

Coexistence of tree species promotes the similarity of elementome in soil profiles

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Abstract

Purpose: The soil elementome has been recently proposed as a promising novel approach for describing the response of soil bioelemental composition to tree species. Using bioelement stoichiometry, we explored the effects of soil biogeochemical processes and tree species coexistence on soil elementome.

Methods: Soil bioelements were analyzed at three soil layers (A, B and C horizons) in four forests (*Picea asperata* (PA), *Larix principis-rupprechtii* (LP), *Betula Platyphylla* (BP), and *Betula Platyphylla* - *Larix principis-rupprechtii* (L-B) mixed forest) in Chongli District, Zhangjiakou City, Hebei Province, China., The soil elementomes of 11 bioelements (C, N, P, O, S, K, Ca, Na, Mg, Mn and Cr) were analyzed by principal component analysis (PCA) based on soil C:N:P stoichiometry. We calculated elementome distance (ED) to examine differences between soil horizons and forests.

Results: We found that soil elementomes in the soil layers decreased with depth and that ED between the B and C horizons was larger than that between A and B horizons. Moreover, differences in soil elementomes were smaller for tree species that often coexist compared to those that rarely live together.

Conclusions: Our results suggest that tree species coexistence promotes similarity in soil elementomes probably due to creation of similar soil conditions. The findings of this research provide a new understanding about the relationship between tree species coexistence and soil bioelemental composition or stoichiometry.

Introduction

All living beings are made of various bioelements in constant ratios (Zhang et al. 2012). Carbon (C), hydrogen (H), and oxygen (O) are the three bioelements that constitute the skeleton of organic molecules. Nitrogen (N), phosphorus (P), and sulfur (S) are the main bioelements involved in biochemical reactions. The stable concentrations and ratios of bioelements in organisms are important indicators for understanding the balance of multiple chemical elements in ecological interactions (Elser et al. 2000a; Elser et al. 2000b; Sardans et al. 2014). In 1958, Redfield (1960) reported that planktonic biomass contains C, N, and P in a comparatively steady atomic ratio of 106:16:1, similar to the proportions of C, N, and P in marine water. The well-known “Redfield ratio” provides promising insight into the nutrient limitation of ocean C storage and contributes to the knowledge of the biogeochemical cycling of N and P in the world’s oceans (Cooper et al. 1996). Afterwards, the study of ecological stoichiometry, which focuses on the balance of multiple chemical elements in ecological interactions, has become a fundamental feature of understanding biogeochemical cycles (Sternner and Elser 2002).

The elegant simplicity of the Redfield ratio prompted the research on searching for similar patterns and relationships in terrestrial ecosystems (Elser and Hassett 1994). McGroddy et al. (2004) reported that C:N:P in plant rootlets at a global scale was 1157:24:1, and the ratios of tree leaves and litters were highly variable. Conversely, Han et al. (2005) studied 753 terrestrial plant species in China and found that the N:P of grass leaves was stable at approximately 14.4. Parallel interactions existed between the terrestrial

environment and vegetation, resulting in similar ratios of C:N:P in soils and plants (McGroddy et al. 2004; Reich and Oleksyn 2004). Cleveland and Liptzin (2007) found that C:N:P ratios in soils and biomass were 186:13:1 and 60:7:1 at the global scale and concluded that a relationship existed between C, N and P in soils, which was similar to the concept of the Redfield ratio.

Concentrations and ratios of soil C, N, and P in terrestrial ecosystems were used to indicate plant physiology, nutrient cycles, and nutrient limitations in ecosystem productivity (Deng et al. 2015; Kirkby et al. 2011; Xu et al. 2015); for instance, C:N in soil or litter was a quality indicator of organic matter (Ostrowska and Porębska 2015), and N:P was related to nutrient constraints in ecosystems (Bui and Henderson 2013). In recent decades, the soil ecological stoichiometry of forest ecosystems has also attracted much attention. Aponte et al. (2010) investigated the stoichiometry of C, N, and P in the soil of Mediterranean forests and found that vegetation and soil depth simultaneously regulated C:N:P stoichiometry. Tian et al. (2010) reported that the soil C:N, C:P, and N:P ratios in China were 11.9, 61, and 5.2, respectively, and that the ratios of C:N:P and especially the C:N ratios were relatively consistent in the topsoil (0–10 cm). Fan et al. (2015) found that soil C and P decreased with the age of trees, and the plant N:P ratio was strongly related to the soil N:P ratios in subtropical plantations in Fujian Province, China.

However, an elementome based on C, N, and P only may miss key information that could be offered by additional elements (Kaspari 2021). Beyond C, N, and P, bioelements such as potassium (K), sodium (Na), magnesium (Mg), calcium (Ca), manganese (Mn), and chromium (Cr) have specific functions even though they are normally present at low concentrations in the environment. For instance, the compositions and ratios of K are related to drought resistance, Mg to the light environment, and K, Ca, Mg, and S to the levels of N and S deposition (Rivas-Ubach et al. 2012; Sardans et al. 2016; Sardans et al. 2011). Introducing additional elements in the analysis of the elementome can effectively improve the prediction of ecosystem functioning (Hofmann et al. 2021; Huang et al. 2019) and should be considered as an entirety in ecological stoichiometric studies. One efficient way to deal with the entirety of bioelements was to perform a dimensionality reduction analysis such as principal components analysis (PCA) (Peñuelas et al. 2019; Sardans et al. 2021).

The “biogeochemical niche” (BN) concept, which is an elementome defined as the content of all (or most) bioelements has been recently proposed (Peñuelas et al. 2019). It is effective in measuring ecological stoichiometry and can be regarded as an extension of the ecological niche concept. Peñuelas et al. (2019) investigated tree species in a holm-oak evergreen Mediterranean forest distribution and found that species with more overlapping ecological niches had greater differences in their BNs. Plants growing in diverse communities tended to change their elemental compositions to either reduce or enhance N and P concentrations depending on the species compared to monocultures (Dehuang et al. 2020; Guiz et al. 2018). Fernández-Martínez et al. (2021) further revealed that pairwise differences in elementomes between species were large as the possibility of coexistence increased. Based on these empirical approaches, it was hypothesized that “at equilibrium, coexisting species tend to have distinct elementomes to minimize competitive pressure” (Sardans et al. 2021). This BN hypothesis suggested that each species would have a specific need for certain bioelement to avoid nutritional competition with

other species. In a forest, the fierce competition between species under similar soil properties would result in remarkable differences in the plant elementome with their likelihood of coexistence (Bai et al. 2018; Fernández-Martínez et al. 2021). Considering that coexisting species are able to adjust ecological strategies by competing for soil resources, it can be further hypothesized that the similarity of the soil elementome leads to elementome segregation for coexisting species in competition.

In this study, we assessed the soil stoichiometry of different soil horizons in four different forests, i.e. *Picea asperata*, *Larix principis-rupprechtii*, *Betula platyphylla* and a mixture of *Betula platyphylla*-*Larix principis-rupprechtii* in Hebei Province, China. The objectives of this study were (1) determining the distribution of C:N:P ratio and concentrations of bioelements C, N, O, S, P, K, Ca, Na, Mg, Mn and Cr, and (2) investigating the soil profiles of different horizons and forest types and their relationships with soil elementomes. We suppose that: (1) the extent soil elementome was affected by biological and chemical processes decreased with the soil depth, and (2) coexisting of tree species reduced the differences in the soil elementome of the forests.

Materials And Methods

Study area

The study area is located in Chongli District, Zhangjiakou City, Hebei Province, P.R. China. The latitudes and longitudes of Chongli are 40°47' N to 41°17' N and 114°17' E to 115°34' E. The altitude extends from 814 to 2174 meters. The climate is classified as continental monsoon with average annual temperatures of 3.7 - 19°C and annual precipitation of 483.3 mm. Eighty percent of the territory in Chongli is mountainous, and the forest coverage rate reaches 67% in 2021. The main tree species are *Picea asperata*, *Larix principis-rupprechtii*, and *Betula platyphylla*, among which *Picea asperata* and *Larix principis-rupprechtii* are artificially planted.

Soil sample collection and chemical analyses

In July 2019, four different sampling plots in the forests of *Picea asperata* (PA), *Larix principis-rupprechtii* (LP), *Betula platyphylla* (BP) and the mixed forest of *Betula platyphylla* and *Larix principis-rupprechtii* (B-L) were selected in the study area. The four plots were all on mountainous slopes, and the size of each plot was set as 100 m × 100 m. In each plot, three quadrat subplots (20 m × 20 m) were uniformly arranged from the bottom to the top of the slope. One sampling point was set in the center of each subplot.

The steps of sample collection were as follows: first, the surface coverages of litter and other sundry were removed from the sampling points; second, a vertical soil profile of approximately 1 m depth was dug using shovels, and the soil profile was found to be three soil formation layers (A, B and C horizons) according to the soil textures; finally, in each soil layer, two samples (each approximately 100 cm³) were collected with a ring knife to analyze the soil physicochemical properties and bioelements. Samples were put into sealed bags and brought to the laboratory for analysis.

Soil pH was measured using a pH meter (type:PHS-3Cby China) with the soil and water ratio as 2.5:1. Soil bulk density (BD) was measured using the ring knife method. Soil organic matter (SOM) was determined by the external heating method of potassium dichromate and concentrated sulfuric acid (Liu et al. 1996). Purging and trapping techniques were used to determine O, N, and S concentration by an elemental analyzer (type: Elementar Vario Macro cube by Germany). The total concentrations of several nutrients (P, K, Ca, Na, Mg, Mn, and Cr) in soils were determined by inductively coupled plasma–optical emission spectrometry (Bremner. 1996). (type: Agilent 5110 ICP–OES by the USA). Table 1 summarizes the results of the soil chemical and physical properties.

Table 1. Soil chemical and physical properties

Forest	Horizon	Bulk	Specific	pH _(H2O)	SOM	TN
		density	gravity			
		g/cm ³	%		g/kg	
PA	A	0.85	2.14	6.74	70.7	3.60
	B	1.02	2.08	6.65	67.0	3.34
	C	1.28	2.22	6.72	49.0	2.46
LP	A	1.09	2.05	6.83	53.7	2.85
	B	1.12	2.09	7.00	47.3	2.53
	C	1.32	2.26	7.01	40.0	2.07
BP	A	1.05	2.18	6.84	45.9	2.61
	B	1.19	2.26	6.91	31.4	1.78
	C	1.65	2.42	7.00	13.0	0.71
B-L	A	0.79	2.05	6.40	85.9	4.35
	B	0.87	2.04	6.63	68.2	3.41
	C	1.13	2.16	6.34	43.2	2.35

SOM: soil organic matter; TN: total nitrogen; PA: *Picea asperata*; LP: *Larix principis-rupprechtii*; BP: *Betula Platyphylla*; L-B: *Betula Platyphylla* - *Larix principis-rupprechtii* mixed forest

Statistical analysis

All data in this study were described by the mean and standard deviation. SOM and elemental concentrations were described by mass content, the values of C:N, C:P, and N:P were molar ratios. A significance level of $p < 0.05$ was specified in this study. Analysis of variance (ANOVA) and Least significant difference (LSD) at a 5% level of significance were used to compare the difference among

horizon and forest. PCA was performed on elemental concentrations to estimate elementomes. Elementome Euclidean distance (ED) was used to quantitatively indicate the difference between elementomes.

All statistical analyses mentioned above were implemented using SPSS 25.0 (IBM, Armonk, New York, NY, USA). Related graphs were drawn by Origin 2021b (Hampton, MA, USA). Biological and chemical processes within the soil profile (Figure 3) were generated in BioRender with authorization.

Results

Soil C, N, P stoichiometry of different forests

The soil chemical and physical properties, which varied greatly with soil depth across all sampling plots. BD was significantly influenced by soil horizons, whereas pH was not significantly affected. SOM and N concentrations were the highest in the A horizon ($P < 0.05$) and declined with soil depth. Comparing the data in different forests, it was found that have SOM_{B-L} SOM_{BP} SOM_{LP} SOM_{PA} and the same trend for the N concentration.

Table 2. Soil C:N, N:P, and C:P in different forest types of this study

Forest	Horizon	C:N	C:P	N:P	C:N:P
PA	A	12.15±1.04Ba	134.77±17.98Ba	11.26±2.36ABa	137:11:1
	B	12.12±1.47Ba	97.85±22.29Bb	8.14±1.80Bb	99:08:1
	C	12.55±1.24Aa	54.66±18.20Cc	4.32±1.24Cc	54:04:1
LP	A	12.74±0.42ABa	127.64±25.50Ba	9.99±1.71Ba	127:10:1
	B	12.67±0.44ABa	103.53±7.33Bb	8.18±0.55Bb	104:08:1
	C	13.39±1.42Aa	96.65±15.26Bb	7.32±1.50Bb	98:07:1
BP	A	13.32±0.38Aa	166.86±13.18Aa	12.55±1.8Aa	167:13:1
	B	13.50±0.23Aa	146.47±17.01Ab	10.85±1.24Ab	146:11:1
	C	13.50±0.39Aa	148.73±8.99Ab	11.03±0.91Ab	149:11:1
B-L	A	13.08±0.53Aab	123.51±18.59Ba	9.43±1.17Ba	123:9:1
	B	12.73±0.67ABb	103.48±16.42Ba	8.10±1.00Ba	103:8:1
	C	13.64±0.59Aa	115.97±39.24Ba	8.46±2.75Ba	115:8:1

Note: Different uppercases mean the significant differences between forests ($p < 0.05$); different lowercases mean the significant difference between soil horizons $p < 0.05$.

The C:N ratios did not differ significantly between the PA, LP, and BP forests during the three horizons (Table 2) and were significantly lower in the soil A and B horizons than in the C horizon of the B-L mixed forest. All forests showed no significant differences in the C:N of the C horizon. A lower C:N ratio was observed in PA surface soil than that in BP and B-L mixed forests. As the soil depth increased, the C:P and N:P ratios decreased. BP forest obtained highest C:P and N:P ratios. There was no significant differences in the C:P and N:P ratios between the A and B horizons of other three forests. PA forests had the lowest ratios of C:P and N:P at the C horizon. Overall, the SOM in broad-leafed forests (BP) was higher than that in coniferous forests (PA and LP). In addition, the soil C:N, C:P and N:P ratios were higher in the B-L mixed forest than in the *Larix principis-rupprechtii* monoculture, indicating that mixed forest can effectively enhance soil organic matter quality in *Larix* forest.

Compared to the average N:P and C:N ratios in China (13.83 and 8.43), all four forests had lower soil N:P ratios (4.32 - 12.55) and higher C:N ratios (12.12 - 13.50) (Tian et al. 2010). In general, when N:P was less than 14:1, plant growth was more restricted by N; when N:P was higher than 16:1, plant productivity was more restricted by P; and when N:P was in the middle, plant growth was restricted by both nitrogen and phosphorus (Olde Venterink et al. 2003). Our study found that soil N in BP, LP, PA, and B-L mixed forests was all N-limited for plant growth.

Soil elementome distribution from PCA

The distribution of elementomes analyzed by PCA method are shown in Figure 2. Three principal components was able to explain a total of 86.05% of the variance. According to the results, loading values and explained variance were mapped to each component after PCA.

PC1 accounted for 52.46% of the total variance and was significantly correlated to C, N, O, S, and P contents. Thus, PC1 remarkable described the biological elements, i.e. C, N, O, S, and P, which are indispensable nutrients for the growth and development of all plants in forest ecosystems.

PC2 explained 22.17% of the variance in the original data, with K, Ca, Na, and Mg having the major loadings. These elements are nutrient cations that are subjected to biological activity and chemical activity to maintain their normal growth.

Accounting for 11.42% of the variance, PC3 substantially described the contents of Mn and Cr in the study area. This component can be described as soil bedrock which is the main influencer of these elements.

Soil elementome differences between horizons and forests

The elementome distances (ED) between horizons in four forests (*Picea asperata*, *Larix principis-rupprechtii*, *Betula platyphylla* and *Betula platyphylla* - *Larix principis-rupprechtii* mixed forest) in this study were calculated and shown in Figure 3.

As with the genome, the soil elementomes can represent the state of soil development. The soil elementomes were defined as the element concentrations in soil (Fernández-Martínez et al. 2019). In all four forests, elementomes decreased along with the depth of the soil. The elementome distances (ED) between the B and C horizons were larger than the ED between A and B horizons (Figure 3), among which ED_{BC} accounted for 61%~91% of the entire soil profile. In comparison with ED_{BC} , the proportion of ED_{AB} was as low as 9%~39%, which showed a larger difference in the bottom two horizons.

Soil is formed by the interaction of geological and biological cycles (Chen et al. 2014). Biological and chemical processes take place throughout the soil profile, interacting at a wide range of temporal scales and together driving the elemental cycle of the soil profile (Kirkby 2018). Our results show that the biological cycle was more vigorous than the chemical cycle, and soil elementomes were more affected by the biological activity rather than the bedrock. Organisms played an important role in soil ecosystem balance and stability as the most active factors in soil formation.

We found that soils of different forest had different elementomes. In mixed forests of *Betula platyphylla* and *Larix principis-rupprechtii*, the soil elementomes were higher than those in pure forests (Figure 4A). Among all forests, *Picea asperata* had the lowest soil elementomes. Successive plantation planting can degrade forest soil fertility, and nutrient accumulation can be effectively increased by mixed needle and broad-leaved planting.

Based on the forest survey, we can obtain the distribution and coexistence situation of tree species. We found that species rarely living together show larger differences in soil elementomes than those that frequently coexist (Figure 4B). The highest elementome distance (ED) value, 1.69, appeared between *Picea asperata* and *Betula Platyphyllaplatyphylla*, and the lowest ED value, 0.53, appeared between *Picea asperata* and *Larix principis-rupprechtii*.

Discussion

Effects Of Forests On Soil C, N, P Stoichiometry

The proportional relationship between C, N, and P is an important indicator of soil nutrient status (Wang et al. 2021). The C:N and C:P ratios of soil determined the decomposition of SOM, whereas the N:P ratio reflected the element restriction of ecosystem (Hui et al. 2021). In this study, we found that the SOM in the broad-leaved forest was better than that in the coniferous forest. According to previous studies, dissolved organic matter in forest soil was mainly formed by litter decomposition and plant root exudates (Goller et al. 2006; Huang and Schoenau 1998). Therefore, a high level of SOM was associated with broad-leaved trees which suggested a high litter decomposition rate. Some research found that keratin prevented microorganisms from adhering and invading leaves with high keratin content, thus causing the slow decomposition of leaves with high keratin content (Garnier and Laurent 1994). As a consequence, in the present study, the litter decomposition rate of *Betula platyphylla* was significantly higher than that of pure *Larix principis-rupprechtii*.

Soil C:N:P stoichiometry in the B-L mixed forest was higher than in the LP monoculture. More studies found that a mixed forest composed of multiple tree species was stronger in soil nutrient protection, which was mainly based on three theories, namely, the natural enemy hypothesis (R. 1973), resource-concentration hypothesis (Freney 1986) and associational resistance hypothesis (Hambäck et al. 2000). In mixed forests, chemical differences in litter, the transfer of nutrients and secondary metabolites between litter, and variations in the microhabitat of decomposers led to the accelerated decomposition of mixed litters (Gartner and Cardon 2004; Song et al. 2010). Our study provided evidence that stand conversion from BP to B-L mixed culture substantially improved soil quality.

In our results, the stoichiometric ratios of soil C, N, and P varied dramatically from forest to forest. As reported by Xu (2012), soil C:N:P ratios ranged from 64:5:1 to 1347:72:1, with an average of 287:17:1. According to Tian (2010), the average C:N:P ratio of China's soils was 60:5:1. The results we obtained were within these reported ranges. We found that the C:N:P ratios decreased with soil depth, consistent with some previous reports such as Bing et al. (2015) reported that C:N:P ratios decreased from 343:16:1 in the A horizon to 63:3:1 in the C horizon.

Elementomes Between Horizons And Mechanisms Of Soil Formation

The adsorption, analysis, decomposition, and aggregation of various elements in soil constitute the biogeochemical cycle of the soil environment (Chen et al. 2014). The biological process is mainly composed of two parts: biological residue is decomposed into inorganic compounds via humification and mineralization by soil microorganisms, and living organisms absorb soil elements. In geological processes, leaching and diagenesis fix soil elements into bedrock while weathering releases them (Banfield et al. 1999; Waroszewski et al. 2019).

The study of soil formation and classification has made significant advances since the mid-1800s, evolving from conceptual frameworks to descriptive studies and finally to more quantitative approaches (Hartemink and Bockheim 2013). Schaetzl et al. (2013) proposed that soil formation was directly affected by the nature and direction of parent materials. By analyzing the elemental composition and weathering rate of Zr and Ti particles, Anda et al. (2009) concluded that soil profiles can be specifically characterized by different parent materials due to their varying weathering processes and rates. Jackson and Sheldon (1949) addressed the role of tree roots in limestone disintegration. Almeida (1994) examined the ability of higher plants to promote weathering. Plants also changed the weathering process and impacted the nutrient characteristics of the profile (Hasenmueller et al. 2017).

Soil geochemical properties are important parameters of soil development. Soil C, N, O, S, and P are major structural components in living organisms and also participate in many biochemical organisms (Melville et al. 1971). Moreover, K, Ca, Na and Mg, are essential elements for plant growth. Therefore, the changes in the main mineral elements in the ecosystem and the mechanism of their recycling are important

contents of the primary succession theory since they represent the main functional process of an ecosystem and determine its pattern. Healthy ecosystems depend heavily on the normal circulation of mineral elements that related to their stability and sustainability (Diaz et al. 2016; Reich and Oleksyn 2004). In addition, manganese (Mn) and chromium (Cr) are also required for normal plant growth and development which cannot be decomposed by soil microorganisms, so they are easy to accumulate. Nevertheless, excessive concentrations of Mn and Cr would be detrimental to plant growth. (Guo et al. 2020; Zemunik et al. 2020).

The elements in this study were significantly different between soil layers and were decreased with soil depth, in particular, a more significant difference in the bottom two horizons. Soils in different forests showed quite different environments. Based on our results, soil elementomes under different forest types were mainly affected by biological processes.

Soil Elementomes Controlled By The Coexistence Of Tree Species

Plant species controlled the composition of soil elements (Zederer et al. 2017). Tree species created soil environments that improved their competitive abilities, thus increasing their fitness (Cools et al. 2014). The nutrient content of tree species determined leaf-fall decomposition, nutrient return, and nutrient release into the soil in forests, affecting soil fertility. In many studies, differences in litter lignin and nutrient content were found to influence microbial decomposition, i.e, litters with higher lignin forms decomposed slower, which subsequently affected the soil elements of the forest floor (Hansson et al. 2011; Hobbie et al. 2006; Lovett et al. 2002; Vesterdal et al. 2012). Each species generated soil conditions that reflected the environmental conditions where it dominated, at a local level, with its life history and nutritional strategies (Pérez-Ramos and Marañón 2011; Vivanco and Austin 2008). According to Aponte et al. (2013), tree species-induced variations in soil conditions created positive feedback through niche partitioning that enabled the coexistence of tree species. Species were unique genetic pools and products of long-term evolutionary processes. The genotypic elements shaped coexistence and accounted for a large part of foliar element composition (Sardans et al. 2021).

Tree species-induced variations in soil nutrient contents influenced elementomes, enabled the separation of biogeochemical niches and maintained their coexistence. According to our results, elementome distances (ED) between PA and BP/LP were more significant than those between BP and LP. Differences in soil elementomes were minor for tree species that often coexist. Numerous studies have demonstrated that elementomes differed more for coexisting species and individuals than for noncoexisting ones (Fernández-Martínez et al. 2021). Additionally, there was evidence that species would compete for resources under similar soil elementomes, causing niche partitioning (Loreau and de Mazancourt 2013) with the likelihood of coexistence. A limited amount of research has focused on applying soil elementomes, and we attempted to analyze soil biogeochemistry through soil elementomes.

The evolution and bioelemental composition of ecosystems were bidirectional because nutrient supply could affect evolutionary processes and the effects of evolution on nutrient supply (Durston and El-Sabaawi 2017). We can understand the processes underlying species shifts in bioelemental composition by studying their responses to environmental changes (Leal et al. 2017; Yamamichi et al. 2015) and, therefore, the effects of organisms on ecosystem functioning and services (Leal et al. 2017). In this way, elementomes constitute a quantifiable tool for detecting, quantifying, and understanding the mechanisms and processes underlying community evolution and species turnover (Peñuelas et al. 2019). Under global change, the study of ecosystem functioning should be based on an elementomes approach.

Conclusion

In this study, we investigated the soil elementomes in four forests to reveal the effects of species coexistence on soil biogeochemistry. The following results were obtained:

- (1) The SOM in the broad-leaved forest was better than the coniferous forest.
- (2) Soil C, N, and P stoichiometry was higher in the B-L mixed forest than in the *Larix principis-rupprechtii* monoculture. In mixed forests, chemical differences, transfer of nutrients, and secondary metabolites in litters led to accelerated decomposition of mixed litters.
- (3) Elementome distances (ED) between the B and C horizons were larger than ED between A and B, which indicated that soil elementomes were more affected by biological activity.
- (4) Differences in soil elementomes were smaller for tree species that often coexist compared to those that rarely live together. Tree species-induced changes in soil nutrient content affected the elementomes and created a soil condition that allowed for biogeochemical niche separation and sustained their coexistence.

The results provide implications for understanding of the processes underlying species shifts in soil bioelemental composition and the responses of organisms to environmental changes and, in turn, the effects of organisms on ecosystem functioning and services. Elementomes constitute a quantifiable tool to detect, quantify and thus better comprehend the mechanisms and processes underlying community evolution and species turnover. Further studies are warranted to discern the ecological and evolutionary processes based on an elementomes approach involved in all types of species, habitats, and ecosystems.

Declarations

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Authors' Contributions

HY Zhang, XC Wu and TS Huang designed and supervised this study; XC Wu and SJ Zhang conducted the experiments, performed data interpretation, and drafted the manuscript; YL Tian and CF Yu helped to revise the manuscript grammatically. TS Huang and YL Tian critically reviewed and revised the final manuscript. All authors read and approved the final manuscript.

Declaration of Competing Interest

We declare we have no competing interests.

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Figures

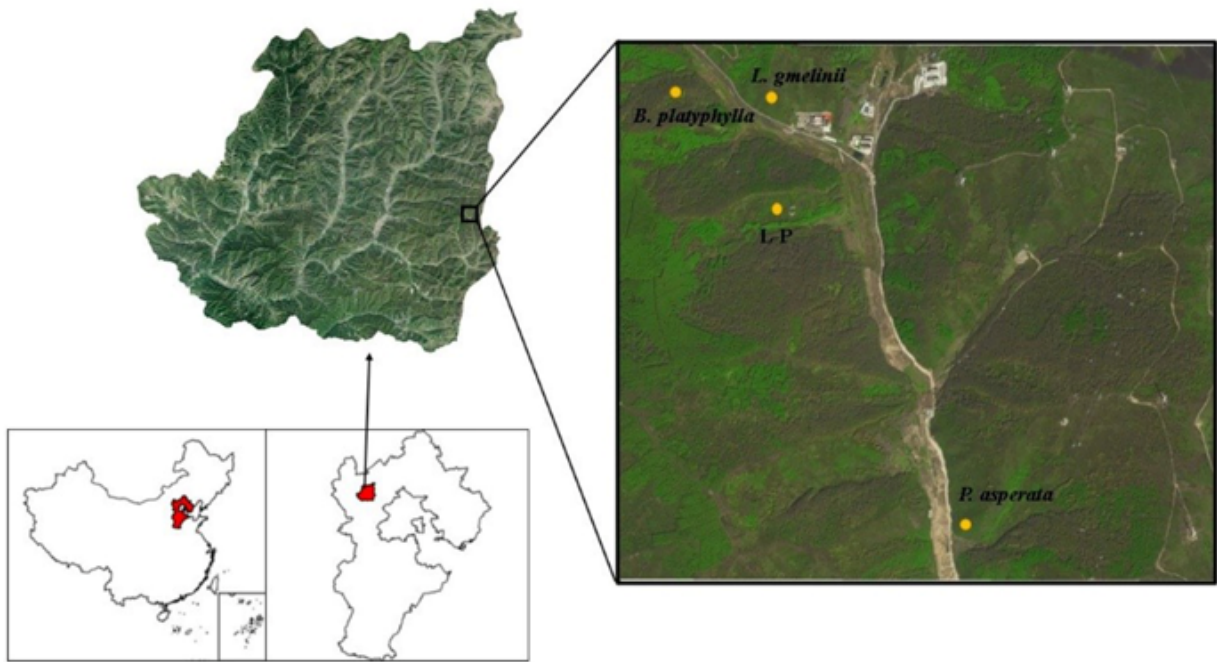


Figure 1

Study area and soil sampling plots

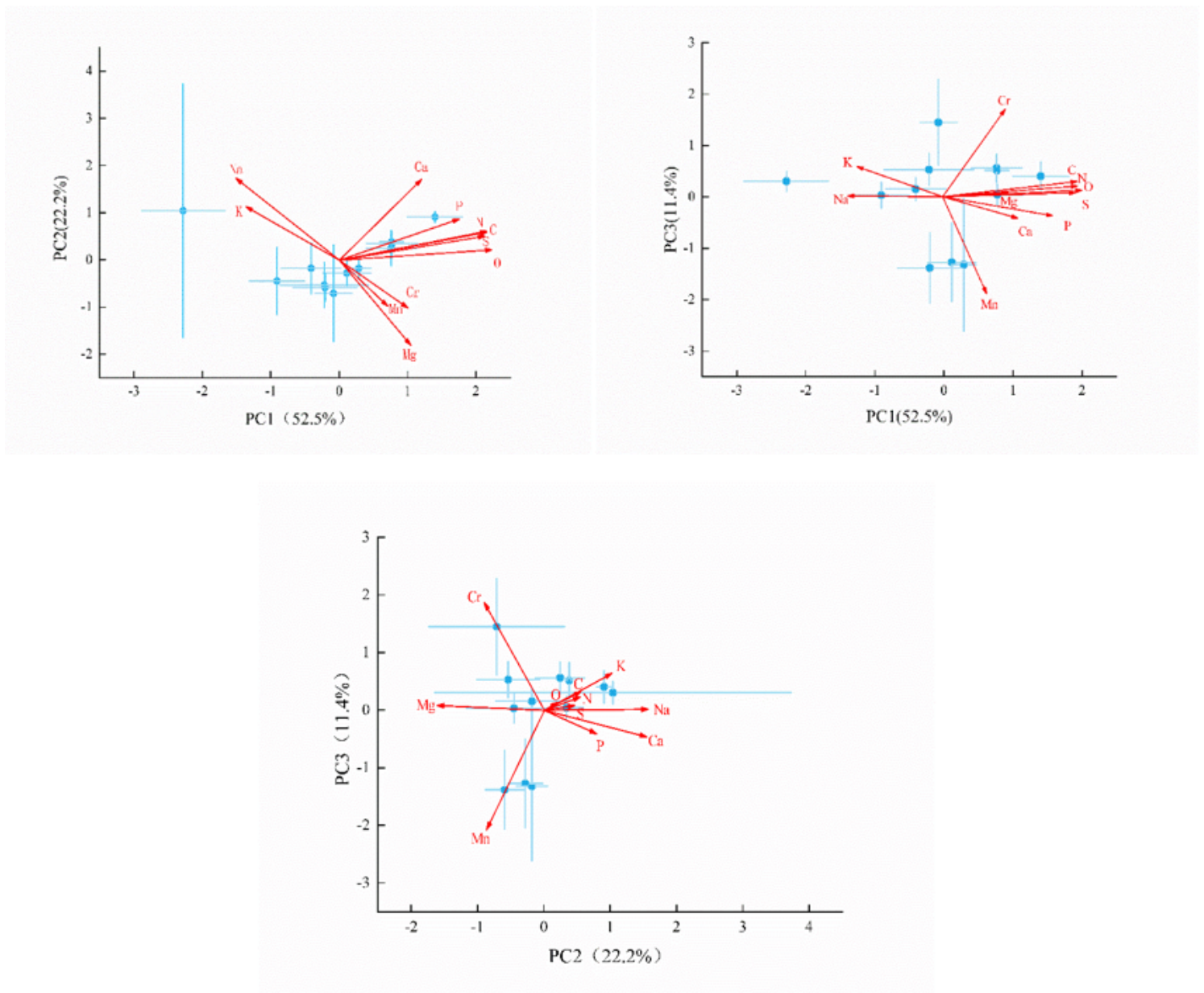


Figure 2

Distribution of elementomes analyzed by PCA method. Biplots showing loadings and mean \pm SE scores. Red arrows indicate factor loadings, and blue dots indicate the mean \pm SE scores per sample.

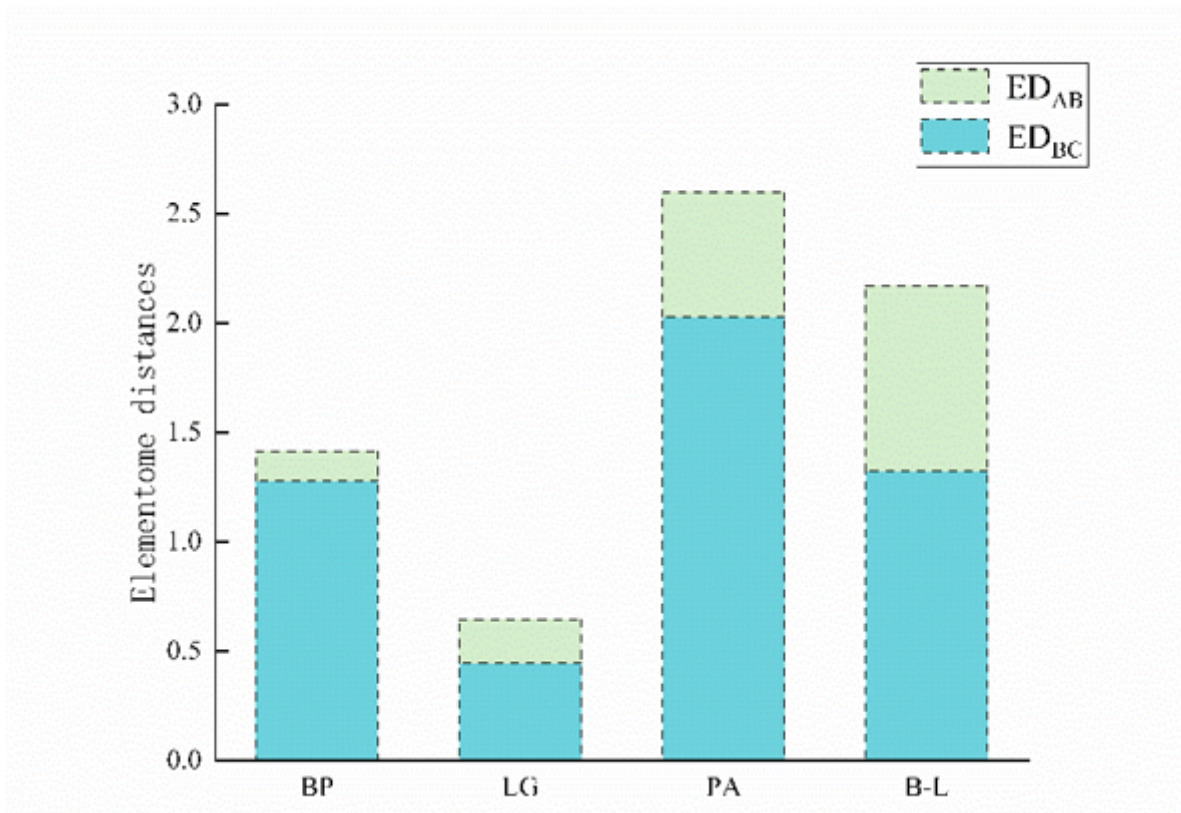


Figure 3

Elementome distances between horizons

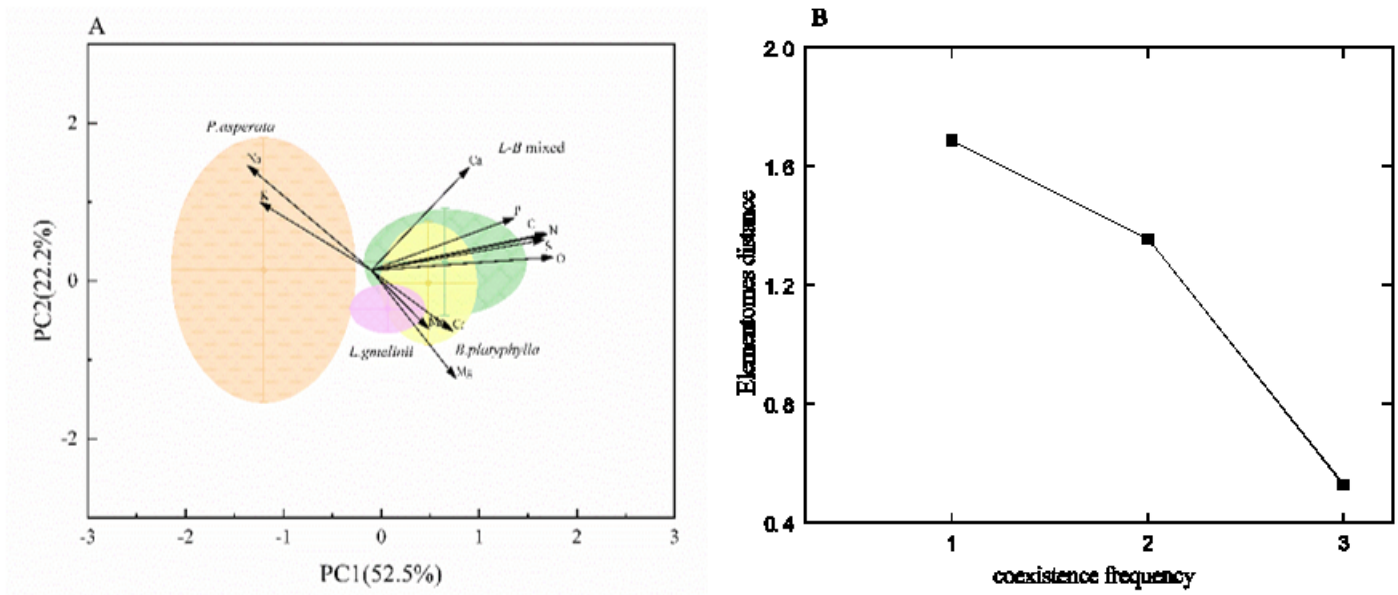


Figure 4

Soil elementome segregation and distances among forest species. **(A)** Soil elementome segregation among forest species. We plotted the soil scores for the first two principal components of the principal component analysis (PCA) conducted with C, N, O, P, S, K, Ca, Na, Mg, Mn, and Cr concentrations as variables. **(B)** Score distances for PC1 and PC2 of the PCA of the soil stoichiometry in 3 species, dominant species as a function of the frequency of species coexistence. Numbers represent 1, no coexistence; 2, occasional coexistence; 3, frequent coexistence. Based on Wen et al. (2017), Liu et al. (2011) and Kang (2013).

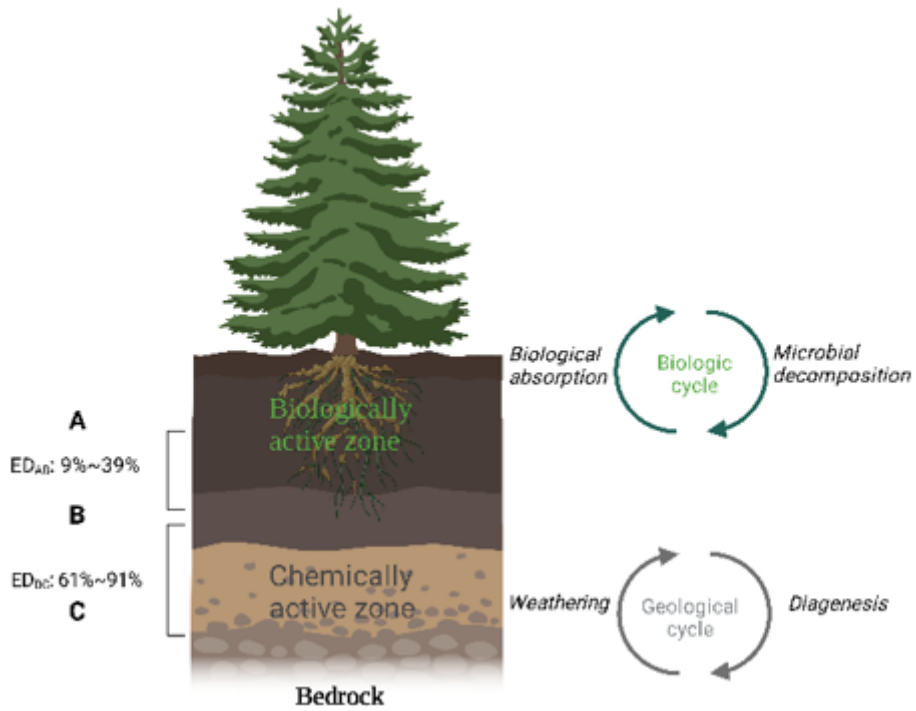


Figure 5

Biological and chemical processes within the soil profile