New
Phytologist

Plant evolutionary history mainly explains the variance in biomass responses to climate warming at a global scale

Junjiong Shao[1,2], Tengfei Yuan[1], Zhen Li[1], Nan Li[1], Huiying Liu[1,2], Shahla Hosseini Bai[3], Jianyang Xia[1,2], Meng Lu[4] and Xuhui Zhou[1,2,5]

[1]State Key Laboratory of Estuarine and Coastal Research, Tiantong National Field Observation Station for Forest Ecosystem, School of Ecological and Environmental Sciences, East China Normal University, Shanghai 200241, China; [2]Center for Global Change and Ecological Forecasting, East China Normal University, Shanghai 200241, China; [3]Faculty of Science, Health, Education and Engineering, University of the Sunshine Coast, Maroochydore, DC, Qld 4558, Australia; [4]Smithsonian Environmental Research Center, Edgewater, MD 21037, USA; [5]Shanghai Institute of Pollution Control and Ecological Security, 1515 North Zhongshan Rd, Shanghai 200437, China

Author for correspondence:
Xuhui Zhou
Tel: +86 21 54341275
Email: xhzhou@des.ecnu.edu.cn

Received: *29 October 2018*
Accepted: *8 January 2019*

New Phytologist (2019) **222:** 1338–1351
doi: 10.1111/nph.15695

Key words: evolutionary history, global warming, intraspecific variation, leaf traits, phylogenetic relatedness, plant biomass, variance partitioning.

Summary

- Evolutionary history shapes the interspecific relatedness and intraspecific variation, which has a profound influence on plant functional traits and productivity. However, it is far from clear how the phylogenetic relatedness among species and intraspecific variation could contribute to the observed variance in plant biomass responses to climate warming.
- We compiled a dataset with 284 species from warming experiments to explore the relative importance of phylogenetic, intraspecific, experimental and ecological factors to warming effects on plant biomass, using phylogenetic eigenvector regression and variance decomposition.
- Our results showed that phylogenetic relatedness could account for about half the total variance in biomass responses to warming, which were correlated with leaf economic traits at the family level but not at species level. The intraspecific variation contributed to approximately one-third of the variance, whereas the experimental design and ecological characteristics only explained 7–17%.
- These results suggest that intrinsic factors (evolutionary history) play more important roles than extrinsic factors (experimental treatment and environment) in determining the responses of plant biomass to warming at the global scale. This highlights the urgent need for land surface models to include evolutionary aspects in predicting ecosystem functions under climate change.

Introduction

Projections of Earth system models suggest a positive feedback loop between the ecosystem carbon (C) cycle and global warming caused by the increasing anthropogenic CO_2 emissions (Jones *et al.*, 2013). This feedback might be attenuated by enhanced C sequestration from the climate-induced increase in plant biomass. Plant biomass not only provides food and wood and supports biodiversity, but it is also a primary driver of other ecosystem processes such as production and decomposition. Plant biomass responses to global warming are thus extremely critical to maintaining ecosystem functions and sustaining human welfare in the context of climate change (Jenkins, 2015; Lohbeck *et al.*, 2015). Although hundreds of manipulative experiments world-wide have been carried out to examine the responses of plant biomass to global warming, the results are largely divergent (Lin *et al.*, 2010; Way & Oren, 2010; Gornish & Prather, 2014). For example, the biomass of prickly sida (*Sida spinosa*) increased 40-fold when the growth temperature was elevated from 23 to 36°C (Tungate *et al.*, 2007), whereas a 15-fold decrease was detected in perennial ryegrass (*Lolium perenne*) when the temperature was elevated from 7 to 33°C (Hunt & Halligan, 1981). Identifying the sources of this large variation may provide insights into reducing model uncertainty and thus deepen our understanding of ecosystem functioning under future climate change.

Considerable efforts have been undertaken to assess the extent to which experimental and ecological factors would affect responses of plant biomass to warming (e.g. Lin *et al.*, 2010; Way & Oren, 2010). However, few studies have examined the importance of plant evolutionary history (e.g. interspecific relatedness and intraspecific variation) in biomass responses to climate warming. Global meta-analyses concluded that mean annual temperature (MAT) and precipitation, warming magnitude, experimental duration, nitrogen (N) addition and plant functional type (PFT) all regulated biomass responses (Lin *et al.*, 2010; Way & Oren, 2010), but the relative importance of these factors had not been quantified. Based on a dataset of 38 species, Gornish & Prather (2014) suggested that leaf traits (e.g. leaf longevity, N concentration and photosynthetic capacity) could explain 21–46% of the total variance, leaving the majority of variance to be resolved.

The unresolved variance may result partly from the phylogenetic relatedness among species. At the community level, phylogenetic diversity represents the net amount of genetic changes in a group of species and could be a significant driver of ecosystem functioning (Cadotte, 2015). At the species level, phylogenetic niche conservatism (PNC) drives closely related species to share similar ecological and biological attributes in a suite of traits related to plant morphology, phenology, leaf economics, water conduction and nutrient utilization (Crisp & Cook, 2012; Davies *et al.*, 2013; Liu *et al.*, 2015). The importance of these plant traits to C sequestration and biomass accumulation has been widely recognized (Bonan *et al.*, 2012; Reich, 2014; Galmés *et al.*, 2015). However, no studies have investigated to what extent phylogenetic relatedness would explain the observed variance in the responses of plant biomass to warming, at either the local or the global scale.

Intraspecific variation, which arises from genetic diversity and phenotypic plasticity (Violle *et al.*, 2012; Moran *et al.*, 2016), might be another factor in affecting plant biomass responses to global warming. A recent synthesis quantified the variation of intraspecific traits as 25% of the total trait variation within communities and 32% among communities (Siefert *et al.*, 2015). By conducting manipulative experiments (Lepš *et al.*, 2011; Jung *et al.*, 2014; Malyshev *et al.*, 2015) and synthesizing multiple experimental results (de Dios *et al.*, 2016), intraspecific variations have been shown to regulate plant responses to environmental changes such as warming, elevated CO_2, drought, nutrient enrichment and grazing. In the global warming experiments, strong intraspecific responses were found among genotypes or ecotypes for photosynthesis, growth and biomass in trees, herbs and crops, suggesting differential tolerances or sensitivities to global warming (Gesch *et al.*, 2003; Bauerle *et al.*, 2007; Glaubitz *et al.*, 2014). However, intraspecific variation is usually neglected in examining the broad-scale patterns of plant responses to climate change, irrespective of the fact that it is an important component of biodiversity and functional diversity (Hulshof *et al.*, 2013; Siefert *et al.*, 2015; Moran *et al.*, 2016).

In this study, we compiled a dataset of warming experiments consisting of 1765 entries with 284 species. Based on the dataset, we primarily aimed to quantify the relative contribution of phylogenetic relatedness among species (indicated by the phylogenetic information, i.e. the species relatedness expressed by a phylogenetic tree), intraspecific variation, experimental design and ecological characteristics to the total variance in responses of plant biomass to warming. We also partitioned the biomass responses into phylogenetic, intraspecific, experimental and ecological components and explored the patterns and drivers of each component to further develop a comprehensive understanding of the variation of plant biomass response to global warming.

Materials and Methods

Data source and preprocessing

The data used in this study were extracted from peer-reviewed papers published before October 2016 (Supporting Information Notes S1), which were searched for in the Web of Science (www.webofknowledge.com) and China National Knowledge Infrastructure (www.cnki.net) in relation to the English and Chinese literature, respectively. The keywords included experimental warming ('warming', 'elevated temperature', 'temperature raising', 'temperature increase', 'increasing temperature' or 'temperature regime') and biomass ('biomass', 'growth', 'production' or 'productivity'). We searched for the three terms – 'growth', 'production' and 'productivity' – for biomass, as many studies have used plant biomass as the indicator of plant growth or productivity, especially in grasslands and croplands. Although these studies focused on growth or productivity, their measurements of biomass met our requirements. Only studies meeting the following criteria were selected: the study species were terrestrial plants; the study included two or more temperature regimes, and the altered temperature regime was achieved by warming rather than cooling (for experiments that had more than two temperature regimes, the one closest to the natural growth temperature was regarded as the control, and all higher temperature regimes were considered as treatments); and the recorded variables included at least one of the following variables: total biomass, root biomass, shoot biomass, stem biomass or leaf biomass. For those studies reporting multiyear results, only the values from the last year were extracted.

The compiled dataset consisted of 1765 entries from 284 species, which were from 185 genera and 63 families in bryophytes, gymnosperms, monocots and eudicots (Fig. S1; Tables S1, S2). As some experiments were conducted on communities and some on individuals or populations, we separated the dataset into Dataset Com (for species grown in communities) and Dataset Ind (for species grown individually or in populations). This separation was necessary because for plants in a community, interspecific competition may regulate biomass responses to warming.

The magnitude of biomass responses to warming was quantified by the natural logarithm of the response ratio ($\log_e RR$) (Hedges *et al.*, 1999):

$$\log_e RR = \log_e \left(\frac{X_t}{X_c} \right) \quad \text{Eqn 1}$$

where X_t and X_c are the biomass of the treatment and control groups, respectively. If there was no report on total biomass, the $\log_e RR$ of biomass in different plant organs (i.e. root, shoot, stem and leaf biomass) was converted to that of total biomass via the linear relationships between them across the whole dataset. The best fit was used to convert in the order of the r^2 of regression models: shoot biomass ($r^2 = 0.92$), followed by leaf ($r^2 = 0.91$), stem ($r^2 = 0.87$) and root ($r^2 = 0.86$) biomass (Fig. S2). As these linear models had high r^2 values, the conversion would not significantly influence the subsequent results. $\text{Log}_e RR$ can be translated to a percentage change in biomass by using $[\exp(\log_e RR) - 1] \times 100\%$.

To investigate the relationships between phylogenetic components and leaf traits, we collected the leaf traits data from TRY datasets (www.try-db.org) for each species. The relevant variables included specific leaf area (SLA), leaf dry mass content (LDMC), leaf C concentration based on mass (leafC_{mass}) and area (leafC_{area}), leaf N concentration based on mass (leafN_{mass}) and area (leafN_{area}), leaf C : N ratio, leaf longevity (LL), and maximum carboxylation rate at 25°C based on mass ($V_{cmax,mass}$) and area ($V_{cmax,area}$). Each species-specific leaf trait was calculated as the average value across the TRY dataset for each species. We applied this approach rather than using distinct leaf traits from warming experiments for two reasons. First, our purpose was to relate the phylogenetic components to species-specific leaf traits. However, the values of leaf traits from warming experiments could have large intraspecific variation, which could bias the results. The average values across numerous observations could reduce the influence of intraspecific variation and derive more robust results. Second, only few warming experiments reported these leaf traits. Therefore, the TRY dataset was appropriate and feasible for our study. TRY provides the most complete dataset for leaf traits around the world. Although it is not possible to completely eliminate the uncertainty from intraspecific variation, we might be able to ignore the effects because a previous global synthesis indicated that the leaf traits were relatively unchanged compared with the variation in plant size (Price *et al.*, 2014).

Partitioning the total variance

The total variance in biomass responses to experimental warming ($\log_e$RR) was partitioned into phylogenetic, intraspecific, experimental and ecological categories. The main challenge was to disentangle the phylogenetic effects from other ones. Many methods had been proposed to account for the phylogenetic effects, such as phylogenetic signals (Münkemüller *et al.*, 2012), phylogenetic independent contrasts (Ackerly, 2009), phylogenetic generalized least-squares model (Revell, 2010), phylogenetic mixed model (Housworth *et al.*, 2004) and phylogenetic eigenvector maps (Guénard *et al.*, 2013). These methods relied on the underlying evolutionary models such as Brownian motion and Ornstein–Uhlenbeck models. However, as the evolutionary processes might be more complicated than the model assumption (Castiglione *et al.*, 2018; Revell *et al.*, 2018), these methods could underestimate the contribution of phylogenetic effects (Cadotte *et al.*, 2017). For that reason, we applied a purely data-driven variance partitioning approach, the phylogenetic eigenvector regression (PVR; Diniz-Filho *et al.*, 1998; Desdevises *et al.*, 2003), to partition the total variance in biomass responses. PVR was based on multiple linear regression models with the explanatory variables being both phylogenetic and nonphylogenetic ones (experimental and ecological in this study). This method has the potential to extract as many phylogenetic effects as possible. Specifically, the phylogenetic variables were species scores along eigenvectors. These eigenvectors were derived from phylogenetic distance matrix by applying principal coordinate analysis. The distance matrix was calculated from the phylogenetic tree of the 284 species being studied (Desdevises *et al.*, 2003). The phylogenetic tree was extracted from a global phylogenetic tree with 31 749 plant species using the online software PHYLOMATIC v.3 (phylodiversity.net/phylomatic; Zanne *et al.*, 2014). The original phylogenetic tree was based on seven gene regions (18S rDNA, 26S rDNA, ITS, *matK*, *rbcL*, *atpB* and *trnL-F*), available in GenBank (www.ncbi.nlm.nih.gov/genbank). The experimental variables included experimental type (field or pot), environmental type (natural or control), warming facility (glasshouse, open-top chamber, electric cable, infrared reflector, or infrared radiator), experimental duration (in $\log_{10}$(d)), warming magnitude (ΔT, in °C), water treatment (drought, ambient or irrigation), CO_2 treatment (ambient or CO_2 enrichment), N treatment (low than ambient, ambient or higher than ambient) and O_3 treatment (ambient or O_3 exposure; not included in the models for Dataset Com because of insufficient data). The ecological variables included MAT, mean annual precipitation (MAP), PFT (moss, forb, graminoid, deciduous shrub, evergreen shrub, deciduous needleleaf tree, evergreen needleleaf tree, deciduous broadleaf tree, or evergreen broadleaf tree) and photosynthetic pathway (C_3 or C_4).

The original PVR method only contained two categories of the phylogenetic and nonphylogenetic variables (Diniz-Filho *et al.*, 1998; Desdevises *et al.*, 2003). However, as we have three classes of variables (phylogenetic, experimental, and ecological), a modified version of PVR was applied. Basically, seven linear regression models ($2^3 - 1$) containing each class of variable and their combinations were fitted and the corresponding r^2 was used as the measure of explanatory power for each model. Based on the seven values of r^2, the individual and joint contributions of each class of variables and their combinations could be calculated (see detailed descriptions in Methods S1). For models with experimental variables (models D and DE; Methods S1), ΔT^2 was considered as an explanatory variable to account for the nonlinear effects of warming magnitude. Interactions of ΔT (and ΔT^2) with experimental and ecological variables were also included to examine the potential interactive effects. Model selection technique based on Akaike information criterion (Burnham & Anderson, 2002) was applied to obtain the most parsimonious models when necessary (Methods S1).

The relative contribution of intraspecific variation was quantified on the basis of the residuals (RES_{DEP}) of model PDE (the PVR model with all the three classes of variables as explanatory variables; Methods S1). A linear regression model (model S) was conducted with the response variable being RES_{DEP} and the explanatory variable being the species identities (i.e. species names). The relative importance of intraspecific variation was $(1 - r^2_{\mathrm{PDE}})(1 - r^2_{\mathrm{S}})$, where $1 - r^2_{\mathrm{PDE}}$ and $1 - r^2_{\mathrm{S}}$ are the proportions of variance unexplained by models PDE and S, respectively.

Phylogenetic component analysis

The effect size of phylogenetic relatedness on biomass responses to experimental warming was expressed as the predictive values of model P (PVR model with the explanatory variables only including the phylogenetic ones; Methods S1), which was referred to as the phylogenetic component in this study. The magnitude of the divergence and the relative contribution to tree-wide variation in the phylogenetic component were calculated at each node in the phylogenetic tree (Moles *et al.*, 2005). The size of the divergence was represented as the standard deviation of the phylogenetic component across daughter clades of the focal node. The contribution of each node to tree-wide variation (relative contribution index, CI) is the product of the variation in the focal clade that is directly attributable to the focal divergence and the amount of tree-wide trait variation that is attributable to terminal taxa within the focal clade (Moles *et al.*, 2005; Swenson & Enquist, 2007). We also calculated the average CI for each phylogenetic group at levels from family to phylum to examine whether any particular groups made large contributions to total variation. We applied this approach to discover the importance of phylogenetic information, rather than directly comparing the phylogenetic components among different phylogenetic groups for three reasons. First, the data among species were not independent, which could create difficulties in testing significant differences. Second, we could not expect systematic trends among different phylogenetic groups because the evolutionary processes might be random. Third, even for the situation where there is a systematic trend in the phylogenetic tree, the evolutionary rate could vary in different clades. Therefore, a detailed investigation of the relative contribution of each split in a phylogenetic tree to the total variance in biomass responses should be better than comparisons among phylogenetic groups.

Relationships between phylogenetic components and leaf traits were examined at the species, family and order/class levels to elucidate the potential importance of phylogenetic conservatism. The leaf traits at the family level were averaged from those at the species level, and the leaf traits at the order level were averaged from those at the family level. As the averages based on small samples might not be as reliable as those based on large ones, the relationship at the family and order/class levels was quantified by weighted linear regression, with the numbers of species and families being the weights. The results based on the weighted linear regression showed significant relationships between the phylogenetic components and SLA, LDMC, leafC_{area}, leafN_{area} and LL at the family level in Dataset Ind. To elucidate the interrelated influences among these variables, path analysis was applied (Shipley, 2004). The potential path model included the causal effects of SLA on LDMC, leafC_{area}, leafN_{area}, LL and the phylogenetic components; the causal effects of LDMC, leafC_{area} and leafN_{area} on LL; the causal effects of LDMC, leafC_{area}, leafN_{area} and LL on the phylogenetic components; and the covariance between any two of LDMC, leafC_{area} and leafN_{area}. As there were missing data for leaf traits, a pairwise correlation matrix was used as the input data for the path model. The maximum likelihood estimator was applied to parameterize the path model (Beaujean, 2014). The χ^2 test was conducted to obtain an acceptable model. If the corresponding P-value of the model was < 0.05, the most nonsignificant path was deleted and the model was re-parameterized. This procedure was repeated until the P-value was > 0.05.

Intraspecific component analysis

The effect size of intraspecific variation on biomass responses to experimental warming was expressed as the residuals of model S, which was referred to as the intraspecific component. The standard deviation of intraspecific components within each species was regarded as the magnitude of intraspecific variation for the corresponding species. This measure of intraspecific variation represented a greater extent of genetic diversity rather than phenotypic plasticity, because the impacts of experimental and ecological factors were precluded. Differences in intraspecific variation at different phylogenetic levels and among PFTs were examined using the Kruskall–Wallis test. Model DE (PVR model with the explanatory variables including both experimental and ecological ones; Methods S1) was applied to each species with > 10 entries to investigate the relative contributions of genetic diversity and phenotypic plasticity at the species level. The distribution characteristics of intraspecific variations were explored by fitting four probability density functions (PDFs) with parameters ≤ 2 (i.e. the power-law, log-normal, exponential and Weibull distributions) against the data.

The power law distribution has a PDF of:

$$p(x) = \frac{\alpha - 1}{x_{\min}} \left(\frac{x}{x_{\min}} \right)^{-\alpha} \qquad \text{Eqn 2}$$

where $\alpha > 1$, and $x_{\min} > 0$.

The PDF of log-normal distribution is:

$$p(x) = \frac{1}{\sqrt{2\pi}\sigma x} e^{-\frac{(\log x - \mu)^2}{2\sigma^2}}. \qquad \text{Eqn 3}$$

The PDF of exponential distribution is:

$$p(x) = \lambda e^{-\lambda x} \qquad \text{Eqn 4}$$

The PDF of Weibull distribution is:

$$p(x) = \frac{a}{b} \left(\frac{x}{b} \right)^{a-1} e^{-\left(\frac{x}{b}\right)^{a}}. \qquad \text{Eqn 5}$$

Note that the PDF of exponential distribution has one parameter and those of other distributions have two parameters.

Experimental and ecological components

The effect sizes of experimental design and ecological characteristics were expressed as the predictive values of models D and E (PVR models with the explanatory variables being only the experimental and ecological ones, respectively; Methods S1), which were referred to as the experimental and ecological components, respectively. The relative contribution of each experimental and ecological variable was further separated by variance partitioning based on model DE. Lindeman–Merenda–Gold values, which provided a decomposition of the explained variance (Bi & Chung, 2011), were used as the relative importance of each variable (Lindeman *et al.*, 1980; Murray & Conner, 2009). In multiple regression models, the sequential r^2 (proportion of type I sum of squares (SS) to total SS) depends on the order of the regressors (i.e. the explanatory variables in the regression model). The Lindeman–Merenda–Gold value of a regressor is the mean sequential r^2 obtained by averaging over all possible orderings. However, in model DE, the numbers of regressors were large (21 and 11 for Dataset Ind and Dataset Com, respectively) and thus the numbers of potential arrangements were also huge (5×10^{19} and 4×10^{7}, respectively), making the regression practically impossible. Therefore, it was necessary to modify the procedure.

The regressors in model DE were first classified into three categories: the experimental variables, the ecological variables and the interactions. In regression analysis, the interactive effects should always be considered after the main effects, so there were only two possible orders for the regressors entering model: experimental variables, ecological variables, and their interactions; or ecological variables, experimental variables, and their interactions. Within each category, the regressors could fully change their orders. The SS accounted for by each variable was averaged across the corresponding type I SS from all the potential models. For interactive terms, the SS was equally partitioned into the relevant variables. Finally, the relative contribution of a variable was the percentage contributed by its SS to the total SS of the category to which it belonged.

Results

Relative importance of phylogenetic information, intraspecific variation, experimental design and ecological characteristics

Warming largely changed the plant biomass, with effects ranging from a 93% reduction to a 44-fold increase in Dataset Ind (for species grown individually or in populations), and from a 97% reduction to a 28-fold increase in Dataset Com (for species grown in communities). The relative contributions of phylogenetic information (an index for phylogenetic relatedness), intraspecific variation, experimental design and ecological characteristics to the total variance in biomass responses to warming were similar between Dataset Ind and Dataset Com (Fig. 1). In both datasets, phylogenetic information accounted for the largest proportion of the total variance (56.29% and 42.69%, respectively), followed by intraspecific variation (30.62% and 39.43%), experimental design (16.51% and 9.05%) and ecological characteristics (14.5% and 6.52%), leaving a small part of variance unexplained (4.98% and 11.21%). The joint contributions of phylogenetic information and experimental design were 12.66% and 8.54%, whereas those of phylogenetic information and ecological characteristics were 12.33% and 9.20% in Dataset Ind and Dataset Com, respectively (Fig. 1). Compared with experimental design and ecological characteristics, the contributions of phylogenetic information alone to the total variance were also the largest: 29.97% and 28.17% for Dataset Ind and Dataset Com, respectively (Fig. 1). Note that we used phylogenetic, intraspecific, experimental and ecological components to represent the effect sizes of the four classes of factors on biomass responses to warming (log$_e$RR (TB), where TB represents the total biomass). The results showed that the phylogenetic and intraspecific components were more closely correlated with log$_e$RR(TB) and their slopes were nearer to 1 than those of the experimental and ecological components in both Dataset Ind and Dataset Com (Fig. S3).

Phylogenetic components and their relationships to leaf traits

The phylogenetic components varied extensively along the phylogenetic tree (−64% to +1841% and −94% to + 805% in Dataset Ind and Dataset Com, respectively; Fig. S4) but changed in a more restricted manner among families (Fig. S5). As the phylogenetic component was not independent among species, the relative contribution to tree-wide variation (CI) was a more appropriate index for determining the importance of each split in the phylogenetic tree. In Dataset Ind, the splits between the bryophytes and seed-bearing plants (CI = 0.1293) and between Gymnospermae and Angiospermae (CI = 0.0804) had the largest contributions (Fig. 2a; Table S3). However, in Dataset Com, the most important splits were found at finer scales (Fig. 2b; Table S4). The CI was not correlated with the time of divergence in either dataset (Tables S3, S4).

The mean CI of species was also calculated from family to phylum levels (Tables S5, S7). At the family level, variations within Fabaceae (mean CI = 0.0092), Pinaceae (mean CI = 0.0064), Myrtaceae (mean CI = 0.0042) and Poaceae (mean CI = 0.0023) were highly important in Dataset Ind, whereas only that within Fabaceae (mean CI = 0.0112) was important in Dataset Com

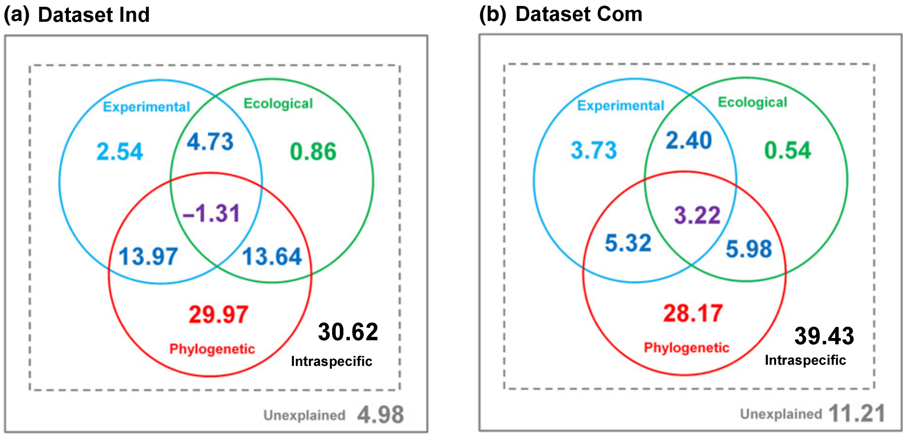

Fig. 1 Relative contributions (%) to total variance in biomass responses to experimental warming (log$_e$(response ratio)). The four classes of factors were phylogenetic information, intraspecific variation, environmental design and ecological characteristics. (a) Dataset Ind, for species grown individually or in populations; (b) Dataset Com, for species grown in communities.

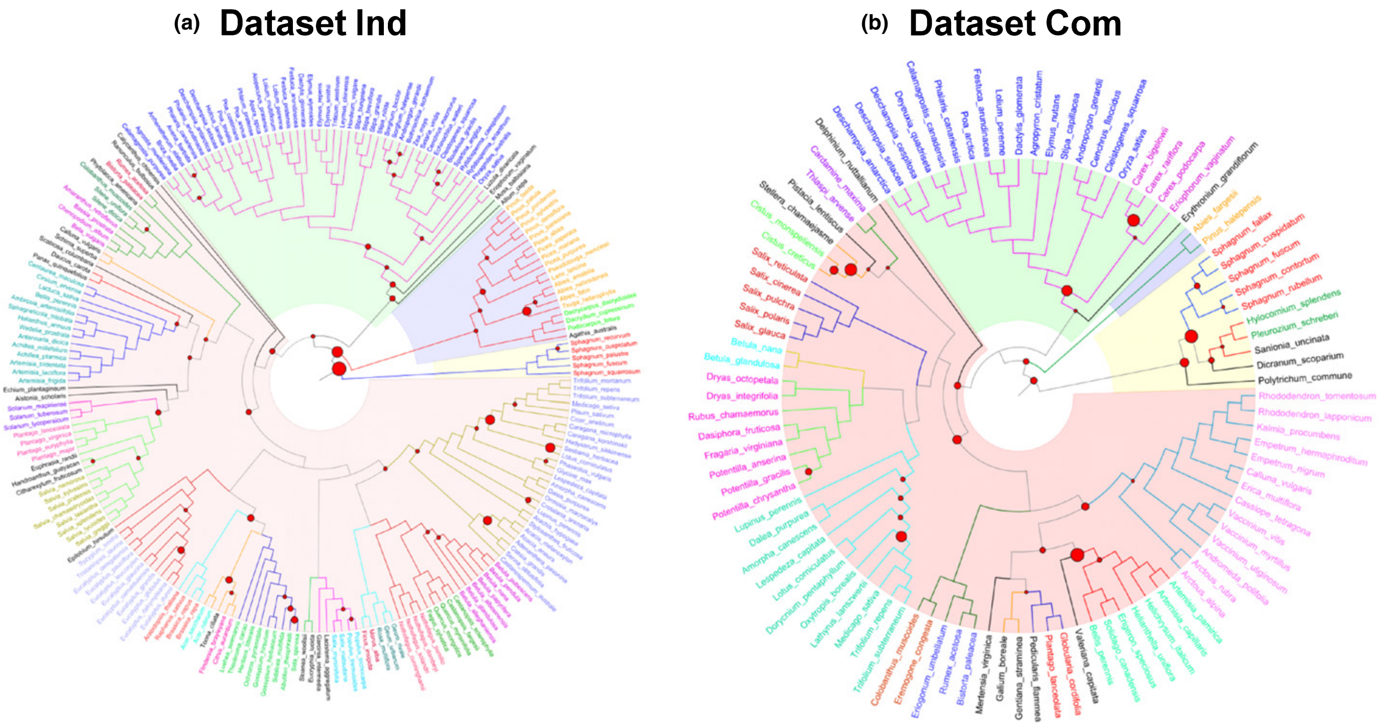

Fig. 2 The relative contribution of each divergence node to tree-wide variation in the phylogenetic component. The phylogenetic component indicated the biomass response that could be attributed to phylogenetic relatedness. The relative contribution index (CI) is indicated by the size of the red circle. The exact CI value of the most important divergences can be found in Supporting Information Tables S3 and S4. (a) Dataset Ind, for species grown individually or in populations; (b) Dataset Com, for species grown in communities.

(Table S5). The results at the order level were basically consistent with those at the family level, but highlighted the importance of Poales (mean CI = 0.0082) in Dataset Com (Table S6). At the broader scale, bryophytes had a much larger mean CI with a lower sample size than did gymnosperms, monocots and eudicots (Table S7).

To examine the potential influence of PNC in leaf traits on biomass responses to warming, the relationships between phylogenetic components and leaf traits were examined at different phylogenetic levels and among PFTs (Table S8; Figs S6–S13). However, strong relationships between phylogenetic components and leaf traits were only found in Dataset Ind at the family level (Figs 3, S14). The family-averaged phylogenetic component in Dataset Ind was significantly correlated with SLA ($r^2 = 0.19$, $P < 0.01$), LDMC ($r^2 = 0.35$, $P < 0.01$), leafC$_{\text{area}}$ ($r^2 = 0.25$, $P < 0.01$), leafN$_{\text{area}}$ ($r^2 = 0.13$, $P < 0.05$), leaf C : N ratio ($r^2 = 0.13$, $P = 0.05$), and LL ($r^2 = 0.31$, $P < 0.05$; Fig. 3a–f). The results of path analysis showed that LDMC and LL had direct effects on the phylogenetic components (standardized path coefficients, $\rho = 0.41$ and 0.37, respectively; $P < 0.05$), whereas SLA had indirect effects by regulating both LDMC and LL (Fig. 3g).

Intraspecific components and their distributions

The intraspecific component ranged from −92% to +1068% and from −89% to +460% in Dataset Ind and Dataset Com, respectively. The relative contribution of experimental and ecological factors to intraspecific variation varied dramatically from species to species, with no robust explanatory factor being identified (Fig. 4a–b). The results based on PVR models also showed that the intraspecific variation (here referred to the variation within the same species but could not be explained by experimental or ecological factors) did not show distinctive differences among different phylogenetic groups or plant growth forms (Figs S15–S18). However, as the frequency distributions of the intraspecific variation in both datasets exhibited right-skewed patterns (the occurrence of small values was more frequent than that of large values; Fig. 4c–d), four candidate PDFs were fitted to the observed intraspecific variation: the power-law, log-normal, exponential and Weibull distributions. The results showed that only the Weibull function fitted observed distributions well (Fig. 4e–f).

Relative importance of experimental and ecological factors

The experimental components ranged from −47% to +284% and from −40% to +180% in Dataset Ind and Dataset Com, respectively, whereas the ecological components ranged from −25% to +225% and from −38% to +50%. Among the experimental factors, warming magnitude (ΔT) and environmental type (natural or control) were the two most important. The importance of ΔT arose mainly from the interactions with other factors, whereas environmental type was independent of the other factors (Fig. 5a–b). Among the ecological factors, PFT and thermal niche (indicated by the MAT) were the two most important

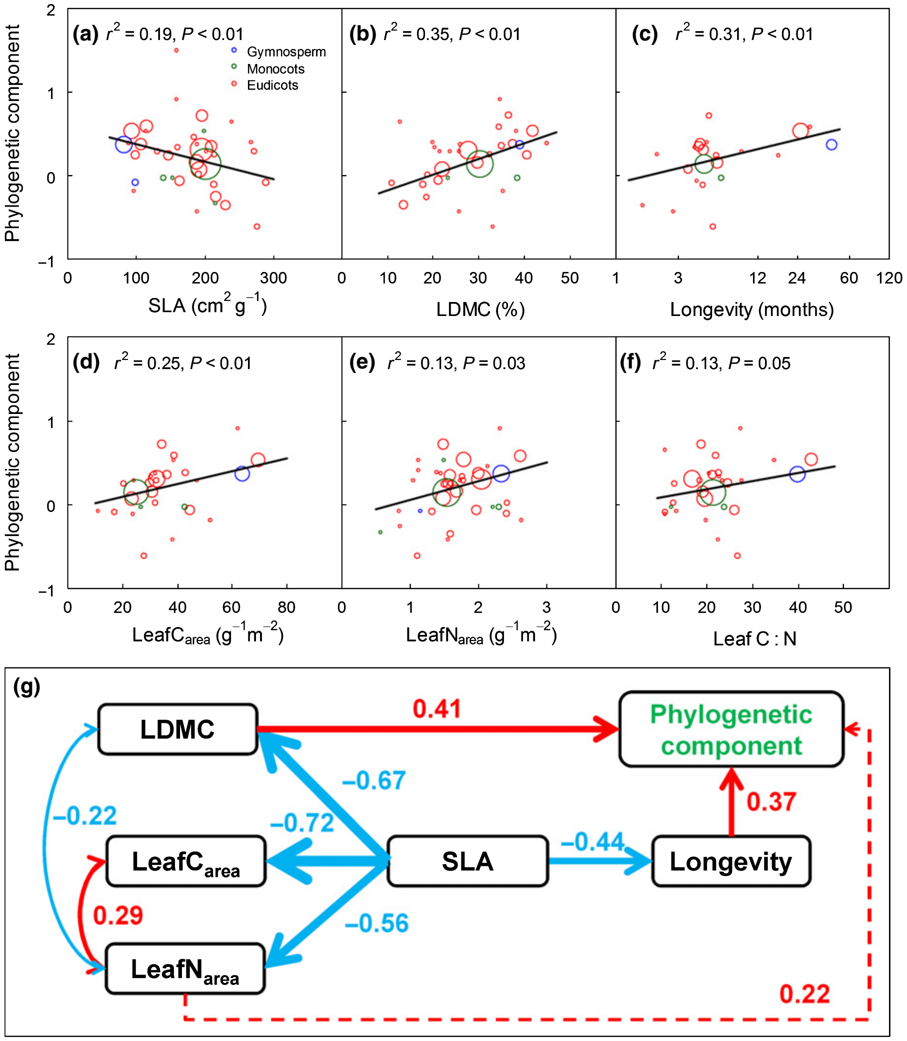

Fig. 3 Relationships between the phylogenetic components and leaf traits at the family level for Dataset Ind (for species grown individually or in populations). The phylogenetic component indicated the biomass response that could be attributed to phylogenetic relatedness. The regression lines in (a)–(f) are from weighted linear regression, with the weights being the number of species (indicated by the size of the open circles) in a certain family. The result in (g) is from path analysis, with $n = 43$, $\chi^2 = 9.345$, df = 6, $P = 0.155$, CFI (comparative fit index) = 0.974, $r^2 = 0.51$ (for the phylogenetic component). Single arrows show the casual effects; double arrows indicate the covarying variables. Solid and dashed arrows are the significant and nonsignificant effects, respectively. The standardized path coefficient (ρ) is shown beside the arrows. LDMC, leaf dry mass content; leafC$_{area}$, leaf C concentration based on area; leafN$_{area}$, leaf N concentration based on area; SLA, specific leaf area; longevity, leaf life span (log-transformed).

factors, with their importance mainly coming from the main effects (Fig. 5c–d).

In Dataset Ind, the biomass responses to warming first increased with ΔT and then decreased, exhibiting parabolic patterns despite a series of covariates (experimental type, environmental type, PFT, MAT, photosynthetic pathway, and MAP; Fig. 6a–f). However, this pattern was not obvious in Dataset Com (Fig. S19). In addition, significant main effects were also found for water treatment, ozone treatment and experimental duration in Dataset Ind (Fig. 6g–i), and for experimental and environmental types, N treatment and PFT in Dataset Com (Fig. S19c–f).

Discussion

Importance of phylogenetic niche conservatism

The differences in plant biomass responses to global warming among PFTs, experimental conditions and taxonomic groups (i.e. seed vs spore plants) have been well documented (Lin *et al.*, 2010; Way & Oren, 2010). However, plant evolutionary history (i.e. interspecific and intraspecific relatedness) received less attention in explaining the variance in biomass responses to warming at a global scale. Among the four explanatory factors (phylogenetic information, intraspecific variation, experimental design and ecological characteristics), phylogenetic information (an index for phylogenetic relatedness) was the most important, accounting for half the total variance in biomass responses to warming (Fig. 1). The importance of phylogenetic relatedness largely stemmed from the tendency of closely related species to have more similar traits compared with more distant relatives, which was referred to as PNC (Wiens *et al.*, 2010; Crisp & Cook, 2012). Previous studies suggested the strong PNC of leaf economic spectrum (LES) traits (Liu *et al.*, 2015), which played a critical role in carbon sequestration (Wright *et al.*, 2004). Therefore, these traits may mediate the phylogenetic patterns in biomass responses to warming. However, our results showed that LES trait-mediated PNC was not prevalent at the species level, except for those in the Fabaceae family (i.e. legumes). LES traits were shaped not only by evolutionary relatedness but also by local adaptation to utilize resources (Wright *et al.*, 2004). The strong selection pressure induced by these resources could introduce variation that is independent of phylogenetic relatedness, thus weakening the relationship between traits and the phylogenetic

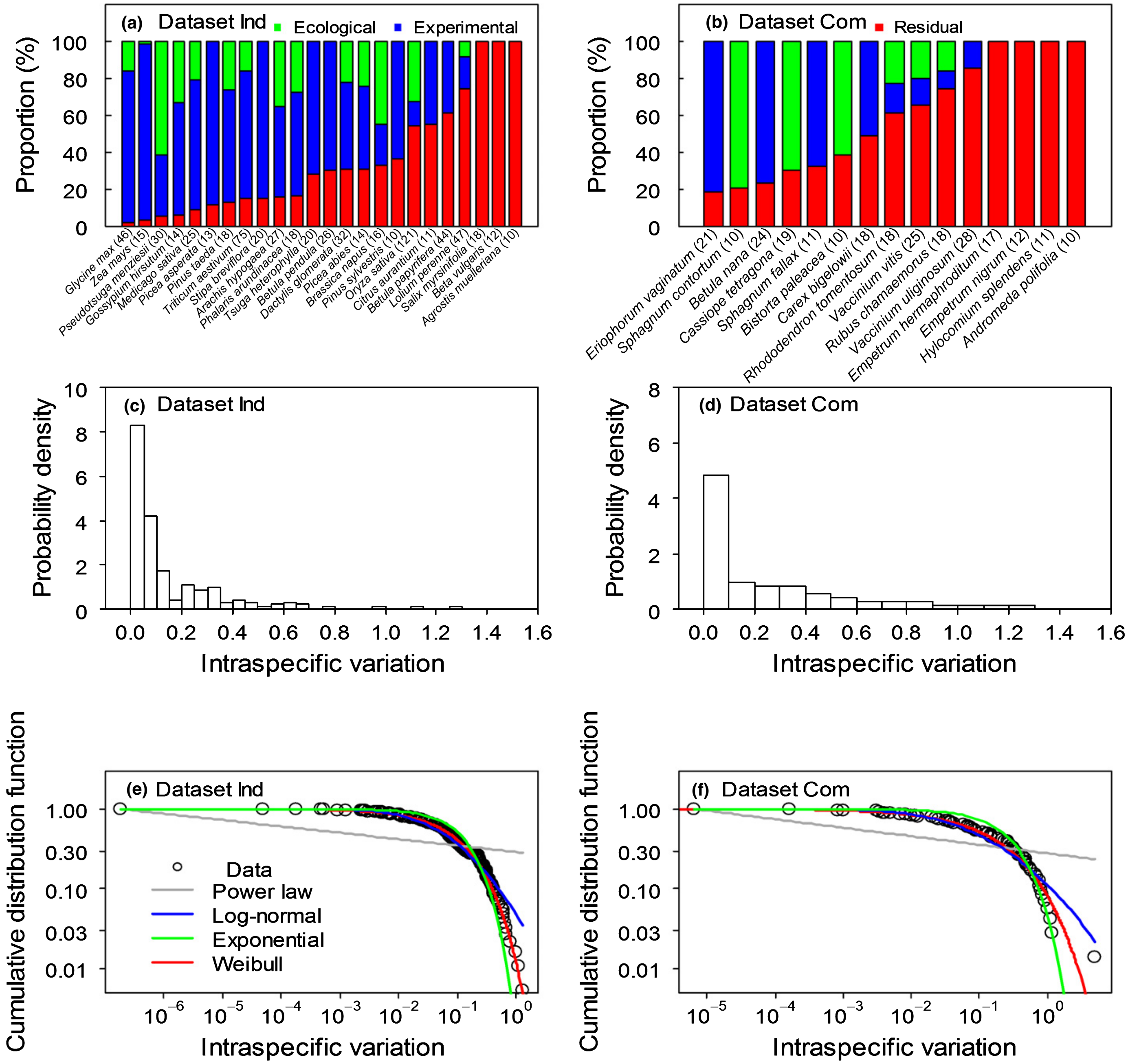

Fig. 4 The intraspecific variation of biomass response to experimental warming for Dataset Ind (for species grown individually or in populations) (a, c, e) and Dataset Com (for species grown individually or in populations) (b, d, f). (a, b) Relative contribution of ecological characteristics (green bars) and experimental designs (blue bars) to intraspecific variation in species with a sample size larger than 10. The residuals (red bars) contain all the information that could not be explained by ecological and environmental factors, thus largely indicating the intraspecific variation caused by genetic diversity; these also contain the effects of unconsidered factors or random errors. (c, d) Distribution of intraspecific variation (standard deviation of intraspecific component within species) derived using the phylogenetic eigenvector regression method. (e, f) The fit of the four probability density functions to the observed intraspecific variation. The *y*-axis indicates the cumulative distribution function across the corresponding *x*-value to the largest possible values.

component of biomass responses to warming. Within the Fabaceae family, specific leaf area (SLA) positively regulated the phylogenetic component (Fig. S7a), because nitrogen (N) fixation relieved the limitation of N on biomass accumulation (Adams *et al.*, 2016). As a result, the LES traits of Fabaceae species might largely mirror their evolutionary relatedness and were closely related to the phylogenetic components.

Contrary to the patterns at the species level, LES traits were strongly correlated with phylogenetic components at the family level in Dataset Ind (Fig. 3). According to the path analysis, LDMC and longevity had directly positive effects on the family-averaged phylogenetic components, whereas SLA exhibited an indirectly negative effect (Fig. 3g). This suggests that slower-growing plants may be more sensitive to global warming. By

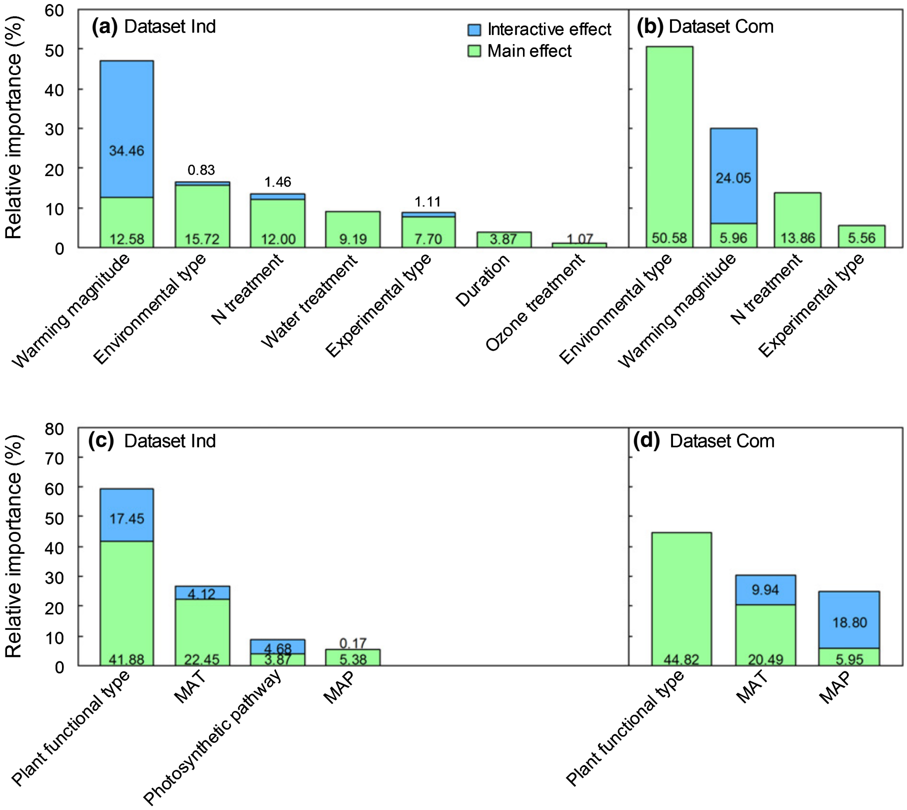

Fig. 5 Relative importance of experimental (a, b) and ecological factors (c, d). The values were relative to the variance explained by experimental and ecological components, respectively for Dataset Ind (for species grown individually or in populations) (a, c) and Dataset Com (for species grown in communities) (b, d). The interactive effect for warming magnitude indicates the interactions between warming magnitude and other factors, whereas that for other factors indicates their interactions with the warming magnitude. MAT, mean annual temperature; MAP, mean annual precipitation.

contrast, Gornish & Prather (2014) showed that the biomass responses were negatively correlated with leaf longevity and positively with photosynthetic capacity across 38 species, suggesting that faster-growing species had greater thermal sensitivity. The contradictory results may imply the importance of plant evolutionary history in explaining biomass responses to warming, as the latter did not consider evolutionary aspects. Thus, the apparent significant correlations between leaf traits and biomass responses to warming at the species level in Gornish & Prather (2014) could be primarily caused by ecological or experimental factors rather than evolutionary ones. Moreover, with decreasing MAT across large local and global regions, the leaf longevity of needleleaf and evergreen trees increased and SLA decreased (Wright *et al.*, 2004; van Ommen Kloeke *et al.*, 2012; Reich, 2014; Rosbakh *et al.*, 2015). The results indicated that, at least for these PFTs, slower-growing species tended to exhibit high sensitivity to global warming. This is because plants with a colder thermal niche might respond more strongly to global warming on a large scale (Way & Oren, 2010).

At a broader level, the early divergence among bryophytes, gymnosperms and angiosperms accounted for 21% of the total variance in Dataset Ind (Fig. 2a; Table S3). The higher warming sensitivity of biomass in spore (bryophytes) than in seed-bearing plants (gymnosperms and angiosperms; Fig. S5) was the reverse of Lin *et al.*'s (2010) results. In the latter, the suppressed bryophyte biomass caused by climate warming in natural ecosystems could be a result of the competition among species (Lin *et al.*, 210), as compared with our results with no competition. The divergence between gymnosperm and angiosperm species about 350 million yr ago (Table S3) triggered the increase in angiosperm leaf vein density, which enhanced leaf hydraulic efficiency and dramatically increased the photosynthetic capacity (Crisp & Cook, 2012). Angiosperms were also found to have thinner roots with higher specific root length and smaller root diameter and tissue density (Liese *et al.*, 2017). Thinner roots were associated with ectomycorrhizal fungi which were more efficient in acquiring nutrients than were arbuscular mycorrhizal fungi (Chen *et al.*, 2016). A recent study on root organization of 369 plant species suggested that thinner roots might reflect the general evolutionary trend of root life strategies from conservatism to opportunism, and from dependence on mycorrhizal fungi to independence (Ma *et al.*, 2018). These advantages with thinner roots could increase the plant's efficiency to absorb water and nutrients (Chen *et al.*, 2013), and shape the different responses of biomass to warming between gymnosperms and angiosperms. However, in general, the divergence age could not predict the magnitude of the phylogenetic components well (Tables S3, S4), indicating that the evolutionary rate might vary among different clades (Revell *et al.*, 2018).

Stochastic feature of intraspecific variation

Intraspecific variation was the second most important contributor to warming effects on biomass (30–40%; Fig. 1). The significance of intraspecific variation has also been highlighted for species' geographic distribution (Garzón *et al.*, 2011), species' coexistence (Lichstein *et al.*, 2007), and ecosystem responses to extreme events (Messier *et al.*, 2010; Shi *et al.*, 2013; Malyshev

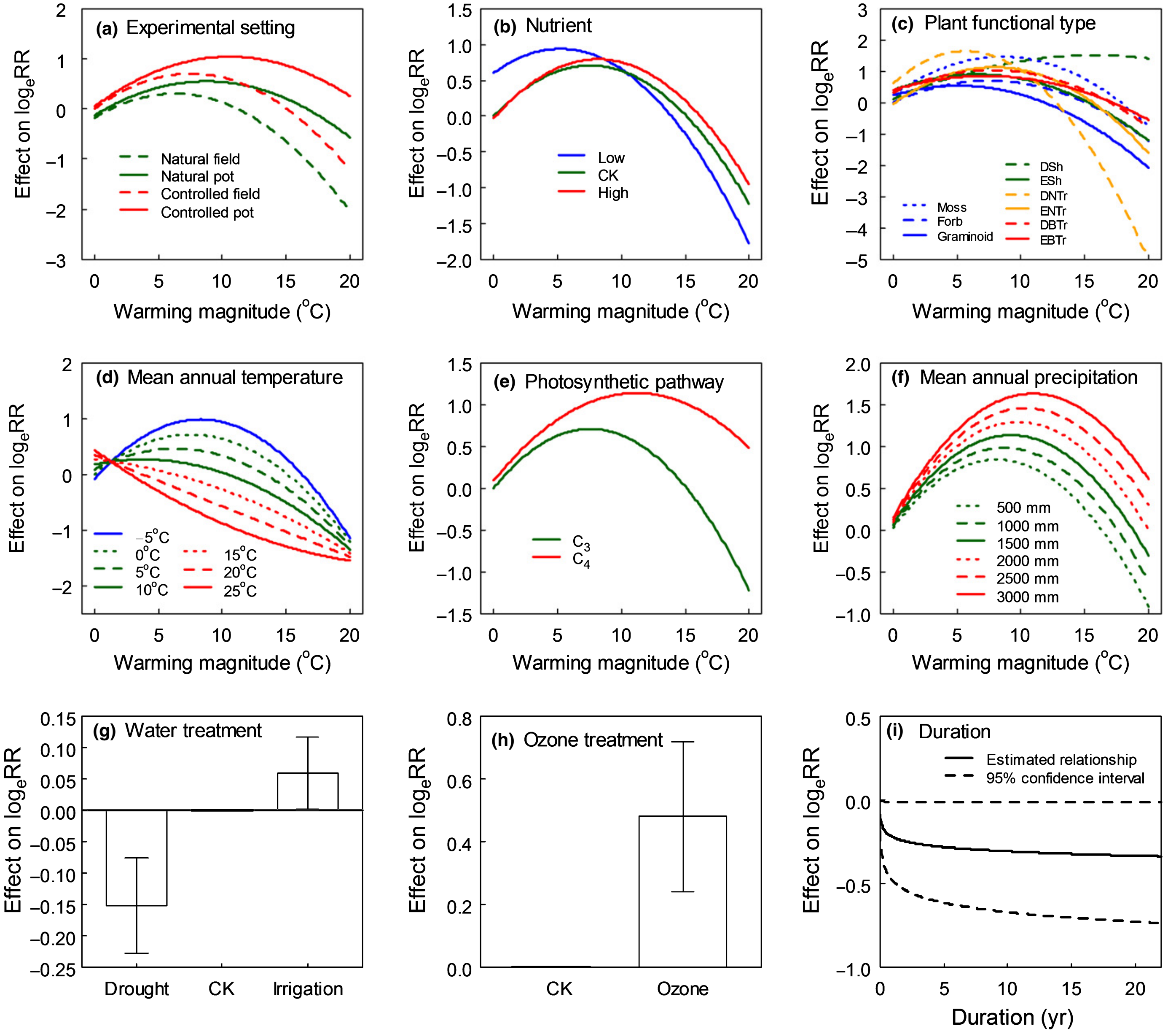

Fig. 6 Effects of warming magnitude and other experimental or ecological factors on the biomass response to warming. If a certain factor has a significant interaction with warming magnitude, the response of the function lines of $\log_e$(response ratio) ($\log_e$RR) to warming magnitude (ΔT) are shown for different groups (a–f); otherwise, the main effect relative to the control condition is presented (g–i). Error bars in panels (g) and (h) are the 95% confidence intervals. DSh, deciduous shrub; ESh, evergreen shrub; DNTr, deciduous needleleaf tree; ENTr, evergreen needleleaf tree; DBTr, deciduous broadleaf tree; EBTr, evergreen broadleaf tree; CK, control.

et al., 2015). However, consistent with previous studies, the relative contribution of genetic diversity and phenotypic plasticity varied dramatically from species to species (Fig. 4a–b), and no explicit drivers could be identified at the levels of family, order, class/phylum or PFTs (Figs S13–S16; Moran *et al.*, 2016).

Theoretically, crops and species with larger geographic distributions may exhibit larger intraspecific variation because of more diverse selection pressures (Martin *et al.*, 2017) and stronger local adaptation (Münzbergová *et al.*, 2017). However, these expectations could not be tested in our datasets, because most of the global warming experiments were not designed to capture the intraspecific variation but rather to examine the average response of a species. Indeed, some common-garden experiments were carried out with multiple genotypes or ecotypes, especially for crops, but few of them were able to fully examine the potential intraspecific variation (Gesch *et al.*, 2003; Shi *et al.*, 2013; Glaubitz *et al.*, 2014). For example, there are at least > 40 000 varieties of rice (*Oryza sativa*) worldwide (Brown, 2008), but the most extensive warming experiments we found examined only 36 varieties (Zhang *et al.*, 2013), covering only a very small proportion of the potential intraspecific variation.

Despite these difficulties, the pattern of intraspecific variation was well fitted by the Weibull PDF which had only two parameters (Fig. 4e–f). For poorly studied taxonomic groups, individual-based models constructed communities by using virtual (simulated) species (Mokany *et al.*, 2016). This approach was usually applied to validate theoretical models and predict biodiversity composition and ecosystem functioning (Mokany *et al.*, 2016). Therefore, incorporating the Weibull PDF into these models might provide insights into the potential influence of intraspecific variation on ecosystem functioning and the theoretical mechanisms behind these phenomena.

Implications for future experiments and model development

In this study, we underscored the importance of phylogenetic relatedness and intraspecific variation in plant biomass responses to climate change. The variation induced by phylogenetic relatedness was correlated with leaf traits at the family level, suggesting that the phylogenetic conservatism signals could be passed to the warming effects on plant biomass. PNC could be weakened under a warming climate if plants fail to adapt to the rapidly changing environment. Therefore, isolating the contribution of phylogenetic information from those of other factors will not only probe the importance of phylogenetic relatedness but also potentially provide deeper insights into the ecological roles of plant traits.

The importance of intraspecific variation to community dynamics and ecosystem functioning might challenge the conclusions drawn from average species traits (Violle *et al.*, 2012; Malyshev *et al.*, 2015). This is because the complicated nonlinear relationships could introduce large uncertainty into ecosystem models (Bolnick *et al.*, 2011; Moran *et al.*, 2016). Such uncertainties remained in this study because the magnitude of intraspecific variation could not be explained by any of the factors investigated. However, if the different magnitudes in intraspecific variation among species can be treated as a stochastic pattern, they could be adequately represented by the Weibull distribution in individual-based models.

Interspecific interactions should also be investigated because some inconsistent results were found between Dataset Ind and Dataset Com. However, it is difficult to disentangle the effects of interspecific interactions from those of other factors without well-designed experiments. A series of coordinated common-garden experiments are needed to elucidate the regulation mechanisms of each factor, as well as to separate the effects of phylogenetic conservatism and differential environments, and attribute the intraspecific variation to either genetic diversity or phenotypic plasticity.

This study, for the first time (to the best of our knowledge), has quantified the relative contribution of evolutionary history to the responses of plant biomass to global warming, using a purely data-driven approach. Our study suggests that intrinsic drivers (phylogenetic relatedness among species and intraspecific variation derived from evolutionary history) play more important roles than extrinsic drivers (experimental treatment and environment) in determining the responses of plant biomass to warming. In this regard, the changes in terrestrial ecosystem functions associated with global warming might be unrealistically represented by current ecosystem models (e.g. Bouskill *et al.*, 2014). Therefore, our study highlights the urgent need for global land surface models to include evolutionary aspects in simulating plant responses to climatic change, which requires further exploration of the combined and interactive effects of ecological and evolutionary factors on terrestrial ecosystems.

Acknowledgements

The authors thank the five anonymous reviewers for their insightful comments. This study was financially supported by the National Natural Science Foundation of China (grant no. 31770559, 31600387), the National Key R&D Program of China (2017YFA06046), and the 'Thousand Young Talents' Program in China. We would like to acknowledge the work carried out by the researchers whose published data were used for this meta-analysis.

Author contributions

JS and XZ conceived the study; JS, JX and ML compiled the dataset; JS analyzed the data; and JS, TY, ZL, NL, HL, SHB, JX, ML and XZ contributed to the writing.

ORCID

Shahla Hosseini Bai https://orcid.org/0000-0001-8646-6423
Meng Lu https://orcid.org/0000-0001-6923-7493
Jianyang Xia https://orcid.org/0000-0001-5923-6665
Xuhui Zhou https://orcid.org/0000-0002-2038-9901

References

Ackerly DD. 2009. Phylogenetic methods in ecology. In: Maccarrone M, Clarke A, Zheng Y, Tickle C, Kehrer-Sawatzki H, Cooper DN, Delves P, Candi E, Perkel DJ, Hetherington AM *et al.* eds. *Encyclopedia of Life Sciences*. Chichester, UK: John Wiley & Sons, 1–9. doi: 10.1002/9780470015902.a0021223.

Adams MA, Turnbull TL, Sprent JI, Buchmann N. 2016. Legumes are different: leaf nitrogen, photosynthesis, and water use efficiency. *Proceedings of the National Academy of Sciences, USA* **113**: 4098–4103.

Bauerle WL, Bowden JD, Wang GG. 2007. The influence of temperature on within-canopy acclimation and variation in leaf photosynthesis: spatial acclimation to microclimate gradients among climatically divergent *Acer rubrum* L. genotypes. *Journal of Experimental Botany* **58**: 3285–3298.

Beaujean AA. 2014. *Latent variable modeling using R: a step-by-step guide*. New York, NY, USA: Routledge.

Bi J, Chung J. 2011. Identification of overall liking – determination of relative importances of regressor variables: identification of drivers of overall liking. *Journal of Sensory Studies* **26**: 245–254.

Bolnick DI, Amarasekare P, Araújo MS, Bürger R, Levine JM, Novak M, Rudolf VHW, Schreiber SJ, Urban MC, Vasseur DA. 2011. Why intraspecific trait variation matters in community ecology. *Trends in Ecology and Evolution* **26**: 183–192.

Bonan GB, Oleson KW, Fisher RA, Lasslop G, Reichstein M. 2012. Reconciling leaf physiological traits and canopy flux data: use of the TRY and FLUXNET databases in the Community Land Model version 4. *Journal of Geophysical Research* **117**: G02026.

Bouskill NJ, Riley WJ, Tang JY. 2014. Meta-analysis of high-latitude nitrogen-addition and warming studies implies ecological mechanisms overlooked by land models. *Biogeosciences* **11**: 6969–6983.

Brown A. 2008. *Understanding food, principles and preparation.* Belmont, CA, USA: Thomson/Wadsworth Learning.

Burnham K, Anderson DR. 2002. *Model selection and multimodel inference: a practical information-theoretic approach.* New York, NY, USA: Springer.

Cadotte MW. 2015. Phylogenetic diversity-ecosystem function relationships are insensitive to phylogenetic edge lengths. *Functional Ecology* **29**: 718–723.

Cadotte MW, Davies TJ, Peres-Neo PR. 2017. Why phylogenies do not always predict ecological differences. *Ecological Monographs* **87**: 535–551.

Castiglione S, Tesone G, Piccolo M, Melchionna M, Mondanaro A, Serio C, Febbraro MD, Raia P. 2018. A new method for testing evolutionary rate variation and shifts in phenotypic evolution. *Methods in Ecology and Evolution* **9**: 974–983.

Chen W, Koide RT, Adams TS, DeForest JL, Cheng L, Eissenstat DM. 2016. Root morphology and mycorrhizal symbioses together shape nutrient foraging strategies of temperate trees. *Proceedings of the National Academy of Sciences, USA* **113**: 8741–8764.

Chen W, Zeng H, Eissenstat DM, Guo D. 2013. Variation of first-order root traits across climatic gradients and evolutionary trends in geological time. *Global Ecology and Biogeography* **22**: 846–856.

Crisp MD, Cook LG. 2012. Phylogenetic niche conservatism: what are the underlying evolutionary and ecological causes? *New Phytologist* **196**: 681–694.

Davies TJ, Wolkovich EM, Kraft NJB, Salamin N, Allen JM, Ault TR, Betancourt JL, Bolmgren K, Cleland EE, Cook BI *et al.* 2013. Phylogenetic conservatism in plant phenology. *Journal of Ecology* **101**: 1520–1530.

de Dios VR, Mereed TE, Ferrio JP, Tissue DT, Voltas J. 2016. Intraspecific variation in juvenile tree growth under elevated CO_2 alone and with O_3: a meta-analysis. *Tree Physiology* **36**: 682–693.

Desdevises Y, Legendre P, Azouzi L, Morand S. 2003. Quantifying phylogenetically structured environmental variation. *Evolution* **57**: 2647–2652.

Diniz-Filho JAF, de Sant'Ana CER, Bini LM. 1998. An eigenvector method for estimating phylogenetic inertia. *Evolution* **52**: 1247–1262.

Galmés J, Kapralov MV, Copolovici LO, Hermida-Carrera C, Niinemets Ü. 2015. Temperature responses of the Rubisco maximum carboxylase activity across domains of life: phylogenetic signals, trade-offs, and importance for carbon gain. *Photosynthesis Research* **123**: 183–201.

Garzón MB, Alía R, Robson TM, Zavala MA. 2011. Intra-specific variability and plasticity influence potential tree species distributions under climate change. *Global Ecology and Biogeography* **20**: 766–778.

Gesch RW, Kang I-H, Gallo-Meagher M, Vu JCV, Boote KJ, Allen LH, Bowes G. 2003. Rubisco expression in rice leaves is related to genotypic variation of photosynthesis under elevated growth CO_2 and temperature. *Plant, Cell & Environment* **26**: 1941–1950.

Glaubitz U, Li X, Köhl KI, van Dongen JT, Hincha DK, Zuther E. 2014. Differential physiological responses of different rice (*Oryza sativa*) cultivars to elevated night temperature during vegetative growth. *Functional Plant Biology* **41**: 437–448.

Gornish ES, Prather CM. 2014. Foliar functional traits that predict plant biomass response to warming. *Journal of Vegetation Science* **25**: 919–927.

Guénard G, Legendre P, Peres-Neto P. 2013. Phylogenetic eigenvector maps: a framework to model and predict species traits. *Methods in Ecology and Evolution* **4**: 1120–1131.

Hedges L, Gurevitch J, Curtis PS. 1999. The meta-analysis of response ratios in experimental ecology. *Ecology* **80**: 1150–1156.

Housworth EA, Martins EP, Lynch M. 2004. The phylogenetic mixed model. *The American Naturalist* **163**: 84–96.

Hulshof CM, Violle C, Spasojevic MJ, McGill B, Damschn E, Harrison S, Enquist BJ. 2013. Intra-specific and inter-specific variation in specific leaf area reveal the importance of abiotic and biotic drivers of species diversity across elevation and latitude. *Journal of Vegetation Science* **24**: 921–931.

Hunt WF, Halligan G. 1981. Growth and developmental responses of perennial ryegrass grown at constant temperature. I. Influence of light and temperature on growth and net assimilation. *Australian Journal of Plant Physiology* **8**: 181–190.

Jenkins DG. 2015. Estimating ecological production from biomass. *Ecosphere* **6**: 49.

Jones C, Robertson E, Arora V, Friedlingstein P, Shevliakova E, Bopp L, Brovkin V, Hajima T, Kato E, Kawamiya M *et al.* 2013. Twenty-first-century compatible CO_2 emissions and airborne fraction simulated by CMIP5 earth system models under four representative concentration pathways. *Journal of Climate* **26**: 4398–4413.

Jung V, Albert CH, Violle C, Kunstler G, Loucougaray G, Spiegelberger T. 2014. Intraspecific trait variability mediates the response of subalpine grassland communities to extreme drought events. *Journal of Ecology* **102**: 45–53.

Lepš J, de Bello F, Šmilauer P, Doležal J. 2011. Community trait response to environment: disentangling species turnover vs intraspecific trait variability effects. *Ecography* **34**: 856–863.

Lichstein JW, Dushoff J, Levin SA, Pacala SW. 2007. Intraspecific variation and species coexistence. *The American Naturalist* **170**: 807–818.

Liese R, Alings K, Meier IC. 2017. Root branching is a leading root trait of the plant economics spectrum in temperate trees. *Frontiers in Plant Science* **8**: 315.

Lin D, Xia J, Wan S. 2010. Climate warming and biomass accumulation of terrestrial plants: a meta-analysis. *New Phytologist* **188**: 187–198.

Lindeman RH, Merenda PF, Gold RZ. 1980. *Introduction to bivariate and multivariate analysis.* Glenview, IL, USA: Scott Foresman.

Liu H, Xu Q, He P, Santiago LS, Yang K, Ye Q. 2015. Strong phylogenetic signals and phylogenetic niche conservatism in ecophysiological traits across divergent lineages of Magnoliaceae. *Scientific Reports* **5**: 12246.

Lohbeck M, Poorter L, Martínez-Ramos M, Bongers F. 2015. Biomass is the main driver of changes in ecosystem process rates during tropical forest succession. *Ecology* **96**: 1242–1252.

Ma Z, Guo D, Xu X, Lu M, Bardgett RD, Eissenstat DM, McCormack ML, Hedin LO. 2018. Evolutionary history resolves global organization of root functional traits. *Nature* **555**: 94–97.

Malyshev AV, Arfin Khan MAS, Beierkuhnlein C, Steinbauer MJ, Henry HA, Jentsch A, Dengler J, Willner E, Kreyling J. 2015. Plant responses to climatic extremes: within-species variation equals among-species variation. *Global Change Biology* **22**: 449–464.

Martin AR, Rapidel B, Roupsard O, Van den Meersche K, de Melo Virginio Filho E, Barrios M, Isaac ME. 2017. Intraspecific trait variation across multiple scales: the leaf economics spectrum in coffee. *Functional Ecology* **31**: 604–612.

Messier J, McGill BJ, Lechowicz MJ. 2010. How do traits vary across ecological scales? A case for trait-based ecology. *Ecology Letters* **13**: 838–848.

Mokany K, Ferrier S, Connolly SR, Dunstan PK, Fulton EA, Harfoot MB, Harwood TD, Richardson AJ, Roxburgh SH, Scharlemann JPW *et al.* 2016. Integrating modelling of biodiversity composition and ecosystem function. *Oikos* **125**: 10–19.

Moles AT, Ackerly DD, Webb CO, Tweddle JC, Dickie JB, Westoby M. 2005. A brief history of seed size. *Science* **307**: 576–580.

Moran EV, Hartig F, Bell DM. 2016. Intraspecific trait variation across scales: implications for understanding global change responses. *Global Change Biology* **22**: 137–150.

Münkemüller T, Lavergne S, Bzeznik B, Dray S, Jombart T, Schiffers K, Thuiller W. 2012. How to measure and test phylogenetic signal. *Methods in Ecology and Evolution* **3**: 743–756.

Münzbergová Z, Hadincová V, Skálová H, Vandvik V. 2017. Genetic differentiation and plasticity interact along temperature and precipitation gradients to determine plant performance under climate change. *Journal of Ecology* **105**: 1358–1373.

Murray K, Conner MM. 2009. Methods to quantify variable importance: implications for the analysis of noisy ecological data. *Ecology* **90**: 348–355.

Price CA, Wright IJ, Ackerly DD, Niinemets Ü, Reich PB, Veneklaas EJ. 2014. Are leaf functional traits 'invariant' with plant size and what is 'invariance' anyway? *Functional Ecology* **28**: 1330–1343.

Reich PB. 2014. The world-wide "fast–slow" plant economics spectrum: a traits manifesto. *Journal of Ecology* **102**: 275–301.

Revell LJ. 2010. Phylogenetic signal and linear regression on species data. *Methods in Ecology and Evolution* **1**: 319–329.

Revell LJ, González-Valenzuela LE, Alfonso A, Castellanos-García LA, Guarnizo CE, Crawford AJ. 2018. Comparing evolutionary rates between trees, clades and traits. *Methods in Ecology and Evolution* **9**: 994–1005.

Rosbakh S, Römermann C, Poschlod P. 2015. Specific leaf area correlates with temperature: new evidence of trait variation at the population, species and community levels. *Alpine Botany* **125**: 79–86.

Shi W, Muthurajan R, Rahman H, Selvam J, Peng S, Zou Y, Jagadish KSV. 2013. Source–sink dynamics and proteomic reprogramming under elevated night temperature and their impact on rice yield and grain quality. *New Phytologist* **197**: 825–837.

Shipley B. 2004. *Cause and correlation in biology: a user's guide to path analysis, structural equations and causal inference.* Cambridge, UK: Cambridge University Press.

Siefert A, Violle C, Chalmandrier L, Albert CH, Taudiere A, Fajardo A, Aarssen LW, Baraloto C, Carlucci MB, Cianciaruso MV *et al.* 2015. A global meta-analysis of the relative extent of intraspecific trait variation in plant communities. *Ecology Letters* **18**: 1406–1419.

Swenson NG, Enquist BJ. 2007. Ecological and evolutionary determinants of a key plant functional trait: wood density and its community-wide variation across latitude and elevation. *American Journal of Botany* **94**: 451–459.

Tungate KD, Israel DW, Watson DM, Rufty TW. 2007. Potential changes in weed competitiveness in an agroecological system with elevated temperatures. *Environmental and Experimental Botany* **60**: 42–49.

van Ommen Kloeke AEE, Douma JC, Ordoñez JC, Reich PB, van Bodegom PM. 2012. Global quantification of contrasting leaf life span strategies for deciduous and evergreen species in response to environmental conditions. *Global Ecology and Biogeography* **21**: 224–235.

Violle C, Enquist BJ, McGill BJ, Jiang L, Albert CH, Hulshof C, Jung V, Messier J. 2012. The return of the variance: intraspecific variability in community ecology. *Trends in Ecology and Evolution* **27**: 244–252.

Way DA, Oren R. 2010. Differential responses to changes in growth temperature between trees from different functional groups and biomes: a review and synthesis of data. *Tree Physiology* **30**: 669–688.

Wiens JJ, Ackerly DD, Allen AP, Anacker BL, Buckley LB, Cornell HV, Damschen EI, Davies TJ, Grytnes J-A, Harrison SP *et al.* 2010. Niche conservatism as an emerging principle in ecology and conservation biology. *Ecology Letters* **13**: 1310–1324.

Wright IJ, Reich PB, Westoby M, Ackerly DD, Baruch Z, Bongers F, Cavender-Bares J, Chapin T, Cornelissen JHC, Diemer M. 2004. The worldwide leaf economics spectrum. *Nature* **428**: 821–827.

Zanne AE, Tank DC, Cornwell WK, Eastman JM, Smith SA, FitzJohn RG, McGlinn DJ, O'Meara BC, Moles AT, Reich PB *et al.* 2014. Three keys to the radiation of angiosperms into freezing environments. *Nature* **506**: 89–92.

Zhang Y, Tang Q, Peng S, Zou Y, Chen S, Shi W, Qin J, Laza MRC. 2013. Effects of high night temperature on yield and agronomic traits of irrigated rice under field chamber system condition. *Australian Journal of Crop Science* **7**: 7–13.

Supporting Information

Additional Supporting Information may be found online in the Supporting Information section at the end of the article:

Fig. S1 Phylogenetic tree of species in this study.

Fig. S2 Conversion of $\log_e$RR from plant part biomass to total biomass.

Fig. S3 Relationship between responses of total biomass to warming and the four components.

Fig. S4 Phylogenetic component of biomass responses along phylogenetic tree.

Fig. S5 Phylogenetic component of biomass responses for families with more than five species.

Fig. S6 Relationships between the phylogenetic component and leaf traits at the species level in different families.

Fig. S7 Relationships between the phylogenetic component and leaf traits at the species level in different orders.

Fig. S8 Relationships between the phylogenetic component and leaf traits at the species level in bryophytes, gymnosperms, monocots and eudicots.

Fig. S9 Relationships between the phylogenetic component and leaf traits at the species level in woody and nonwoody plants.

Fig. S10 Relationships between the phylogenetic component and leaf traits at the species level in trees and shrubs.

Fig. S11 Relationships between the phylogenetic component and leaf traits at the species level in forbs and graminoids.

Fig. S12 Relationships between the phylogenetic component and leaf traits at the species level in deciduous broadleaf trees, evergreen broadleaf trees and evergreen needleleaf trees for Dataset Ind.

Fig. S13 Relationships between the phylogenetic component and leaf traits at the species level in C_3 and C_4 graminoids.

Fig. S14 Relationships between the phylogenetic component and leaf traits at the family level for Dataset Com.

Fig. S15 The variation in the intraspecific components in different families.

Fig. S16 The variation in the intraspecific components in different orders.

Fig. S17 The variation in the intraspecific components in gymnosperms, monocots and eudicots.

Fig. S18 The variation in the intraspecific components in different plant functional types.

Fig. S19 Effects of warming magnitude and other experimental or ecological factors on the biomass response to warming based on Dataset Com.

Methods S1 Detailed procedures of variance partitioning based on the phylogenetic eigenvector regression.

Notes S1 Papers used in this meta-analysis.

Table S1 Dataset Ind.

Table S2 Dataset Com.

Table S3 The most important divergences in the plant biomass response to warming for Dataset Ind.

Table S4 The most important divergences in the plant biomass response to warming for Dataset Com.

Table S5 The species-level average contribution to tree-wide variation in different families for Dataset Ind and Dataset Com.

Table S6 The species-level average contribution to tree-wide variation in different orders.

Table S7 The species-level average contribution to tree-wide variation in different groups.

Table S8 The correlation matrix of leaf traits for the 284 species in this study.

Please note: Wiley Blackwell are not responsible for the content or functionality of any Supporting Information supplied by the authors. Any queries (other than missing material) should be directed to the *New Phytologist* Central Office.

About *New Phytologist*

- *New Phytologist* is an electronic (online-only) journal owned by the New Phytologist Trust, a **not-for-profit organization** dedicated to the promotion of plant science, facilitating projects from symposia to free access for our Tansley reviews and Tansley insights.
- Regular papers, Letters, Research reviews, Rapid reports and both Modelling/Theory and Methods papers are encouraged. We are committed to rapid processing, from online submission through to publication 'as ready' via *Early View* – our average time to decision is <26 days. There are **no page or colour charges** and a PDF version will be provided for each article.
- The journal is available online at Wiley Online Library. Visit **www.newphytologist.com** to search the articles and register for table of contents email alerts.
- If you have any questions, do get in touch with Central Office (np-centraloffice@lancaster.ac.uk) or, if it is more convenient, our USA Office (np-usaoffice@lancaster.ac.uk)
- For submission instructions, subscription and all the latest information visit **www.newphytologist.com**

© 2019 The Authors
New Phytologist © 2019 New Phytologist Trust