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Global patterns and controlling factors of tree bark C:N:P stoichiometry in forest ecosystems consistent with biogeochemical niche hypothesis

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Summary

- Bark serves crucial roles in safeguarding trees physically and chemically, while also contributing to nutrient cycling and carbon sequestration. Despite its importance, the broader biogeographical patterns and the potential factors influencing bark C:N:P stoichiometry in forest ecosystems remain largely unknown.
- In this study, we compiled a comprehensive dataset comprising carbon (C), nitrogen (N), and phosphorus (P) concentrations in bark with 1240 records from 550 diverse forest sites to systematically analyze the large-scale patterns and the factors controlling bark C:N:P stoichiometry.
- The geometric means of bark C, N, and P concentrations were found to be 493.17±1.75 mg g^{-1}, 3.91±0.09 mg g^{-1}, and 0.2±0.01 mg g^{-1}, respectively. Correspondingly, the C:N, C:P, and N:P mass ratios were 135.51±8.11, 3313.19±210.16, and 19.16±0.6, respectively. Bark C:N:P stoichiometry exhibited conspicuous latitudinal trends, with the exception of N:P ratios. These patterns were primarily shaped by the significant impacts of climate, soil conditions, and plant functional groups. However, the impact of evolutionary history in shaping bark C:N:P stoichiometry outweigh climate, soil, and plant functional group, aligning with the biogeochemical niche (BN) hypothesis.
- These finding enhance our understanding of the spatial distribution of bark nutrient stoichiometry and have important implications for modelling of global forest ecosystem nutrient cycles in a changing environment.

Key words： bark, carbon, forest ecosystems, nitrogen, phosphorus, stoichiometry.

Introduction

Ecological stoichiometry refers to the balance and flow of chemical elements through biological systems and has been used to explore physiological processes of plants and other taxonomic groups and in general the functions and structure of terrestrial and aquatic ecosystems (Elser et al., 2000; Sterner & Elser, 2002; Sardans et al., 2012). Carbon (C), nitrogen (N), and phosphorous (P) are considered to be the most basic elements, which are essential for plant growth and ecosystem function (Allen & Gillooly, 2009; Marschner, 2011; Wang et al., 2022a). The stoichiometry of C, N, and P in plant organs largely reflects physiological constraints, evolutionary history, and ecological adaptation strategies (Ågren, 2004; Wang et al., 2022a; Yan et al., 2023a). Thus, evaluating C, N, and P stoichiometry patterns and their potential controlling factors at the large scales are helpful for understanding ecosystem functions and biogeochemical cycling under changing climate. The large-scale patterns of plant C:N:P stoichiometry have been widely studied from the perspective of different organs (e.g., leaf, stem, and root) at the global (McGroddy et al., 2004; Reich & Oleksyn, 2004; Yuan et al., 2011; Hu et al., 2021), national (Han et al., 2005; Tang et al., 2018; Zhang et al., 2018; Wang et al., 2019; Dynarski et al., 2023), and regional scales (Liu et al., 2010; Zhao et al., 2018; Cao et al., 2020; Xiong et al., 2022). Bark contains higher nutrient concentrations than wood per unit volume (Franceschi et al., 2005; Martin et al., 2015). However, compared to plant leaves, stems and roots, a comprehensive understanding of the patterns and potential controlling factors of C:N:P stoichiometry in the bark of diverse tree species at a broad spatial scale remains unclear.

Previous studies have showed that the C:N:P stoichiometry of plant organs may exhibit clear patterns along geographic or environmental gradients, and climate, soil, or plant functional type plays important roles in regulating the C:N:P stoichiometry of plant organs (Sardans & Peñuelas, 2014). For example, using global dataset, an empirical synthesis study showed that leaf C:N:P ratios were significantly correlated with latitude in forest ecosystem (McGroddy et al., 2004), and that temperature, precipitation, and soil nutrients influence the spatial variations of leaf C:N:P ratios (Reich & Oleksyn, 2004). Similar latitudinal patterns in C:N:P stoichiometry have also been observed in stems and roots in forest ecosystems (Yuan et al., 2011; Zhang et al., 2018; Wang et al., 2020). Climate and plant type were the dominant factors regulating spatial variations of stem and fine-root C:N:P ratios across the forest ecosystems of China. However, whether climate, soil and plant variables are the key factors influencing global bark stoichiometry is still unknown.

Bark is the outermost tissues of tree stems and branches of woody plants that can protect the living tree from cold, heat and fire (Rosell, 2016; Pausas, 2017). In addition, bark acts as a defensive barrier against herbivory and pathogens (Paine et al., 2010). For living trees, bark is here defined as all the tissues external to the vascular cambium (Esau, 1967; Rosell et al., 2014; Tuo et al., 2021). Notably, bark constitutes a significant proportion of forest biomass and plays an essential role as a carbon sink and nutrient reservoir (Rosell, 2016). In particular, the complex secondary tissue system in woody species can comprise up to 2-20% as a percent of forest biomass (Jones et al., 2019), and its associated cambium (i.e., phellogen) and living tissues (phelloderm and phloem) can store a substantial amount of nutrients (Dossa et al., 2018; Jones et al., 2019). Unfortunately, previous studies have considered stems as a single homogeneous organographic “unit”, without distinguishing between wood (xylem) and bark (or either of their component tissues). However, the available data indicate that stem tissues can differ markedly in their chemical composition as well as their structure (Dossa et al., 2016) and can therefore perform very different functions (Rosell et al., 2014). For example, the living tissues in bark often participate in photosynthesis (Pfanz et al., 2002; Cernusak & Hutley, 2011) and can have high nutrient transport rates and nutrient storage capacities (Aschan & Pfanz, 2003; Scholz et al., 2007; Rosell & Olson, 2014; Rosell et al., 2014, 2016; Ryan & Asao, 2014; Staver et al., 2020; Li et al., 2022). In light of the diverse ecological functions and chemical elements of the bark, exploring C:N:P stoichiometry in bark is crucial for improving our understanding of the evolutionary history and environmental adaptations of tree species. Furthermore, considering the absence of bark roles in global biogeochemical cycling models, making sense of bark stoichiometry could provide valuable insights and aid in parameterizing and benchmarking such models.

Recently, the biogeochemical niche (BN) hypothesis was proposed to investigate species' niche space via bio-elements (Peñuelas et al., 2019; Sardans et al., 2021; Sardans et al., 2023). The BN hypothesis states that all living organisms on earth are composed of atoms from various bioelements, which are utilized in the formation of molecules, tissues, organisms, and communities. These bioelements are required in specific quantities and proportions for an organism to survive and grow. Different species have evolved unique functions and life strategies, leading to the development of distinct structures and the adoption of specific metabolic and physiological processes. Consequently, each species is anticipated to have varying requirements for each bioelement (Peñuelas et al., 2019). The species-specific elementome and BN are founded on three fundamental complementary rules. Firstly, distinct taxonomic groups exhibit different elementomes, with larger differences as taxonomic distance and evolutionary time increase. Secondly, at equilibrium, coexisting species typically possess distinct elementomes to minimize competitive pressure. Thirdly, trade-offs between adaptation to a stable environment for competition and success in more fluctuating environments result in variations in homeostasis and plasticity among species along a continuum of strategies. Recently, it has been shown that the evolutionary history has greater effect on foliar elements (Vallicrosa et al., 2022a, b) and photosynthetic traits (Yan et al., 2023b) than environment factors (i.e., climate and soil). However, the genetic legacy effects on bark elemental composition remain unknown.

In this study, we compiled a large comprehensive world-wide dataset of bark C, N, and P concentrations for tree species from peer-reviewed studies to explore the patterns and potential controlling factors of bark C:N:P stoichiometry. The main objectives were to (1) reveal the bark C, N, and P concentrations and C:N:P ratios in different plant functional groups, (2) explore the latitudinal patterns of bark C:N:P ratios, (3) identify the relative contributions of climate, soil, and plant functional groups on bark C:N:P ratios; and (4) verify whether bark C:N:P stoichiometry is consistent with the BN hypothesis. This research endeavors to bridge existing knowledge gaps concerning bark C:N:P stoichiometry worldwide, enhancing our comprehension of forest stoichiometry and the pivotal role of bark in biogeochemical cycle.

2. Materials and Methods

2.1 Data collection

We compiled a global database of bark C, N, and P concentrations for tree species from the published literatures by means of Web of Science (http://apps.webofknowledge.com), Google Scholar (http://scholar.google.com), and National Knowledge Infrastructure Database (http://cnki.net). Combinations of keywords such as “bark”, “elements”, “stoichiometry”, “carbon”, “nitrogen”, and “phosphorous” were used to search studies published from 1980 to 2022. The data were extracted from the tables, figures, and appendices. GetData Graph Digitizer v2.26

software (http://getdata-graph-digitizer.com) was used to extract the data from figures when data were only presented graphically. Published data were included in data set using four stringent criteria: (1) the studies included C, N, and P concentrations of bark for tree species, (2) the bark were all tissues outside of the vascular cambium (including the phloem), (3) the collected data must include species names and detailed site information (longitude and latitude), and (4) we excluded data from fertilized or polluted sites, or from plants grown in greenhouses to avoid misattributing natural nutrient limitations due to anthropogenic impacts. These resources are also available as part of the AusTraits database (Falster et al., 2021). In total, our database contained 655 observations from bark C concentration and 1240 observations from bark N and P concentrations for a total 324 tree species spanning 550 independent sampling sites worldwide (Fig. S1; A list of the literature sources can be found in the supporting information). All species were classified into two plant functional groups (broad leaved versus needle leaved species, and evergreen versus deciduous species) based on the descriptions from published literature.

We retrieved climate variables, and soil properties for each site based on coordination information if the data were missed in the original literatures. Specifically, climatic variables including mean annual temperature (MAT), mean annual precipitation (MAP), solar radiation (SR), and water vapor pressure (WVP) at each site were obtained from WorldClim data website (www.worldclim.org) with a resolution of 1 km × 1 km. Aridity index (AI) was obtained from the global map of Global Aridity Index (Global-Aridity_ET0) and Global Reference Evapo-Transpiration (Global-ET0) datasets with a resolution of 1 km × 1 km (Trabucco & Zomer, 2018) (https://csidotinfo.wordpress.com/). Soil properties including soil organic carbon (SOC), total nitrogen (STN), total phosphorus (STP), pH, and soil texture (ST: silt +

clay) were extracted from SoilGrids-global gridded soil information at a spatial resolution of 1 km × 1 km at 0-15cm of depth (https://soilgrids.org/). The source and detail information of all the variables used in this study were listed in Table S1.

2.2 Statistical analysis

Because the frequency distributions of bark C, N, and P concentrations and C:N:P ratios were highly skewed (Fig. S2), we calculated geometric means and compared their geometric means among different plant functional groups using One-way ANOVA with the Student's t test. Then, the biogeographical patterns of bark C, N, and P concentrations and C:N:P ratios were mapped at a global scale (Fig. 1). Ordinary least squares (OLS) regressions were used to explore latitudinal patterns of bark C, N, and P concentrations and C:N:P ratios at a global scale. The Pearson correlation matrix was used to analyze the relationships of bark C, N, and P concentrations and C:N:P ratios with climatic and edaphic variables (Fig. S3).

To quantify the relative importance of climate (MAT, MAP, and SR), soil (SOC, STN, STP, pH and ST) and plant functional groups (broad leaved versus needle leaved species; and evergreen versus deciduous species) on bark C, N, and P concentrations and their mass ratios, we used the machine learning technique “random forest models” using the “randomForest” packages of R software (Breiman, 2001; Hapfelmeier et al., 2014). To avoid the multicollinearity among the independent variables, we conducted the variable clustering in the “Hmisc” package of R software before performing the random forest model. Specifically, for highly correlated variables (pearson’s $r^2 > 0.6$), only one of them was kept in subsequent analysis. For example, MAP & AI, MAT & WVP have high correlations, respectively (Fig. S4), MAP and MAT were retained in the subsequent analysis, with the removal of AI and WVP. To further determine the relative importance of all variables, we calculated the values of increased mean squared errors for each potential predictor in our constructed random-forest models using the “rfPermute” R package (Archer, 2021). The values were further transformed into relative importance (%) to facilitate interpretation (Fig. 4). Similarly, the significance of each predictor on the response variables was assessed using the “rfPermute” R package.

To estimate the effect of phylogenetic structure on bark C, N, and P concentrations and their mass ratios of these species, we first constructed a phylogenetic tree for all recorded species in this study by using the “V. phylomaker” package (Jin & Qian, 2019) in R. Then, the parametric Blomberg’s K (Blomberg et al., 2003) and Pagel’s λ indices (Pagel, 1999) were used to assess the strength of phylogenetic signals for bark C, N, and P concentrations and their mass ratios. Parametric indices based on evolutionary models, like Blomberg’s K and Pagel’s λ, tend to be close to zero when trait evolution is random. The R package “ape”, “picante” and “phytools” were used in this analysis (Kembel et al., 2010; Revell, 2012; Paradis & Schliep, 2019).

Bayesian phylogenetic linear mixed models were used to assess the relative contributions of environmental drivers and evolutionary history (i.e., phylogeny and species) to bark C, N, and P concentrations and their mass ratios. The climate (i.e., MAT, MAP, and SR) and soil variables (i.e., SOC, STN, STP, pH, ST) were set as independent variables (the fixed effects), with phylogeny and species set as random variables. If the relative weight of legacy effects (phylogeny and species) exceeds that of environmental factors (climate and soil), this would support the BN hypothesis. Phylogeny represents the long-term implications of evolutionary history, while species reflect interspecific variability that is independent of shared ancestry. This variability includes effects from recent epigenetic evolutionary mechanisms, as well as recent convergence and divergence in evolutionary processes among species that are closely related within phylogenetic clades (Peñuelas et al. 2019; Sardans et al. 2021, 2023; Yan et al., 2023b).

To conduct this analysis, we employed the "MCMCglmm" R package (Hadfield, 2010). All statistical analyses were performed using R version 4.2.2 (R Core Team, 2022).

3. Results

3.1 Variations in bark C, N, and P stoichiometry

Across global tree species, the geometric means of bark C, N, and P concentrations were 493.17±1.75 mg g^{-1}, 3.91±0.09 mg g^{-1}, and 0.2±0.01 mg g^{-1}, respectively. Those of bark C:N, C:P, and N:P ratios were estimated to be 135.51±8.11, 3313.19±210.16, and 19.16±0.60, respectively (Table S2). Bark C, N, and P concentrations and C:N:P ratios varied markedly across different plant functional groups. The bark C concentration, C:N and C:P ratios of needle leaved species were significant higher than in broad leaved species, whereas broad leaved species showed the higher N and P concentrations than in needle leaved species. However, the bark N:P ratio of needle leaved and broad leaved species did not show a significant difference. For deciduous species, C concentration, C:N and C:P ratios were significant lower than those of evergreen species, whereas the bark N and P concentrations in deciduous species were higher than those in evergreen species. Meanwhile, evergreen and deciduous species showed no significant differences in bark N:P ratio (Table S2; Fig. 2).

3.2 Changes in bark C, N, and P stoichiometry along latitudinal gradients

Bark C, N and P concentrations and their mass ratios exhibited significant latitudinal trends, except for N:P ratio (Fig. 3). The bark C concentration, C:N and C:P ratios significantly increased with increasing latitude, whereas bark N and P concentrations decreased with increasing latitude ($P < 0.001$). However, no clear trend was observed for bark N:P ratio with latitude ($P = 0.094$). Bark C concentration was negatively correlated with all climate factors (MAT, MAP, and SR), but only positively correlated with some of soil factors (STP and pH). Bark N and P concentrations increased significantly with the increase in MAP, STP, and ST, but decreased with SR, STN, and pH. Besides, bark C:N, C:P and N:P ratios decreased with increasing SOC and ST, whereas SR and pH displayed the opposite trends (Fig. S3).

3.3 The relative effects of climate, soil, and plant functional group on bark C:N:P stoichiometry

The results of the better fitted random forest models demonstrated that climate, soil and plant functional group variables collectively influence bark C, N, and P concentrations and their mass ratios, and the explanatory power of random forest models were more than 50% of the total variance for bark C:N:P stoichiometry (Fig. 4). Plant functional groups had the strong influence in bark C, N, P concentrations, C:N and C:P ratios (Fig. 4A-E), whereas SR was the key factor in determining the bark N:P ratio (Fig. 4F). The total relative contributions of plant functional groups to bark C concentration and C:N ratio were 38.61% and 39.99%, respectively, overriding those contribution of climate and soil variables, whereas the relative contribution of soil variables to bark N (43.11%) and P (44.06%) concentrations and C:N (36.67%) and N:P (51.03%) ratios were much higher than climate and plant functional groups.

3.4 The effects of phylogenetic signals and evolutionary history on bark C:N:P stoichiometry

Two phylogenetic parametric indices Blomberg's K (range from 0.06 to 0.18) and Pagel's λ (range from 0.40 to 0.70) were significant ($p < 0.01$) for bark C, N, and P concentrations and their mass ratios with the exception of Blomberg's K value for bark C concentration (Table S3), indicating that the bark stoichiometry was strongly constrained by phylogeny.

From the results of the Bayesian phylogenetic linear mixed model, we found that evolutionary history (indicated by phylogeny and species) has the largest effect on bark

C, N, and P concentrations and C:N:P ratios compared to current environmental factors (climate and soil) (Table 1). Specifically, in a general view of bark C:N:P stoichiometry, evolutionary history (indicated by phylogeny and species) explained between 54-85% of the total variance, whereas current environmental factors explained only 5-14% of total variance. In addition, environmental factors played different roles in influencing bark C:N:P stoichiometry. Namely, STP had a significant effect on bark C; MAT and STN had significant effects on bark N; MAT, MAP, SR, STN, and ST have significant effects on bark P; MAP and SR had significant effects on bark C:N ratio; MAP, SR and STN had significant effects on bark C:P ratio, whereas MAT, SR, STN, STP, and ST had significant effects on bark N:P ratio (Table 1).

4. Discussion

4.1 The variation of bark C, N, and P stoichiometry in forest ecosystems

This study presents the first report about global bark C, N, and P stoichiometry in tree species across plant functional groups. The bark C concentration of tree species in our study is higher than the C concentration of previously reported leaf, twig, and root, whereas N and P concentrations are lower than that in the global leaf, twig, and root dataset at national and global scales (Table 2). This result was consistent with the observed carbon accumulation with the tree growth (Rosell et al., 2014, 2015; Dossa et al., 2018). Throughout the ontogeny of tree species, the bark undergoes potentially dramatic changes, including maturation of thin-walled parenchyma cells into thick-walled sclerotia cells and accumulation of fragmented phloem (Srivastava, 1964; Rosell et al., 2015). These processes are accompanied by changes in bark density, thickness, and water content, which may favor the carbon storage per unit of dry biomass via the accumulation of dense wall material (Rosell et al., 2015; Rosell et al., 2017), supporting the notion that the proportions of galactose, mannose and starch are higher in bark than in wood (Romero, 2014).

Moreover, bark in this study encompasses both the outer bark and the inner bark, each playing distinct roles throughout a tree’s lifetime (Dossa et al., 2018). The outer bark in living trees serves to protect the underlying tissue from fire (Pausas, 2017), herbivory, and pathogens (Paine et al., 2010). Conversely, the inner bark plays a crucial role in water storage and the transportation of organic compounds, particularly those involved in photosynthesis (Ryan & Asao, 2014; Rosell et al., 2023). Consequently, the outer bark requires a higher accumulation of carbonaceous material to fulfill its protective function, while the inner bark, akin to other active organs, exhibits high levels of N and P concentrations to support plant growth and metabolic demands. However, due to the diluting effect of the outer bark, N and P concentrations throughout the bark were lower compared to other organs (Table 2).

The bark C:N:P ratios were higher than those of other plant organs such as leaves, twigs, and roots reported by previous studies (Table 2). This result could be explained by higher C concentration and lower N and P concentrations in bark. Plant N:P ratios are considered to be reliable indicators of the relative nutrient limitations of N and P in terrestrial ecosystems (Koerselman & Meuleman, 1996; Güsewell, 2004; Elser et al., 2010). Generally, leaf N:P ratio less than 14 tends to indicate N limitation, whereas N:P ratio greater than 16 frequently indicates P limitation (Aerts & Chapin, 2000). The higher bark N:P ratio (19.16±0.60) in our study can be interpreted to indicate that tree species tend to be more limited by P than by N, which is consistent with the previous studies with leaves (Reich & Oleksyn, 2004; Wang et al., 2022b). However, given the uncertainty of the N:P ratio as a threshold for plant nutrient limitation (Yan et al., 2017) and the divergence in nutrient use strategies of tree species from different locations (Sardans et al., 2016), whether the bark N:P can indicate N and P limitation of tree species still needs to be discussed.

The bark C, N, and P concentrations and C:N:P ratios differed across different plant functional groups, supporting the interpretation that bark nutrients can be highly variable across species (Cornwell et al., 2009; Jones et al., 2019). One possible reason was that bark in this study contains phloem, the great variation in volume and proportion of the outer bark also caused great differences in the chemical elements of the bark. Our results indicate that the bark C concentration is higher in needle leaved species than that in broad leaved species, consistent with a previous study suggesting that gymnosperms often have thicker outer bark than angiosperms (Rosell et al., 2017). Needle leaved species frequently grown in cold areas with harsh environment, the bark of these species maybe increase protection (more C accumulation) to resistant low temperature (Reich, 2014; Augusto et al., 2015). In contrast, the bark N and P concentrations are higher in broad leaved than needle leaved species, supporting the notion that short-lived, fast-growing species tend to have higher N and P concentrations and lower N:P ratio than those of short-lived, slow-growing species, which have lower N and P concentrations and higher N:P ratio (Güsewell, 2004; Wang et al., 2022b). Moreover, higher bark C:N and C:P ratios were observed in needle leaved species, providing additional evidence that species with thicker bark, which is of lower density, tended to have lower P concentrations (Richardson et al., 2015; Jones et al., 2019; Rosell et al., 2023).

In comparison to deciduous trees, higher concentration of bark C but lower concentrations of N and P were observed in evergreen species. We speculate that the possible reasons for this result is that this result may be attributed to the bark of evergreen trees typically being smooth, and relatively thin, but dense, resulting in a higher concentration of C. In contrast, the bark of deciduous trees may exhibit a rougher or cracked texture, aiding in trunk expansion during growth, thus leading to the lower C concentration. Additionally, to facilitate rapid expansion during the shorter growing season, the bark of deciduous trees may contain higher concentrations of N and P to meet elevated metabolic demands. However, bark characteristics may vary among individuals of the same tree species, and different tree species may exhibit similar bark characteristics (Rosell, 2016). Therefore, further investigation into the variation in bark stoichiometry across different plant functional groups is warranted in future studies.

4.2 Latitudinal patterns of bark C, N, and P stoichiometry in forest ecosystems

Significant latitudinal patterns were observed in bark C, N, and P stoichiometry across global forest ecosystems, except for N:P ratio (Fig. 3). However, these results were inconsistent with the findings of leaves from whole terrestrial (Reich & Oleksyn, 2004), global forest (McGroddy et al., 2004) and coastal wetland ecosystems (Hu et al., 2021). The differences between our results and the results of leaves in previous studies might be related mainly to the divergences of functions in distinct plant organs. Specifically, based on the temperature plant physiology and the soil substrate age hypothesis, Reich & Oleksyn (2004) proposed that plant leaves need to accumulate higher N and P concentration to increase metabolism rate to adjust to short growing seasons in higher latitudinal regions. While outer bark needs to increase its protective properties by accumulating secondary metabolites (mainly C), rather than increasing N and P concentrations to enhance the metabolic capacity.

The latitudinal patterns observed in bark C:N:P stoichiometry are clearly influenced by environmental factors. Climate and soil variables exhibited significant correlations with bark C, N, and P concentrations and C:N:P ratios. Evidences have indicated that climate variables are the most important factors that can drive vegetation distribution, community structure and physiological metabolism to affect C:N:P stoichiometry of different plant organs at species and community level (Wright et al., 2001; Reich, 2005; Wang et al., 2020), despite these studies have been not taken into account the legacy effects. Moreover, soil physical and chemical properties also have significant correlations to bark C, N, and P concentrations and C:N:P ratios in this study. This is probably because soil conditions may influence the nutrient uptake and acquisition and then affect plant C:N:P stoichiometry (Wang et al., 2020).

4.3 The driving factors of bark C, N, and P stoichiometry in forest ecosystems

As shown in the results of random forest model, climate, soil, and plant functional group collectively influence the bark C, N, and P concentrations and their mass ratios (Fig. 4). It is known that climate drives plant distributions and community structures (Hu et al., 2021) and alter soil nutrient availability (Wang et al., 2020), resulting in the changes in bark C:N:P stoichiometry. We also found that plant functional groups were very significant in determining bark C, N, P concentrations, C:N and C:P ratios. Plant functional groups are not only regulated by external environmental factors but also controlled by the internal vegetation attributes (Valverde-barrantes et al., 2017). These results are in line with species composition hypothesis proposed by Reich & Oleksyn (2004), suggesting that plant species was one of the most important factors regulating the variations of plant C:N:P stoichiometry. However, due to limitations in explanatory variables, we still need to further explore more potential factors (e.g., topography, microclimate, warming, N deposition, and fire) that have an impact on bark C:N:P stoichiometry.

In addition, compared to climate, soil, and plant functional group, evolutionary history had an important role in explaining global bark C:N:P stoichiometry evident from the obtained results from phylogenetic signal and Bayesian phylogenetic linear mixed model analyses. First, the significant phylogenetic signals existed for bark C, N, and P concentrations and their mass ratios (Fig. S5; Table S3), consistent with the observations in leaves and fine roots (Wang et al., 2022b; You et al., 2023). Second, the results of the Bayesian phylogenetic linear mixed model indicated that legacy factors (phylogeny and species) have higher relative weight over environmental factors in explaining bark C:N:P stoichiometry (Table 1). Phylogeny reflects long-term evolutionary processes including ancient adaptation and differentiation, whereas species is related to more recent environmental selections and phenotypic changes that are not directly detectable by phylogenetic information such as epigenetic and divergent and convergent evolution processes (Sardans et al., 2021; Yan et al., 2023b). Previous studies of multi-elemental concentrations and photosynthetic traits have also consistently shown that evolutionary history plays a dominant role in explaining large-scale variation in various leaf traits (Sardans et al., 2021, 2023; Vallicrosa et al., 2022a,b; Yan et al., 2023b). Our results reveal the phylogenetic relatedness of bark C:N:P stoichiometry at global scales, suggesting that bark stoichiometry is mainly regulated by long-term evolutionary processes, and thus it has singular values for each species/genotype, consistently with the BN hypothesis (Peñuelas et al., 2019; Sardans et al., 2021). Additionally, it is worth noting that the explanatory strength and significance of fixed current environmental variables were very different for bark C, N, and P and their mass ratios in Bayesian phylogenetic linear mixed model analysis (Table 1). This is attributed to that various plant organs have different elemental requirements, and the assimilation of these elements is influenced by different environmental factors (Wang et al., 2020).

5. Limitations and implications

While the present study offers valuable insights into the global patterns and controlling factors of bark C:N:P stoichiometry in tree species, it is essential to acknowledge three main limitations. Firstly, in this study ‘bark’ encompasses all tissues outside the vascular cambium and is regarded as a homogeneous tissue (Dossa et al., 2018). However, bark typically consists of two distinct parts: the inner bark (e.g., successive periderms), responsible for photosynthate transport and storage, and the outer bark (e.g., secondary cortex), which primarily provides physical and chemical protection (Rosell, 2016). These two components have significant differences in morphological characteristics, physical properties, and chemical composition, and perform entirely different functions (Rosell et al., 2014; Rosell, 2016). A prior study has pointed out that the outer bark has relatively lower nutrients than that in the inner bark, and their findings only focused on N and P stoichiometry of the inner bark and sapwood, but do not considered the outer bark (Rosell et al., 2023). Therefore, expanded dataset on the inner and outer bark globally are warranted to provide more evidence for the effects of climate and evolutionary history on shaping bark C:N:P stoichiometry in various tree species. Secondly, due to limited data from the Southern Hemisphere (i.e., Southern Africa, South America, and Southeast Asia), our understanding of the patterns and drivers of bark C:N:P stoichiometry at a global scale remains restricted. Consequently, future research in these crucial regions is warranted and necessitates further investigation. Thirdly, the study's limited inclusion of soil and climate explanatory variables may hinder the identification of additional potential factors (e.g., topography and microclimate) influencing bark C:N:P stoichiometry. Thus, further research is needed to elucidate the underlying mechanisms governing the dynamics of bark C:N:P stoichiometry under changing environments. Additionally, while all bark element data in our study are collected from natural conditions, it is important to test the responses of bark C:N:P stoichiometry to global change factors (e.g., fire, precipitation change, CO_2 enrichment, and N deposition).

To the best of our knowledge, this study represents the first comprehensive exploration of bark C:N:P stoichiometry in tree species at a global scale. Despite several limitations, this study holds significant implications for our understanding of ecological C:N:P stoichiometry and for modeling nutrient cycling in global forest ecosystems under changing environments. Firstly, as bark constitutes 2-20% of woody plant biomass in forests and represents significant N and P pools (Jones et al., 2019; Rosell, 2019), our results will enhance the evaluation of bark's contribution to forest C storage, nutrient turnover, and biogeochemical cycles at a global scale. Secondly, since bark contains more nutrients than wood and serves as a high-quality substrate for decomposers (Dossa et al., 2018), our study may also enhance predictive models of bark decomposition in response to environmental changes.

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Competing interests

None declared.

Author contributions

ZW and JP conceived and designed the research. HG, ZW and HH collected the data. HG performed the analyses. HG, ZW, JS, HH, ZY and JP interpreted the results. ZW and HG wrote the first draft of the manuscript. All authors contributed to the final version of the manuscript.

Data availability

Any data that support the findings of this study are included within the article. The list of references for dataset is publicly available and can be accessed in the appendix.

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Table 1 Summary of the Bayesian phylogenetic linear mixed model of bark C, N, and P concentrations and their mass ratios.

Bayesian model	**The statistics of fixed variables**						**Model statistics**
	Variable	**Post.mean**	**Lower 95% CI**	**Upper 96% CI**	**Eff.samp**	**pMCMC**	
Bark C ~ MAT + MAP + SR + STN + STP + pH + ST + (random = phylogeny + species)	MAT	-0.16	-0.34	0.02	1700	0.09	$R_m^2 \approx 0.12$ $R_c^2 \approx 0.79$ $R_p^2 \approx 0.47$ $R_s^2 \approx 0.19$
	MAP	-0.04	-0.18	0.10	2030	0.59	
	SR	0.04	-0.14	0.25	1700	0.69	
	STN	0.04	-0.05	0.14	1700	0.40	
	STP	-0.11	-0.20	-0.03	1700	**0.01**	
	pH	0.07	-0.07	0.23	1573	0.37	
	ST	-0.40	-0.54	-0.25	1332	**<0.001**	
Bark N~ MAT + MAP + SR + STN + STP + pH + ST + (random = phylogeny + species)	MAT	-0.03	-0.13	0.07	1700	0.56	$R_m^2 \approx 0.06$ $R_c^2 \approx 0.75$ $R_p^2 \approx 0.41$ $R_s^2 \approx 0.28$
	MAP	0.31	0.20	0.42	1700	**<0.001**	
	SR	-0.05	-0.14	0.04	1700	0.24	
	STN	-0.07	-0.13	-0.01	1700	**0.02**	
	STP	0.06	-0.01	0.13	1700	0.11	
	pH	0.09	-0.03	0.21	2059	0.15	
	ST	-0.04	-0.13	0.04	1432	0.31	
Bark P ~ MAT + MAP + SR + STN + STP + pH + ST + (random = phylogeny + species)	MAT	-0.25	-0.33	-0.15	948	**<0.001**	$R_m^2 \approx 0.13$ $R_c^2 \approx 0.73$ $R_p^2 \approx 0.26$ $R_s^2 \approx 0.33$
	MAP	0.21	0.12	0.31	1027	**0.001**	
	SR	-0.16	-0.24	-0.08	1700	**<0.001**	
	STN	-0.14	-0.20	-0.09	1700	**<0.001**	
	STP	-0.04	-0.10	0.02	1579	0.21	
	pH	0.04	-0.06	0.16	1700	0.42	
	ST	0.14	0.06	0.21	1378	**<0.001**	
Bark C:N ~ MAT + MAP + SR + STN + STP + pH + ST +	MAT	0.00	-0.17	0.17	1700	0.95	$R_m^2 \approx 0.13$
	MAP	-0.33	-0.47	-0.17	1700	**<0.001**	$R_c^2 \approx 0.89$
	SR	-0.27	-0.47	-0.05	1700	**0.01**	$R_p^2 \approx 0.56$
	STN	0.02	-0.06	0.11	1831	0.64	$R_s^2 \approx 0.20$

(random = phylogeny + species)	STP	-0.05	-0.13	0.03	1700	0.28	
	pH	-0.13	-0.25	0.02	1518	0.08	
	ST	0.17	0.03	0.32	1700	**0.02**	
Bark C:P ~ MAT + MAP + SR + STN + STP + pH + ST + (random = phylogeny + species)	MAT	-0.06	-0.21	0.08	1700	0.41	$R_m^2 \approx 0.05$ $R_c^2 \approx 0.90$ $R_p^2 \approx 0.79$ $R_s^2 \approx 0.06$
	MAP	-0.13	-0.26	-0.01	1700	**0.04**	
	SR	0.36	0.18	0.55	2023	**<0.001**	
	STN	0.08	0.01	0.15	1356	**0.04**	
	STP	-0.04	-0.11	0.03	1700	0.31	
	pH	0.06	-0.06	0.19	2604	0.33	
	ST	0.04	-0.07	0.16	1361	0.44	
Bark N:P ~ MAT + MAP + SR + STN + STP + pH + ST + (random = phylogeny + species)	MAT	0.28	0.18	0.38	1700	**<0.001**	$R_m^2 \approx 0.14$ $R_c^2 \approx 0.68$ $R_p^2 \approx 0.15$ $R_s^2 \approx 0.39$
	MAP	0.02	-0.09	0.12	1700	0.72	
	SR	0.15	0.07	0.24	1700	**<0.001**	
	STN	0.11	0.06	0.17	1700	**<0.001**	
	STP	0.10	0.03	0.17	1700	**0.01**	
	pH	0.02	-0.11	0.13	1700	0.75	
	ST	-0.19	-0.28	-0.11	1519	**<0.001**	

Note: Full names of each predictor were listed in Table S1. R_c^2, percentage of variance explained by all the model (fixed + random); R_m^2, percentage of variance explained by fixed factors; R_p^2, percentage of variance explained by phylogeny; R_s^2, percentage of variance explained by species; Post.mean, posterior mean; Eff.samp, the effective sample size; pMCMC, p-value from Monte Carlo sampling by Markov Chain.

Table 2 Comparisons of the mean values of bark C, N, and P concentrations and C:N:P ratios in different plant tissues at global or national scale.

Tissues	Study area	C (mg g^{-1})	N (mg g^{-1})	P (mg g^{-1})	C: N	C: P	N: P	Reference
Leaf	Global terrestrial ecosystems	—	20.09	1.77	—	—	13.8	Reich and Oleksyn (2004)
Leaf	Global forest ecosystems	—	—	—	37.37	516.4	12.55	McGroddy et al. (2004)
Leaf	Global terrestrial ecosystems	476.1	17.4	1.23	23.4	—	12.28	Kattge et al. (2011)
Leaf	China's terrestrial ecosystems	436.8	14.14	1.11	—	—	—	Tang et al. (2018)
Twig	Global terrestrial ecosystems	—	9.33	1.12	—	—	10.16	Wang et al. (2022a)
Twig	China's forest ecosystems	472	9.8	1.15	—	—	—	Yao et al. (2015)
Root	Global terrestrial ecosystems	447	9.8	0.78	65.8	1415	16	Yuan et al. (2011)
Root	China's terrestrial ecosystems	448.81	10.73	0.9	41.84	508.32	11.73	Wang et al. (2020)
Bark	Global forests ecosystems	493.17	3.91	0.2	135.51	3313.19	19.16	This study

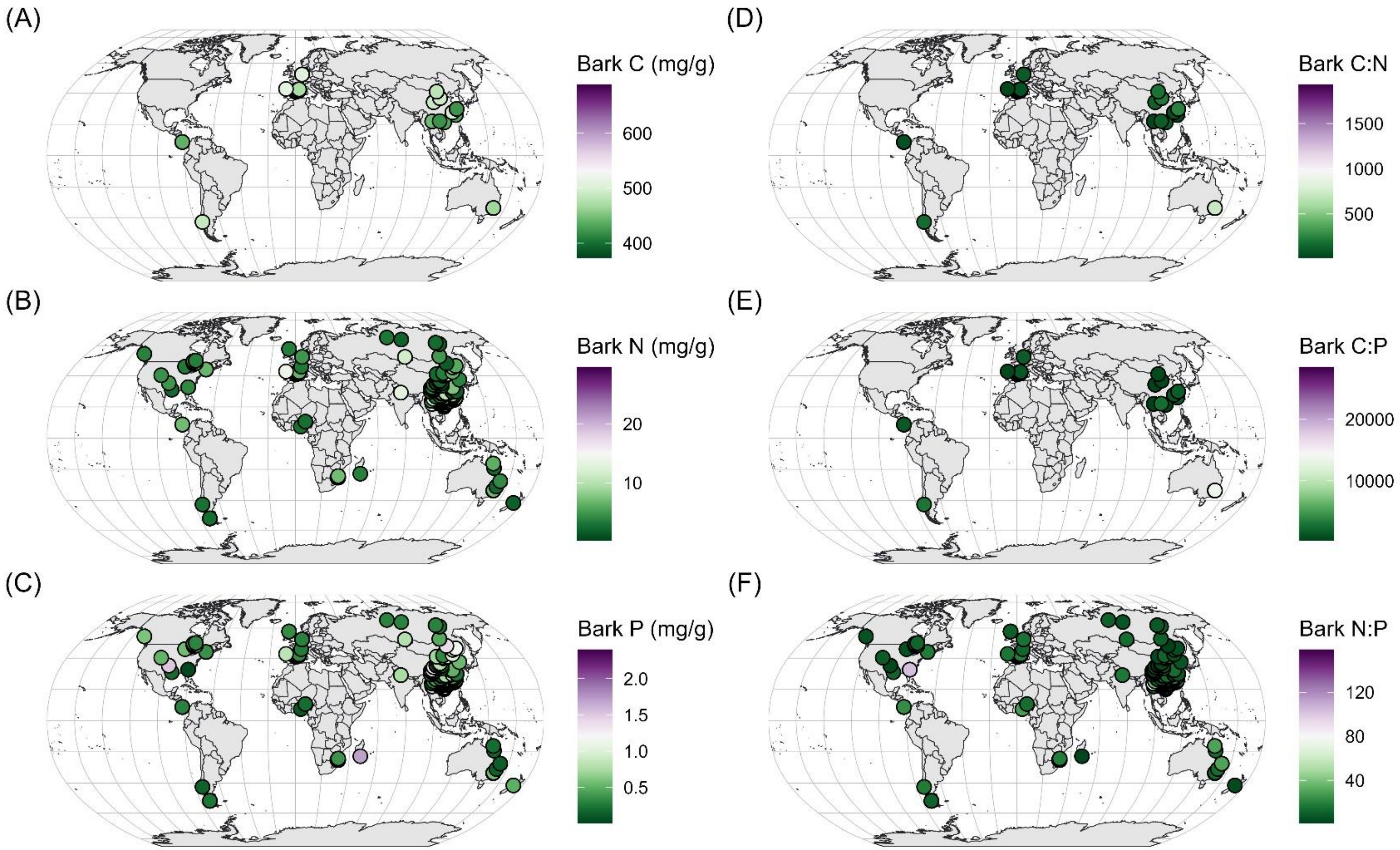

Fig. 1 Global biogeographical patterns of bark C, N, and P concentrations and their mass ratios.

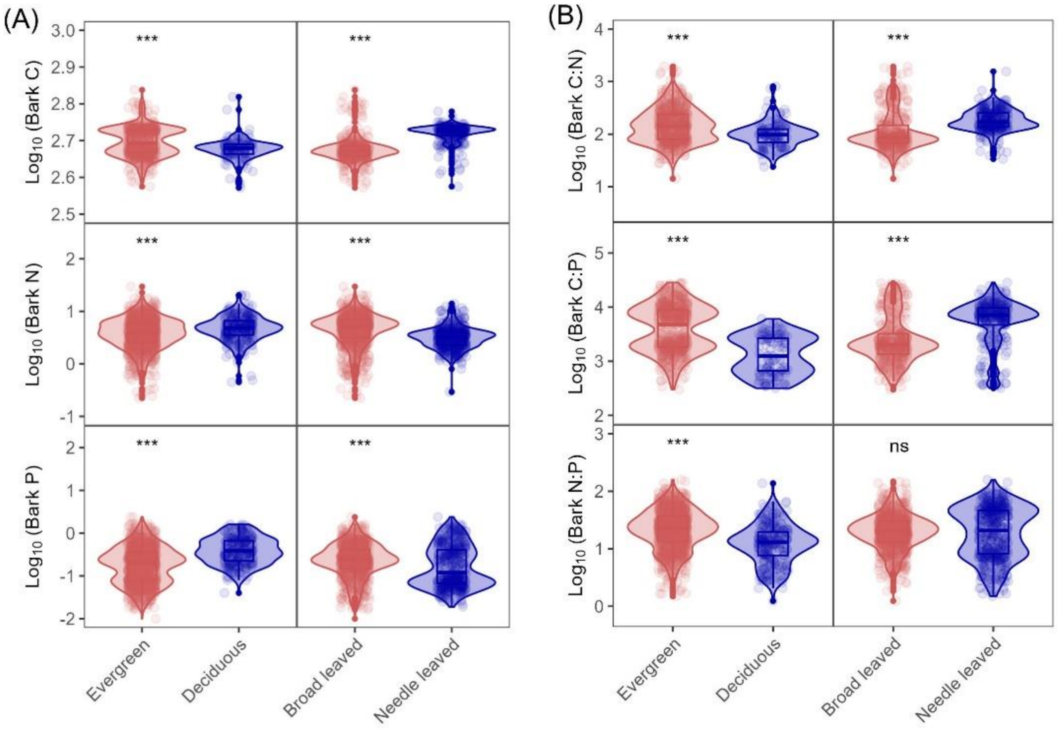

Fig. 2 Comparisons of bark C, N, and P concentrations (A) and C:N:P ratios (B) between different plant functional groups (i.e., evergreen vs. deciduous species; broad leaved vs. needle leaved species). * $p < 0.05$; ** $p < 0.01$, *** $p < 0.001$, ns $p > 0.05$.

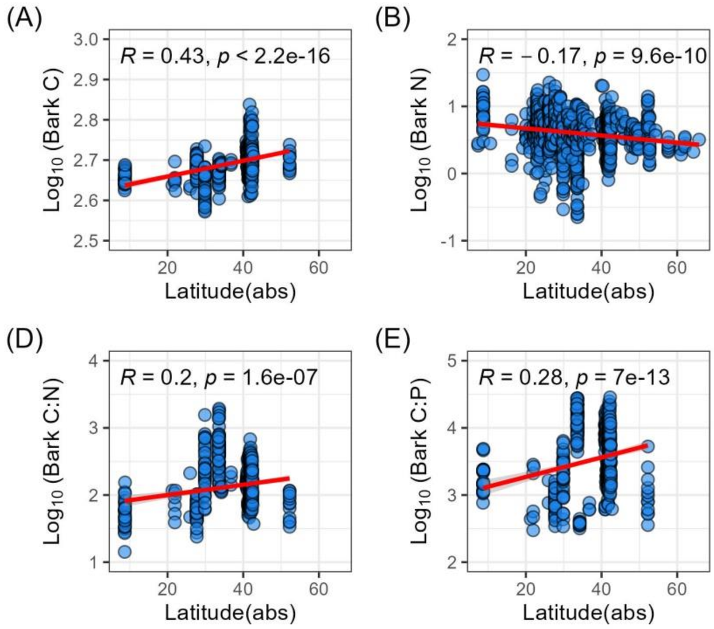

Fig. 3 Correlations of absolute latitudinal with bark C, N, and P concentrations (A-C) and C:N:P ratios (D-F) at a global scale.

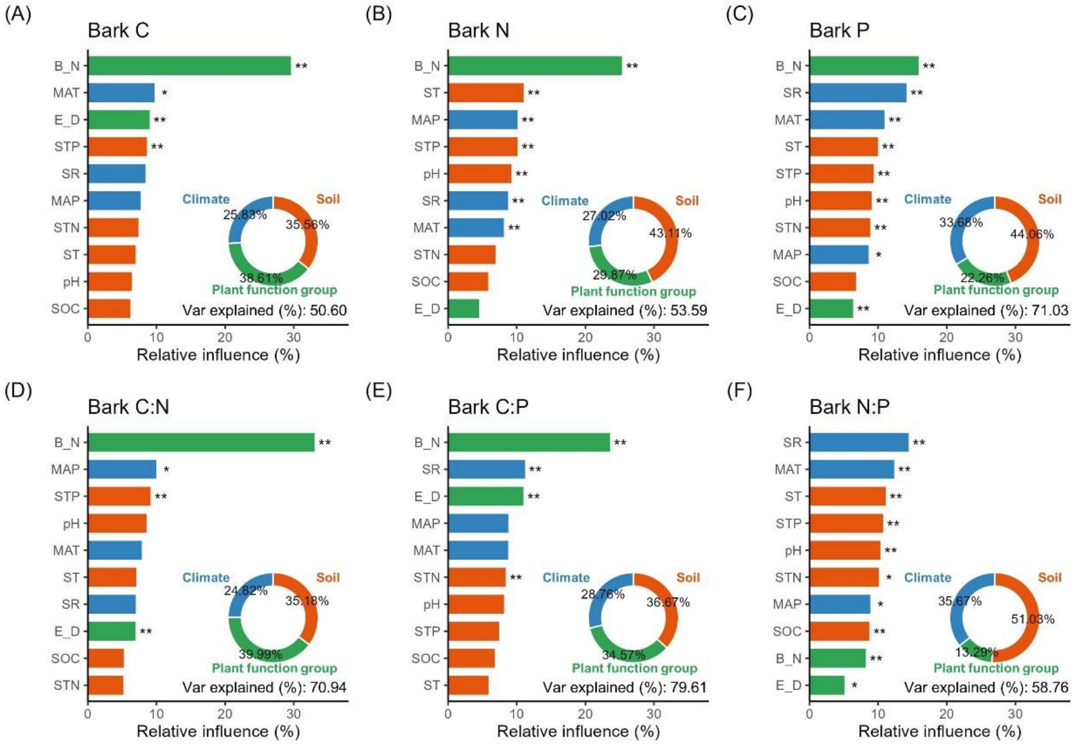

Fig. 4 Random forest model results of the relative influences of climate, soil and plant functional groups variables on bark C:N:P stoichiometry. The annular chart represents the percentages of cumulative relative contributions of climate, soil and plant functional group. MAT, mean annual temperature; MAP, mean annual precipitation; SR, solar radiation; pH, soil pH; ST, soil texture; SOC, soil organic carbon; STN, soil total nitrogen; STP, soil total phosphorous; B_N, broad leaved or needle leaved trees; E_D, evergreen or deciduous trees; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.