Linking performance trait stability with species distribution: the case of *Artemisia* and its close relatives in northern China

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Abstract

Aims: Understanding the relationship between species and environments is at the heart of ecology and biology. Ranges of species depend strongly on environmental factors, but our limited understanding of relationships between range and trait stability of species across environments hampers our ability to predict their future ranges. Species that occur over a wide range (and thus have wide niche breadth) will have high variation in morpho-physiological traits in response to environmental conditions, thereby permitting stability of performance traits and enabling plants to survive in a range of environments. We hypothesized that species' niche breadth is negatively correlated with the rate of performance trait change along an environmental gradient.

Location: Northern China.

Methods: We analysed standing biomass and height of 48 species of Asteraceae (*Artemisia* and its close relatives) collected from 65 sites along an environmental gradient across northern China.

Results: In support of our hypothesis, there were significant negative correlations between climatic niche breadth and rate of change in biomass, a performance trait, but not in height, which is both a morphological and a performance trait.

Conclusions: These findings have implications for risk assessment of species under climate change and prediction of unknown distributions of species. They also offer a new avenue of research for species distribution models.

Introduction

Scientists have long observed consistent relationships between species' phenotypic properties (traits), distributions and the environment (e.g. Westerman & Lawrence 1970; Chapin et al. 1993; Grime et al. 1997; Cornelissen et al. 2003; Gilbert & Lechowicz 2004; Guisan & Thuiller 2005; Elith & Leathwick 2009), which helps to understand and predict how species are spatially and temporally distributed. How species are sorted over an environmental gradient reflects the interplay of a large number of geographic, environmental and biotic processes operating over multiple scales of space and time (Maurer & Taper 2002; Shipley et al. 2006; Elith & Leathwick 2009; Laughlin et al. 2012; Ulrich et al. 2014), making it extremely difficult to accurately predict species distributions (Buckley et al. 2010).

For plants, genetic constraints on the values of their functional traits limit the range along environmental gradients within which they can obtain sufficient resources for growth and survival, thus determining species distribution (Violle et al. 2007; Russo et al. 2010). Research on species traits and environments has yielded several important findings. (1) Much of the trait variation reflects the direct effects of environment on plant growth and development (Ackerly et al. 2000). (2) Covarying traits are considered evidence of coordinated ecological strategies (Westoby et al. 2002; Reich et al. 2003). (3) A species' trait values have implications for both species interactions and ecosystem processes (McGill et al. 2006; Cornwell & Ackerly 2009). Furthermore, global trends in trait variation are congruent with species distributions along environmental gradients (Cornwell & Ackerly 2009).

Because traits are selected along environmental gradients over evolutionary time, trait-based approaches may simultaneously offer prediction and explanation for community ecology (Ackerly et al. 2000; Webb et al. 2010; Laughlin et al. 2011; Laughlin 2014). Trait–environment relationships also form the basis for predicting shifts in species distributions in response to on-going global change (McGill et al. 2006; Laughlin et al. 2011; Schwilk & Caprio 2011). Yet, to date, no hypothesis has been proposed to explain the relationships between species distribution and trait stability along environmental gradients. Furthermore, no study has quantified the relationship between species' ranges and the way their traits respond to environmental variables, which is the primary aim of our study.

Our research is based on a hierarchical perspective on plant traits: both functional and performance traits are considered in evaluating plant performance and individual fitness. The plant functional trait concept has been widely used in plant ecology (e.g. Díaz & Cabido 2001; Lavorel & Garnier 2002; Kattge et al. 2011), and it refers to any trait that impacts fitness indirectly via its effects on growth, reproduction and survival (Violle et al. 2007). Following a framework of performance paradigms first proposed by Arnold (1983), Violle et al. (2007) suggested three performance traits for plants that directly determine fitness: vegetative biomass, reproductive output and survival. They also proposed that these three performance traits are influenced by functional traits, i.e. morphological, physiological and phenological traits operating from cell to whole plant levels; and that vegetative biomass represents the net cumulative outcome of all growth and loss processes. Plant height is a central aspect of plant ecological strategies and is a major determinant of a species' ability to compete for light (Westoby et al. 2002; Moles et al. 2009). The height of a plant observed in the field is determined both by its genetically determined species-specific maximum height and by environmental drivers that constrain the phenotypic expression of plant height (Moles et al. 2009; see also Table 4 in Kattge et al. 2011). For allometric reasons, it also tends to scale with plant above-ground biomass (Niklas 1994). Thus, plant height is both a morphological and a performance trait.

Following from the above, correlations between species distributions and the abiotic environment are used to calculate and predict species geographic ranges. But it is inherently difficult to predict species distributions in practice because community assembly depends not only on abiotic but also on biotic factors. It is now known that trait variation correlates with environmental variation and thereby determines range limits. Yet, we have a very limited understanding of the variation of the relationships between traits and environments both at the interspecific and intraspecific level, because we still know little about the way in which species' traits react to changes or variation in the environment. Ecologists have long recognized two general ways in which species react to changing environments: (1) developmental stability (Westerman & Lawrence 1970), i.e. a genotype produces a particular phenotype that can buffer against environmental variation, while the genotype itself is subject to natural selection; and (2) developmental flexibility (plasticity; Thoday 1953), i.e. a genotype develops different phenotypes in different environments. At the species level, morpho-physiological traits collectively influence performance traits that determine species' fitness (Arnold 1983; Violle et al. 2007). Keeping in mind such hierarchical nature of traits, we can expect that species that occur over a wide environmental range will have high (genetic or plastic) flexibility in morpho-physiological traits, which will enable successful adaptation to different environmental conditions. This flexibility of morpho-physiological traits permits the stability of performance traits (such as vegetative biomass, reproductive output, plant survival, etc.) enabling plants

to survive and replace themselves in a range of different environments (cf. Ackerly et al. 2000).

Therefore, the sensitivity of a performance trait to environmental conditions may determine the range of these species' distributions. Given the positive relationship between species distribution range and niche breadth (Slatyer et al. 2013), the rate of performance change should also determine niche breadth of these species. If a set of species has similar performance trait range and these species reach a maximum performance trait value within their range, a species that has a steeper response of performance traits to environmental conditions will have a narrower niche breadth along an environmental gradient than a species that has a shallower response (Fig. 1a). Hence, we can hypothesize that the relationship between niche breadth and relative performance trait response to the environment should be negative: the less a performance trait varies along environmental gradients or geography, the wider the species distribution and niche breadth (Fig. 1b). This negative relationship will also be true if, as is likely in the real world, different species occupy different sections of the overall performance trait range or overall niche range seen across all species that are compared (e.g. Species 1 vs 2 and 3 in Fig. 1a).

To test this hypothesis, we quantified the stability of biomass and height in 48 *Artemisia* species and their close relatives collected along a climatic gradient across northern China, to determine the relationships between climatic niche breadth and the rate of trait change for each species. *Artemisia* species and their close relatives are widely distributed in China, making them suitable for testing hypotheses relating to niche breadth. We used closely related species to partially control the effects of phylogeny and life form on the trait change along environmental gradients.

Methods

Plant collection and trait measurements

We collected 48 species of *Artemisia* (Asteraceae) and its close relatives (*Ajania, Filifolium, Hippolytia, Neopallasia* and *Seriphidium*) from 65 sites across northern China in August and early September 2012 (Fig. 2, Appendices S1 and S2). Recent molecular phylogenetic data, together with other characters, have suggested that *Neopallasia* and *Seriphidium* are nested within the genus *Artemisia* (Oberprieler et al. 2009; Pellicer et al. 2011). However, *Ajania, Filifolium* and *Hippolytia* are related to but distinct from *Artemisia*. Our sampling locations were selected to cover a range of environmental conditions, although they did not cover the entire distribution ranges of these species. We collected plants from natural vegetation and recorded altitude, latitude and longitude of each location.
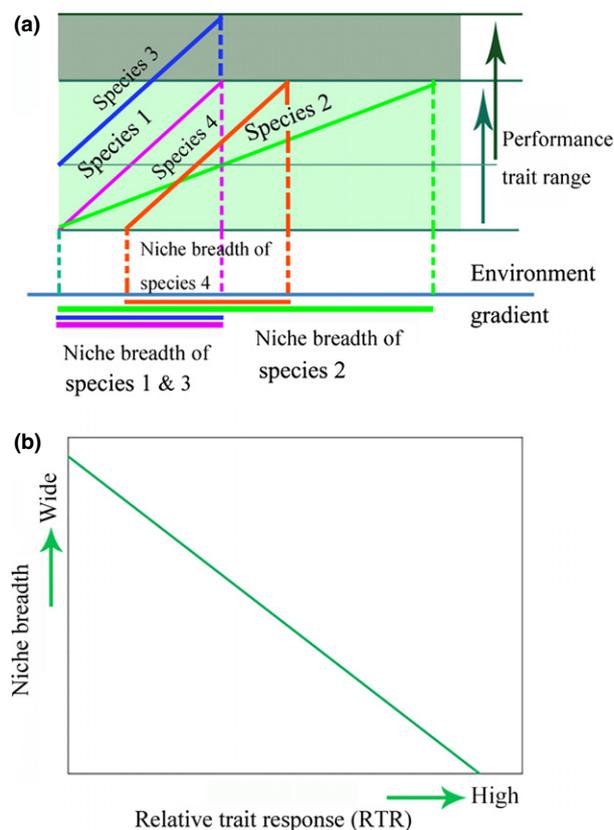

Fig. 1. Relationships between an environmental gradient, performance trait stability and niche breadth. (**a**) Four illustrative hypothetical cases of relationships between species trait stability and niche breadth along an environment gradient. Species 1, 3 and 4 have steeper response with changing environmental conditions than Species 2 does, resulting in narrower niche breadth along the environment gradient. (**b**) The relationship between relative trait response (RTR, see Methods for the definition) and niche breadth implied by (**a**). Note that the relationship may not necessarily be linear.

Temperature, precipitation and bioclimatic parameters were derived from the WorldClim data set (Hijmans et al. 2005). Most plants (>95%) were fully mature (in flowering stage) at sampling time, and plants that had been damaged by herbivores were excluded. Because biomass and height continue to increase with age, even while flowering, mature individuals, perennials and shrubs <3 years old (mostly in their second year; age determined by counting bud scale scars on the stem) were sampled to account for the age or size effects. In addition, even within species and individuals traits can change drastically throughout the growing season (Dubey et al. 2011; McKown et al. 2013). Since we collected plants at the same fully mature stage and the sampling period was relatively short in this study, sampling time probably did not affect the appearance of the trait–environment relationship substantially. Species nomenclature followed

the Flora of China (ECCAS 1974–1999). In each location, three 10 m × 10 m plots were divided into 100 1 m × 1 m subplots, and we haphazardly sampled (mostly three) individuals of each species in at least three subplots (Appendix S3). A total of 585 individuals were sampled at the 65 locations. Plant height of sampled individuals was determined using a meter stick. We collected entire plants above ground, and above-ground biomass (a performance trait) was measured to the nearest 0.0001 g using an analytical balance (Sartorius Group, DE) after oven-drying for 48 h at 65 °C.

Statistical analyses

Plant biomass and height were $\log_{10}$-transformed before analysis to improve the normality of the residuals. To identify environmental gradients in the climate data, a principal components analysis (PCA) was performed using the function princomp from the R-package stats (R Foundation for Statistical Computing, Vienna, AT). To determine which PCA components were significant, PCAsignificance function in R package BiodiversityR was performed after the climate data were analysed by RDA function. We then used a multiple regression analysis (the lm function in R) to identify the relationship between the first three PCA axes and the two plant traits (height and biomass) of all 48 species. Graphs of traits against PCA axis did not suggest non-linearity or humped relationships. Additionally, Bayesian information criterion (BIC) value for the linear model and of biomass with the three PC axes (493.07) was lower than that for a nonlinear model of a quadratic term (502.16), which
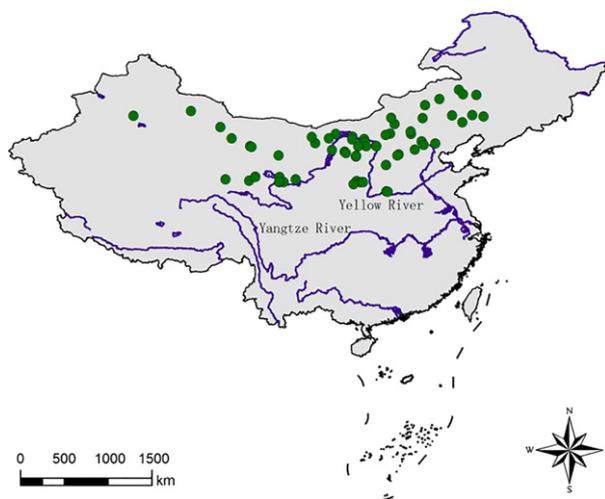
was also true for height (linear: −303.40; nonlinear: −304.78), indicating a better fit of linear models.

To further reveal the relationships between climatic gradients and plant traits for each species, analysis of covariance (ANCOVA; Crawley 2005) was conducted to compare regression slopes of the 17 species (16 *Artemisia* and one *Neopallasia* species) that occurred at more than three locations. To compare the trait response of different species to the PCA axes, we calculated the relative trait response (RTR) of each species as:

$$\text{RTR}_i = \sum\nolimits_{j=1}^{k} |\text{slope}_{ij}| / \left(\frac{1}{n} \times \frac{1}{k} \times \sum\nolimits_{i=1}^{n} \sum\nolimits_{j=1}^{k} |\text{slope}_{ij}| \right)$$

where $|\text{slope}_{ij}|$ is the absolute value of the regression slope of species i to PCA axis j from ANCOVA. Since the PCA axis scores are calculated from correlation matrices, variables are standardized relative to their respective SD, permitting a comparison of slopes of different PCA axes. The absolute value was used because the regression slope can be either positive or negative. Note that RTR_i is the ratio of the average steepness of the slopes for species i, relative to the average steepness of the slopes of all species (where a steep slope can be either positive or negative). RTR will be >1 for a species with steeper than average slopes and <1 for species with shallower than average slopes along an environmental gradient.

We further calculated the climatic niche breadth (species tolerance) for each species via OMI (outlying mean index) analysis (Dolédec et al. 2000). In this analysis, species with high values of tolerance occur across widely varying environmental conditions (generalists; wide habitat niche breadth), and those with low values occur only across a limited range of conditions (specialists; small habitat niche breadth). This analysis is suitable for describing both unimodal and linear responses of species to environmental gradients (Dolédec et al. 2000; Heino 2005). We then used linear regression to describe relationships between the rate of trait change (RTR, $\log_{10}$-transformed) and climatic niche breadth ($\log_{10}$-transformed) across species.

A potential source of bias in the estimate of RTR is that species occurring over a smaller range of environments and with fewer samples may have a larger standard error of slope. While this does not create any bias in slope estimation, the larger error for species with smaller environmental ranges may result in them having estimated slopes of the wrong sign more often than species with broader environmental ranges. In other words, species with fewer data points may have a larger chance to achieve a wrong slope in estimates of their response to environmental gradients. This could inflate the average of absolute values taken in RTR calculations. To address this potential source of bias we did two things. First, we conducted simulations

Fig. 2. The locations of 65 sampling sites in this study. Each green dot represents a sampling site. See Appendix S1 for more details.

of a null model of the regression of the absolute value of regression slopes vs the range of species niche breadth for randomly generated data sets using random normal distributions of species' ecological ranges and trait values reflective of observed distributions. If the distribution of R^2 for this simulation does not differ significantly from zero, the potential bias is negligible. Second, we repeated the regression of RTR vs true niche breadth, but first truncated the data sets so that all RTR calculations were done with niche breadths set equal to the average niche breadth of the five narrowest species.

Statistical analyses were performed with packages within R v 2.15.2.

Results

The PCA of 19 climatic variables revealed that the first three axes explained 85.7% of the variation in the original climatic variables. After the third axis, variance explained decreased substantially (the fourth axis only explained 8.5% variance). The first three PCA axes were all significant, with higher cumulative percentage of variance than broken-stick cumulative percentage (first: 99.83% vs 51.88%; second: 99.91% vs 59.58%; third: 99.95% vs 66.24%). Annual mean temperature (AMT), minimum temperature of the coldest month (MTCM) and annual precipitation (AP) were the major climatic variables that contributed (all positively) to the first axis. Increasing values for the second axis were associated with the seasonality of temperature and precipitation, and values for the third axis were environmental extremes of temperature and moisture in the wettest and warmest months (Appendix S4). Thus, our sampling sites covered a climatic gradient with important variation in both average temperature and precipitation and seasonality of temperature and precipitation and provided a suitable region to test our hypothesis.

Multiple regression analyses revealed significant relationships between the first three PCA axes and the two plant traits, biomass and height (all $P < 0.01$; Table 1). The first two PCA axes were positively related to biomass, while the third axis showed a negative relationship with biomass. There were overall positive relationships between

the three PCA axes and plant height (Table 1). Although the left-most point in Fig. 3 for height is leveraged, regression did not change after its removal. Furthermore, influences of the PCA axes on the two traits differed among species (Fig. 3).

The ANCOVA revealed that regression slopes differed between species in response to the same environmental gradient (PCA axis) and between different PCA axis scores for the same species (Appendices S5 and S6). This indicates that species respond differently to the environment.

Consistent with our hypothesis, we found significant negative relationships between climatic niche breadth and relative trait response (RTR) estimated from biomass (a performance trait; Fig. 4). The simulations with our null model suggested little bias in the estimates of RTR using absolute slope values (Appendix S7). Also, the relationship between climatic niche breadth and RTR estimated from biomass remained significantly negative when the data sets were truncated to equal ranges before calculating RTR (Appendix S8). Thus, the widely distributed species (i.e. wide niche breadth) would appear to have higher performance trait stability (i.e. smaller RTR) than narrowly distributed ones. In contrast, relationships between climatic niche breadth and RTR estimated from height (which is both a morphological trait and a performance trait) were not significant (Fig. 4). There was no clear difference in trait response–niche breadth between annuals and perennials or in vegetation types (Appendices S2 and S5).

Discussion

Is there a consistent relationship between performance trait stability and climatic niche breadth? Given that performance traits directly measure plant performance that determines fitness of plants over a range of environments, determining how performance traits change along environmental gradients can provide key information about mechanisms underlying species distribution. Here, we hypothesized that species climatic niche breadth should be negatively correlated with the rate of performance trait change along an environmental gradient. We found robust support for this hypothesis with a large, new multi-species

Table 1. Multiple regression analyses of the scores of the first three PCA axes and the two plant traits (biomass and height).

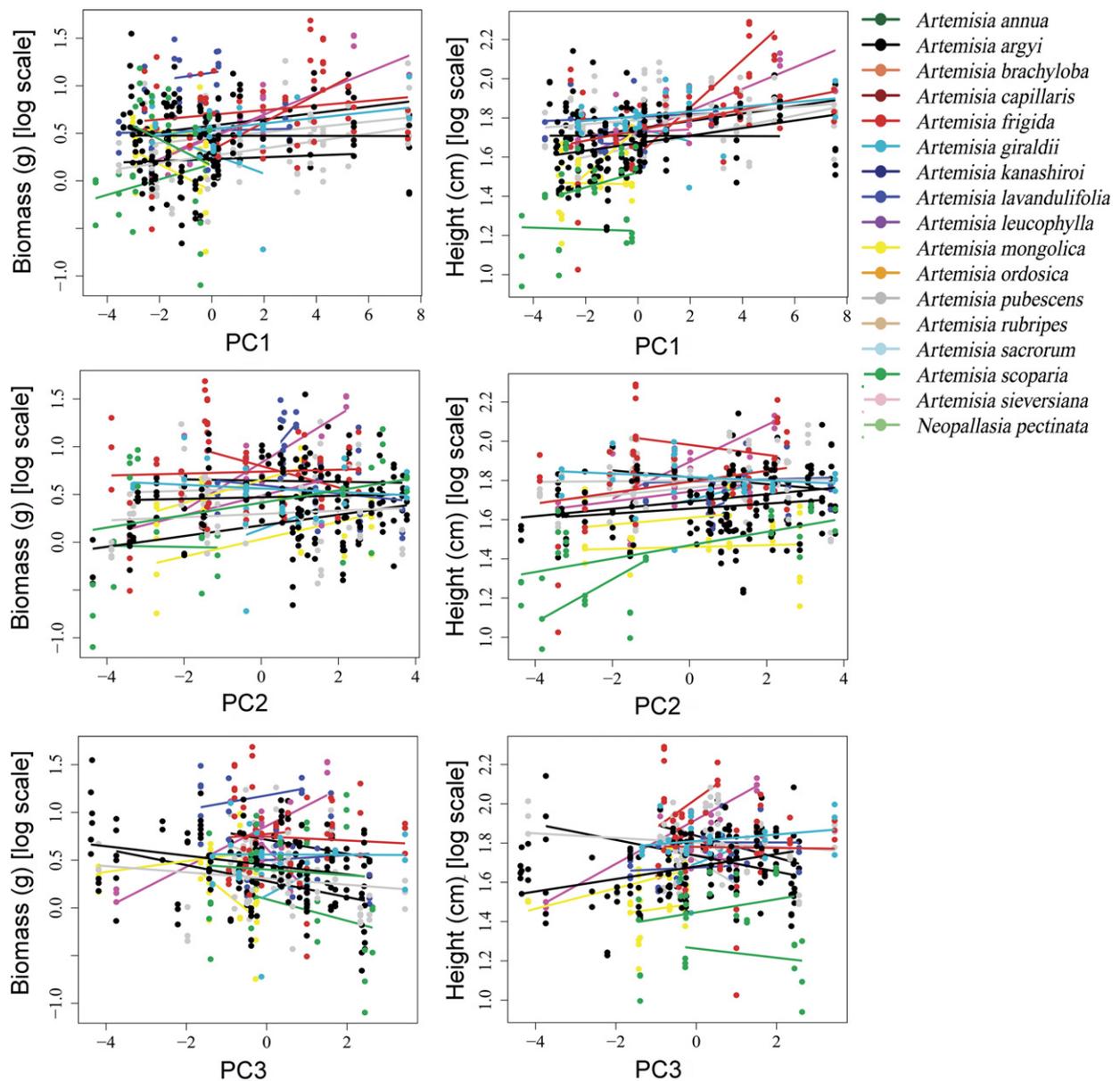| Variables	Biomass			Height		
	Estimate	SE	t-value	Estimate	SE	t-value
Intercept	0.453	0.019	24.315 ***	1.6932	0.0088	212.748***
PC1	0.040	0.0066	6.087***	0.034	0.0029	12.201***
PC2	0.033	0.0086	3.818***	0.023	0.0037	6.155***
PC3	−0.035	0.0118	−2.921**	0.0182	0.0051	3.592 ***

$**P < 0.01$; $***P < 0.001$.

Fig. 3. Relationships between the ranges of values for each of the two plant traits (biomass and height) of each species and the first three PCA axes representing climatic variation across the gradient.

trait data set along a large climatic gradient in China. Thus determination of the rate of performance trait change along environmental gradients may be useful for predicting the size of a species' range. Our approach therefore provides a new perspective for understanding the environment–trait–distribution continuum.

We used a set of phylogenetically related species (*Artemisia* and its close relatives) growing along a climatic gradient in testing our hypothesis. But might more distantly related plants be less likely to show this negative relation between niche breadth and slope of performance trait

response to environmental gradients? In a study of five vegetation types with many distantly related species in 44 plots across coastal California, species that occurred in fewer plots showed steeper slopes of traits (height, seed mass, leaf area, etc.) to environmental gradients than species that occurred in more plots (Ackerly & Cornwell 2007; Cornwell & Ackerly 2009), which is consistent with our hypothesis. Moreover, differential drought sensitivity shapes plant distributions in tropical forests at both regional and local scales (Engelbrecht et al. 2007), and we thus can expect that traits of less drought-tolerant species will
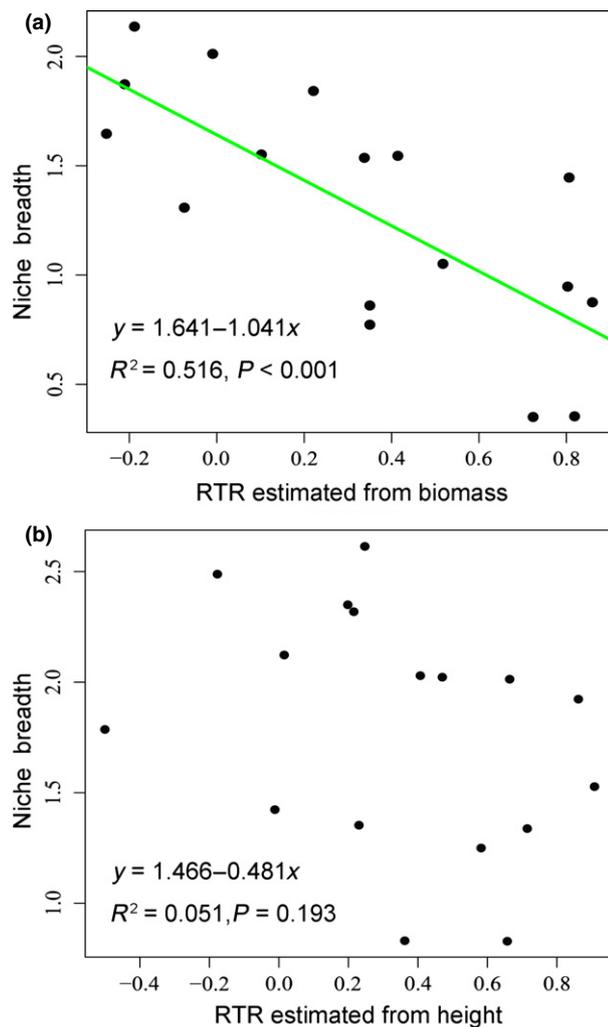
Fig. 4. The relationship between niche breadth and relative trait response (RTR, see Methods for the definition of RTR) estimated from plant biomass (**a**; a performance trait) and height (**b**; both a morphological and a performance trait) for each species. Note that axis values were log-transformed.

have steeper slopes along water availability than those of more drought-tolerant ones. These studies suggest that our hypothesis probably also applies to distantly related taxa and at a range of scales.

Another possible caveat is that we only used climatic variables to describe the environment. Indeed, edaphic and topographic variables may impact the distribution of the species in our study. We used climatic variables based on the knowledge that plants are most intimately connected to climatic conditions through exchanges of energy and mass and that climate exerts the principal control over the distribution of vegetation (Lenoir et al. 2008; Kearney & Porter 2009). It should be noted that our sampled area might cover only a portion of the total distribution range of

some species. Thus, RTR might be different if the entire range were sampled for these species. If so, we suggest further research to sample a larger area when species with wide distribution ranges are involved. For the species sampled in our study, we checked the species distribution range described in the *Flora of China* and found that our sampled individuals per species were proportional to their ranges: species that have wider geographic range have more plants sampled than species that have narrower range. This suggests that our sampling did reflect the real distribution pattern for most species and largely excludes the possibility of a biased estimation of performance traits caused by sampling some species merely on the range edge and others throughout the entire range. This also means that, for the majority of species, our data set likely included values close to the maximum that can be found in nature.

At first glance, our hypothesis may seem to contradict the idea that phenotypic plasticity is an important contributor to ecological range. Biomass can be considered to be a performance trait (*sensu* Violle et al. 2007). If a species has a strong response of performance traits to a gradient, it can mean that it performs poorly in certain environments along the gradient (cf. Violle et al. 2007). However, certain morpho-physiological traits (Agrawal 2001; Lavorel & Garnier 2002; Angert et al. 2007; Violle et al. 2007) may show high plasticity in response to environmental variation. For instance, specific leaf area may be responsive to light or moisture gradients (Poorter et al. 2009), and so its plasticity may help species to be distributed more widely. The distinction between performance traits and morpho-physiological traits may help to reconcile the two theories. However, our analyses do not allow us to determine the mechanisms underlying our hypothesis. We provide two possible underlying patterns: either there is larger performance trait homeostasis for more widespread species, as we have assumed, or performance trait variations along environmental gradients directly reflect a species' adaptability, thus determining the range. These possibilities merit further exploration. In addition, other performance traits (e.g. total seed mass) and morphological traits (e.g. specific leaf area) need to be studied further to confirm our hypothesis.

Our findings have important implications for both conservation biology and ecology. First, we can use the negative relationship for risk assessment under climate change. Climate change has caused changes in species distributions worldwide (Pounds et al. 1999; Root et al. 2003; Lenoir et al. 2008; Bertrand et al. 2011). We can predict from our hypothesis that climate change may have more profound effects on the distribution of species with steeper performance trait gradients than on those with shallower gradients. Second, knowledge of performance trait stability in species with known range sizes

should help in making predictions of range size for species in which range size is not known. However, confounding influences of evolutionary and biogeographic history, as well as human interference, pose challenges to do so reliably. Third, species distribution models (SDMs) are used to make spatial predictions of habitat suitability or probability of species occurrence (McGill et al. 2006; Austin 2007; Webb et al. 2010), but predicting species distribution from traits without any theoretical context has largely failed (Shipley et al. 2006). To represent biota as a continuous distribution of traits can enhance the ability to predict the impact of global change on ecosystem functioning across biogeographic gradients (Violle et al. 2014). Incorporating our hypothesis into SDMs would offer a new avenue for prediction of niche breadth along environmental gradients via performance trait stability. Variable selection is a major issue for SDMs (Guisan & Thuiller 2005; Austin 2007; Kearney & Porter 2009; Laughlin 2014), and likewise not all trait stability is useful for prediction with our framework. Based on our findings, predictions may be more accurate when using performance traits. Also, one trait may integrate a whole suite of traits, and trait–environment relationship may differ for different environmental factors. For example, leaf traits are associated with species distributions on an insolation gradient, but not on an elevation gradient (Ackerly et al. 2002). Thus, selections of appropriate traits and environmental variables are both important. We suggest a two-step procedure: first, select environmental gradients that are relevant to plant performance and reduce the dimensionality with PCA if necessary; second, select the performance traits that exhibit strong relationships along the selected environmental variables.

To conclude, we have proposed, and partly confirmed, a hypothesis that offers a framework for understanding the linkage between species climatic niche breadth and trait stability along an environmental gradient. Further testing is needed to determine how well our hypothesis and approach will stand up across a wider range of phylogenetic distance. When comparing the trait stability including a wide set of species, such as trees and herbs, it is important that RTR should be standardized. In the case of biomass as a performance trait, a species with a large mean biomass might have the same trait–environment slope as a species with much smaller biomass (different intercepts, same slope). The RTRs would be similar, but the species with the smaller mean biomass might actually be more 'responsive' to the environmental gradient because a severe unit biomass increase per environmental unit increase results in a larger proportional increase in biomass relative to the mean trait value for that species. Nonetheless, we believe that the distribution–trait stability relationship will not only help to understand patterns of present-day plant species distribution but also to predict future patterns as influenced by the Earth's fast-changing climate.

Acknowledgements

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Supporting Information

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

Appendix S1. Locations of the sampling sites in this study arranged from west to east in Fig. 2.

Appendix S2. Species collected in this study.

Appendix S3. Sampled plants per species in each site.

Appendix S4. Results of a principal component analysis of values for climatic variables at our sampling locations.

Appendix S5. Slopes and intercepts for regressions of biomass to the first three PCA axes for each species (ANCOVA).

Appendix S6. Slopes and intercepts for regressions of height to the first three PCA axes for each species (ANCOVA).

Appendix S7. The R^2 values of simulations of a null model of the regression of the true value (a) and absolute value (b) of regression slopes (for trait values vs niche breadths of randomly generated data sets) vs the range of species niche breadth for randomly generated data sets using random normal distributions of species ecological ranges and trait values reflective of observed distributions.

Appendix S8. The regression of RTR vs true niche breadth, after first truncating the data sets so that all RTR calculations were done with niche breadths set equal to the average niche breadth of the five narrowest species.