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Global patterns of leaf litter C:N:P stoichiometry under current and future climate scenarios

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Abstract

Plant litter carbon (C), nitrogen (N), and phosphorus (P) stoichiometry can indicate ecosystem nutrient use efficiency and limitation. Yet a comprehensive quantification of plant litter C:N:P ratios at global scale remain elusive, limiting our understanding on how their variation responds to future climate change. We constructed a database comprising 11807 records of leaf litter C:N:P ratios, quantifying their global patterns under current and future (2041-2100) climate scenarios by using the random forest method. We found that global mean leaf litter C:N, C:P and N:P ratios were 46.5, 669.4 and 16, respectively, while they were dependent on mycorrhizal association, taxonomic division, and/or plant functional type. Leaf litter C:N and N:P ratios showed opposite latitudinal patterns, being larger in high and low latitude regions, respectively, while C:P ratio remained relatively stable in low latitude regions but increased significantly toward the poles. Our simulations further revealed that increasing climate warming decreased leaf litter C:N ratio but increased C:P and N:P ratios in terrestrial plants, despite that their variations were largely dependent on ecosystem type. These findings clearly benefit us to understand the role of leaf litter in regulating the cycling of C and nutrients, responding to ecosystem plant development with climate change.

Plain Language Summary

In this study, we used to the machine learning-based random forest models to understand how global patterns of leaf litter C:N:P stoichiometry responds to future climate change. Our simulations reveal that increasing climate warming decreases leaf litter C:N and C:P ratios but increases N:P ratio in terrestrial vegetation. Despite that their variations are largely dependent on ecosystem type, but these findings clearly benefit us to understand the role of leaf litter in regulating the cycling of C and nutrients, responding to ecosystem vegetation development with the climate change.

Key Points

- Using random forest models constructs a database of global leaf litter C:N:P stoichiometry, responding to future climate change
- Variations of global mean leaf litter C:N, C:P and N:P ratios are dependent on mycorrhizal association, taxonomic division, and/or plant functional type
- Increasing climate warming decreases leaf litter C:N ratio but increases C:P and N:P ratios in terrestrial plant

1. Introduction

Carbon (C), nitrogen (N), and phosphorus (P) are three prevalent essential elements in the majority of plants (Sterner & Elser, 2002). Carbon serves as the fundamental building block, constituting the structural basis for plant tissues (such as leaves, stems, and roots), while N and P play pivotal roles as indispensable nutrients, acting as significant factors that exert a profound influence on primary production in ecosystems (Cebrián & Duarte, 1995; Galloway et al., 2008; White & Hammond, 2008). Plant tissues maintain the elements supplied by their resources in a specific ratio being conducive to growth and reproduction, which is usually referred to homeostasis (Sterner & Elser, 2002). Plant litter stands out as the primary source of C and nutrients in soil ecosystems (Hobbie, 2015), while the litter C:N:P ratios play a crucial role in regulating ecosystem functions, such as nutrient use efficiency, primary production, and nutrient cycling processes (Aerts et al., 2012; Manzoni et al., 2008). Indeed, litter C to nutrient ratio (i.e., C:N and C:P) can be helpful for predicting litter decomposition and the associated release of nutrients, and N:P ratio serves as a critical indicator of nutrient limitation, with higher ratios typically signaling P limitation in terrestrial plants (Güsewell, 2004; Vallicrosa et al., 2022; Zhou et al., 2019). Although extensive studies have investigated the patterns of C:N:P ratios for plants and soils (Chen & Chen, 2021; Du et al., 2020; Hu et al., 2021; McGroddy et al., 2004; Vallicrosa et al., 2022), a comprehensive global-scale assessment on plant litter C:N:P ratios is still lacking.

To mitigate direct competition and preserve different metabolic and functional properties, distinct plant species demonstrate variations in elemental ratios (Peñuelas et al., 2008; Sardans et al., 2021). And plants being characterized by high growth rates can necessitate significant protein synthesis, leading to an increased requirement of P rich ribosomal RNA (rRNA) and a reduced C:P and N:P ratios (Elser et al., 2000). Thus, factors such as plant functional types (PFTs, woody *vs*. herbaceous plants) and taxonomic divisions (gymnosperm *vs*. angiosperm plants) may modulate litter C:N:P ratios. Also, an expanding body of studies suggests that mycorrhizal association can act as a functional link between plant and soil in nutrient uptake, particularly for N and P, as well as in organic C stabilization (Cibichakravarthy et al., 2015; Smith & Smith, 2011). This directly impacts the regulation of plant C:N:P ratios (Liu et al., 2021). Recent studies have shown that most of the vascular plants have mycorrhizas, with 78% arbuscular mycorrhizal (AM) plants and 2% ectomycorrhizal (ECM) plants (Brundrett & Tedersoo, 2018; Tedersoo et al., 2020). Plants associated with AM fungi excel in acquiring inorganic nutrients, while plants associated with ECM fungi demonstrate proficiency in mineralizing nutrients from organic matter (Phillips et al., 2013). Difference in nutrient accumulation strategies may thus lead to divergence in litter C:N:P ratios. Plants associated with AM fungi exhibit faster leaf litter decomposition and thrive in warm, humid low-latitude ecosystems, whereas litter from ECM plants usually show slower decomposition rate and occur dominantly in dry, cold high-latitude ecosystems (Phillips et al., 2013; Zhang et al., 2018; Zhong et al., 2021). Therefore, the dissimilar nutrient acquisition strategies and geographical distribution of AM and ECM plants can result in differences of litter C:N:P ratios, but have not been assessed at the global scale.

Plant litter C:N:P ratios may be also vulnerable to climate change, because changes in temperature and precipitation affect plant growth and soil nutrient uptake (He et al., 2021; Smith et al., 2023). Also, soil nutrient availability can affect the uptake of N and P, ultimately affecting litter C:N:P ratios (Cornwell et al., 2008; Freschet et al., 2012; Hu et al., 2024; Pausas & Bond, 2020). Tropical/subtropical ecosystems primarily face P limitation, while temperate/boreal regions exhibit N limitation, with transitional zones showing N-P co-limitation (Du et al., 2020). Therefore, climatic and geographic factors are likely important drivers of the global patterns of litter C:N:P ratios, but have not been quantified in the literature

Here, we perform a global synthesis with 11807 observations assembled from 1664 publications to quantify the global patterns and driving factors of leaf litter C:N:P ratios. We focused on leaf litter because most publications in our database have only focused on leaf litter. The objectives of this study were to: (1) assess the patterns and controlling factors of leaf litter C:N, C:P, and N:P ratios on a global scale; and (2) predict the global patterns of leaf litter C:N:P ratios under future climate warming scenarios. We hypothesize that (i) C:N:P ratios are controlled by plant functional types such as PFT, mycorrhizal association, and taxonomic division; (ii) leaf litter C:N ratio would be high in temperate, boreal, and polar regions but C:P ratio high in tropical and subtropic regions, while N:P ratio would decrease with latitude; and (iii) leaf litter C:N and C:P ratios will increase under future climate warming scenarios because of a higher plant primary production and the limitations in soil N and P.

2. Methods

2.1. Data collection

To compile published data for our analysis, peer-reviewed articles, book chapters and academic theses that were published before November 2021 were searched on *Google Scholar*, *Web of Science*, and *China Knowledge Resource Integrated* using of the following search terms: "plant litter" OR "leaf litter" OR "litter decomposition" OR "litter processing" OR "litter decaying". To select appropriate data, we used the following criteria: (i) data were sourced from field experiments and the study site with geographic coordinates were reported; (ii) at least one of the response variables (i.e., C:N, C:P, or N:P ratios) was reported or can be calculated based on the concentration data; (iii) the Latin names of plants from which leaf litter was collected was reported; and (iv) leaf litter should be collected from plants under natural conditions, namely plants were not affected by artificial treatments such as warming, N deposition, drought, and/or elevated CO_2. Data was collected directly from the main text, tables, or appendixes of each primary studies. When data were presented in figures, we used the Engauge Digitizer version 12.2 to digitize the data (Mitchell et al., 2020). After the compilation of all data, we identified and removed the outliers as data points exceeding two times of the standard deviation (Vallicrosa et al., 2022). Finally, our database included 11807 observations (4566 for C:N ratio, 2696 for C:P ratio, and 4545 for N:P ratio) collected from 1664 independent publications (Fig. 1) that represented 2192 unique species met the criteria (2073 for angiosperms, 119 for gymnosperms in Fig. S1), and the database encompassed comprehensive biomes (Fig. S2).

The Latin names for all the species included in our database were cross-referenced with *the World Flora Online*. To identify the mycorrhizal associations, the *FungalRoot* dataset (Soudzilovskaia et al., 2020) was utilized to categorize species as AM, ECM or plant associated with both AM and ECM fungi (Dual) (Teste et al., 2020). For species associated with both AM and ECM fungi, we categorized such species as ECM (Cosme, 2023) because these dual-mycorrhizal plants tend to predominantly utilize AM fungi only during the seedling stages (Brundrett & Tedersoo, 2018; Teste et al., 2020). We classified the PFTs based on a previous review (Richardson & Rejmánek, 2011), and identified the taxonomic divisions according to the online website of *Missouri Botanical Garden*, *eFloras*, and *Arbolapp Canarias* if this information was not directly reported in the primary studies. To examine if leaf litter C:N:P ratios varied between mycorrhizal associations, taxonomic divisions, and PFTs, we employed generalized linear mixed-effects models (Table S1). For each model, each variable was treated as a fixed-effect factor and the identity of publications was treated as the random-effect factor.

2.2. Predictor variables

To identify the drivers of litter C:N:P ratios globally, we compiled a set of 56 global gridded environmental predictors that have been reported to influence terrestrial C and nutrient dynamics (Vallicrosa et al., 2022; Yang et al., 2022; Yuan et al., 2024), including 32 soil variables for the 0-45 cm soil layer, 21 climate variables between the period of 1970-2000, gross primary production (GPP), slope, and elevation (see Table

S2 for details). All the predictor variables were inputted into the georeferenced leaf litter C:N:P ratio dataset using the *raster* package (Hijmans, 2023). Climatic, plant, geographic, and soil data were integrated with leaf litter C:N:P ratios based on the geographic coordinates. We used two types of predictors to train the models for C:N:P ratios under current and future climate scenarios: full models with predictors of climate, plant, geographic, and soil properties and climate models only with climate variables.

To mitigate the impact of multicollinearity among predictor variables, the variance inflation factors (VIFs) were computed for each variable and variables with the highest VIFs were removed until all VIFs for the remaining variables were within a predetermined threshold of five (Haaf et al., 2021). We then profiled a variable selection procedure using the *VSURF* package (Genuer et al., 2015). After these procedures, four, five, and six predictor variables were included in the full predictive models for leaf litter C:N, C:P, and N:P ratios, respectively (Fig. S3), and four predictor variables were included in the climate models for leaf litter C:N, C:P, or N:P ratios (Fig. S4).

2.3. Predictive models

We employed the machine learning-based random forest models (Breiman, 2001) to assess the relationships between leaf litter C:N:P ratios and predictor variables using full models and climate models. To assess the accuracy of models and minimize the over-fitting potential, we employed ten-fold cross-validation and repeated data for ten times divided into training (80%) and validation (20%) subsets. During the cross-validation, we used the rooted mean squared error (RMSE) as an evaluation metric to minimize prediction error. We also computed the determination coefficient (R^2) to assess the proportion of variance explained by the models. According to the cross-validation results (Table S3), the climate models were ultimately selected due to their comparable R^2 to the full models, direct isolation of climatic drivers, and enhanced compatibility with future climate projections.

To visualize the relationships between leaf litter C:N:P ratios and individual predictor variables, we employed partial dependence analysis. This analysis utilize partial dependence plots (PDPs) to illustrate the effect of a single predictor on the predicted response of the RF model, while keeping the average of all others constant (Friedman, 2001). By examining partial dependence plots, we can gain insights into how changes in a specific predictor variable may affect the predicted values of leaf litter C:N:P ratios.

2.4. Prediction of C:N:P ratios under current and future climate scenarios

European space agency land-cover (CCI-LC) v2.0.7 was utilized to determine the worldwide distribution of plants. We specifically focused on the terrestrial vascular plants, i.e., forests, shrubs, and herbaceous systems (Table S4). Therefore, we used the climate models to predict leaf litter C:N:P ratios under current climate scenario. To predict leaf litter C:N:P ratios under future climate warming scenario, we used climate data from the International Coupled Model Intercomparison Project Phase 6 (CMIP6) (O'Neill et al., 2016). We selected two Shared Socioeconomic Pathways (SSPs) scenarios, namely the low forcing sustainability pathway SSP1-2.6 and the high radiative forcing pathway SSP5-8.5, and each scenario fitted bias-corrected climate inputs from five global climate models (GCMs) (Table S5) for future (2041-2070 and 2071-2100) projections (Karger et al., 2021). These two SSPs scenarios were chosen because they represent the most plausible (SSP1-2.6) and the worst scenarios (SSP5-5.8) of emissions at the end of the 21st century, respectively. To explore the effects of future climate warming on leaf litter C:N:P ratios, we calculated the changes between change of leaf litter C:N:P ratios (ΔC:N:P ratios) under current and future (the two SSPs scenarios) climate. To explore the relationship between climate and ΔC:N:P ratios, we analyzed their univariate relationships with projected changes in mean annual temperature under future climate scenarios.

To evaluate the uncertainty of random forest models, we calculated the coefficient of variance (CV) for leaf litter C:N:P ratios for each pixel based on observation and future CMIP6 simulations (Fig. S5), which represents the ratio of standard deviation to the mean of C:N:P ratios. The CV maps of prediction accumulated after 500 model runs from best-performing random forest model. Spatial autocorrelation holds significance in spatial data analysis, and failure to account for it may result in an overestimation of the prediction performance of the model (Cai et al., 2023; Ploton et al., 2020). Thus, we conducted semi-variograms, which help to identify spatial autocorrelation patterns in our database, prior to performing spatial analyses (Fig. S6). We examined the residuals of the model to check for spatial autocorrelation (Fig. S7), and results showed that spatial autocorrelation had negligible effect on random forest models. All the statistical analyses were performed in R version 4.4.0 (R Core Team, 2024).

3. Results

3.1. Leaf litter C:N:P ratios worldwide

Averaged across the 11807 observations, leaf litter C:N, C:P, and N:P ratios ranged from 2.6 to 145.5 (mean 46.5), 24 to 2410.5 (mean 669.4), and 0.1 to 50.6 (mean 16), respectively (Fig. 1). Leaf litter C:P and N:P ratios were significantly higher from woody plants compared to herbaceous plants, but no difference found for C:N ratio between PFTs (Fig. 2). Leaf litter from the plants associated with AM fungi had significantly lower C:N and C:P ratios compared to ECM fungi, while N:P ratio in Dual group was higher than in AM/ECM types. As to taxonomic division, leaf litter from gymnosperm species had significantly higher C:N and C:P ratios compared to those from angiosperm species, while N:P ratio in gymnosperm leaf litter was significantly lower than that in angiosperm leaf litter.

3.2. Global leaf litter C:N:P ratios under current climate scenario

The ten-fold validation showed that climate models had good performance in predicting the global patterns of leaf litter C:N:P ratios (Table S3). The R^2 of estimating leaf litter C:N, C:P, and N:P ratios using climate models were 0.56, 0.66, and 0.64, respectively, (Fig. 3). The percentage values reported in Fig. S8 indicated the percentage increase in mean square error (%IncMSE) of each predictor in the climate models for C:N, C:P, and N:P ratio datasets. Among the four predictor variables, precipitation seasonality was the most important variable for leaf litter C:N and C:P ratios, while mean temperature of the wettest quarter was the most important one for N:P ratio. We generated PDPs to better understand the relationships between each predictor variable and leaf litter C:N:P ratios (Fig. 3). These plots showed nonlinear trends in leaf litter C:N:P ratios with precipitation and temperature predictors, suggesting strong interactions among predictor variables.

Globally, the predicted mean C:N, C:P, and N:P ratios under current climate scenario were 45.58, 669.87, and 15.3, respectively (Fig. 4). For leaf litter C:N ratio, the higher values were found in northern Asia and Europe, southern Africa, northern North America, and southern South America, while lower values were observed near the equator. The lower leaf litter C:P ratio was found near the equator, while northern Asia, and southern Africa had high values. For leaf litter N:P ratio, southern Asia, northern Africa and North America, and northern South America had higher values, while central Asia, and northern America had low values. The estimated global map of leaf litter C:N:P ratios showed clear latitudinal patterns, with C:N ratio increasing, but N:P ratio decreasing, from the equator to the two poles. In contrast, the C:P ratio showed little variation across low latitude regions but increased markedly at higher latitude regions.

3.3. Global leaf litter C:N:P ratios under future climate warming scenario

Leaf litter C:N:P stoichiometry from future period (2041-2100) under SSP1-2.6 climate warming scenario with values ranged from 14.82 to 82.31 (mean 43.5) for C:N ratio, 224.6 to 1578.6 (mean 742.3) for C:P ratio, and 5.43 to 38.49 (mean 15.2) for N:P ratio

(Fig. S9). And under SSP5-8.5 climate warming scenario, C:N ratio ranged from 15.63 to 82.42 (mean 43.05), C:P ratio from 281.7 to 1574.5 (mean 740.9), and N:P ratio from 5.28 to 35.26 (mean 15.3). Under both the SSP1-2.6 and SSP5-8.5 climate warming scenarios, leaf litter C:N ratio was high in Asia and central North America, but low in northern South America and central Africa. In contrast, C:P ratio was high in northern South America and central Africa, but low in Asia and southern Africa. As to N:P ratio, higher values were observed in northern South America and Africa, and low values in Asia and North America. The future climate PDPs demonstrated distinct climate-nutrient interactions under SSP1-2.6 and SSP5-8.5 scenarios during 2071-2100 (Fig. S10). Leaf litter C:N ratio for precipitation seasonality showed a hump-shaped response in both scenarios, while leaf litter C:P ratio under mean temperature of the wettest quarter exhibited steeper declines in SSP5-8.5. Notably, precipitation of the warmest quarter displayed the amplified N:P ratio increases under high-emission SSP5-8.5.

The global leaf litter ΔC:N ratio decreased from -2.7 in the SSP1-2.6 scenario to -3.15 in the SSP5-8.5 scenario by the year 2100, while ΔC:P ratio declined from 70.18 in the SSP1-2.6 to 62.37 in the SSP5-5.8 (Fig. 5). Conversely, ΔN:P ratio increased from 0.11 in the SSP1-2.6 scenario to 0.49 in the SSP5-8.5 scenario. Leaf litter ΔC:N:P ratio under both the SSP1-2.6 and SSP5-8.5 climate warming scenarios showed similar global patterns in the two time periods (2071-2100 in Fig. 5 and 2041-2070 in Fig. S11). Leaf litter ΔC:N and ΔC:P ratios were projected to be higher in northern and eastern Asia and central North America, but lower in northern South America and central Africa. Leaf litter ΔC:P ratio showed high values in northern South America and northern

Africa, but low values in Asia and North America.

Leaf litter ΔC:N:P ratios within each biome type had similar patterns under SSP1-2.6 and SSP5-8.5 climate scenarios for the periods 2041-2070 (Fig. S12) and 2071-2100 (Fig. 6). In total, leaf litter ΔC:N and ΔN:P ratios between current and future climate scenarios showed the largest decrease in tundra, but ΔC:P ratio in Xeric shrublands. And C:N ratio decreased in most biomes, while C:P and N:P ratios were increased. Compared to two SSP scenarios, ΔC:N and ΔN:P ratios for SSP5-8.5 scenario were greater than SSP1-2.6 scenario. And for ΔC:P ratio, the change rate under SSP5-8.5 was smaller than that under SSP1-2.6 except for tropical conifer, tropical shrubland, and xeric shrubland. Finally, we found that temperature significantly affected changes of C:N:P ratio (Fig. S13).

4. Discussion

Our analytical results supports our first hypothesis, clearly revealing significant global differences in leaf litter C:N:P ratios by PFT, mycorrhizal association, and taxonomic division. The difference between woody and herbaceous plants can be attributed to the distinct growth strategies and functional characteristics of these plant types. Woody plants are slower growing species containing higher lignin concentrations, as they usually require proportionally more C input at the cellular scale to synthesize lignin for supporting the low-rate of growth (Ma et al., 2018). In contrast, herbaceous plants are characterized by faster growth rates and a stronger capacity for photosynthesis and nutrient absorption from the soil (Cornwell et al., 2008; Grime, 2006). These plants have a greater demand for P to support their rapid growth and maintain optimal leaf function and structure, requiring more P at a given N level (Kerkhoff et al., 2006). Consequently, they exhibit lower C:P and N:P ratios.

Interestingly, we observed a consistent trend in leaf litter C:N:P ratios between mycorrhizal associations and taxonomic divisions. This alignment can be attributed to the prevalence of two major types of mycorrhizal fungi worldwide: AM and ECM fungi (Tedersoo et al., 2020). AM Plants fungi are predominantly low-latitude broadleaf species, whereas ECM plants are primarily high-latitude coniferous species (Lin et al., 2017; Soudzilovskaia et al., 2015). We found that the C:N and C:P ratios of leaf litter from ECM plants were significantly higher than those from AM plants. These variations in leaf litter C:N:P ratios can be attributed to variations in N and P use efficiency of fungi across different ecosystems (Lü et al., 2012; Richardson et al., 2005). The AM fungi specialize in P acquisition from soil inorganic P pools through hyphal extension and P secretion. This strategy enables AM plants to achieve efficient P acquisition in low-P environments (Zhou et al., 2022). Specifically, AM fungi establish a symbiotic relationship with plant roots, benefiting their host plants by improving nutrient acquisition and stress tolerance (Tedersoo et al., 2020), while ECM fungi hydrolyze complex polymers by producing extracellular enzymes in association with saprotrophic fungi, releasing C and nutrients required for plant growth and metabolic function (Cibichakravarthy et al., 2015). ECM fungi decompose soil organic matter through oxidizing enzyme secretion, releasing organically bound N (Jörgensen et al., 2024; Peng et al., 2022). Soil nutrient availability influences leaf nutrient concentrations, which, in turn, affects the nutrient resorption efficiency during leaf senescence. This resorption process regulates the initial nutrient content of leaf litter (Güsewell, 2004; McGroddy et al., 2004; Yuan et al., 2011). Notably, over 90% of plant N and P can be derived from nutrients recycled from the previous year's litterfall (Chapin et al., 2011). ECM-dominated gymnosperm plants tend to grow in relatively nutrient-poor soils that lack nutrients like N and P, having relatively greater C:N and C:P ratios (Sulman et al., 2017; Yang & Luo, 2011). Additionally, although we found that both AM and ECM plants exhibited a lower N:P ratio than Dual types, the reasons may be different. Firstly, AM fungi may reduce the residual N proportion in litter by enhancing plant N acquisition efficiency (Yin et al., 2021). Secondly, ECM fungi enhance P mineralization through organic acid and enzyme secretion, resulting in relative P accumulation in plant litter (Cibichakravarthy et al., 2015). In contrast, Dual types possessing both AM and ECM characteristics may exhibit elevated N:P ratio due to reduce N and P metabolic efficiency caused by synergistic interactions between the two mycorrhizal types (Teste et al., 2020).

It is consistent with our second hypothesis, as leaf litter C:N:P ratios exhibited a distinct latitudinal pattern. This effect is attributed to the Growth Rate Hypothesis (GRH). Indeed, we found that leaf litter in low-latitude regions displayed lower C:N and C:P ratios but higher N:P ratio (Elser et al., 2000). The GRH considers that plants with high growth rates require greater quantities of ribosomal RNA to support protein synthesis, consequently exhibiting lower C:P and N:P ratios (Matzek & Vitousek, 2009). Conversely, in high-latitude regions, the retarded decomposition promotes P immobilization in organic matter (low litter C:P ratio), with concomitant N accumulation (elevated C:N ratio) compensating for metabolic constraints (Liu et al., 2023b; Pan et al., 2025). This dual-strategy paradigm aligns precisely with the GRH predictions regarding resource optimization under growth-limiting conditions (Isanta-Navarro et al., 2022; McGuire et al., 2006). Generally, tropical regions are generally faster growing angiosperm plants, while high latitudes are generally slower growing gymnosperm plants, and N:P is positively correlated to growth rate (FAO, 2020; Sardans et al., 2012). And there is a correlation within growth rate and increased P requirement for synthesizing the P rich rRNA, which results in a reduction of the cytoplasmic N:P ratio (Elser et al., 2000; Karpinets et al., 2006). Thus faster growing plants usually are greater N and P concentrations (fewer C:N and C:P ratios) and lower N:P ratio (Zechmeister-Boltenstern et al., 2015). Elevated C:N and C:P ratios in high-latitude regions drive soil organic carbon accumulation through suppressed decomposition processes, thereby amplifying terrestrial C sequestration potential. On the one hand, elevated C:N ratio in high-latitude litter significantly suppress decomposition rates, leading to prolonged residence time of particulate organic matter (Sardans & Peñuelas, 2013). Concurrently, reduced microbial C use efficiency drives the reallocation of residual C into stabilized mineral-associated organic matter through mineral adsorption processes (Feng et al., 2022; Konrad et al., 2025). On the other hand, under prevailing P-limited conditions, microbial activity becomes predominantly reliant on litter-derived nutrients, resulting in diminished priming effects and consequently lower SOC loss (Dai et al., 2019). Conversely, temperate-boreal systems with high litter C:N ratio constrain decomposer activity, ultimately establishing more persistent soil C reservoirs (Liu et al., 2023a; Wu et al., 2022).

The worldwide modeling of leaf litter C:N:P ratios are closely related to soil properties. P required for plant growth and development can be taken up directly from soil, while N needs to be accumulated slowly through N deposition or biological N fixation (Vitousek et al., 2010). Thus, younger soils are often N-limited, and continued soil weathering, and N input resulting in N enrichment and P deprivation, while ancient tropic soil had reduced ability to discharge P from the parent material (Richardson et al., 2005; Vitousek et al., 2010). Due to the relative nutrient poverty and lower availability of soil nutrients in northern soils, plants in high-latitude regions have higher nutrient uptake rates and will absorb more N and P form senescing leaves. Therefore, C:N and C:P ratios are relatively higher at high latitude regions (Sardans & Peñuelas, 2013). This difference may affect the evolution of soil fertility. In tropical regions, N released from litter of low C:N ratio decomposition maintains ecosystem N balance through biological N fixation and rapid mineralization, but persistent P loss may lead to long-term soil degradation (Martínez-García et al., 2021; Zhang et al., 2025); high C:N litter of high-latitude accumulates humus through slow decomposition which may promote the release of mineral-bound nutrients through freeze-thaw in the long term (Schwieger et al., 2025). It is noteworthy that litter C:N and C:P ratios are influenced by soil microbial C:N ratio. Recent study has revealed divergent nutrient limitations between plants and microorganisms (Liu et al., 2023a). Microorganisms efficiently mineralize organic matter through extracellular enzyme secretion, prioritizing their P acquisition. While under P-limited conditions, enhanced microbial P activity may accelerate organic P release, potentially alleviating plant P limitation indirectly (Čapek et al., 2018; Cui et al., 2022).

We found a consistent trend in leaf litter ΔC:N:P ratios in both SSP1-2.6 and SSP5-8.5 scenarios over the next two (2041-2070 and 2071-2100) periods, supporting our third hypothesis. Climate plays a crucial role in influencing global leaf litter C:N:P ratios. Climate influences not only plant litter decomposition (Berg & McClaugherty, 2020), and release of soil nutrients (Yuan et al., 2021), but also the growth and development of plants (Dolezal et al., 2021). Globally, atmospheric temperature drives variations in plant growth rates, requiring faster growth rates (needing higher nutrient level) to accomplish growing and reproducing during shorter growing periods in temperate landscapes than in tropic landscapes (Kerkhoff et al., 2005; Lovelock et al., 2007). Moreover, our results also reveal that elevated temperature significantly affected leaf litter C:N:P ratios. Under the SSP5-8.5 scenario, C:N ratio decreases in most biomes, while C:P and N:P ratios increase. This indicates that higher temperatures will lead to an accumulation of leaf litter N concentration, while the availability of P concentration will be limited. Elevated temperature accelerates soil microbial activity, promoting the decomposition of organic matter and mineralization process of N, thereby increasing the amount of available N in the soil (Song et al., 2018). Higher temperatures also expedite the release of N, making more N available for plant absorption and utilization, which leads to a decrease in the leaf litter C:N ratio (Pei et al., 2019; Suseela & Tharayil, 2018). And high temperatures may enhance P adsorption in the soil, making P more difficult to be taken up by plant roots (Bai et al., 2017; Reich & Oleksyn, 2004). However, high C:P litter compels decomposers to secrete additional phosphatases for P acquisition, thereby reducing decomposition rates (Berg & McClaugherty, 2020). This may lead to growth suppression in tropical trees whereas it is dependent on rapid P cycling, while boreal conifers with conservative P use strategies may gain competitive advantages (Lai et al., 2024; Liu et al., 2025). It is noteworthy that the SSP5-8.5 scenario exacerbates this trend, potentially leading to the decreased net primary productivity in P-sensitive biomes. Additionally, latitudinal variations in C:N ratios driven by climate warming will differentially influence soil C sequestration. Decreasing C:N ratios in high-latitude systems may accelerate litter decomposition, simultaneously promoting mineral-associated organic matter formation through microbial residues (Bradford et al., 2016; Lavallee et al., 2020; Schwieger et al., 2025). Tropical forests exhibit high sensitivity to reduced precipitation and climate warming, significantly elevating leaf litter C:P ratio. This likely stems from AM-dominated P acquisition strategies: while it enhances P uptake, they reduce foliar P resorption efficiency, ultimately forming high C:P litter that establishes a negative feedback loop by suppressing decomposition (Lyu et al., 2023; Weber et al.; Zhang et al., 2019). In contrast, boreal forests display decreasing leaf litter C:N ratio under climate warming. As early evidenced (Cui et al., 2024; Yang et al., 2019), this originates from freeze-thaw cycle-enhanced N mineralization combined with fire-derived pyrogenic C regulation on litter C:N ratio.

5. Conclusions

By constructing a comprehensive global database of leaf litter C:N:P ratios, we generated worldwide maps for leaf litter C:N:P ratios using random forest regression models. Our results revealed that the average leaf litter C:N, C:P, and N:P ratios were 46.5, 669.4, and 16, respectively. These ratios were significantly influenced by mycorrhizal association, taxonomic division, and/or PFT. Leaf litter C:N and C:P ratios increased with absolute latitude, while N:P ratio showed an opposite pattern. Under future climate warming scenarios, ΔC:N and ΔC:P ratios decreased from SSP1-2.6 to SSP5-8.5 scenarios, while ΔN:P showed an opposite pattern. This indicates that higher temperatures would lead to an accumulation of leaf litter N concentration, while the availability of P concentration will be limited. Overall, our results clearly show the global patterns of leaf litter C:N:P ratios under current and future climate warming scenarios, which will help us to better understand the role of leaf litter in global C and nutrient cycling.

CRediT authorship contribution statement

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Competing interests

The authors declare that there are no competing financial or personal interests that could inappropriately influence this study.

Data Availability Statemen

All the raw data and source code used in the study were deposited in figshare at https://doi.org/10.6084/m9.figshare.28917632.v4 (Yue & Yuan, 2025).

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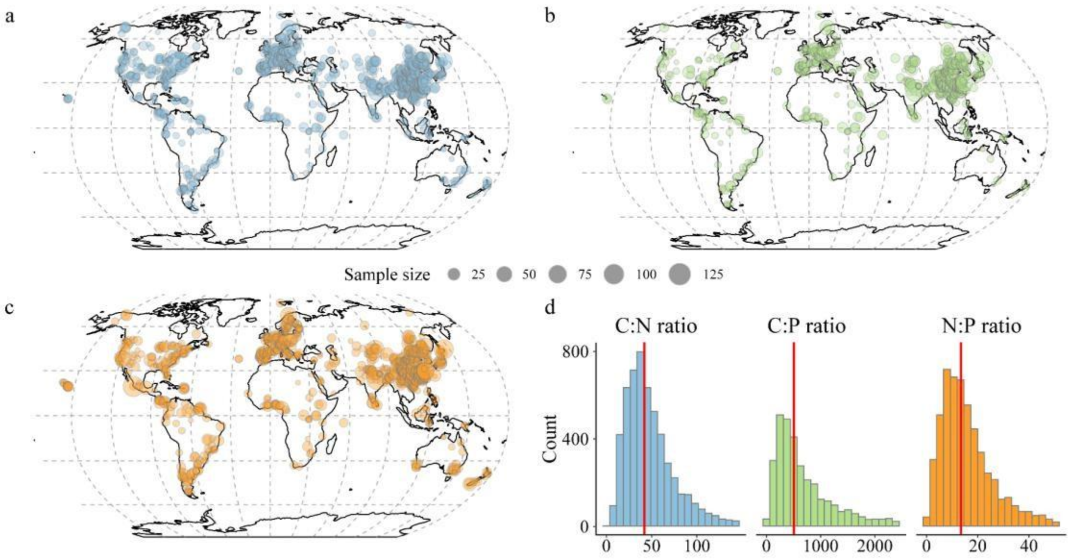

Fig. 1 Dataset used in the study. Distribution of leaf litter (a) C:N ratio, (b) C:P ratio, (c) N:P ratio. (d) Frequency distribution histogram of leaf litter C:N, C:P, and N:P ratios. Red vertical lines represent mean values in the frequency distribution.

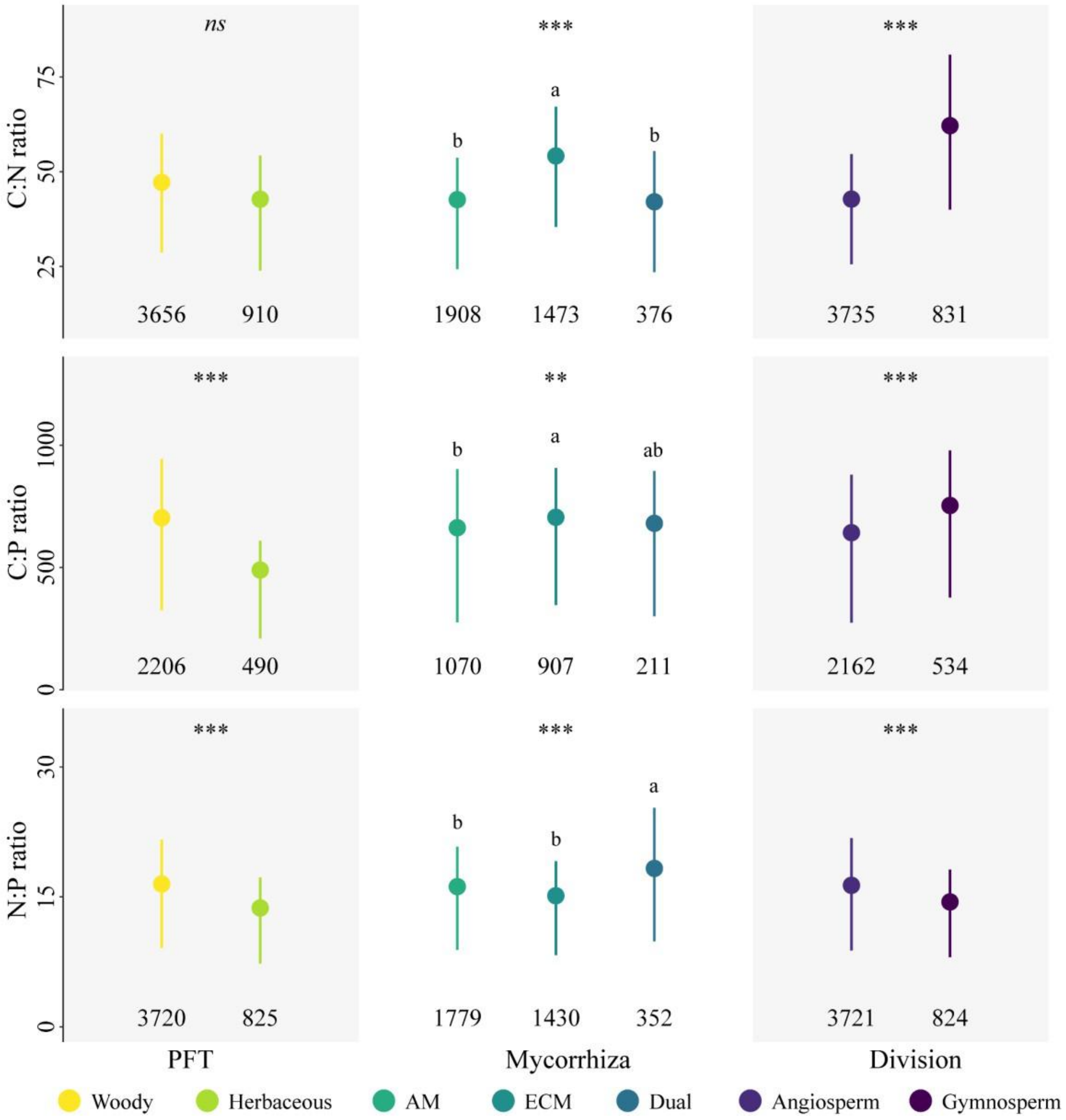

Fig. 2 Leaf litter C:N (a), C:P (b), and N:P (c) ratios in relation to plant functional type (PFT), mycorrhizal association, and taxonomic division. Different letters indicate significant differences among various plant mycorrhizal associations at *$p<0.05$, **$p<0.01$, and ***$p<0.001$. *ns*, not significant between groups ($p>0.05$). Data are presented as the mean with inner bars from the first to the third quartile. Numbers represent sample sizes within each group. AM, arbuscular mycorrhiza; ECM, ectomycorrhiza; Dual, plant associated with both AM and ECM fungi.

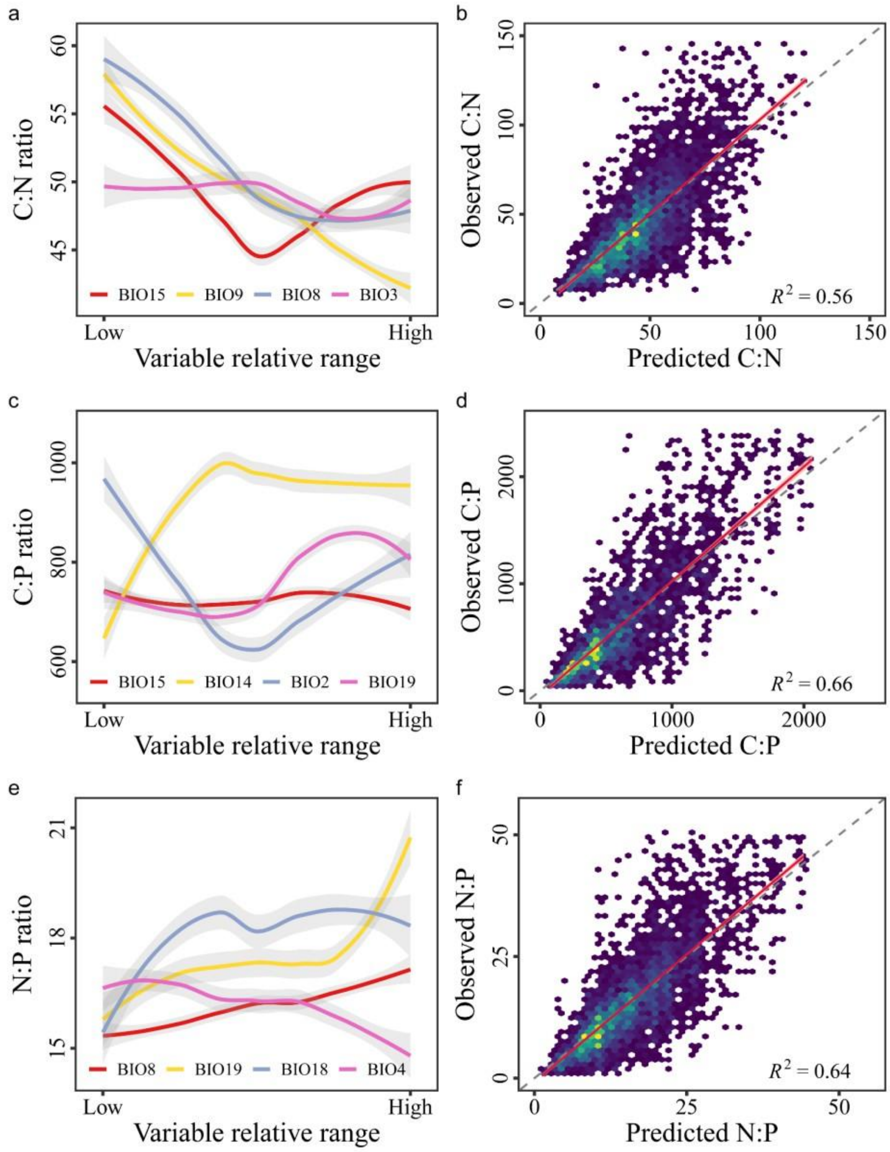

Fig. 3 Spatiotemporal changes in the leaf litter C:N:P ratios and their main climate drivers. The illustrations on the left showed the partial dependence of leaf litter C:N (a), C:P (c), and N:P (e) ratios on the climate factors. The illustrations on the right showed the performance of random forest models to explain the leaf litter C:N (b), C:P (d), and N:P (f) ratios. The grey line indicates the 1:1 line; the red line indicates the regression line between predicted and observed values. BIO2, mean diurnal range; BIO3, isothermality; BIO4, temperature seasonality; BIO8, mean temperature of the wettest quarter; BIO9, mean temperature of the driest quarter; BIO14, Precipitation of the driest month, BIO15, precipitation seasonality; BIO18, precipitation of warmest quarter; BIO19, precipitation of coldest quarter.

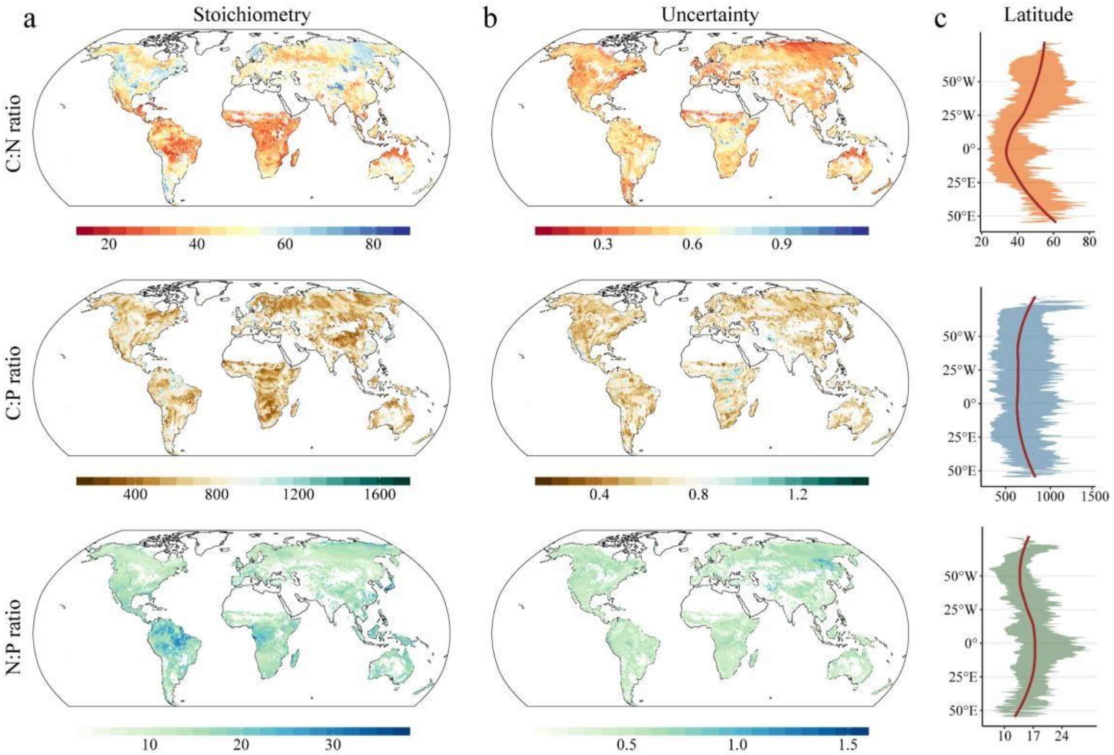

Fig. 4 The global patterns (a), uncertainty (b) and latitudinal patterns (c) of C:N C:P, and N:P ratios in leaf litter based on observation simulations. Uncertainty maps indicate coefficient of variation (standard deviation divided by the mean value). In panels (c), red line indicates the locally weighted regression, and grey ribbon spans the range between the 5% and 95% quantiles. All maps are projected at 0.5° resolution.

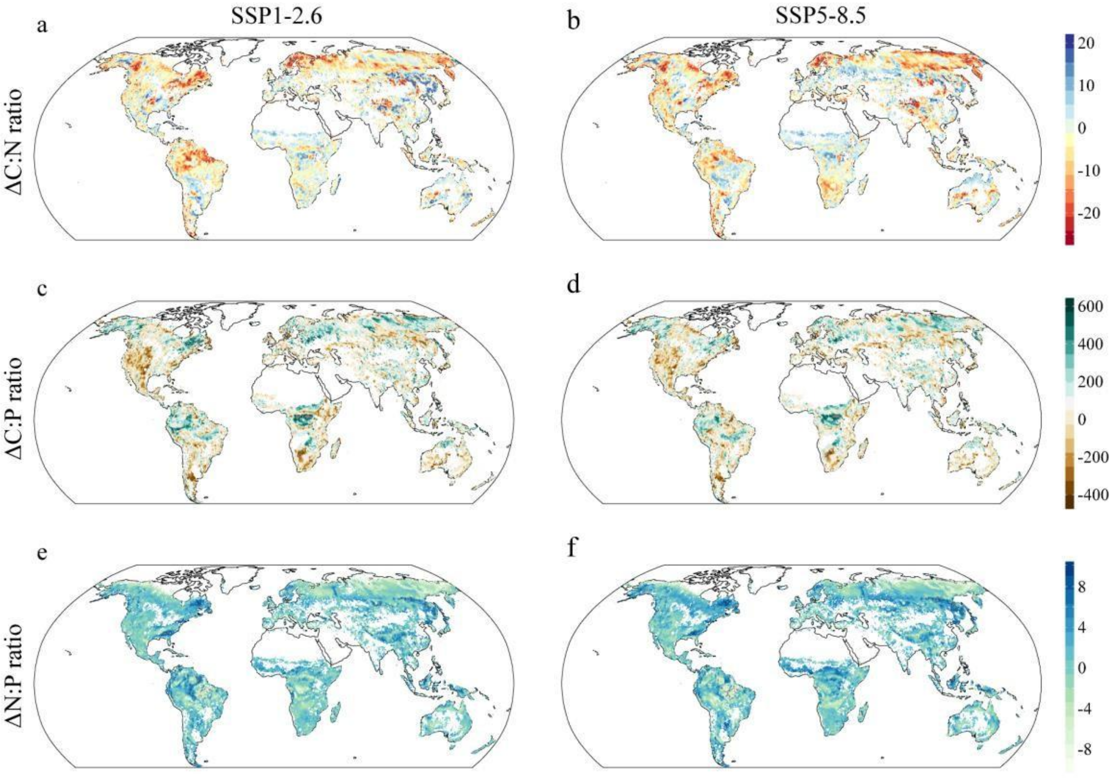

Fig. 5 Response of leaf litter C:N:P stoichiometry to climate change in period 2071-2100 relative to observation simulations under CMIP6 simulations. The maps on the left and right show the change of leaf litter C:N:P (ΔC:N:P) ratios under SSP1-2.6 and SSP5-8.5 scenarios. To better illustrate the findings, the results are presented with 99% confidence intervals (Fig. S14), and the full results could be found in Fig. S15. All maps are projected at 0.5° resolution. Change of C:N:P ratios were calculated as the future simulation minus the observation simulation. CMIP6, Shared Socioeconomic Pathways 6; SSP, Shared Socioeconomic Pathways.

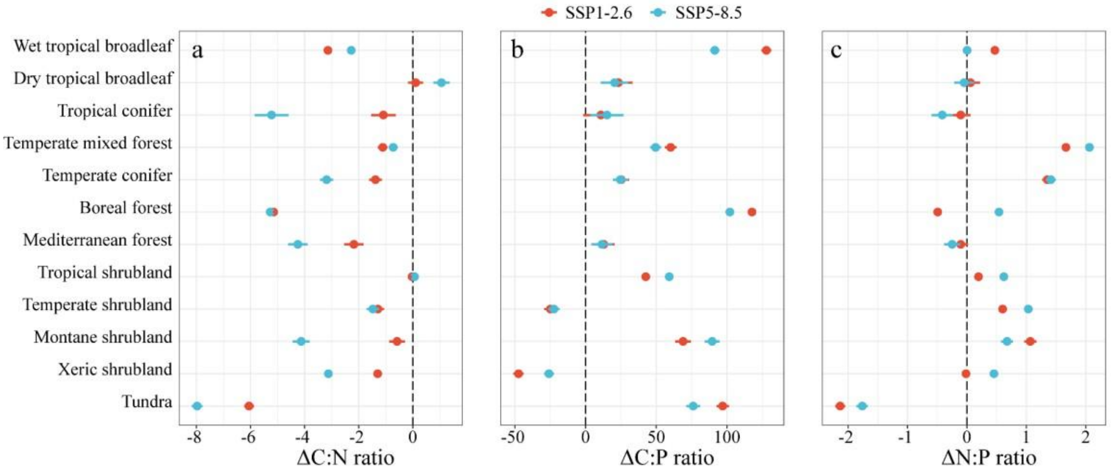

Fig. 6 The distribution of change of leaf litter C:N (a), C:P (b), and N:P (c) ratios across biomes in period 2071-2100 under SSP1-2.6 and SSP5-8.5 scenarios. The data are presented as means, with error bars representing standard errors (SE). SSP, Shared Socioeconomic Pathways.