



C:N:P stoichiometry in China's forests: From organs to ecosystems

Jiahui Zhang^{1,2†} | Ning Zhao^{3†}  | Congcong Liu¹ | Hao Yang¹ | Meiling Li¹ | Guirui Yu^{1,2} | Kevin Wilcox⁴ | Qiang Yu⁵ | Nianpeng He^{1,2,6} 

¹Key Laboratory of Ecosystem Network Observation and Modeling, Institute of Geographic Sciences and Natural Resources Research, Chinese Academy of Sciences, Beijing, China; ²College of Resources and Environment, University of Chinese Academy of Sciences, Beijing, China; ³Key Laboratory of Remote Sensing of Gansu Province, Cold and Arid Regions Environmental and Engineering Research Institute, Chinese Academy of Sciences, Lanzhou, China; ⁴Department of Microbiology and Plant Biology, University of Oklahoma, Norman, OK, USA; ⁵National Hulunber Grassland Ecosystem Observation and Research Station/Institute of Agricultural Resources and Regional Planning, Chinese Academy of Agricultural Sciences, Beijing, China and ⁶Institute of Grassland Science, Northeast Normal University and Key Laboratory of Vegetation Ecology, Ministry of Education, Changchun, China

Correspondence

Nianpeng He and Qiang Yu

Emails: henp@igsrr.ac.cn; yuqiang@caas.cn

Funding information

National Key Research Project of China, Grant/Award Number: 2016YFC0500202; National Natural Science Foundation of China, Grant/Award Number: 31290221 and 31570471; Chinese Academy of Sciences, Grant/Award Number: KFJ-SW-STS-167

Handling Editor: Shuli Niu

Abstract

1. Ecological stoichiometry connects different levels of biology, from the gene to the globe, by scaling up elemental ratios (e.g. carbon [C], nitrogen [N] and phosphorus [P]). Thus, ecological stoichiometry could be a powerful tool for revealing certain physiological processes of plants. However, C:N:P stoichiometry remains unclear at the community and ecosystem levels, despite it being potentially important for primary productivity.
2. In this study, we measured the C, N and P contents of different plant organs, litter and soil in nine natural forest ecosystems (from cold-temperate to tropical forests along a 3,700-km transect in China) to explore C:N:P stoichiometry and the main influencing factors. C:N:P stoichiometry was evaluated for different components in the forest ecosystems (plant community, soil, litter and ecosystem) and, at the community level, for different organs (leaves, branches, trunks and roots) from 803 plant species.
3. The ratios of C:P and N:P decreased with increasing latitude, with spatial patterns being primarily regulated by climate. Interestingly, the homeostasis of N, P and N:P was highest in leaves, followed by branches, roots and trunks, supporting the hypothesis that more active organs have a higher capacity to maintain relatively stable element content and ratios. At the community level, the leaf N:P ratio indicated increasing P limitation in forests of lower latitude (i.e. more southerly) in China's forests.
4. Our findings demonstrate the spatial patterns of C:N:P stoichiometry and the strategies of element distribution among different organs in a plant community, providing important data on C:N:P to improve the parameterization of future ecological models.

KEYWORDS

C:N:P, community, ecological stoichiometry, homeostasis, latitudinal pattern, limiting element

†Jiahui Zhang and Ning Zhao contributed equally to this work.

1 | INTRODUCTION

All plants are composed of more than 16 elements that are essential for growth and development (Marschner, 2011), of which carbon (C), nitrogen (N) and phosphorus (P) are considered primary elements. The C:N:P ratio can be used to estimate the growth rate of some organisms (Elser, Sterner, et al. 2000), determine limiting elements (Koerselman & Meuleman, 1996) and demonstrate the allometric growth and distribution of mineral elements (Yang et al., 2014; Zhao, Yu, He, Xia, et al. 2016). In fact, these three items represent the main research focus of ecological stoichiometry. Ecological stoichiometry refers to the balance of energy and multiple chemical elements by element ratios (Sterner & Elser, 2002). It has been considered a major progress in ecology over the last two decades, with many ecologists being devoted to this field of research. As shown in Figure 1, most of studies on C, N and P stoichiometry in terrestrial ecosystems have focused on the organ level, and only a few have been conducted at the plant community and ecosystem levels. Previous studies have focused on averaging the element content of dominant species (through randomly collected data of some species in practice), which directly promoted the research process of ecological stoichiometry. However, this method of data processing is open to discussion. First, there are no standards for selecting dominant species, such as the number. Second, the different roles of different species or functional types were overlooked in the methods originally used. In nature, communities and ecosystems are formed as a result of the adaptation of species to a specific environment and mutual competition between species. Thus, structure and functioning of terrestrial ecosystems should be explored at this important community/ecosystem level. Therefore, investigations at the community level which include more species and functional types as well as community structure, rather than the organ level, might better reflect the characteristics of an ecosystem and provide a better foundation for improving ecological models.

The C, N and P content of plants is closely related to the environment; therefore, their stoichiometry might vary with changing environments (Li, Niu, & Yu, 2015; Zhang, Zhang, Slik, & Cao, 2012). Chapin, Matson, and Vitousek (2011) observed that plants obtain more than 90% of their N and P from the nutrients that plants returned to soil the previous year. Plants principally acquire N and P from the soil, with soil nutrient content representing an important factor regulating plant C:N:P stoichiometry (Gusewell, 2004). Reich and Oleksyn (2004) presented the Soil Substrate Age hypothesis to explain this process, whereby tropical soils that are considered to be older than temperate soils and to be more leached lead to increased C:N and C:P in leaves. In addition, climate (i.e. mean annual temperature [MAT] and mean annual precipitation [MAP]) vary dramatically with changing latitude and longitude. The mechanisms underlying the influence of climate on the spatial patterns of plant C:N:P stoichiometry remain unclear. However, several hypotheses have been proposed, including the Temperature–Plant Physiological hypothesis and the opposing Temperature–Biogeochemistry hypothesis (Reich & Oleksyn, 2004). In the former, leaves have higher N and P in colder climates to compensate for reduced efficiency and rate of biochemical reactions. In the latter, low temperatures suppress the mineralization and decomposition of organic matter, and then restrain plant N and P uptake (Reich & Oleksyn, 2004). However, these hypotheses have not been verified using data from the plant community level.

Organisms with homeostasis can keep the content of different elements, and their ratios, relatively stable in changing environments (Sterner & Elser, 2002). This phenomenon reflects the adaptation of organisms to their environment in long-term evolution (Yu et al., 2011). Homeostasis has been confirmed in plankton (Andersen & Hessen, 1991), algae (Rhee, 1978) and herbaceous plants (Yu et al., 2010, 2015). However, to date, the homeostasis of forest communities has not been reported. In fact, different plant organs play different roles to keep a plant alive. For example, leaves are mainly responsible for photosynthesis, transpiration and gas

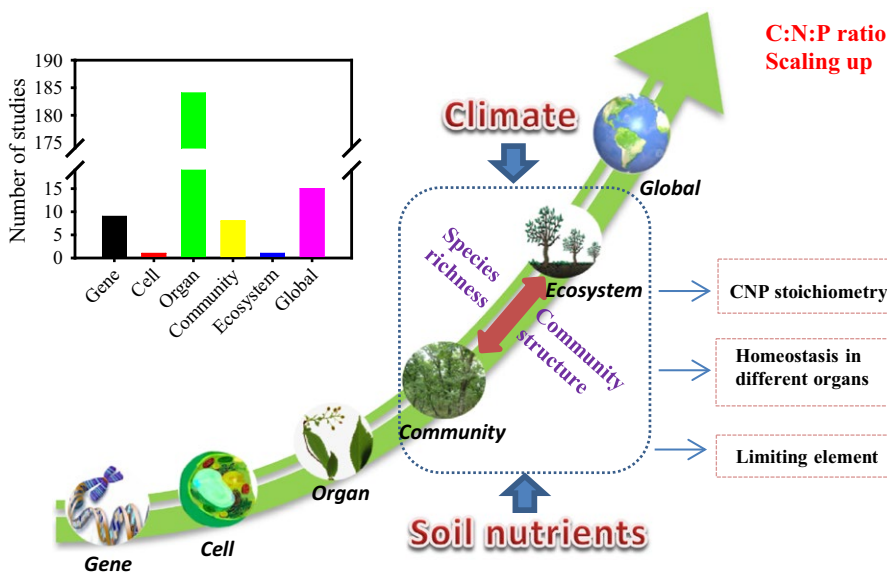


FIGURE 1 Theoretical framework of ecological stoichiometry and the key scientific issues at a terrestrial ecosystem scale. The small panel shows the number of stoichiometric studies in terrestrial ecosystems (meta-analysis)

exchange; roots are responsible for nutrient absorption and support; and trunks are responsible for support and storage. Typically, the most active organ has the highest requirements for requisite elements (e.g. N and P). Therefore, we hypothesized that more active organs would have higher N:P stoichiometry homeostasis to achieve optimal material and energy efficiency (the homeostasis hypothesis).

According to the law of the minimum (Liebig, 1840), the limiting element is the one whose content is below the minimum requirement of plants, because its supply cannot meet the need of plant growth and development, resulting in low forest productivity. Previous research has identified such element limitations at regional (Han, Fang, Guo, & Zhang, 2005) and global (Elser et al., 2007) scales. Furthermore, based on leaf element content for several species, these studies have noted that the limiting element has higher homeostasis (Avolio et al., 2014; Yu et al., 2015). Because the characteristics of the community can reflect nature better, the limiting element required to be investigated at the community level (considering most plant species and community structure).

The north-south transect of eastern China (NSTEC) is 4,700-km long, and includes almost all forest types in the northern hemisphere, and is mainly influenced by a thermal gradient. This transect provides a unique natural laboratory to investigate C:N:P stoichiometry in forest ecosystems and, in particular, to verify the suggested homeostasis hypothesis at the community level. The main objectives of this study were to: (1) reveal the C:N:P stoichiometry of ecosystem components and plant organs at the community level, (2) explore their latitudinal patterns and influencing factors (climate and soil) and (3) determine the limiting element of the forest community. Our results are expected to help improve the parameterization of future ecological models.

2 | MATERIALS AND METHODS

2.1 | Study site

Nine typical forest ecosystems along the NSTEC (cold-temperate to tropical zones) were included in the study (Figure 2). From north to the south, the sites spanned latitudes from 51.8 to 18.7°N, MAT from -4 to 23°C and MAP from 470 to 2,270 mm respectively. The soil types included podzol, greyzem, luvisol, ferralsol and Acrisol (Table S1). The vegetation types correspondingly varied from cold-temperate coniferous forest to tropical monsoon forest (Figure 2).

2.2 | Field sampling

In this study, we investigated the C, N and P contents of the different organs (leaves, branches, trunks and roots) in different plant species (total of 803 tree, shrub and herb species), as well as litter and soil. In 2013, field sampling was conducted during the period of peak growth (July and August). Each forest contained four experimental plots (30 m × 40 m), with plant species, number and community structure being investigated in each plot. For trees and shrubs, we measured

height and diameter at breast height (DBH) to calculate biomass (Wang et al., 2015). For herbs, we measured biomass by removing plants at ground level.

For all trees and shrubs in each plot, the leaves (only those sun exposed and fully expanded), end branches (diameter <1 cm, collected randomly), cores (gathered using increment borer at breast height) and fine roots (diameter <2 mm) were collected (in Jianfengling [JF], we only collected leaf samples due to the disturbance of typhoon in 2013). When we collected root samples, we removed the surrounding soil along certain main root until we found the fine roots to distinguish different species. For herbs, the whole plant was removed for subsequent processing. Soil samples were also collected using a soil sampler (40–50 random points in each plot) in the 0–10 cm and 10–30 cm layers.

The leaf, branch, trunk (or core), fine root and litter samples were carefully cleaned and oven-dried at 60°C. Soil samples were air-dried after being sieved (2-mm mesh), and visible roots and organic debris were separated by hand. All samples were ground to fine powder, using a ball mill (MM400 Ball Mill, Retsch, Germany) and an agate mortar grinder (RM200, Retsch, Haan, Germany), for element analysis (Zhao, Yu, He, Wang, et al. 2016).

2.3 | Measurement of element content

The C and N contents of the plant and soil samples were determined with an elemental analyser (Vario MAX CN Elemental Analyzer, Elementar, Hanau, Germany). Before measuring P, plant samples were acidified with 68% HNO₃, while soil samples were acidified with HNO₃ and HF, all night (Zhao, Yu, He, Wang, et al. 2016). Samples were then digested with a microwave digestion system (Mars X press Microwave Digestion system, CEM, Matthews, NC, USA). All samples were analysed for P with an inductively coupled plasma optical emission spectrometer (ICP-OES, Optima 5300 DV, Perkin Elmer, Waltham, USA).

2.4 | Historical data

We extracted climatic data (MAT and MAP) from the meteorological database, which was generated by the ANUSPLIN interpolation software, based on the data from 740 China Meteorological Administration climate stations during 1961–2007 (Li, He, Yu, Wang, & Sun, 2016; Tian, Yu, He, & Hou, 2016). The P content of litter was extracted from the published literature for experimental sites that was similar to our sites. A mini meta-analysis, using the search term “ecological stoichiometry” in Web of Science, was conducted to determine the number of stoichiometric studies in terrestrial ecosystems (Figure 1).

2.5 | Calculations and data analysis

To better reflect relative contribution of each species in the community, the C, N and P contents of the individual, community and ecosystem were calculated using the biomass-weighted mean method. Species-specific allometric equations were used to calculate the biomass of

leaves, branches, trunks and roots for each studied species in the community. However, some species' specific organ biomass was unavailable. Therefore, allometric equations from the same genera or mixed-species equations of a forest were used to deal with the problem (see equations from Table S7). C:N, C:P and N:P were used as the mass ratios in this study. We derived element content for the plant species, community and ecosystem using Equations 1, 2 and 3 respectively.

For the plant species:

$$E_{\text{Spe}} = E_L \times \frac{B_L}{B_{\text{Spe}}} + E_B \times \frac{B_B}{B_{\text{Spe}}} + E_T \times \frac{B_T}{B_{\text{Spe}}} + E_R \times \frac{B_R}{B_{\text{Spe}}} \quad (1)$$

where E_{Spe} is the element (C, N or P) content (g/kg) of the plant species. E_L , E_B , E_T and E_R are the element (C, N or P) content (g/kg) of the leaves, branches, trunks and roots of the species respectively. B_L , B_B , B_T and B_R are the biomass (t/ha) of the leaves, branches, trunks and roots of the species respectively. B_{Spe} is the biomass (t/ha) of the species.

For the plant community:

$$E_{\text{Com}} = \sum E_j \times \frac{B_j}{B_{\text{Com}}} \quad (2)$$

where E_{Com} is the element (C, N or P) content (g/kg) of the plant community, E_j is the element (C, N or P) content (g/kg) of the plant species j , B_j is the biomass (t/ha) of species j and B_{Com} is the biomass (t/ha) of the community.

For the ecosystem:

$$E_{\text{Eco}} = \frac{100 \times \sum E_j \times B_j + \sum E_{\text{sk}} \times \text{BD}_k \times T_k}{100 \times \sum B_j + \sum \text{BD}_k \times T_k} \quad (3)$$

where E_{Eco} is the element (C, N or P) content (g/kg) of the ecosystem, E_j and B_j are as defined for Equation 2, E_{sk} is the soil element (C, N or P) content (g/kg) of soil layer k , BD_k is the soil bulk density (g/cm³) of soil layer k , T_k is the thickness (cm) of soil layer k and 100 is the unit conversion factor.

Furthermore, to explore the C:N:P stoichiometry of the different organs, we also used the biomass-weighted mean method (Equation 4).

$$E_{\text{Org}} = \sum E_i \times \frac{B_i}{B_{\text{Org}}} \quad (4)$$

where E_{Org} is the element (C, N or P) content (g/kg) of the organ in a plot, E_i and B_i are the element (C, N or P) content (g/kg) and biomass (t/ha) of the organ of plant species i , respectively, and B_{Org} is the organ biomass (t/ha) of all species in the plot.

We used homeostatic regulation coefficient (H) to depict the homeostatic regulation capacity of different organs for different elements (Sterner & Elser, 2002) (Equation 5).

$$y = cx^{1/H} \quad (5)$$

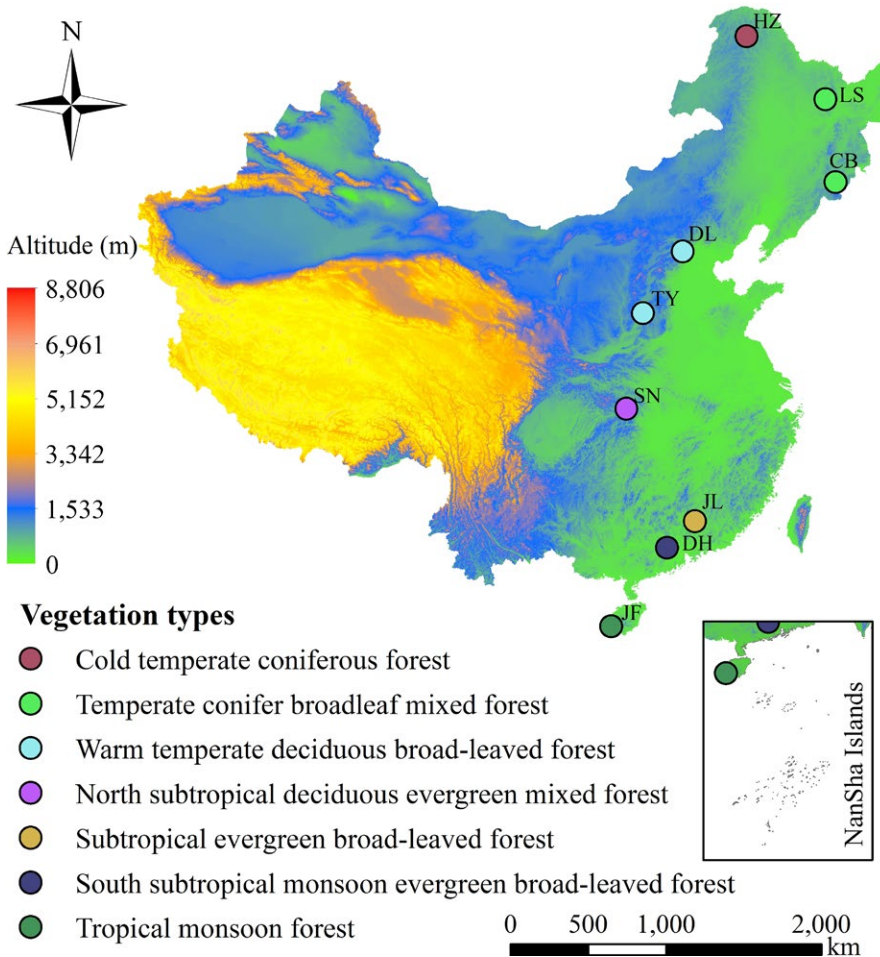


FIGURE 2 Locations of the selected forest ecosystems. HZ, Huzhong; LS, Liangshui; CB, Changbai; DL, Dongling; TY, Taiyue; SN, Shennongjia; JL, Jiulian; DH, Dinghu; JF, Jianfengling

where y is N or P content (g/kg) or the N:P ratio of plant organs at the community level calculated by Equation 4, x is N or P content (g/kg) or the N:P ratio of soil and c is a constant.

One-way ANOVA with Duncan's post hoc multiple comparisons was used to compare differences in the C:N:P ratio among ecosystem components and plant organs. Paired-samples t tests were used to test the differences between the two scaling-up methods; namely, the biomass-weighted mean and arithmetic mean (averaging species element content directly). Linear regressions were performed to describe the relationships among C:N, C:P, N:P, latitude, MAT, MAP and soil N and P contents. Redundancy analysis was used to determine influencing factors for the latitudinal pattern of N:P. All analyses were conducted by SPSS (version 19.0) statistic software or R (3.1.2) software. The significance level for all tests was $p = .05$.

3 | RESULTS

3.1 | Changes in C:N:P stoichiometry in different components of forest ecosystems

The estimated C:N:P ratios in China's forest ecosystem, plant community, litter and soil were 186:5:1, 1359:13:1, 714:21:1 and 73:5:1 respectively (Figure 3a). The variable coefficient (CV) of C:N was highest in the plant community, followed by litter and soil; however, the opposite trend was obtained for C:P and N:P (Table S2). Significant differences ($p < .05$) were observed for the C:N, C:P and N:P ratios of each component (ecosystem, plant community, litter and soil) among the nine forest ecosystems (Table S3).

In general, the C:P and N:P ratios for each ecosystem component were correlated with latitude, MAT, MAP and soil N and P contents. These two ratios were negatively correlated with latitude and soil N and P contents, but were positively correlated with MAT and MAP (Table 1). Redundancy analysis showed that climate (MAT and MAP) was the dominant factor regulating the spatial patterns of these two ratios, followed by soil (soil N and P contents). Together, climate and soil explained 97.2%, 62.9%, 86.8% and 90.1% of spatial variation in

the N:P ratio for the plant community, litter, soil and forest ecosystem respectively (Figure 4).

3.2 | Changes in C:N:P stoichiometry in different plant organs

The estimated leaf, branch, trunk and root C:N:P ratios were 447:19:1, 633:11:1, 5394:14:1 and 706:15:1 respectively (Figure 3b). The C:N, C:P and N:P ratios were significantly different among the different organs ($p < .05$), with the highest C:N and C:P occurring in the trunks, the highest N:P occurring in the leaves and the lowest N:P occurring in the branches. The CV of C:N and C:P was lowest in the branches and highest in the trunks. In contrast, the CV of N:P was lowest in the leaves and highest in the roots (Table S4). Furthermore, the C:N:P stoichiometry in each organ was significantly different among the nine forests (Table S5).

C:P and N:P ratios decreased with increasing latitude and soil N and P contents, and increased with increasing MAT and MAP, irrespective of plant organ (Table 2; Figure 5). However, no clear relationship was observed for C:N. Together, climate and soil explained 95.8%, 95.4%, 76.8% and 98.5% of N:P spatial variation in the leaves, branches, trunks and roots respectively (Figure 4).

3.3 | Changes in homeostasis among different plant organs

Different plant organs showed different homeostasis for N, P and N:P. Overall, leaves showed strong homeostasis for N, P and N:P. The branches and roots showed relatively strong homeostasis for P or N:P. In contrast, the trunks showed no homeostasis for any element (Table 3).

4 | DISCUSSION

4.1 | C:N:P stoichiometry in forest ecosystems

Our study is the first to report the C:N:P stoichiometry of several ecosystem components and plant organs at a large scale (Table S6).

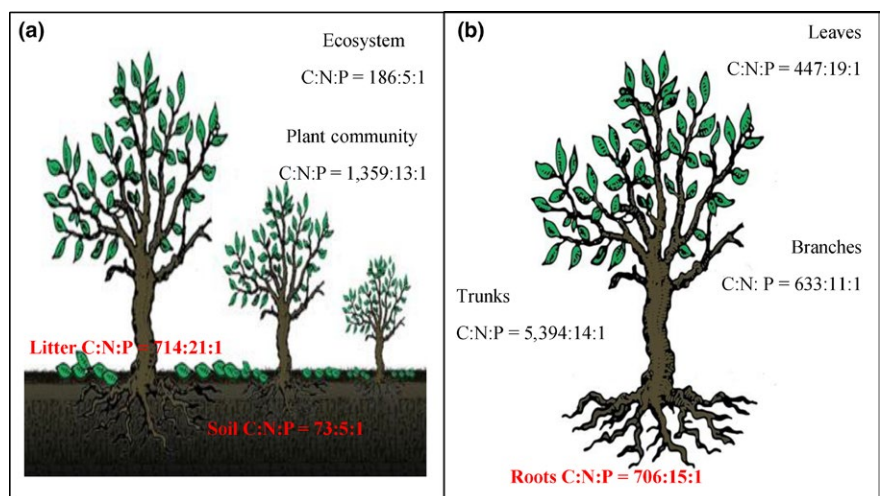


FIGURE 3 Changes in C:N:P ratios at the community level among different components (a) and different organs (b) in China's forests, which were calculated using the biomass-weighted mean method

| | Ratio | Latitude | MAT | MAP | Soil N content | Soil P content |
|-----------------|-------|----------------|---------------|--------------|----------------|----------------|
| Ecosystem | C:N | -0.58 | 0.66 | 0.69 | -0.73* | -0.75* |
| | C:P | -0.64 | 0.76* | 0.71* | -0.63 | -0.80* |
| | N:P | -0.59 | 0.72* | 0.63 | -0.55 | -0.83* |
| Plant community | C:N | 0.45 | -0.36 | -0.19 | -0.11 | 0.08 |
| | C:P | -0.37 | 0.53 | 0.38 | -0.79* | -0.59 |
| | N:P | -0.66 | 0.76* | 0.44 | -0.74* | -0.67 |
| Litter | C:N | 0.07 | -0.07 | -0.17 | -0.07 | -0.16 |
| | C:P | -0.80** | 0.83** | 0.79* | -0.82** | -0.66 |
| | N:P | -0.73** | 0.75* | 0.77* | -0.68* | -0.50 |
| Soil | C:N | 0.28 | -0.21 | -0.29 | -0.28 | -0.32 |
| | C:P | -0.53 | 0.62 | 0.61 | -0.59 | -0.85** |
| | N:P | -0.64 | 0.71* | 0.72* | -0.56 | -0.76* |

MAT, mean annual temperature; MAP, mean annual precipitation.

* $p < .05$, ** $p < .01$.

TABLE 1 Correlation coefficients of C:N, C:P and N:P of different components with respect to latitude, MAT, MAP, soil N and soil P contents in forest ecosystems. The bold fonts indicated significant correlations

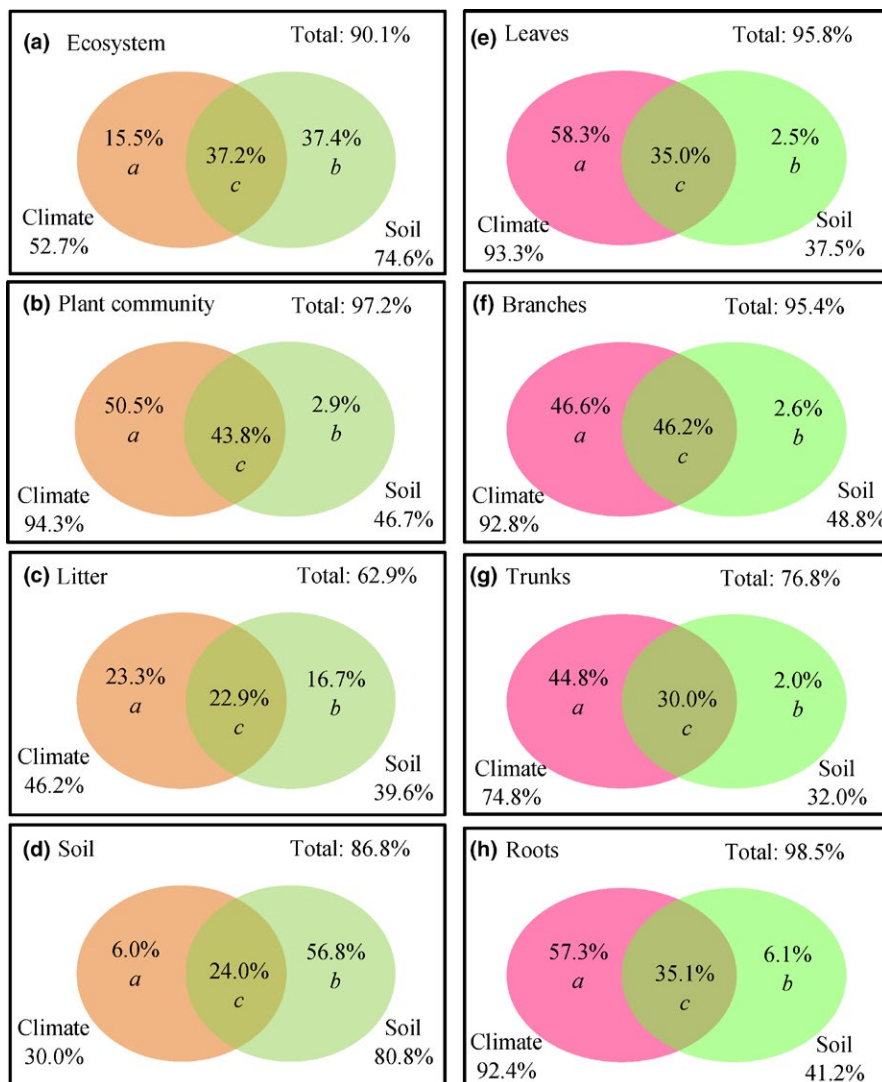


FIGURE 4 Variance in the latitudinal pattern of N:P in different ecosystem components and different plant organs might be explained by climate (MAT and MAP) as well as soil N and P contents using redundancy analysis. *a* and *b* are the single effects; *c* is the interaction effect

TABLE 2 Correlation coefficients of C:N, C:P and N:P of plant organs with respect to latitude, MAT, MAP, soil N and soil P contents in forest ecosystems. The bold fonts indicated significant correlations

| | Ratio | Latitude | MAT | MAP | Soil N content | Soil P content |
|--------|-------|----------------|---------------|---------------|----------------|----------------|
| Leaf | C:N | -0.53 | 0.52 | 0.54 | -0.76* | -0.53 |
| | C:P | -0.93** | 0.96** | 0.86** | -0.81** | -0.77* |
| | N:P | -0.90** | 0.94** | 0.80* | -0.67 | -0.72* |
| Branch | C:N | 0.40 | -0.29 | -0.23 | -0.18 | -0.25 |
| | C:P | -0.72* | 0.82* | 0.56 | -0.81* | -0.83* |
| | N:P | -0.78* | 0.85** | 0.58 | -0.73* | -0.72* |
| Trunk | C:N | 0.35 | -0.25 | -0.24 | -0.25 | 0.08 |
| | C:P | 0.03 | 0.12 | 0.04 | -0.45 | -0.15 |
| | N:P | -0.61 | 0.76* | 0.52 | -0.61 | -0.52 |
| Root | C:N | -0.30 | 0.20 | 0.58 | -0.09 | -0.05 |
| | C:P | -0.77* | 0.84** | 0.63 | -0.86** | -0.67 |
| | N:P | -0.51 | 0.59 | 0.23 | -0.70 | -0.56 |

MAT, mean annual temperature; MAP, mean annual precipitation.

* $p < .05$, ** $p < .01$.

In general, our results differed from those obtained by a previous global-scale study. For example, root C:N:P was 706:15:1 in our study, whereas it was 522:12:1 in the previous global-scale study (Gordon & Jackson, 2000). However, due to the use of different scaling-up methods, some results reported here were not able to compare with those of previous studies. In this study, the biomass-weighted mean method was used for scaling-up, whereas most previous studies only collected data on the dominant species, and used the arithmetic mean method for scaling-up. In general, the biomass-weighted mean method should better reflect reality, because it considers the relative contribution of each species in the community. To determine if there were any differences between the two scaling-up methods, we used our data to calculate means using both methods. As a result, we confirmed that there are significant differences ($p < .05$) between the two methods, especially for C:N and C:P. For instance, most of the means were higher using the biomass-weighted mean method compared to the arithmetic mean method (Figures S1 and S2). These results suggest that calculating C:N:P stoichiometry without considering plant community structure might underestimate the elemental ratios, with this issue requiring future consideration in ecological models.

We only found one previous study using the biomass-weighted mean method (Jackson, Mooney, & Schulze, 1997). However, our study obtained higher root C:N:P (706:15:1) compared to that obtained by in Jackson et al. (1997) (450:11:1). This difference might be attributed to systematic sampling and investigation in this study rather than collecting data from other studies. In general, the data of species' traits collected from published literature can well only explain the characteristics of dominant species. However, C:N:P ratios of non-dominant species were also shown in this study, which is significantly different from the dominant species. In addition, we only focused on forest ecosystems in China rather than all kinds of ecosystems, including tundra, desert and grassland globally, in which N and P contents of fine root were high (Yuan, Chen, & Reich, 2011).

Significant differences in C:N:P stoichiometry were detected among the different organs (Table S4). The ratios of C:N and C:P were higher in trunks than in the other organs. This difference is likely due to more N and P being allocated to active organs (e.g. leaves and branches) to meet the requirements of plant growth and development (Sternier & Elser, 2002). Trunks are primarily responsible for support; consequently, trunks contain more carbohydrates (i.e. carbon) than other organs. In contrast, leaves are responsible for photosynthesis, and need sufficient N and P to synthesize various enzymes for biochemical reactions. In comparison, branches contain abundant N and P, because they are responsible for the development of new shoots and nutrient exchange. Because fine roots connect the plant to the soil, they are important for absorbing water and mineral nutrients (Taiz & Zeiger, 2002) and exchanging materials. Consequently, roots require adequate N and P to support metabolism and transfer excess N and P to leaves and branches. In general, the activity of organs determines the level of the element ratios.

4.2 | Climate is the main factor influencing spatial patterns in C:N:P stoichiometry

The ratios of C:P and N:P in different ecosystem components and plant organs showed decreasing trends with increasing latitude (Tables 1 and 2). These results are consistent with the Temperature-Plant Physiological hypothesis and the Soil Substrate Age hypothesis (Reich & Oleksyn, 2004). In high-latitude areas, the growing season is short, and accompanied by lower temperature. Therefore, plants might increase their absorption of nutrient elements to compensate for lower enzyme efficiency and RNA. In contrast, low-latitude regions with a tropical climate (i.e. higher MAP and MAT) have no decrease in enzyme efficiency or RNA, but do have a larger loss in soil nutrients through leaching than in high-latitude regions. Consequently, P content is lower in low-latitude regions. In addition, plants mainly absorb P from the soil, whereas they obtain N from

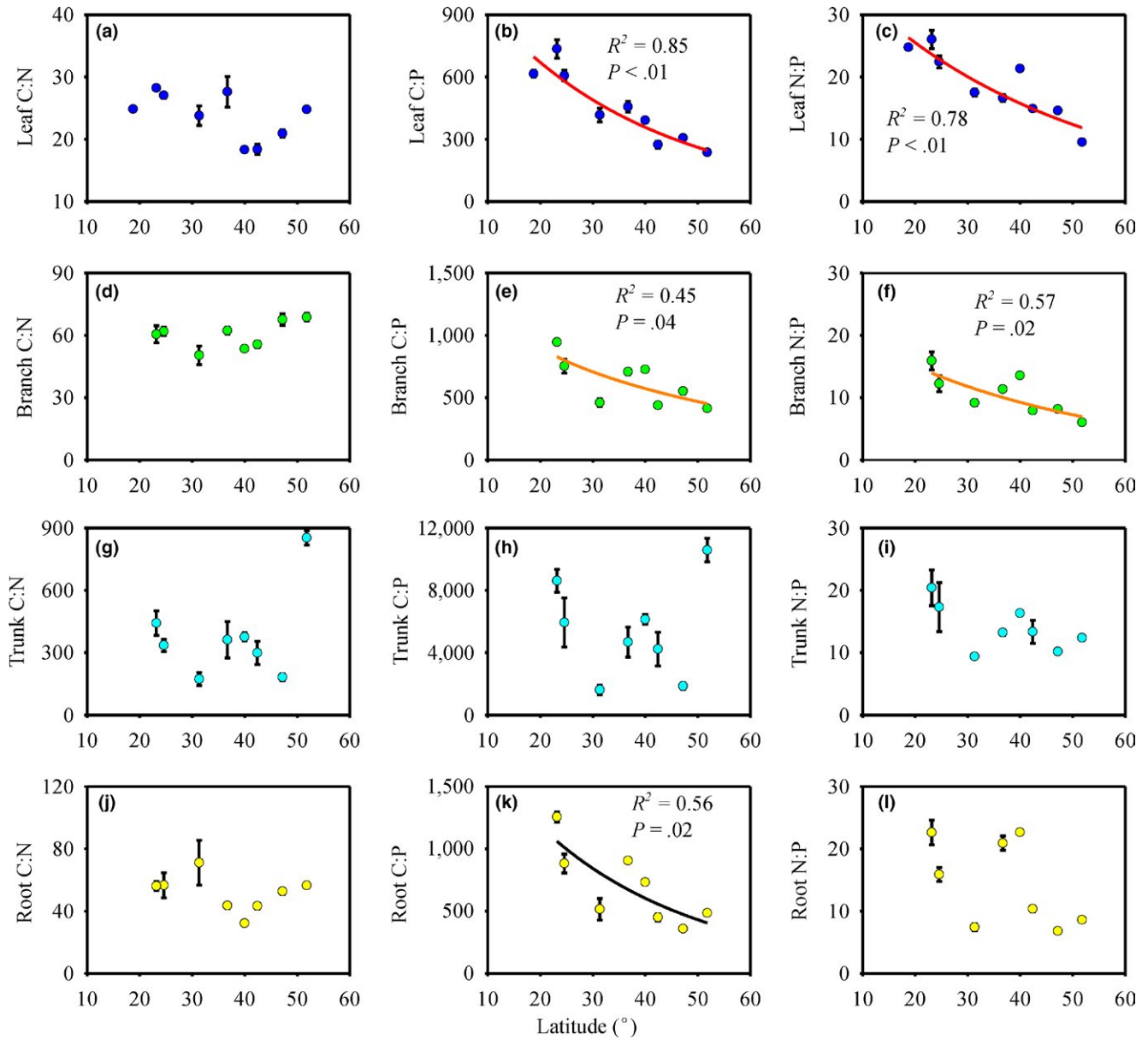


FIGURE 5 Latitudinal patterns of C:N, C:P and N:P of different plant organs. R^2 is the coefficient of determination; p is the significance level at $p = .05$ level

several sources, that is, the soil, biological N fixation and significantly increasing atmospheric N deposition (Jia et al., 2014; Zhu et al., 2015, 2016). Thus, the source of elements might explain N:P spatial pattern. Previous studies on the spatial patterns of C:N:P stoichiometry were mostly conducted using leaf (Elser, Fagan, et al. 2000; Han et al., 2005; Kerkhoff, Enquist, Elser, & Fagan, 2005) and root (Yuan et al., 2011) data collected from published literature, resulting in it being fragmentary and biased. The results from our comprehensive study provide important information on different ecosystem components and plant organs and therefore help to fill the knowledge gap on C:N:P stoichiometry, as we provide the first results on this subject for forest ecosystem and community.

The latitudinal patterns of C:N:P stoichiometry in forest ecosystems are controlled by many factors. Using redundancy analysis, we

found that climate factors (MAT and MAP) and edaphic factors (soil N and P contents) explain most of the variation in the N:P ratio in forests at a large scale (Figure 4). In general, more of the variation was explained by climate ($a + c$) than by edaphic factors ($b + c$). This difference might occur because the studied plant species had different tolerances to climatic conditions, which resulted in regular changes in community structure along the NSTEC. However, whether climate influences these patterns by regulating plant species composition or phylogenetic properties remains unclear and requires further investigation. Furthermore, changes in climate altered the hydrothermal conditions along the NSTEC, which might have resulted in different nutrient allocation among different plants, and even among different plant organs. Soils provide the main nutrient elements (including trace elements) to maintain plant growth, but have weak capacity to alter

TABLE 3 Homeostatic regulation coefficient (H) of different plant organs, which was calculated using $y = cx^{1/H}$

| Organ | N | | P | | N:P | |
|--------|-------|-------|-------|-------|-----------|-------|
| | H_N | R^2 | H_P | R^2 | $H_{N:P}$ | R^2 |
| Leaf | 3.14 | 0.45 | 2.05 | 0.63 | 2.08 | 0.35 |
| Branch | — | — | 2.29 | 0.71 | 2.14 | 0.29 |
| Trunk | — | — | — | — | — | — |
| Root | — | — | 2.02 | 0.45 | — | — |

H_N , H_P and $H_{N:P}$ were homeostatic regulation coefficient for N, P and N:P, respectively; R^2 , coefficient of determination; —, no significant difference at $p < .05$.

species composition or vegetation types. Therefore, for N:P spatial patterns, climate was the dominant influencing factor.

4.3 | Element allocation in different organs represents the adaptation strategy of plants

At the community level, the N, P and N:P levels in leaves were well regulated, which showed a high homeostasis that was not observed in other organs (Table 3). This phenomenon might occur because leaves are responsible for supplying energy (through photosynthesis) to support plant growth; therefore, leaves need to be able to maintain a suitable nutrient level (i.e. homeostasis). These findings support the hypothesis that active organs are able to maintain nutrient levels to ensure optimal material and energy use efficiency. This mechanism is unique, allowing plants to adapt to changing environments.

In general, better constraint was exhibited for P compared to N in the different plant organs (Table 3). Based on the theory stating that limiting elements are better regulated in homeostasis (Avolio et al., 2014; Yu et al., 2015), our results suggest that P was the more restricted element in the plant community. Under low phosphorus stress, plants form a self-regulating mechanism, through strengthening P absorption from the soil or re-absorption from the senescent organs (Aerts, 1996; Yuan et al., 2005), which keeps the element at a relatively stable state to ensure a variety of plant biochemical reactions.

4.4 | Forests in low-latitude regions are more restricted by P limitation

At the community level, the ratio of leaf N:P ranged from 9.6 in Huzhong (HZ) (cold-temperate forest) to 24.8 in JF (tropical forest), which were logarithmic decreases with increasing latitude (Table S5, Figure 5). Based on the standard (Koerselman & Meuleman, 1996), $N:P < 14$ indicates N limitation, $N:P > 16$ indicates P limitation and $14 < N:P < 16$ indicates that the plant is co-limited by N and P. Therefore, we concluded that high-latitude forests are not subject to P limitation, whereas low-latitude forests are restricted by P supply, with this limitation effect strengthening with decreasing latitude.

In natural forests, P mainly originates from the soil, through rock weathering (Tiessen, Stewart, & Cole, 1984; Walbridge, Richardson, & Swank, 1991). In the short term, available P mainly exists in soil organic matter and organisms. In tropical soil, P is the main limiting element, whereas N is the limiting element in high-latitude soil (Reich & Oleksyn, 2004). Soils in low-latitude areas, such as red soil and laterite in this study, have lower available P because of the tropical climate, with faster mineralization and stronger eluviation (Reich & Oleksyn, 2004). In addition, higher N deposition in south China (Zhu et al., 2015) accelerates plant growth. This phenomenon increases plant demand for P, resulting in higher P limitation in the future (Elser et al., 2009; Li et al., 2015). Furthermore, P limitation of plant growth also results from limiting microbial growth in tropical forests (Cleveland, Townsend, & Schmidt, 2002). Considering the inhibition of limiting element for forest development, these results suggest that further consideration should be given to element limitations in forest management strategies in China and in other forest systems globally.

5 | CONCLUSIONS

This study was the first comprehensive field investigation (cold-temperate to tropical ecosystems) of C:N:P stoichiometry in different organs, plant species and soils. Our results provided important information on ecological stoichiometry at the natural community/ecosystem level. The C:P and N:P ratios of different components and organs decreased with increasing latitude. Variations in the spatial patterns of N:P were better explained by climate than by soil factors. However, the influencing mechanisms require further investigation. The findings of the study supported the homeostasis hypothesis, with this unique mechanism allowing plants to adapt to their environment. Furthermore, at the community level, leaf N:P ratio decreased (logarithmic) with increasing latitude, indicating that the limiting effect of P supply increases with decreasing latitude. This finding has important implications on forest management practices. In particular, our study provides valuable data for improving and establishing new forest ecosystem models, as well as providing a basis for future research on global C, N and P coupling cycles.

ACKNOWLEDGEMENTS

This work was supported by the National Key Research Project of China (2016YFC0500202), the National Natural Science Foundation of China (31290221, 31570471), STS of the Chinese Academy of Sciences (KFJ-SW-STS-167) and by the program of Youth Innovation Research Team Project (LENOM2016Q0005).

AUTHORS' CONTRIBUTIONS

J.Z., N.Z. and N.P. conceived the ideas and designed methodology; J.Z., Z.N., H.Y., M.L. and N.H. collected the data; J.Z., Q.Y. and N.H. analysed the data; J.Z., N.H., G.Y. and K.W. led the writing of the

manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA ACCESSIBILITY

Relative data are appended in the Supporting Information. Data used in this manuscript are available from Dryad Digital Repository <https://doi.org/10.5061/dryad.2r8v4> (Zhang et al., 2017).

ORCID

Ning Zhao  <http://orcid.org/0000-0002-6915-3828>

Nianpeng He  <http://orcid.org/0000-0002-0458-5953>

REFERENCES

- Aerts, R. (1996). Nutrient resorption from senescing leaves of perennials: Are there general patterns? *Journal of Ecology*, *84*, 597–608.
- Andersen, T., & Hessen, D. O. (1991). Carbon, nitrogen, and phosphorus content of freshwater zooplankton. *Limnology and Oceanography*, *36*, 807–814.
- Avolio, M. L., Koerner, S. E., La Pierre, K. J., Wilcox, K. R., Wilson, G. W., Smith, M. D., & Collins, S. L. (2014). Changes in plant community composition, not diversity, during a decade of nitrogen and phosphorus additions drive above-ground productivity in a tallgrass prairie. *Journal of Ecology*, *102*, 1649–1660.
- Chapin III, F. S., Matson, P. A., & Vitousek, P. (2011). *Principles of terrestrial ecosystem ecology*. New York, NY: Springer Science & Business Media.
- Cleveland, C. C., Townsend, A. R., & Schmidt, S. K. (2002). Phosphorus limitation of microbial processes in moist tropical forests: Evidence from short-term laboratory incubations and field studies. *Ecosystems*, *5*, 680–691.
- Elser, J. J., Andersen, T., Baron, J. S., Bergstrom, A. K., Jansson, M., Kyle, M., ... Hessen, D. O. (2009). Shifts in lake N: P stoichiometry and nutrient limitation driven by atmospheric nitrogen deposition. *Science*, *326*, 835–837.
- Elser, J. J., Bracken, M. E. S., Cleland, E. E., Gruner, D. S., Harpole, W. S., Hillebrand, H., ... Smith, J. E. (2007). Global analysis of nitrogen and phosphorus limitation of primary producers in freshwater, marine and terrestrial ecosystems. *Ecology Letters*, *10*, 1135–1142.
- Elser, J. J., Fagan, W. F., Denno, R. F., Dobberfuhl, D. R., Folarin, A., Huberty, A., ... Sterner, R. W. (2000). Nutritional constraints in terrestrial and freshwater food webs. *Nature*, *408*, 578–580.
- Elser, J. J., Sterner, R. W., Gorokhova, E., Fagan, W. F., Markow, T. A., Cotner, J. B., ... Weider, L. J. (2000b). Biological stoichiometry from genes to ecosystems. *Ecology Letters*, *3*, 540–550.
- Gordon, W. S., & Jackson, R. B. (2000). Nutrient concentrations in fine roots. *Ecology*, *81*, 275–280.
- Gusewell, S. (2004). N: P ratios in terrestrial plants: variation and functional significance. *New Phytologist*, *164*, 243–266.
- Han, W. X., Fang, J. Y., Guo, D. L., & Zhang, Y. (2005). Leaf nitrogen and phosphorus stoichiometry across 753 terrestrial plant species in China. *New Phytologist*, *168*, 377–385.
- Jackson, R. B., Mooney, H. A., & Schulze, E. D. (1997). A global budget for fine root biomass, surface area, and nutrient content. *Proceedings of the National Academy of Sciences of the United States of America*, *94*, 7362–7366.
- Jia, Y., Yu, G., He, N., Zhan, X., Fang, H., Sheng, W., ... Wang, Q. (2014). Spatial and decadal variations in inorganic nitrogen wet deposition in China induced by human activity. *Scientific Reports*, *4*, 3763. <https://doi.org/10.1038/srep03763>
- Kerkhoff, A. J., Enquist, B. J., Elser, J. J., & Fagan, W. F. (2005). Plant allometry, stoichiometry and the temperature-dependence of primary productivity. *Global Ecology and Biogeography*, *14*, 585–598.
- Koerselman, W., & Meuleman, A. F. M. (1996). The vegetation N: P ratio: A new tool to detect the nature of nutrient limitation. *Journal of Applied Ecology*, *33*, 1441–1450.
- Li, N., He, N., Yu, G., Wang, Q., & Sun, J. (2016). Leaf non-structural carbohydrates regulated by plant functional groups and climate: Evidences from a tropical to cold-temperate forest transect. *Ecological Indicators*, *62*, 22–31.
- Li, Y., Niu, S., & Yu, G. (2015). Aggravated phosphorus limitation on biomass production under increasing N addition: A meta-analysis. *Global Change Biology*, *22*, 934–943.
- Liebig, J. V. (1840). *Organic chemistry in its application to vegetable physiology and agriculture. Readings in ecology*. New York, NY: Prentice Hall.
- Marschner, H. (2011). *Marschner's mineral nutrition of higher plants*. London, UK: Academic Press.
- Reich, P. B., & Oleksyn, J. (2004). Global patterns of plant leaf N and P in relation to temperature and latitude. *Proceedings of the National Academy of Sciences of the United States of America*, *101*, 11001–11006.
- Rhee, G. Y. (1978). Effects of N-P atomic ratios and nitrate limitation on algal growth, cell composition, and nitrate uptake. *Limnology and Oceanography*, *23*, 10–25.
- Sterner, R. W., & Elser, J. J. (2002). *Ecological stoichiometry: The biology of elements from molecules to the biosphere*. Princeton, NJ: Princeton University Press.
- Taiz, L., & Zeiger, E. (2002). *Plant physiology*, (3rd edn.). Sunderland, MA: Sinauer.
- Tian, M., Yu, G., He, N., & Hou, J. (2016). Leaf morphological and anatomical traits from tropical to temperate coniferous forests: Mechanisms and influencing factors. *Scientific Reports*, *6*, 19703. <https://doi.org/10.1038/srep19703>
- Tiessen, H., Stewart, J., & Cole, C. (1984). Pathways of phosphorus transformations in soils of differing pedogenesis. *Soil Science Society of America Journal*, *48*, 853–858.
- Walbridge, M. R., Richardson, C. J., & Swank, W. T. (1991). Vertical distribution of biological and geochemical phosphorus subcycles in two southern Appalachian forest soils. *Biogeochemistry*, *13*, 61–85.
- Wang, R. L., Yu, G. R., He, N. P., Wang, Q. F., Zhao, N., Xu, Z. W., & Ge, J. P. (2015). Latitudinal variation of leaf stomatal traits from species to community level in forests: Linkage with ecosystem productivity. *Scientific Reports*, *5*, 14454. <https://doi.org/10.1038/srep14454>
- Yang, X., Tang, Z. Y., Ji, C. J., Liu, H. Y., Ma, W. H., Mohamot, A., ... Zheng, C. Y. (2014). Scaling of nitrogen and phosphorus across plant organs in shrubland biomes across northern China. *Scientific Reports*, *4*, 5448. <https://doi.org/10.1038/srep05448>
- Yu, Q., Chen, Q. S., Elser, J. J., He, N. P., Wu, H. H., Zhang, G. M., ... Han, X. G. (2010). Linking stoichiometric homeostasis with ecosystem structure, functioning and stability. *Ecology Letters*, *13*, 1390–1399.
- Yu, Q., Elser, J. J., He, N. P., Wu, H. H., Chen, Q. S., Zhang, G. M., & Han, X. G. (2011). Stoichiometric homeostasis of vascular plants in the Inner Mongolia grassland. *Oecologia*, *166*, 1–10.
- Yu, Q., Wilcox, K., La Pierre, K., Knapp, A. K., Han, X. G., & Smith, M. D. (2015). Stoichiometric homeostasis predicts plant species dominance, temporal stability, and responses to global change. *Ecology*, *96*, 2328–2335.
- Yuan, Z. Y., Chen, H. Y. H., & Reich, P. B. (2011). Global-scale latitudinal patterns of plant fine-root nitrogen and phosphorus. *Nature Communications*, *2*, 344. <https://doi.org/10.1038/ncomms1346>
- Yuan, Z. Y., Li, L. H., Han, X. G., Huang, J. H., Jiang, G. M., Wan, S. Q., ... Chen, Q. S. (2005). Nitrogen resorption from senescing leaves in 28 plant species in a semi-arid region of northern China. *Journal of Arid Environments*, *63*, 191–202.
- Zhang, S. B., Zhang, J. L., Slik, J. W. F., & Cao, K. F. (2012). Leaf element concentrations of terrestrial plants across China are influenced by taxonomy and the environment. *Global Ecology and Biogeography*, *21*, 809–818.

- Zhang, J., Zhao, N., Liu, C., Yang, H., Li, M. L., Yu, G., ... He, N. (2017). Data from: C:N:P stoichiometry in China's forests: from organs to ecosystems. *Dryad Digital Repository*, <https://doi.org/10.5061/dryad.2r8v4>
- Zhao, N., Yu, G., He, N., Wang, Q., Guo, D., Zhang, X., ... Li, N. (2016). Coordinated pattern of multi-element variability in leaves and roots across Chinese forest biomes. *Global Ecology and Biogeography*, *25*, 359–367.
- Zhao, N., Yu, G., He, N., Xia, F., Wang, Q., Wang, R., ... Jia, Y. (2016). Invariant allometric scaling of nitrogen and phosphorus in leaves, stems, and fine roots of woody plants along an altitudinal gradient. *Journal of plant research*, *129*, 1–11.
- Zhu, J. X., He, N. P., Wang, Q. F., Yuan, G. F., Wen, D., Yu, G. R., & Jia, Y. L. (2015). The composition, spatial patterns, and influencing factors of atmospheric wet nitrogen deposition in Chinese terrestrial ecosystems. *Science of the Total Environment*, *511*, 777–785.
- Zhu, J., Wang, Q., He, N., Smith, M. D., Elser, J. J., Du, J., ... Yu, Q. (2016). Imbalanced atmospheric nitrogen and phosphorus depositions in

China: Implications for nutrient limitation. *Journal of Geophysical Research: Biogeosciences*, *121*, 1605–1616.

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

How to cite this article: Zhang J, Zhao N, Liu C, et al. C:N:P stoichiometry in China's forests: From organs to ecosystems. *Funct Ecol*. 2017;00:1–11. <https://doi.org/10.1111/1365-2435.12979>