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Carbon, Nitrogen and Phosphorus Stoichiometry in Natural and Plantation Forests in China

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Abstract: Ecological stoichiometry is essential for understanding the biogeochemical cycle in forest ecosystems. However, previous studies of ecological stoichiometry have rarely considered the impacts of forest origins, which could help explain why to date so much uncertainty has been reported on this subject. In this study, we tried to reduce this uncertainty by examining carbon (C), nitrogen (N) and phosphorus (P) in roots, litter and soil in both natural and plantation forests throughout China. The sampled forest sites were divided into three groups according to the identified succession stages: early (ES), middle (MS) and late (LS) stages. Our results show that soil C, N and P concentrations were significantly higher in natural (NF) than in plantation (PL) forests. As succession/growth proceeded, P concentrations significantly increased in litter, roots and soil in NF, while the opposite occurred in PL. These results indicate that NF are able to use P more efficiently than PL, especially in the LS. Furthermore, the higher root N:P ratio indicates that the growth of PL was limited by P in both MS and LS. Our results also suggest that geographical and climatic factors are not the dominant factors in the differences in P between NF and PL, and, even more clearly and importantly, that native forests with native species are more capable of conserving P than planted forests, which are frequently less diverse and dominated by fast-growing non-site native species. These results will help improve biogeochemical models and forest management throughout the world.

Keywords: C N P stoichiometry; natural forests; plantations; succession stage; climatic factors

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1. Introduction

Carbon (C) is one of the base materials that support vegetation growth [1], in which nitrogen (N) and phosphorus (P) are the two most important limiting elements [2,3]. The ratios of carbon to nitrogen (C:N), carbon to phosphorus (C:P) and nitrogen to phosphorus (N:P) can therefore be used to explore the relationships and feedback between organisms and the environment [4], as well as biogeochemical processes [2]. C, N and P in forest ecosystems are exchanged between plants, litter and soil [5]. However, the determination of stoichiometry in root–litter–soil systems still needs clarifying. The importance of roots, in particular, is often ignored, even though they play a vital role in connecting plants' aboveground and underground structures [6]. More than 90% of the N and P nutrients in vegetation are returned to the soil through litter [7].

China possesses abundant forest resources with rich forest types spread over a climatic gradient that ranges from cold temperate to tropical [8]. These forests, either naturally regenerated (natural forests, NF) or artificially planted (plantation forests, PL), greatly differ in terms of both species composition and management. As previously reported, China's PL provide fewer ecosystem services than NF since they are monocultures, and as a result of inappropriate management, there is excessive use of fast-growing pioneer successional species, use of non-native species such as *Pinus* and *Eucalyptus*, less biodiversity, and declining forest productivity [9,10]. Thus, there is an urgent need to explore differences in nutrient cycling between NF and PL, a process that is seldom reported but which is essential for improving forest management.

Despite intensive studies that have investigated the stoichiometric characteristics of plant tissues [11–13] and controlling factors at different temporal-spatial scales [3,12,14–16], debate continues as to the influence of climatic factors on stoichiometric ratios. For example, by compiling published data relating to global experiments conducted in natural environments, Yuan and Chen [17] found that the ratio of terrestrial plant N:P decreases with greater atmospheric concentrations of CO_2, increased rainfall, and P fertilization, but increases with warming, drought, and N fertilization. By comparison, Reich and Oleksyn [3] used a global data set of 5087 observations of leaf N and P to demonstrate that leaf N and P increase from the tropics towards cooler and drier mid-latitudes, and that the N:P ratio increases with mean annual temperature (MAT) and towards the equator. Yet, Townsend [18] found no relationship between the N:P ratios and either latitude or mean annual precipitation (MAP) in the tropics. In addition to these discrepancies, the interactions between root–litter–soil are often not taken into account in studies of the stoichiometric characteristics in forests, even though they could give rise to important feedbacks between the above- and below-ground components of ecosystems [19]. As such, the internal mechanisms of C, N and P balances in different forest stands during succession/growth stages still need to be further explored.

In this study, we examined the C, N and P concentrations and stoichiometric ratios in roots, litter and soil in different forest stands in China's forest ecosystems. We predicted that the C, N and P concentrations and their stoichiometric ratios in roots, litter and soil are likely to be closely linked. Therefore, our objectives were to (1) quantify the patterns of C, N and P concentrations and stoichiometric characteristics in roots, litter and soil during succession stages in NF and PL throughout China's forest ecosystems; and (2) determine the factors affecting C, N and P concentrations and ecological stoichiometry in roots, litter and soil, and the differences between NF and PL.

2. Materials and Methods

2.1. Samples and Measurement

Root, litter and soil samples were collected in China during the years 2011–2015. Samplings and laboratory analyses were all conducted following a consistent standardized protocol [20,21]. We divided the country into three grid sizes (100, 400 and 900 km^2) based on vegetation distribution using a 1: 1,000,000 vegetation map. A grid size of 100 km^2 was designed for tropical and subtropical regions with rich species diversity, and 400 and 900 km^2 were for temperate and alpine vegetation regions where species diversity is relatively poor. Then we overlaid the grid maps with administrative maps and randomly select 3% to 5% of the grid for the field surveys by considering forest origin, age and type [22]. At each site, a 1000-m^2 plot was established (600 m^2 in some cases in plantations), each of which consisted of 10 subplots (10 m × 10 m) for the field survey. In each plot, plant roots were collected from the commonest tree species (diameter breast height $\geq$ 5 cm, 1–5 species). We also set up three 1 m × 1 m quadrats in each subplot for litter sampling. After removing the litter layer, soil samples at 0–50 cm were collected in each plot with a soil auger. Fertilized sites, sites with missing measurements in any depth of 0–50 cm in the soil matrix, and missing root of tree samples were filtered, and in total of 1112 sites were retained for analysis (Figure 1). All the root and litter samples were oven-dried at 65 °C to a constant weight and ground into fine powder with a plant sample grinder. Soil samples were air dried. C and N concentrations in the root, litter and soil were analyzed using an elemental analyzer (2400 II CHNS; Perkin-Elmer, Boston, MA, USA). P concentrations were determined using the molybdate/ascorbic acid method after H_2SO_4-H_2O_2 digestion. The sampled sites were divided into two groups, natural (NF) and plantations (PL) forests. Three successional stages or growth stages were identified for each (early, middle and late stages). Details of the identification of the successional and growth stages can be found in Yu et al. [22]. Dominant species of different successional stages in different forest origins were shown in detail in Table A1.

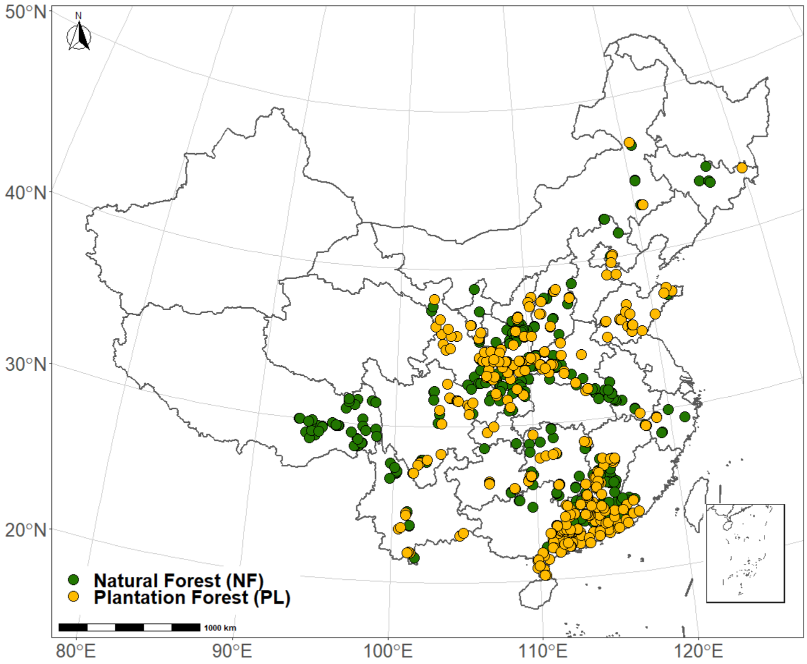

Figure 1. Sampling locations of the natural forests and plantations in this study.

2.2. Climate Data

Climate data (MAT and MAP) were obtained from the National Ecosystem Research Network of China (http://data.cma.cn/en, accessed on 16 January 2021).

2.3. Statistical Analyses

The mean and standard error of the investigated variables (including C, N and P contents, and C:N, C:P and N:P ratios) of root, litter and soil mixtures were calculated separately. Independent-samples T-tests were used to examine the differences between the C, N and P concentrations and ratios in the different forest types. One-way analyses of variance (ANOVA) were used to examine the differences in C, N and P concentrations and the ratios between the different succession/growth stages. Pearson's correlation was used to analyze the association between the studied variables (C, N and P concentrations, and geographical and climatic factors). All values were considered statistically significant at $p < 0.05$ and the results are reported as the means ± standard errors. All statistical analyses were performed using SPSS v22.0 (IBM Crop.) (Chicago, IL, USA), and the statistical data were plotted using OriginPro 2021 (Hampton, USA).

3. Results

3.1. C, N and P Concentrations in Roots, Litter and Soil in Forests of Different Origins in China

Significantly higher root C and N concentrations were found in PL than in NF (Table 1, $p < 0.05$); root P concentrations were significantly lower in PL than in NF (Table 1, $p < 0.05$). For litter C concentrations, no differences were found between PL and NF (Table 1, $p > 0.05$). However, litter N concentrations were significantly higher in PL than in NF. In contrast, litter P concentrations were significantly higher in NF than PL (Table 1, $p < 0.05$). Soil C, N and P concentrations were significantly lower in PL than in NF (Table 1, $p < 0.05$).

Table 1. Concentrations of C, N, and P in roots, litter and soil in NF and PL in forest ecosystems in China.

Parameter	Forest Origin	C Concentration ($g \cdot kg^{-1}$)	N Concentration ($g \cdot kg^{-1}$)	P Concentration ($g \cdot kg^{-1}$)
Root	NF	443.30 ± 1.87 B	4.4 ± 0.12 B	0.73 ± 0.03 A
	PL	451.80 ± 2.41 A	6.64 ± 0.26 A	0.56 ± 0.03 B
Litter	NF	412.71 ± 2.69 A	10.48 ± 0. 13 B	0.93 ± 0.03 A
	PL	410.40 ± 4.05 A	10.96 ± 0.19 A	0.71 ± 0.02 B
Soil	NF	22.00 ± 0.83 A	1.56 ± 0.05 A	0.48 ± 0.02 A
	PL	16.83 ± 0.69 B	1.14 ± 0.06 B	0.39 ± 0.01 B

Note: Capital letters indicate significant differences in C, N and P concentrations in roots, litter and soil between different forest origins ($p < 0.05$); n = 667 and 445 for NF and PL, respectively.

The C:N, C:P, and N:P ratios did not significantly differ between NF and PL in soils (Table 2, $p > 0.05$). For roots and litter, the N:P ratios were significantly higher in PL than in NF (Table 2, $p < 0.05$). By comparison, the C:N and C:P ratios in NF and PL only significantly differed in roots and litter (Table 2, $p < 0.05$), respectively.

Table 2. Stoichiometry of the C, N, and P in roots, litter and soil in NF and PL in forest ecosystems in China.

Parameter	Forest Origin	C:N Ratio	C:P Ratio	N:P Ratio
Root	NF	128.71 ± 2.70 A	1352.19 ± 62.18 A	11.86 ± 0.45 B
	PL	109.79 ± 4.16 B	1421.91 ± 50.82 A	16.56 ± 0.65 A
Litter	NF	46.19 ± 1.02 A	674.38 ± 20.95 B	16.19 ± 0.42 B
	PL	43.74 ± 1.11 A	853.67 ± 36.52 A	19.22 ± 0.48 A
Soil	NF	17.58 ± 0.75 A	64.18 ± 5.76 A	4.20 ± 0.40 A
	PL	19.21 ± 1.27 A	60.64 ± 2.62 A	3.79 ± 0.18 A

Note: Capital letters indicate significant differences in the C, N and P stoichiometry of roots, litter and soil between the different forest origins ($p < 0.05$); n = 667 and 445 for NF and PL, respectively.

Although the C concentrations were not significantly different in the three succession stages, both in NF and PL and in roots and litter (Figure 2a,d, $p > 0.05$) soil C concentrations significantly increased with succession/growth stages in both NF and PL (Figure 2g, $p < 0.05$). Root N concentrations generally decreased in NF during succession (Figure 2b, $p < 0.05$) but did not change significantly in PL (Figure 2b, $p > 0.05$). However, compared to the ES and MS, soil N increased significantly in NF and decreased significantly in PL in the LS (Figure 2h, $p < 0.05$). P concentrations generally increased in NF during succession in roots, litter and soil but significantly decreased in PL (Figure 2c,f,i, $p < 0.05$).

The C:N, C:P and N:P ratios did not significantly differ in NF in roots during succession (Figure 3, $p > 0.05$). Root C:P and N:P ratios generally increased in PL during succession (Figure 3b,c, $p < 0.05$). Litter C:P and N:P ratios significantly increased with age in PL but decreased in NF (Figure 3e,f, $p < 0.05$). Soil C:N and C:P ratios significantly increased in PL (Figure 3g,h, $p < 0.05$). The difference in soil N:P ratios in NF and PL during succession was not significant (Figure 3i, $p < 0.05$).

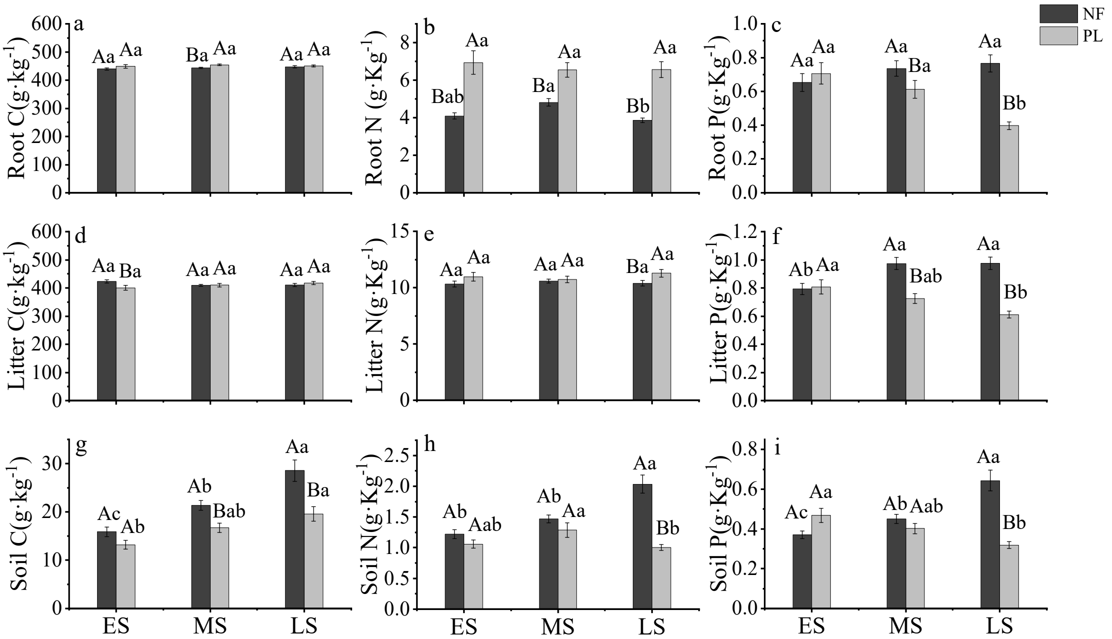

Figure 2. C, N and P concentrations in roots (**a**–**c**), litter (**d**–**f**) and soil (**g**–**i**) in different succession stages in NF and PL. Note: The error bars indicate standard errors of the means. Capital letters indicate significant differences in concentrations in different forest origins at the same succession stage ($p < 0.05$), while lowercase letters indicate significant differences in concentrations in the same forest origin at different succession stages ($p < 0.05$); $n = 149$, 344, 174, 102, 199 and 144 for NF−ES, NF−MS, NF−LS, PL−ES, PL−MS and PL−LS, respectively.

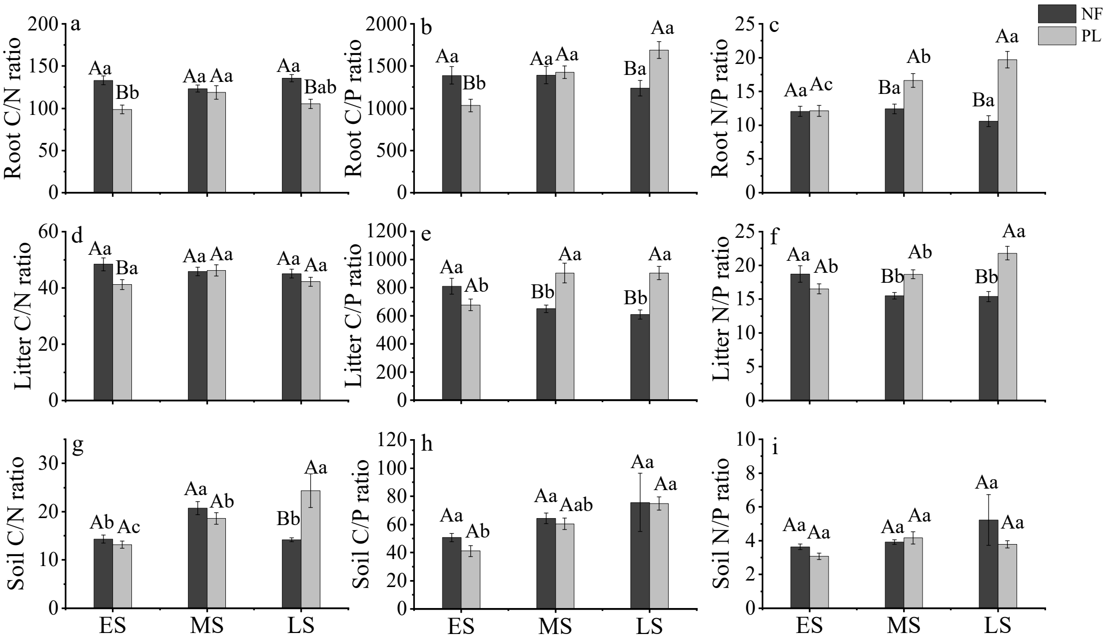

Figure 3. C, N and P stoichiometry in roots (**a**–**c**), litter (**d**–**f**) and soil (**g**–**i**) in different succession stages in NF and PL. Note: The error bars indicate standard errors of the means. Capital letters indicate significant differences in concentrations in different forest origins in the same succession stage ($p < 0.05$), while lowercase letters indicate significant differences in concentrations in the same forest origin at different succession stages ($p < 0.05$); $n = 149$, 344, 174, 102, 199 and 144 for NF−ES, NF−MS, NF−LS, PL−ES, PL−MS and PL−LS, respectively.

3.2. Relationships in C, N and P Concentrations and Ecological Stoichiometry in Roots, Litter and Soil in Different Forests

The relationships in C, N and P concentrations and in C:N, C:P and N:P ratios in root–litter–soil in NF and PL are shown in Figure 4. In NF, roots, litter and soil C concentrations were significantly positively correlated. P concentrations were significantly correlated positively in roots, litter and soil but had a strong negative influence on root N and litter N concentrations. Moreover, no clear relationship was observed between the soil N concentrations and root and litter N concentrations (Figure 4a). Roots, litter and soil C:P ratios were very positively correlated (Figure 4b). Soil C:N and N:P ratios were significantly positively correlated with soil C: P. Similar patterns were also observed in roots, litter and soil P concentrations in both PL and NF. (Figure 4c). The C:N, C:P and N:P ratios in roots and litter were significantly positively correlated. The significant positive correlations between litter and soil were linked by their C:P and N:P ratios (Figure 4d).

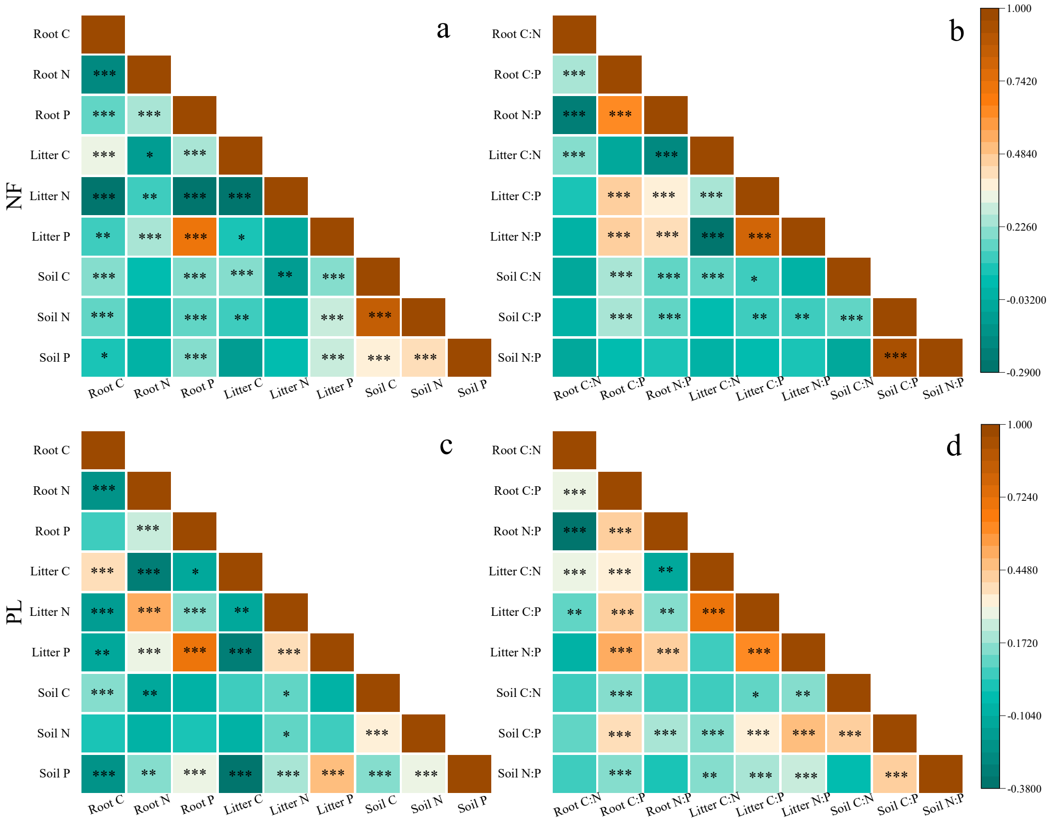

Figure 4. Pearson's correlation matrix between plant root, litter and soil C, N and P concentrations and stoichiometric ratios in NF and PL. (**a**,**b**) The correlation between the concentrations of C, N and P and the stoichiometric ratios of C:N, C:P and N:P in roots, litter and soil in NF; (**c**,**d**) the correlation between the concentrations of C, N and P and the stoichiometric ratios of C:N, C:P and N:P in roots, litter and soil in PL. * $p < 0.05$, ** $p < 0.01$,*** $p < 0.001$.

3.3. Relationships in Determinants and C, N and P Concentrations and Ecological Stoichiometry in Roots, Litter and Soil between NF and PL

C concentrations in roots, litter and soil do not significantly change with latitude, longitude, MAP, MAT or altitude in different succession stages in PL (Figures A1–A3). However, in NF, litter C concentrations were positively correlated with altitude in the ES, but were significantly negatively correlated with altitude in the MS ($p < 0.05$) and did not change with altitude in the LS (Figures A1–A3). Root and litter N concentrations were significantly positively correlated with longitude, while soil N concentrations were negatively correlated with longitude over all three succession stages ($p < 0.05$) (Figures A4–A6). MAP, MAT and altitude had completely different effects on the N concentrations in roots, litter and soil in NF and PL. Overall, MAP and MAT had positive influences on root and litter N concentrations and a negative influence on the soil N concentrations in NF in all three succession stages. By contrast, MAP was inversely correlated with root and litter N concentrations and positively correlated with soil N concentrations in PL across the three successional stages (Figures A4–A6). MAP and MAT were significantly negatively correlated with P concentrations in roots, litter and soil in both NF and PL, while latitude had positive correlations with P concentrations in litter and soil in both NF and PL (except for litter in the ES in NF) (Figures 5–7). The P concentrations of the roots were only significantly positively correlated with latitude in the MS in NF, and in both the ES and MS in PL. Furthermore, the P concentrations of the roots, litter and soil decreased markedly with longitude in both the ES and LS in NF (Figures 5 and 7) ($p < 0.05$) but did not change with longitude in the MS (Figure 6). They increased with longitude in both the ES and MS (Figures 5 and 6) ($p < 0.05$) but did not change with longitude in the LS in PL (Figure 7).

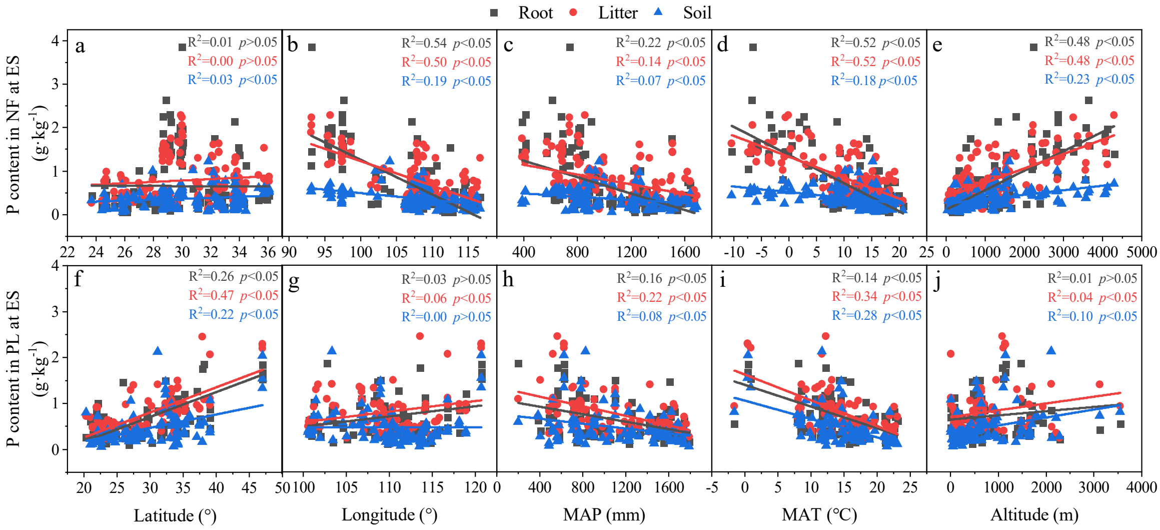

Figure 5. P concentration changes with latitude (**a**,**f**), longitude (**b**,**g**), mean annual precipitation (MAP) (**c**,**h**), mean annual temperature (MAT) (**d**,**i**) and altitude (**e**,**j**) in different forest origins in the early stage (ES). The numbers of forest sites are 149 and 102 for NF−ES and PL−ES, respectively.

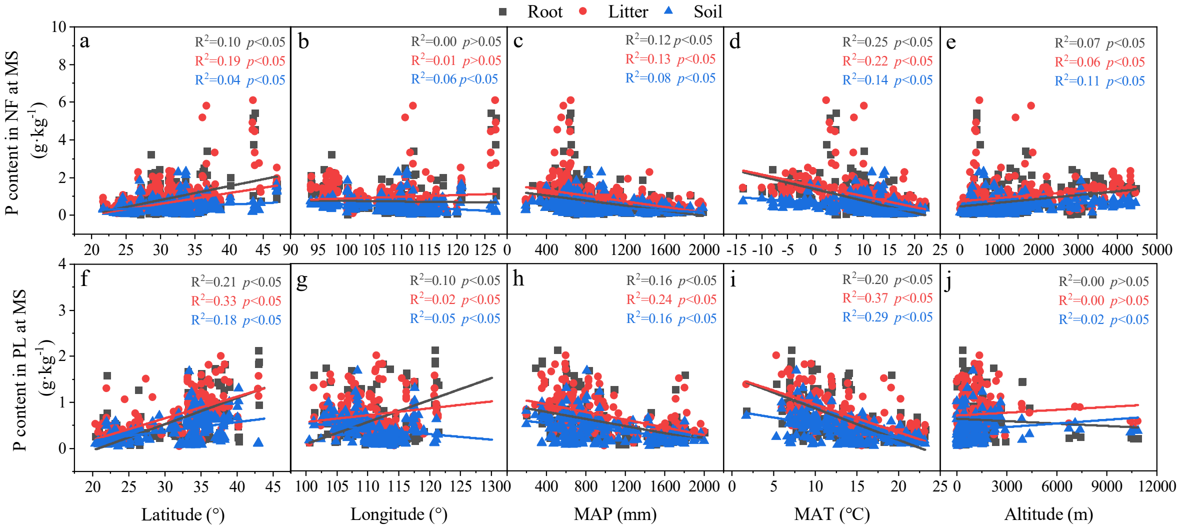

Figure 6. P concentration changes with latitude (**a**,**f**), longitude (**b**,**g**), mean annual precipitation (MAP) (**c**,**h**), mean annual temperature (MAT) (**d**,**i**) and altitude (**e**,**j**) in different forest origins in the middle stage (MS). The numbers of forest sites are 344 and 199 for NF−MS and PL−MS, respectively.

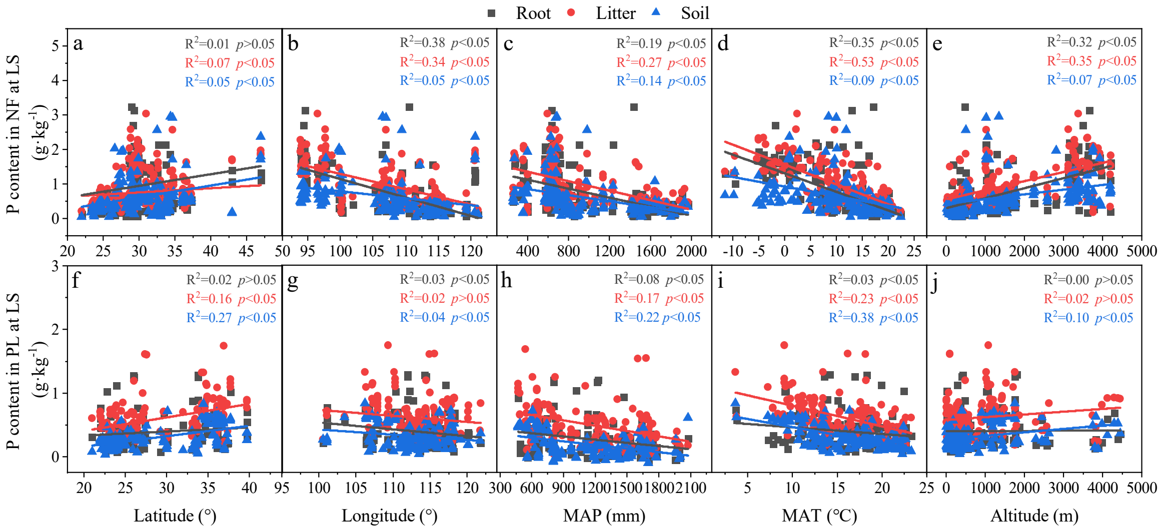

Figure 7. P concentration changes with latitude (**a**,**f**), longitude (**b**,**g**), mean annual precipitation (MAP) (**c**,**h**), mean annual temperature (MAT) (**d**,**i**) and altitude (**e**,**j**) in different forest origins in the late stage (LS). The numbers of forest sites are 114 and 144 for NF−LS and PL−LS, respectively.

4. Discussion

4.1. C, N and P Concentrations and Stoichiometry in Roots, Litter and Soil in Different Forests

Ecosystem C, N and P are transferred and recycled in plants, litter and soil [23], and play an important role in maintaining the nutrient balance in forest ecosystems. For example, litter nutrients are important inputs for soil and help sustain the growth of plants [24]. Roots are not only an organ used by plants to absorb nutrients such as N and P [25], but are also an important source of nutrients themselves. Indeed, Vogt et al. [26] found that the carbon and nutrients (N and P) returned to the soil through the turnover of fine roots exceeded the ground litter in forest ecosystems on a global scale.

Our results showed that C, N and P concentrations were closely correlated between roots, litter and soil in both NF and PL (Figure 4), and significantly differed between different forest stands in China's forest ecosystems. Root C and N concentrations in PL (451.8 g·kg^{-1} and 6.64 g·kg^{-1}) were significantly higher than those in NF (443.3 g·kg^{-1} and 4.4 g·kg^{-1}), and were also higher than the levels (417.8 g·kg^{-1} for root C, 4.87 g·kg^{-1} for root N) for China's terrestrial ecosystems reported by Tang et al. [24]. By comparison, root P concentrations in PL (0.56 g·kg^{-1}) were significantly lower than in NF (0.73 g·kg^{-1}) ($p < 0.05$), and were smaller than the average root P in fine roots (0.78 g·kg^{-1}) at a global level, as reported by Yuan et al. [27]. This may be related to the different morphological characteristics of roots and the different environment bases of the two forest stands [28,29]. Previous hypotheses have also claimed greater plant diversity with deeper roots, since more soil animals can capture and exploit P from the deeper soil [30]. Liu et al. [31] have reported for surface soil layers (0–10 cm) C (31.01 g·kg^{-1}), N (1.71 g·kg^{-1}) and P (0.39 g·kg^{-1}) concentrations in China's forests that are close to the C, N and P concentrations in the PL in our study. We found that soil C, N and P in NF were significantly higher than those in PL.

Forest restoration is the key factor affecting soil C, N and P concentrations [23]. In this study, we found that, as succession progressed, the C concentrations in roots and litter did not change significantly, while the soil C concentrations increased significantly in both NF and PL ($p < 0.05$). More specifically, the soil C concentrations were obviously higher in later successional stages in NF than in PL ($p < 0.05$). Zhou [32] have shown that old-growth forests can still accumulate carbon in soils. Our results imply that PL soils have a high C sequestration potential in China. Gu et al. [33] report that the soil physical and chemical properties change after vegetation restoration, which can be beneficial to the development of plant roots and thus to the accumulation of soil organic carbon. In addition, increases in community species richness and underground biomass may also contribute to the accumulation of soil organic carbon. N concentrations gradually increase as succession progresses, which could be attributable to nutrients released from the litter. In turn, the increase in soil N increases the soil carbon sequestration capacity of the forest [34]. However, P concentrations in roots, litter and soil significantly increase in NF as succession progresses but significantly decrease in PL. Plants have different nutrient strategies to survive and thrive in P-limited soils [35]. Previous studies have indicated that NF might obtain P from deeper layers of soil via roots and mycorrhizal fungi in the LS [22]. However, decreased P in PL might be due to its low P-retention ability, which is mainly due to the loss from erosion, harvest and the low efficiency of the P retention system. Yu et al. [22] also hypothesized that the P loss caused by horizontal (i.e., surface and subsurface runoff) and vertical (i.e., leaching into subsoils) transport played an important role in systems with low P efficiency.

C:N:P ratios are critical indicators of ecosystem processes [17]. The concentrations and stoichiometry of elements in our study between roots, litter and soil in different forest stands were highly correlated (Figure 4). From a single tissue to the entire community, a strong correlation is essential for measuring plants' responses to global change [24]. The C:N and C:P ratios of plants reflect the efficiency of a plant's use of N and P and their growth rates [4,36]. Litter C:N is also significantly correlated with the litter decomposition rate [6,37]. In our study, we found that root C:N and C:P ratios were higher than litter, both in NF and PL, which indicates that plants tend to recycle nutrients to ensure their growth and development [38]. As the succession/growth progressed, root C:P ratios significantly decreased ($p < 0.05$) in NF but significantly increased ($p < 0.05$) in PL, which also shows how a low-P soil environment can improve nutrient utilization efficiency in PL compared to NF. Plant N:P ratios have been proven to be useful for accessing the limitations of N and P on primary production of terrestrial ecosystems [12,18,39], in which a N:P ratio below 14 and above 16 can be used as indicators of N and P limitation, respectively [40]. Previous studies have also reported that China's forests are more generally limited by P than by N concentrations [31]. Here we found that both the roots and litter N:P in PL were significantly higher than NF, thereby suggesting a greater P vs. N retention capacity (e.g., retranslocation) in native than planted forests. As the succession progressed, root N:P in NF did not change significantly ($p > 0.05$) but did significantly increase from 12.12 to 19.67 in PL. Such changes indicate that P is not the limiting nutrient in the ES in PL, but, rather, gradually becomes the limiting factor as the forest grows; this also suggests that the P retention capacity is worse in PL than in NF. As well, N gradually became the limiting nutrient in the LS in NF. In general, forests are usually limited by N in the early stage of succession and will become restricted by both N and P, or by just P, in later stages, a process that is more evident in PL (as indicated by our study). Soil C:P ratios can act as indicators of the potential of microbial mineralization in soil organic matter to release P or to absorb and store environmental P [41]. In our study we found that the soil C:P ratios in PL increased significantly as the succession progressed ($p < 0.05$) but did not change significantly in NF ($p > 0.05$). Decreasing P concentrations might therefore reduce the P availability in PL, which may further inhibit microbial activity and reduce long-term C storage capacity [42,43]. Wardle et al. [44] also found that in most long-term observational studies the N:P ratio in litter rose as the age of the soil substrate increased. This indicates that there are similar degradation trends in forest ecosystems from tropical to temperate zones, which generate a decrease in soil P availability as the succession advances. In our study, trends were observed to be more intense in PL than in NF. The frequent use of fast-growing, mostly non-native trees in plantations, above all in wet tropical and subtropical areas, tends to impoverish soil nutritional quality, which is especially evident in the case of P conservation in the plant–soil system [9,10]. Native forests, on the other hand, are generally more diverse and have several adaptations for coping with limited P availability, mainly in the late successional stages when there is a greater capacity for retaining P in the plant soil system [9,18,22].

4.2. Factors Affecting C, N and P Concentrations and Their Stoichiometry in Different Succession Stages in NF and PL

Recent analyses have shown that temperature [3,12], precipitation [18,27], functional group [31] and soil and litter nutrients [18,19,45,46] are strongly correlated with plant nutrients and stoichiometry. However, most of these previous studies have focused on changes at global or regional scales using published data and did not consider forest origins. Our results show that the changes in C concentrations along latitude, longitude, MAP and altitude gradients were similar in NF and PL. Tang et al. [20] report that vegetation and litter C concentrations decreased with increasing MAT. However, our study shows that during the three stages MAT had different effects on root and litter C concentrations in NF (negative) and PL (positive). This may be because of the differences in tree species composition in forest stands [47]. Sardans and Peñuelas [48] have demonstrated that water resources are an important driving force for increasing plant nutrient-use efficiency in ecosystems, and droughts will habitually change the internal N and P cycles in terrestrial ecosystems. Precipitation decreases from the southeast to the northwest in China, a pattern that shapes the distribution of the soil water content and further limits soil nutrient availability [49]. Certain studies report that climatic factors only have a weak impact on plant N concentrations, which are mainly determined by plant functional groups [31]. Moreover, the Temperature-Plant Physiological Hypothesis also indicates that higher N and P content help enhance the metabolic activity and growth rate of plants, which offsets the low impact of temperature at high latitude by decreasing the biochemical reaction rate of N-rich enzymes and P-rich RNA in plants [3,50]. The results of our study show that latitude and longitude affect the distribution of vegetation N content through temperature and precipitation. Moreover, MAP and MAT showed opposite effects on the root and litter N content between NF and PL, while they only had a significantly effect on the soil N content in the middle and later stage of NF. These results also suggested that plant species, rather than climatic variation, was the major determinant of plant N concentrations [51].

Like previous studies [3,12,18], climatic factors (MAT and MAP) were significantly and negatively correlated with P concentrations in both NF and PL ($p < 0.05$), but were related to the strong weathering and eluviation of soil in high MAT and MAP areas [52]. As succession progressed, P concentrations in root, litter and soil increased with greater longitude in the ES and MS stages in PL, but then decreased with longitude in the LS stages. However, we found that MAT, MAP, latitude, longitude and altitude all had the same effect on P concentrations in NF and PL in the LS, which indicates that geographical and climatic factors were not the reasons for differences in P concentrations between NF and PL. Yu et al. [53] have proved that high long-term N deposition significantly reduces total soil TP concentrations but has no significant influence on total soil TN concentrations, which has thus increased the C:P and N:P ratios over the past 60 years in subtropical China. These studies provide strong evidence that China’s total soil P concentrations have been decreasing over the past few decades, which has led to P limitations and higher N:P ratios in its forest ecosystems [31]. However, our results also support the idea that, given P limitation in forest ecosystems, natural forests (NF) seem to be more able to retain P than plantations (PL), which are frequently dominated by fast-growing non-native species. The overarching reason, as pointed out by Yu et al. [22], is that natural native vegetation during succession grows, retains and accumulates P from deeper soil layers and has a greater P-retention capacity [9,18,22]. However, we found that MAT, MAP, latitude, longitude and altitude all had the same effect on P concentrations in NF and PL in the LS, thus indicating that geographical and climatic factors were not the reasons for the differences in P concentrations between NF and PL. Instead, our results strongly suggest that species composition is the main cause of the different evolution of P limitation in soil in PL and in NF.

5. Conclusions

Ecological stoichiometry in forest ecosystems were different between forest origins. In this study, we found that P concentrations significantly decreased in the litter, root and soil in plantation forests (PL) as succession/growth proceeded, while the opposite occurred in natural forests (NF). Our results indicate that NF maybe more capable as growth progresses of storing P nutrients than PL. Different plant N:P ratios in NF and in PL during the progress of succession/growth also suggests that the difference between forest origins should be considered in the future research. Our study also reveals that geographical and climatic factors were not the dominant drivers of the differences in P concentrations between NF and PL in China, although more studies are still required to confirm this finding.

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Informed Consent Statement: Informed consent was obtained from all subjects involved in the study.

Data Availability Statement: By 2022, the data will available for download at the website: http://dhf.cern.ac.cn/meta/metaData, accessed on 16 January 2021.

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Abbreviations

The following abbreviations are used in this manuscript:

C	Carbon
N	Nitrogen
P	Phosphorus
NF	Natural forests
PL	Plantation forests
ES	Early stage
MS	Middle stage
LS	Late stage
MAT	Mean annual temperature
MAP	Mean annual precipitation

Appendix A

Table A1. Tree species of each growth stages in NF and PL.

Forest Origin	*n*	Growth Stages	N	Dominant Species
NF	667	ES	149	*Quercus wutaishansea* Mary, *Populus simonii* Carr, *Betula platyphylla* Suk., *Betula albosinensis* Burk., *Quercus variabilis* Bl., *Quercus acutissima* Carruth., *Pinus tabuliformis* Carr., *Pinus massoniana* Lamb., *Quercus glandulifera* var. *brevipetiolata* Nakai, *Abies fabri* (Mast.) Craib, *Quercus semicarpifolia* Smith, *Pinus yunnanensis* Franch., *Cyclobalanopsis glauca* (Thunb.) Oerst., *Lithocarpus glaber* (Thunb.) Nakai, *Pinus densata* Mast., *Picea spinulosa* (Griff.) A. Henry, *Cunninghamia lanceolata* (Lamb.) Hook., *Abies georgei* Orr var. *smithii* (Viguie et Gaussen) Cheng et L.
		MS	344	*Fraxinus rhynchophylla* Hance, *Quercus mongolica* Fisch. ex Ledeb, *Juglans mandshurica* Maxim., *Populus davidiana* Dode, *Betula dahurica* Pall., *Quercus aliena* Bl. var. *acuteserrata* Maxim. ex Wenz., *Robinia pseudoacacia* L., *Betula platyphylla* Suk., *Quercus wutaishansea* Mary, *Pinus armandii* Franch., *Pinus tabuliformis* Carr., *Picea crassifolia* Kom., *Sabina przewalskii* Kom., *Larix gmelinii* (Rupr.) Kuzen., *Quercus acutissima* Carruth., *Acer ginnala* Maxim., *Quercus variabilis* Bl., *Juniperus formosana* Hayata, *Quercus aliena* Bl. var. *acuteserrata* Maxim. ex Wenz., *Vernicia fordii* (Hemsl.) Airy Shaw, *Populus tomentosa* Carr, *Pinus tabuliformis var. henryi* (Masters) C. T. Kuan, *Cunninghamia lanceolata* (Lamb.) Hook., *Pinus massoniana* Lamb., *Bothrocaryum controversum*, *Abies fabri* (Mast.) Craib, *Pinus yunnanensis* Franch., *Quercus semicarpifolia* Smith, *Abies georgei* Orr var. *smithii* (Viguie et Gaussen) Cheng et L., *Picea spinulosa* (Griff.) A. Henry
		LS	174	*Ulmus pumila* L., *Larix gmelinii* (Rupr.) Kuzen., *Quercus variabilis* Bl., *Cyclobalanopsis glauca* (Thunb.) Oerst., *Quercus aliena* Bl. var. *acuteserrata* Maxim. ex Wenz., *Pinus tabuliformis* Carr., *Picea crassifolia* Kom., *Pinus armandii* Franch., *Platycladus orientalis* (L.) Franco, *Quercus wutaishansea* Mary, *Betula albosinensis* Burk., *Quercus acutissima* Carruth., *Quercus aliena* Bl. var. *acuteserrata* Maxim. ex Wenz., *Pinus massoniana* Lamb., *Liquidambar formosana* Hance, *Quercus glandulifera* var. *brevipetiolata* Nakai, *Pinus yunnanensis* Franch., *Schima superba* Gardn. et Champ., *Loropetalum chinense* (R. Br.) Oliver, *Castanopsis fargesii* Franch., *Bothrocaryum controversum*, *Castanopsis sclerophylla* (Lindl.) Schott., *Cinnamomum porrectum* (Roxb.) Kosterm., *Castanopsis hystrix* J. D. Hooker et Thomson ex A. De Candolle, *Castanopsis carlesii* (Hemsl.) Hayata., *Cunninghamia lanceolata* (Lamb.) Hook., *Abies georgei* Orr, *Abies delavayi* Franch., *Abies georgei* Orr var. *smithii* (Viguie et Gaussen) Cheng et L., *Pinus densata* Mast., *Quercus semicarpifolia* Smith, *Picea spinulosa* (Griff.) A. Henry
PL	445	ES	102	*Larix gmelinii* (Rupr.) Kuzen., *Populus gansuensis* C. Wang et H. L. Yang, *Robinia pseudoacacia* L., *Platycladus orientalis* (L.) Franco, *Pinus tabuliformis* Carr., *Populus simonii* Carr, *Betula albosinensis* Burk., *Populus euramericana* cv.'I-214', *Pinus massoniana* Lamb., *Abies fabri* (Mast.) Craib, *Quercus semicarpifolia* Smith, *Cinnamomum camphora* (L.) Presl., *Pinus yunnanensis* Franch., *pinus elliottii*, *Eucalyptus robusta* Smith, *Cunninghamia lanceolata* (Lamb.) Hook., *Acacia mangium* Willd., *Schima superba* Gardn. et Champ., *E. urophylla* × *E. grandis*
		MS	199	*Larix gmelinii* (Rupr.) Kuzen., *Pinus sylvestris* var. *mongolica* Litv., *Picea asperata* Mast., *Pinus tabuliformis* Carr., *Larix gmelinii* var. *principis-rupprechtii* (Mayr) Pilger, *Robinia pseudoacacia* L., *Larix kaempferi* (Lamb.) Carr., *Pinus thunbergii* Parlatore, *Quercus acutissima* Carruth., *Styphnolobium japonicum* (L.) Schott, *Populus tomentosa* Carr, *Quercus aliena* Bl. var. *acuteserrata* Maxim. ex Wenz., *Populus tomentosa* Carr, *Quercus variabilis* Bl., *Cunninghamia lanceolata* (Lamb.) Hook., *Cupressus funebris* Endl., *Eucalyptus robusta* Smith, *Acacia mangium* Willd.
		LS	144	*Pinus tabuliformis* Carr., *Larix gmelinii* (Rupr.) Kuzen., *Populus davidiana* Dode, *Pinus densiflora* Sieb. et Zucc., *Platycladus orientalis* (L.) Franco, *Pinus thunbergii* Parlatore, *Populus simonii* Carr, *Populus cathayana* Rehd., *Populus tomentosa* Carr, *Larix kaempferi* (Lamb.) Carr., *Cunninghamia lanceolata* (Lamb.) Hook., *Pinus massoniana* Lamb., *pinus elliottii*, *Cinnamomum camphora* (L.) Presl., Quercus variabilis Bl., *Loropetalum chinense* (R. Br.) Oliver, *Acacia mangium* Willd., *Schima superba* Gardn. et Champ., *Liquidambar formosana* Hance

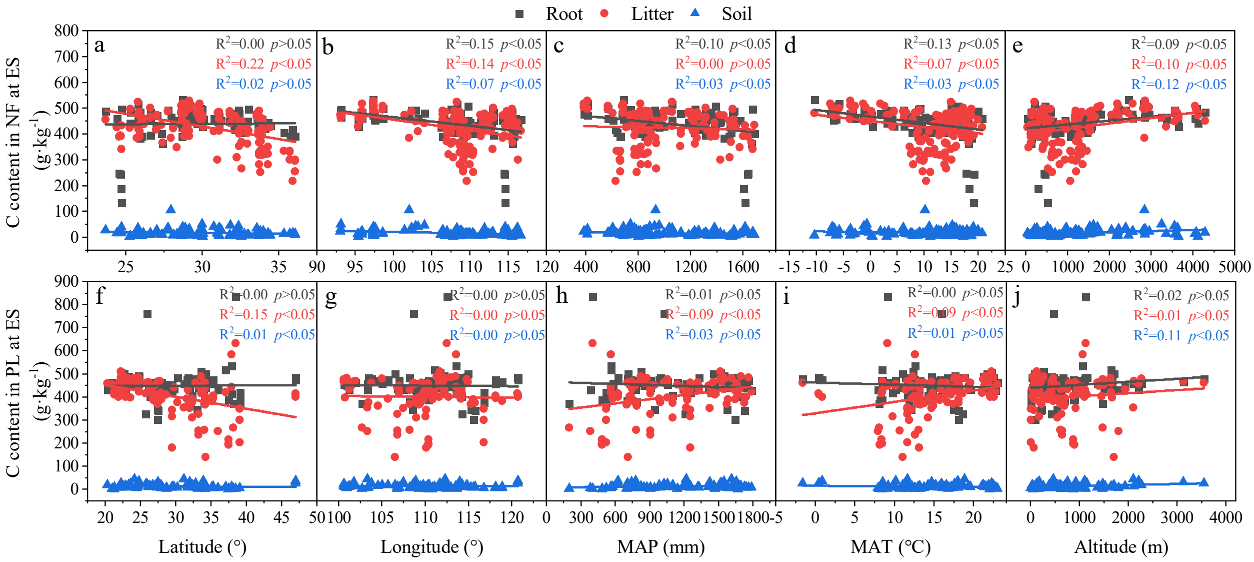

Figure A1. C content changes with latitude (**a**,**f**), longitude (**b**,**g**), mean annual precipitation (MAP) (**c**,**h**), mean annual temperature (MAT) (**d**,**i**) and altitude (**e**,**j**) in different forest origins in the early stage (ES). The number of forest sites are 149 and 102 for NF−ES and PL−ES, respectively.

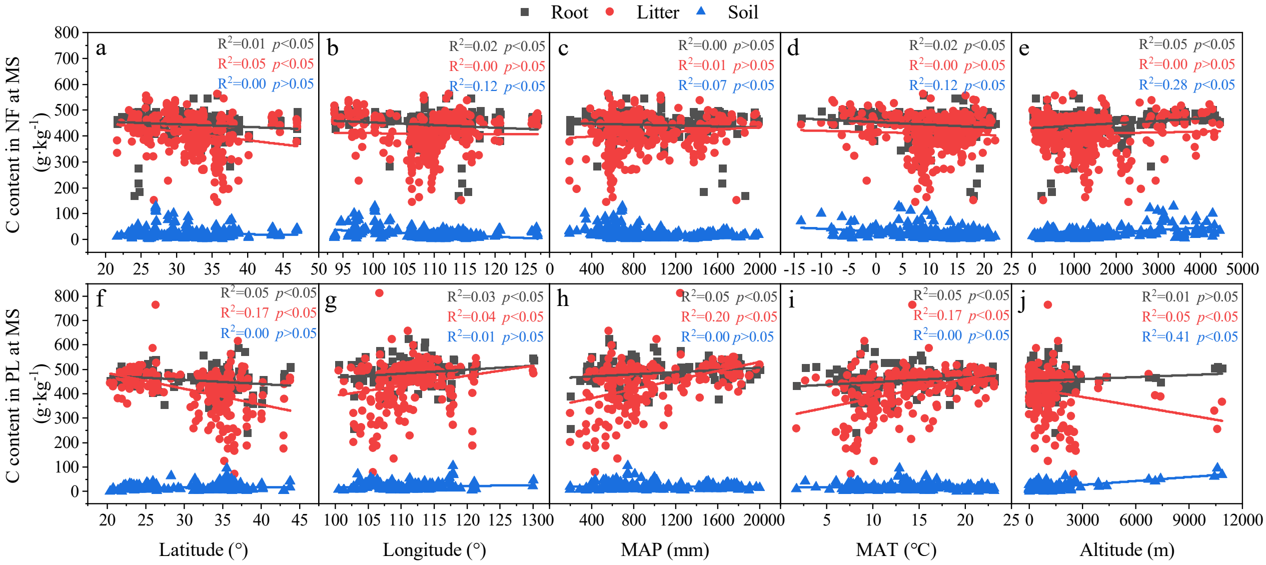

Figure A2. C content changes with latitude (**a**,**f**), longitude (**b**,**g**), mean annual precipitation (MAP) (**c**,**h**), mean annual temperature (MAT) (**d**,**i**) and altitude (**e**,**j**) in different forest origins in the middle stage (MS). The number of forest sites are 344 and 199 for NF−MS and PL−MS, respectively.

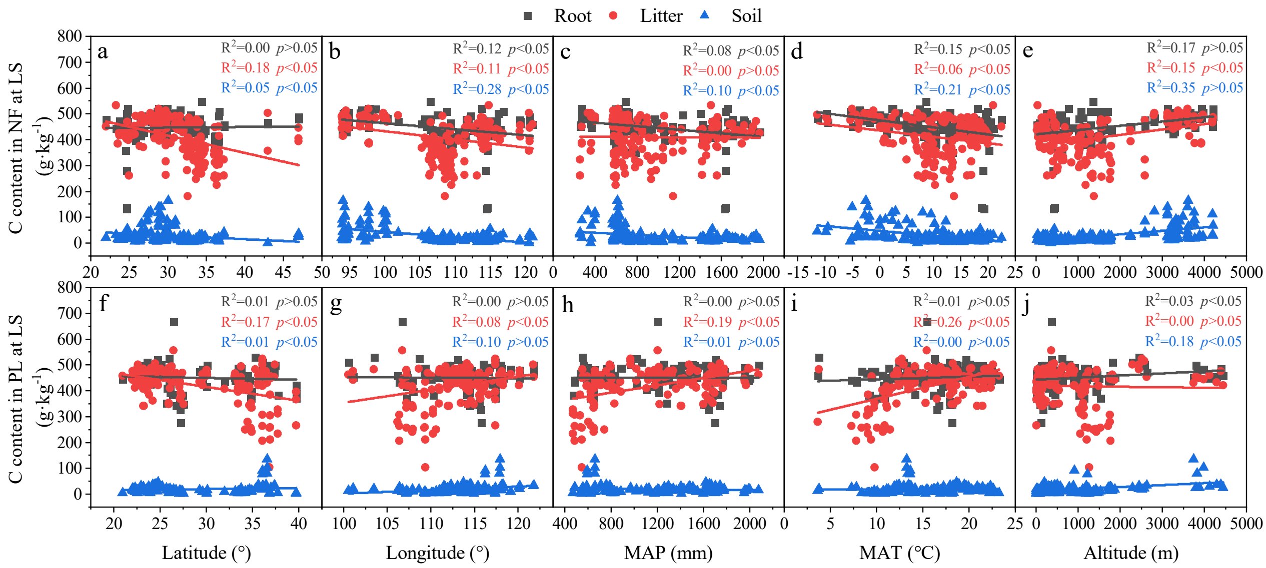

Figure A3. C content changes with latitude (**a**,**f**), longitude (**b**,**g**), mean annual precipitation (MAP) (**c**,**h**), mean annual temperature (MAT) (**d**,**i**) and altitude (**e**,**j**) in different forest origins in the late stage (LS). The number of forest sites are 114 and 144 for NF—LS and PL—LS, respectively.

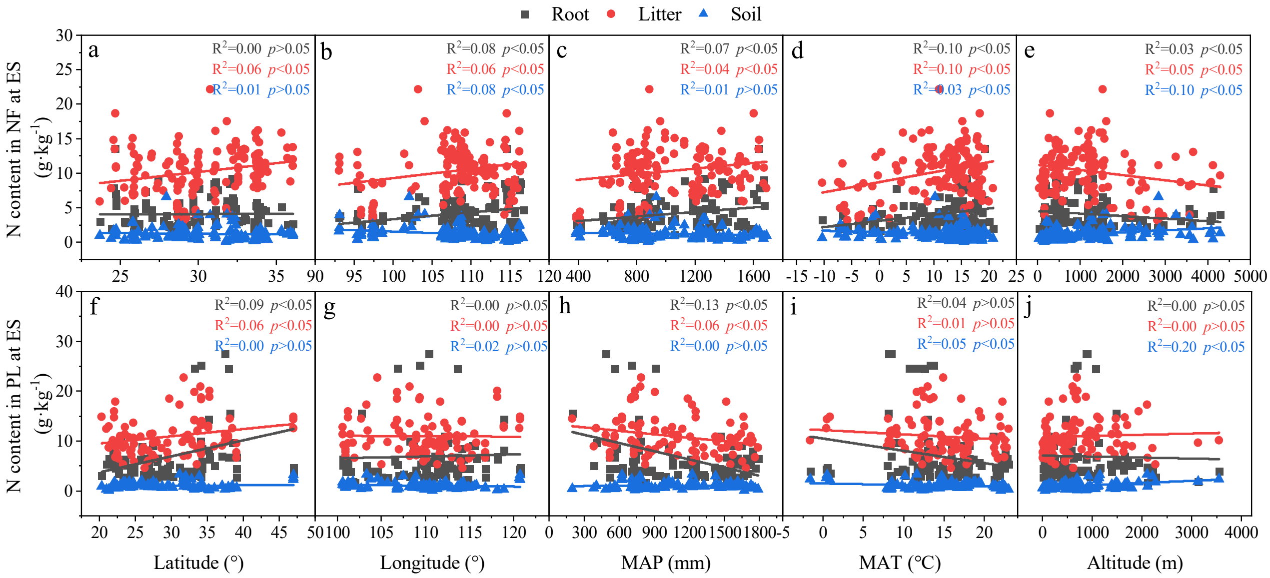

Figure A4. N content changes with latitude (**a**,**f**), longitude (**b**,**g**), mean annual precipitation (MAP) (**c**,**h**), mean annual temperature (MAT) (**d**,**i**) and altitude (**e**,**j**) in different forest origins in the early stage (ES). The number of forest sites are 149 and 102 for NF—ES and PL—ES, respectively.

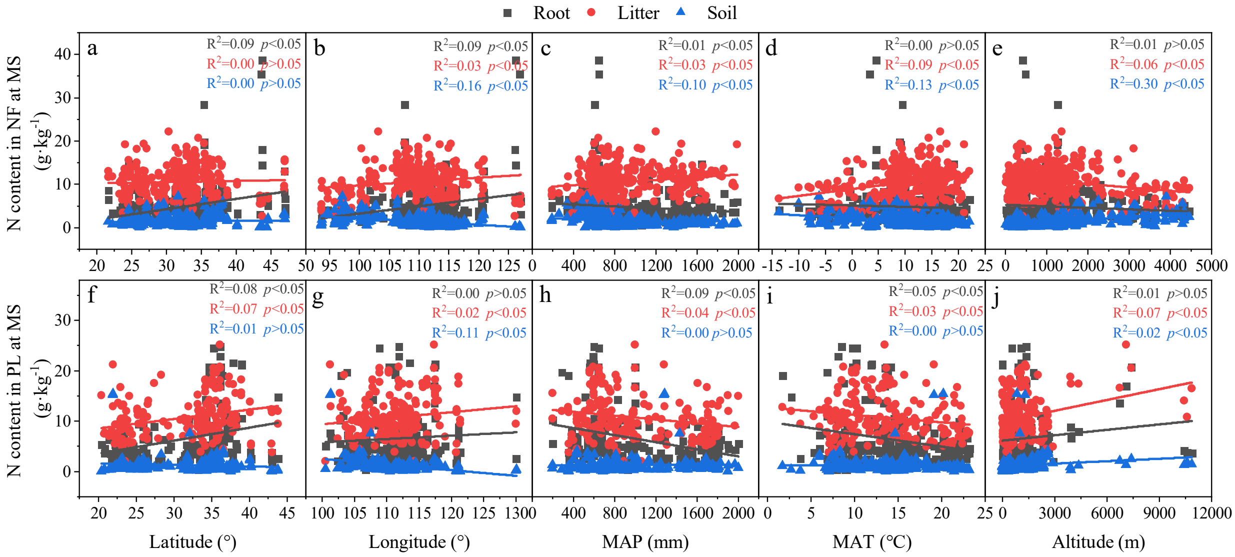

Figure A5. N content changes with latitude (**a**,**f**), longitude (**b**,**g**), mean annual precipitation (MAP) (**c**,**h**), mean annual temperature (MAT) (**d**,**i**) and altitude (**e**,**j**) in different forest origins in the middle stage (MS). The number of forest sites are 344 and 199 for NF−MS and PL−MS, respectively.

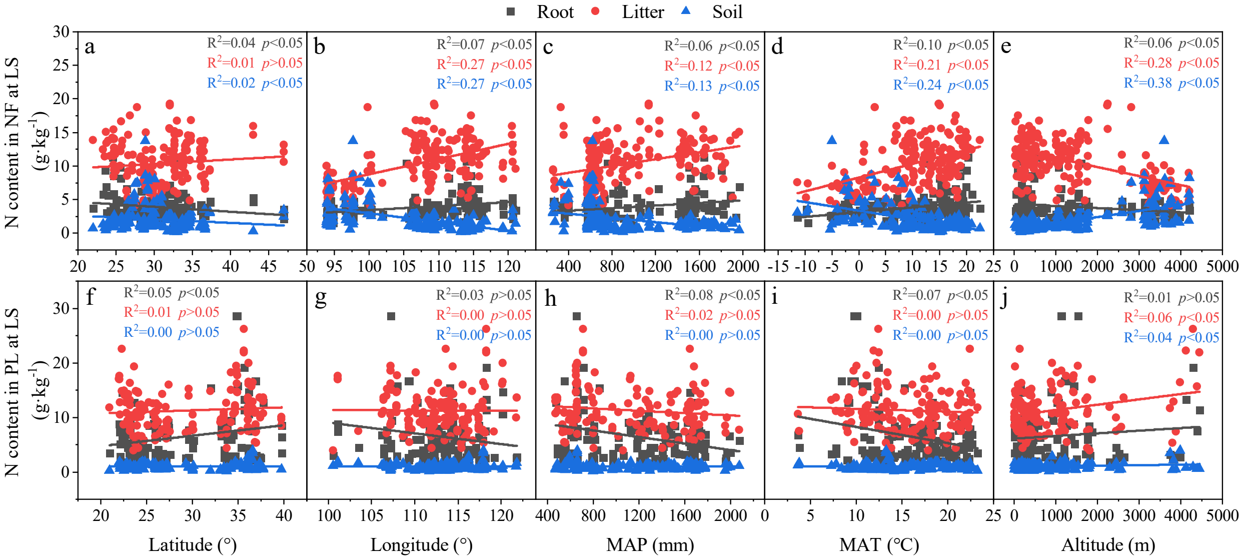

Figure A6. N content changes with latitude (**a**,**f**), longitude (**b**,**g**), mean annual precipitation (MAP) (**c**,**h**), mean annual temperature (MAT) (**d**,**i**) and altitude (**e**,**j**) in different forest origins in the late stage (LS). The number of forest sites are 114 and 144 for NF−LS and PL−LS, respectively.

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