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Nitrogen use efficiency of terrestrial plants in China: geographic patterns, evolution, and determinants

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Abstract

Background: Plant nitrogen use efficiency (NUE) is an important ecological indicator that reflects the capacity of a plant to transform nitrogen into production, which is essential for further elucidating plant growth and terrestrial ecosystem productivity. Although there are a growing number of studies that address NUE changes at local scales, the variations of NUE over large spatial scales remain unclear. In this study, we analyzed the geographic patterns of NUE and explored its phylogenic and environmental drivers across 1452 species at 1102 sites in China.

Results: NUE tended to decrease with latitude ($r = -0.56$), whereas it increased with longitude ($r = 0.54$), and varied widely in different ecosystems and plant life forms. Furthermore, NUE was negatively correlated with plant foliar phosphorus concentration ($r = -0.53$), soil pH ($r = -0.10$), soil total phosphorus ($r = -0.13$) and available phosphorus ($r = -0.05$), but positively with the mean annual temperature ($r = 0.32$), annual precipitation ($r = 0.27$), and aridity index ($r = 0.26$). NUE was significantly altered with phylogeny and evolved toward a lower value ($r = -0.28$), which may have been due to increasing nitrogen deposition and fixation in biogeochemical evolution. Overall, the combination of foliar phosphorus concentration, phylogeny, climate, and soil properties accounted for 52.7% of the total variations of NUE. In particular, foliar phosphorus concentration was the most important factor, whereas plant evolutionary history was second in contributing to NUE variations.

Conclusions: Our study emphasizes the pivotal role of plant stoichiometry and phylogeny in nitrogen cycling and suggests incorporating them into earth system models to better understanding plant growth and nitrogen cycling in the context of environmental changes.

Keywords: Nitrogen use efficiency, Foliar phosphorus, Geographic pattern, Stoichiometry, Plant phylogeny, Climate, Soil properties

Introduction

The efficient use of nitrogen (N) is essential for plants, as it is one of the most limiting factors for plant growth (Pellegrini 2016). Plant nitrogen use efficiency (NUE) is defined as the net dry mass production per unit of N uptake, which is extensively employed for research into plant N use strategies (Hirose 2011). Plants with higher NUE can better integrate limited N resources to gain advantages in barren environments (Vitousek 1982). Currently, human-generated N is continuously introduced into the environment, which has led to a general increase in atmospheric N deposition (Canfield et al. 2010; Peñuelas et al. 2012). Simultaneously, increasing global carbon dioxide (CO_2) levels promote plant photosynthesis, which induces plants to absorb additional N from the soil to support their growth (Ainsworth and Rogers 2007; Reich et al. 2006a, b). Hence the effects of global CO_2 fertilization largely depend on the availability of nutrients

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(LeBauer and Treseder 2008; Reich et al. 2006a, b; Wang et al. 2020). However, the correlation between the increased atmospheric N deposition and plant N demand is uncertain, which increases the complexity of plant N use strategies.

The limitation of N on primary plant productivity is common in most ecosystems worldwide (Agren et al. 2012; Du et al. 2020; Elser et al. 2007; Zhu et al. 2016). Thus, plant N use strategies play a critical role in determining primary plant productivity and ecosystem responses to global environmental changes. Several previous studies have examined NUE and its responses to climate and soil factors in some ecosystems (Fu et al. 2019; Hirose 2012; Yin et al. 2021; Zuo et al. 2016). However, exactly how NUE changes at large scales and what are its determinants remain unknown for the most part.

The NUE of wild plant species varies greatly in the natural environment (Chapin 1980), which may be due to changes in soil properties, climate conditions, and other environmental factors. Among these factors, the relationship between NUE and the availability of soil N has been extensively explored. Studies on coniferous pine at various sites found that NUE decreased as the availability of N increased (Vitousek 1982), as well as when plants were subjected to high N concentrations (Aerts and Decaluwe 1994). These observations appeared to confirm that plants growing in soils with poor N can adapt to these environments by improving their NUE; however, this rule is not always the case. In addition to the availability of soil nutrients, when plant growth is limited by other factors, NUE will also change (Chapin 1980; Yasumura et al. 2002). For example, several studies reveal that temperature can affect both the foliar N content and NUE (Chadwick et al. 1999). Plant nitrogenase reduces activity at low temperatures and inactivates at high temperatures (Weih 2001). Precipitation can also impact NUE by modifying both plant and soil moisture conditions, as appropriate water conditions benefit N exchange and use (Fu et al. 2019; Wright et al. 2001; Yuan et al. 2006). Conversely, NUE will be limited under drought conditions although N is available. In the future, global warming and drought will continue to affect NUE (Estiarte and Peñuelas 2015).

In addition to environmental factors, stoichiometry constraints may also impact NUE. There are specific proportional relationships between the various elements of plants that enable them to maintain stable stoichiometric characteristics when they are subjected to environmental changes (McGroddy et al. 2004; Zeng et al. 2013). In particular, the N and phosphorus (P) of plants have a strict proportional relationship. For instance, most plants have a close N:P ratios and N–P scaling exponents (Reich and Oleksyn 2004; Reich et al. 2010; Tian et al. 2017), to keep their nutrient composition relatively constant regardless of changing supplies of nutrients in the environment, which is referred to as stoichiometric homeostasis (Sterner and Elser 2002; Wang et al. 2018). This relationship limits the nutrient cycling process of plants (Elser and Hamilton 2007; Gressel and McColl 1997; Vitousek and Hobbie 2000). Changes in the availability of P will significantly influence plant growth and NUE (Hong et al. 2013). Nevertheless, the relative importance of plant stoichiometry constraints versus environmental factors on NUE remains unclear.

Many biologists have assumed negligible evolutionary effects on plant ecology as evolution occurs over such long time scales (Lewontin 2000; Orians 1962). However, evidence has revealed that evolution can operate over a range of temporal and spatial scales (Urban et al. 2020). Recently, the impacts of plant phylogeny on plant traits have been observed in many studies (Caruso et al. 2020; Ma et al. 2018; Zhang et al. 2020). The conservative phylogenetic hypothesis proposes that related species have higher trait similarities than distant evolutionary species (Losos 2008). Hirose (1975) compared the NUE of different plant species and found that the NUE of perennial plants was higher than that of annual plants, and are generally more common than annual plants in poor nutrient environments. This type of natural selection for plant traits is widespread (Caruso et al. 2020; Zhan et al. 2018). A recent study found a significant phylogenetic signal in the C:N stoichiometry of plant leaves and branches, and they both showed a low C:N evolutionary trend (Zhang et al. 2020). However, current research on NUE associated phylogeny has focused more on crop cultivation from the perspective of genetic engineering (Cormier et al. 2016; Liu et al. 2020). The large-scale phylogenetic study of NUE in wild plants is still lacking.

China is suitable for conducting large-scale NUE research as it is home to various types of terrestrial ecosystems and plant species across tropical and cold regions. This study was designed to investigate the spatial patterns of NUE and its controlling factors at the national scale. We analyzed the NUE of 1452 species at 1102 sites in China, and collected relevant climate and soil data to address the following questions: (1) how does NUE change geographically, or across different ecosystem types, or plant life forms at large spatial scales? (2) Are there any specific observable phylogenetic signals or evolutionary directions for NUE variations that occur when plants interact with their environment? (3) What are the main controlling factors of NUE: climate, soil properties, plant stoichiometry, or phylogeny?

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Materials and methods

Data collection and preprocessing

We developed a paired N and P concentrations database that was derived from fully developed green leaves, with detailed site information in China (Tian et al. 2019a). This data set was partly compiled from an open data source *the TRY-Plant Trait Database* (Fraser 2020), an integrated data set of China established by Han et al. (2005) and four major original sampling studies (He et al. 2008; Chen et al. 2013; Yang et al. 2016; Luo 2017). The database provides paired records of N and P concentrations in green leaves from July to August 2000–2016, which contains matched information of geographical location (longitude, latitude), environmental factors [mean annual temperature (MAT), mean annual precipitation (MAP)], life forms (ferns, woody plants, herbs, shrubs, vines, and subshrubs), and taxonomic data (family, genus, and species). The MAT ranged from -10.4 to 24.8 °C, whereas the MAP ranged from 18 to 2366 mm. Furthermore, to represent soil water conditions more comprehensively, we added the Aridity Index (AI) from the *Global Aridity Index and Potential Evapotranspiration (ET0) Climate Database v2* with a grid resolution of $0.5° \times 0.5°$ according to the latitude and longitude (Trabucco and Zomer 2019). According to database methodology, AI was calculated as

$$AI = \frac{MA\text{-}Pr}{MA\text{-}ET0} \qquad (1)$$

where MA-Pr = mean annual precipitation, MA-ET0 = mean annual reference evapotranspiration. Therefore, lower AI values indicated drier climatic conditions.

We also extracted soil data, including soil texture (percentage content of clay, sand, and silt), soil pH, total nitrogen content (TN), total phosphorus content (TP), available nitrogen content (AN), available phosphorus content (AP), exchangeable cation content (CEC) and soil organic matter content (SOM) from *The Soil Database of China for Land Surface Modeling* database with a grid resolution of $0.5° \times 0.5°$ according to the latitude and longitude (Shangguan et al. 2013). Since the physical and chemical properties of topsoil are most related to plant physiological activities, we extracted the soil data at the depth of 0–4.5 cm.

Data pertaining to the Chinese terrestrial ecosystem types were derived from *The Spatial distribution data of China's terrestrial ecosystem types (*http://www.resdc.cn/data.aspx?DATAID=105*)*, which includes seven ecosystem categories: forest, desert, grassland, farmland, settlement, wetland, and others (Additional file 1: Fig. S1).

To analyze the geographical patterns of plant traits, the geometric means of foliar N and P concentrations data for each species at each site under three taxonomic levels (family, genus, species) were initially calculated (Han et al. 2005; Reich and Oleksyn 2004). As all leaf traits and soil nutrients data were approximately log-normally distributed, we converted the data to natural logarithms for plant and soil N and P concentrations to attain the approximate normality and homogeneity of residuals. The final data set contained 1102 sites from seven different ecological regions (Additional file 1: Fig. S1), with 1452 species in 628 genera and 123 families (Additional file 1: Fig. S2).

Statistical analysis

First, we used the definition of plant N use efficiency (NUE) as the flux ratio between plant dry matter production (ΔW) and N uptake (ΔN) (Chapin 1980; Yin et al. 2021). This definition is also known as N utilization efficiency (the ratio of plant yield to plant N) (Congreves et al. 2021; Dobermann et al. 2007; Moll et al. 1982):

$$NUE = \frac{\Delta W}{\Delta N} \qquad (2)$$

Though plant N uptake could be allocated to different organs, such as leaves, roots, branches, and stems, most of plant N is allocated to leaves and is directly involved in photosynthesis (Evans 1989). Leaf N concentration influences the entire plant N concentration consequently plant growth. Thus, an analysis of N use at the leaf level facilitates its elucidation at the plant level NUE (Hirose 2012; Heberling and Fridley 2013). Here, we assume that the N concentration of leaves is NC, the dry matter is ΔW, and the N uptake is:

$$\Delta N = \Delta W \times NC \qquad (3)$$

Then, a useful index of NUE can be derived (i.e., the inverse of nitrogen concentration of leaves) (An et al. 2005; Vitousek 1982; Zuo et al. 2016):

$$NUE = 1/NC \qquad (4)$$

Second, we tested differences of NUE between ecosystems and between plant life forms using one-way ANOVA analysis. General linear regression models were employed to analyze the relationship between NUE and foliar phosphorus, geographic factors (latitude and longitude), climatic factors (MAT, MAP, AI), soil properties (pH, Clay, Sand, Silt, TN, TP, AN, AP, CEC, SOM), and plant evolution time, respectively. Following regression analysis, the random forest algorithm was utilized to explore the relative importance of different explanatory variables to NUE (Wang et al. 2019), which was performed with the R package "randomForest" (Breiman 2001). Random forest has been proven to be an effective

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machine learning tool due to its ability to identify complex nonlinear or multicollinearity relationships between variables (Reichstein et al. 2019) and deal with overfitting (Xu et al. 2018). Then, we used "IncNodePurity" as a measure of variable importance (this method is based on the total decrease in node impurities from splitting on the variable, averaged over all trees). The significance level of all analyses was $\alpha = 0.05$.

We employed phylogenetic analysis to test the relationship between NUE and its phylogeny/evolution. We first used the R package "plantlist" (Zhang 2018) to confirm the species names followed by the APG III phylogenetic system. Next, the family/genus/species list data were imported into the R package "phytools" (Revell 2012) to construct the phylogenetic trees (Qian and Jin 2016), which was visualized by the iTOL tool (Interactive Tree Of Life) (Letunic and Bork 2019). Subsequently, we defined the evolution time of a given plant family using the earliest diverging genus within that family (Ma et al. 2018; Zhang et al. 2020). We calculated Blomberg's *K* statistic using the 'Picante' package in R and evaluated the strength of the phylogenetic signal for NUE (Kembel et al. 2010). A large Blomberg's *K* value was thought to indicate phylogenetic conservatism (Blomberg et al. 2003). Data preprocessing and statistical analyses were performed using R software (version 3.6.1) and ArcMap 10.5.

Results

Spatial pattern of NUE in China

NUE tended to decrease from low to high latitudes ($r = -0.56$, $p < 0.05$; Fig. 1a), whereas NUE increases with the longitude in China ($r = 0.54$, $p < 0.05$; Fig. 1b). The mean NUE in terrestrial plants in China was 53.28 g g^{-1} N (SD = 24.11).

There were significant differences in the NUE between different ecosystems ($p < 0.05$) (Fig. 2a). The mean NUE was 65.08 g g^{-1} N (SD = 32.64) in the settlement ecosystem, which was higher than those of the farmland ecosystem (58.71 g g^{-1} N, SD = 31.40), forest ecosystem (54.22 g g^{-1} N, SD = 21.54), wetland ecosystem (53.11 g g^{-1} N, SD = 17.53), and grassland ecosystem (49.53 g g^{-1} N, SD = 21.24). The mean NUE was lowest in the desert ecosystem (48.48 g g^{-1} N, SD = 21.72).
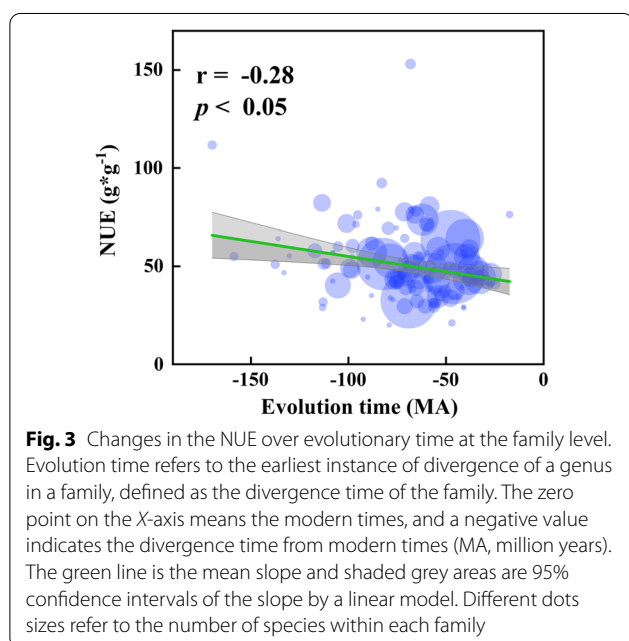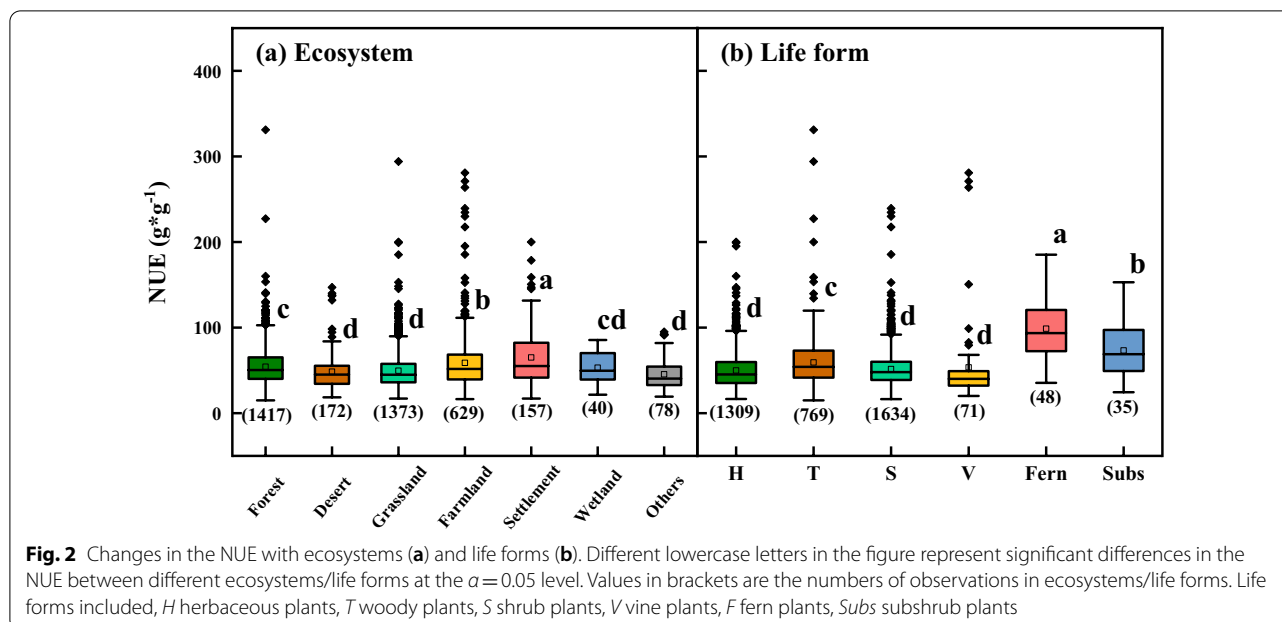
There were also significant differences in the NUE between different life forms ($p < 0.05$) (Fig. 2b). The average NUE was the greatest in fern plants (98.64 g g^{-1} N, SD = 34.20), and the average NUE was lowest in herbaceous plants (49.85 g g^{-1} N, SD = 21.42). The average NUE of other life forms were: subshrub plants (73.22 g g^{-1} N, SD = 31.36), woody plants (59.27 g g^{-1} N, SD = 26.73), vine plants (53.39 g g^{-1} N, SD = 50.11) and shrub plants (51.45 g g^{-1} N, SD = 20.29).

Changes in NUE with plant phylogeny

We constructed a phylogenetic tree using NUE data (Additional file 1: Fig. S2). Species shown at closer distances on the tree represent a closer genetic relationship, where the lengths of the tree branch indicate the evolutionary history of the species. Blomberg's *K* method was employed to calculate the phylogenetic signals of NUE. At the taxonomic level of genera, significant phylogenetic signals of NUE were observed ($K = 0.746$, $p < 0.05$), which indicated that NUE and plant evolutionary history were
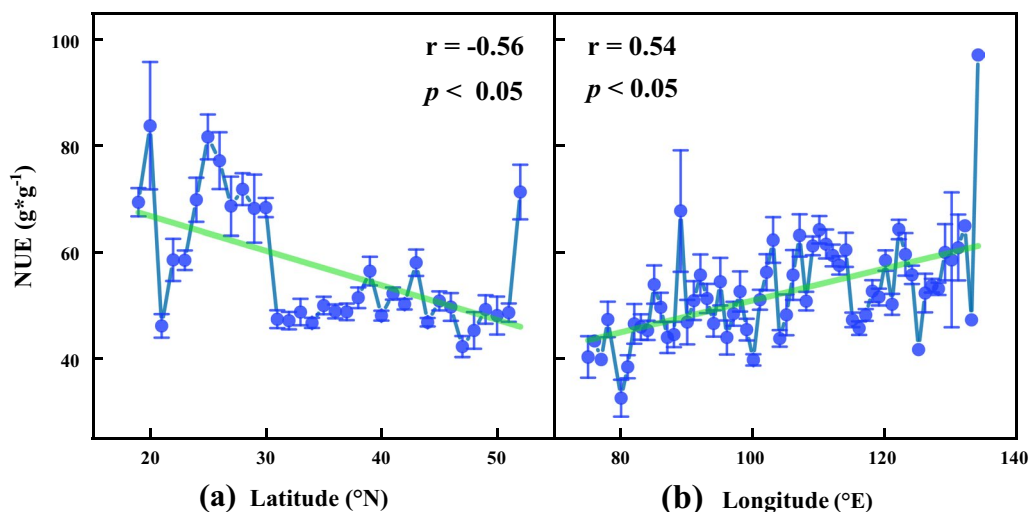
Fig. 1 Changes in NUE with latitude (**a**) and longitude (**b**). The latitudinal and longitudinal patterns of NUE were fitted by a linear function. These figures are drawn with 1° latitudinal/longitudinal resolution. Dots are the mean NUE values and the bars represent the standard errors (SE)

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Fig. 2 Changes in the NUE with ecosystems (**a**) and life forms (**b**). Different lowercase letters in the figure represent significant differences in the NUE between different ecosystems/life forms at the $a = 0.05$ level. Values in brackets are the numbers of observations in ecosystems/life forms. Life forms included, *H* herbaceous plants, *T* woody plants, *S* shrub plants, *V* vine plants, *F* fern plants, *Subs* subshrub plants

Fig. 3 Changes in the NUE over evolutionary time at the family level. Evolution time refers to the earliest instance of divergence of a genus in a family, defined as the divergence time of the family. The zero point on the *X*-axis means the modern times, and a negative value indicates the divergence time from modern times (MA, million years). The green line is the mean slope and shaded grey areas are 95% confidence intervals of the slope by a linear model. Different dots sizes refer to the number of species within each family

intimately linked. We then tested the role of evolutionary history in NUE and found that NUE decreased temporally with evolution, that is, the plant evolved toward a lower NUE ($r = - 0.28$, $p < 0.05$) (Fig. 3).

Controlling factors for the variations of NUE
NUE was negatively related to the concentration of plant foliar P ($r = - 0.53$, $p < 0.05$). Of the climatic factors, NUE significantly increased with MAT ($r = 0.32$, $p < 0.05$) and

MAP ($r = 0.27$, $p < 0.05$). In addition, NUE was positively related to AI ($r = 0.26$, $p < 0.05$) (Fig. 4; Additional file 1: Figs. S3, S4).

Of the soil properties, NUE decreased slightly with soil pH ($r = - 0.10$, $p < 0.05$) and soil sand content ($r = - 0.11$, $p < 0.05$). Moreover, NUE significantly increased with soil clay content ($r = 0.17$, $p < 0.05$), but did not significantly change with soil silt content (Additional file 1: Figs. S5, S6).
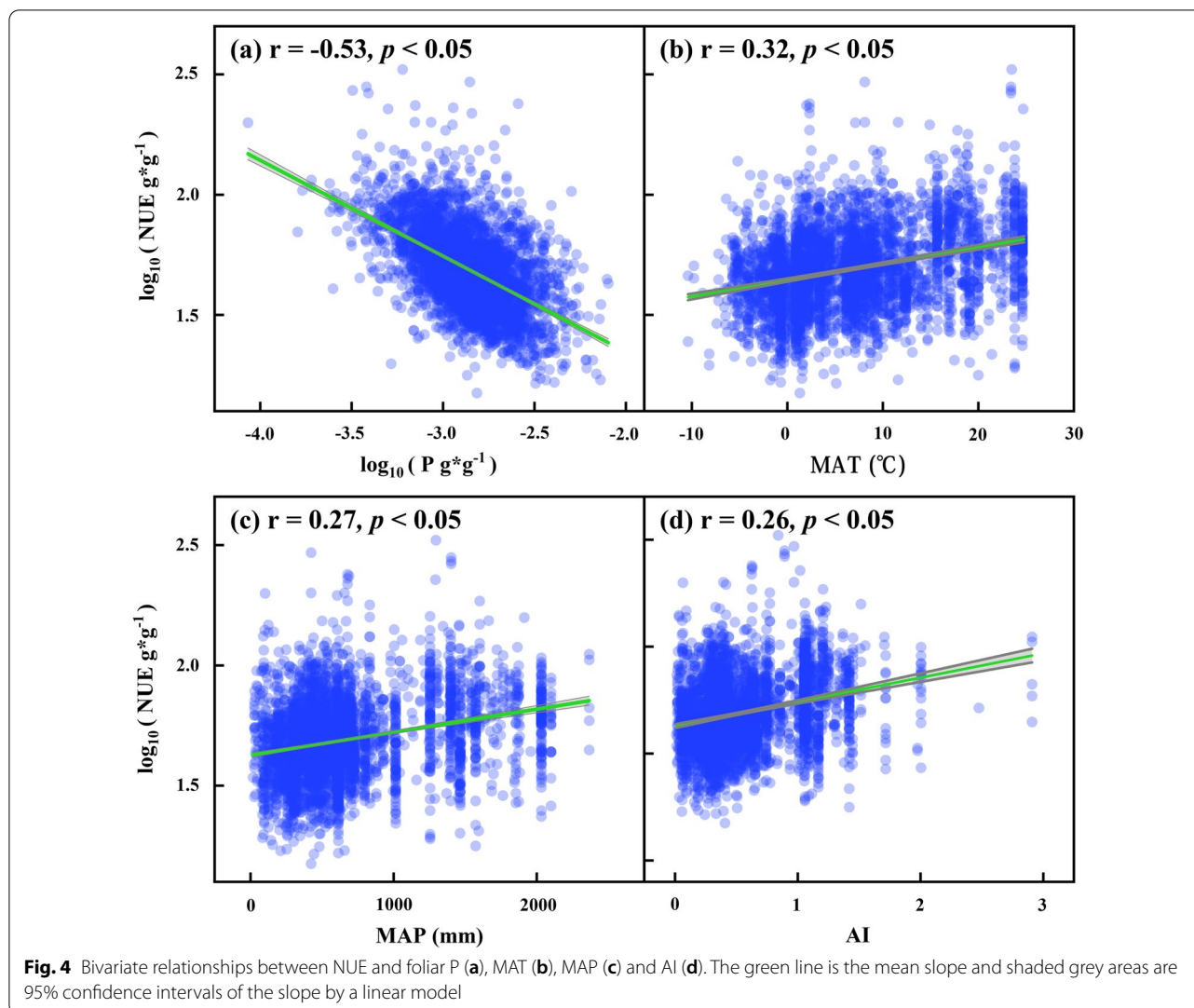
Specifically, NUE was slightly decreased with TP ($r = - 0.13$, $p < 0.05$), AP ($r = - 0.05$, $p < 0.05$), and CEC ($r = - 0.09$, $p < 0.05$). There was no significant relationship between NUE and TN, AN, or SOM (all $p > 0.05$) (Additional file 1: Figs. S7, S8).

Random forest analysis revealed that plant foliar P was the most dominant predictor that affected NUE, while the second most important factor was the evolution time, and climatic factors slightly predicted it. However, all soil properties explained little in the way of NUE variations (Fig. 5).

Discussion
This study revealed the large-scale variations and controlling factors of the NUE across different ecosystems and plant life forms in China. The mean NUE in China's terrestrial ecosystem was 53.31 ± 24.40 g g^{-1} N, which indicated that every unit of N uptake produced about 53 units of dry matter. Significant changes in NUE along latitude and longitude suggested that the spatial variations of NUE were related to zonal factors, such as temperature, moisture, and other climate

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Fig. 4 Bivariate relationships between NUE and foliar P (**a**), MAT (**b**), MAP (**c**) and AI (**d**). The green line is the mean slope and shaded grey areas are 95% confidence intervals of the slope by a linear model
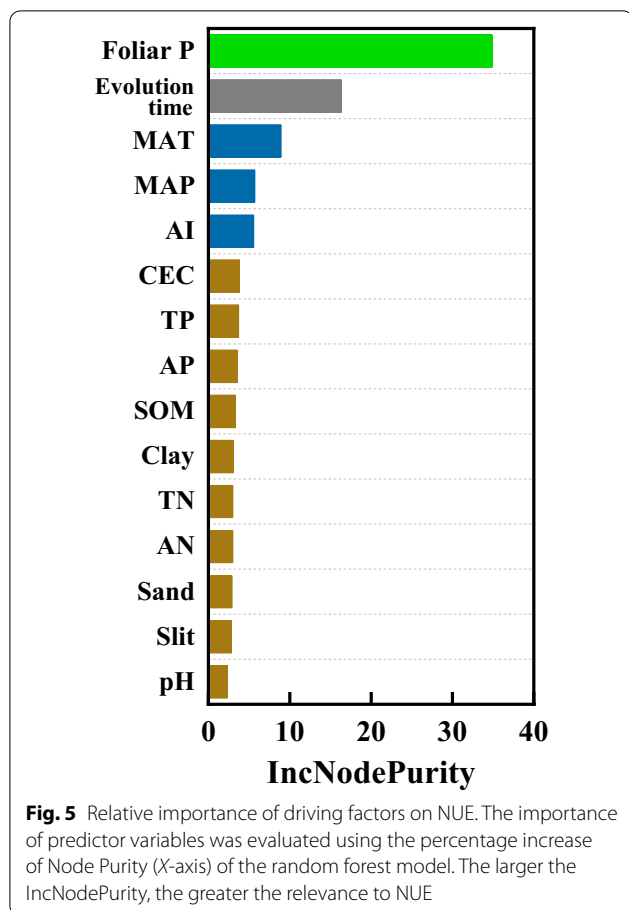
factors (Liu et al. 2020; Reich and Oleksyn 2004). In China, temperature gradually decreases from low latitude to high latitude and precipitation becomes less as longitude decreases (Piao et al. 2010), while low temperature and low precipitation significantly inhibit NUE (Fig. 4). Among different ecosystems, the spatial patterns of NUE were similar to the net primary productivity (NPP) in China (Chen et al. 2011). Ecosystems with a high NUE may have high NPP. Thus, the NUE may be an important ecological indicator that reflects a plant's capacity to transform N into production. The difference in NUE between different life forms may be related to the plant root: shoot ratios (Jackson et al. 1996). For example, herbaceous plants often have large root:shoot ratios and tend to be nutrient conservative (Guerrero-Ramirez et al. 2021); thus, the NUE of herbaceous plants was low,

while fern plants and woody plants exhibited higher NUE (Fig. 2).

Distinct from the traditional viewpoint that soil N availability determines NUE, we observed that the plant foliar P concentration contributed the most. The evolutionary history of plants contributed indirectly to the variation in NUE, whereas climate and soil properties played a less significant role. Our results emphasized the necessity of incorporating plant stoichiometry constraints and phylogenetic data into biogeochemical models to better predict N cycling.

Foliar phosphorus content primarily impacted NUE

Among all of the factors that affected NUE, plant foliar P content was the most important determinant (Fig. 5). Plant foliar P was negatively correlated to NUE (Fig. 4a; Additional file 1: Figs. S3a, S4), which may be due to the following mechanisms. First, plant P content was

Fig. 5 Relative importance of driving factors on NUE. The importance of predictor variables was evaluated using the percentage increase of Node Purity (*X*-axis) of the random forest model. The larger the IncNodePurity, the greater the relevance to NUE

intimately related to N content due to their stoichiometric homeostasis (Koerselman and Meuleman 1996). This is because N is allocated to protein synthesis, whereas P is allocated to rRNA for maintaining any specific quantity of protein (Niklas et al. 2005). Therefore, the ratio of N to P in plants has a limited range (Reich and Oleksyn 2004), where the geometric means of N:P ratios was 15.8 globally, although it had both biological and ecological variations (SD = 5.2) (Tian et al. 2017, 2019b), while N:P ratios in our database were 16.49 ± 7.29 (Additional file 1: Fig. S9). Thus, plants with high P content generally maintain a high N content, which translates to a low NUE (Chapin 1980; Yin et al. 2021). Second, there is a cooperative relationship between N and P, which together limit the nutrient cycling processes of plants (Elser and Hamilton 2007; Gressel and McColl 1997; Vitousek and Hobbie 2000). P is an essential element for the synthesis of ATP and plants consume much energy to absorb N through active transport (Reed et al. 2010; Simpson and Burris 1984). Therefore, the P content of plants affects their capacity to absorb N. For example, an efficient P-acquisition strategy, carboxylate release can promote soil P mobilization (Lambers et al. 2013, 2015) and may also affect N cycling

through accelerating soil organic matter decomposition which is called a priming effect (Zhu et al. 2014). Besides, P can directly control NUE by affecting N processes, such as mineralization, organic matter decomposition (Yu et al. 2017), and fixation (Pons et al. 2007). Thus, P-rich plants have better N uptake capacity. While the increase in total N content of plant is not as fast as the increase in N uptake, which causes the N mean residence time (the ratio of total N to N uptake) to decrease (Hirose 2011; Zhu et al. 2020). Low mean residence time means that the same N can only fix C for a shorter time, which leads to a decrease in NUE. Otherwise, when plants lack P they may absorb less N, which induces them to improve N use efficiency to overcome this disadvantage.

Another view suggests that the interactions between N and P do not always exist. For example, Schleuss et al. (2020) found that P had no significant impact on the aboveground N stocks or N fixation processes of plants. This may have been due to that the effects of P on NUE being dependent on different levels of N limitation. Although the addition of P had no significant effects on foliar N and NUE under low N conditions, its addition enhanced the plant N content as plant growth gradually transitions from N limitation to P limitation under high N conditions (Long et al. 2016).

Currently, imbalances in N:P ratios initiated by climate change and anthropogenic activities were found in the global ecosystems, which affected a series of ecosystem structures and functionalities (Delgado-Baquerizo et al. 2013; Peñuelas et al. 2013). In general, N:P ratios are increasing, and ecosystems tend to be P limited rather than N limited (Du et al. 2020; Peñuelas et al. 2020) (Additional file 1: Fig. S9). In this case, NUE will be more dependent on the availability of P, as revealed in this study. Therefore, in the future, the important role of foliar P should be considered more in the study of NUE and N cycles.

Plants evolved toward lower NUE
Evolutionary history is the second most important driver of NUE. In our results, different life forms of plants have significantly different NUE (Fig. 2). Furthermore, there are significant phylogenetic signals ($K = 0.746$, $p < 0.05$) and evolutionary direction for NUE (Fig. 3). These results indicated that the variations in the NUE of wild plants are intimately related to the phylogenetic process, which has seldom been revealed previously.

The evolutionary history of plants reflects their active adaptation to environmental changes during growth and development. The results of this study show that plants have evolved toward a lower NUE (Fig. 3). Plants and the terrestrial environment have been co-evolving for millennia. Since the establishment of Earth's biosphere,

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plant communities have interacted with the soil environment. Soil provides plants with the water and nutrients required for growth and development. Meanwhile, plants can alter the physical and chemical properties of the soils through their root systems and litter (Chapin et al. 2011). During the early evolution of terrestrial ecosystems, due to the parent material not weathering further, most soils remained in a barren state with a low nutrient content (Chadwick et al. 1999). The low availability of soil N largely limited plant growth; thus, plants with high NUE were more competitive (Zhang et al. 2020). However, over time, plants continuously release organic matter into the soil, and the continuous weathering of the parent material increases the nutrient content (Chadwick et al. 1999). Particularly in the modern environment following the Industrial Revolution, immense quantities of anthropogenic N was introduced into the ecosystems, which significantly enhanced the availability of soil N (Canfield et al. 2010; Galloway et al. 2004). For these reasons, plants with high NUE have gradually lost their competitive advantage, and plants have evolved toward a low NUE.

Although a few recent studies have found decreasing leaf N and ^{15}N isotope concentrations in locations, such as the Qinghai-Tibet Plateau (Kou et al. 2020) and North America (Brookshire et al. 2020), these phenomena may be anomalies caused by biomass accumulation under increasing atmospheric CO_2 concentrations since the Industrial Revolution (Chapin et al. 2011; Finzi et al. 2007). Conversely, increasing leaf N and ^{15}N isotope have been observed in tropical forests due to the continuous increases in N inputs (Hietz et al. 2011). Ecosystem N concentrations will continually increase via anthropogenic N inputs that occurs across China and the world (Fowler et al. 2013; Xu et al. 2020). We also tested the evolution trend of leaf ^{15}N isotope through a global database (Carine et al. 2018) and found that leaf ^{15}N isotope evolved toward a higher value (Additional file 1: Fig. S10), which indicated the N availability is increasing. A similar study revealed that the C:N ratios of plants gradually decreased through evolution under such a background (Zhang et al. 2020). In summary, the availability of N tends to increase and NUE tends to decrease over the long history of plant evolution. We thus projected that in the future, with increasing atmospheric N deposition and anthropogenic terrestrial N inputs, plants may reduce N investments by reducing their NUE and turn to secure other limited resources, such as P.

Climate factors affect NUE more than soil
Although being less important than plant P content and phylogenetic impacts, climate factors (MAT, MAP, AI) are also critical in influencing NUE. The rise in temperature helps the movement of water and nutrients in soil and plant cells (Schulze et al. 2019). In addition, appropriate high temperatures also lead to high microbial activity and enzyme activity which are related to various physiological activities of plants (Reich and Oleksyn 2004; Romero-Olivares et al. 2017). Higher temperature is beneficial for the transfer of N in some processes, such as absorption, assimilation, and transportation, which ultimately improves NUE (Bai et al. 2013; Xu et al. 2012). Tian et al. (2019b) also found that leaf nitrogen content is negatively correlated with MAT and MAP across global terrestrial plants, which was corroborated with our results. NUE also increases with higher MAP and has a significantly negative correlation with drought (smaller AI index), which aligns with previous studies (Lv 2010; Su and Shangguan 2020). For example, NUE of grassland plants in Inner Mongolia increased with higher rainfall levels (Lv 2010). Moreover, the significant relationship between NUE and MAT or MAP could be explained by the growth rate of plants in different environments. The slower growth under low MAT or MAP tends to condense N inside the plants, while faster growth results in lower N concentration and higher NUE (Chapin 1980; Hirose 2011; Lambers and Poorter 2004). In addition, more frequent drought events result in a significant decrease in the NUE of leaves and roots (Fu et al. 2019). With increased humidity, NUE is higher as more precipitation alleviates plant water restrictions, while stimulating plant growth and N utilization (Yuan et al. 2006). Conversely, humid conditions are of benefit for N transport from soil to plants, which increases the possibility of plants N use; however, drought limits the above process (Gupta et al. 2020).

Soil factors had a negligible effect on NUE in our study. The weak negative correlation between NUE and pH (Additional file 1: Figs. S5a, S6a) indicates soil pH is not a pivotal factor determining NUE variation. Luo et al. (2021) found globally positive responses of photosynthetic leaf nitrogen to soil pH, because soil pH influences the soil nutrients availability. A higher pH means more available nutrient cations for plant use as acid soils replace nutrient cations with H^+. Besides, soil P is more available at high pH, since P can be easily fixed by some cations (e.g., Fe, Al) at low pH (Lambers and Plaxton 2018), which may explain the low NUE in high pH. Other factors, including soil texture [the percentage content of sand (20–2000 μm), clay (2–20 μm) and silt (0–2 μm)], are also related to NUE. Our results show a positive correlation between NUE and soil clay (Additional file 1: Figs. S5d; S6d), because soils with less clay (means tighter or looser soil) tend to have low permeability and absorption rates, which reduces water and nutrient use efficiency (Ishaq et al. 2001; Liu et al. 2020). Another

explanation is that low permeability caused by less clay would affect the processes of nitrification and denitrification to control the ratio of ammonium to nitrate which is also related to NUE (Chapin et al. 2011).

Several previous studies have revealed that the NUE is reduced with higher soil N content (Enoki et al. 1997; Vitousek 1982), and proposed the hypothesis that plants have higher NUE in locations with lower N availability to adapt to the low nutrient environments. However, our study failed to find the above relationship between NUE and N availability (Fig. 5; Additional file 1: Figs. S7; S8). In addition, many other investigations have also come to a different conclusion and posited that there is not necessarily a significant correspondence between NUE and the availability of soil N (Bridgham et al. 1995; Su et al. 2000). The relationship between N availability and NUE is not a simple linear relationship. Only when the availability N drops to a certain level, NUE is positively related to N availability (Bridgham et al. 1995). When N availability is at a higher level, the response of NUE is reduced or even disappears (De Aldana and Berendse 1997). Instead, soil P content in this study had a more significant impact on NUE (Additional file 1: Fig. S7b, d). It had been shown that soil P significantly promoted plant N and P content due to increased P supply (Chen et al. 2013), and they both have strong control effects on plant NUE.

Implications and limitations

According to our results, we proposed a hypothesis regarding NUE determinants: NUE is mostly affected by both plant P content and evolutionary history that reflects the long history of N supply conditions due to continuous weathering during evolution. However, these two factors dominate the changes in NUE at different stages (Fig. 6).

First, at a historically low N supply period (point a), plants tend to have a higher NUE. At that time, the N supply dominates NUE changes rather than the P availability. As the N supply continues to increase and meets plant demand, NUE begins to decrease (a→b, c, d). When N is gradually abundant, or even attains the saturation stage (points b, c, and d), plants are limited by P, where the plant P content begins to dominate changes in NUE. Plants under high P conditions are more proficient at obtaining N; thus, their NUE is lower, whereas a low P content limits N access, leading to a higher NUE. Under this basic framework, climate factors and soil properties regulate the variations in NUE to a certain extent.
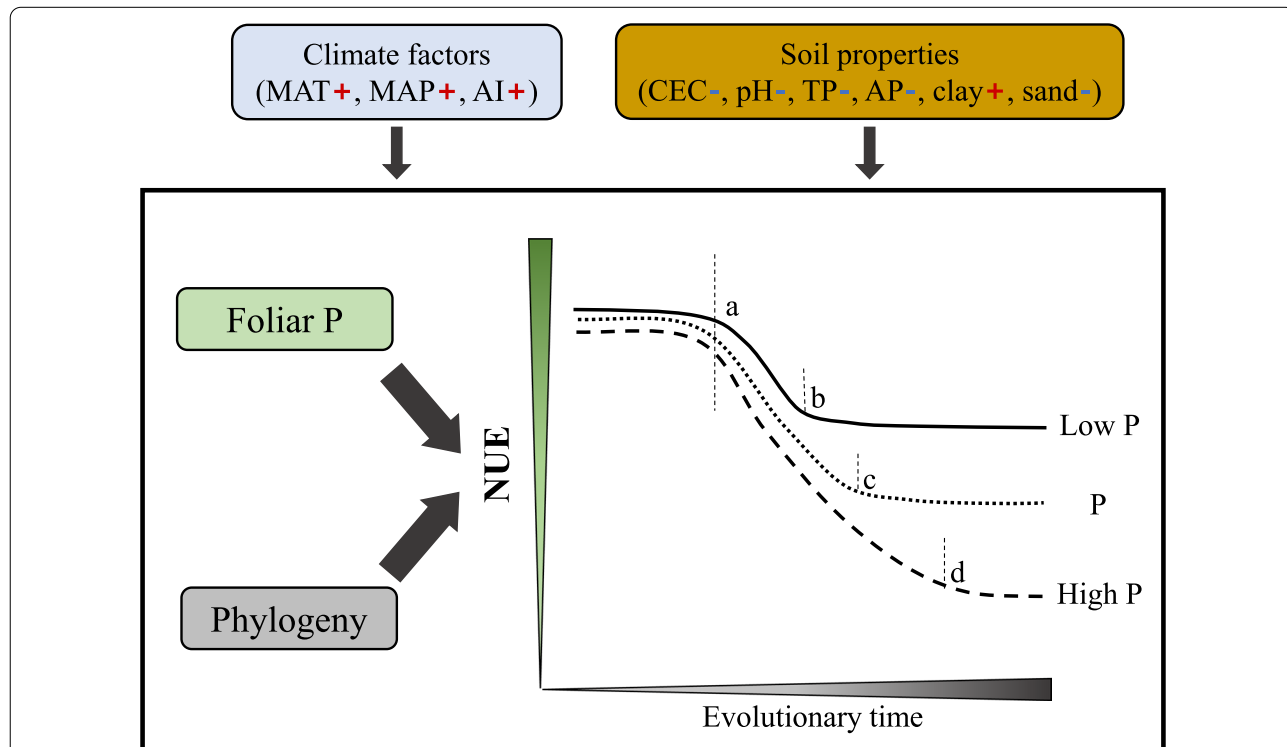
Fig. 6 Conceptual diagram of the influence of P, phylogeny, climate factors, and soil properties on NUE. This mechanism emphasizes the important effects of plant phosphorus content and evolutionary history that reflects the long history of environmental nitrogen supplies due to continuous weathering during evolution. **a** Refers to low nitrogen conditions at the onset of evolution, and **b–d** refers to an ample nitrogen environment under different phosphorus conditions

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Disentangling the drivers of NUE can improve the elucidation and prediction of plant–soil N cycling. Since plant foliar P and phylogeny play important roles in determining NUE changes, plant stoichiometry and phylogeny should be incorporated within ecosystem N cycle models. Furthermore, we are aware that there may be some additional critical factors, such as mycorrhizal fungi (Han et al. 2020; Wooliver et al. 2018) and soil microorganisms (Kuypers et al. 2018; Moreau et al. 2019) that affect NUE. Due to data scarcity, we were unable to quantify their impact in this study; however, they certainly warrant examination in future studies.

Conclusion

To the best of our knowledge, this study is among the first to quantify the large-scale patterns, long evolutionary history, and drivers of NUE. We found that the foliar P content was the main driving factor for the variations in NUE, whereas plant evolutionary history was the second most important factor for its regulation. In contrast to our original expectation, climate and soil properties contributed relatively less to this large-scale variation in NUE. Our findings provide a new perspective of NUE and we suggest that future studies should pay more attention to plant N–P stoichiometric relationships and phylogeny to further understand the biogeographic mechanisms underlying NUE variations.

Abbreviations
NUE: Nitrogen use efficiency; C: Carbon; N: Nitrogen; P: Phosphorus; MAT: Mean annual temperature; MAP: Mean annual precipitation; AI: Aridity index; TN: Soil total nitrogen content; TP: Soil total phosphorus content; AN: Soil available nitrogen content; AP: Soil available phosphorus content; CEC: Exchangeable cation content; SOM: Soil organic matter.

Supplementary Information
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Additional file 1: Fig. S1. Spatial site distributions in the NUE database. **Fig. S2.** Phylogenetic tree and phylogenetic signals of NUE. **Fig. S3.** Bivariate relationships between NUE and plant foliar phosphorus (a), MAT (b), MAP (c) and AI (d) of different ecosystems. **Fig. S4.** Bivariate relationships between NUE and plant foliar phosphorus of different life forms. **Fig. S5.** The bivariate relationships between NUE and soil physical properties. **Fig. S6.** The bivariate relationships between NUE and soil physical properties of different ecosystems. **Fig. S7.** The bivariate relationships between NUE and soil chemical properties. **Fig. S8.** The bivariate relationships between NUE and soil chemical properties of different ecosystems. **Fig. S9.** The bivariate relationships between NUE and N:P ratios. **Fig. S10.** Changes in the leaf δ^{15}N over evolutionary time at the family level.

Authors' contributions
SN and JL conceived the idea and wrote the first draft of manuscript. JL carried out the analyses. All authors contribute to the data collection and paper writing. All authors read and approved the final manuscript.

Availability of data and materials
The data that support the findings of this study are derived from the following resources available in the public domain: Leaf nitrogen and phosphorus concentrations data are available in Tian et al. (2019a). Aridity Index data are from *CGIAR Consortium for Spatial Information (CGIAR-CSI)* https://doi.org/10.6084/m9.figshare.7504448.v3 *(Trabucco and Zomer 2019). Soil data are from The Soil Database of China for Land Surface Modeling* http://globalchange.bnu.edu.cn/research/soil2 *(Shangguan et al. 2013).*

Declarations

Ethics approval and consent to participate
Not applicable.

Consent for publication
All authors agreed and approved the manuscript for publication in Ecological Processes.

Competing interests
The authors declare no competing financial interests.

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