuscript.

I would also really like to see another plot, similar to figure 2, but with **PFTs plotted in trait space** to highlight to massive overlap in trait values among PFTs.

We have included a new Figure (Fig. 5), which illustrates exactly this point.

Specific comments

Table 1 seems unnecessary. With most of the important information contained within it repeated in figure 1. I would suggest moving it to the Supplementary info.

We have moved the Table as suggested.

DGVMs typically use A_{max} and V_{cmax} as parameters to describe photosynthetic rates. I understand that chlorophyll florescence offer advantages over A_{max}/V_{cmax}, but perhaps the authors should state this because otherwise it seems that it would have been more appropriate to measure parameters used by DGVMs.

V_{cmax} can be inferred from A_{max} using the so-called one-point method, but even simply measuring A_{max} requires taking a heavy infrared gas analysis (IRGA) apparatus to the field sites. Fluorescence is a different measure, not a substitute for A_{max}. However, we sacrificed the added value of providing A_{max} and V_{cmax} data for the ability to assemble a very large trait data set, including sampling forest reserves in South China that would have been challenging to reach with an IRGA.

It is not stated in the methods what the sampling unit is that is being analyzed. Are the GLMs applied to trait values of individual plants and the environmental variable at the site levels or (as is plotted in figure 3 and 4) species-level means?

The sampling unit analysed is a species at a site. We have now added this information in the Methods.

I would be interested to know how the analyses look when they are repeated within and between species rather than PFTs. In terms of trait change along environmental gradients this is more relevant as species are real entities rather than PFTs which are the invention of modelers. There isn't room for this in this manuscript, which is focused on the utility of traits and PFTs for models, but I look forward to seeing this analysis in anther publication.

We agree that there is scope for this analysis to be done in future, and that it would be of great interest. However we agree that this manuscript doesn't have room for it; it would be a separate study.

Does the entire PCA analysis of climate space in China and the climate space covered by the sites only exist to make the point that the sites cover a wide range of climate conditions that are representative of Chinese climate? This point seems to be adequately made in figure 1. I would suggest moving this analysis to the supporting information.

Yes, this is the only purpose of this complete PCA. So we agree, and we have moved this analysis out of the main text (apart from a brief mention of its similarity to the analysis of our sampling sites).

Please add some discussion of the confounding role of nutrients. Many of the traits included in this analysis would be expected to be profoundly altered by different soil nutrient conditions. It is understandable given the poor quality of most soil nutrient maps that this was not included as a predictor variable in the analysis, but I believe further discussion and an acknowledgment of their role should be included.

We fully agree; we have added new text in the Discussion, with appropriate references, making this clear.

Technical corrections

In the discussion it is stated: "On the other hand, the LPJ-family models treat SLA as a PFT-specific parameter and thus do not allow for covariation of SLA with N_{area}." This is not true. Please see the recently published LPJml-FIT model:

Sakschewski, B., von Bloh, W., Boit, A., Rammig, A., Kattge, J., Poorter, L., Peñuelas, J. and Thonicke, K. (2015), Leaf and stem economics spectra drive diversity of functional plant traits in a dynamic global vegetation model. Global Change Biology. doi: 10.1111/gcb.12870

We have modified this statement, and cited this paper.

Anonymous referee #2

General comments

This manuscript addresses a scientifically interesting and important topic – the connection between biophysical, biochemical and physiological leaf traits and climate. It is asking the question how temperature and water availability influence selected leaf traits, and if observed variability in leaf traits is due to continuous adaptive trait shifts within plant functional types (PFTs), or due to PFT replacements along climatic gradients. Although many contemporary Dynamic (Global) Vegetation Models (DGVMs) still rely on the PFT concept, more recent developments in vegetation modeling focus on PFT-less trait-based approaches, arguing that the conventional PFT-based approaches may be too rigid, general, and over-simplifying. As PFTs are usually assigned a fixed set of parameter values in many DGVMs, continuous adaptive variation cannot be modeled directly, but needs to be mimicked by PFT replacement, disregarding that within-PFT variability of traits can equal or exceed between-PFT variability. Especially with respect to the more recent development of trait-based DGVMs that allow continuous trait variation within defined ranges of trait space this study provides valuable new data material for model parameterization, calibration and evaluation. Moreover, it contributes to an improved understanding of the linkages between different leaf traits and climate.

The abstract is clearly structured, presenting the motivation for the presented study, the methods used to address the problematic, a very short summary of the main results found in the study, and a brief outlook on the significance of the presented results. The introduction provides background information on the PFT concept in vegetation modeling and its inherent drawbacks, and establishes a connection to related studies in the field. However, **although the scientific questions acting as motivation for this study are inherently present hidden in the introduction text, I would like to**

see them listed and phrased directly as such (bullet points, listed by numbers, or in a similar way) at the end of the second paragraph (p. 7097, l. 21).

We have made this change: now the third paragraph starts by stating the main scientific questions addressed, as a numbered list.

The scientific methods used to address the research questions are well-established and appropriate to address the presented research questions. Results and conclusions are generally presented in a transparent, structured and concise way and sufficiently illustrated with figures and tables. The discussion part is well-structured, but section 4.3 (Comparison with previous studies of trait variation within and between PFTs) is rather short and basically only focuses on Kattge et al. (2011) and Zhang et al. (2012). If available, it would be desirable to (shortly) include a few more studies related to this topic here.

The literature on this topic is actually quite limited; we have found a couple of additional papers to cite, but both use the examples of N and SLA and rely on a graphical demonstration – they add little to the analysis by Kattge et al. However, we realize that the original section looked unbalanced, so we have re-structured it, added the new references, and altered the section heading to a more general one.

The only part where I do not fully agree with the authors is the last section (4.4 Implications for modelling). Their results nicely show that within-PFT trait variability is often continuous and can be as high or higher as between-PFT trait variability, and that PFT replacement only partially explains trait variation along climate gradients. Nonetheless, they strongly argue in favor of PFT-based vegetation models, when in fact their results justify and support the development and existence of PFT-less trait-based models that allow dynamic plant community assembly in dependence of prevailing environmental conditions. I would have liked to have seen a slightly **more balanced discussion here with respect to the advantages/limitations of PFT-based vs. trait-based vegetation models**, as in my opinion both model types have their right to exist, depending on the research questions under consideration.

This was a thought-provoking comment. On reflection, we realized that although simply retaining PFT distinctions would be one way to account for differences between PFTs, in fact the phenomenon described (trait-environment relationships being contingent on PFT membership) could as well or better be represented as an effect of 'PFT-defining traits' on the relationships between other traits and environment. We have amended our discussion accordingly.

In general, the manuscript is sufficiently referenced to allow making connections to related research. In a few places where more references would be desirable, it is highlighted in the "Detailed Comments" section of this review. The provided supplementary material is of good quality and sufficient to transparently present the results in a more in-depth way than possible in the manuscript itself. Overall, I consider this study to be a valuable contribution to the field, and suggest its publication in BG after minor revisions.

Detailed comments

p. 7096, l. 19-22: " 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 and the possibility that such variation is "universal" – that is, manifested similarly within and between species, PFTs and communities." Should phrase this even more clearly: the definition of a limited number of PFTs with fixed parameter values is an artificial generalization concept used by vegetation modelers to discretize continuous trait combinations into a manageable number of seemingly distinct categories. However, this oversimplification neglects that the range of trait variations within these artificial PFT-categories in reality may be as large or larger than between PFT categories, which leads to an underestimation of the plasticity and adaptive potential of vegetation to environmental change and vegetation feedbacks to climate.

We fully agree. We have strengthened our statement on the subject.

p. 7097, l. 10-21: this part reads a bit confusing, as the arguing in favor of trait-based approaches vs. PFT-based approaches goes back and forth and from the phrasing is not clear enough. Please first talk about the advantages of trait-based modeling, and then make it clear that afterwards you are talking about circumstances in which leaf traits have been discovered to be distinctly different between PFTs, thus indicating that PFT-based modeling also can be justified based on focus and circumstances. "An advantage of trait-based modelling is that it can take better advantage of the wealth of georeferenced data now available on plant functional traits (Kattge et al., 2011)." This may indeed be one advantage, but in my opinion the more relevant advantage of trait-based modeling is that it allows to simulate continuous trait variation, thereby allowing the development of plant community assemblies that are adapted to site-specific biotic and abiotic environmental conditions and can react more flexibly to environmental change, as well as allowing new approaches to simulate functional diversity and competition (see, e.g., the trait-based aDGVM2 model as described in Scheiter et al., 2013).

We agree, and we have added a statement to this effect.

"On the other hand, some leaf traits can have different relationships to climate depending on the PFT": I'm not entirely sure I understand correctly what you mean to say with this sentence. Do you mean that certain leaf traits within one PFT behave one way along a climate gradient, while they behave the opposite way along the same climate gradient for plants that belong to another PFT, or do not vary with climate at all for a third PFT? If possible, rephrase this to make it more clear.

We have clarified the wording of this statement.

p. 7097, l. 25: "on all of the species present at 80 sites, with a wide geographic spread.": How many species did you sample overall? And what was the range of species numbers between sites (minimum and maximum number of species per site)?

This information was available in Table S2. However, we have now extracted key statistics (number of species-site combinations; range of species number) and put them into the text.

p. 7098, l. 2-4: “Area-based nutrient contents provide no independent information, as they are simply derived from mass-based nutrient contents and SLA, but they provide an alternative perspective on the regulation of leaf nutrient contents.” In what way do they provide an alternative perspective? Please elaborate a bit more closely, or else it becomes hard to justify why you are presenting both if they are not independent.

We have added a senetence expanding on this point, and provided a key reference in support of our reasoning.

p. 7098, l. 12: “The sites (Table 1) represent...”: Please also point out Figure 1 here, as you show the location of your sampling sites on a map in Figure 1. I find it helpful to also see the location of the sites on a map, and would have asked for a map figure, but then realized that the sites are actually highlighted in Fig. 1 when looking at the figure later on.

Done.

p. 7099, l. 11/12: “except for a few species with very small leaves at the driest sites”: What did you do for these? No sampling, or sample as much as was available?

We took a smaller sample (at least 2 g). This is now stated.

p. 7099, l. 19: “Leaf C was measured by the potassium dichromate volumetry method and leaf N by the microkjeldahl method.” Please add a reference if possible, as it is not instantaneously clear to everybody how these methods work.

Done.

p. 7103, l. 7/8: “Figure 1 also shows the frequency of different GDD0-α combinations among grid cells, and the site positions in this climate space.”, and p. 7121, Fig. 1: frequency distribution and location of sampling sites in climate space: The chosen sampling sites cover a large range of the occurring GDD0-α combinations and are therefore well-suited for the pursued study purpose. However, no sites cover the very low end of GDD0 values, and in the area of GDD0-values between 6000 and 9000 and α between 0.4 and 0.9. Which areas of China would these combinations correspond to? Probably high-altitude grid cells for the low GDD0-values, and places in Southern China with high GDD0 and intermediate to high α values? Maybe point this out briefly either in the Figure caption or in the text.

We have provided this information in the revised text.

p. 7103, l. 14-16: “Deciduous trees and deciduous shrubs favor cooler and drier climates, corresponding to the deciduous forests of central eastern China.” I generally agree with your four PFT groups based on optimum and tolerance thresholds, except maybe for this group, as their tolerance range compared to the ones of the PFTs in the other groups is very wide, and therefore makes these two PFTs overlap with group (1) and group (3).

Their range is particularly wide, certainly, and we have now commented on this.

p. 7104, l. 3-6: “Inclusion of PFTs as predictors (Fig. S1 in the Supplement) shows that there are some 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." Are the differences statistically significant? (Same question applies to Fig. S3)

Yes. The original text mentioned the fact that we applied a quite conservative ($P < 0.01$) criterion in order to minimize the chance of "false positives" in analyses (2) and (3), where a large number of parameters are estimated. However, it was stated kust once and without elaboration. So we have now expanded this statement in the Methods, explained that by "significant" we always mean $P < 0.01$ (or better), and provided frequent "reminders" of this in the Results section.

p. 7104, l. 25/26: "Warmer climates also show somewhat reduced potential and actual quantum yield." So both dry conditions and warm climate show reduced QY. Can you make a judgment which of these two factors has the greater effect? I suppose that, since dry conditions and warm conditions are not statistically independent, the decrease in QY is a combination of both, but nonetheless it would be interesting to know more about the relative importance of each factor.

As should now be clear (from our more explicit treatment of "significance", QY shows independently significant effects of both drought and heat. We can't say whether one is more important than the other: that would depend on the conditions sampled.

p. 7105, l. 24/25: "The observed continuous biophysical trait variations with moisture availability are consistent with previous studies..." Please add some references for these studies.

This was an oversight. We have now added a list of relevant papers.

p. 7108, l. 24-28: "Our findings suggest that vegetation models should retain the PFT concept and a minimal set of PFTs, because the distinctions between woody and herbaceous, de- ciduous and evergreen, and angiosperm and gymnosperm plant types systematically influence the values of key biophysical traits in ways that would not be predictable from assumed universal relationships." I do not agree with this statement. Vegetation models using the PFT concept may be useful and sufficient to address many scientific questions with respect to vegetation dynamics, but it is not true that using the PFT concept is the only way to get clear distinctions between key biophysical traits. Trait-based vegetation models not necessarily need to assume universal relationships, but may define a potentially allowed maximum range of values for key biophysical traits. If plants are assigned values from within these ranges at birth, selection through environmental conditions such as temperature and water availability will lead to the emergence of successful trait value combinations, whereas unsuccessful combinations will be eliminated through competition and/or environmental pressure. Whether woody or herbaceous, deciduous or evergreen, plants with low or high SLA, etc. will prevail therefore is not predefined, but will be an emergent property of simulated trait selection through environmental filtering. No PFTs need to be predefined, but an *a posteriori* classification of simulated plants into PFT categories based on simulated successful trait combinations is possible and will also pick up PFT replacement over time and space where it occurs. Trait-based vegetation models such as, e.g., the aDGVM2 model (Scheiter et al., 2013) therefore offer completely new approaches to simulate changes in functional diversity, trait selection through environmental conditions, and competition for resources (water, light) that in such a way are not possible with classical PFT-based vegetation models.

See our response to the related general comment previously. Although a broad discussion of model construction principles is outside our scope here, we accept the point and have modified our statements accordingly.

p. 7122, Fig. 2: Change “boardleaf” to “broadleaf in figure caption.

Done.

What are the grey background points? The GDD0 vs. α combinations of all the 10 km grid pixels in China?

Presumably this comment refers to Fig. 2? We have amended the caption to point out that the grey points are, indeed, all of the grid cells across China.

p. 7123, Fig. 3: Change “boardleaf” to “broadleaf” in figure caption

Done.

p. 7124, Fig. 4: Change “boardleaf” to “broadleaf” in figure caption

Done.

Supplementary Material: Please also change “boardleaf” to “broadleaf” in figure captions where applicable.

Done.

Anonymous referee #3

This article provides an impressive dataset and very insightful analysis of the modulation of plant functional traits within and between functional groups according to environmental conditions broadly related to moisture availability and temperature. Although several studies on this subject exist, few can provide such a large, uniformly measured dataset together with high quality environmental data. The analysis is aimed at disentangling the effects of adaptive trait shifts within functional types (PFT) versus PFT replacement along environmental gradients on trait variability. This question is extremely relevant not only to improve our understanding of functional trait modulation in general but also due to the (still) frequent and arguably problematic use of the PFT concept in dynamic vegetation models.

Specific comments

The paper is very well written and generally easy to follow. Apart from some minor points, which are outlined in "technical corrections", I have only three **main points of critique**.

Firstly, the relative lack of discussion of the issues related to the use of plant functional groups, such as inferring functional similarity in groups where trait syndromes vary widely and **functional group membership may be dependent on**

environmental conditions (e,g. species generally known as growing in tree form growing in shrub-like forms in harsher environments). Although this is addressed to some extent, e.g. on page 7096, I think such a fundamental issue should be highlighted even more. This is particularly important since the conclusions seem to point towards the authors interpreting their study as being supportive of the PFT concept, when their results could easily be interpreted otherwise.

This is a good point. The revised Discussion draws attention to this further limitation of the PFT concept.

Related to this, **I miss references to species-specific, or at least genus specific trait differences**. Again, this is briefly mentioned in the discussion but without providing any data or analyses. Although repeating the analyses performed on species rather than functional group level might change the scope of this work too much, at least giving an indication to the degree of within as opposed to between species functional variability in their data would add a lot to the paper.

As this referee notes, consideration of trait differences between taxa, as opposed to PFTs, would require different analyses and change the scope of the paper in a major way. Our goal in this MS was to compare variation within and between PFTs (basically a modelling construct), rather than addressing the separate question of trait plasticity within species. But this question is relevant to modelling too; so we have added a little more Discussion material on it.

Secondly, the argumentation for using GDD0 instead of e.g. the Principle Component scores of axes one or MAT, which has a higher loading than GDD0 on the first axis, is insufficient. There are good reasons for using GDD0 but the authors should clarify these.

We have added a sentence explaining why we use GDD_0. *The main argument in favour of* GDD_0 *as opposed to MAT is that in climates with cold winters, such as in northern China, large spatial variations in MAT can be induced by conditions in midwinter that do not relate to conditions during the time when growth occurs.*

Also, since a lot of traits are highly dependent on soil nutrient status and other environmental conditions, which have not been measured in this study, their likely effect should at least be mentioned.

This is now mentioned in the Discussion, as a potential field for investigation which we have not attempted.

Finally, unless I have overlooked this, no statistical tests of differences between the linear model regression fits have been performed. The authors talk about "significant differences" (e.g.pp. 7104 line 16) but it is not clear how significance can be inferred without such tests.

See our response to the same point as made by referee #2. Indeed, all statements made in the original manuscript had been carefully checked for significance using a conservative ($P < 0.01$) *criterion. We hope that this is now abundantly clear in the revised MS.*

Technical corrections

Pp. 7099 - line 11: clarify what you did in case of the very small leaves at the driest sites.

Done (also requested by referee #2).

Pp. 7099 - line 15: how many leaves were scanned?

We have included this information now.

Pp. 7100 - line 14: the results of the country-wide PCA should be provided in the appendix.

Done (also recommended by referee #1).

Pp. 7101 - line 1: clarify how you divided the variables into bins - how did you decide on the size of the bins?

This is now briefly described.

Pp. 7101 - line 6: GLM should be GZLM to avoid confusion between General linear models (GLM) and the Generalized linear models (GZLM) used here.

We disagree. GLM is a very widely accepted abbreviation for generalized linear models; whereas we have never encountered "GZLM". Given the context, we believe there should be no confusion.

Pp. 7105 - line 25: please provide references to the "previous studies".

Done (also requested by referee #2).

Figure 1: if possible, please choose another colour scheme to cater for red-green blindness, it would be very useful if you could code the plot symbols according to region

Done.

Please check your spelling of "broadleaf" in the figure captions.

Corrected.

It would be useful to include a table with the number of species per site to give the reader an idea of differences in the geographic spread of the species you measured and whether the PFTs within certain regions are represented by many or few species.

This information is already in Table S1. We have also provided summary statistics in the revised text.

Editor

Please provide a revised manuscript according to your answers to the reviewer queries. When doing so, please add a short statement wrt to the reviewer #1 query on the relevance of fluorescence vs Vcmax/Amax to the paper.

Done. As a response to reviewer #1 query on the relevance of fluorescence vs Vcmax/Amax*, we have added some discussion on quantifying* V_{cmax}*-environment relationships for DGVMs in the last second paragraph.*

Changes in the manuscript

We have made some changes in the manuscript as indicated in the above response.
Those changes are clearly illustrated by the marked-up manuscript as following.

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 *versus* 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., 2007; Scheiter and Higgins, 2009) and vegetation feedbacks to climate (Alton et al., 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 & 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 proportional 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) 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 ≥ 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 several days and then oven-drying at 75°C for 48 hours. Leaf C was measured by the potassium dichromate volumetry method (e.g. Slepetiene et al., 2008) and leaf N by the microkjeldahl method (e.g. Bremner, 1960). Leaf P was analyzed 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 of precipitation seasonality and timing (defined as in Prentice et al., 2011) were calculated for each site. 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 growing season (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 digitized from Shi et al. (2004).

Principal components analysis was performed on standardized 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.

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 linearize 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, *versus* 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 minimize 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 & 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 & 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 summarized 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 *versus* 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 summarized 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. Fig. 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 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.

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 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., 2014a) because of the high transpirational cost of keeping stomata open under conditions of high atmospheric aridity (vapour pressure deficit). Increased photosynthetic 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., 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.

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., 2005). 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., 2014b). 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 faclitate community-level adaptation to environmental change. In effect, current DGVMs largely ignore the potential stabilizing 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 capitalize on the growing body of quantitative plant trait data sets based on comprehensive floristic sampling in different environments.

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Figures

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.

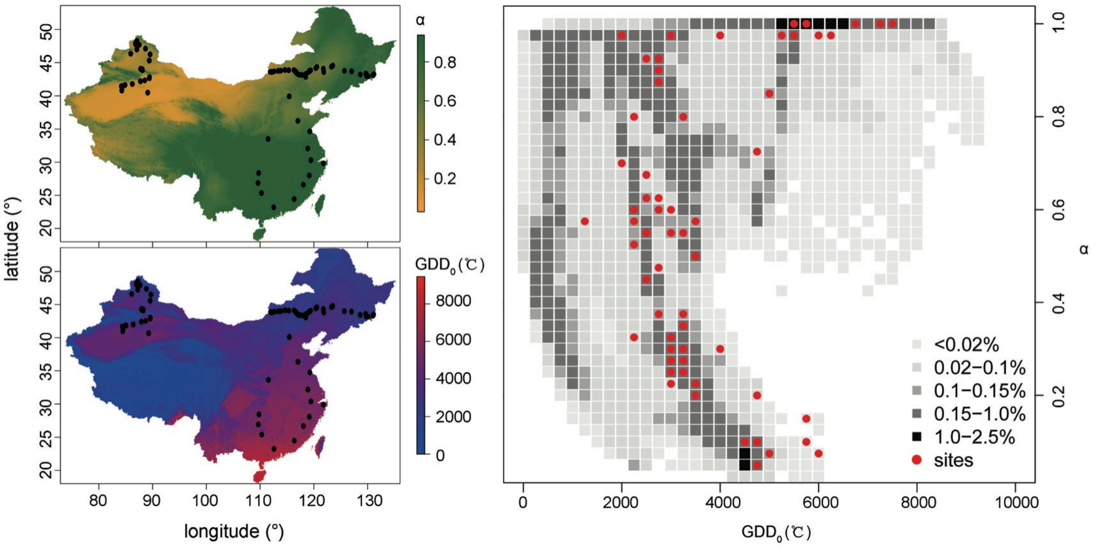


Figure 2: Optima and tolerances of PFTs in climate space, based on data from the sampling sites. The grey dots represent the climates of all grid cells in China.

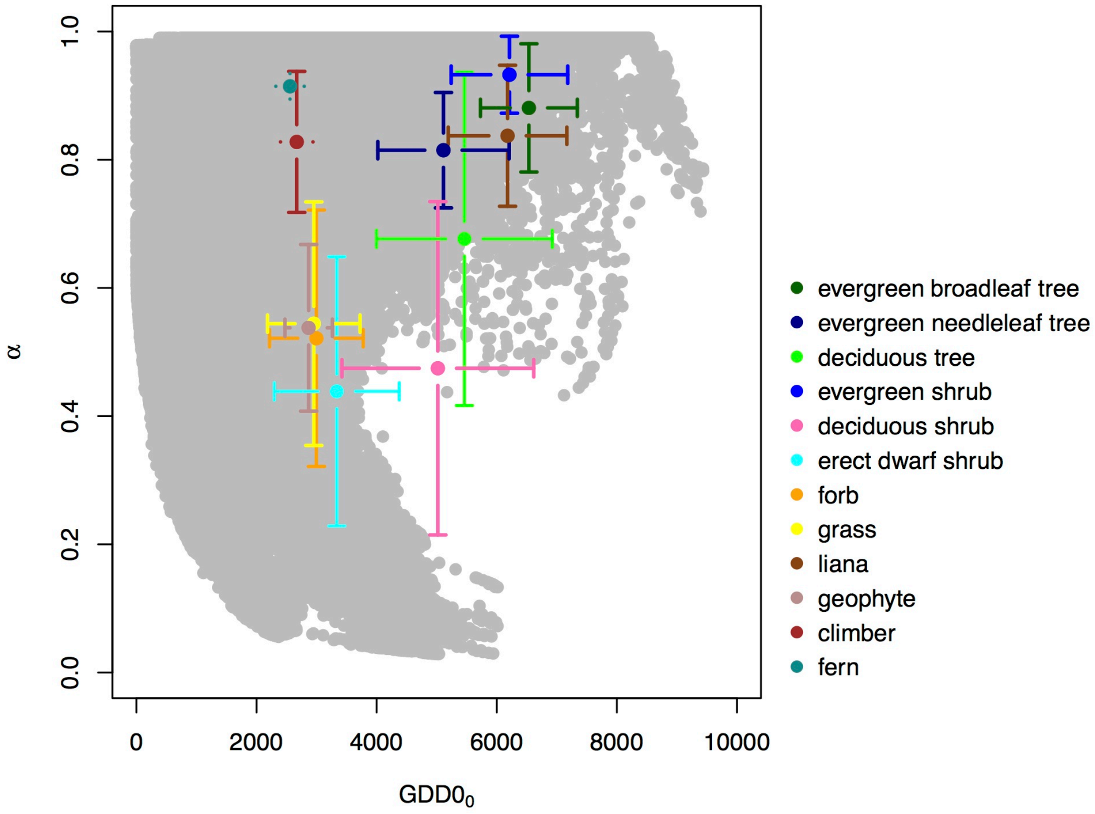


Figure 3: Partial residual plots for the relationships between leaf traits and the Cramer-Prentice moisture index (α), from the GLM analysis summarized in Table 2. Each point denotes a species-site combination; PFTs are indicated by colours. Only significant regression slopes (P < 0.01) are shown.

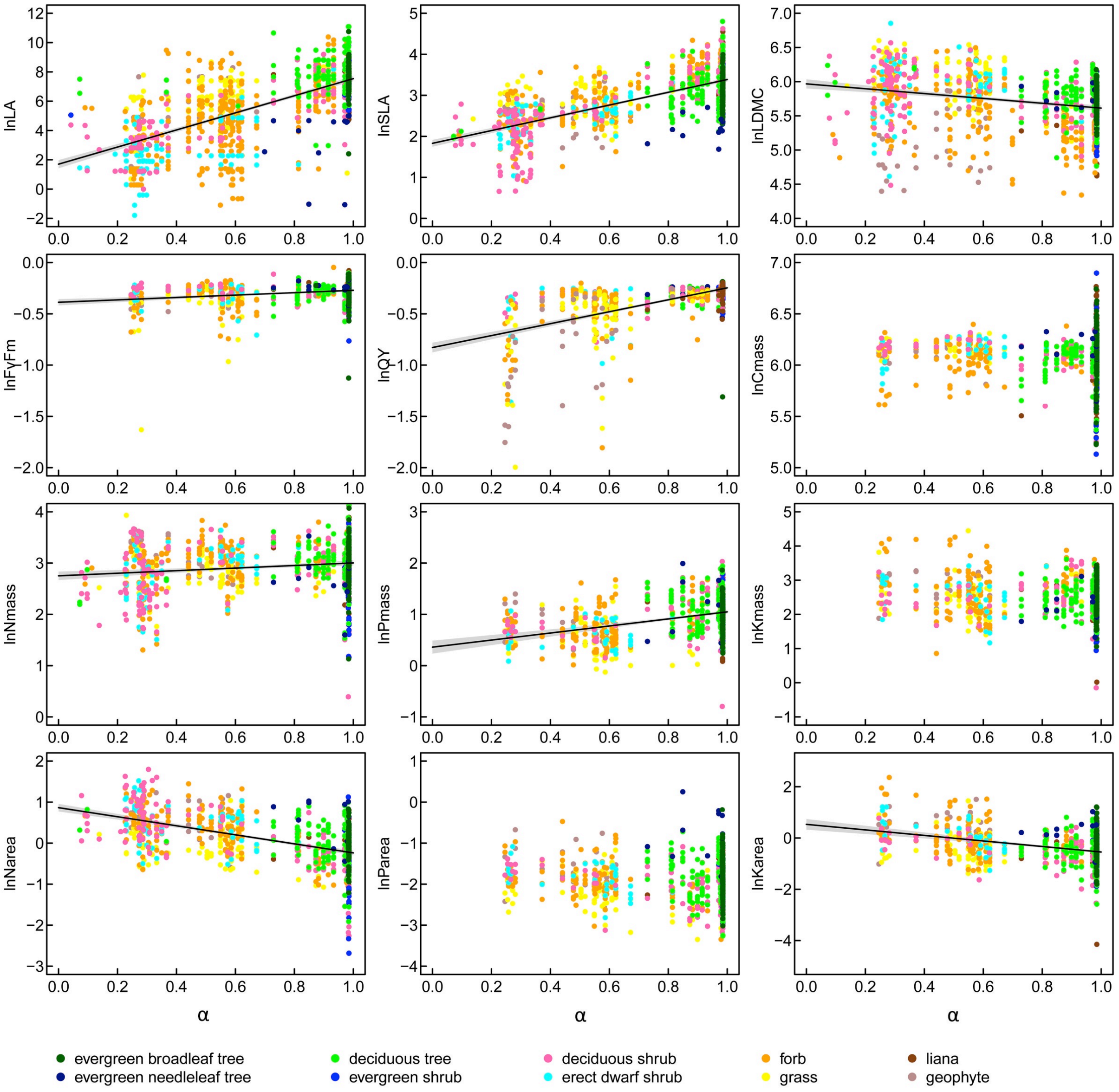


Figure 4: Partial residual plots for the relationships between leaf traits and growing degree days (GDD_0), from the GLM analysis summarized in Table 2. Each point denotes a species-site combination; PFTs are indicated by colours. Only significant regression slopes ($P < 0.01$) are shown.

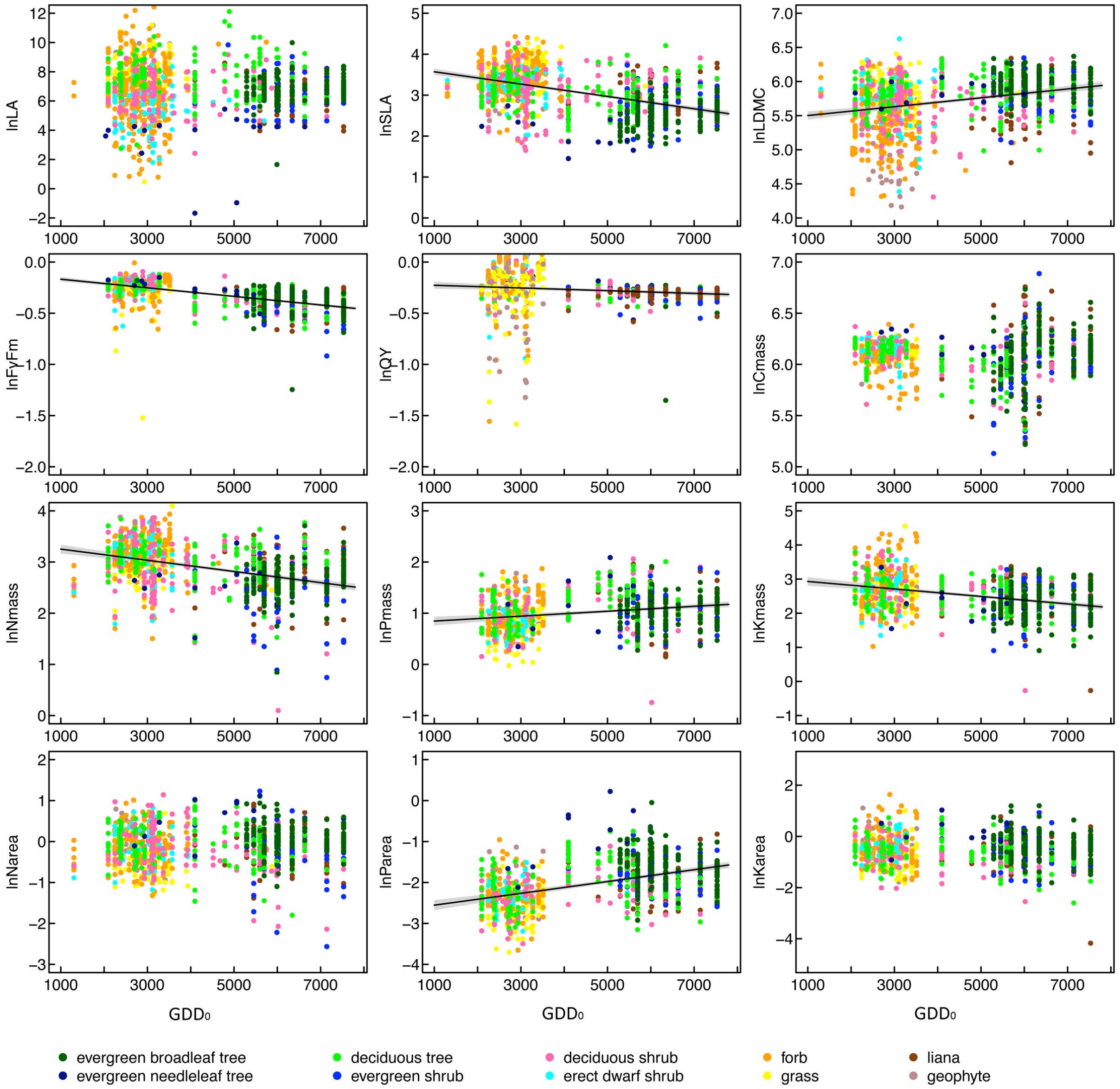
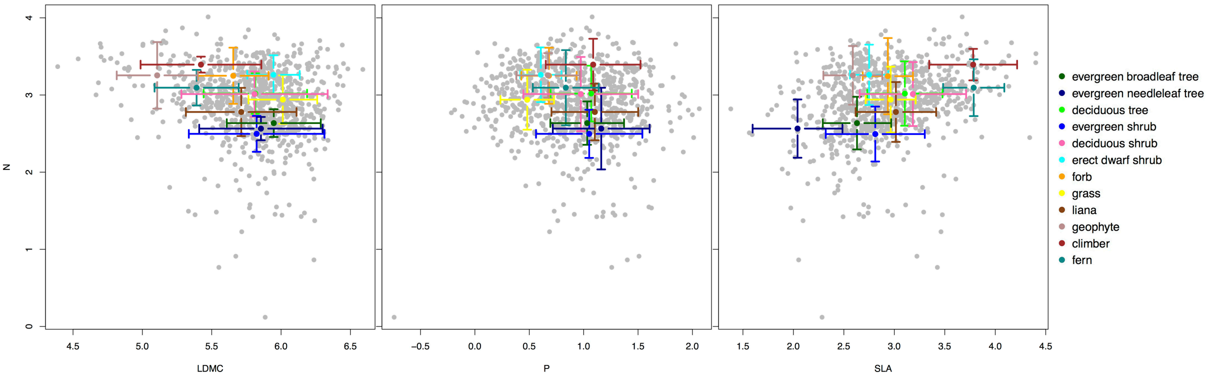


Figure 5: Illustrative plots showing means and standard deviations of trait values within PFTs for ln N_{area} combined with LDMC, ln P_{area} and SLA.



Tables

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%

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

	intercept		alpha		GDD0	
	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

Table 3: Variation (%) in traits accounted for by climate 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*