Foliar functional traits that predict plant biomass response to warming

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Abstract

Question: Ecologists are increasingly interested in making accurate predictions of plant response to climate change. Many studies have attempted to document plant response to warming by grouping species into functional groups. Within functional groups, however, species often display divergent responses. Determining how foliar functional traits might be used to predict plant responses to warming could reduce analytical complexity while maintaining generalizations across systems.

Methods: We conducted a meta-analysis on 18 studies (consisting of 38 species) of plant biomass response to experimental or natural warming. We determined whether plant trait estimates associated with the leaf economics spectrum [leaf life span (LL), leaf mass per area (LMA), leaf nitrogen (N_{mass}), leaf phosphorus (P_{mass}), photosynthetic capacity (A_{max}) and stomatal conductance (G_s)] from a global plant database of experimentally unmanipulated plants, GloPNet, could be used to predict biomass response to experimental warming.

Results: We found that three single leaf traits (LL, N_{mass} and A_{max}) were significant predictors for the response of plant biomass to warming treatments, perhaps due to their association with plant growth rates, adaptation rate and ability, each explaining between 21–46% of the variation in plant biomass responses. The magnitude of response to warming decreased with increasing LL, but increased with increasing N_{mass} and A_{max}. We found no linear combination of any of these traits that predicted warming response.

Conclusions: These results show that foliar traits can aid in understanding the mechanisms by which plants respond to temperature across species. Because each trait only explained a portion of variation in how plant growth responded to warming, however, future studies that examine how plant communities respond to warming should simultaneously measure multiple leaf traits, especially those most sensitive to warming, across plant species, to determine whether the predictive ability of functional traits changes between different ecosystems or plant taxonomic groups.

Introduction

Recent research has documented a variety of biotic responses to warming, including adaptations, changes in the ranges of species and changes in the abundance and biomass of particular groups (Hughes 2000; Peterson et al. 2001). Accurately predicting species response to a warmer global environment is difficult, however, and, given that the effects of warming are often context-dependent (Arft et al. 1999), making extrapolations from species-specific studies is also difficult. Identifying traits that are good indicators of response across species is a useful alternative to studying individual responses (McGill et al. 2006). For example, traits such as generation time, metabolic rate and dispersal ability have been used to accurately predict biotic responses to other kinds of environmental change (Foster et al. 1990; Schweiger et al. 2011). However, although there has been limited research regarding how multiple foliar traits simultaneously respond to environmental change (Wright et al. 2005; Kattge et al. 2011; Soussana

et al. 2012), we do not yet understand the utility of plant traits in predicting how species will respond to warming.

To address our incomplete knowledge of the relationship between plant traits and warming response, researchers have documented growth responses of plant functional groups and growth forms to warming using both meta-analyses (e.g. Arft et al. 1999; Dormann & Woodin 2002; Lin et al. 2010) and long-term studies (e.g. Harte et al. 1995; Wahren et al. 2005). This approach allows researchers to organize species by multiple traits that directly impact fitness (Violle et al. 2007). Collectively, these studies have highlighted interesting patterns in functional group response to warming. For example, woody plants appear to increase in biomass more than herbaceous plants in response to warming (Lin et al. 2010), resulting in significant changes within plant communities (Gornish & Tylianakis 2013). However, mechanistic interpretation from these studies is limited, because functional groups can be characterized by multiple functional traits. Therefore, similar responses among different functional groups (Cunningham & Read 2002) could obscure ecologically relevant relationships between factors of climate change and functional traits (Matesanz et al. 2009). The diversity of plant responses that are seen within functional groups may be due to differences within traits in a functional group. Indeed, trait-mediated differences across individual species can be responsible for differences in the way plants respond to environmental changes (e.g. Kardol et al. 2010). Therefore, analyses examining multiple functional traits of *individual species*, which can provide information about plant- and community-level function (Smith & Knapp 2003; Wardle & Zackrisson 2005; McGill et al. 2006; Shipley & Garnier 2006), could be a useful metric to predict responses to warming (Berg et al. 2010; Kloeke et al. 2012).

Multiple traits can influence plant responses to environmental factors (Price & Waser 1998; De Valpine & Harte 2001) in complex ways. This interaction can occur as a result of trade-offs where, for example, a reduction in plant growth can be compensated by an increase in reproductive output (Grime 1977). Plant traits can also differ in how they mediate responses to the environment factors across local, regional and global scales (e.g. Hamilton et al. 2005). Due to the various ways in which plants traits can interact both with the environment and with other traits, leaf traits are expected to demonstrate different relationships (slope value and sign) with warming due to differences in the vulnerability of traits to treatment effects.

We attempted to determine whether foliar functional traits could be used to predict biomass response to warming using leaf functional trait data from GloPNet (Wright et al. 2004). Evaluating a pool of species within a trait spectrum associated with biomass accumulation addresses the limitation of evaluating functional group response. We used a meta-analysis approach, and combined the results of published studies that reported the total plant biomass responses to experimental warming with measurements of different foliar characteristics (under non-warmed conditions) from the GloPNet data set. We chose to investigate the relationship among warming, biomass and leaf traits because changes in biomass have been one of the most well documented effects of warming (Wu et al. 2011), and leaf traits are often involved in modifying the direct and indirect effects of warming on plants (Luo 2007). We focused on six traits – leaf life span (LL), leaf mass per area (LMA), leaf nitrogen (N_{mass}), leaf phosphorus (P_{mass}), photosynthetic capacity (A_{max}) and stomatal conductance (G_s) – that have been shown to be important for plant response to warming in different ecosystems (Llorens et al. 2002; Oyarzabal et al. 2008; Hudson et al. 2011). Species used in our study included individuals from different growth forms (trees, shrubs, herbaceous and graminoids) as well as different life cycles (annuals, biennials and perennials; see SOM).

We had several hypotheses regarding the role of plant traits in mediating warming effects. Specifically, since warming often results in increased nutrient availability through increased rates of soil organic matter decomposition (Aerts 2006) and N mineralization (MacDonald et al. 1995), we expected that leaf traits more directly related to rates of plant growth (N_{mass} and A_{max}) would be disproportionately affected by warming. Thus, these traits should be the best predictors of responses of plant biomass to experimental warming. We also expected P_{mass} to have a positive relationship with the magnitude of warming effect on total biomass. This is because P uptake is often enhanced through mycorrhizal associations (Read & Perez-Moreno 2003), and mycorrhizal associations [which encourage plant growth (Janos 1980) occur in most vascular plants (Brundrett 2009)] with increase in temperature (Grey 1991). Plants with high foliar P availability are therefore more likely to significantly increase in size in response to warming.

Methods

Data collection

Suitable studies for our meta-analysis were identified using the Web of Science (ISI) searches, with the keywords: 'warming', 'OTC (open top chamber)', 'temperature' and 'climate change', and keywords related to the response variable: 'plant biomass' and 'primary production'. We only used references found between 1950 and 2011 that included the responses to experimental warming of total (above-ground + below-ground) terrestrial plant biomass for species that are included in the GloPNet data set. We

found a total of 18 studies and 38 species (Data, SOM). Means, sample sizes and SD were recorded for both control and for experimentally warmed plants (Data, SOM). Biomass values were standardized to $g \cdot m^{-2}$. Data were collected from published tables, and were estimated from published figures using datathief III (http://datathief.org/).

In cases where single articles published multiple responses to a warming treatment (e.g. response over time), we recorded biomass for the last data point of the experiment to avoid pseudoreplication of longer-term studies (Gurevitch & Hedges 2001). Studies were analysed together irrespective of warming facility type used (OTC; greenhouse; soil warming) as biomass response has been shown to be independent of facility type (Lin et al. 2010). Further, an ANOVA showed that facility type did not contribute to differences in biomass response to experimental warming ($F_{3,34} = 0.966$, $P = 0.42$).

Publications are often biased towards statistically significant results and large effect sizes, and therefore, against small or few treatment effects, so meta-analyses may overestimate the effects of warming on plant biomass. We estimated the magnitude of publication bias in our data by calculating Rosenthal's fail-safe number (Rosenthal 1979), a commonly used metric in meta-analyses that estimates the number of studies showing no warming effect required to reverse patterns identified in our study. Our fail safe number was considerably higher (28 419) than the generally accepted value of $5n + 10$, suggesting that publication bias was unlikely to have affected our results.

To obtain numerical information about plant functional traits, we used data for each species from GloPNet. If there was more than one entry for a species in GloPNet, we used the studies that had the most data available (most entries filled in). If multiple studies had the same number of entries, we randomly picked one study from which to use values. Finally, if the study we picked had missing values that could be filled in using another study, we used the other study values to fill in the missing entries. In most cases (27 out of 38 species), the system from which the species data were collected from GloPNet matched the system from the experimental study. In almost all cases where systems did not match, the warming experiment was performed in a cold, high latitude biome and the GloPNet data were from a temperate forest system; so in these few cases, the biomass response of the experimental species would be smaller than expected for the species from which the traits were derived (Lin et al. 2010).

We are confident that our choices from the GloPNet database did not bias our results for two reasons. First, we calculated the average values of foliar traits reported in GlopNet for every species that we chose (see Species Averages, SOM), and on average, because most values only had one or two reported values, most of the values that we chose fell within ± 1 SE of the average (in 34 of 38 cases). Second, multiple analyses using different values (in the case of multiple entries in GloPNet) demonstrated no significant differences in the slope of the relationship between trait and effect size.

Published data were derived from plants across different life stages (see Data, SOM). Moreover, data available from GloPNet were likely collected from plants that varied in age and stage. Although the role of plant traits in mediating warming effect can be different across plant life stages, in addition to the trait values themselves, we did not distinguish between studies from plants of different ages.

Analyses

To facilitate comparison across studies, we estimated the experimental effect as a change in plant biomass proportional to warming (Hedges et al. 1999). We used the log response ratio ($\ln R$) as our estimate of effect size, calculated as

$$\ln R = \ln(X^E/X^C) \qquad (1)$$

where X^E and X^C are means of the experimental and control groups, respectively. The variance of the response ratio is calculated as:

$$V_{\ln R} = (s^E)^2/N^E(X^E)^2 + (s^C)^2/N^C(X^C)^2 \qquad (2)$$

where s^E and s^C are SD of the experimental and control groups, respectively, and N^E and N^C are sample sizes of the experimental and control groups, respectively. These metrics reduce the effect of plant size on our response variable (Hedges et al. 1999; Hawkes & Sullivan 2001), and makes our continuous data amenable to a weighted regression (Hedges et al. 1999).

To reduce the bias introduced from differences in sample size among studies, a weighted average (the reciprocal of the sampling variance) was applied to our response ratios to determine a cumulative effect size for our studies. The final log response ratios were normally distributed with Q-Q plots. The magnitude of warming applied across studies differed (range of warming = 0.5–12.0 °C; mean warming = 3.75 °C, mode warming = 5.0 °C). However, since we found no relationship between magnitude of warming and the log response ratio (slope = −0.04, $P = 0.10$), we did not further weight the log response ratios by the magnitude of warming applied in each study.

Since our data were normally distributed, we did not employ resampling techniques. The cumulative effect size was determined as significant if the confidence interval for that effect size did not bracket zero. We also looked at the total heterogeneity (Q_T; heterogeneity among the results)

of effect sizes across studies, which suggest whether other factors, in addition to the warming treatment, alter effect sizes across studies.

We used weighted least squares regression to analyse the relationship between log-transformed continuous predictors (LL, LMA, N_{mass}, A_{max}, P_{mass} and G_s) on the log response ratio of each species in each study. Outliers, as identified from diagnostic plots, were omitted from the regression to reduce a disproportionate leverage of single data points on the analysis. Removing these outliers, however, did not alter our results or conclusions. These analyses were conducted in Metawin v 2.0 (Rosenberg et al. 1999).

We calculated Pearson's correlations among traits to determine whether our traits were statistically related to one another. We used regression trees, which use binary recursive partitioning, to assess the effects of multiple traits together using the {tree} package in R v 2.15 (R Foundation for Statistical Computing, Vienna, AT).

Results

Warming had a significant and positive effect on plant biomass (warmed plants were about 11% larger than non-warmed plants), as indicated by significantly positive effect sizes (0.31 with CI 0.069–0.511). The statistically significant high heterogeneity (Q_T; 7745), however, suggests that predictors other than treatment effects (such as functional traits) might be responsible for differences in effect size across studies.

Leaf life span (LL) was the only factor investigated that was negatively related to effect size (Fig. 1a; slope = −0.45, R^2 = 0.46, Q_T = 37.7, P = 0.001). Alternatively, both N_{mass} (Fig. 1c; Q_T = 41.73, P = 0.06) and A_{max} (Fig. 1e; Q_T = 60.34, P = 0.01) were positively related to effect size (slope = 0.97, R^2 = 0.276 and 0.39, R^2 = 0.213, respectively). Finally, the relationship between LMA (Fig. 1b; Q_T = 35, P = 0.199), P_{mass} (Fig. 1d; Q_T = 47, P = 0.374) and effect size and G_s (Fig. 1f; Q_T = 20, P = 0.373) and effect size were not significant (slope = −0.504, 0.405 and 0.203, respectively).

As expected, we found significant correlations among many of the traits investigated (Table 1). For example, leaf nutrient content (both N_{mass} and P_{mass}) had mostly positive correlations with almost all other plant traits. When controlling for correlated factors, the regression tree analysis did not identify significant effects of interacting plant traits on biomass response.

Discussion

Using a large database that catalogues species-specific leaf functional traits, we were able to identify three foliar traits that might be suitable for making predictions of warming effects. In general, if a plant has short LL, high N_{mass} and high A_{max} (at the high end of the leaf economics spectrum; Wright et al. 2005), the species-specific biomass response of the plant to warming should be higher than a plant with long LL, low N_{mass} and low A_{max}. One complication with our approach is that the predictors we found to be important for explaining biomass change in response to warming have significant correlations with one another (Table 1), thus making it hard to disentangle the predictive value of a single trait. However, given that most studies do not measure multiple traits and a species' response to warming, this approach is a good start at identifying candidate predictive traits that may be used in the future.

Our results support the strong relationship previously documented between LL and warming (Cavender-Bares et al. 2005; Kikyzawa & Lechowicz 2005; Pensa et al. 2010). Plants with shorter LL demonstrated a larger change in total biomass in response to experimental warming. Species with shorter LL often grow faster, and thus could exploit the benefits of warmer temperatures more quickly and at a lower energetic cost than species with a longer leaf life span (Reich et al. 1999). For example, species with short LL can modify their carbon intake through photosynthetic acclimation more quickly than species with longer LL (e.g. Shen et al. 2009). Alternatively, leaf longevity could be indicative of other leaf traits, including photosynthetic rates and leaf thickness (Reich et al. 1999; Westoby et al. 2002), which have been shown to modify a species' response to changing abiotic conditions (Saar et al. 2012).

Leaf nitrogen (N_{mass}) is associated with rapid plant growth (Laliberte et al. 2012), and it demonstrated a positive relationship with effect size of experimental warming. Higher N_{mass} could indicate more efficient N absorption, N retention, or both. Nitrogen use efficiency (Coleman & Bazzaz 1992; but see Berendse & Aerts 1987), N reabsorption efficiency (Yuan & Chen 2009) and stress management strategies that require N (Ougham & Howarth 1988) can be reduced at high temperatures. Therefore, species that are already growth-limited by inadequate N capture or storage capabilities would be restricted in their ability to take advantage of the extended growing period that often accompanies warming, demonstrating little or no biomass response to increased temperature.

There is a rather complicated relationship between temperature and A_{max} (Long 1991). In general, A_{max} is a plastic trait, and increases with temperature (Liang et al. 2013), but only until A_{max} rates have reached their highest capacity (Bunce 2000). This increase, however, is not seen for all species (Niu et al. 2008), which may be why A_{max} only predicts 21% of the variation in how plant biomass responds to warming. Moreover, the average amount of
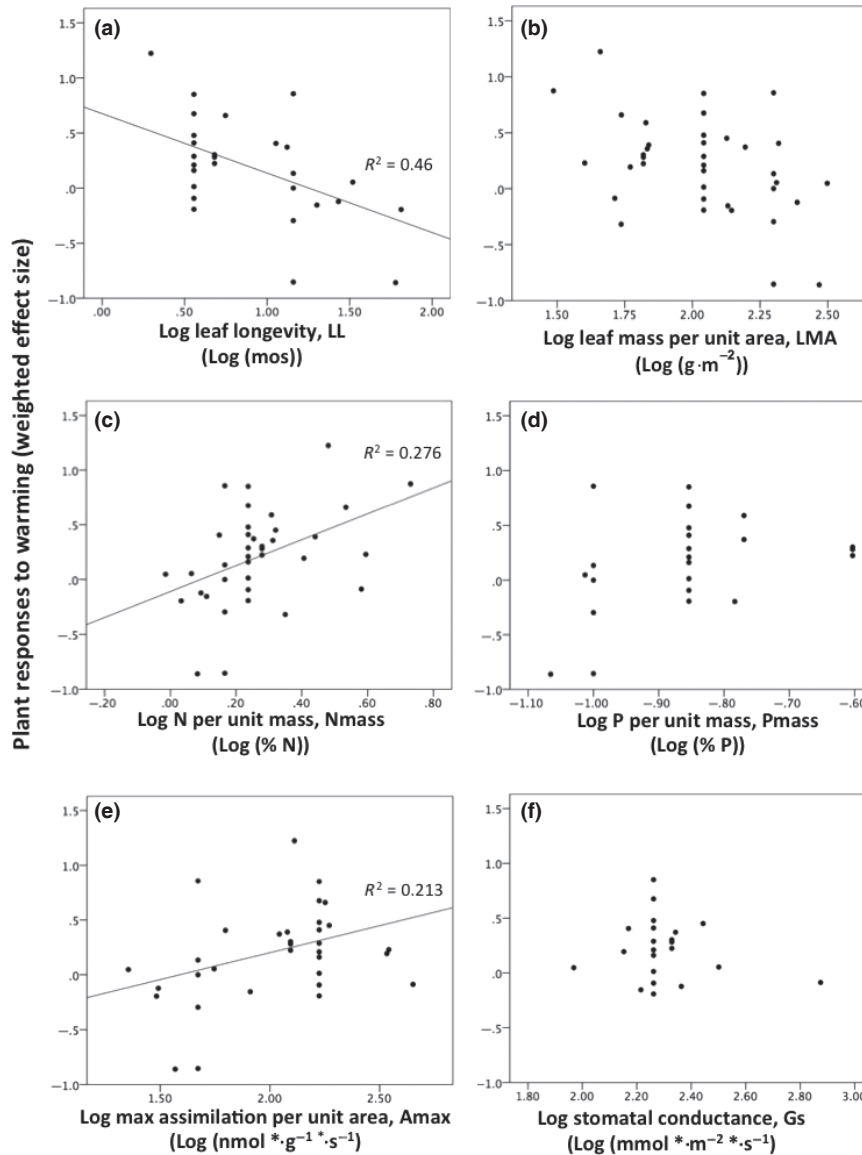
Figure 1. Relationships between plant responses to warming (weighted effect size) and various leaf traits. Relationships were significant for LL (**a**), N_{mass} (**c**) and A_{max} (**e**), but not for LMA (**b**), P_{mass} (**d**) and G_s (**f**). All data points are shown.

Table 1. Pearson's product-moment correlation matrix. Values in bold indicate significant relationships.

	A_{max}	G_s	LL	LMA	N_{mass}	P_{mass}
A_{max}	1.00					
G_s	0.06	1.00				
LL	**−0.94**	0.04	1.00			
LMA	−0.37	−0.40	0.59	1.00		
N_{mass}	**0.76**	**0.69**	**−0.68**	−0.60	1.00	
P_{mass}	**0.10**	**0.87**	−0.17	**−0.77**	**0.68**	1.00

warming for studies in our data set was 3.75 °C, and could possibly not be high enough for most species to reach their maximum potential assimilation rate, given that in nature most species rarely surpass a fraction of their maximum A_{max} (Starr et al. 2008), limiting the predictive power that A_{max} would have in an analysis such as this.

Alternatively, the role of A_{max} in modifying biological processes (e.g. decomposability of a leaf) can be a function of indirect effects on other leaf traits (e.g. SLA, N or P; Santiago 2007). We found significant correlations between A_{max} and both N_{mass} and P_{mass} (Table 1). Therefore, the predictive power of A_{max} for biomass response to warming could be increased with the assessment of interacting leaf traits not investigated in our study. Moreover, plants may adapt their carbon metabolism to locally warmer temperatures (Silim et al. 2010; Barron-Gafford et al. 2012), so

A_{max} could be particularly useful for determining how species at range edges respond to warming.

Three of the traits investigated (LMA, P_{mass} and G_s) did not appear to be useful predictors for plant biomass response to warming. Similar to LL (a trait to which it is often correlated; Wright et al. 2005; but see Table 1) LMA demonstrated a, not entirely unexpected, negative (non-significant) relationship with effect size. LMA, which is often used as an indicator of different ecological plant strategies (Westoby et al. 2002), has been shown to have idiosyncratic relationships with other plant traits (e.g. Drenovsky et al. 2012). In our study, for example, LMA demonstrated a positive (non-significant) correlation with LL and a negative correlation with all other plant traits (Table 1), and these relationships may be important for warming response. The low correlation between LMA and warming response may result from factors important for response to temperature change, such as mass-based nutrient concentrations or plant life span, which can correlate in opposing ways with LMA (Poorter et al. 2009). In our study, we found that LMA demonstrated negative correlations with P_{mass}, possibly obscuring significant relationships between LMA and warming.

We expected an interaction between warming and mycorrhizal associations would drive the predictive power of P_{mass} (Zavalloni et al. 2012). This hypothesis was developed from studies conducted (mostly) in natural systems. In total, 78% of our studies were conducted in greenhouses, where soil mycorrhizal diversity can be restricted compared to natural (outside of greenhouse) soils (e.g. Jiao et al. 2011). Perhaps the mycorrhizal contributions to foliar P_{mass} were limited in most of the experimental systems used in our analysis. Alternative explanations could include the release of labile N from soils with warming, leading to increasing P limitation on the growth of plants (Dijkstra et al. 2012), as shown by decreasing the amount of P in leaves with warming (Yang et al. 2011) or co-limitation by N and P (Elser et al. 2007). Because of this, we expected that the amount of P in plant tissues would be important for plant response to warming. The lack of a significant relationship between foliar P_{mass} and the magnitude of plant biomass response to warming could be explained by the modest duration of experiments included in our analysis (median experimental duration = 9 months). It is reasonable to expect that most of the experimental plant species are N-limited (Vitousek & Howarth 1991). If the majority of the experiments did not proceed long enough to alleviate N limitation, then the foliar availability of P is likely to be less important to warming response traits related to the uptake of N in plants.

Although we found no relationship between G_s and warming, stomatal conductance is a plastic trait within an individual species and commonly demonstrates a positive relationship with temperature (Bunce 2000; Silim et al. 2010). An increase in G_s in response to warming, however, does not necessarily result in an increase in biomass because photosynthesis or assimilation rate might not increase. Because G_s can continue to increase at temperatures where carbon assimilation rates have reached their maximum across many species (Bunce 2000), this may make G_s a poor predictor of how plant biomass would respond to warming. Alternatively, G_s rates can be susceptible to seasonal changes and microsite characteristics (e.g. Hiyama et al. 2005), and this variation might not be adequately captured in the GloPNet database.

We found that LL, N_{mass} and A_{max} are particularly useful traits for predicting the magnitude of biomass response to elevated temperature. These three traits, however, each only have modest predictive ability (R^2 between 0.21 and 0.46), and we found that no pair-wise combination of these traits was better at predicting this response to warming because most traits were correlated. The limitation of this predictive ability could be due to foliar functional traits and warming responses being measured at different times and locations; the GloPNet database itself can be subject to bias (e.g. a majority of studies conducted in a particular system; see below). Moreover, the strong correlation among plant traits (e.g. Wright et al. 2004) increases the complexity associated with confident identification of individual plant traits driving warming response. Thus, there is a need to rigorously test these relationships with studies that simultaneously measure both multiple foliar functional traits and plant responses to warming to detect whether multiple traits are indeed indicative of plant responses to warming. Meanwhile, however, the recognition that leaf traits broadly correlate with how plant biomass responds to warming may be useful in making robust predictions of how productivity of individual species, and even plant communities, might change in a warmer future. Finally, we expect that this approach could be useful when examining how other factors associated with climate change also affect plants (e.g., CO_2, precipitation), but a different suite of traits might be more important for these other factors.

Incorporating this understanding into future work could improve predictions of biotic responses to a changing climate, as well as elucidate the mechanisms driving global trends in plant biomass responses to warming. Using plant traits to make predictions about the response of plants to global change would be particularly valuable when paired with information highlighting how landscapes are expected to change (Chessman 2012). In order to test the strength of these relationships across different ecosystems and plant taxonomic groups, future warming studies should include measures of a wide range of plant functional traits. Moreover, expanding the breadth of

ecosystems in which warming studies are commonly implemented would also be beneficial. In our data set, many of the experiments were from montane and tundra ecosystems, as a result of a historical bias with warming studies (Gornish & Tylianakis 2013). This system bias could skew our result applicability to cold and high-latitude biomes. In order to facilitate broader trait-based predictions of plant biomass response to climate change, warming experiments conducted in tropical and lower latitude systems should become more common. We especially encourage studies that could investigate the candidate traits that we have identified here to measure multiple traits simultaneously, given that these traits are correlated with one another.

Acknowledgements

References

Aerts, R. 2006. The freezer defrosting: global warming and litter decomposition rates in cold biomes. *Journal of Ecology* 94: 713–724.

Arft, A.M., Walker, M.D., Gurevitch, J., Alatalo, J.M., Bret-Harte, M.S., Dale, M., Diemer, M., Gugerli, F., Henry, G.H.R. (…) & Wookey, P.A. 1999. Responses of tundra plants to experimental warming: meta-analysis of the international tundra experiment. *Ecological Monographs* 69: 491–511.

Barron-Gafford, G.A., Scott, R.L., Jenerette, G.D., Hamerlynck, E.P. & Huxman, T.E. 2012. Temperature and precipitation controls over leaf- and ecosystem-level CO_2 flux along a woody plant encroachment gradient. *Global Change Biology* 18: 1389–1400.

Berendse, F. & Aerts, R. 1987. Nitrogen-use-efficiency: a biologically meaningful definition? *Functional Ecology* 1: 293–296.

Berg, M.P., Kiers, E.T., Driessen, G., van der Heijden, M., Kooi, B.W., Kuenen, F., Liefting, M., Verhoef, H.A. & Ellers, J. 2010. Adapt or disperse: understanding species persistence in a changing world. *Global Change Biology* 16: 587–598.

Brundrett, M.C. 2009. Mycorrhizal associations and other means of nutrition of vascular plants: understanding the global diversity of host plants by resolving conflicting information and developing reliable means of diagnosis. *Plant and Soil* 320: 37–77.

Bunce, J.A. 2000. Acclimation of photosynthesis to temperature in eight cool and warm climate herbaceous C-3 species: temperature dependence of parameters of a biochemical photosynthesis model. *Photosynthesis Research* 63: 59–67.

Cavender-Bares, J., Cortes, P., Rambal, S., Joffre, R., Miles, B. & Rocheteau, A. 2005. Summer and winter sensitivity of leaves and xylem to minimum freezing temperatures: a comparison of co-occurring Mediterranean oaks that differ in leaf life-span. *New Phytologist* 168: 597–611.

Chessman, B.C. 2012. Biological traits predict shifts in geographical ranges of freshwater invertebrates during climatic warming and drying. *Journal of Biogeography*. 39: 957–969.

Coleman, J.S. & Bazzaz, F.A. 1992. Effects of CO_2 and temperature on growth and resource use of co-occurring C_3 and C_4 annuals. *Ecology* 73: 1244–1259.

Cunningham, S.C. & Read, J. 2002. Comparison of temperate and tropical rainforest tree species: photosynthetic responses to growth temperature. *Oecologia* 133: 112–119.

De Valpine, P. & Harte, J. 2001. Plant responses to experimental warming in a montane meadow. *Ecology* 82: 637–648.

Dijkstra, F.A., Pendall, E., Morgan, J.A., Blumenthal, D.M., Carrillo, Y., LeCain, D.R. & Williams, D.G. 2012. Climate change alters stoichiometry of phosphorus and nitrogen in a semiarid grassland. *New Phytologist* 196: 807–815.

Dormann, C.F. & Woodin, S.J. 2002. Climate change in the Arctic: using plant functional types in a meta-analysis of field experiments. *Functional Ecology* 16: 4–17.

Drenovsky, R.E., Grewell, B.J., D'Antonio, C.M., Funk, J.L., James, J.J., Molinari, N., Parker, I.M. & Richards, C.L. 2012. A functional trait perspective on plant invasion. *Annals of Botany* 110: 141–153.

Elser, J.J., Bracken, M.E., Cleland, E.E., Gruner, D.S., Harpole, W.S., Hillebrand, H., Ngai, J.T., Seabloom, E.W., Shurin, J.B. & Smith, J.E. 2007. Global analysis of nitrogen and phosphorus limitation of primary producers in freshwater, marine and terrestrial ecosystems. *Ecology Letters* 10: 1135–1142.

Foster, D.R., Schoonmaker, P.K. & Pickett, S.T.A. 1990. Insights from paleoecology to community ecology. *Trends in Ecology & Evolution* 5: 119–122.

Gornish, E.S. & Tylianakis, J. 2013. Plant community effects of global climate change at different scales: a review. *American Journal of Botany* 100: 1–13.

Grey, W.E. 1991. Influence of temperature on colonization of spring barleys by vesicular arbuscular mycorrhizal fungi. *Plant and Soil* 137: 181–190.

Grime, J.P. 1977. Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *The American Naturalist* 111: 1169–1194.

Gurevitch, J. & Hedges, L.V. 2001. Meta-analysis: combining the results of independent experiments. In: Scheiner, S.M. & Gurevitch, J. (eds.) *Design and analysis of ecological experiments*, pp. 347–369. Oxford University Press, Oxford, UK.

Hamilton, M.A., Murray, B.R., Cadotte, M.W., Hose, G.C., Baker, A.C., Harris, C.J. & Licari, D. 2005. Life-history correlates of plant invasiveness at regional and continental scales. *Ecology Letters* 8: 1066–1074.

Harte, J., Torn, M.S., Change, F.R., Feifarek, B., Kinzig, A.P., Shaw, R. & Shen, K. 1995. Global warming and soil

microclimate: results from a meadow-warming experiment. *Ecological Applications* 5: 132–150.

Hawkes, C.V. & Sullivan, J.J. 2001. The impact of herbivory on plants in different resource conditions: a meta-analysis. *Ecology* 82: 2045–2058.

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

Hiyama, T., Kochi, K., Kobayashi, N. & Sirisampan, S. 2005. Seasonal variation in stomatal conductance and physiological factors observed in a secondary warm-temperate forest. *Ecological Research* 20: 333–346.

Hudson, J.M.G., Henry, G.H.R. & Cornwell, W.K. 2011. Taller and larger: shifts in Arctic tundra leaf traits after 16 years of experimental warming. *Global Change Biology* 17: 1013–1021.

Hughes, L. 2000. Biological consequences of global warming: is the signal already apparent? *Trends in Ecology & Evolution* 15: 56–61.

Janos, D.P. 1980. Vesicular-arbuscular mycorrhizae affect lowland tropical rain forest plant growth. *Ecology* 61: 151–162.

Jiao, H., Chen, Y.L., Lin, X.G. & Liu, R.J. 2011. Diversity of arbuscular mycorrhizal fungi in greenhouse soils continuously planted to watermelon in North China. *Mycorrhiza* 21: 681–688.

Kardol, P., Cregger, M.A., Campany, C.E. & Classen, A.T. 2010. Soil ecosystem functioning under climate change: plant species and community effects. *Ecology* 91: 767–781.

Kattge, J., Diaz, S., Lavorel, S., Prentice, I.C., Leadley, P., Bönisch, G., Garnier, E., Westoby, M., Reich, P.B. (…) & Wirth, C. 2011. TRY – a global database of plant traits. *Global Change Biology*, 17: 2905–2935.

Kikyzawa, K. & Lechowicz, M.J. 2005. *Ecology of leaf longevity*. Springer, Tokyo, JP.

Kloeke, A.E.E.V., Douma, J.C., Ordonez, J.C., Reich, P.B. & van Bodegom, P.M. 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.

Laliberte, E., Shipley, B., Norton, D.A. & Scott, D. 2012. Which plant traits determine abundance under long-term shifts in soil resource availability and grazing intensity? *Journal of Ecology* 100: 662–677.

Liang, J., Xia, J., Liu, L. & Wan, S. 2013. Global patterns of the responses of leaf-level photosynthesis and respiration in terrestrial plants to experimental warming. *Journal of Plant Ecology*. doi:10.1093/jpe/rtt003.

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

Llorens, L., Penuelas, J. & Emmett, B. 2002. Developmental instability and gas exchange responses of a heathland shrub to experimental drought and warming. *International Journal of Plant Sciences* 163: 959–967.

Long, S.P. 1991. Modification of the response of photosynthetic productivity to rising temperature by atmospheric CO_2

concentrations – has its importance been underestimated. *Plant, Cell and Environment* 14: 729–739.

Luo, Y.Q. 2007. Terrestrial carbon-cycle feedback to climate warming. *Annual Review of Ecology, Evolution and Systematics* 38: 683–712.

MacDonald, N.W., Zak, D.R. & Pregitzer, K.S. 1995. Temperature effects on kinetics of microbial respiration and net nitrogen and sulfur mineralization. *Soil Science Society of American Journal* 59: 233–240.

Matesanz, S., Brooker, R.W., Valladares, F. & Klotz, S. 2009. Temporal dynamics of marginal steppic vegetation over a 26-year period of substantial environmental change. *Journal of Vegetation Science* 20: 299–310.

McGill, B.J., Enquist, B.J., Wiher, E. & Westoby, M. 2006. Rebuilding community ecology from functional traits. *Trends in Ecology & Evolution.* 221: 178–185.

Niu, S.L., Li, Z.X., Xia, J.Y., Han, Y., Wu, M.Y. & Wan, S. 2008. Climatic warming changes plant photosynthesis and its temperature dependence in a temperate steppe of northern China. *Environmental and Experimental Botany* 63: 91–101.

Ougham, H.J. & Howarth, C.J. 1988. Temperature shock proteins in plants. *Symposia of the Society for Experimental Biology* 42: 259–280.

Oyarzabal, M., Paruelo, J.M., Federico, P., Oesterheld, M. & Laurenroth, W.K. 2008. Trait differences between grass species along a climatic gradient in South and North America. *Journal of Vegetation Science* 19: 183–192.

Pensa, M., Karu, H., Luud, A. & Kund, K. 2010. Within-species correlations in leaf traits of three boreal plant species along a latitudinal gradient. *Plant Ecology* 208: 155–166.

Peterson, A.T., Sanchez-Cordero, V., Soberon, J., Bartley, J., Buddemeier, R.W. & Navarro-Siguenza, A.G. 2001. Effects of global climate change on geographic distributions of Mexican Cracidae. *Ecological Modelling* 144: 21–30.

Poorter, H., Niinemets, U., Poorter, L., Wright, I.J. & Villar, R. 2009. Causes and consequences of variation in leaf mass per area (LMA): a meta-analysis. *New Phytologist* 182: 565–588.

Price, M.V. & Waser, N.M. 1998. Effects of experimental warming on plant reproductive phenology in a subalpine meadow. *Ecology* 79: 1261–1271.

Read, D.J. & Perez-Moreno, J. 2003. Mycorrhizas and nutrient cycling in ecosystems – a journey towards relevance? *New Phytologist* 157: 475–492.

Reich, P.B., Ellsworth, D.S., Walters, M.B., Vose, J.M., Gresham, C., Volin, J.C. & Bowman, W.D. 1999. Generality of leaf trait relationships: a test across six biomes. *Ecology* 80: 1955–1969.

Rosenberg, M.S., Adams, D.C. & Gurevitch, J. 1999. *MetaWin: statistical software for meta-analysis. Version 2.0.* Sinauer Associates, Sunderland, MA, US.

Rosenthal, R. 1979. The "file drawer" problem and tolerance for null results. *Phycological Bulletin* 86: 638–641.

Saar, L., Takkis, K., Pärtel, M. & Helm, A. 2012. Which plant traits predict species loss in calcareous grasslands with extinction debt? *Diversity and Distributions* 18: 808–817.

Santiago, L.S. 2007. Extending the leaf economics spectrum to decomposition: evidence from a tropical forest. *Ecology* 88: 1126–1131.

Schweiger, O., Heikkinen, R.K., Harpke, A., Hickler, T., Klotz, S., Kudrna, O., Kühn, I., Pöyry, J. & Settele, J. 2011. Increasing range mismatching of interacting species under global change is related to their ecological characteristics. *Global Ecology and Biogeography* 21: 88–99.

Shen, H.H., Klein, J.A., Zhao, X.Q. & Tand, Y.H. 2009. Leaf photosynthesis and simulated carbon budget of *Gentiana straminea* from a decade-long warming experiment. *Journal of Plant Ecology* 2: 207–216.

Shipley, B.D. & Garnier, E. 2006. From plant traits to plant communities: a statistical mechanistic approach to biodiversity. *Science* 314: 812–814.

Silim, S.N., Ryan, N. & Kubien, D.S. 2010. Temperature responses of photosynthesis and respiration in *Populus balsamifera* L.: acclimation versus adaptation. *Photosynthesis Research* 104: 19–30.

Smith, M.D. & Knapp, A.K. 2003. Dominant species maintain ecosystem function with non-random species loss. *Ecology Letters* 6: 509–517.

Soussana, J., Maire, V., Gross, N., Bachelet, B., Pages, L., Martin, R., Hill, D. & Wirth, C. 2012. Gemini: a grassland model simulating the role of plant traits for community dynamics and ecosystem functioning. Parameterization and evaluation. *Ecological Modelling* 231: 134–145.

Starr, G., Oberbauer, S.F. & Alhquist, L.A. 2008. The physiological response of tundra plants to an experimental lengthening of the growing season and soil warming. *Arctic, Antarctic and Alpine Research* 40: 181–191.

Violle, C., Navas, M., Vile, D., Kazakou, E., Fortunel, C., Hummel, I. & Garnier, E. 2007. Let the concept of trait be functional! *Oikos* 116: 882–892.

Vitousek, P.M. & Howarth, R.W. 1991. Nitrogen limitation on land and in the sea – how it can occur. *Biogeochemistry* 13: 87–115.

Wahren, C.H.A., Walker, M.D. & Bret-Harte, M.S. 2005. Vegetation responses in Alaskan arctic tundra after 8 years of a summer warming and winter snow manipulation experiment. *Global Change Biology* 11: 537–552.

Wardle, D.A. & Zackrisson, O. 2005. Effects of species and function group loss on island ecosystem properties. *Nature* 435: 806–810.

Westoby, M., Falster, D.S., Moles, A.T., Vesk, P.A. & Weight, I.J. 2002. Plant ecological strategies: some leading dimensions of variation between species. *Annual Review of Ecology and Systematics* 33: 125–159.

Wright, I.J., Reich, P.B., Westoby, M., Ackerly, D.D., Baruch, Z., Bongers, F., Cavender-Bares, J., Chapin, T., Cornelissen, J.H.C. (…) & Villar, R. 2004. The worldwide leaf economics spectrum. *Nature* 428: 821–827.

Wright, I.J., Reich, P.B., Cornelissen, J.H.C., Falster, D.S., Groomm, P.K., Hikosaka, K., Lee, W., Lusk, C.H., Niinemets, Ü. (…) & Westoby, M. 2005. Modulation of leaf economic traits and trait relationships by climate. *Global Ecology and Biogeography* 14: 411–421.

Wu, Z., Dijkstra, P., Koch, G.W., Penuelas, J. & Hungate, B. 2011. Responses of terrestrial ecosystems to temperature and precipitation change: a meta-analysis of experimental manipulation. *Global Change Biology* 17: 927–942.

Yang, Y., Wang, G., Klanderud, K. & Yang, L. 2011. Responses in leaf functional traits and resource allocation of a dominant alpine sedge (*Kobresia pygmaea*) to climate warming in the Qinghai-Tibetan Plateau permafrost region. *Plant and Soil* 349: 377–387.

Yuan, Z.Y. & Chen, H.Y.H. 2009. Global-scale patterns of nutrient resorption associated with latitude, temperature and precipitation. *Global Ecology and Biogeography* 18: 11–18.

Zavalloni, C., Vicca, S., Buscher, M., de la Providencia, I.E., de Boulois, H.D., Declerck, S., Nijs, I. & Ceulemans, R. 2012. Exposure to warming and CO_2 enrichment promotes greater above-ground biomass, nitrogen, phosphorus and arbuscular mycorrhizal colonization in newly established grasslands. *Plant and Soil* 359: 121–136.

Supporting Information

Additional supporting information may be found in the online version of this article:

Appendix S1. Data from all studies used in the meta-analysis

Appendix S2. Notes on the data set.

Appendix S3. Citations used in the data set.

Appendix S4. Species averages for all traits and effect sizes. Grey depicts where GloPNet did not report any values, and yellow depicts when the value we chose fell outside 1 SE of the average value for each species.

Appendix S5. Averages of traits and effect sizes for each growth form.

Appendix S6. Species that had disproportionate effects on regressions.