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Driving Mechanism of Vegetation Succession on Leaf-Soil Ecological Stoichiometric Coupling in the Jingpo Lake Lava Plateau

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Abstract

This study explored ecological stoichiometric coupling of plant-soil systems during vegetation succession in extremely oligotrophic habitats. We selected five vegetation types at distinct successional stages on the Jingpo Lake lava plateau: grassland, shrubland, deciduous broad-leaved forest, coniferous and broad-leaved mixed forest, and coniferous forest. We quantified carbon (C), nitrogen (N), phosphorus (P) concentrations and stoichiometric ratios in plant leaves and topsoil, and analyzed their interaction mechanisms and driving factors via geostatistics and structural equation modeling (SEM). Results showed that: Leaf C, N, P contents differed significantly across successional stages. Broad-leaved forests had significantly higher leaf C than other types ($p < 0.05$), with opposite trends for N and P; all leaf N:P ratios were < 14, indicating N limitation on plant growth. Soil C increased with succession, with forest soils having significantly higher C than GLs ($p < 0.05$); coniferous forests had significantly higher soil N and P than all other stages ($p < 0.05$). Leaf N-P allometric scaling exponent (α) for all five types was < 1, indicating faster P turnover than N, supporting plant acclimation to N limitation. Redundancy analysis revealed soil C:N ratio explained 45.8% of leaf stoichiometry variation ($p < 0.05$), as the dominant driver. Overall, vegetation mitigates N limitation by regulating P turnover. Leaf N-P allometric pattern reveals synergistic adaptation of plant-soil systems during succession, verifying vegetation's ecological adaptability to severely nutrient-impoverished lava habitats.

Introduction

Ecological Stoichiometry is a tool for studying the dynamic stoichiometric balance of organismal elements (Sterner et al. 2002), revealing the regulatory effects of biotic factors on biological metabolism, and clarifying the nutrient linkage and supply between organisms and the environment. C, N and P are key elements studied in ecological stoichiometry, and their concentrations and ratios can characterize the physiological and ecological traits of plants and reflect the nutrient limitation status underlying ecological stoichiometric balance. As the core interface for material cycling and energy flow in plants, plants accumulate carbon via photosynthesis and leaf carbon sequestration, and rely on root systems to take up and transform soil nutrients. Plant-soil material cycle focuses on photosynthesis in leaves and nutrient uptake and metabolism in roots (Ding et al. 2022), and they drive material transformation and energy flow of the ecosystem (Peng et al. 2025). Leaves, as the primary organs responsible for transpiration and photosynthesis in plants, are sensitive to variations in soil environmental conditions (Zhao et al. 2017). Their ecological stoichiometric characteristics can effectively characterize the mechanisms underlying ecosystem stoichiometric balance, reveal plant growth strategies, nutrient utilization efficiency, and the sustainability of ecosystem nutrient retention (Gao et al. 2023;Ozdemir et al. 2025). The ecological stoichiometric characteristics of soil C, N and P can comprehensively reflect soil physicochemical properties, organic matter level and soil ecological health (Su et al. 2021), and are the core indicators characterizing soil nutrient supply capacity. Based on the theory of ecological chemometrics, the allometric growth relationship can effectively reveal the nutrient utilization strategies of organisms. Organismal elemental stoichiometry is a core indicator of nutrient limitation status during its growth process (Zeng et al. 2005), among which the N:P ratio of plant leaves has become a key

indicator for identifying N vs. P limitation in plant communities (Güsewell 2004). The leaf N-P allometric scaling exponent can further reveal the dynamic rates of change and patterns of elemental allocation of N and P in plants (Chen et al. 2024;Li et al. 2021), and reflect their differential responses to environmental variations (Chen et al. 2022).Significant differences exist in leaf N-P allometric scaling exponents across different ecosystems. (Liu et al. 2025;Tian et al. 2021). Such differences essentially reflect nutrient regulatory strategies resulting from long-term plant adaptation to the environment (Frouz et al. 2011). Coupled analysis of leaf and soil ecological stoichiometry can help elucidate patterns of nutrient migration and transformation between plants and soil, and clarify their co-evolutionary dynamics (Li et al. 2025).

Volcanic lava plateaus are typical extremely oligotrophic habitats. Their porous and permeable substrates and strongly weathered surface horizons result in poor soil water-holding capacity and nutrient deficiency. However, their vegetation communities present a clear successional sequence, making them ideal sites for exploring the succession and evolution of ecosystem vegetation (Huang et al. 2014;Wang et al. 2016). We do not have systematic studies on coupled feedbacks and driving mechanisms of leaf-soil ecological stoichiometry in vegetation succession in this kind of extreme habitats, and dynamic regulatory effects of soil nutrient evolution on allometric growth of plants. We take Jingpo Lake lava plateau and select vegetation types representing different succession stages, including grassland (GL), shrubland (SL), deciduous broad-leaved forest (DB), coniferous and broad-leaved mixed forest (CB), and coniferous forest (CF). We combine field sampling with laboratory analysis, the ecological stoichiometric characteristics of C, N and P in plant leaves and soil, the effects of soil edaphic conditions on the ecological stoichiometry of both plant leaves and soil, together with the coupling relationship and underlying driving factors between the two compartments. We examined the ecological stoichiometric characteristics of plant leaves and soil in different succession stages of the community. We give references to vegetation restoration, ecological conservation and sustainable ecosystem management in this area.

Overview of the Study Area and Research Methods

Overview of the study area

Jingpo Lake is located within Ning 'an City in the southeast of Heilongjiang Province and the southwest of Mudanjiang City (120°30 'to 129° 30'E, 43°46' to 44° 18'N) (Zhang et al. 2025). The average annual relative humidity is 71.5%, and the average annual precipitation is 619.8 mm. It belongs to the cold temperate continental monsoon climate (Cong et al. 2023). The main soil types are basic rock volcanic stony soil and dark brown loam volcanic ash soil. Due to the varying distances of lava from the crater and the different degrees of weathering, factors such as topography, soil, and germplasm sources affect the different stages of vegetation succession, which can be classified into GL,SL, DB, CB, CF (Ma et al. 2001).The sampling points are shown in the Fig. 1.

Research Methods

Sample Point Setting and Sample Collection and Processing

Field sampling was conducted in July 2025. Select GL,SL, DB, CB, CF Set up sample points for five typical vegetation types, The basic information of each vegetation type sample plot is shown in Table 1.All plots were established in areas with gentle terrain and a uniform slope of < 5° to eliminate topographic interference. For each vegetation type, three replicate 10 m × 10 m main plots were established. Within each main plot, five 1 m × 1 m subplots were randomly set up for vegetation community investigation. For each main plot, fully expanded, healthy mature leaves were collected from the dominant species. Leaf samples from the same main plot were pooled into one composite sample. Three replicate composite samples were obtained for each vegetation type, and all samples were placed in pre-labeled breathable paper envelopes to prevent sample deterioration. Given the shallow, poorly differentiated soil profile characteristic of the lava plateau habitat in the study area, the five-point sampling method was applied within each main plot. After removing the surface litter layer (≈ 2 cm thick), topsoil samples from the 0–15 cm depth were collected. Soil samples from the five subplots in each main plot were pooled into one composite sample, with a fresh weight of approximately 1 kg per sample. Each composite sample was sealed in a sterile sampling bag, which was double-labeled inside and outside to avoid label loss. All leaf and soil samples were immediately stored in a 4°C portable cooler, and transported back to the laboratory within 24 h for subsequent processing and analysis.Leaf samples were oven-dried at 65°C to a constant weight, then ground and passed through a 0.25 mm sieve for elemental content determination. Soil samples were naturally air-dried in a cool, ventilated room after removing visible plant roots, gravel, and debris. The air-dried samples were ground and sequentially passed through 1 mm and 0.149 mm sieves. The 1 mm fraction was used for the determination of soil physicochemical properties, and the 0.149 mm fraction was used for the analysis of soil C, N, and P concentrations.

Table 1
Geographic coordinates, altitude, and dominant species of sampling plots

Vegetation type	longitude	Latitude	/(m) Altitude	Dominant species
GL	128°56'52.38"E	44°03'56.82"N	354.0	*Artemisia mongolica*、*Vicia sepium*、*Campanula glomerata*
	128°57'01.01"E	44°04'05.90"N	357.0	
	128°56'47.06"E	44°03'56.86"N	362.1	
SL	128°56'51.37"E	44°04'18.67"N	356.9	*Lespedeza davurica*、*Lonicera maackii*、*Acer tataricum* subsp *ginnala*
	128°56'51.37"E	44°04'27.06"N	357.6	
	128°56'53.30"E	44°04'22.41"N	361.2	
DB	128°57'39.50"E	44°02'31.61"N	417.3	*Populus davidiana*、*Quercus mongolica*、*Betula platyphylla*
	128°57'53.26"E	44°02'31.37"N	417.5	
	128°57'46.36"E	44°02'31.43"N	415.8	
CB	128°59'24.72"E	44°02'50.25"N	417.6	*Populus davidiana*、*Quercus mongolica*、*Betula platyphylla*、*Pinus koraiensis*
	128°59'13.63"E	44°02'50.25"N	417.4	
	128°59'17.94"E	44°02'50.41"N	417.1	
CF	128°59'12.78"E	44°02'16.65"N	417.7	*Pinus koraiensis*
	128°59'22.67"E	44°02'20.44"N	419.0	
	128°59'19.57"E	44°02'16.34"N	418.1	

Note: Grassland (GL), Shrubland (SL), Deciduous Broad-Leaved Forest (DB), Coniferous and Broad-Leaved Mixed Forest (CB), Coniferous Forest (CF).

Sample Determination Method

Soil moisture content (SMC) was determined via the 105°C gravimetric oven-drying method, soil pH was determined via the potentiometric method with a glass electrode, soil electrical conductivity (EC) was determined with a benchtop conductivity meter (Hu 2014). Total organic carbon in plant leaves and soil was determined via the potassium dichromate oxidation-external heating method, total nitrogen in plant leaves was determined via the Kjeldahl digestion method, total phosphorus in plant leaves was determined via the molybdenum-antimony anti-spectrophotometric method (Bao 2000). Soil total nitrogen was determined via the semi-micro Kjeldahl method. Soil total phosphorus was extracted via sodium hydroxide fusion method, and TP concentration in the extracting solution was determined via the molybdenum-antimony anti-spectrophotometric method (Aierxiding et al. 2026). For each sample, three

technical replicates were performed for all indicators, and the mean value was used as the final analytical result.

Data Processing

All data processing and statistical analyses in this study were performed using Microsoft Excel 2019 and IBM SPSS Statistics 27.0. One-way analysis of variance (ANOVA) was applied to test for significant differences in leaf and soil C, N, P contents and their stoichiometric ratios among different vegetation successional stages. Duncan's multiple range test was used for post hoc multiple comparisons at the significance level of $p < 0.05$. Pearson correlation analysis was performed to assess the bivariate correlations between indicators. Box plots and correlation heatmaps were generated using Origin 2024 and R software. Redundancy analysis (RDA) between leaf and soil stoichiometric characteristics was performed using Canoco 5. Structural equation modeling (SEM) was constructed to quantify the effects of soil environmental factors (including SMC, EC, and soil C-N-P stoichiometric traits) on leaf ecological stoichiometric ratios. Path analysis and SEM plotting were performed using IBM SPSS Amos. All data in the tables are presented as mean ± standard deviation (SD). The leaf N-P allometric scaling exponent for the five vegetation types was calculated via standardized major axis (SMA) regression using IBM SPSS Statistics 27.0, with the calculation formula as follows:

$$N = \beta P^{\alpha}$$

In the formula, N and P represent the total nitrogen and total phosphorus contents in plant leaves, respectively; α is the slope (N-P allometric scaling exponent), and β is the intercept (normalization constant) of the log-linear regression between leaf N and P concentrations. Prior to regression analysis, leaf N and P content data were log10-transformed to meet the normality assumption of linear regression (Aierxiding 2026).

Results

Contents of C, N, and P in Leaves and ecological stoichiometric ratios of plants of Different vegetation types

In the study area, leaf C content exhibited an exponential increasing trend with the progression of vegetation succession, with the highest value observed in CF. In contrast, leaf N and P contents showed a significant decreasing trend along the successional gradient. Leaf C:N and C:P ratios showed a consistent increasing trend along the successional gradient, with the ratios in CF significantly higher than those in the other four vegetation types ($p < 0.05$). Leaf N:P ratios across all vegetation types were consistently < 14, indicating that plant growth in the study area was uniformly limited by N, with consistent nutrient limitation patterns across all successional stages.

Table 2
The influence of vegetation types on the contents of C, N and P in plants and their ecological stoichiometric ratios

Vegetation type	Organ	C:N	C:P	N:P
GL	Leaf	23.49^{d}	225.49^{d}	9.61^{b}
SL	Leaf	24.87^{cd}	272.87^{c}	10.99^{a}
DB	Leaf	26.19^{bc}	285.62^{bc}	10.92^{a}
CB	Leaf	27.25^{b}	302.26^{b}	11.13^{a}
CF	Leaf	34.16^{a}	321.38^{a}	9.41^{b}

Contents of C, N and P in plant soil and ecological stoichiometric ratios of different vegetation types

In the study area, soil C content in CF was significantly higher than that in all other vegetation types ($p < 0.05$), while soil N and P contents showed a trend of first increasing then decreasing along the vegetation successional gradient, with values in GL significantly higher than those in all forest vegetation types ($p < 0.05$). Soil C:N and C:P in CF were significantly higher than the other four vegetation types ($p < 0.05$), and soil N:P ratios differed significantly among all five vegetation types ($p < 0.05$). As shown in Table 3, vegetation successional stage was the key factor driving the accumulation of soil C, N and P, as well as the variation in their ecological stoichiometric characteristics.

Table 3
The influence of vegetation types on the contents of C, N and P in soil and their ecological stoichiometric ratios

Vegetation type	soil	C:N	C:P	N:P
GL	soil	8.6^{d}	50.10^{d}	5.96^{a}
SL	soil	10.73^{d}	56.17^{d}	5.33^{ab}
DB	soil	15.61^{c}	75.56^{c}	4.87^{b}
CB	soil	22.11^{b}	90.33^{b}	4.15^{c}
CF	soil	28.71^{a}	98.22^{a}	3.47^{d}

Correlation analysis of Leaf and Soil Ecological stoichiometric Mantel test

Mantel test results revealed there was a significant coupling relationship between the leaf and soil ecological stoichiometric characteristics of the Jingpo Lake lava plateau ($p < 0.05$). SC, SC: N, SC:P, SMC,

EC were significantly positively correlated with LC ($p < 0.05$). In contrast, SN, SP, SN:P, pH were highly significantly negatively correlated with LC ($p < 0.05$). Secondly, LN was highly significantly positively correlated with SN, SN:P and pH ($p < 0.05$), while SC, SC:N, SC:P, SMC and EC were significantly negatively correlated with LN ($p < 0.05$). SN, SN:P, and soil pH were significantly positively correlated with each other ($p < 0.05$). The leaf N-P allometric scaling exponents (α) of the five vegetation types in the study area was 0.17, 0.63, 0.45, 0.14 and 0.73, respectively. Further Mantel test results showed that leaf N-P allometric scaling exponent was significantly positively correlated with C, C:N, C:P, soil C:P and C:N, C:P, SMC, EC. The normalization constant (β) was significantly positively correlated with LN, LP, LN:P, SN, SN:P, pH and EC. Significant differences in leaf N-P allometric scaling exponent were observed among different vegetation successional stages ($p < 0.05$)

Note

LC: Carbon content of leaves; LN: Nitrogen content in leaves; LP: Phosphorus content in leaves; LC:N: Carbon-nitrogen ratio of leaves; LC:P: Carbon-phosphorus ratio of leaves; LN:P: Leaf nitrogen-phosphorus ratio; SC: Soil carbon content; SN: Soil nitrogen content; SP: Soil phosphorus content; SC:N: Soil carbon-nitrogen ratio; SC:N: Soil carbon-phosphorus ratio; SN:P: Soil nitrogen-phosphorus ratio; SMC: Soil moisture content; EC: Electrical conductivity

Regulatory Pathways of Environmental factor Soil element cascade Effect on Leaf ecological stoichiometric

Structural equation modeling (SEM) results demonstrated that soil environmental factors exerted direct driving effects on soil C-N-P ecological stoichiometric characteristics. SMC exhibited a negative path coefficient with soil N and P, while EC promotes the accumulation of soil C content. Regarding the coupling relationship between soil and leaf ecological stoichiometry, soil C and soil N were significantly positively correlated with the ecological stoichiometry of leaves, while soil P was significantly negatively correlated with leaf ecological stoichiometric ratios.

RDA results showed that the cumulative variance explanation amount is 72.25%, among which the variance explained by all measured environmental factors reached 72.25%, with the first and second ordination axes explaining 63.23% and 9.03% of the total variance, respectively. Monte Carlo permutation test results indicated that soil C:N ratio had the highest explanatory power for the variation in leaf ecological stoichiometric characteristics (45.8%), with a statistically significant effect ($p < 0.05$). Soil C:N ratio was the core factor driving the variation in leaf ecological stoichiometric characteristics in the study area. Compared with other measured soil environmental factors, it exhibited stronger explanatory power for leaf stoichiometric variation, while the effects of other environmental factors were not significant influence.

Discussion

The influence of different succession stages of the Jingpo Lake lava Plateau on the ecological stoichiometric characteristics of leaf C:N:P

Leaf nutrient concentrations are core indicators reflecting plant physiological status and habitat nutrient supply capacity. In this study, leaf C content of vegetation at different successional stages in the study area was slightly higher than the global mean level of terrestrial plants, while N and P content were significantly lower than global mean for leaves of terrestrial plants (McGroddy et al. 2004;Han et al. 2005). This pattern is a direct result of the constraint of extremely oligotrophic habitats on plant nutrient uptake. The soil of the lava plateau has poor water-holding capacity and severe nutrient deficiency, making it difficult for plant roots to take up and assimilate sufficient N and P from the soil. In contrast, sustained photosynthesis and carbon sequestration maintain a relatively high leaf C content. Leaves are the most sensitive organs of plants for environmental changes (Zhao 2017), and C, N and P contents vary markedly along the vegetation succession gradient in the Jingpo Lake lava plateau: As succession progresses from the early stage to the middle and late stages, plants require more developed vascular tissues and mechanical support structures to enhance stress resistance and resource competitive capacity. The main components of these structures are carbon-rich compounds such as cellulose and lignin, which directly drive the continuous accumulation of C in leaves. Meanwhile, woody plants (especially CF) have a higher photosynthetic efficiency. The amount of carbon fixed via photosynthesis is far higher than that consumed by growth, and the excess carbon is stored in leaves in the form of starch and cellulose, further promoting leaf C accumulation. This ultimately results in a gradual increase in leaf C content along the succession gradient (Liu et al. 2022;Niklas 1994;Feng et al. 2008;Lerdau et al. 2023). Leaf functional traits are tightly linked to plant growth strategies: high leaf mass per area usually corresponds to a low growth rate and high stress resistance, whereas high N and P contents indicate stronger capacity and competitive ability (Poorter et al. 2006;Wright et al. 2004). In this study, the gradual decrease in the contents of N and P in plant leaves as vegetation succession, indicating that GL had a dominant advantage in nutrient competition during vegetation succession in the Jingpo Lake lava plateau (Tian et al. 2010). As succession progresses, plant growth rate decreases, and the instantaneous demand for N and P is reduced. This forms an efficient nutrient utilization strategy, whereby plants can meet their metabolic demands without maintaining high leaf N and P contents. This is an important adaptive strategy for plants to cope with the oligotrophic habitat of the lava plateau. Leaf C:N and C:P ratios are positively correlated with plant carbon sequestration capacity and nutrient use efficiency, but negatively correlated with plant growth rate (Yu et al. 2021). CF had the highest C: N and C: P ratios, indicating strong carbon assimilation capacity, high nutrient use efficiency, and slow growth rate. This corresponds to the classic "high stress resistance, low growth rate" functional trait syndrome. Leaf N:P ratios across all vegetation types were consistently below 14. According to Koerselman & Meuleman’s classic nutrient limitation theory, plant growth in the study area was limited by N (Yu et al. 2022), This N limitation pattern is closely related to low soil total N content, inhibited nitrogen mineralization under low temperature, and insufficient soil N supply. In summary, the leaf nutrient traits of vegetation in the Jingpo Lake lava plateau shift toward a stronger stress resistance strategy with

reduced competitive capacity along the succession gradient, with nitrogen limitation as the dominant nutrient constraint throughout the succession process.

The influence of Different succession Stages of the Jingpo Lake Lava Plateau on Soil C:N:P Ecological stoichiometric characteristics

In this study, soils in the Jingpo Lake lava plateau were characterized by high C and N contents but low P content, which was significantly different from the soil stoichiometric patterns in the alpine regions of western Sichuan (Tan et al. 2015). This pattern is driven by the combined effects of low temperature under the humid/semi-humid climate of the cold temperate zone, and the basalt parent material of the study area. Low temperature inhibits soil microbial metabolic activity, reduces the decomposition rate of soil organic C and N, and thus promotes their accumulation in soils (Chen et al. 2022;Li et al. 2020;Zheng et al. 2021). Meanwhile, cations released during basalt weathering bind with phosphate to form insoluble precipitates, which reduces soil P content (Jin et al. 2025). This process ultimately shapes the unique stoichiometric pattern of the study area, characterized by C and N enrichment coupled with P deficiency. In this study, soil C content increased continuously along the vegetation succession gradient, with values in forest vegetation significantly higher than those in GL. This trend is attributed to the synergistic effects of increased organic matter input and improved soil structure during vegetation succession. Compared with GL, the plant biomass, litter, and root exudate input of CF and SL increased exponentially, providing a large amount of organic matter input to the soil (Zheng et al. 2023). In the middle and late successional stages, soil organic colloids bind with mineral particles to form primary aggregate structures, which enhances the soil's adsorption and retention capacity for organic carbon, reduces organic carbon mineralization loss, and further promotes soil C accumulation (Jiang et al. 2017). Soil N and P contents reached their maximum values in SL, which was a direct result of the efficient nutrient mineralization driven by the physicochemical properties of SL litter. SL litter has a relatively low C:N and lignin, easily decomposed by microorganisms and efficiently released N and P nutrients (Wang et al. 2021). However, GL litter has a fast turnover rate but low total input to the soil. Forest litter has a high C:N ratio, high lignin and tannin contents, and its decomposition is inhibited by secondary metabolites, resulting in an extremely slow decomposition rate. Moreover, the competition for nutrients in forest communities is more intense, resulting in the accumulation of soil N and P in both types being lower than that in SL (Qin et al. 2016). Soil P content in GL and SL was significantly higher than that in forest vegetation.Soil P is mainly derived from bedrock weathering, and its content is mainly regulated by soil parent material and plant uptake (Kang et al. 2010;Cui et al. 2023). Forest vegetation has a more developed and extensive root system, and its uptake of soil P is far higher than that of GL and SL. This leads to soil P depletion, as the rate of biological P uptake exceeds the rate of natural P replenishment via bedrock weathering (Xie et al. 2023).

In the early stage of succession, the C: N and C: P in GL soil are relatively low, which conforms to the rapid nutrient turnover strategy of herbaceous plants: the shallow root systems of herbaceous plants will preferentially utilize surface nutrients and stimulate microbial activity through rhizodeposition, thereby alleviating the soil P fixation effect. Soil C:N and C:P ratios in the CF were the highest among all

successional stages. This was attributed to the complex composition and high recalcitrance of CF litter, which is difficult to decompose. The accumulation rate of soil organic C was faster than that of available N and P (Zhu et al. 2021), which exacerbated the nutrient imbalance. Soil N: P ratio is a widely recognized core indicator reflecting soil nutrient limitation status. In this study, soil N:P ratios in the study area were lower than the global mean value of terrestrial forest soils (Cleveland et al. 2007), and were consistently below 14 across all successional stages (He et al. 2020) indicates that the soil in this area simultaneously has the problem of insufficient supply of N and P, and the restriction of N supply is more prominent. Soil N:P is negatively correlated with plant growth rate (Fan et al. 2015). A high growth rate will lead to a decrease in the N:P ratio (Elser et al. 2003), reflecting the rapid nutrient turnover adaptation strategy formed by plants in oligotrophic habitats. The soil in CF stage has the lowest N: P ratio. This might be due to the combined effect of organic acids produced by the decomposition of litter and rainfall leaching (Ren et al. 2025;Xiao et al. 2024), which inhibits the mineralization and availability of N. Meanwhile, CF has a higher N demand, which together intensify N limitation and ultimately form a co-limitation pattern of N and P, with N limitation as the dominant constraint.

The Influence of different vegetation types on the allometric growth of leaves and ecological stoichiometric

The allometric growth relationship of N-P in plant leaves reflects the plants' adaptive response to nutrient allocation patterns, utilization strategies and habitat nutrient supply, and is a key entry point to explore the plant nutrient homeostasis regulation mechanism (Yang et al. 2023). In this study, the N and P allometric scaling exponents (α) of the leaves of the five succession stages of vegetation were all < 1. According to the allometric power law, α < 1 indicates that the rate of change of P content in leaves is faster than that of N (Duan 2023). This result indicates that the turnover rate of P in the leaves of plants in the study area is significantly higher than that of N, which is the core nutrient strategy for plants to cope with the N-limited habitat of the lava plateau. This is in line with the "growth rate hypothesis", that is, plants with a high growth rate have a higher demand for P and show a lower leaf N: P ratio (Hu et al. 2020). Against the backdrop of a persistent shortage of available N in the soil, plants find it difficult to maintain homeostasis by rapidly regulating N uptake. Instead, they accelerate the uptake, turnover and reutilization of P, using the rapid dynamic changes of P to compensate for the insufficient supply of N, thereby achieving nutrient homeostasis and ensuring basic growth and metabolic needs. This is an important evolutionary adaptation of plants to extremely oligotrophic habitats. The differences in α values at different succession stages reflect the adjustment of plant adaptation strategies: The α values of CF and SL are relatively high, approaching the global average level of temperate plants, indicating that their regulatory ability over P is stronger and their nutrient strategies are more adapted to local habitats. The α value of CB is the lowest, possibly because at this stage, the competition for interspecific resources is the most intense, and plants allocate more resources to growth competition, weakening their regulatory ability on P homeostasis. As the initial stage of succession, GL has shallow root systems and low nutrient use efficiency, which made it difficult to achieve efficient turnover of P. The results of

this study are slightly lower compared with the global species-level plant leaf N-P allometric scaling exponent (3/4) (Atawula et al. 2024), which reflects the particularity of the extreme habitat of the lava plateau. In addition to the N limitation, factors such as poor soil water-holding capacity, simple structure, and low microbial activity further restrict the uptake and regulation of P by plants, resulting in their overall regulatory capacity still being lower than that of conventional habitats. This result enriches the understanding of N-P allometric growth of plants in extreme habitats and provides a new perspective for understanding the nutrient adaptation of plants in volcanic landforms. In addition, the Mantel test indicated that leaf N-P allometric scaling exponents were significantly positively correlated with factors such as leaf C, C:N, C:P, as well as soil C, C:N, SMC, and EC. This indicates that environmental factors and the stoichiometric characteristics of plant ecology jointly regulate leaf N-P allometric growth. Soil water and salt conditions and carbon supply patterns indirectly regulate the distribution and turnover of N and P within plants by influencing their photosynthetic carbon sequestration and nutrient uptake, ultimately driving differences in allometric scaling exponents. This confirms that plant allometric growth characteristics are the result of the synergistic effects of plant physiological traits and habitat environmental factors.

The influence of soil environmental factors of different vegetation types on the ecological stoichiometric ratios of C, N, and P in leaves

The regulation of leaf-soil ecological stoichiometry by soil environmental factors exhibits a significant cascading effect, and is dominated by a factor-driven regulatory mode. SMC and EC are the basic underlying environmental factors, which indirectly regulate leaf ecological stoichiometry. Soil C:N is the driving factor which directly controls coupling and differentiation of leaf-soil ecological stoichiometry. This regulation model is the result of long-term co-evolution between plants and highly oligotrophic environments. The regulation of nutrients by soil water and salt factors is site-specific: soil moisture is negatively related to the contents of soil N and P but positively related to EC, reflecting the particularity of soil in lava plateau. The soil in the study area is shallow and has poor water-holding capacity. The moisture increase reduces soil aeration, inhibits nitrification and mineralization of microbes, and reduces N and P availability. Water transport promotes surface accumulation of salt, increasing EC, forming chain reaction “more water, salt and less available nutrients”. Positive regulation of soil C by EC may be related to promote soil aggregate formation by moderate salinity, enhances the physical protection of soil organic carbon, reduction of mineralization loss. Soil C, N and P exert differential effects on leaf ecological stoichiometry: soil C and N are positively related to soil C and negatively associated with soil P. Promoting effect of soil C and N conforms to the "priming effect". The accumulation of soil C and N can enhance soil microbial activity, promote the mineralization of insoluble nutrients, provide more available nutrients for plants, and thus enhance leaf carbon assimilation capacity. Negative regulation of soil P is the result of “dilution effect” under N limitation. Under N limitation, soil P is more readily available to plants, but it cannot be converted into growth advantage. Instead, due to relative enrichment of P in the body, the N:P ratio of leaves is reduced and the overall ratio of leaves is decreased.

RDA indicated that soil C:N ratio was the core driver of variation in leaf ecological stoichiometric characteristics, which was mainly mediated by soil N supply capacity and soil microbial activity. Soil total N content directly influenced soil N mineralization and release rate. In the study area with N-limited, the supply of soil N directly determines the N uptake of plants and the stoichiometric properties of leaves. Soil C:N ratio was therefore the core link of leaf-soil stoichiometric coupling, via the regulatory pathway of "regulating soil N availability-influencing plant N uptake-driving leaf stoichiometric variation". This indicates that in ecological restoration, soil C:N ratio is the key to positive coupling of system nutrients. The Pearson correlation and structural equation models also show that plant stoichiometric homeostasis regulation is the basis of a co-evolutionary relationship relationship between leaf element content and soil nutrients (Liu et al. 2024). In the same area, a nutrient limitation pattern dominated by N and supplemented by P was adopted that allowed plants to adapt cross-scale to multiple stresses by elastically controlling their own homeostasis. This interaction provides a basis for ecological restoration model of “soil-plant coordinated regulation” in lava plateauand also a regulatory direction for ecological restoration of extremely infertile habitats.

Conclusion

In this study, five typical vegetation types representing different successional stages on the Jingpo Lake lava plateau, GL, SL, DB, CB and CF, as the research objects. It systematically analyzed the ecological stoichiometric characteristics of C, N, and P in plant leaves and surface soil, revealing the coupling law of leaf-soil ecological stoichiometry in extreme oligotrophic habitats, the adaptation mechanism of N-P allometric growth, and the key driving factors. The main conclusions are summarized as follows:

The leaf-soil ecology shows a staged differentiation pattern in vegetation succession of the lava plateau. The key change is adaptive response of plants to change their own metabolism and nutrient allocation strategies according to the habitat supply characteristics. The entire succession system takes N limitation as the main stress factor. The leaf N-P allometric scaling exponent revealed the core adaptive strategy of plants in the study area: increase turnover of P and use of N to compensate for lack of N supply. This allometric growth pattern is a key evolutionary adaptation of plants to extremely oligotrophic habitats. differentiation of plant stoichiometric is also controlled by the stoichiometric characteristics of plants and habitat factors like soil water, salt, carbon pool. The regulation of leaf ecological stoichiometry by soil environmental factors exhibited a typical cascading effect, and was dominated by a factor-driven mode. Soil SMC and EC directly affect leaf stoichiometry by controlling soil nutrient reservoirs, while soil C:N directly controls the coupling and differentiation pattern of leaf-soil ecological stoichiometric by controlling soil N mineralization and availability. This study confirmed that the soil nutrient transformation process is the core link mediating the interaction of leaf-soil systems in extreme oligotrophic habitats. It is recommended to prioritize the N fertilizer supplementation to alleviate regional dominant N restriction and return straw to the field and biological agents to activate the P retained in the soil and optimize the soil nutrient supply. For GL and SL stages early succession, one would like to protect the nutrient pool of the surface soil and reduce human interference for natural accumulation of soil nutrients. For forest succession stage, one would want to rationally regulate the community

structure, improve the efficiency of soil organic matter accumulation, promote positive coupling and circulation of nutrients between leaves and soil, and so to stabilize the recovery and positive succession.

The coupling law of leaf-soil ecological stoichiometric and the mechanism of vegetation nutrient adaptation in extreme oligotrophic habitats presented in this paper enrich ecological chemometrics theory of vegetation succession in volcanic lava landform area, and also provides new perspective for understanding co-evolution between plant-soil systems in extreme habitats. The targeted N supplementation, soil P activation and phased vegetation and soil nutrient reservoir protection proposed in this paper provide scientific theory and practical models for vegetation restoration, biodiversity conservation and sustainable management in Jingpo Lake lava Plateau and other volcanic lava landform areas around the world, and theoretical framework for construction of soil-plant coordinated regulation model for ecological restoration in extreme habitats.

Abbreviations

GL	Grassland
SL	Shrubland
DB	Deciduous Broad-Leaved Forest
CB	Coniferous and Broad-Leaved Mixed Forest
CF	Coniferous Forest
SMC	Soil moisture content
EC	Electrical conductivity
LC	Carbon content of leaves
LN	Nitrogen content in leaves
LP	Phosphorus content in leaves
LC:N	Carbon-nitrogen ratio of leaves
LC:P	Carbon-phosphorus ratio of leaves
LN:P	Leaf nitrogen-phosphorus ratio
SC	Soil carbon content
SN	Soil nitrogen content
SP	Soil phosphorus content
SC:N	Soil carbon-nitrogen ratio
SC:P	Soil carbon-phosphorus
SN:P	Soil nitrogen-phosphorus ratio
ANOVA	A One-way analysis of variance
RDA	Redundancy Analysis
SEM	Structural equation modeling

Declarations

Author Contributions: Y.Z. and J.H. conceived of and conducted the study. Laboratory work were performed by Z.Y. and Y.Y. The first draft of the manuscript was written by Y.Y. and Z.Y. L.S. and Z.H. collected specimens. Y.S. and J.J. review and editing of the manuscript, obtained research funding. All authors read and approved the final manuscript.

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Data availability statement

The datasets used and/or analyzed during the current study are included in the manuscript

Conflict of interest The authors have no competing interests to declare that are relevant to the content of this article

Ethics approval statement

Not applicable

Consent for publication

Not applicable

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Figures

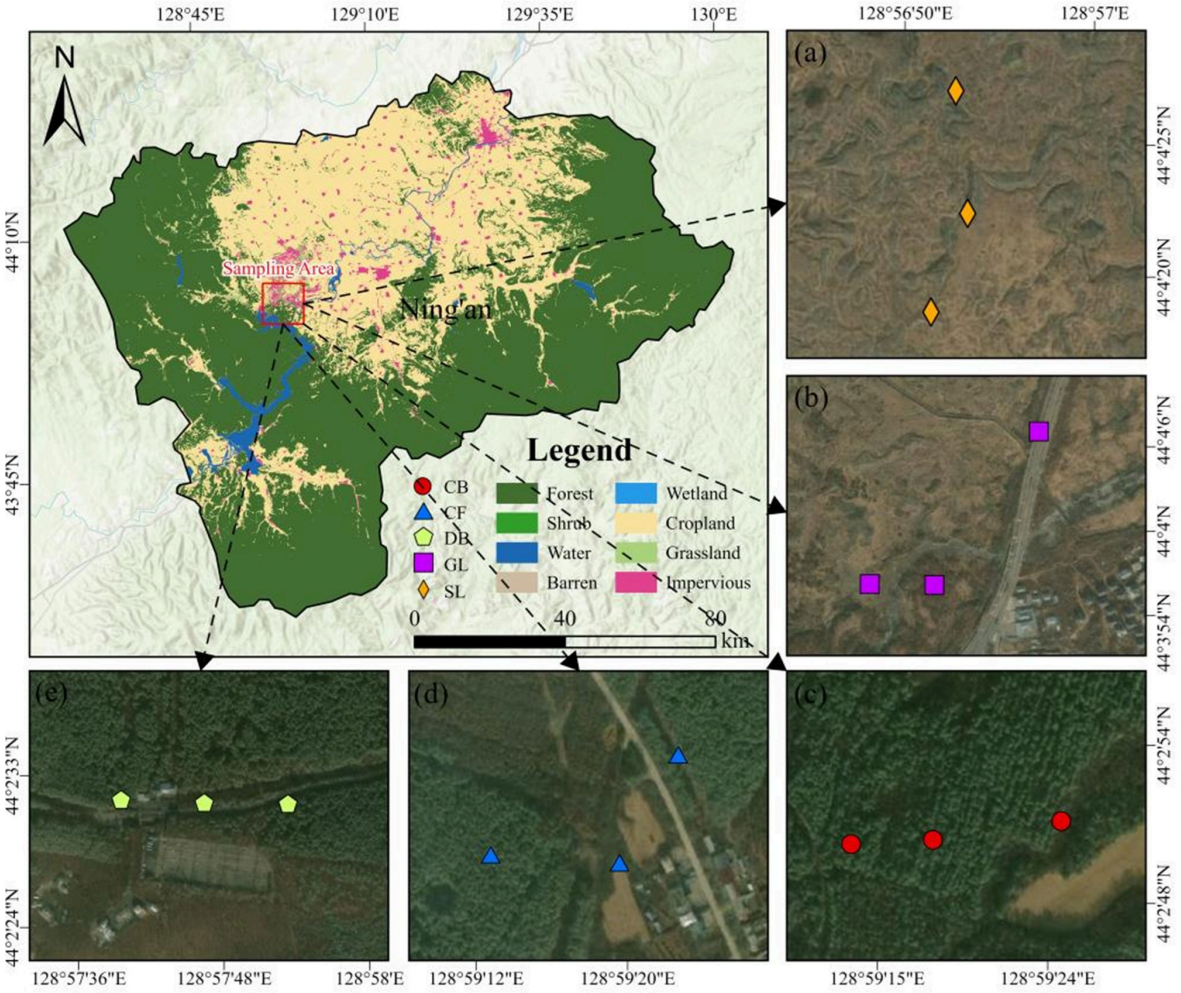


Figure 1

Overview of Jingpo Lake National Geopark.

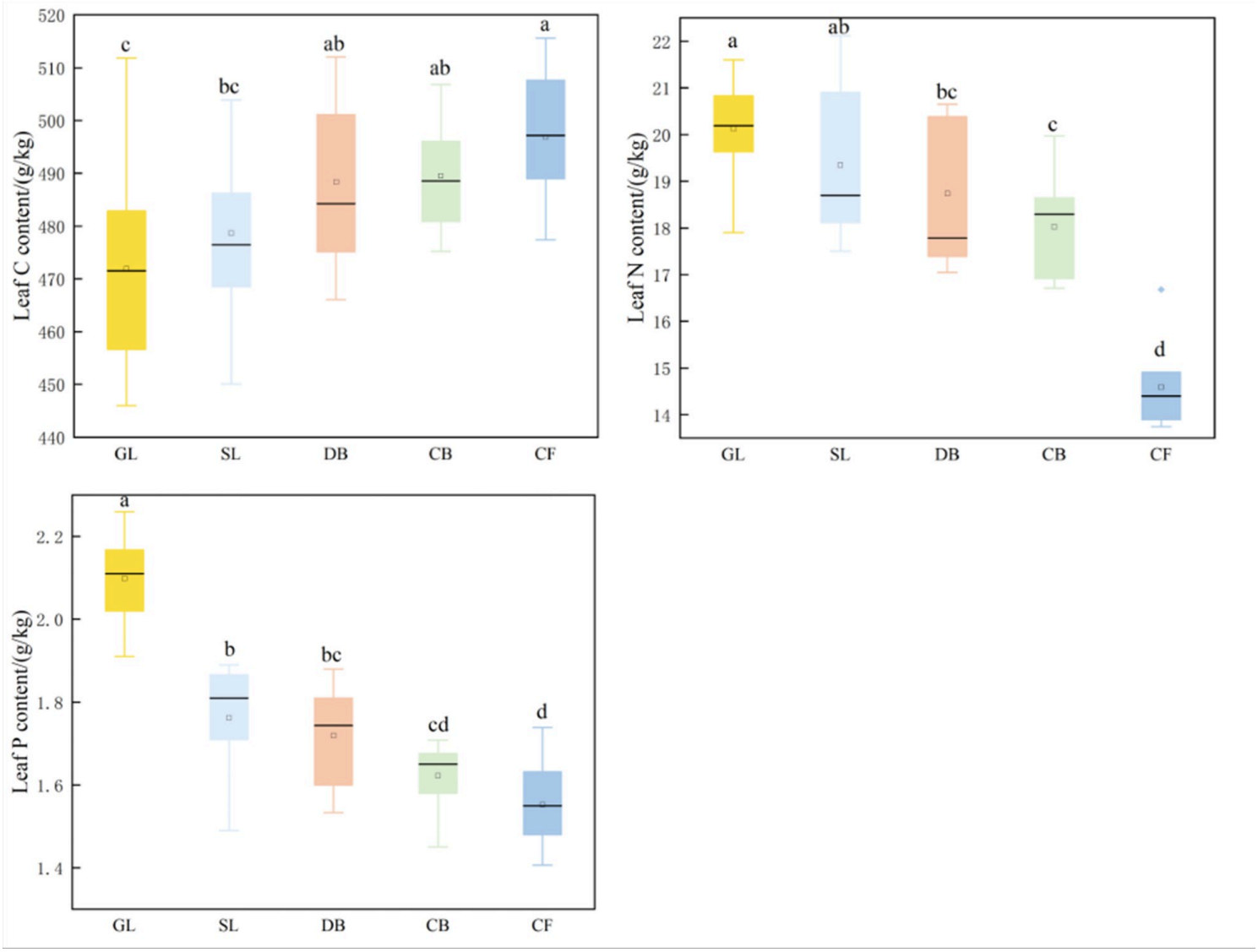


Figure 2

Leaf C, N, and P contents across five vegetation successional stages. Different lowercase letters indicate significant differences among stages ($p < 0.05$).

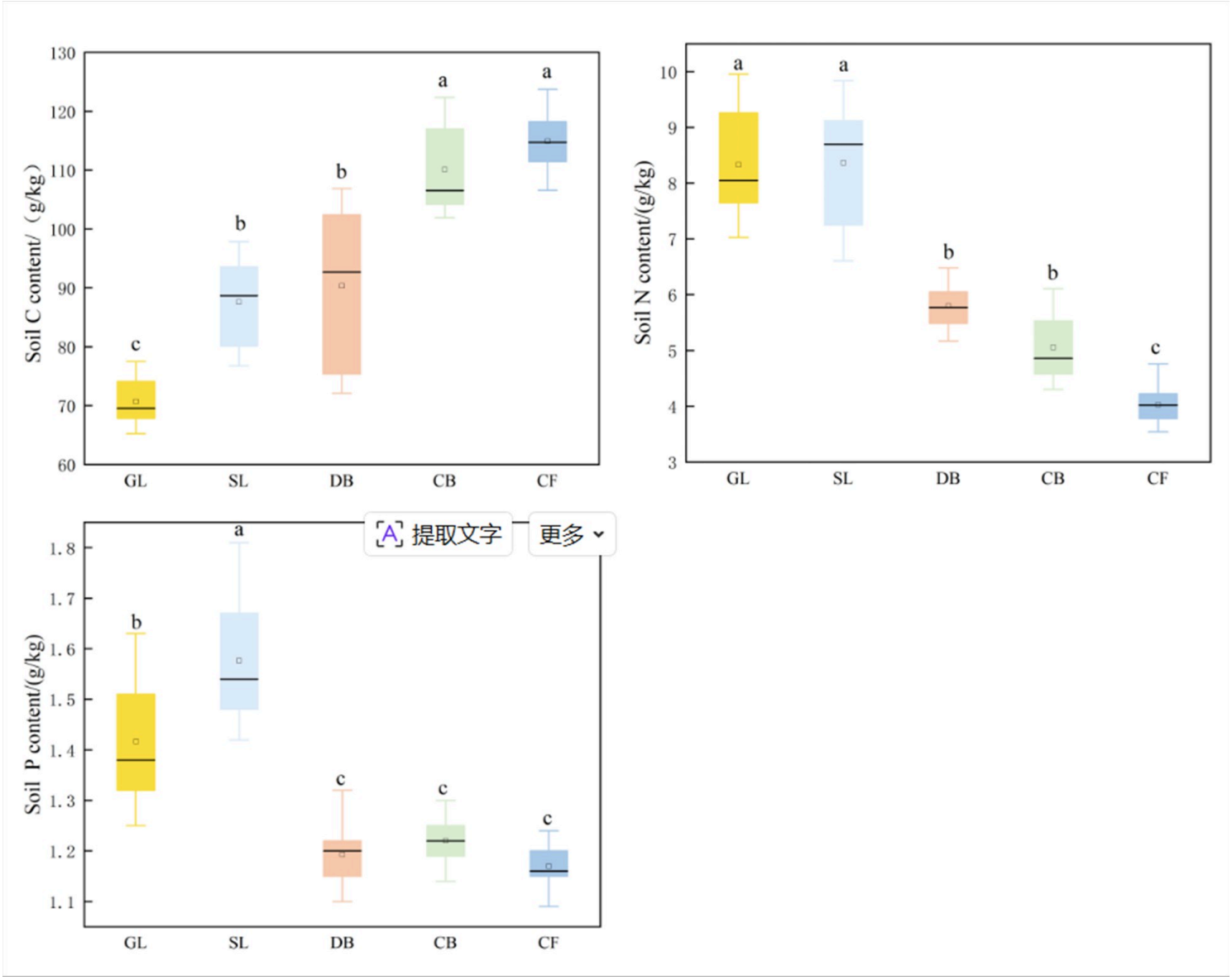


Figure 3

shows the different contents of C, N, and P in the soil of plants of different vegetation types. Lowercase letters indicate the significance of the differences among different vegetation types ($p < 0.05$)

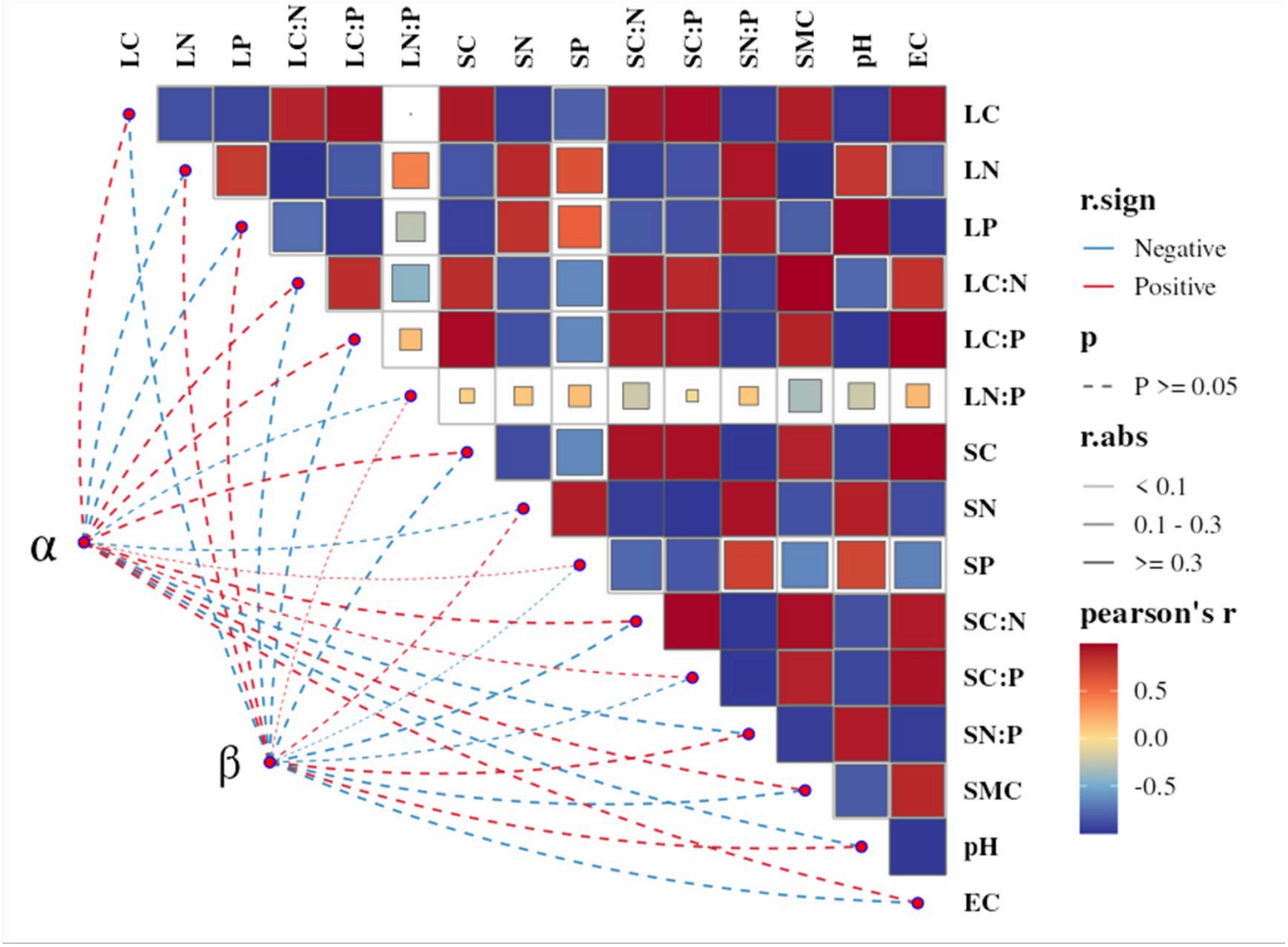


Figure 4

Correlation analysis of allometric scaling exponent with leaf-soil C, N, P contents and ecological stoichiometric

Note: LC: Carbon content of leaves; LN: Nitrogen content in leaves; LP: Phosphorus content in leaves; LC:N: Carbon-nitrogen ratio of leaves; LC:P: Carbon-phosphorus ratio of leaves; LN:P: Leaf nitrogen-phosphorus ratio; SC: Soil carbon content; SN: Soil nitrogen content; SP: Soil phosphorus content; SC:N: Soil carbon-nitrogen ratio; SC:N: Soil carbon-phosphorus ratio; SN:P: Soil nitrogen-phosphorus ratio; SMC: Soil moisture content; EC: Electrical conductivity

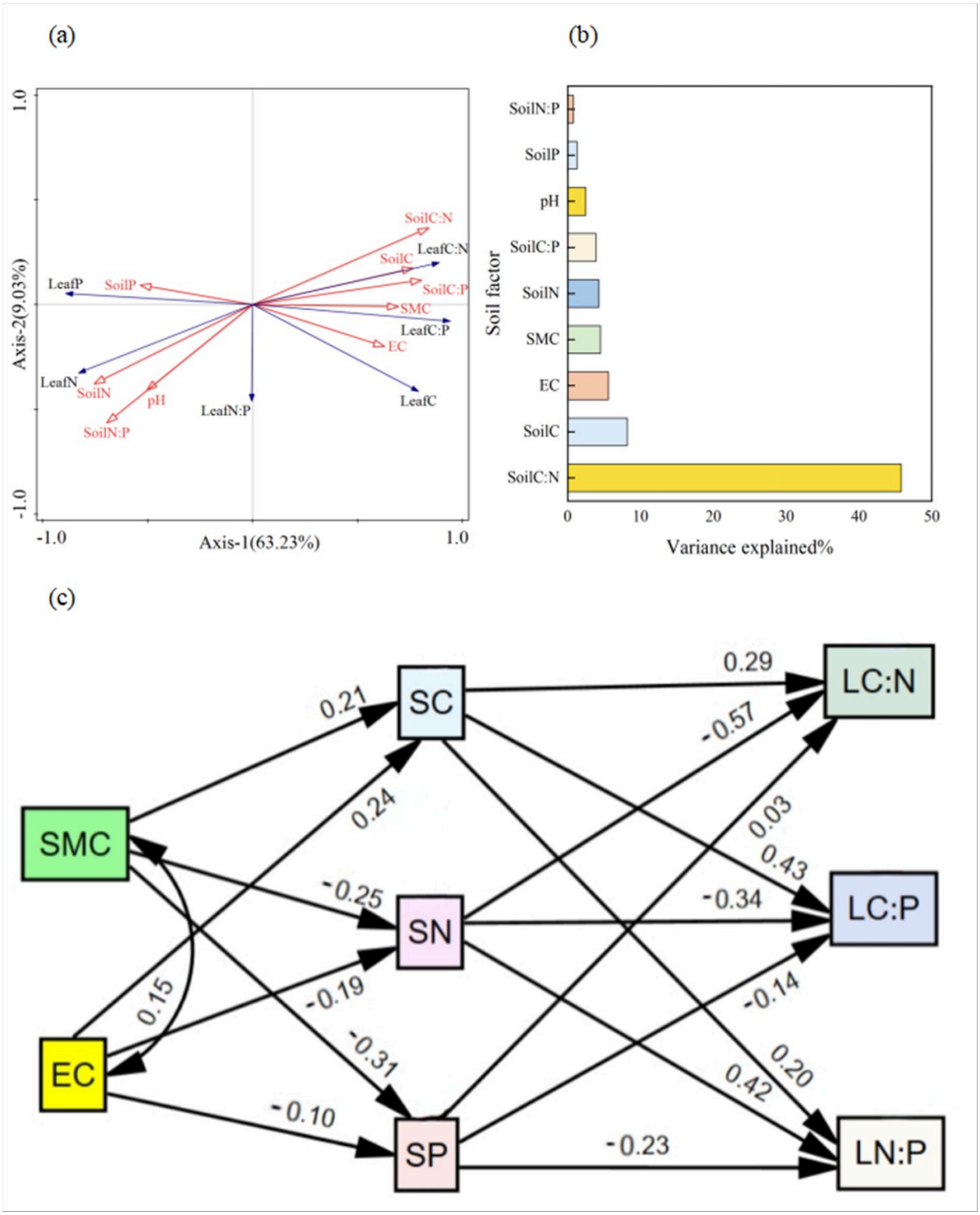


Figure 5

Redundant analysis of the relationship between ecological stoichiometric characteristics of plant leaves and soil environmental factors: (a) Redundant analysis (RDA) of ecological stoichiometry of leaf C:N:P and soil environmental factors; (b) The explanatory quantities of each factor influencing the ecological stoichiometry of leaves by soil factors. (c) Path model for predicting the association between soil environmental factors and plant leaves.