

Abstract

Concentrations of leaf nitrogen (N) and phosphorus (P) are key leaf traits in ecosystem functioning and dynamics. Foliar stoichiometry varies remarkably among life forms. However, previous studies have focused on trees and grasses, leaving the knowledge gap for the stoichiometric patterns of shrubs. In this study, we explored the intra- and interspecific variations of leaf N and P concentration in relation to climate, soil property and evolutionary history based on 1486 samples composed of 163 shrub species from 361 shrubland sites in northern China expanding 46.1° (86.7–132.8° E) in longitude and 19.8° (32.6–52.4° N) in latitude. The results showed that leaf N concentration decreased with precipitation, leaf P concentration decreased with temperature and increased with precipitation and soil P concentration. Both leaf N and P concentrations were phylogenetically conserved, but leaf P concentration was less conserved than leaf N concentration. At community level, climates explained more interspecific, while soil nutrient explained more intraspecific, variation of leaf nutrient concentrations. These results suggested that leaf N and P concentrations responded to climate, soil, and phylogeny in different ways. Climate influenced the community chemical traits through the shift in species composition, whereas soil directly influenced the community chemical traits.

1 Introduction

Understanding how and why plant stoichiometry vary among species and sites is the most important single step towards understanding land ecosystem properties in general, including biogeochemical cycles, plant trait evolution, plant communities and their functional characteristics in a changing climate (Westoby and Wright, 2006). Concentrations of leaf nitrogen (N) and phosphorus (P) play crucial roles in ecosystem functioning and dynamics (Sterner and Elser, 2002; Wright et al., 2004; Kerkhoff et al., 2006; Ordoñez et al., 2009; Vitousek et al., 2010). Leaf N concentration is critical

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for photosynthesis, plant production and litter decomposition (LeBauer and Treseder, 2008), while P is a limiting nutrient responsible for the energy storage, cell structure, and the composition of DNA and RNA. Plant leaves vary dramatically in N and P concentrations, despite their shared key functional purpose of photosynthetic carbon assimilation and transpiration (Elser et al., 2003; Reich and Oleksyn, 2004; Wright et al., 2004; Kerkhoff et al., 2006; Chen et al., 2013). This is partly because of the differences in climate, soil, vegetation types, and developing history among sites (Westoby and Wright, 2006). For example, leaf N and P concentrations are higher in herbs than in woody plants and in deciduous than in evergreen species (Kerkhoff et al., 2006) and decrease with latitude at large scales (McGroddy et al., 2004; Reich and Oleksyn, 2004; Han et al., 2005, 2011; Kerkhoff et al., 2006). Studying the patterns of leaf N and P concentrations is important in understanding the macroecological patterns in plant stoichiometry and related driving factors (Han et al., 2005).

Several hypotheses have been proposed to explain the patterns of plant stoichiometry (Elser et al., 2003; Reich and Oleksyn, 2004), among which the plant physiology hypothesis (Woods et al., 2003; Reich and Oleksyn, 2004), the biogeochemical hypothesis (McGroddy et al., 2004; Reich and Oleksyn, 2004) and the species composition hypothesis (Reich and Oleksyn, 2004; He et al., 2006) have been mostly reported. The plant physiology hypothesis proposes that concentrations of N and P in plant tissues increase as the ambient temperature decreases to offset the decreases in plant metabolic rate (Woods et al., 2003; Reich and Oleksyn, 2004). Studies in arid regions also proposed that plants tend to have higher leaf N concentration to better adapt to arid environments (Cunningham et al., 1999; Wright et al., 2003) through exploiting greater light availability (Cunningham et al., 1999) while reducing stomatal conductance and transpiration rate (Wright et al., 2003). The biogeochemical hypothesis suggests that concentrations of N and P in plant tissues are controlled by the availabilities of soil N and P, therefore concentrations of N and P in plant tissues are highly correlated with those in the soils (McGroddy et al., 2004; Reich and Oleksyn, 2004).

the patterns of foliar stoichiometry for shrubs and shrublands in relation to climate, soil property and species composition (and phylogeny).

In this study, we explored the patterns of leaf N and P concentrations of shrubs in relation to climate, soil and evolutionary history in northern China. We have following hypotheses. First, in contrast to soil N, P is particularly low in soils in China (Han et al., 2005), plants may absorb P from soil when it is available; we therefore hypothesize that leaf P concentration is more strongly correlated with soil nutrient availability than leaf N concentration. Second, as plants in arid regions may contain higher N concentrations to better adapt to arid environments, we hypothesize that leaf N concentration may decrease with precipitation; and both leaf N and P concentrations may decrease with MAT based on the plant physiology hypothesis. Third, traits remarkably influenced by environments tend to be weakened in phylogenetic conservation during adaptive evolution (Losos, 2008); most vascular plants uptake P through the “mycorrhizal” pathway (Smith et al., 2003) and the infection of mycorrhizal fungi mainly depends on environments (Allen et al., 1995); in contrast, N is relatively sufficient. We therefore hypothesize that leaf N concentration is more phylogenetically conserved than leaf P concentration.

2 Materials and methods

2.1 Sampling collection and measurements

This study was conducted based on an investigation of 361 shrubland sites, including 289 temperate shrubland, 69 desert shrubland and 3 subalpine shrubland sites, expanding 19.8° in latitude (32.6–52.4° N) and 46.1° in longitude (86.7–132.8° E) in northern China (Fig. 1). The sampling was conducted in the summer (July to September) of 2011, 2012 and 2013. At each site, three plots of 5 m × 5 m, with distances of 5–50 m between edges of nearby plots, were selected to present the natural shrubland communities. We identified all shrub species in each plot, and harvested leaf, stem and root biomass separately for each species. Fully expanded sun leaves of at least five

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individuals of each species were collected and assembled in fabric bags then dried in the sun. Leaf samples were transported to the laboratory and oven-dried at 65°C for 72 h. In total, we collected 1486 samples composed of 163 species from 38 families and 86 genera, with 91 species sampled from more than one sites.

At each plot, we excavated three pits to the depth of 1 m to collect soil samples at the diagonal of the plot; for each profile, soil samples were taken at the depths of 0–10, 10–20, 20–30, 30–50, 50–70 and 70–100 cm, and the soil samples from the same depth were mixed.

An elemental analyzer (2400 II CHNS; Perkin-Elmer, Boston, MA, USA) was employed to measure the total N concentration of the soils (STN) and leaves under 950°C for combustion then reduced to 640°C. The molybdate/ascorbic acid method was applied to measure total P concentration in the soils (STP) and leaves after H₂SO₄-H₂O₂ digestion (Jones, 2001). As STN and STP from 0–10 cm depth interval were highly correlated with those from other depth intervals, we only used STN and STP from 0–10 cm depth interval.

We also extracted mean annual temperature (MAT) and precipitation (AP) from the WorldClim spatial climate data (resolution at ca 1 km, available at www.worldclim.org/). MAT in the study sites ranged from –4.1 to 16.0°C, and AP ranged from 15 to 974 mm. Please refer to Yang et al. (2014) for more detailed information on data collections.

2.2 Phylogenetic tree and phylogenetic signal test

We developed a phylogenetic tree for the 163 species by using Phylomatic (Webb and Donoghue, 2005) based on APG III topology to the family level (Bremer et al., 2009). We then conducted K statistic (Blomberg et al., 2003) to quantify the magnitude of phylogenetic signal of leaf N, P concentrations and N:P ratio. For each species, we first calculated the mean leaf N and P concentrations. To test if the phylogenetic conservatism of leaf N concentration is caused by the legumes (species from Fabaceae), we also conducted K statistic of leaf N after dropping the clade of Fabaceae. The signifi-

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cance (P values) was evaluated by comparing the variance of independent contrasts for each trait to the expected values calculated by shuffling the tips for 999 times.

To quantify the magnitude of phylogenetic signal of species' environmental niches, we calculated K statistics of mean climate (MAT and AP) and soil chemistry (STN and STP) of all sites each species occurring.

2.3 Data analysis

We first examined effects of climate, soil property and evolutionary history on the leaf N, P concentrations and N : P ratio by plotting the concentrations against environmental factors using all data (treating all observations as equal). Leaf N and P concentrations were base 10 log transformed to normalize their distributions before analysis as their frequency distributions were skewed. To eliminate the possible bias resulted from the higher chances of abundant species to be included in raw data, we also analyzed the data at the community level by calculating average values of each species for each site and then averaging them to get mean value for each site.

We followed Lepš et al. (2011) to assess the relative contributions of intra- and interspecific variability effects on biomass weighted site-average leaf N, P concentration and N : P ratio along the climatic and soil nutrient gradients. For each site, we calculated "specific" site-average leaf N, P concentration and N : P ratio and "fixed" site-average leaf N, P concentration and N : P ratio with the formulas below:

$$\text{Specific average} = \sum_{i=1}^S p_i x_{i_{\text{site}}} \quad (1)$$

$$\text{Fixed average} = \sum_{i=1}^S p_i x_i \quad (2)$$

where S is the number of species in a study site, p_i is the proportion of the i th species based on aboveground biomass (leaf and stem biomass) in the site, x_i is the fixed

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mean leaf N, P concentration or N : P ratio of the i th species for all study sites where the species exists, and $x_{i, \text{site}}$ is the specific mean leaf N, P concentration or N : P ratio of the i th species for the given site. We assumed that the variation of specific average values is caused by both intra- and interspecific leaf chemical trait variation, while the variation of fixed average values is solely affected by interspecific leaf chemical trait variation. Hence, the effect of intraspecific variability can be estimated using a parameter calculated as follow:

$$\text{Intraspecific variability} = \text{Specific average} - \text{Fixed average} \quad (3)$$

We then used each of the three parameters as a single response variable in general linear model (GLM) regressions and explain them by climatic and soil nutrient factors. The decomposition of sum of squares (SS) can be used across the three GLM models:

$$SS_{\text{Specific}} = SS_{\text{Fixed}} + SS_{\text{Intraspecific}} + SS_{\text{covariation}} \quad (4)$$

We can then extract the SS for each of the three GLM models explained by each of the environmental factors. In this way, we decomposed the total variation of leaf N, P concentration or N : P ratio into parts explained by intraspecific variation, interspecific variation and their covariation, we also quantified how much variability in each part can be explained by each environmental factor. We analysed both main-effect GLM models and GLM models with interaction terms. Since the results for the main effects of environmental variables are same, and the variation explained by interaction terms are relatively small compare to the main-effects, we only presented the main-effect models for simplicity, and showed the models with interaction terms in the supplementary material (Table S1 in the Supplement).

Ecological data on large scale often display spatial autocorrelation, and the presence of such pattern in the residuals of a statistical model may increase type I error rates (Dormann, 2007). We tested for spatial independence of the residuals of the models using Moran's I index (Moran, 1950), and found that the Moran's I of residuals of all

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models were not significant (Fig. S1 in the Supplement), indicating that the environments included in the models removed the spatial auto-correlation in the leaf nutrient concentration (Diniz-Filho et al., 2003). Therefore, we did not apply the spatial linear autoregressive models (SLM) in our analyses, because the SLM may underestimate the effects of predictors at large scales (Diniz-Filho et al., 2003).

Statistical and phylogenetic analyses were performed using R 3.1.1 (R Development Core Team, 2014) with the basic, ape (Paradis et al., 2004) and picante packages (Kembel et al., 2010). Spatial analyses were conducted using SAM 4.0 (Rangel et al., 2010).

3 Results

Leaf N and P concentrations changed from 4.26 to 46.80 mg g⁻¹ (mean = 21.91, SD = 6.84) and 0.16 to 4.80 mg g⁻¹ (mean = 1.30, SD = 0.53) for shrubs in northern China. Leaf N:P changed from 4.07 to 145.76 (mean = 18.69, SD = 8.40) (Fig. S2). Leaf N concentration decreased ($R^2 = 0.1$, $p < 0.001$), while leaf P concentration increased ($R^2 = 0.03$, $p < 0.001$), with AP. Leaf P concentration decreased ($R^2 = 0.03$, $p < 0.001$), while leaf N concentration showed no significant correlation ($R^2 < 0.01$, $p = 0.227$), with MAT. Leaf N concentration decreased with STN ($R^2 = 0.13$, $p < 0.001$), while leaf P concentration increased with STP ($R^2 = 0.02$, $p < 0.001$) (Fig. 2). Leaf N:P ratio increased with MAT ($R^2 = 0.04$, $p < 0.001$), while decreased with AP ($R^2 = 0.18$, $p < 0.001$), STN ($R^2 = 0.07$, $p < 0.001$) and STP ($R^2 = 0.06$, $p < 0.001$) (Fig. 3). All these patterns remained almost unchanged at community level (Figs. 2 and 3).

Leaf N concentration exhibited significant non-random phylogenetic signal ($K = 0.31$, $p < 0.001$), while leaf P concentration showed significant but weaker non-random phylogenetic signal ($K = 0.24$, $p < 0.01$) among all species (Table 1). When excluding legumes from the dataset, the phylogenetic signal for leaf N concentration remained significant ($K = 0.30$, $p < 0.001$) (Table 1).

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Climatic variables explained 5.7 % of the variation in leaf N concentration, and 10.8 % of the variation in leaf P concentration. Only AP significantly influenced leaf N concentration ($p < 0.001$), while all environmental factors except STN significantly influenced leaf P concentration ($p < 0.001$). MAT, AP, STP and STN explained 1.96, 24.64, 0.49 and 0.73 % of variation in leaf N : P ratio (Table 2).

When the total variation of leaf N and P concentrations were decomposed into intra- and interspecific variations, GLM analyses showed that AP and STN explained 7.2 % ($p < 0.001$) and 2.7 % ($p < 0.01$) of the interspecific variation of leaf N concentration, respectively. None of MAT, AP, STN and STP significantly influenced intraspecific variation of leaf N concentration ($p > 0.05$ for all). For leaf P concentration, MAT and AP accounted for 1.7 % ($p < 0.001$) and 3.4 % ($p < 0.001$) interspecific variation; MAT, STN and STP explained 1.2 % ($p < 0.01$), 1.4 % ($p < 0.01$) and 4.3 % ($p < 0.001$) of intraspecific variation, respectively (Table 2; Fig. 4). Come to the leaf N : P ratio, MAT, AP and STN accounted for 0.6 % ($p < 0.01$), 21.9 % ($p < 0.001$) and 0.5 % ($p < 0.05$) of the interspecific variation; STP explained 1.27 % ($p < 0.001$) of the intraspecific variation, respectively (Table 2; Fig. 4).

4 Discussion

Using the foliar stoichiometry of 163 shrub species from 361 shrubland sites, we investigated patterns of leaf N and P concentrations in shrublands of northern China. We focused our discussion on leaf N and P concentrations instead of their ratio because leaf N : P was strongly driven by both leaf N and P concentrations and was predictable based on leaf N and P concentrations. Given that leaf C concentration is relatively stable, leaf N and P concentrations can also be good indicators of C : N and C : P ratios (Reich, 2005). We found that mean leaf N (21.91 mg g^{-1}) and P (1.30 mg g^{-1}) concentrations of shrubs in northern China shrubland were similar to those in shrubs across China (mostly distributed in forests as understory species, Han et al., 2005), but lower than those in grasses (Han et al., 2005; He et al., 2006, 2008) and higher than those

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in trees in China (Han et al., 2005) (Fig. S3). According to the “leaf economics spectrum”, an “expensive” strategy was characterized by low rates of metabolism, low N and P concentrations, and extended leaf longevity; while a “cheap” strategy was defined by high rates of metabolism, high N and P concentrations, and short leaf longevity (Wright et al., 2004). Our result indicated that the life strategy of shrubs is “cheaper” compared with that of trees but more expensive than herbaceous plants. Our results also suggested that the inclusion of shrub is necessary to explore the patterns of leaf stoichiometry in relation to climate and soil property.

There are some novel findings concerning the patterns of leaf stoichiometry, which we discuss below.

4.1 Influence of climate on leaf N and P concentrations

Leaf N and P concentrations responded to climate in different ways (Figs. 3 and 4). Consistent with our hypothesis, leaf N concentration decreased with precipitation. This is partly due to the higher leaf N concentration of plants in desert shrublands (Figs. 3 and 4). Higher leaf N concentration has been suggested as a general property of arid-zone plants (Wright et al., 2003). It is widely reported that plants tend to increase leaf N to exploit greater light availability while reducing stomatal conductance and transpiration rate (Cunningham et al., 1999; Wright et al., 2003). Succulence is such an adaption for plants to drought and salinity by accumulating nitrogen-containing compounds in their leaves to maintain water balance and therefore succulent plants are higher in leaf N concentration than other plants (Mansour, 2000) (Fig. S3). In contrast, leaf P concentration increased with precipitation. P is derived primarily from the weathering of soil inorganic components and the degradation of organic matters, and diffuses in soil (Aerts and Chapin, 1999). Increase in precipitation may amplify the P availability in soil by facilitating the decomposition of litters. The positive correlation between STP and precipitation ($R^2 = 0.21$, $p < 0.001$) and the lower STP in desert shrubland (Figs. 3 and 4) confirmed such hypothesis.

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Leaf P decreased with MAT, which was consistent with the plant physiology hypothesis that plant P may increase to offset the decreases in plant metabolic rate as ambient temperature decreases (Reich and Oleksyn, 2004). However, inconsistent with other studies (Reich and Oleksyn, 2004; Han et al., 2005; Chen et al., 2013), we did not observe a decrease in leaf N concentration with temperature. Given the significant impact of precipitation on leaf N concentration, a possible reason for this pattern might be the weak but significant negative correlation between MAT and AP in the study region ($R^2 = 0.02$, $p < 0.001$).

4.2 Influence of soil N, P concentration on leaf N and P concentration

We observed a significant positive correlation between leaf P concentration and STP, but not for leaf N concentration and STN. Such positive correlation between leaf and soil P concentrations might be caused by following reasons. Although leaf P concentration is higher in shrublands of northern China than in forests in China (Han et al., 2005), it is significantly lower than those in the rest of the world (Reich and Oleksyn, 2004). It is widely reported that a leaf N and P ratio (N : P) < 14 indicates N limitation, whereas a N : P > 16 indicates P limitation, in the ecosystem (Aerts and Chapin, 1999; Koerselman and Meuleman, 1996). In this sense, shrublands of northern China is P limited with a mean N : P of 18.69, though soil P concentration is higher than in southern part of China (Zhang et al., 2005). In the P limited ecosystems, plants may absorb P and deposit P in an inorganic form when P in soil is abundant (Sterner and Elser, 2002), resulting a positive correlation between leaf and soil P concentrations. However, leaf N concentration did not increase with soil N concentration, since N is not limited in soil. The negative correlation between leaf and soil N concentrations might be attributed to the highly positive correlation between STN and precipitation ($R^2 = 0.52$, $p < 0.001$), since higher precipitation facilitates the decomposition of litters in water-limiting environments.

Soil available N and P are small portion but important components of soil total N and P, because they can be readily absorbed and utilized by plants (Bünemann and

Condrón, 2007; McNeill and Unkovich, 2007) and therefore better indicators of soil fertility (Zhang et al., 2005; Ordoñez et al., 2009). Soil available N and P concentration were not measured in this study. However, a recent study on leaf chemical traits of shrub species across Inner Mongolia suggested that total soil nutrient concentrations explained similar amount of variance in leaf N and P concentrations with available soil nutrient concentrations (Liu et al., 2012), indicating that selection of total or available soil nutrient concentrations will not result in big difference in predicting nutrient concentrations in leaves from the studied region.

4.3 Influence of environmental factors on intra- and interspecific variation of leaf N and P concentrations

Environmental factors explained nearly 15% of total variance in leaf P concentration on community level, which was two times more than that of leaf N concentration, indicating that leaf P concentration is more affected by environmental factors. However, the explanatory powers of climate and soil for leaf N and P concentrations are comparably low, partly because other factors may profoundly affect the leaf stoichiometry, such as soil age (Vitousek et al., 2010; Hayes et al., 2014), but were not included in our model. Interspecific variation of leaf N and P concentrations is caused by changes in species composition, and intraspecific variation of leaf N and P concentrations is driven by environmental variations. Leaf P was jointly influenced by climate and soil nutrient. Climate influences the community leaf P concentration through shift in species composition, whereas soil influences the community P concentration directly. Leaf N concentration is mainly driven by precipitation, which affects species turnover.

The phylogenetic signal analysis also indicated that the temperature and precipitation niches of species exhibited phylogenetic signal, while the soil niche did not (Table 1). This result was consistent with the previous conclusion that climate explained more interspecific variation of leaf chemical traits and influenced species composition. Both results indicated that climate influences the community chemical traits mainly through the shift in species composition (He et al., 2008), whereas soil directly influ-

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ences the community chemical traits. Changes in leaf chemical traits along climate gradient are mainly due to difference in species composition along the gradient. Particularly, AP showed the strongest phylogenetic signal, largely due to the large gradient in precipitation across the study region and the dramatic variation in species composition adapted to aridity gradient.

4.4 Influence of phylogeny on leaf N and P concentrations

Leaf N concentration exhibited strong, while leaf P concentration exhibited weak, phylogenetic conservatism (Table 1). Furthermore, phylogenetic effect explained more variation in leaf N concentration than leaf P concentration. Legumes (species from the Fabaceae family) are higher in leaf N concentrations (Fig. S3) because of their ability of nitrogen fixation, and therefore may significantly increase the K value of leaf N concentration. However, when legumes were excluded, the K value remained almost unchanged (Table 1). Therefore, the phylogenetic conservatism of leaf N concentration is not resulted from the inclusion of legumes.

Plants disperse and evolve in response to changing environment in both time and space (Kerkhoff et al., 2006). In this process, traits that are easily changed by environment tend to be weakened in conservation during adaptive evolution (Losos, 2008). In this study, leaf N concentration was weakly influenced by soil nutrient, and the influence of climate on leaf N concentration mainly works through species turnover. Leaf N concentration therefore exhibited significant phylogenetic signal (Table 1). Leaf P concentration was significant influenced by soil nutrient, and its conservation was therefore weakened. This could also be attributed to the uptaking mechanism of P. The “mycorrhizal” pathway is the major pathway of P uptake in most vascular plants (Smith et al., 2003; Plassard and Dell, 2010) and the infection of mycorrhizal fungi mainly depends on environmental conditions rather than the host plants (Allen et al., 1995).

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5 Conclusions

In this study, we explored the patterns leaf N and P concentrations in relation to climate, soil and evolutionary history in northern China, based on 163 shrub species from 361 sites. We found that leaf N and P concentrations were mainly influenced by different factors, and thus responded to climate, soil, and evolutionary history differently. Leaf P concentration is jointly driven by soil P concentration and climate, whereas leaf N concentration is mainly driven by precipitation. Both leaf N and P concentrations are phylogenetically conserved, but leaf P concentration is less conserved than leaf N concentration, which could be attributed to the mechanism that plants utilize P. Changes in leaf chemical traits along climate gradient are mainly due to difference in species composition along the gradient, whereas soil influences the community chemical traits directly. Future studies of the biogeochemical implications and the evolutionary basis of plant nutrient concentrations in various regions, plant forms and other plant organs are important to understand the macroecological patterns and mechanisms of plant nutrient concentrations.

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Author contributions. X. Yang and Z. Tang conceived and designed the study, X. Yang, Z. Tang and X. Chi, conducted analyses and wrote the paper. X. Yang, C. Ji, H. Liu, W. Ma, A. Mohhammat, Z. Shi, X. Wang, S. Yu, M. Yue, and Z. Tang contributed data, discussed the draft manuscript and interpreted the results.

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Table 1. Arithmetic mean, range and phylogenetic signal (K value) of leaf N and P concentrations and environmental variables for shrubs in northern China.

	Mean (SD)	Range	K		Mean (SD)	Range	K
Leaf N (mg g^{-1})	21.91 (6.84)	4.26–46.80	0.31 ^a	MAT ($^{\circ}\text{C}$)	7.18 (3.42)	−4.05–15.98	0.26 ^a
Leaf N (mg g^{-1}) non-legumes	20.95 (6.47)	4.26–45.81	0.30 ^a	AP (mm)	478.79 (215.51)	15–974	0.53 ^a
Leaf P (mg g^{-1})	1.30 (0.53)	0.16–4.80	0.24 ^b	STN (mg g^{-1})	1.84 (1.67)	0.05–18.03	0.23 ^{NS}
Leaf N : P	18.69 (8.40)	4.07–145.76	0.24 ^a	STP (mg g^{-1})	0.56 (0.32)	0.12–3.20	0.17 ^{NS}

Abbreviations: MAT, mean annual temperature.

AP, annual precipitation.

STN, soil total nitrogen.

STP, soil total phosphorus.

^a $p < 0.001$.

^b $p < 0.01$.

^{NS} non-significance.

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Table 2. Summary of main-effect general linear models for leaf N (a), P (b) concentrations and N : P (c) of shrubs in northern China.

	Interspecific variation		Intraspecific variation		Total variation		SS%
	F	SS	F	SS	F	SS	
(a) MAT	0.01	0.2 ^{NS}	0.07	1.0 ^{NS}	0.01	0.3 ^{NS}	< 0.01
AP	47.67	932.1 ^a	0.79	10.8 ^{NS}	21.71	742.9 ^a	5.73
STN	17.62	344.6 ^a	0.91	12.5 ^{NS}	6.61	226.2 ^c	1.74
STP	0.01	0.2 ^{NS}	2.17	29.8 ^{NS}	0.74	25.3 ^{NS}	0.2
Residual	6844.1		4740.3		11 979		
Total	8121.2		4794.4		12 973.7	7.67	
(b) MAT	15.77	1.8 ^a	9.88	1.3 ^b	23.38	6.0 ^a	5.69
AP	31.38	3.6 ^a	1.45	0.2 ^{NS}	20.86	5.4 ^a	5.07
STN	2.44	0.3 ^{NS}	12.07	1.5 ^b	2.04	0.5 ^{NS}	0.5
STP	0.24	0.0 ^{NS}	35.65	4.6 ^a	14.88	3.8 ^a	3.62
Residual	40.4		43.4		90.2		
Total	46.2		51		106	14.88	
(c) MAT	6.73	103 ^b	3.59	58.44	9.86	312 ^b	1.96
AP	227.58	3487 ^a	0.83	13.48	124.11	3927 ^a	24.64
STN	5.42	83 ^c	0.02	0.26	2.45	78 ^{NS}	0.49
STP	0.73	11 ^{NS}	12.47	203.13 ^a	3.69	117 ^{NS}	0.73
Residual	5792		5605.56		11 504		
Total	9476		5879		15 938	27.82	

Abbreviations: MAT, mean annual temperature. AP, annual precipitation. STN, soil total nitrogen. STP, soil total phosphorus.

^a $p < 0.001$. ^b $p < 0.01$. ^c $p < 0.05$. NS = non-significance.

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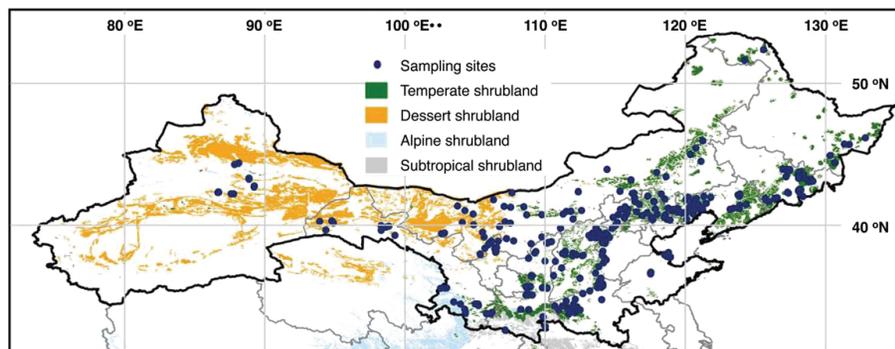


Figure 1. Locations of the sampling sites based on shrublands in northern China.

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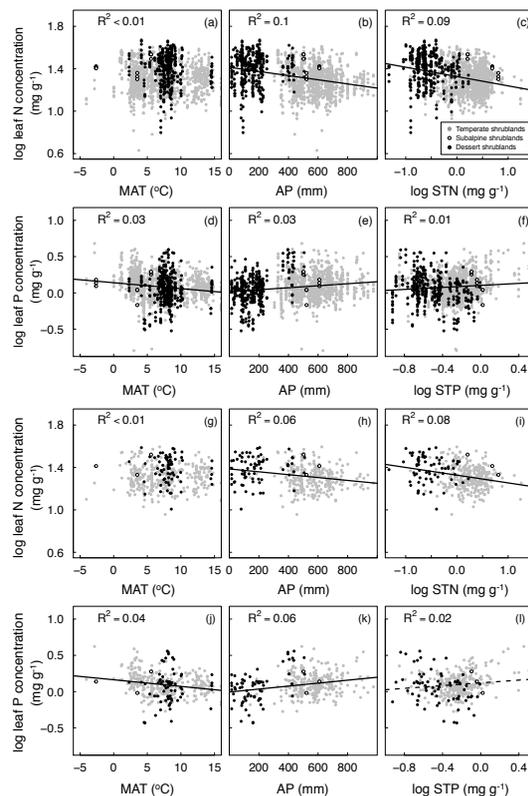


Figure 2. Individual (a–f) and community level (g–l) changes of logarithm transferred leaf nitrogen and phosphorus concentrations in relation to climate (mean annual temperature and annual precipitation, MAT and AP) and soil nutrient (soil total nitrogen and phosphorus concentrations, STN and STP) for shrubs in northern China. Solid lines represent regressions significant at $P < 0.001$, and dashed line represents regressions significant at $P < 0.01$.

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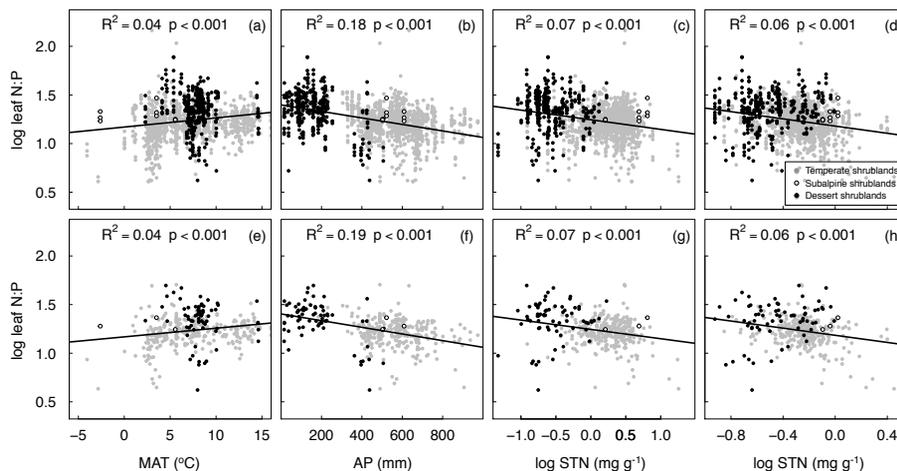


Figure 3. Individual (a–d) and community level (e–h) changes of logarithm transferred leaf N : P ratio in relation to climate (mean annual temperature and annual precipitation, MAT and AP) and soil nutrition (soil total nitrogen and phosphorus concentrations, STN and STP) for shrubs in northern China. Grey solid dots, black open circles and black solid dots represent samples from temperate, subalpine, and desert shrublands, respectively. Solid lines represent regressions significant at $P < 0.001$, and dashed line represents regressions significant at $P < 0.01$.

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