

## CLIMATE CHANGE AND SPECIES RANGE SHIFTS Convergent effects of elevation on functional leaf traits within and among species

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### Summary

1. Spatial variation in filters imposed by the abiotic environment causes variation in functional traits within and among plant species. This is abundantly clear for plant species along elevational gradients, where parallel abiotic selection pressures give rise to predictable variation in leaf phenotypes among ecosystems. Understanding the factors responsible for such patterns may provide insight into the current and future drivers of biodiversity, local community structure and ecosystem function.
2. In order to explore patterns in trait variation along elevational gradients, we conducted a meta-analysis of published observational studies that measured three key leaf functional traits that are associated with axes of variation in both resource competition and stress tolerance: leaf mass:area ratio (LMA), leaf nitrogen content per unit mass ( $N_{\text{mass}}$ ) and N content per unit area ( $N_{\text{area}}$ ). To examine whether there may be evidence for a genetic basis underlying the trait variation, we conducted a review of published results from common garden experiments that measured the same leaf traits.
3. Within studies, LMA and  $N_{\text{area}}$  tended to decrease with mean annual temperature (MAT) along elevational gradients, while  $N_{\text{mass}}$  did not vary systematically with MAT. Correlations among pairs of traits varied significantly with MAT: LMA was most strongly correlated with  $N_{\text{mass}}$  and  $N_{\text{area}}$  at high-elevation sites with relatively lower MAT. The strengths of the relationships were equal or greater within species relative to the relationships among species, suggesting parallel evolutionary dynamics along elevational gradients among disparate biomes. Evidence from common garden studies further suggests that there is an underlying genetic basis to the functional trait variation that we documented along elevational gradients.
4. Taken together, these results indicate that environmental filtering both selects locally adapted genotypes within plant species and constrains species to elevational ranges based on their ranges of potential leaf trait values. If individual phenotypes are filtered from populations in the same way that species are filtered from regional species pools, changing climate may affect both the species and functional trait composition of plant communities.

**Key-words:** community structure, elevational gradient, environmental filtering, functional traits, intraspecific variation, leaf nitrogen, LMA, meta-analysis, phenotypic plasticity, plants

### Introduction

Understanding variation in functional traits among organisms enables ecologists to make predictions about community structure (McGill *et al.* 2006), to describe factors

influencing the geographical ranges of species (Kelly *et al.* 2003; Westoby & Wright 2006) and to infer why processes such as nutrient cycling and plant productivity vary among systems (Díaz & Cabido 2001). In most ecosystems, the environment can act as a selective filter on plant species along abiotic gradients. This process, often referred to as abiotic filtering, mediates the assembly of

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plant communities so that species with similar functions tend to co-occur more often than would be expected by chance (Keddy 1992; Weiher, Clarke & Keddy 1998; Kraft, Valencia & Ackerly 2008; Swenson & Enquist 2009). For instance, to cope with abiotic gradients across elevations, plants in disparate taxa have evolved parallel morphological and physiological traits at high and low elevations (Clausen, Keck & Hiesey 1940; Ackerly & Reich 1999; Swenson & Enquist 2007). Despite the apparent ubiquity of variation in plant functional traits with elevation, and the growing literature documenting patterns along single elevational gradients, global-scale analyses are needed to show repeated elevational gradients in form and function within and among species across systems that may point to universal underlying mechanisms (Poorer *et al.* 2009; Körner 2012). To assess whether such patterns in form and function are similar, both within and among species and across disparate systems, we conducted a meta-analysis that focused on a few key leaf functional traits from the leaf economics spectrum (Reich, Walters & Ellsworth 1997; Wright *et al.* 2004, 2005).

#### KEY FUNCTIONAL TRAITS ALONG ELEVATIONAL GRADIENTS

A global spectrum of morphological and chemical leaf traits, often referred to as the leaf economics spectrum, spans a continuum of plant life-forms and life histories (Reich, Walters & Ellsworth 1997; Wright *et al.* 2004, 2005). Generally speaking, fast-growing species with a resource-acquisitive life strategy tend to have short-lived leaves, while slow-growing, conservative species invest more resources into thick, durable leaves. Leaf mass:area ratio (LMA) and leaf nitrogen (N) content per mass ( $N_{\text{mass}}$ ) and per area ( $N_{\text{area}}$ ) are correlated with relative growth rate and serve as cornerstones of this trait spectrum. Species exhibiting the acquisitive syndrome tend to have lower LMA, higher  $N_{\text{mass}}$  and lower  $N_{\text{area}}$  than conservative species (Shipley *et al.* 2006). A principal component analysis of the GLOPNET data base, including plant trait values from a variety of ecoregions and growth forms, showed that roughly three-quarters of trait variation was loaded onto a single axis, which differentiated acquisitive species from conservative species, including significant loadings on LMA and  $N_{\text{mass}}$  (Wright *et al.* 2004). The GLOPNET analysis suggests that easily measured traits on which a number of researchers have collected data can provide ecologically relevant information on the life-history strategies of plants and their contribution to ecosystem functioning.

The trade-off between competitiveness for limiting resources and stress tolerance mediates the assembly of at least some plant communities and may be responsible for functional trait gradients observed along latitudinal (Stott & Loehle 1998) and elevational gradients around the globe (Cornwell & Ackerly 2009; Körner 2012). Of course, the plants are not responding to latitude or elevation directly,

but rather to a suite of factors that covary with latitude and elevation. For instance, as elevation increases, temperature and atmospheric pressure decrease, and clear-sky solar radiation increases, although mountain ranges around the world exhibit different trends of moisture, growing season length and cloudiness (Körner 2007). Despite the variability in elevation-climate relationships, it may be that at lower elevations, conditions tend to favour acquisitive species that can take advantage of high resource levels, since higher temperature stimulates microbial activity and increases resource availability (Raich & Schlesinger 1992). Conversely, at higher elevations, harsh environmental conditions and lower resource availability promote stress-tolerant species that invest more carbon on a per-leaf basis (Körner *et al.* 1989; Körner 2012). Therefore, we expect individual plants at higher elevations to have increased LMA, increased  $N_{\text{area}}$  and decreased  $N_{\text{mass}}$  relative to low-elevation individuals.

Variation in plant functional traits along elevational gradients, whether caused by phenotypic plasticity or genetic divergence, may influence how communities and ecosystems respond to global change. The resource conservation-acquisition trade-off, for which LMA and leaf N may represent useful proxies, is critical in predicting the responses of plant species to changing environmental conditions (Suding *et al.* 2008; Bardgett & Wardle 2010; Reu *et al.* 2011). Spatial variation in plant traits along elevational gradients may parallel trends associated with ongoing and projected anthropogenic climate warming (Dunne *et al.* 2004; Fukami & Wardle 2005), which is predicted to affect the functional trait composition of plant communities (Suding *et al.* 2008). The degree to which genetic variation and phenotypic plasticity are responsible for variation in plant traits will influence the responses of plants to climate change: phenotypic plasticity will allow short-term responses to abiotic changes, while genetic variation may permit evolutionary responses to abiotic changes.

Based on predictions made by leaf economics spectrum theory, LMA and  $N_{\text{area}}$  should increase with elevation and that  $N_{\text{mass}}$  should decrease, and that the mechanisms contributing to these patterns would include phenotypic plasticity, genetic divergence within a species and changing species composition along gradients of elevation. We hypothesized that intraspecific and interspecific variation would contribute roughly equally to elevational patterns in functional traits, because particular species and functional trait compositions are ultimately the result of filtering processes acting on individuals (Lavorel & Garnier 2002). We further hypothesized that parallel evolution, the independent evolution of similar phenotypes in response to similar selective pressures, is largely responsible for parallel trait patterns along elevational gradients. Previous studies have documented parallel evolution in a variety of organisms both within and across species (Schluter & McPhail 1992); parallel genetic changes in different populations often give rise to parallel changes in interspecific interactions and

ecosystem properties (Fussmann, Loreau & Abrams 2007; Harmon *et al.* 2009; Agrawal *et al.* 2013). The role of parallel genetic divergence relative to phenotypic plasticity in causing patterns of trait variation that are similar across plant functional types and biomes can be determined using common garden experiments, reciprocal transplants or hybridization studies (Clausen, Keck & Hiesey 1940; Whitham *et al.* 2006).

Using a meta-analysis approach (Borenstein *et al.* 2009), we assessed whether general patterns of variation exist in key plant functional traits along elevational gradients. Trait values that vary consistently with elevation would suggest that abiotic factors associated with elevation, particularly temperature, represent a selective gradient to which plants respond consistently. In addition, we asked whether variation within species was greater than variation among species assemblages. Finally, we conducted a qualitative review of experimental common garden studies to test the hypothesis that genetic divergence explains a significant proportion of intraspecific variation in important plant functional traits.

## Materials and methods

### TRAIT SELECTION

We selected three leaf functional traits for analysis based on the availability of data and their significant association with the resource conservation-acquisition trade-off axis. LMA,  $N_{\text{mass}}$  and  $N_{\text{area}}$  are relatively easy to measure (Pérez-Harguindeguy *et al.* 2013) and are associated with plant resource acquisitiveness and stress tolerance (Grime 1977; Shipley *et al.* 2006; Poorter *et al.* 2008, 2009), composite traits that are difficult or impossible to measure (Wright *et al.* 2004, 2005). While natural selection does not operate at the level of traits or even trait syndromes, functional trait approaches provide insight into selective processes occurring at the individual-fitness level that scale up to higher levels of organization (Violle *et al.* 2007). LMA is the product of leaf thickness and density, increasing with the proportion of leaf biomass that consists of cell wall (Niinemets 2001; Poorter *et al.* 2009). Leaf N content corresponds to the amount of protein and other secondary compounds present within the leaf, which are necessary for photosynthesis and growth (Wright *et al.* 2004). Leaves with high LMA are more tolerant of abiotic stress including cold temperatures (Poorter *et al.* 2009). However, high-elevation plants that have high LMA due to increased leaf tissue thickness experience constraints on their maximum photosynthetic rate per unit area due to diffusion and shading constraints in the interior of the leaf (Körner & Diemer 1987; Poorter *et al.* 2009). Therefore, high-LMA leaves are constrained to have low N content per unit mass and long life spans to repay leaf construction costs (Reich, Walters & Ellsworth 1997). For these reasons, we selected studies where LMA,  $N_{\text{mass}}$  or  $N_{\text{area}}$  were sampled along elevational gradients for the meta-analysis.

### LITERATURE SEARCH

In March 2012, we conducted a literature search on Web of Knowledge and Google Scholar, using combinations of the search terms plant, trait, altitude and elevation. After screening the initial list of over 10 000 articles generated by our data base searches and retaining only studies that measured plant functional traits at

multiple elevations, we selected additional literature from parent and child citations, that is, articles that cited or were cited by articles on the reduced list. For each published study, we recorded the identities of the focal species, the traits measured, whether variation was examined within or among species, the number and elevations of sites sampled, the mean latitude of the gradient, the number of individuals sampled at each site and the plant functional types represented in the study: angiosperm tree, conifer, fern, forb, graminoid, legume or shrub (see Table S1, Supporting information). In addition, we extracted the raw trait data where possible.

We modelled mean annual temperature (MAT) and precipitation at all the study sites by georeferencing all site coordinates, extracting elevation, temperature and precipitation data from the SRTM (Jarvis *et al.* 2008) and Bioclim (Hijmans *et al.* 2005) data sets over a rectangular area spanning  $1^\circ \times 1^\circ$  at 0.5' resolution, then generating functions relating elevation and MAT (McCain & Colwell 2011). MAT showed a significantly negative relationship with elevation in every case, but mean annual precipitation did not vary consistently, with a positive trend at 61 of the 116 study sites and a negative trend at 55 of the sites (data not shown). We analysed 46 independent regressions of LMA on MAT modelled as a function of elevation using data extracted from 29 papers, 39 regressions of  $N_{\text{mass}}$  (23 papers) and 29 regressions of  $N_{\text{area}}$  (16 papers; see Appendix S1, Supporting information). Our analysis was global in scope, including study sites distributed across a wide range of latitudes and both hemispheres (see Fig. S1, Supporting information).

We conducted an additional literature search using the terms common garden, genetic, plant, trait, leaf nitrogen and leaf area. We compiled a second data base of studies in which plants from a single species collected at multiple sites along an elevational or latitudinal gradient were grown under controlled environmental conditions in a common garden, and where the investigators measured LMA,  $N_{\text{mass}}$  and  $N_{\text{area}}$ . This data base included the focal species, the traits measured, the number of sites sampled and the statistical technique used to test the hypothesis that populations at different elevations vary genetically (see Appendix S2, Supporting information).

### META-ANALYSIS OF TRAIT-ELEVATION RELATIONSHIPS

For each study, we obtained the correlation coefficient, Pearson's  $r$ , of the trait regressed on MAT along the elevational gradient and used it to calculate the effect size for that study. The effect that each study estimated was a correlation or relationship between MAT and a leaf trait. The Pearson's  $r$  is a standardized estimate of the strength of that relationship. When transformed to an effect size  $z$ , it can be compared among studies, and the mean effect size among many studies can be estimated. If necessary, we extracted raw elevation and mean trait values from tables or scatter plots using GETDATA GRAPH DIGITIZER 2.24 software (Fedorov 2008) and calculated  $r$  from the raw data. We calculated degrees of freedom from the number of sampling sites along the elevational gradient, instead of treating each sampled individual as independent. Averaging trait values at each site in this way ignores variation within a site, avoiding inflation of degrees of freedom at the expense of increasing the absolute value of the effect size estimate. We calculated the variance around each effect size estimate using the formula  $v_i = \frac{1}{n_i - 3}$ , where  $n_i$  is the number of sites sampled in study  $i$  (Zar 1999).

We transformed effect sizes using Fisher's  $r$ -to- $z$  transformation,  $z = \tanh^{-1}r$ , to ensure that the distribution of effect sizes approximated a normal distribution (DeCoster 2004), and conducted a random-effects meta-analysis on the transformed correlation coefficients (Field 2001). A random-effects meta-analysis

assumes that the true effect size differs among studies and weights each effect size with a parameter accounting for variance across effect sizes (see Appendix S3, Supporting information). We back-transformed all mean effect sizes to  $r$  values for ease of interpretation.

We also investigated trends in the pairwise relationships among all three trait pairs using a moving-window regression analysis (Loader 1999). The pairwise data included all studies within the meta-analysis that measured two or more traits at each site (16 studies for LMA:N<sub>area</sub>, 19 for LMA:N<sub>mass</sub> and 15 for N<sub>mass</sub>:N<sub>area</sub>). We sorted data points by modelled MAT, and we calculated the correlation coefficient  $r$  between the two traits at each point within a surrounding bandwidth of 10 data points. The moving-window regressions used estimated mean annual temperature values as a predictor instead of elevation so that we could compare elevational gradients across all latitudes. We fit linear and quadratic regression models to the moving-window coefficients for each trait pair and selected the best model using Akaike's information criterion (AIC).

#### SOURCES OF VARIATION IN EFFECT SIZE

We constructed generalized linear models with plant functional type, latitude, elevational range, minimum elevation and type of variation (within or among species) as predictors, then used a stepwise model selection procedure based on AIC to find the best reduced models. We conducted  $z$ -tests for effect size heterogeneity (Borenstein *et al.* 2009) to compare the weighted mean effect sizes among groups of studies. Finally, we assessed publication bias using a number of tests. We found only limited evidence for publication bias in favour of positive results in LMA studies, and no evidence for bias in N<sub>mass</sub> or N<sub>area</sub> studies (see Appendix S4, Supporting information). All analyses were done using R 2.14.1 (R Development Core Team 2011), including the packages meta (Schwarzer 2012) and raster (Hijmans & van Etten 2013).

#### REVIEW OF EXPERIMENTAL STUDIES

We did not conduct a quantitative meta-analysis of the common garden and reciprocal transplant studies due to low availability of published data. Instead, we determined whether each study reported significant genetic effects among elevations, using F-statistics from analyses of variance or correlation coefficients from linear regressions. We used a vote-counting approach (DeCoster 2004) to qualitatively assess the genetic basis of variation in LMA, N<sub>mass</sub> and N<sub>area</sub> across elevations.

## Results

Overall, we found that (i) LMA and leaf N content varied with mean annual temperature along elevational gradients in similar fashion among plant species, (ii) both intraspecific and interspecific variation in these traits are of similar magnitude across disparate and extensive elevational gradients and (iii) much intraspecific variation in leaf traits along elevational gradients may be explained by convergent evolution.

#### META-ANALYSIS OF TRAIT-TEMPERATURE RELATIONSHIPS

Across 46 elevational gradients spanning a total of over 4800 m, the mean effect of modelled MAT on LMA was

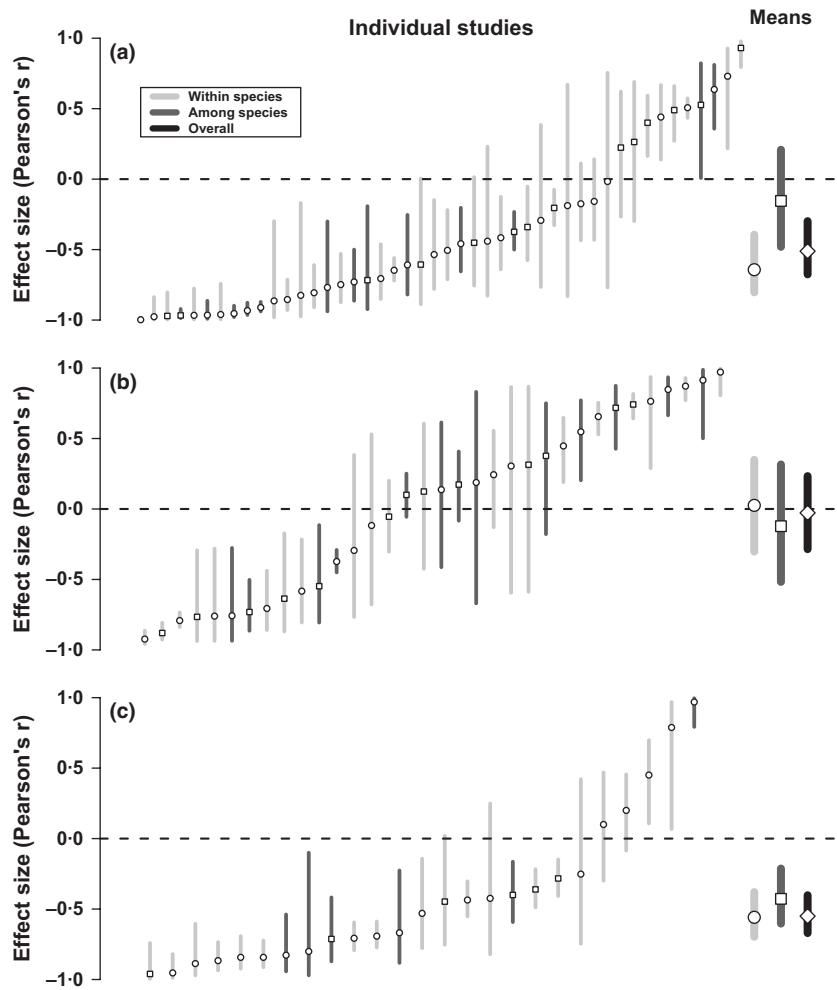
negative [mean  $r = -0.51$ , 95% CI = (-0.30, -0.68),  $P = 1 \times 10^{-6}$ , Fig. 1a]. For N<sub>mass</sub>, the mean effect size did not differ significantly from zero ( $P = 0.84$ , Fig. 1b). On average for each gradient, there was a significantly negative relationship between N<sub>area</sub> and MAT [mean  $r = -0.55$ , 95% CI = (-0.40, -0.67),  $P < 1 \times 10^{-6}$ , Fig. 1c]. The absolute trait values showed only weak trends with MAT when compared among all gradients (Fig. S2, Supporting information).

The strengths of the correlations among each of the three trait pairs changed significantly with increasing mean annual temperature, as revealed by moving-window regression analyses (Fig. 2). A change in the magnitude or direction of pairwise trait relationships across different environments represents strong evidence for environmental filtering across elevations. A quadratic least-squares regression model fit the pairwise trait correlation data best for all three pairs. At sites with lower mean annual temperature, generally corresponding to high elevations, LMA and N<sub>area</sub> tended to be positively correlated, but the positive relationship decreased with increasing temperature ( $r^2 = 0.77$ ,  $P < 1 \times 10^{-6}$ , Fig. 2a). Conversely, at sites with relatively lower temperatures, LMA and N<sub>mass</sub> tended to be negatively correlated, but the correlation tended to approach zero as temperature increased ( $r^2 = 0.24$ ,  $P < 1 \times 10^{-6}$ , Fig. 2b). The relationship between N<sub>mass</sub>:N<sub>area</sub> correlation and mean annual temperature tended to be most positive at intermediate temperature ( $r^2 = 0.39$ ,  $P < 1 \times 10^{-6}$ , Fig. 2c).

#### SOURCES OF VARIATION IN EFFECT SIZE

Studies that measured variation in LMA within species had a significantly more negative mean effect size than did studies that measured community-level variation ( $Z = 2.35$ ,  $P = 0.02$ ). For N<sub>mass</sub>, there was no significant difference between intraspecific and interspecific studies, neither of which had an overall mean effect size different from zero ( $Z = 0.52$ ,  $P = 0.60$ ). Mean effect sizes for N<sub>area</sub> within species and among species were both significantly negative ( $P < 1 \times 10^{-6}$ ,  $P = 1 \times 10^{-6}$ ) and did not differ from one another ( $Z = 0.31$ ,  $P = 0.95$ ).

Plant functional types varied in their average trait response to decreasing MAT with increasing elevation. LMA decreased with increasing MAT in forbs [mean  $r = -0.47$ , 95% CI = (-0.24, -0.65),  $P = 0.002$ ] and angiosperm trees [mean  $r = -0.74$ , 95% CI = (-0.44, -0.90),  $P = 0.0001$ ], with no significant trend in conifers ( $P = 0.81$ ). N<sub>area</sub> was negatively correlated with MAT in forbs [mean  $r = -0.46$ , 95% CI = (-0.27, -0.62),  $P = 2 \times 10^{-5}$ ] and angiosperm trees [mean  $r = -0.65$ , 95% CI = (-0.46, -0.79),  $P < 1 \times 10^{-6}$ ]; as before, conifers showed no trend. No individual functional type showed a significant relationship between MAT and N<sub>mass</sub>. Small sample size in shrubs and graminoids did not permit analysing them separately.



**Fig. 1.** Effect size plots for (a) LMA, (b)  $N_{\text{mass}}$  and (c)  $N_{\text{area}}$ . Points represent Pearson's  $r$  values from each independent regression of trait on modelled mean annual temperature with asymmetrical 95% confidence intervals. Within-species studies are circular points with light-shaded confidence bars, and among-species studies are square points with dark-shaded confidence intervals. The large points at left shows the weighted mean effect size with 95% confidence bar from a random-effects meta-analysis of within-species studies, among-species studies and overall (diamond point with black-shaded confidence bar; LMA,  $n = 46$ ,  $r = 0.51$ ;  $N_{\text{mass}}$ ,  $n = 39$ ,  $r = 0.03$ ,  $N_{\text{area}}$ ,  $n = 29$ ,  $r = 0.55$ ).

Model selection did not show a consistent effect of any one factor in determining variation in effect size across the three traits (see Table S2, Supporting information). For LMA, type of variation (within species vs. among species) explained the most variation in effect size in the best models, with within-species studies having a more negative mean effect size. For  $N_{\text{mass}}$ , plant functional type was retained as a significant predictor in the best models because conifers tended to have a weaker relationship between  $N_{\text{mass}}$  and MAT, while other functional groups tended to have greater  $N_{\text{mass}}$  at low-MAT, high-elevation sites. Finally, for  $N_{\text{area}}$ , only gradient length was retained as a significant predictor in the best models, indicating that studies conducted over a wider range of elevations tended to have larger absolute effect sizes, as expected.

#### REVIEW OF EXPERIMENTAL STUDIES

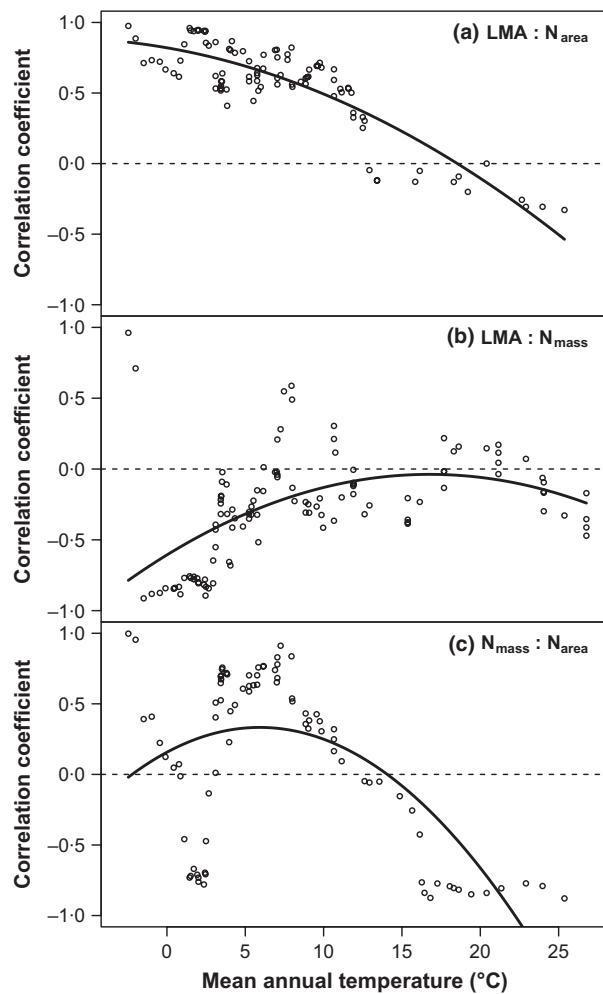
In a majority of the common garden studies we reviewed, genetic divergence among populations from different elevations or latitudes was a significant driver of variation (Fig. 3). Of 17 studies measuring LMA, 13 (76%) showed significant genetic effects. Of 12 studies measuring  $N_{\text{mass}}$ , 9

(75%) showed genetic effects and four of five (80%) studies measuring  $N_{\text{area}}$  showed these effects.

#### Discussion

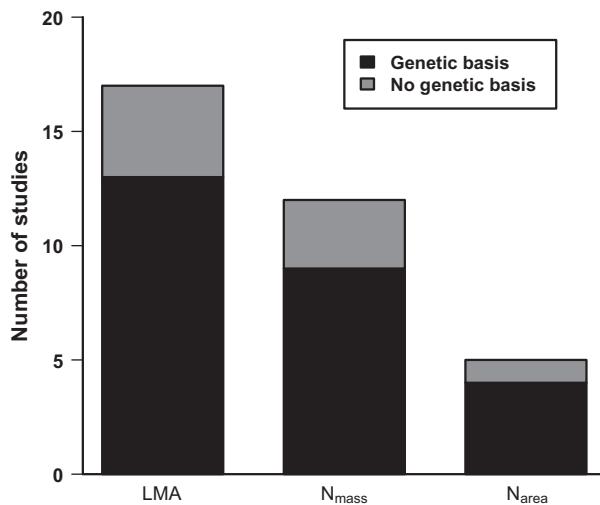
The most salient results of our meta-analysis are (i) general patterns emerge with elevation in leaf economic traits due to consistent abiotic gradients associated with elevation; (ii) trait variation within plant species is equal to or greater than community-level variation, supporting the view that plant community composition is the result of a hierarchy of processes acting on individuals (Sundqvist *et al.* 2011; Kichenin *et al.* 2013); (iii) a significant proportion of the variation observed in the field is driven by genetic effects, consistent with our expectation that parallel evolutionary processes and phenotypic plasticity act in concert to produce functionally meaningful patterns in plant traits.

Across many taxa and systems, LMA was positively associated with elevation; previous studies have found that LMA increases with elevation in alpine plants (Körner *et al.* 1989) and trees (Körner 2012). Furthermore, LMA varies significantly with light, temperature, CO<sub>2</sub> concentration and nutrient stress across plant taxa (Poorter *et al.* 2009), all variables that change with elevation above sea



**Fig. 2.** Moving-window regression plots for (a) LMA:N<sub>area</sub> ( $R^2 = 0.77$ ), (b) LMA:N<sub>mass</sub> ( $R^2 = 0.24$ ) and (c) N<sub>mass</sub>:N<sub>area</sub> ( $R^2 = 0.39$ ). Points represent the correlation coefficient between the two traits at a particular site and the ten surrounding data points, sorted by estimated mean annual temperature. A quadratic trendline was fit to each pairwise comparison.

level. Although LMA in some functional groups increased with elevation (forbs, angiosperm trees) and did not vary in others (conifers), LMA did not decline significantly as elevation increased for any group. Similarly, the meta-analysis of Poorter *et al.* (2009) found that plant functional groups differed in their plasticity with respect to environmental gradients. We found significantly positive trends in LMA not only among populations of the same species, but also among species assemblages at different elevations along a gradient. Increased leaf density that often accompanies increased LMA is associated with a higher percentage of biomass in N-poor cell walls (Craine 2009; Poorter *et al.* 2009). The lack of response in N<sub>mass</sub>, contrary to our hypothesis, suggests that variation in N<sub>mass</sub> is limited by physiological constraints that vary independently of elevation. Coupled with an increase in LMA and N<sub>area</sub> with elevation, constant N<sub>mass</sub> leads to higher C:N ratios in leaf tissue. Elevated C:N ratios in leaves should,



**Fig. 3.** Bar plot showing the proportion of studies that found a significant genetic basis to variation along an elevational or latitudinal gradient from the quantitative reviews of common garden experiments measuring each of the three traits (LMA, 13/17 studies; N<sub>mass</sub>, 9/12 studies; N<sub>area</sub>, 4/5 studies).

in turn, influence foliar herbivory, decomposition, nutrient cycling and transpiration, ultimately feeding back into plant community structure (Bardgett & Wardle 2010). Our pairwise correlation analysis showed that at sites with relatively lower mean annual temperature (at high elevations), LMA and N<sub>area</sub> were more positively correlated and LMA and N<sub>mass</sub> were more negatively correlated, although the trend was relatively weaker for LMA:N<sub>mass</sub>. The tightness of the relationship among traits was strongest where temperature was lowest, providing additional support for the hypothesis that the strength of environmental filters, which operate on whole organisms and not individual traits, changes along environmental gradients.

We found that N<sub>mass</sub> was as likely to decrease with elevation as increase, which may be explained by biological constraints on the range of leaf N content within a species or local community coupled with different optimum N concentrations in different environmental contexts. Although N content in plant tissue is often closely linked with soil N availability, which shows no global trend with elevation (Körner 2007), developmental constraints on high-elevation plants may decouple N<sub>mass</sub> and N<sub>area</sub> from soil N content (Körner 1989), contributing to the trends observed here. In particular, constraints on tissue formation in high-elevation plants may inhibit the dilution of N and other nutrients in leaf tissue (Körner 1989), leading to higher-observed N<sub>area</sub> values and higher metabolic activity per leaf area at high elevations, regardless of the degree of soil nutrient limitation. Below-ground functional traits, such as specific root length or root nutrient content, show similar patterns due to similar constraints on tissue formation and growth resulting from stressful environments at high elevations (Körner & Renhardt 1987; Álvarez-Uría & Körner 2011). Unfortunately, sufficient data do not yet exist to conduct a similar meta-analysis for below-ground traits.

While the overall relationship between elevation and  $N_{\text{mass}}$  was not negative as we predicted, we found that at least two traits which are associated with plant life-history strategies, LMA and  $N_{\text{area}}$  (Wright *et al.* 2004), varied predictably with elevation. This finding lends support to the hypothesis that selection imposed by the environment on linked traits leads to trait convergence along similar environmental gradients. Specifically, selective pressures associated with lower temperatures at higher elevations promote leaf trait syndromes associated with superior stress tolerance but inferior competitiveness; this supports the hypothesis that the role of environmental filtering in community assembly increases with elevation (Callaway *et al.* 2002). However, in many cases, LMA and leaf N content do not fully capture the syndrome of responses exhibited by high-elevation plants; for example, due to colder temperatures and shorter growing seasons at higher elevations, tissue formation is highly constrained (Körner *et al.* 1989). As a result, leaf size tends to decrease with elevation (Körner, Bannister & Mark 1986; Kouwenberg, Kurschner & McElwain 2007; Bresson *et al.* 2011), causing allometric responses in leaf morphological traits including LMA. Although abiotic constraints at high elevations may explain some of the variation we observed without invoking adaptation, our review of common garden studies provides additional support for the existence of adaptive trade-offs along elevational gradients.

In our meta-analysis, population-level variation equalled or exceeded community-level variation along elevational gradients, suggesting a consistent selective effect of environmental factors associated with elevation across multiple levels of organization. The composition of a plant assemblage is the result of a hierarchy of filters that select species and traits from a regional pool over both ecological and evolutionary time, comprising both abiotic filters and biotic interactions (Lavorel & Garnier 2002). Intraspecific variability enables plants to pass through abiotic filters across a wider range of elevations (Jung *et al.* 2010). Intraspecific variation was equal to or greater than interspecific variation, suggesting that the filter imposed by elevation on individual plants may dictate the composition of local communities found along elevational gradients, and that intraspecific variation is an important driver of community structure and ecosystem function.

In general, the consistent responses we observed can be explained by a combination of phenotypic plasticity and genetic variation. Our qualitative review of common garden studies using plants from multiple sites along elevational and latitudinal gradients showed that genetic divergence often explains a significant amount of variation in our three functionally important leaf traits, LMA,  $N_{\text{mass}}$  and  $N_{\text{area}}$ . Genetic variation is essential for plants to adapt to long-term climate change. Phenotypic plasticity is the most important mechanism by which plants can react to short-term environmental changes (Agrawal 2001; Matesanz, Gianoli & Valladares 2010), but if the magnitude of change is severe enough, plastic responses will be insuffi-

cient to cope with change (Valladares, Gianoli & Gómez 2007). Unless the reaction norm evolves to fit the new environmental conditions, the species will suffer long-term fitness consequences or become locally extinct (Sultan 2000). It is important to note that plasticity is itself a trait under genetic control (Schlichting & Pigliucci 1993) and that evolution by natural selection may lead to increased plasticity for important plant functional traits in variable environments and in a changing climate (Agrawal 2001; Matesanz, Gianoli & Valladares 2010).

With climate change, plants are being forced to evolve, move, be plastic or go locally extinct (Bellard *et al.* 2012). For example, movement towards mountaintops and towards the poles is taking place, resulting in the reshuffling of plant genotypes, species and communities on the landscape (Parmesan & Yohe 2003; Beckage *et al.* 2008; Lenoir *et al.* 2008; but see Crimmins *et al.* 2011). Global patterns of plant functional traits with elevation may be useful as a space-for-time substitution to provide insights into the responses of plant species and communities to temporal change caused by humans (Dunne *et al.* 2004; Fukami & Wardle 2005). Plant taxa that show relatively higher levels of genetic and phenotypic variation along elevational gradients may have a higher capacity to respond to global change, in addition to expected uphill or poleward dispersal (Beckage *et al.* 2008; Rapp *et al.* 2012). Physiological changes driven by both genetic divergence and phenotypic plasticity may contribute to the overall response of plant communities to the selective agent of climate change (Bellard *et al.* 2012), just as they determine the ability of plants to pass through existing environmental filters. Regardless of the mechanism, our results indicate that different locally adapted ecotypes, and different species within assemblages, are associated with changes in the abiotic environment along elevational gradients. Our results speak to the paramount role of abiotic filtering in community assembly, with potential implications for changing community structure and ecosystem function on a warming planet.

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## Conflict of interest

The authors declare no conflict of interest.

## Data accessibility

Data are accessible at <http://dx.doi.org/10.5061/dryad.4q2f3> (Read *et al.* 2013).

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## Supporting Information

Additional Supporting Information may be found in the online version of this article:

**Appendix S1.** References from the meta-analysis.

**Appendix S2.** References from the review.

**Appendix S3.** Mathematical formulae used.

**Appendix S4.** Assessment of publication bias.

**Fig. S1.** Maps of study locations.

**Fig. S2.** Meta-regression plots for each trait.

**Table S1.** Summary information about each study.

**Table S2.** ΔAIC values of GLMs.