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RESEARCH ARTICLE

Global spectra of plant litter carbon, nitrogen and phosphorus concentrations and returning amounts

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Abstract

1. Litter decomposition is a key ecological process that determines carbon (C) and nutrient cycling in terrestrial ecosystems. The initial concentrations of C and nutrients in litter play a critical role in this process, yet the global patterns of litter initial concentrations of C, nitrogen (N) and phosphorus (P) are poorly understood.
2. We employed machine learning with a global database to quantitatively assess the global patterns and drivers of leaf litter initial C, N and P concentrations, as well as their returning amounts (i.e. amounts returned to soils).
3. The medians of litter C, N and P concentrations were 46.7, 1.1, and 0.1%, respectively, and the medians of litter C, N and P returning amounts were 1.436, 0.038 and 0.004 Mg ha^{-1} year^{-1}, respectively. Soil and climate emerged as the key predictors of leaf litter C, N and P concentrations. Predicted global maps showed that leaf litter N and P concentrations decreased with latitude, while C concentration exhibited an opposite pattern. Additionally, the returning amounts of leaf litter C, N and P all declined from the equator to the poles in both hemispheres.
4. *Synthesis*: Our results provide a quantitative assessment of the global concentrations and returning amounts of leaf litter C, N and P, which showed new light on the role of leaf litter in global C and nutrients cycling.

KEYWORDS
carbon cycle, global map, leaf litter, lifeform, machine learning, mycorrhizal association

1 | INTRODUCTION

The decomposition of plant litter, which is the main source of soil carbon (C) and nutrients, is a crucial ecological process that determines the C and nutrient cycling in terrestrial ecosystems (Guo et al., 2021; Hobbie, 2015). It is also the main way by which plants return C and nutrients to soil, driving the accumulation and formation of soil organic matter (Berg & McClaugherty, 2020; Elser et al., 2003). Nitrogen (N) and phosphorus (P) are recurrent limiting nutrients in terrestrial ecosystems and are crucial for the physiological and metabolic activities involved in plant growth (Chave et al., 2010; Yuan et al., 2011). While many studies have assessed the litter decomposition process and associated releases of C and nutrients (Manzoni et al., 2008; Xie et al., 2022; Yue et al., 2018; Zhang et al., 2020), few have evaluated the initial concentrations of C, N and P (i.e. concentrations of C, N and P in freshly fallen litter) and the quantity of these elements returned to the soil at the global scale. This lack of data has hindered our ability to quantitatively assess the role of litter in global C and nutrient cycling across terrestrial ecosystems.

Globally, changes in climate factors induced by latitude, such as temperature and precipitation, result in varied patterns of nutrient accumulation in vegetation. Thus, litter initial concentrations of C, N and P are likely to differ across taxonomic divisions (Cornwell et al., 2008; Pietsch et al., 2014; Zhang et al., 2012). Moreover, plants with different lifeform exhibit diverse growth and nutrient use strategies (Killingbeck, 1996; Zhang et al., 2022). In contrast to herbaceous plants, slow-growing woody plants exhibit lower nutrient uptake rates and greater nutrient resorption (Carrera et al., 2000; Huang et al., 2018). Additionally, mycorrhizal association represents a crucial factor influencing litter initial C, N and P concentrations, owing to the varied strategies employed by mycorrhizal fungi for plant nutrients uptake (Chen et al., 2019; Frey, 2019), as more than 90% of the vascular plants on earth are associated with mycorrhizal fungi, with arbuscular mycorrhizal (AM) and ectomycorrhizal (ECM) fungi being the dominant types (Brundrett & Tedersoo, 2018; Keller & Phillips, 2019). Nevertheless, the effects of these factors on the initial concentrations of litter C, N and P remain elusive at the global scale.

The return of plant litter to soil supplies a large proportion of nutrients, such as N and P required for plant growth, while their returning amounts (i.e. amounts returned to soils) are determined by their initial concentrations (Geng et al., 2022; Qin et al., 2019). Evidence suggests that litter production and nutrient return are important drivers of ecosystem processes, including nutrient cycling (Muqaddas & Lewis, 2020), soil and water conservation (Dunkerley, 2015), and soil fertility (Pandey et al., 2007). Moreover, these processes exhibit high spatiotemporal heterogeneity and are influenced by vegetation type, species composition and climate condition (Jasińska et al., 2020; Kitayama et al., 2021; Zhu et al., 2019). Recent studies indicated that plant litter elements in terrestrial ecosystem had clear geographical patterns at region and global scales, which are jointly driven by climate, soil properties and vegetation (Ochoa-Hueso et al., 2019; Xie et al., 2022; Yuan & Chen, 2009). Climate factors, such as precipitation and temperature have a direct impact on plant physiology, phenology, and ecology, including the uptake of C, N and P (Tjoelker et al., 1999; Woods et al., 2003). Similarly, soil nutrients are directly linked to plant growth and their corresponding concentrations in plant tissues (Isaac & Borden, 2019; Moreau et al., 2019), and thus modulate the concentrations of plant litter C, N and P, either individually or interactively with climate. For instance, slow decomposition and mineralization of organic matter under cold climate can reduce soil nutrient availability, leading to reduced nutrient concentrations in plant tissues and consequently in litter (Reich & Oleksyn, 2004; Yuan et al., 2011). In addition, elevation is another important environmental factor affecting litter concentrations of C, N and P, because it is closely related to climate (Weemstra et al., 2021). However, up to date, the global patterns and drivers of litter initial C, N and P concentrations and their returning amounts have not been quantitatively assessed (Hu et al., 2021; Muqaddas & Lewis, 2020), thus limiting our in-depth understanding of the role of litter in terrestrial C and nutrient cycling.

Here, to explore the global patterns of litter concentrations and returning amounts of C, N and P, we constructed a global database of 22,998 records from 2575 sites (Figure 1 and Figure S1). Because limited data available of bryophytes and ferns in our database, we focused our analysis on angiosperm and gymnosperm plants only, as these two groups contained 2099 and 122 species, respectively (Figures S2 and S3). In addition, due to the scarcity of data on other types of litter apart from leaf litter (Figure S4), we focused our statistical analysis primarily on leaf litter.

We used machine learning techniques to identify the key environmental variables and develop the most effective predictive models for leaf litter initial concentrations of C, N and P. Specifically, we constructed linear and non-linear predictive models for predicting leaf litter production and initial concentration of C, N and P based on the best predictors. These models were then used to generate predictions for leaf litter initial concentrations and returning amounts of C, N and P at the global scale. We hypothesised that litter initial concentrations of C, N and P are significantly influenced by lifeform, mycorrhiza association, and taxonomic division. The objectives of this study were to (1) evaluate the leaf litter initial concentrations of C, N and P at the global scale; (2) determine the relative importance of factors on leaf litter initial concentrations of C, N and P; and (3) use eight approaches to predict the global patterns of leaf litter initial concentrations and returning amounts.

2 | MATERIALS AND METHODS

2.1 | Data collection and preprocessing

Peer-reviewed articles, book chapters and academic dissertations including the data of litter initial concentrations of carbon (C), nitrogen (N), and phosphorus (P) were searched on *Web of Science*, *Google Scholar* and *China National Knowledge Infrastructure* in November 2021 using the search terms of ("plant litter" OR "leaf litter" OR

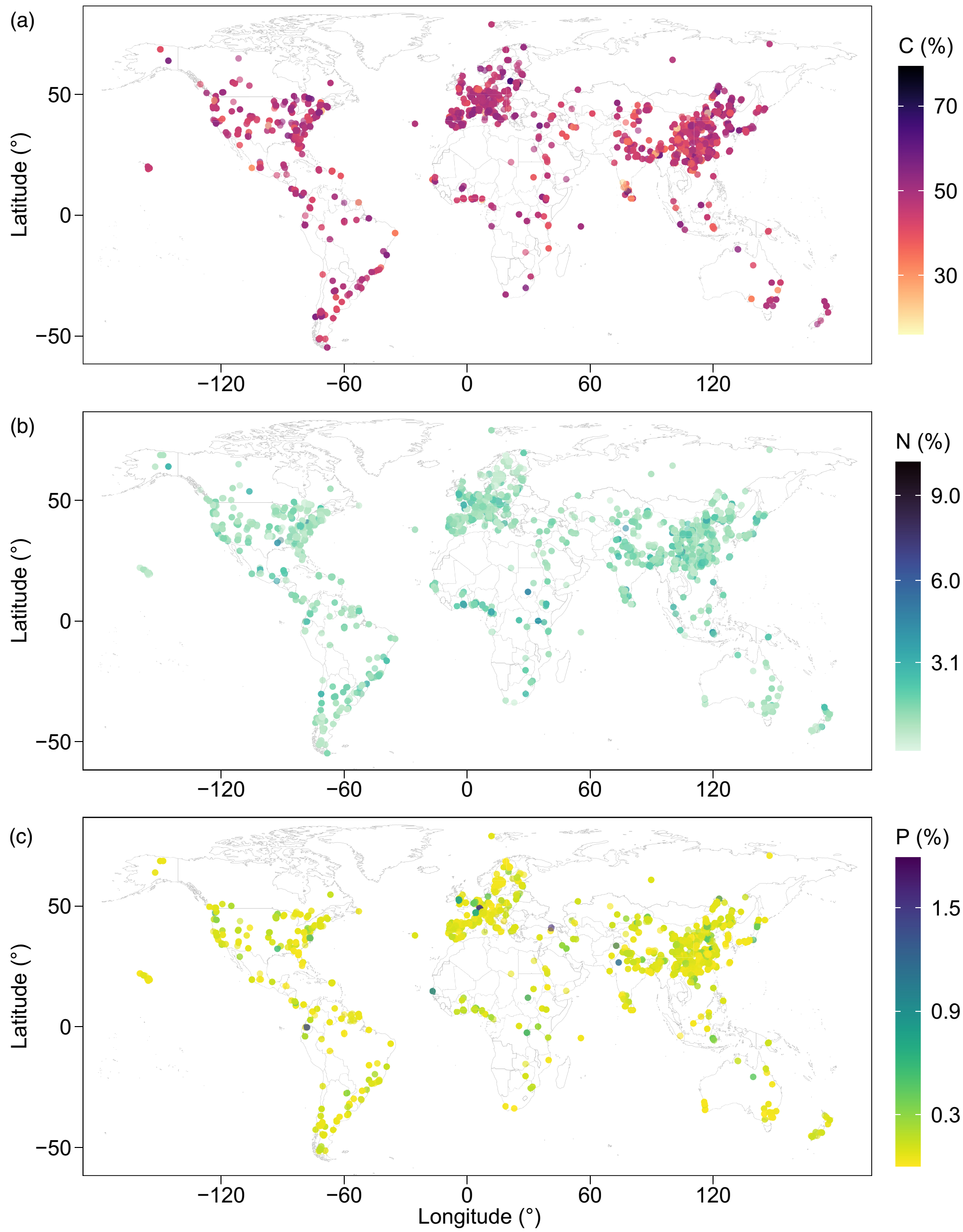

FIGURE 1 Map of study sites where the data of litter carbon (C), nitrogen (N) and phosphorus (P) concentrations are compiled in our database.

"foliar litter" OR bark OR branch OR deadwood OR "woody debris" OR "root litter") and their equivalents in Chinese. To avoid publication bias, only studies meeting the following criteria were included in the database: (1) data were obtained through field experiments or observational studies rather than been estimated or remote sensed; (2) at least one of the concentrations of C, N or P was reported; and (3) the Latin names of plants and litter types should be clearly reported. We focused on terrestrial natural ecosystems, excluding ecosystems such as croplands, urban forests and mangroves. We only considered freshly fallen litter and did not collect senescent or decomposed litter. Specifically, we did not gather data with a decomposition time of 0 days in litter bags, as we consider them not to be initial litter. If different locations or sampling time were studied within the same paper, they were considered as independent observations. Data were obtained from tables, main texts, supplementary materials or figures (using GetData software, https://getdata.com). To avoid data repetition, we cleaned the data by removing records with identical initial litter C, N and P concentrations in samples taken at the same geographical coordinates. After extraction and compilation, a total of 20,032 data points (5722 for C, 8572 for N and 5738 for P) from 1798 publications (Figure 1; Notes S1) were included in our study. Meanwhile, we used several published databases of global litter production (Holland et al., 2015; Jia et al., 2016; Liu et al., 2019; Neumann et al., 2018), which included 2966 data points in total (Figure S1), for calculating the returning amounts of leaf litter C, N and P.

To determine mycorrhizal association of litter-producing plants, we used a currently published peer-reviewed database named FungalRoot (Soudzilovskaia et al., 2020) and divided them based on their Latin names according to the *World Flora Online* (www.worldfloraonline.org). We divided mycorrhizal association into three types, namely arbuscular mycorrhizal fungi (AM), ectomycorrhizal fungi (ECM) and dual (i.e. species associated with both AM and ECM fungi), because the roots of more than 90% of terrestrial plant species are associated with either AM or ECM fungi (Brundrett, 2009). Also, we determined lifeform (woody vs. herbaceous) according to Latin names following a previous review (Richardson & Rejmánek, 2011) and classified taxonomic division (angiosperm vs. gymnosperm) according to online botanical databases of *Missouri Botanical Garden* (http://www.missouribotanicalgarden.org), *eFloras* (http://www.efloras.org), and *Identification guide for the wild trees of the Canary Archipelago* (https://www.arbolappcanarias.es).

To assess the effects of litter type, lifeform, mycorrhizal association and taxonomic division on litter initial concentrations of C, N and P, we used generalised linear mixed-effects model using the "lme4" package (Bates et al., 2015). Each predictor was fitted as a fixed-effects factor and the identity of primary studies from which data were collected as a random-effects factor to account for the potential dependence of data points collected from a single primary study. For factors that showed significant effects, we then tested post hoc comparisons at $\alpha=0.05$ using the "emmeans" package (Russell et al., 2018).

2.2 | Variable selection

To determine the essential factors that control the patterns of leaf litter initial concentrations of C, N and P at the global scale, we collected data of climate, plant, topography and soil properties that were reported to affect plant C and nutrient concentrations (Steidinger et al., 2019; Vallicrosa et al., 2022; Xie et al., 2022). Among them, 21 climate variables represented average for the years of 1970–2000. Gross primary production (GPP) data were average for the years of 1988–2020 in remote sensing datasets. The soil data encompassed 32 variables for the 0–45 cm soil layer. Additionally, elevation and slope data were included (see Table S1 for details). Data for climate, plant, topographic and soil were added to leaf litter production and initial concentrations of C, N and P using the "raster" package (Hijmans, 2023) based on the geographic coordinates from the studies.

To minimise the effects of multicollinearity, the variance inflation factors (VIF) of all independent predictor variables were estimated, and the maximum variance inflation factor was eliminated until the variance inflation factor of all independent variables were below a threshold of five using the "car" package (Fox et al., 2007). We then used "VSURF" package (Genuer et al., 2015) for variable selection procedure through random forest, which used a variable profile based on random forests permutation-based score of importance and using a stepwise forward strategy. This strategy added a variable only when the reduction in error was greater than a threshold, that is the reduction in out-of-bag (OOB) error must be significantly greater than the average change obtained by adding noisy variables. Consequently, we final selected subsets of 6, 7 and 6 environmental variables for leaf litter C, N and P concentrations, respectively, to minimise redundancy and maximise model performance (Figure S5). Notably, multicollinearity among the selected variables was limited, as no pair of predictor variables had a Pearson coefficient greater than 0.64 (Figure S6).

2.3 | Predictive modelling

To quantify the relationships between leaf litter initial concentrations of C, N and P and environmental predictors, we fitted several linear regression and machine learning models. Specifically, we constructed a total of four linear regression models and four machine learning models to evaluate their efficacy in predicting leaf litter C, N and P concentrations, with the aim of identifying the best models for predicting leaf litter C, N and P concentrations. Linear regression models included linear regression (LM) model and linear regression model with (LEAPS) stepwise selection (Ziegel, 2003), least angle regression (LARS) model (Efron et al., 2004), and Elastic Net (ENET) model (Zou & Hastie, 2005). On the other hand, machine learning models included boosted tree (BOOSTED; Friedman, 2001), random forest (RF; Breiman, 2001), extreme gradient boosting (XGBoost; Chen et al., 2015) and cubist (CUBIST; Quinlan, 1992) models. All models except for the LM model incorporated built-in tuning parameters (i.e. hyperparameters), which could determine the training strategy and the relevant efficiency of the algorithm (Bergstra & Bengio, 2012). And we used "train" function from "caret" package (Kuhn, 2008) to optimise the model tuning parameters.

More specifically, LEAPS models were trained for the maximum number of variables. LARS and ENET models were trained with 0, 0.01 and 0.1 quadratic penalty parameter. For each RF models, we set the 500 regression trees for maximum number. In XGBoost models were trained with learning rate of 0.1, 0.2 and 0.3 with two to five maximum depth of a tree, 100, 150 and 200 max number of boosting iterations, 0 of minimum loss reduction required to make a further partition on a leaf node of the tree, and 0.6, 0.7 and 0.8 of subsample ratio of columns when constructing each tree and subsample ratio of the training instance. CUBIST models were trained with between 1 and 9 by 2 neighbours and 1, 5, 10, 50, 75, and 100 communities. The package "leaps" was used to fit Leaps, "lars" to fit Lars, "elasticnet" to fit ENET, "plyr" and "mboost" to fit Boosted, "randomForest" to fit RF, "XGBOOST" to fit XGBoost, "Cubist" to fit CUBIST.

To evaluate the predictive accuracy of model and minimise the risk of overfitting, we conducted tenfold cross-validation repeated 10 times with 80% training to 20% validation data for all models to find out the best model hyperparameters by the lowest rooted mean squared error (RMSE). Finally, we assessed RMSE and determination coefficient (R^2) for all tuned models and ranking model performance to find out best model (lowest RMSE and highest R^2). The results

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showed that the random forest models performed the best for all leaf litter initial concentrations of C, N and P, and were subsequently used for all subsequent analyses (Table S2).

2.4 | Variable importance

To estimate the relative influence of each environmental variables for predicting leaf litter initial concentrations of C, N and P, we evaluated the importance of variables using "caret" package for best-performing random forest models, which enables reciprocal measures of variable importance through the variable importance tool. Specifically, the results of the variable importance in random forest models indicated the influence of predictor variables on the model results (Wei et al., 2015), where each of the predictor variables was normalised within a range of 0%–100% to represent the relative importance to the model results. Specifically, to assess the prediction error in the model, the arrangement variable importance measure used OOB estimation to calculate the RMSE for each given regression tree (Breiman, 2001; Grömping, 2009). The derived variable importance measure for the random forest model presents the impact of the environmental predictors to the model results (Wei et al., 2015).

To visualise the relationships between leaf litter production and initial concentrations of C, N and P, and the single environmental predictors, we used partial dependence analyses using the "pdp" package (Greenwell, 2017). The partial dependence plot can demonstrate the influence of individual predictors on the outcome of the machine learning model by displaying the predicted response to a predictor while holding all other predictors at their average values (Friedman, 2001).

2.5 | Global prediction

To calculate leaf litter returning amounts of C, N and P, we also performed the random forest model with 4 selected soil and climate predictors (Figure S7) for leaf litter production (i.e. yearly leaf litterfall), which showed a better fit (R^2=0.72).To identify the global distribution of vegetation (i.e. trees, shrubs and herbs), we used land cover map from 2018 ESA CCI-LC v2 at 300 m original resolution, and selected "forest", "shrubland" and "grassland" classes using the table of correspondence between the IPCC land categories and the CCI-LC classes to be extracted at 0.5°×0.5° resolution (Table S3). We precluded areas from our prediction maps in which (1) any of the environmental predictors had missing data, and (2) the land cover type varied from the integrated land cover systems illustrated above. Accordingly, we employed the best random forest models to predict leaf litter production (Figure S8) and initial concentrations of C, N and P, and exhibited the projections by predicting pixel geographic coordinates (i.e. latitude and longitude) at 0.5°×0.5° resolution. And, we can calculate annual C, N and P returning amounts of leaf litter as follows (Vitousek, 1982):

$$NR = C_i \times M_i \times 100, \tag{1}$$

where NR is the annual returning amount of litter C, N or P ($\mathrm{Mg\,ha^{-1}\,year^{-1}}$); C is concentration (%) of litter C, N or P; and M is the annual litter production amount ($\mathrm{Mg\,ha^{-1}\,year^{-1}}$).

To evaluate the uncertainty associated with map creation, we computed the mean and standard deviation (SD) for coefficient of variance (CV), that is the ratio of SD to mean, of leaf litter production and initial concentrations of C, N and P in each pixel by randomly sampling 500 trees from global predicted random forest model. Subsequently, we employed the 500 estimates of litter nutrient concentrations and litter production in each pixel to derive 500 estimates of litter nutrient returning amounts, from which we can calculated the mean, SD, and CV (Figure S9).

2.6 | Spatial autocorrelation

Spatial autocorrelation is a common issue in spatial data analysis, and neglecting it can result in an overestimation of the model's predictive performance (Cai et al., 2023; Ploton et al., 2020). Thus, we performed semivariograms to identify the spatial autocorrelation patterns in our plant litter data before conducting spatial analyses (Figure S10), and examined the model residuals for spatial autocorrelation (Figure S11). Results indicated that spatial autocorrelation had minimal impact on our prediction models. All statistical analyses were performed with R v.4.2.2 (R Core Team, 2022).

3 | RESULTS

3.1 | Litter C, N and P concentrations

The initial concentrations of C, N and P differed significantly among litter types. Specifically, wood litter had the highest C concentration, with a median of 48.4%. Likewise, the concentration of N was found to be the highest in flower litter as compared to other litter types, with a median value of 1.5%. Root litter exhibited the highest initial concentration of P, with a median value of 0.1% (Figure S4).

Leaf litter initial concentrations exhibited a wide range of C, N and P, with values ranging from 16.1% to 71.4% (median 46.7%), from 0% to 6.8% (median 1.1%), and 0% to 1.8% (median value 0.1%), respectively (Figure S12). The initial concentrations of C, N and P in leaf litter were found to be significantly influenced by lifeforms, mycorrhizal associations and taxonomic divisions. Specifically, leaf litter C concentration in woody plants was higher than that in herbaceous plants. Gymnosperm plants had higher litter C concentration than angiosperm plants. Additionally, leaf litter from plants associated with ECM or both AM and ECM fungi exhibited higher C concentrations as compared to AM fungi (Figure 2). Leaf litter N concentration was higher from angiosperm plants and plants associated with AM or both AM and ECM fungi, but was not significantly affected by lifeforms. In addition, leaf litter P concentration showed an opposite

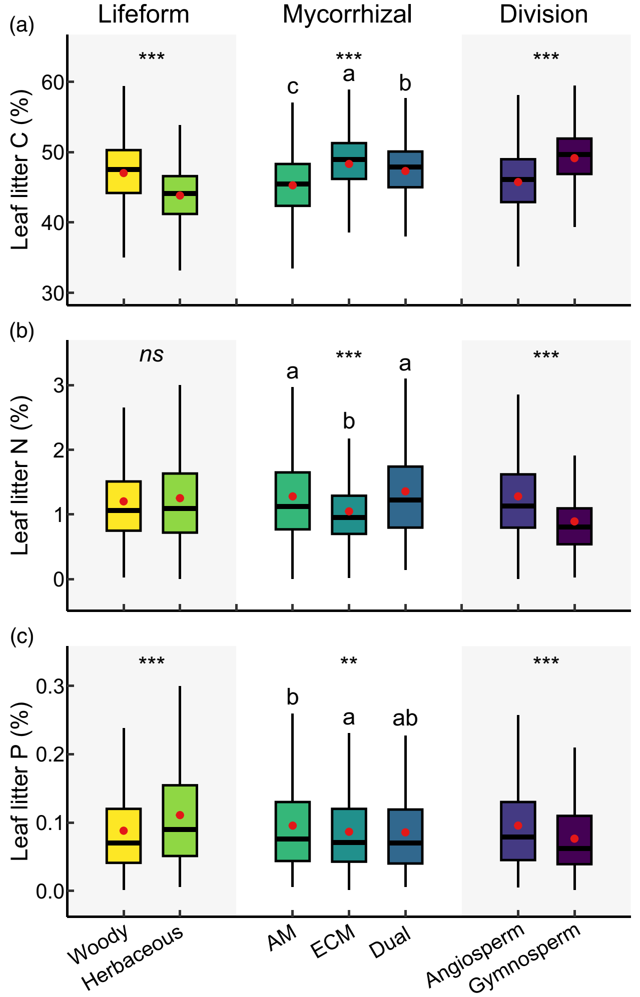

FIGURE 2 Comparison of leaf litter C (a), N (b) and P (c) concentrations within lifeform, mycorrhizal association and taxonomic division. The box spans form the first to the third quartile, with median and mean marked as the black horizontal line and red solid circle of the box. Different letters indicate significant differences among various plant mycorrhizal associations at $^*p<0.05$, $^{**}p<0.01$ and $^{***}p<0.001$. *ns*, not significant between groups ($p>0.05$); AM, arbuscular mycorrhiza; ECM, ectomycorrhiza; Dual, plant associated with both AM and ECM fungi.

trend compared to C concentration, with higher P concentrations in herbaceous, AM or both AM and ECM fungi, and angiosperm plants than in woody, ECM, and gymnosperm plants.

3.2 | Drivers of leaf litter C, N and P concentrations

Our study successfully developed the best random forest regression models, which showed that leaf litter initial concentrations of C, N and P could be predicted by a combination of global-scale soil and climate interactions (Figure 3). Non-linear model approach performed significantly better than linear models for all leaf litter initial concentrations of C, N and P (Table S2). The results also showed that soil properties only explained a relatively small proportion (32.8%) but climate explained a majority proportion (67.2%) of leaf litter C concentration. The most important factor for leaf litter C concentration was isothermality (Figure 3d). Similarly, isothermality was also identified as the most significant factor influencing leaf litter N concentration (Figure 3e), and it was primarily controlled by climate (57.5%) and soil properties (42.5%). Although mean diurnal range emerged as the most important factor for leaf litter P concentration (Figure 3f), only a relatively small portion of it was influenced by climate (48.4%) as compared to leaf litter P concentration regulated by soil properties (51.6%). To better understand the direction of these relationships, we created partial dependence plots that revealed non-linear increasing or decreasing trends in leaf litter initial concentrations of C, N and P in response to soil and climate predicted factors, indicating a strong interaction between these environmental variables (Figure 4).

3.3 | Global maps of leaf litter C, N and P concentrations and returning amounts

At the global scale, leaf litter C concentration was higher in Northern and Eastern Asia, central Africa, Northern and Southern America, and Central Europe compared with other regions. On the other hand, leaf litter N concentration was higher in Oceania, southern Asia, Africa, and southern America. P concentration was found to be higher in central and northern Africa, and southern Asia (Figure 5). In addition, we observed that leaf litter initial concentrations of C, N and P showed latitudinal patterns, with N and P concentrations increasing from the equator to both poles while leaf litter C concentration decreased from the poles to the equator (Figure S13a–c).

Our analysis of leaf litter C, N and P returning amounts across different regions revealed distinct spatial patterns (Figure 5). Specifically, leaf litter C returning amount was predicted to be highest in Central America, Central Africa, Southern Asia and Northern Oceania compared with other regions. Conversely, both leaf litter N and P returning amounts were lowest in Central and Northern Asia, Southern Oceania and Northern America. Furthermore, we founded that leaf litter C, N and P returning amounts also showed a latitudinal gradient, decreasing from the equator to the poles (Figure S13d–f).

4 | DISCUSSION

Supporting our hypothesis, the results showed that leaf litter initial concentrations of C, N and P were significantly affected by lifeforms (woody and herbaceous plants), mycorrhizal associations (AM, ECM and plants with both AM and ECM fungi), and taxonomic divisions (gymnosperms and angiosperms). Our results indicated that litter derived from woody plants had a higher C concentration to that of herbaceous plants, whereas no significant difference was observed in N concentration. Carbon is an important element invested in plant structure and defence through the synthesis of cellulose and lignin (Freschet et al., 2012). In general, leaves of woody plants

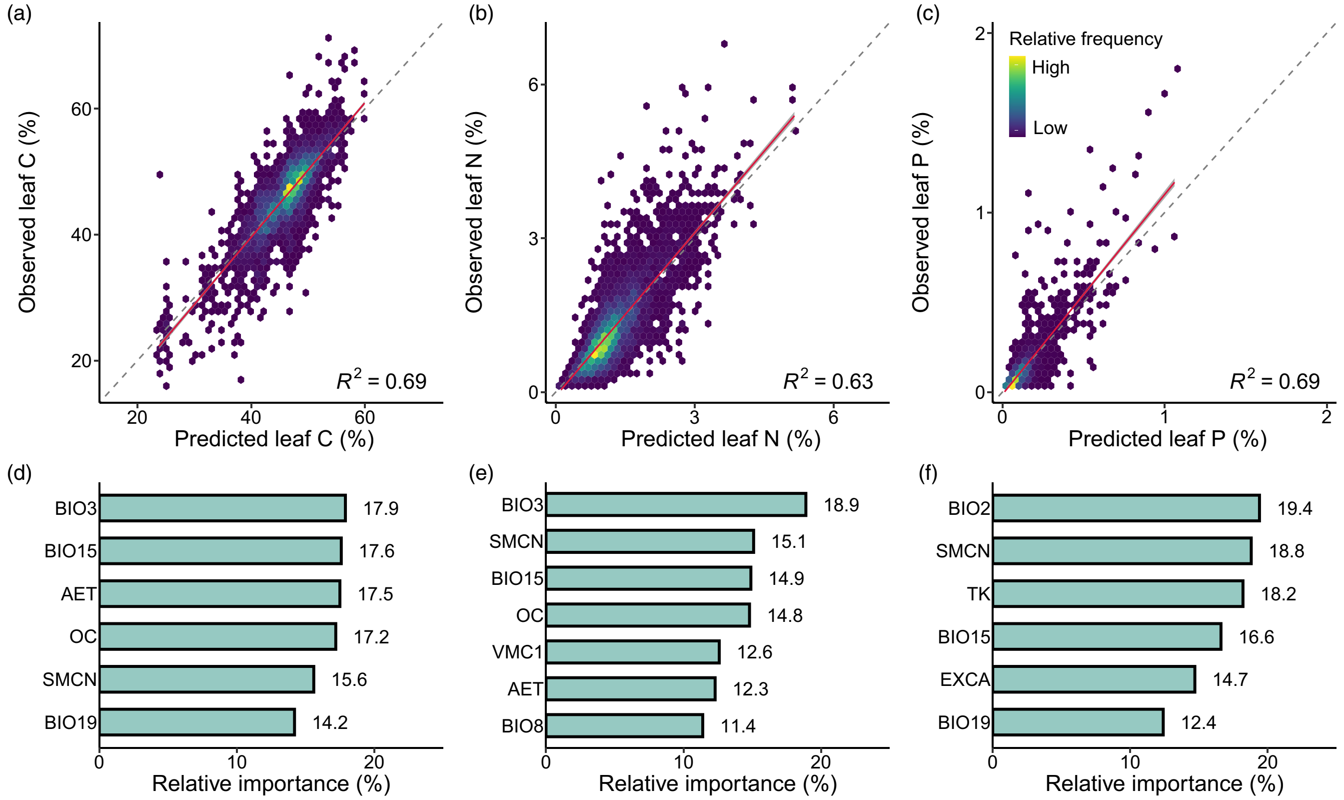

FIGURE 3 Prediction performance and variable relative importance of leaf litter C, N and P concentrations. (a–c) Predictions for leaf litter C (a), N (b), and P (c). The grey dashed lines indicate the 1:1 line, and the red solid lines indicate the regression line between predicted and observed values. (d–f) Relative importance assessed by random forest models run with the most important environmental variables for leaf litter C (d), N (e) and P (f) concentrations. Environment variable abbreviations are listed in Table S1.

typically exhibit greater thickness and contain more cells, along with cell wall components such as lignin, cellulose and hemicellulose (Li et al., 2016; Peng et al., 2022; Popper et al., 2011). These constituents may contribute to the higher C concentration in the leaf litter of woody plants. The P concentration in leaf litter of woody plants were observed to be lower compared to that of herbaceous plants, which may be attributed to the higher demand of herbaceous plants for P to maintain their leaf structure and function as compared to woody plants (Kerkhoff et al., 2006).

Our results revealed that the initial concentrations of C in leaf litter from plants associated with ECM fungi and gymnosperms were higher than those in plants associated with AM fungi and angiosperms, while N and P concentrations showed an opposite trend compared with C concentration. Plants associated with ECM fungi typically have more branched root systems, which can lead them to take up more C in the soil (Cheng et al., 2016). Also, plants associated with ECM fungi generally grow in organic matter-rich forest soil, which may have higher C stocks, resulting in higher C concentration in the leaf litter of ECM plants (Tedersoo & Bahram, 2019; van der Heijden et al., 2015). In general, angiosperm plants had higher nutrient uptake capacity and growth rate (Hobbie et al., 2006; Prescott et al., 2004), and the growth rate hypothesis indicates that fast-growing plants usually have higher leaf N:P ratio, as N is key limiting factor for boreal forests that are required for the metabolic activity of plants (Kerkhoff et al., 2006; Reich & Oleksyn, 2004; Tian et al., 2018). Moreover, the mycorrhizal associations of plants were found to be closely linked to taxonomic divisions and acknowledged as a significant factor influencing ecosystem functions (Soudzilovskaia et al., 2019). Our results reveal that leaf litter derived from plants associated with AM fungi possesses higher litter quality compared to litter from plants associated with ECM fungi. This distinction can be attributed to the prevalence of angiosperm plants with AM fungi in tropical and subtropical regions, where nutrient cycling occurs at a rapid pace. In contrast, ECM fungi tend to dominate in high-latitude ecosystems characterised by slower nutrient cycling processes (Soudzilovskaia et al., 2015; Zhang et al., 2018).

According to our predicted global map, leaf litter initial concentration of C increased with latitude in both hemispheres, whereas litter C returning amount demonstrated an inverse relationship. Conversely, both leaf litter initial concentrations of N and P exhibited a decline with increasing latitude, consistent with previous findings (Xie et al., 2022). This may be associated with the nutrient use efficiency of plants. Plants growing in soils with low nutrient use efficiency tend to have higher N and P absorption efficiency compared to species in fertile soils (Lü et al., 2012; Richardson et al., 2005), which results in nutrients residing longer within the plant, adopting a more conservative nutrient use strategy (Silla & Escudero, 2006). Consequently, nutrient-poor soils receive fewer nutrients from

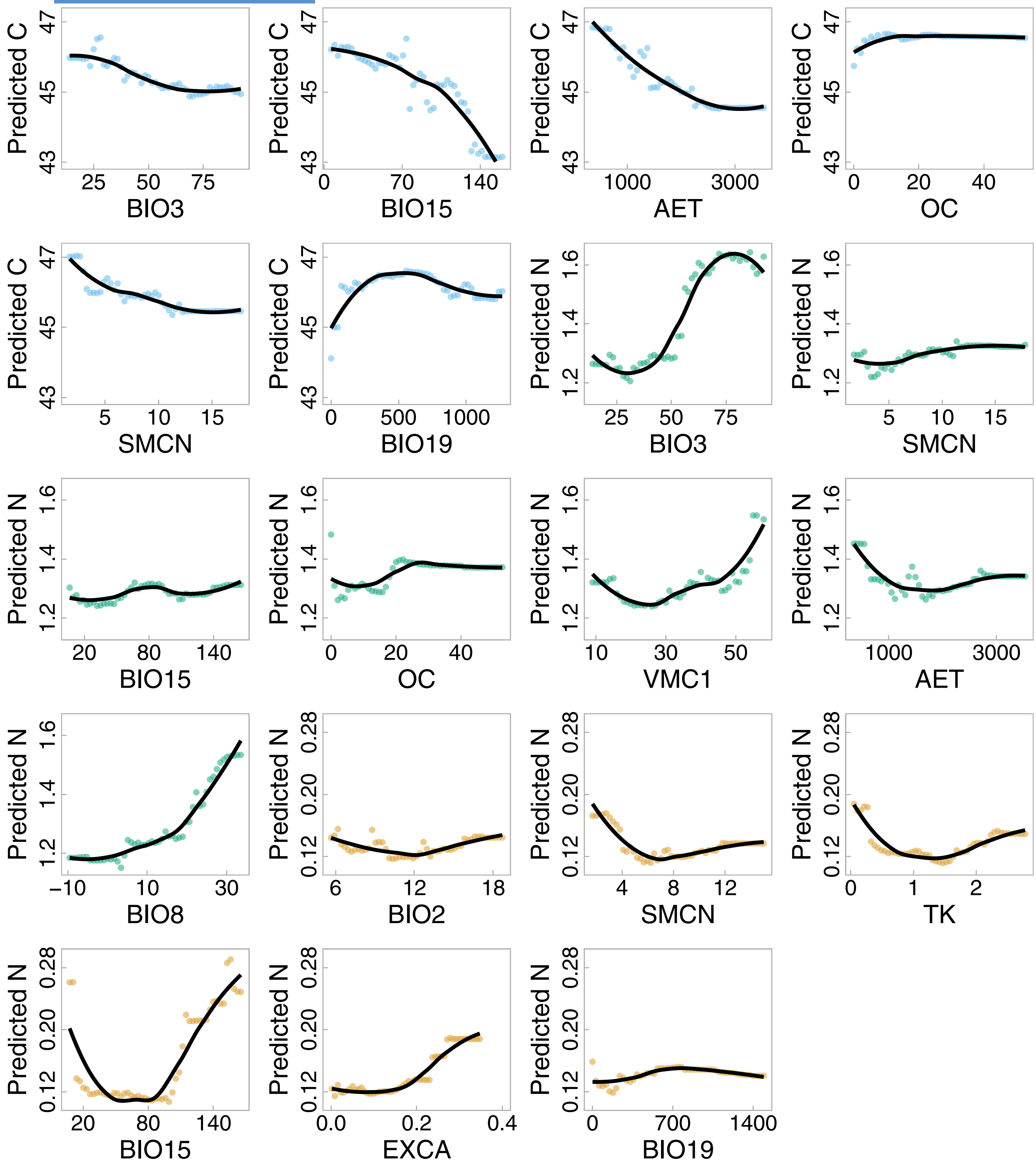

FIGURE 4 Partial dependence plots of the predicted variables for leaf litter C, N and P concentrations. The black solid lines indicated the locally weighted regression. Environment variable abbreviations are listed in Table S1.

plant litter, increasing the plant nutrient use efficiency and creating a further feedback effect on plant litter decomposition (Kitayama et al., 2004; Kobe et al., 2005). However, in contrast to the trend of leaf litter concentrations of N and P, fresh leaf and soil P concentration increased with latitude (Reich & Oleksyn, 2004; Shangguan et al., 2014; Vallicrosa et al., 2022; Xie et al., 2022). Low-latitude regions are predominantly characterised by tropical rainforests and subtropical broadleaf evergreen forests, which are typically limited by P, while high-latitudes regions are dominated by coniferous forests, which are limited by N. Furthermore, fast-growing tropical broad-leaved plants tend to have higher N and P concentrations (FAO, 2020; Sardans & Peñuelas, 2013). The observed patterns of

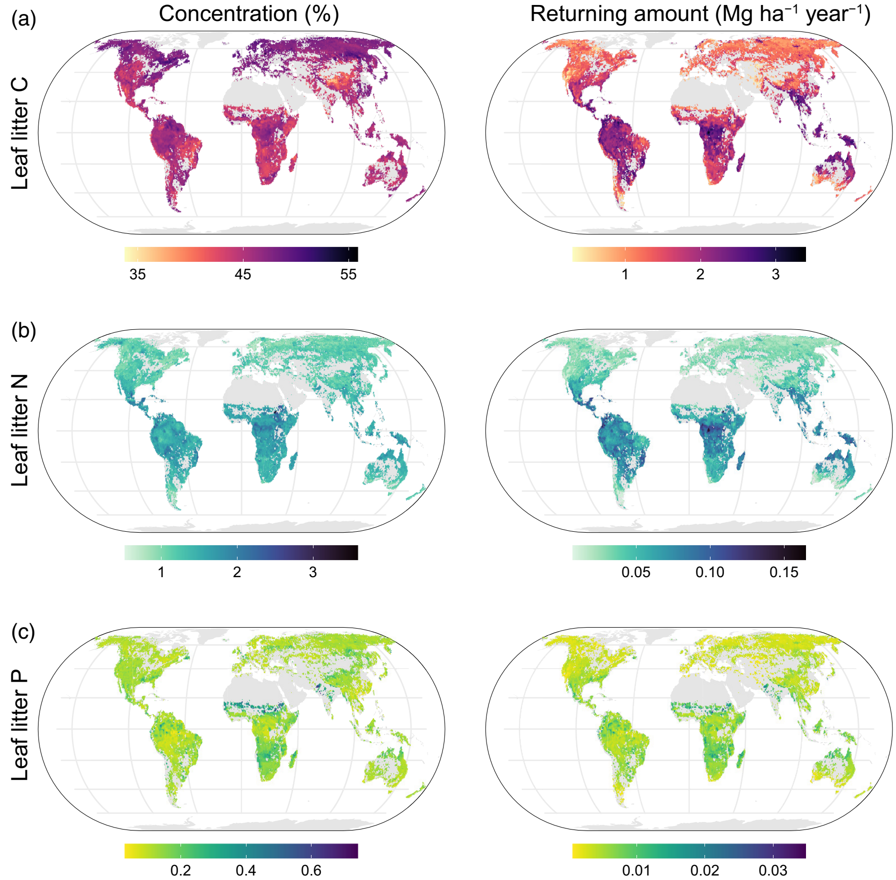

FIGURE 5 The global patterns of C, N and P concentrations and returning amounts in leaf litter. The maps on the left and right show the concentrations and returning amounts for C (a), N (b) and P (c), respectively. All maps are projected at 0.5° resolution.

leaf litter initial N and P concentrations in gymnosperm and angiosperm species align with previous findings that highlights the importance of C in the synthesis of structural (e.g. cellulose) and defensive (e.g. polyphenols) compounds in terrestrial plants, and coniferous plants with conserved nutrient strategies tend to have high C concentration (Freschet et al., 2012). Additionally, differences in growth strategies may contribute to the observed trend, as leaf litter initial concentration of C is typically much higher in hot and rainy tropical areas than in high latitudes.

Broadly speaking, the plant litter initial nutrient concentration is an important factor influencing litter decomposition, while environmental factors are of secondary importance (Ball et al., 2022; García-Palacios et al., 2013). Globally, litter decomposition shows faster rates near the equator, gradually decreasing towards the poles. This phenomenon is primarily attributed to the fact that litter from high-nutrient and low-C concentration plants tends to decompose more rapidly compared to litter from low-nutrient and high-C plants (Freschet et al., 2012; Zhang et al., 2008), which is in agreement with our results for predicting global leaf litter initial concentrations of C, N and P. Plant litter initial C and nutrients concentrations can also indirectly regulate the litter decomposition process by modulating microbial decomposers (Yue et al., 2018), where litter N and P concentrations are considered to be the main determinants of soil microbial colonization-degradation (Cornwell et al., 2008). Microbial stoichiometry underlies the nutrient requirements of microbial communities, and heterotrophic microbes in plant litter are thought to be N- or P-limited (Zechmeister-Boltenstern et al., 2015). Among these, gram-negative bacteria are considered the primary decomposers in litter with high organic matter and N availability (Fierer et al., 2003), while gram-positive bacteria and fungi are more abundant in litter with lower initial nutrient concentrations (Bray et al., 2012). Our results also indicated that soil microbial nutrients influence the litter initial concentrations of C, N and P. This is because microbes largely show homeostatic properties, allowing the microbial community to alleviate limitations imposed on plants by N and P (Zechmeister-Boltenstern et al., 2015). Furthermore, terrestrial litter serves as a significant source of freshwater litter, and their connection is closely intertwined. Interestingly, some studies suggest that the decomposition of freshwater litter is predominantly influenced by microbial communities and initial nutrient elements of the litter, rather than the physical properties of stream (Boyero et al., 2011; García-Palacios et al., 2016). Throughout both aquatic and terrestrial ecosystems, the decomposition of litter C and N is regulated by common driving factors (Yue et al., 2018). It is demonstrated that the study on the distribution of initial concentrations and driving factors for terrestrial litter lays the foundation for a common model of litter decomposition dynamics in both terrestrial and aquatic ecosystems. Overall, the initial concentrations of litter significantly affect the decomposition rate and nutrient release, as well as microbial activity during litter decomposition. Therefore, our study established a global database of the initial litter concentrations and returning amounts of C, N and P, which need to be appropriately parameterised into global litter decomposition models. It is better to simulate litter decomposition processes, aid in predicting nutrient cycling and C dynamics within litter layers, and enhance the accuracy of global C and nutrient cycling models.

Despite the overall patterns were found in our study, limitations still exist because of the availability of data for certain variables or processes. For instance, we observed that plant lifeforms, mycorrhizal associations, and taxonomic divisions significantly influenced litter initial concentrations of C, N and P, but could not be included in the predicting models due to the lack of comprehensive global datasets for these variables. Also, the focus in plant litter studies have been primarily on leaf litter, with limited studies on other litter types, which limits our ability to further analyse and predict global litter C, N and P models in addition to leaf litter. In addition, a majority of the available study sites have been concentrated in the northern hemisphere, especially in China, Europe and the United States. This geographical bias may have limited the generalizability of the results to other regions. Therefore, future studies on litter elements should consider the impacts of factors like lifeforms, mycorrhizal associations and taxonomic divisions, and expand the scope of data coverage to focus more on litter types other than leaf litter.

5 | CONCLUSIONS

Our study quantified the global patterns of litter C, N and P concentrations and returning amounts and found that leaf litter C, N and P concentrations were affected by mycorrhizal association, taxonomic division and/or lifeform. Among the factors that affect litter C, N and P concentrations, climate and soil were the most important ones. Globally, leaf litter C concentration increased with latitude in both hemispheres, while N and P concentrations as well as the returning amounts of leaf litter C, N and P decreased with latitude in both hemispheres. These results provide new insight for understanding the role of litter in biogeochemical cycling of terrestrial ecosystems, and could also improve the predictions of process-based models for terrestrial C, N and P cycling.

AUTHOR CONTRIBUTIONS

Kai Yue and Fuzhong Wu conceived the study. Ji Yuan, Kai Yue, Qiqian Wu, Yan Peng, Zimin Li, Siyi Tan, Chaoxiang Yuan and Xiangyin Ni collected the raw data. Ji Yuan, Kai Yue, Josep Peñuelas, Helena Vallicrosa, Jordi Sardans, Zimin Li, Petr Heděnec and Fuzhong Wu performed statistical analyses. Ji Yuan, Kai Yue, and Fuzhong Wu interpreted the results and wrote the paper with substantial input from all the coauthors.

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CONFLICT OF INTEREST STATEMENT

The authors declare no competing interests.

DATA AVAILABILITY STATEMENT

Raw data used in the study were deposited in figshare: https://doi.org/10.6084/m9.figshare.24439225.v1 (Yue & Yuan, 2023).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Figure S1. The global distribution of leaf litter production in our database.

Figure S2. Phylogenetic tree of plant species included in our study.

Figure S3. Distribution of litter C, N, and P concentrations across taxonomic divisions.

Figure S4. Concentrations of litter C, N, and P grouped by litter types.

Figure S5. Variable selection using random forests.

Figure S6. Pearson Correlation among the most important environmental variables for leaf litter C, N and P concentrations.

Figure S7. Leaf litter production important predict variables.

Figure S8. Global map of predicted leaf litter production.

Figure S9. Uncertainty in predicted leaf litter production and litter C, N, and P concentrations from the random forest models.

Figure S10. Semivariograms showing spatial autocorrelation of leaf litter C, N, and P concentrations, and leaf litter production.

Figure S11. Residual plot for the best random forest models.

Figure S12. Frequency of the distribution of leaf litter C, N, and P concentrations, and leaf litter production.

Figure S13. Global latitudinal patterns of predicted leaf litter C, N, and P concentrations and returning amounts.

Table S1. List of environmental variables used to build the models.

Table S2. Compared the performance of all models using the best predictors.

Table S3. Land cover reclassification table based on the ESA CCI-LC gridded layer.

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