RESEARCH PAPER

Effect of geographical range size on plant functional traits and the relationships between plant, soil and climate in Chinese grasslands

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ABSTRACT

Aim Our aim was to address the potential effect of the geographical range size of species on the relationships between plant traits, soil and climate in Chinese grasslands. Previous analyses tended to examine plant–environment relationships across many species while ignoring that species with different range sizes may respond differently to the environment. Here we hypothesized that leaf traits of narrow-ranging species would be more strongly correlated with soil and climatic variables than those of wide-ranging species.

Location Chinese grasslands.

Methods Data on leaf traits, including nitrogen and phosphorus concentrations, carbon/nitrogen ratio, nitrogen/phosphorus ratio and specific leaf area, as well as species range sizes for 208 species distributed across 178 sites in Chinese grasslands were collected. Soil and climate information for each study site was also gathered. The effects of range size on leaf traits were tested using one-way ANOVA. Correlations between leaf traits, soil and climate were calculated for all species pooled together and for species partitioned into range size quartiles, from the first (narrowest- ranging 25%) to the fourth (widest-ranging 25%).

Results Narrow-ranging species tended to occur at high altitude with lower temperature but higher soil nutrient concentrations compared with wide-ranging species. No direct link between leaf traits and species range sizes was detected. However, patterns of leaf–soil nutrient relationships changed significantly across levels of range size. Narrow-ranging species tended to be more sensitive to variation in soil nutrient availability than wide-ranging species, resulting in a shift from a positive leaf–soil nutrient relationship for narrow-ranging plants to no relationship for wide-ranging plants. Species responses to climatic variables were unrelated to their range sizes.

Main conclusions The close relationship between leaf and soil nutrients indicates a specialization of narrow-ranging species to particular habitats whereas wide-ranging species may be able to better withstand changes in environment such as soil fertility over a large area.

Keywords
Chinese grasslands, climate, Inner Mongolia, leaf functional traits, soil nutrient concentrations, species range size, Tibetan Plateau.

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INTRODUCTION

Since Charles Darwin (1859), biogeographers and ecologists have been fascinated by the question of why some species are widely distributed and abundant while other species have narrow ranges and are rare (e.g. Spalding, 1890; Griggs, 1940; MacArthur, 1972; Brown et al., 1996; Kunin & Gaston, 1997; Jetz & Rahbek, 2002). One of the most striking facts is that as a basic unit of biogeography, the geographical range size (RS) of species, varies dramatically among organisms (Brown et al., 1996). The different RSs of species are believed to relate, at least in part, to ecological strategies (Wilson & Yoshimura, 1994; Pulliam, 2000). As habitat heterogeneity tends to increase with geographical distance, wide-ranging species are usually able to use a wide array of resources and to tolerate broad environmental conditions or physiological stresses, and hence flourish over a larger area; in contrast, narrow-ranging species usually exploit a limited range of resources and adapt to relatively homogeneous environment, and thus are unable to achieve an extensive distribution (Kruckeberg & Rabinowitz, 1985; Futuyma & Moreno, 1988; Thompson et al., 1999; Devictor et al., 2008).

It has been well-documented that plant functional traits usually reflect the adaptation of species to the environment (Chapin et al., 1993; Wright et al., 2004). A question then arises: are there any links between functional traits and species RS? Previous studies have used comparative approaches to test for relationships between plant traits and rarity–commonness (Thompson et al., 1999; Walck et al., 1999; Lavergne et al., 2004; Thuiller et al., 2004). Although a number of plant life-history and ecological attributes have been investigated, no individual trait has been identified to differentiate narrow- and wide-ranging species. Individual traits and trait associations with RS varied substantially for different ecosystems and in different regions and appear to be highly context-dependent (reviewed in Bevill & Louda, 1999; Murray et al., 2002).

Since inherent characteristics of plants do not necessarily reflect species RS (Murray et al., 2002), examining plant–environment interactions may provide some insights into the underlying mechanism. As early as the 19th century, von Humboldt (1814) proposed that relationships between environment and plant traits along environmental gradients could be presented as evidence of environmental control over the distribution of species. Recent studies have assembled considerable data on the correlations between foliar nitrogen (N), phosphorus (P) and soil nutrient supply and showed that the relationships could be either positive or negative, and in many cases no detectable relationship was observed (Güsewell & Koerselman, 2002; Bowman et al., 2003; Parfitt et al., 2005; Frank, 2008). Conventionally, these analyses have looked at overall patterns across many species with different RSs. However, it has been proposed that species with different RSs may respond differently to the environment (Futuyma & Moreno, 1988; Murray et al., 2002). Narrow-ranging species may be more adapted to local habitats and are more likely to be sensitive to environmental changes than wide-ranging species (Thuiller et al., 2005; Broenniman et al., 2006; Devictor et al., 2008). Therefore patterns of species–environment relationships drawn from pooling all species together may suffer from the offset effect among species with different RSs. Moreover, wide-ranging species appear more frequently and are more likely to be investigated than narrow-ranging species. This inconsistency in sampling size has been discussed for birds, with results showing that wide-ranging bird species were more responsible for the observed richness pattern due to sample bias (Jetz & Rahbek, 2002; Lennon et al., 2004), which misrepresents the dynamics of most species in bird research (Kunin & Gaston, 1997). Yet until now, this sample bias has attracted little attention in plant research. Few attempts have been made to examine whether the investigations of plant–environment relationships suffer from the same problem.

Here we addressed the potential effect of species RS on leaf functional traits as well as on the pattern of relationships between leaf traits, soil and climatic variables. Chinese grasslands provide an ideal opportunity for such studies. In the past several years we have systematically collected leaf traits across Chinese grassland biomes (He et al., 2006a,b, 2008, 2009, 2010). At the same time, our research group has built a national database for plant species distributions (Wang et al., 2009). Using both databases, we investigated for the first time the relationships between foliar (N and P) and soil nutrient concentrations (total N, extractable N, total P and extractable P), as well as the response of leaf traits to climatic variables (temperature and precipitation) for species differing in RS across Chinese grasslands. Species were partitioned into RS quartiles, which have been successfully employed in previous bird studies to detect the difference in richness pattern between narrow- and wide-ranging birds (Jetz & Rahbek, 2002). Quartiles range from the first (narrowest-ranging 25% of species) to the fourth (widest-ranging 25% of species). The leaf–soil (and climate) relationships were tested for each quartile. We sought to clarify whether plant responses to changes in soil nutrients and climate are related to species RS. We predicted that narrow-ranging species may be more sensitive to changes in their habitats than wide-ranging species, therefore narrow-ranging species would have a tight coupling between leaf and soil as well as leaf and climate while wide-ranging species may not have such a close relationship. In particular, foliar N and P of narrow-ranging species would be more strongly affected by corresponding soil nutrients compared with wide-ranging species so that the strength of leaf–soil nutrient relationships might decrease from the first to the fourth quartile. By drawing together a large dataset on species RS, leaf traits, soil properties and climatic variables from original measurements with standard protocol rather than the literature, we thoroughly examined whether species RS matters for the sensitivity of the response of plants to changes in soil and climate parameters.

MATERIALS AND METHODS

Site description

The study area encompassed temperate grasslands on the Inner Mongolian Plateau and alpine grassland on the Tibetan Plateau

Table 1 Description of the study regions.

	Overall	Inner Mongolia	Tibetan Plateau
No. of sites	178	66	112
Longitude (°E)	80.75 to 120.12	107.26 to 120.12	80.75 to 101.48
Latitude (°N)	30.31 to 50.19	38.41 to 50.19	30.31 to 37.28
Altitude (m)	553 to 5249 (2998)	553 to 1527 (937)	2925 to 5249 (4195)
MAT (°C)	−9.7 to 11.9 (1.5)	−2.6 to 7.1 (1.2)	−9.7 to 11.9 (1.7)
GST (°C)	−1.0 to 19.6 (10.6)	13.9 to 19.6 (17.0)	−1.0 to 12.0 (6.9)
MAP (mm)	119 to 604 (360)	148 to 436 (298)	119 to 604 (395)
GSP (mm)	91 to 414 (260)	109 to 326 (228)	91 to 414 (278)

Means of altitude, mean annual temperature (MAT), mean annual precipitation (MAP), growing season temperature (GST) and growing season precipitation (GSP) of the sampling sites are shown in parentheses.

(Table 1). Over 178 sites were selected, extending from latitudes 30.31 to 50.19° N and longitudes from 80.75 to 120.12° E, along with altitudes from 553 to 5249 m. Mean annual temperature (MAT) and mean annual precipitation (MAP) ranged from −9.7 to −11.9 °C and 119 to 604 mm, respectively. The vegetation represents natural zonal grassland in these regions, including six main vegetation types: meadow steppe, typical steppe, desert steppe, alpine meadow, alpine steppe and alpine scrubs (Zhang *et al.*, 1988). Field measurements were conducted during late July and early August from 2003 to 2007. Sampling sites were selected by visual inspection of the vegetation, aiming to sample sites subject to minimal grazing and other anthropogenic disturbances (detailed in He *et al.*, 2009, 2010).

Measurement of RS

Species distribution data were compiled using widely accepted national and provincial floras (see Appendix S1 in Supporting Information). Field plant community surveys were also incorporated into the species distribution database. Species ranges were mapped at county level (Appendix S2). For each species, there are complete presence/absence data for every county in China. If a species occurred in one county then its range included the entire area of the county. RS was calculated as the total area of the counties where the species was present. It should be noted that in western China some counties have very large areas, and counting the entire range of these large counties might result in an overestimation of species RS. In order to minimize the effect of this drawback, we further divided each large county into several small units according to the topography and vegetation coverage. To ensure the accuracy of species range data, the distribution map of each species was further verified by local taxonomists. After RS measurement, species were partitioned into RS quartiles, from the first (narrowest-ranging 25%) to the fourth (widest-ranging 25%) (Fig. 1). Each RS quartile contained 52 species.

## Leaf trait measurements and soil survey

A total of 208 species from 100 genera in 33 families were sampled. At each site, leaf samples from 5–10 individuals of each dominant species were collected. A representative subset of fully expanded leaf blades was collected and leaf areas were measured using a portable leaf-area meter (AM200, ADC Bioscientific Limited, Herts, UK). Following area determinations, leaves were oven-dried at 60 °C and weighed to calculate specific leaf area (SLA; leaf area per unit leaf mass, $cm^2\ g^{-1}$). Total carbon (C) and nitrogen (N) concentrations were determined on ground material using an elemental analyser (PE 2400 II CHN elemental analyser, Perkin-Elmer, Boston, MA, USA). Total phosphorus (P) concentrations were measured by a molybdate/stannous chloride method (Kuo, 1996).

At each site three soil pits were excavated to collect samples for analyses of physical and chemical properties. Soil organic carbon (SOC), soil total N (STN) and P (STP), soil extractable N (SEN) and P (SEP), and soil bulk density (SBD) at the depth of 0–10 cm were used as measures of soil fertility. Sampling protocols and analyses for SOC, SBD and STN have been detailed previously (He *et al.*, 2009). SEN was determined photometrically from on-site KCl extractions using a continuous flow analyser (SAN Plus, Skalar, Netherlands) (Baumann *et al.*, 2009). STP was measured from a H_2SO_4 and $HClO_4$ acid digest using a phosphomolybdate blue method. For P extraction, soil samples were extracted with 0.5 M $NaHCO_3$, filtered and analysed for orthophosphate by reaction with acid molybdate and reduction with ascorbic acid (Murphy & Riley, 1962). Soil pH was determined potentiometrically in double-distilled H_2O.

Climate data

The climate data at each site were calculated based on linear models using latitude, longitude and altitude as predictors from 55-year (1951–2005) averaged annual temperature and precipitation records at 680 evenly distributed climate stations across China (Climate Database, National Meteorological Bureau of China). The growing season temperature (GST) (from May to August) and growing season precipitation (GSP) were used in the final analysis to more accurately capture the climatic variation important to plant growth.
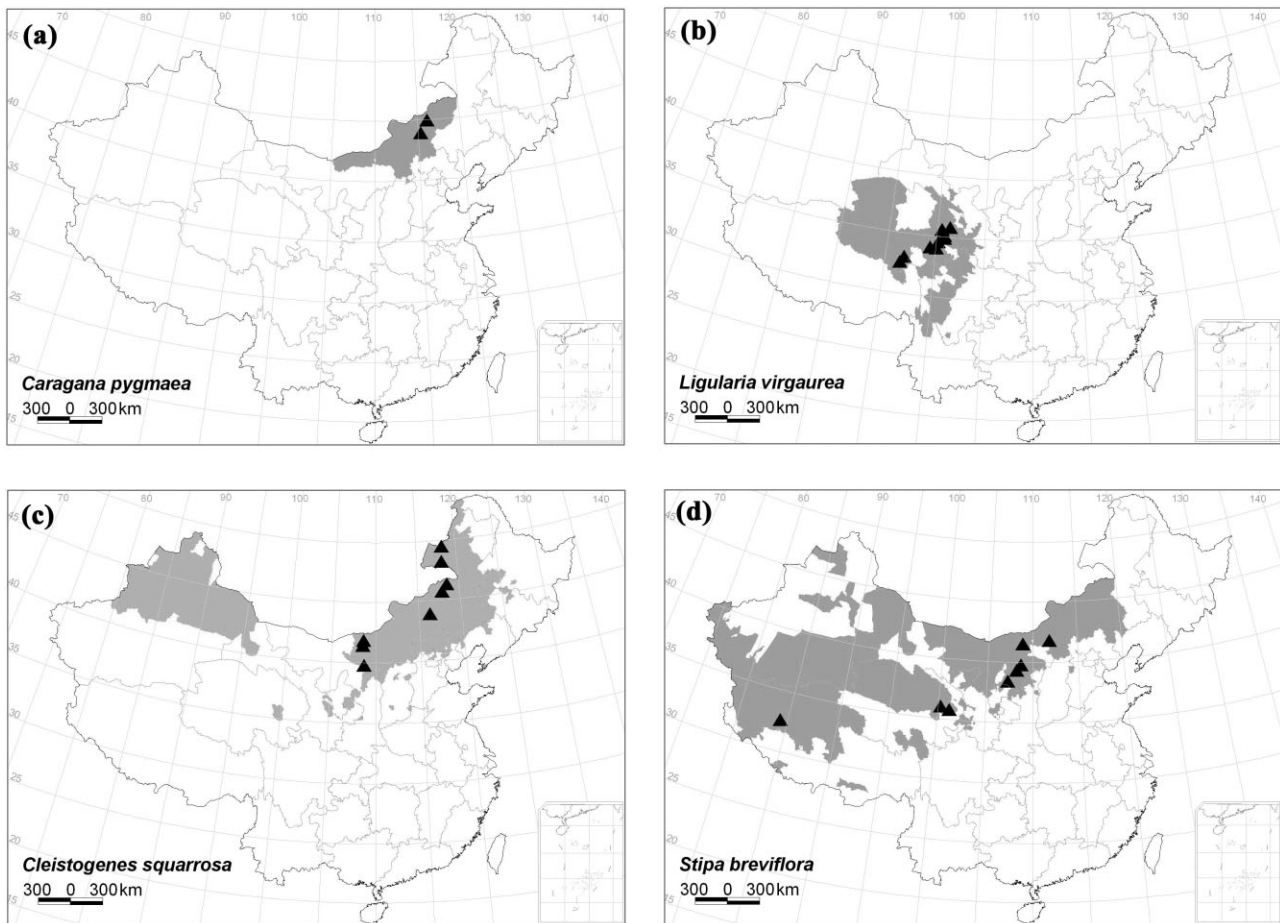
Figure 1 Geographical distributions of plant species in each range size quartile. Quartiles range from the first (narrowest-ranging 25% of species, a) to the fourth (widest-ranging 25% of species, d). The four representative species are *Caragana pygmaea* (a), *Ligularia virgaurea* (b), *Cleistogenes squarrosa* (c) and *Stipa breviflora* (d). Triangles represent the sampling sites of each species.

Statistical analysis

Quantile regression was first used to estimate variations of leaf traits as a function of RS for 5, 25, 50, 75 and 95 percentile distributions of leaf traits. Then we compared leaf traits and habitat characters of species with different RSs. One-way ANOVA with a Tukey's *post hoc* test for differences among the means was used to test the RS effect. Afterwards we conducted multiple regressions with leaf nutrients as the dependent variable and soil nutrients, RS and their interactions as the predictors. RS was treated as a four-level factor (a categorical non-continuous predictor) in the models leaf N (or P) ~ RS + soil N (or P) + RS × soil N (or P) to test whether the soil nutrient effects on corresponding leaf nutrients change across levels of RS. To further illustrate the different responses to environment between narrow- and wide-ranging species, correlations between pairwise leaf and soil nutrient contents were performed separately for each RS quartile. The evaluation of climatic effects followed the same approach. Relationships between selected leaf traits and environmental variables were tested with linear regression. As some species were frequently sampled while some only occurred at one or two sites, to account for this variation in

sample size we analysed the data at two levels: (1) species-by-site level, with individual plant measurements averaged within species at each site and (2) species level, with measurements of leaf and soil variables averaged by species across sites to produce a second dataset of species means. Data of leaf traits (N, P, C : N, N : P and SLA) and soil properties (SOC, STN, STP, SEN, SEP and SBD) were log transformed to normalize statistical distributions. Statistical analyses were conducted with the software R (R Development Core Team, 2007).

RESULTS

General pattern of species RS

The median RS for all species was 1.00×10^6 km^2, whereas mean RS was 1.25×10^6 km^2. The smallest RS was 7.70×10^3 km^2 and the largest was 9.08×10^6 km^2, varying by three orders of magnitude (Appendix S2). The frequency distribution of species RS showed a roughly lognormal distribution for all species pooled together (Fig. 2a), and for Inner Mongolian (Fig. 2b) and Tibetan Plateau datasets individually (Fig. 2c), indicating a large number of narrow-ranging species.
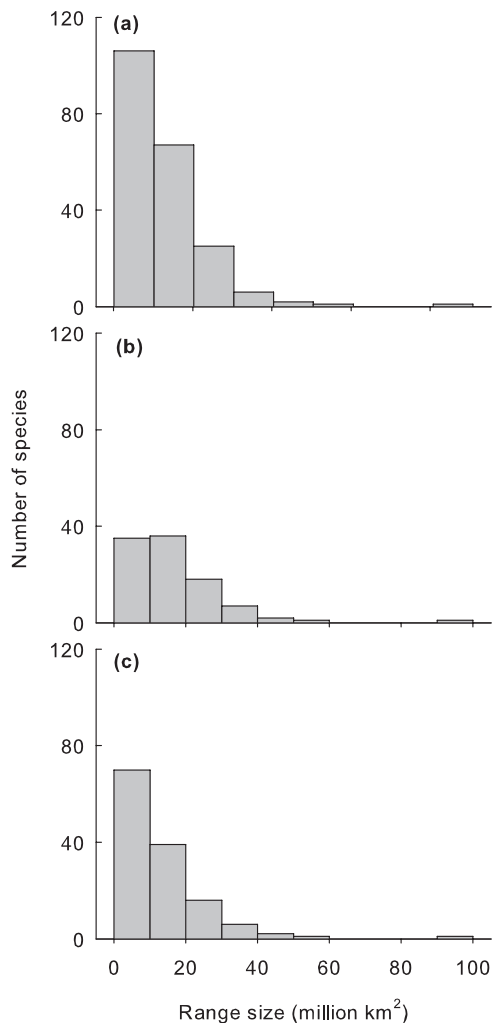
Figure 2 Histograms showing the frequency distribution of species range size for all species pooled together (a), species from Inner Mongolian grassland (b), and species from Tibetan grassland (c).

Species on the Tibetan Plateau showed a tendency towards smaller RS compared with Inner Mongolia (53% vs. 35% species belong to the narrow-ranging half of species) (Fig. 2b, c). Among the five dominant families, Asteraceae and Fabaceae tended to have a large proportion of species with a small RS (65% and 64% belong to the narrow-ranging half of species, respectively), whilst Poaceae and Rosaceae on average had larger RS (1.64×10^6 and 1.57×10^6 km^2, respectively). Cyperaceae exhibited approximately equal numbers of narrow- and wide-ranging species (Appendix S3). With regard to growth form, there were no significant differences in the mean RS between grass, herb and woody species ($F = 1.446$, $P = 0.238$) (Appendix S3).

Leaf traits and habitat preference of species with different RS

Quantile regression indicated a negative relationship between RS and leaf N and a positive relationship between RS and C : N ratio ($P < 0.05$ for H$_0$: $\beta_1 = 0$), whereas leaf P, N : P ratio and SLA did not show a significant relationship with RS (Appendix S4). Among RS quartiles, there were no marked differences in either leaf nutrient concentrations or SLA (Table 2). Trait mean values and variations of the four quartiles were similar.

Narrow-ranging species tended to occur at high altitude with higher soil nutrient concentrations than wide-ranging species (Appendix S5). All soil nutrient contents, except soil extractable N, declined from sites of the first quartile to the fourth (Table 3). This is contrary to previous finding that range-limited species are more common on poor sites (Hodgson, 1986; Thuiller *et al.*, 2004). We found that soil organic C, total N, total and extractable P were significantly higher at sites supporting the narrowest-ranging species than elsewhere. No significant differences in soil bulk density and pH were detected among RS quartiles (Table 3). When climate preference was compared, results showed no significant and consistent difference in mean annual precipitation and growing season precipitation between species with different RSs, while mean annual temperature and growing season temperature increased from the first to the fourth quartile (Appendix S5).

Leaf traits in relation to soil and climate parameters

When species were pooled together, leaf N and P concentrations were poorly correlated with either soil total or extractable N and P concentrations (Fig. 3). The influence of soil variables, though statistically significant ($P < 0.05$), explained a trivial amount of the variation in leaf nutrient concentrations [$R^2 < 0.1$, percentage of sum of squares explained (SS%) < 10] (Fig. 3, Table 4).

In multiple regressions for leaf nutrients as a function of soil nutrients, RS and soil × RS showed that the interaction terms were significant for leaf N ($P < 0.05$) and marginally significant for leaf P ($P < 0.1$), indicating that the soil effects (the slopes of the regressions) on leaf nutrients change across levels of RS (Table 4). When the plant–soil interactions were examined separately for each RS quartile, different patterns emerged between quartiles. For the moderate- and widest-ranging species (the third and the fourth quartiles) there was little association between leaf and soil variables, but for the narrow-ranging species (the first and the second quartiles) significant correlations between leaf and soil variables were detected. Furthermore, correlation coefficients and slopes for the regressions declined gradually from the first to the fourth quartile (Fig. 3). In particular, leaf N and P were consistently more strongly correlated with soil extractable N and P than with soil total N and P (Fig. 3). It should be noted that the degree of leaf–soil correlations tended to decrease from the first to the fourth RS quartile regardless of whether data of species-by-site (data not shown for brevity) or species means was used. Species occurrence frequency (number of sites) had little effect on the above trend as RS did not depend on the frequency of habitat (Appendix S6). We acknowledged that a number of species had a low level of sampling. Therefore to minimize the effect of this drawback, we left out species sampled from few sites (only one site for the first and the second quartiles and

Table 2 Leaf traits of species in each range size quartile.

Leaf traits	First	Second	Third	Fourth
N (mg g^{-1})				
Mean	28.12	25.93	25.91	26.38
Range	14.33–46.96	13.11–43.35	17.03–41.67	17.45–47.47
CV	0.27	0.25	0.23	0.26
P (mg g^{-1})				
Mean	1.72	1.82	1.70	1.70
Range	0.83–2.92	0.80–3.65	0.80–3.05	1.00–3.14
CV	0.32	0.33	0.26	0.32
C : N				
Mean	16.80	18.29	18.08	18.48
Range	9.22–31.85	10.80–35.34	9.41–27.84	8.86–26.00
CV	0.28	0.26	0.22	0.24
N : P				
Mean	17.59	15.32	16.19	16.67
Range	8.75–30.20	7.14–22.96	8.57–27.29	9.02–43.26
CV	0.30	0.26	0.27	0.32
SLA (cm^2 g^{-1})				
Mean	126.1	131.7	126.4	126.2
Range	57.1–219.1	46.0–287.3	46.4–204.6	47.7–206.8
CV	0.31	0.35	0.26	0.28

Quartiles range from first (narrowest-ranging 25% of species) to fourth (widest-ranging 25% of species). None of the trait means differ significantly among quartiles at $P < 0.05$.
CV, coefficient of variation; SLA, specific leaf area (cm^2 g^{-1}).

fewer than three sites for the third and the fourth quartiles) from the original dataset and conducted the same analysis with the new dataset. Narrow-ranging species again showed a more sensitive response to variation in soil nutrient concentrations than did wide-ranging species (data not shown for brevity).

Overall, neither growing season temperature nor growing season precipitation was correlated with leaf nutrient contents or SLA (Table 5). Species responses to climatic variables were unrelated to their RS. For all RS quartiles, variations of foliar N and SLA were unrelated to either growing season temperature or precipitation (Table 5). Leaf P of the narrowest-ranging quartile declined with increasing growing season temperature and tended to be positively correlated with growing season precipitation, but the explanatory power of the regressions was low ($R^2 < 0.1$). Climatic variables had negligible effects on leaf P of the other three quartiles (Table 5). Because temperature increased from the first to the fourth RS quartile, it is conceivable that the observed pattern may be not about narrow-versus wide-ranging species but about leaf–soil nutrient relationships in cold versus warm climates. However, multiple regressions using soil, RS and growing season temperature as predictors showed that neither growing season temperature nor temperature × soil had a significant effect on leaf nutrients (Appendix S7). Moreover, regression models with soil and RS being the predictors had a stronger explanatory power than models with soil and temperature as predictors (Appendix S8). Therefore we conclude that RS, rather than temperature, was

more responsible for the variation in leaf–soil nutrient relationships among RS quartiles.

DISCUSSION

No direct links between leaf functional traits and species RS

A number of studies have explored how plant functional traits relate to plant rarity, but up to now no key characteristics have been identified to distinguish rare and common species (reviewed in Bevill & Louda, 1999; Murray *et al.*, 2002). In the present study, sampling a large number of species from a wide range of sites across Chinese grassland biomes, we failed to detect a link between leaf functional traits and species RS. In addition to existing findings which have already shown no discrepancy in either leaf N or SLA between narrow- and wide-ranging plant species (e.g. Richards *et al.*, 2003; Lavergne *et al.*, 2004), here we further found that leaf P concentration, C : N and N : P stoichiometry did not show systematic variations among species with different RSs.

Based on the theory of natural selection, we would expect species with distinct niche positions and breadth to have different morphological and physiological profiles. Narrow-ranging species have often been found in relatively infertile and more stressful habitats (Hodgson, 1986; Thuiller *et al.*, 2004), therefore species with restricted distributions are expected to have stress-tolerant trait syndromes, such as small stature, low SLA,

Soil variable	First	Second	Third	Fourth
Soil organic C (mg g^{-1})				
Mean	42.54b	40.86ab	38.86ab	27.93a
Range	3.00–193.00	2.03–148.51	3.02–173.57	2.03–148.51
CV	1.037	0.926	0.999	1.008
n	75	128	151	187
Total N (mg g^{-1})				
Mean	5.07b	4.07b	3.88b	3.00a
Range	0.33–18.79	0.27–15.00	0.43–14.90	0.23–13.67
CV	0.893	0.909	0.867	0.929
n	75	126	150	185
Extractable N (µg g^{-1})				
Mean	7.23a	8.71a	7.50a	6.89a
Range	2.11–21.85	2.02–26.07	2.02–34.31	2.02–21.85
CV	0.852	0.807	0.798	0.658
n	23	42	64	87
Total P (mg g^{-1})				
Mean	0.57b	0.51ab	0.51ab	0.48a
Range	0.14–1.26	0.09–0.97	0.16–1.20	0.09–0.97
CV	0.402	0.449	0.423	0.428
n	74	128	151	184
Extractable P (µg g^{-1})				
Mean	14.14b	12.83b	10.81b	8.59a
Range	2.12–58.40	1.47–37.51	1.26–37.51	1.26–37.51
CV	0.854	0.855	0.778	0.882
n	75	128	151	187
Bulk density (g cm^{-3})				
Mean	0.90a	0.99a	0.99a	1.02a
Range	0.30–1.68	0.20–3.15	0.35–1.74	0.20–1.74
CV	0.440	0.487	0.359	0.373
n	58	101	113	139
pH				
Mean	7.18a	7.15a	7.27a	7.35a
Range	6.11–8.51	5.31–8.28	5.97–8.51	5.31–8.84
CV	0.100	0.083	0.086	0.096
n	28	41	66	90

Quartiles range from first (narrowest-ranging 25% of species) to fourth (widest-ranging 25% of species). Means followed by different letters are significantly different at *P* < 0.05.
CV, coefficient of variation; *n*, sample size.

low nutrient contents and assimilation rate, and high concentrations of secondary metabolites (Chapin *et al.*, 1993). However, in the present paper as well as some early studies, traits that capture resource acquisition potential (e.g. SLA, leaf N and maximum photosynthetic rate) do not play an important role in habitat selection and expansion, and competitive hierarchy may not correspond to species RS (Snyder *et al.*, 1994). Alternatively, these traits may be important in reflecting community structure at small scales, but less important at the landscape or biome scale.

He *et al.* (2006a, 2008) reported stable leaf N concentration and C : N ratio for 213 species across distinct regions of China's grasslands, and leaf N : P ratios of Inner Mongolia and Tibet were similar. These constrained foliar traits suggest a convergent evolution in chemical composition and functioning of Chinese grassland plants. Taken together, RS had little direct effect on the plant functional traits we examined across Chinese grassland biomes.

Leaf–soil nutrient relationships vary among species with different RS

Although in the current study RS was poorly related to leaf traits, we did observe an effect of species RS on the relationships between leaf traits and soil variables. The soil effect on leaf nutrients changed across levels of RS. The relationships between leaf and soil nutrient concentrations progressively weakened from the first to the fourth RS quartile, implying a more sensitive response to the changes in soil nutrient supply of narrow-ranging species than wide-ranging species.
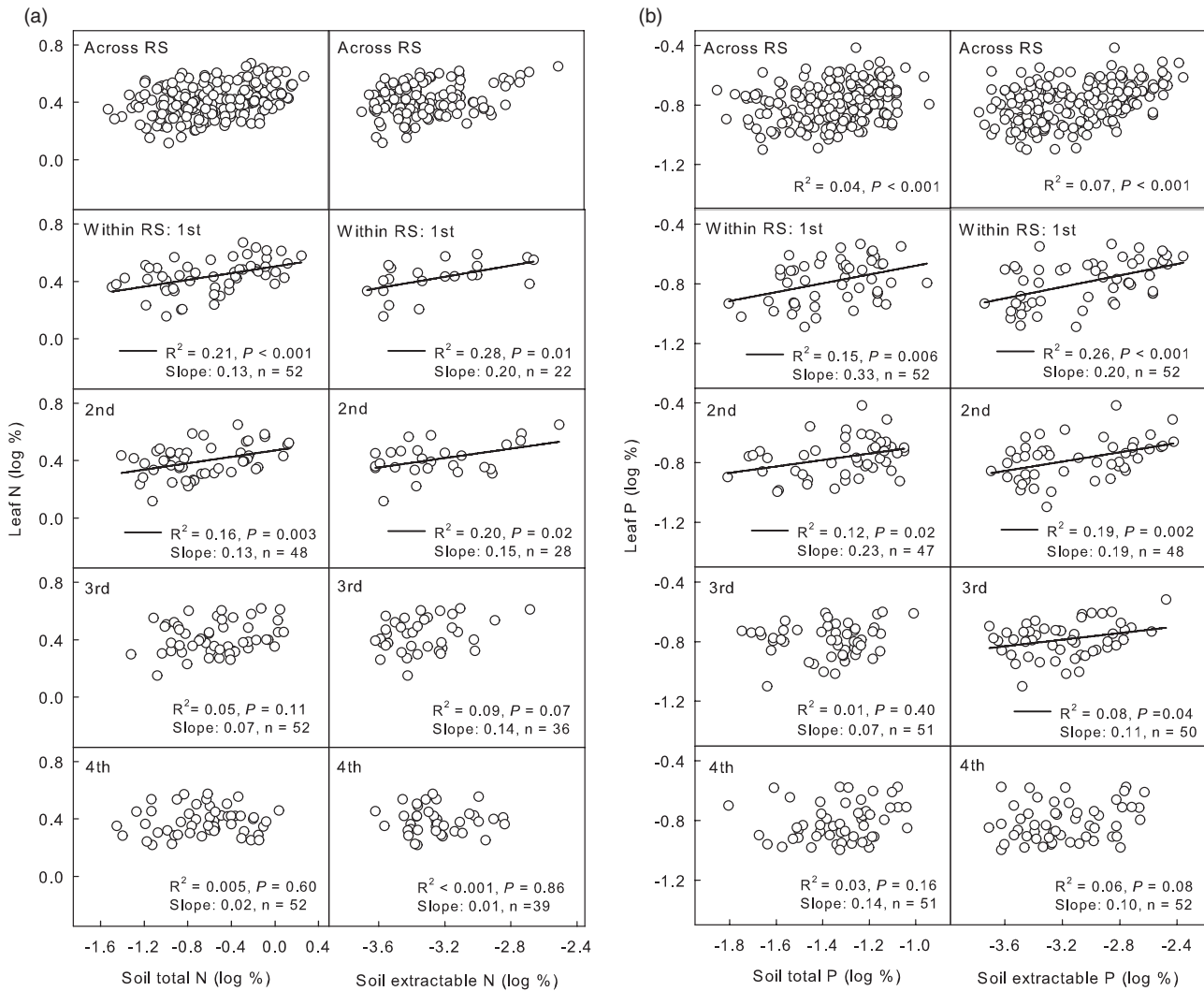
Figure 3 Relationships between leaf N and soil total and extractable N (a), and leaf P and soil total and extractable P concentrations (b) for all species pooled together and for each range size (RS) quartile. Quartiles range from the first (narrowest-ranging 25% of species) to the fourth (widest-ranging 25% of species). Regression lines are shown only for those that are statistically significant ($P < 0.05$).

Table 4 Summary of analysis of variance (ANOVA) of the effects of range size (RS), soil nutrients and the interactions between RS and soil nutrients on leaf N and P concentrations.

		Leaf N					Leaf P		
	d.f.	SS	P	SS%		d.f.	SS	P	SS%
RS	3	0.019	0.660	0.73	RS	3	0.024	0.376	0.78
STN	1	0.242	0.009**	9.36	STP	1	0.198	0.008**	6.45
RS × STN	3	0.211	0.044*	8.16	RS × STP	3	0.180	0.061†	5.86
Residuals	197	2.114		81.75	Residuals	196	2.668		86.91
RS	3	0.031	0.196	1.12	RS	3	0.026	0.426	0.76
SEN	1	0.268	0.003**	9.66	SEP	1	0.265	0.004**	7.74
RS × SEN	3	0.231	0.022*	8.32	RS × SEP	3	0.125	0.088†	3.66
Residuals	114	2.244		80.89	Residuals	197	3.008		87.85

**$P < 0.01$; *$P < 0.05$; †$P < 0.1$.
STN, soil total N concentration; SEN, soil extractable N concentration; STP, soil total P concentration; SEP, soil extractable P concentration; d.f., degrees of freedom; SS, sum of squares; SS%, percentage of sum of squares explained.

Table 5 Correlations (*R*) between leaf traits and climatic variables for all species pooled together and species partitioned into range size (RS) quartiles.

	Across RSs	First	Second	Third	Fourth
Leaf N–GST	−0.12	−0.23	−0.21	0.17	−0.10
Leaf N–GSP	0.13	0.22	0.24	−0.10	0.11
Leaf P–GST	−0.18	−0.43**	−0.20	0.15	−0.13
Leaf P–GSP	0.15	0.32*	0.16	−0.12	0.14
SLA–GST	−0.14	−0.16	−0.14	−0.15	−0.10
SLA–GSP	0.15	0.20	0.15	0.15	0.15

**$P < 0.01$, *$P < 0.05$.
GST, growing season temperature; GSP, growing season precipitation.

This observation could be relevant to the ecological characteristics of wide- and narrow-ranging species. In our study widespread species occupy a broader range of soil and climate types than range-limited species. Most of the widest-ranging species are habitat generalists which appear in all Chinese grassland biomes, ranging from warm and moist areas in east Inner Mongolia, arid and montane areas in west Inner Mongolia and Xinjiang, to alpine landscape on the Tibetan Plateau. In contrast, species with the smallest RS were largely found on isolated regions on either the Tibetan Plateau or Inner Mongolia Plateau with a distinctive combination of environmental conditions. Due to their narrow niche breadth and specific niche position, in order to survive, range-restricted species may have to be more specialized to the constrained environment, especially to the edaphic conditions which directly control mineral uptake. Specialization to the unique habitat characters is a strategy in conflict with widespread species, but the cost of specialization is the loss of attributes necessary for persistence in alternative habitats where range-limited species are supposed to be competitively inferior to wide-ranging species (Griggs, 1940; Walck *et al.*, 1999; Lloyd *et al.*, 2002). Moreover, the reduced phenotypic variation may increase the susceptibility to environmental changes (Kruckeberg & Rabinowitz, 1985; Cole, 2003). Summing up, narrow-ranging species are superior under some but not all conditions. In support of this view, most species of the first RS quartile occurred on the Tibetan Plateau. High altitudes, low growing season temperature, great intensity of solar radiation and other factors of a high-altitude environment on the plateau have been strong selective forces on the flora (Zhang *et al.*, 1988). Some of the narrowest-ranging species that evolved on the plateau are generally excluded from regions that are relatively warm and dry, such as Inner Mongolia and Xinjiang, probably due to the potential trade-off between cold tolerance strategies and competitive ability in warm and dry environments (Loehle, 1998). In view of a larger temporal scale, narrow-ranging species are expected to have evolutionarily adapted to habitat stability, while widespread species are possibly a recent consequence of global change and have a relatively short history of evolution on local habitats. Therefore they may be less prone to fluctuations of environmental variables such as soil fertility and climate (Futuyma & Moreno, 1988).

The lack of correlation between plant and soil for wide-ranging species may also be interpreted by considering their trait regulations. Widely distributed plants are thought to be able to better withstand environmental change and maintain fitness across a broad range of habitats than rare species (Sultan *et al.*, 1998; Thuiller *et al.*, 2005; Broenniman *et al.*, 2006). The constancy in fitness-related traits despite environmental variation of wide-ranging species could be due to their intricate self-regulation of multifactorial physiological traits (Sultan *et al.*, 1998). Thus an absence of close relationships between plant and soil nutrients does not necessarily mean that a species is less adaptive. Instead, a plant may respond to change in soil nutrient supply by altering its growth rate or other physiological characters without affecting leaf nutrient status (Chapin, 1980). The poor synchronization with local edaphic conditions demonstrates a capacity of wide-ranging species to maintain a high level of function at both high and low resource levels, resulting in their broad distributions.

Our observation may partially account for the existing weak relationships between foliar and environmental variables at a large scale. In a global study, plant–soil nutrient relationships showed considerable scatter around the regression lines (Ordoñez *et al.*, 2009). Meanwhile, modulation of leaf traits and trait relationships by climate is surprisingly modest at the global scale (Wright *et al.*, 2004). More specifically, for Chinese grassland biomes climate also only weakly influences leaf functional traits (He *et al.*, 2006a,b, 2008). Obviously, these analyses have only looked at overall patterns. It is often ignored that narrow- and wide-ranging species may differ in their environmental requirements or determinants (Jetz & Rahbek, 2002). As pointed by Kunin & Gaston (1997), there is a bias of the published literature toward studies of common bird taxa. Wide-ranging bird species appear more frequently in the literature whereas the roles of narrow-ranging birds may be underestimated (Lennon *et al.*, 2004). This problem may also exist for the sampling of plants, yet relatively few studies have investigated this issue in plants. So the previously reported poor relationships between plant traits and environmental variables, particularly between leaf and soil nutrients, might be partly due to the sampling bias by incorporating a disproportionately large number of records of wide-ranging plant species while actually most species have RSs below the average. Therefore, patterns of large-scale plant–environment relationships should be obtained with consideration of the inconsistency in plant sampling size.

Species natural habitats will be subject to more disturbances in the future due to climate change and habitat degradation caused by intensive anthropogenic activities. In particular, narrow-ranging plant species are more vulnerable to environmental changes and will suffer greater extinctions than widespread species (Fischer & Stocklin, 1997; Rooney *et al.*, 2004). If our results hold true at broad scales, the conservation of narrow-ranging plant species will largely depend on

stabilization of their habitats. Future work combining plant–environment interactions and species distribution may help to assess the sensitivity of species to environmental changes and establish management plans for biodiversity conservation.

Limitations of the current study

In the present study all species RSs were calculated within China, while in fact some species expand outside of China. This might raise concerns as RSs do not represent the full ranges of some species. However, the bias introduced by using species RS within China should be weak. In previous studies it has been found that species RS within a region or continent correlate with their global RSs (Gregory & Blackburn, 1998). Moreover, most narrow-ranging species in this study are endemic to China while most wide-ranging species are broadly distributed both inside and outside China. Therefore, using RS from China rather than global RS will not substantially change the categorization of wide- and narrow-ranging species and our results should hold up under the global distribution system. Additionally, our grouping of RS may also induce phylogenetic bias among RS quartiles. Within-family and within-genus studies should be informative by minimizing the problem of phylogenetic dependence (Felsenstein, 1985). To control for phylogenetic relatedness, we tested the within-genus pattern using *Stipa* and *Kobresia*, two dominant genera in Chinese grasslands. However, these two genera tended to be widely distributed, with most species occurring in the third and fourth quartiles. As a result, it is hard to detect the within-genus pattern due to the inadequate sampling of narrow-ranging populations compared with their wide-ranging congeners. Within-family analysis suffered the same problem, as none of the 33 families studied had balanced numbers of narrow- and wide-ranging species to address the effect of RS on leaf–environment relationships.

More studies are needed to validate the reported patterns at broader scales and to clarify how species RS links to the nature of plant–soil nutrient relationships. Further investigations are highly desirable to test for these relationships by embracing more taxonomically diverse datasets in more regions, and incorporating additional plant traits with ecological significance such as photosynthetic rate and seed size, together with more environmental variables. In particular, transplant studies might be useful to test the pattern along gradients of experimental environments, allowing a balanced study design where all species occur in more comparable environmental conditions.

CONCLUSIONS

Our results found that narrow-ranging species tended to occur at high altitude with lower temperature but higher soil nutrient concentrations than wide-ranging species across Chinese grasslands. While there was little evidence that narrow-ranging species had particular leaf traits, they did show stronger leaf–soil nutrient relationships compared with wide-ranging species, indicating that they might be more specialized to particular

habitats than their wide-ranging counterparts. In addition, species responses to climatic variables were unrelated to their RSs.

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SUPPORTING INFORMATION

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

Appendix S1 Species list with their estimated range sizes and sampling frequencies. Reference sources for range size measurement are listed below.

Appendix S2 Map of Chinese geography showing the counties which are the basic units for species range sizes estimation. Black triangles represent sampling sites.

Appendix S3 Number of species from dominant families and different growth forms in each range size quartile. Means of range size of the five families and three growth forms are also shown.

Appendix S4 Scatterplots of leaf traits against species range size with 0.95, 0.75, 0.50, 0.25, 0.05 quantile regression estimates (solid lines).

Appendix S5 Altitude (meters a.s.l) and climatic conditions for species range size quartiles. Quartiles range from the first (narrowest-ranging 25% of species) to the fourth (widest-ranging 25% of species). Different letters (a, b, ab) denote significant differences at $P < 0.05$.

Appendix S6 Occurrence frequencies (number of sites) of species with different range sizes.

Appendix S7 Summary of ANOVA of the effects of range size (RS), GST (growing season temperature), soil, and the interactions between soil and RS, soil and GST on leaf N and P concentrations. *df*: degrees of freedom, SS: sum of squares, SS%, percentage of sum of squares explained. ***, $P < 0.001$; **, $P < 0.01$; *, $P < 0.05$; †, $P < 0.1$.

Appendix S8 Summary of regression models of leaf N and P concentrations as a function of soil nutrients, range size (RS) (or growing season temperature, GST) and soil × RS (or soil × GST).

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