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SYNTHESIS

Unveiling Pervasive Soil Microbial P Limitation in Terrestrial Ecosystems Worldwide

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ABSTRACT

Soil microorganisms are crucial in terrestrial ecosystems, influencing carbon (C) sequestration, yet their metabolic activities are often constrained by nitrogen (N) and phosphorus (P) availability. Despite this, a global understanding of microbial nutrient limitation remains elusive. We synthesised 1245 observations from 225 articles to elucidate patterns and factors of microbial nutrient limitation. Contrary to convention, soil microbial P limitation is widespread (83.78% of observations), with N limitation mainly in temperate zones and pronounced P limitation in tropical and cold zones. Soil microbial P limitation correlates positively with mean annual precipitation and clay content, while N limitation correlates negatively with soil pH. Importantly, microbial nutrient limitation directly affects C cycling, as microbial C limitation increases with decreasing N or P limitation. This underscores the significance of microbial nutrient limitation in terrestrial C cycling and the need to incorporate it into Earth system models for accurate predictions under changing conditions.

1 | Introduction

Soil microorganisms play a pivotal role in regulating the decomposition rates of plant litter and soil organic matter (Zechmeister-Boltenstern et al. 2015; Neurauter et al. 2023), thus exerting significant control over soil carbon (C) and nutrient cycling in terrestrial ecosystems (Vitousek et al. 2010; Camenzind et al. 2018; Zhang et al. 2022). The ecological stoichiometry theory posits that the narrowly fluctuating (homeostatic) stoichiometry of three macronutrients – C, nitrogen (N) and phosphorus (P) – found in plant litter and, to a lesser extent, in soil organic matter, often fails to meet the nutritional demands of homeostatic microbial communities, leading to nutrient limitations during microbial growth (Schade et al. 2005; Manzoni and Porporato 2009; Čapek et al. 2016; Cui et al. 2022a; Liu et al. 2023). Under conditions of N and P limitation, microorganisms typically increase enzyme secretion to accelerate organic matter decomposition,

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aiming to acquire additional N and P to sustain their metabolism (Sinsabaugh et al. 2008; Sinsabaugh and Shah 2012; Zhang et al. 2023). However, this enhanced enzymatic activity may also result in increased soil CO_2 emissions. Earth system models further suggest that nutrient-limited soil microbial communities could diminish the capacity of terrestrial ecosystems to sequester C (Exbrayat et al. 2013; Zhang et al. 2023). Conversely, nutrient limitation may impede the mobilisation of soil C by microorganisms, leading to greater C retention in the soil (Cui et al. 2022b). Thus, a comprehensive understanding of the patterns and drivers of nutrient limitation in soil microbial communities is crucial for elucidating ecosystem functions such as C sequestration.

The heterogeneity of soil microbial nutrient limitation in different geographical regions remains poorly understood, with limited research on how geology and climate influence patterns of microbial N and P limitation (Xu, Thornton, and Post 2013; Du et al. 2020). The substrate-age hypothesis posits that P constraint increases from cold to tropical regions due to the scarcity of 'weatherable' rocks (Hou et al. 2021). Conversely, biological N fixation and N mineralisation exhibit latitudinal trends opposite to those of P, generally indicating an increasing N limitation towards cold regions. However, recent studies have indicated that soil P limitation is more prevalent than N limitation for vegetation on a global scale (Darcy et al. 2018; Du et al. 2020; Hou et al. 2020). The intricate relationship between plants and soil microorganisms, characterised by facilitation and competition, further complicates our understanding of N and P limitation patterns (Kuzyakov and Xu 2013; Čapek et al. 2018; Zhang et al. 2024), and it remains largely unknown whether microorganisms and plants share distinctive or similar patterns in N and P limitation. While past research has suggested that microbial metabolism is primarily limited by P in tropical zones and by N in temperate zones (Chen et al. 2018; Mori et al. 2018; Feng et al. 2019), emerging evidence indicates potential colimitation by both N and P in temperate and cold zones (Fanin, Moorhead, and Bertrand 2016; Jing et al. 2020; Wu et al. 2020; Xiao et al. 2020; Zhang et al. 2023). These discrepancies highlight the urgent need to elucidate the spatial patterns of soil microbial metabolic limitation. To date, a comprehensive examination of the patterns and drivers of soil microbial N/P limitation in natural terrestrial ecosystems worldwide has not been undertaken.

Ecoenzymatic stoichiometry has emerged as a valuable tool for assessing the relative nutrient limitation of soil microorganisms, with soil extracellular enzyme activity reflecting microbial responses to meet their metabolic resource demands (Sinsabaugh et al. 2008; Moorhead et al. 2016; Liu et al. 2023; Zhang et al. 2023). However, the validity of the enzymatic stoichiometry method in determining microbial nutrient limitation has been questioned in some studies (Mori et al. 2018; Rosinger, Rousk, and Sandén 2019; Mori 2020). Nonetheless, much of the conflicting evidence arises from disturbed systems, such as agricultural systems or short-term incubation experiments, where plant-derived organic matter may not be the primary energy and nutrient source for microorganisms. In natural ecosystems, ecoenzymatic stoichiometry methods likely remain the most suitable for assessing patterns of microbial nutrient limitations, given the mechanisms of enzyme production and persistence in soil environments (Nannipieri, Trasar-Cepeda, and Dick 2017; Schimel, Becerra, and Blankinship 2017; Moorhead et al. 2023). Stoichiometric modelling based on extracellular enzymes involves measuring the activity of enzymes responsible for the decomposition of specific organic compounds, such as cellulose, organic P and organic N compounds (Sinsabaugh, Hill, and Shah 2009; Zheng et al. 2022). By analysing the relative proportions of these enzymes, researchers can infer the relative limitations of C, N and P in the soil (Moorhead et al. 2016). This approach provides insights into how microorganisms allocate their metabolic resources to produce enzymes that target the most limiting nutrients, thereby reflecting the nutrient dynamics and constraints within the ecosystem. In this study, we assembled a comprehensive global database of ecoenzymatic stoichiometry, comprising 1245 observations from 225 studies (Figure S1; Data S1). We investigated the patterns of soil microbial N/P limitation in terrestrial ecosystems on the global scale. Specifically, we aimed to address two key questions: (1) What is the global pattern of soil microbial N/P limitation? (2) What are the primary controlling factors of soil microbial N/P limitation worldwide?

2 | Materials and Methods

2.1 | Data Compilation

To investigate microbial nutrient limitation in terrestrial ecosystems, we conducted a comprehensive literature search up to 2023 using the Web of Science (http://webofscience.com) and Google Scholar (https://scholar.google.com). The search utilised the following keywords and phrases: (a) 'soil enzyme' or 'soil extracellular enzymes' or 'extracellular enzyme activity' and (b) 'terrestrial' or 'soil' or 'land'. Articles were selected based on the following criteria: (a) Experiments that assessed enzymes involved in the C (β-glucosidase, BG), N (leucine aminopeptidase, LAP and/or β-N-acetyl-glucosaminidase, NAG) and P (acid/alkaline phosphatases, AP) cycles were included. The enzymes mentioned are only a subset of those involved in the C, N and P cycles, which is a potential limitation, especially considering the more comprehensive data available from metagenomics and metatranscriptomics analyses. However, this quantitative stoichiometric tool serves as an indicator of the integrated resource availability and demand of enzyme-producing communities in the soil over time. An increasing number of studies have utilised ecoenzymatic stoichiometry to determine the nutritional status or nutrient limitations of microorganisms (e.g. Sinsabaugh et al. 2012; Hill et al. 2014; Fujita, Miyabara, and Kunito 2019; Rosinger, Rousk, and Sandén 2019; Cui et al. 2022a; Zheng et al. 2022; Zhang et al. 2023). This approach is highly influential as it focuses on microbial allocation to resource acquisition, providing a valuable assessment of the microbial nutrient status. (b) only data from control groups were extracted in studies with multiple manipulated factors (e.g. warming, N deposition and drought); (c) field experiments were included, while laboratory incubation experiments were excluded; (d) data from intensively managed ecosystems (e.g. agroforests, fertilised

plantations, sown pastures, croplands and urban green spaces) were excluded to prevent false attribution of natural nutrient limitations due to human interference; (e) for studies conducted at the same site, data were collected only from the most recent study; (f) when results were reported for different soil layers, only data from the 0–30 cm soil layer were included; and (g) if measurements were reported for multiple years or months at the same site, soil enzyme activities were averaged across those sampling times. In addition, soil enzyme activities were measured simultaneously, and the use of vector methods can rule out the effect of sampling time on activity.

The filtering steps are outlined in Figure S1. Following these selection criteria, a total of 225 publications and 1245 data points were included. The distribution of sampling sites with ecosystem types in the literature is illustrated in Figure S2. From the selected articles, we extracted data on various soil extracellular enzymes, including BG, LAP, NAG and AP. Additionally, we recorded corresponding information on vegetation types, site location (longitude and latitude), mean annual temperature (MAT) in degrees Celsius (°C), mean annual precipitation (MAP) in millimetres (mm) and soil properties such as pH, soil organic carbon (SOC), total N, cation exchange capacity and clay proportion from the literature. In cases where environmental factors (MAT and MAP) were not directly provided in the papers, site information (latitude and longitude) was used to retrieve them from a global database (http://www.worldclim.org/). Tabular data were extracted directly from the publications, while data presented graphically were obtained using the GetData Graph Digitizer v.2.24 (http://getdata-graph-digitizer.com/). The constructed database encompasses an MAT range of −7°C–30°C and MAP range of 65–7400 mm. The terrestrial ecosystem types included in this dataset are limited to forest (981 observations), grassland (204 observations) and shrubland (60 observations), reflecting the relatively few records available for other ecosystems (e.g. wetlands and deserts). Furthermore, all study sites were categorised into three climate zones based on latitude: Tropical ($0° < \text{Tropical} \leq 23°26'$), Temperate ($23°26' < \text{Temperate} \leq 60°$) and Cold (Cold > 60°) (Ferreira et al. 2015; Zhang et al. 2019).

Ecoenzymatic stoichiometry has been proposed as an effective indicator of the relative nutrient limitations of microorganisms (Sinsabaugh and Shah 2012). Extracellular enzymes are proximate agents of microbial metabolism, facilitating the decomposition of litterfall and microbial residue, depolymerising macromolecules and ultimately generating soluble substrates for microbial assimilation (Sinsabaugh and Shah 2012). The relative abundance of enzymes involved in C, N and P cycling reflects the biogeochemical equilibrium between microbial biomass stoichiometry and the elemental composition of organic matter (Sinsabaugh, Hill, and Shah 2009). Consequently, extracellular enzyme activity can serve as a valuable tool for elucidating the relationship between microbial metabolism and nutrient cycle (Sinsabaugh and Shah 2012; Chen et al. 2018). Typically, this method involves measuring four key extracellular enzymes: BG, LAP, NAG and AP. These enzymes are commonly assayed as proxy indicators of overall C, N and P acquisition (Table S1). Within this context, Moorhead et al. (2016) proposed, drawing on the metabolic theory of ecology and the ecological stoichiometry theory (Sterner and Elser 2002), that plotting the proportional activity of C vs. N acquiring enzymes (BG/ [BG + LAP+NAG]) against C vs. P acquiring enzymes (BG/[BG + AP]). Then, the length and angle of the vector created by connecting a line between the plot origin and point are represented by these proportions. The length quantifies the relative C limitation and the angle quantifies the relative P vs. N limitation (Figure S3). Vector length and angle were calculated using the following equations:

$$\text{Vector length} = \sqrt{(\text{BG}/[\text{BG}+\text{AP}])^2 + (\text{BG}/[\text{BG}+\text{LAP}+\text{NAG}])^2} \quad (1)$$

$$\text{Vector angle} = \text{Degrees}\left(\text{Atan2}(\text{BG}/(\text{BG}+\text{AP}), \text{BG}/(\text{BG}+\text{LAP}+\text{NAG}))\right) \quad (2)$$

Greater C limitation (C_{lim}) of microorganisms is associated with a longer vector length. Vector angles < 45° indicate N limitation (N_{lim}) and the magnitude of N_{lim} increases as the vector angle decreases. Conversely, angles > 45° indicate P limitation (P_{lim}) and the magnitude of P_{lim} increases as the vector angle increases (Moorhead et al. 2016; Cui et al. 2022a).

In addition, we evaluated the validity of the ecoenzymatic stoichiometry method by examining the relationships between soil-available nutrients and corresponding nutrient limitations. Our preliminary analysis revealed a negative correlation between the magnitude of microbial nutrient limitation and soil-available nutrients (Figure S4). This supports the resource allocation theory, which posits that enzyme production should increase when simple nutrients are scarce, and confirms the applicability of the ecoenzymatic stoichiometry method (Sinsabaugh and Shah 2012; Zechmeister-Boltenstern et al. 2015). As discussed by Mori (2020) and Moorhead et al. (2023), the ecoenzymatic stoichiometry method is an effective method for evaluating microbial nutrient limitations in natural ecosystems. This is because disturbances, such as manipulation experiments, can affect enzyme production and distort stoichiometric relationships. The method provides insights into microbial resource utilisation and limitations, offering a functional perspective that differs from other measures of microbial community behaviour.

2.2 | Statistical Analyses

Initially, we mapped the global limitation of microbial nutrients using the package '*tmap*' in R (version 4.2.1). Subsequently, we analyse the impacts of climate zones, ecosystem types, and their interactions on microbial nutrients limitation in terrestrial ecosystems. To select the most appropriate model, we utilised mixed-effects meta-regression analysis, employing the '*glmulti*' package in R and considering the corrected Akaike information criterion, as suggested by previous studies (Calcagno and de Mazancourt 2010; Terrer et al. 2016). The relative importance value, indicating the overall support for each predictor across all models, was calculated as the sum of the Akaike weights for the models in which the predictor appeared. A cutoff relative importance value of 0.8 was

established to distinguish between important and unimportant predictors (Terrer et al. 2016; Chen et al. 2020). All model factors were selected based on the following criteria: (a) the factors of each category with > 300 observations were included in the analysis (total C, total P, ammonia N, dissolved organic N, nitrate N, available P, microbial biomass C, microbial biomass N, microbial biomass P were excluded); (b) variance inflation factors (VIFs) were computed using the package '*car*' to assess multicollinearity, with a VIF value < 5 indicating that collinearity was not a problem (latitude was excluded); and (c) compared with sand, clay in soils is an important P binding component in soil and provides many interfaces for P adsorption (Vitousek et al. 2010; Du et al. 2020). Subsequently, model selection analysis was limited to studies ($n = 435$) that simultaneously reported the responses of biome, elevation, MAT, MAP, pH, SOC, TN, CEC and clay. Finally, regression analysis was performed to fit the relationships between the vector angle (P_{lim} and N_{lim}) and these important predictors.

3 | Results

In contrast to soil microbial N limitation, which accounted for 202 observations (16.22% of the total), predominantly within the temperate zone, P limitation was globally prevalent, comprising 1043 observations (83.78% of the total; Figure 1). Specifically, tropical and cold zones exhibited high levels of soil microbial P limitation, while N and P limitations coexisted within the temperate zone (all $p < 0.05$; see Table 1 and Figure 2). Additionally, we identified soil microbial C limitation at a global scale, with

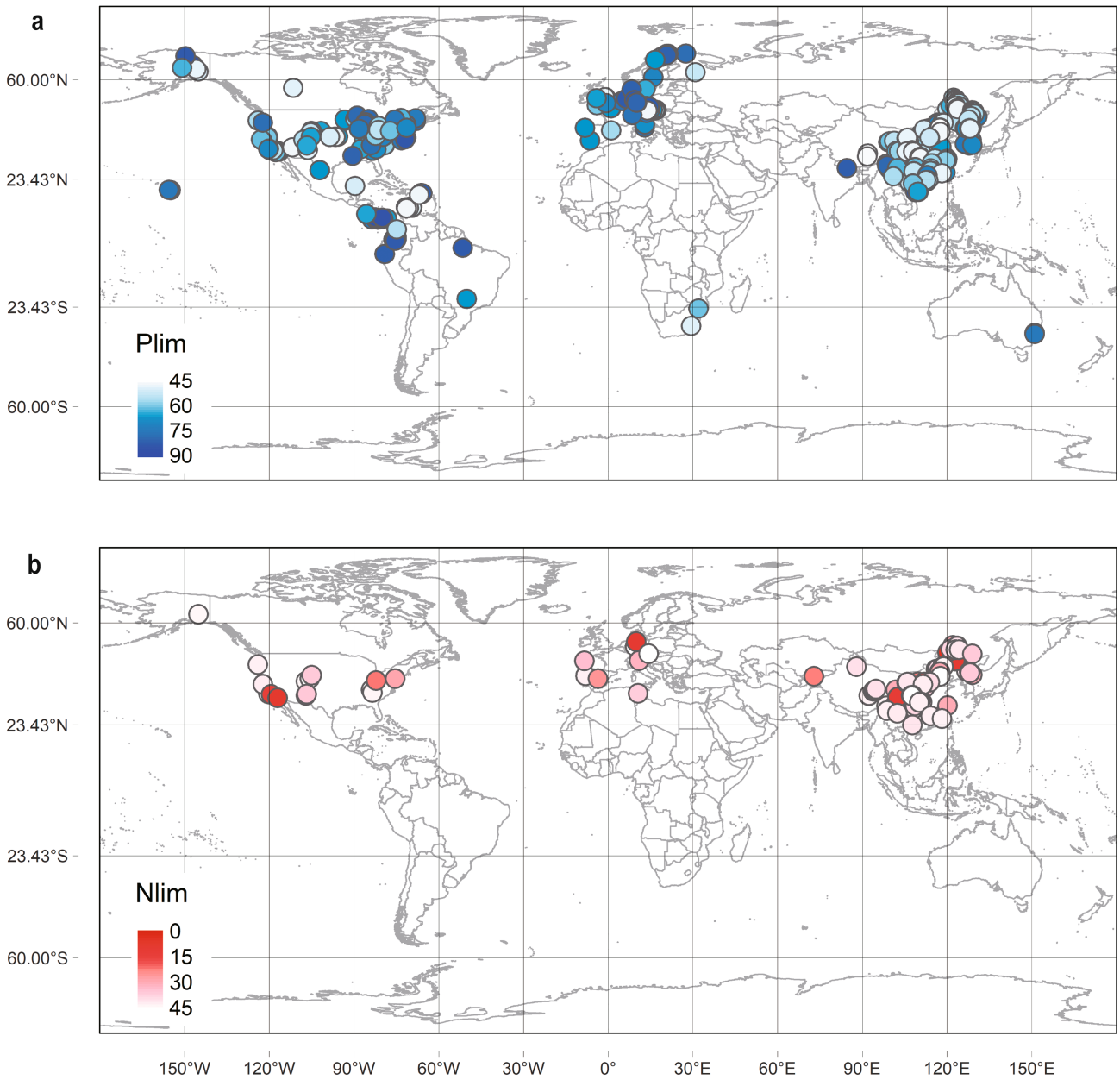

FIGURE 1 | Global distribution of studies on soil microbial phosphorus (P) (a, $n = 1043$) and nitrogen (N) (b, $n = 202$) limitations included in this synthesis. N_{lim} and P_{lim} denote soil microbial N limitation (vector angle < 45°) and P limitation (vector angle > 45°), respectively. The magnitude of N/P limitation is depicted by the shade of the colours.

TABLE 1 | The effects of climate zones, biome types, and their interactions on vector angle and vector length.

	Vector angle (°)				Vector length (unitless)	
	P_{lim} (>45°)		N_{lim} (<45°)		C_{lim}	
	d.f.	*F*, *p*	d.f.	*F*, *p*	d.f.	*F*, *p*
Climate	2	12.44**	2	2.73	2	2.38
Biome	2	3.26*	2	1.55	2	4.21*
Climate × Biome	4	1.88	4	1.56	4	0.96

Note: Statistical significance is denoted as follows: *$p < 0.05$; **$p < 0.001$.

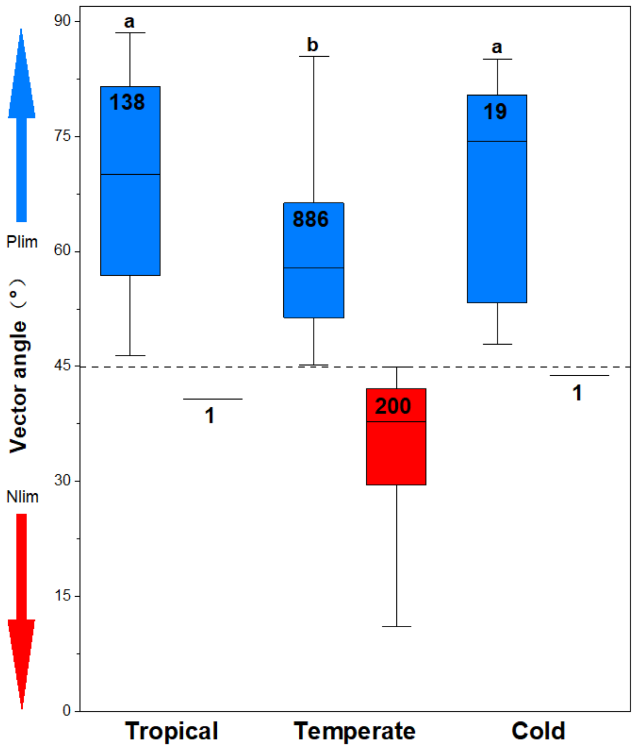

FIGURE 2 | Comparison of vector angles (N/P limitation) among different climate zones. Different lowercase letters on the error bars indicate significant differences between climate zones, determined by the Tukey HSD test at the $p < 0.05$ level. P_{lim} and N_{lim} denote soil microbial P and N limitations, respectively. Vector angles <45° indicate N_{lim} and the magnitude of N_{lim} increases as the vector angle decreases (blue arrow), whereas angles >45° indicate P_{lim} and the magnitude of P_{lim} increases as the vector angle increases (red arrow). The sample size is indicated by the number within each column.

variations observed across different biomes. Particularly, forests exhibited higher levels of C limitation compared to grasslands ($p < 0.05$; Table 1; Figures S5 and S6).

The model selection analysis revealed that MAP and clay content were the most crucial moderators for soil microbial P limitation (Figure 3a). We observed a positive correlation between P limitation and both MAP and clay content, with significance observed for all relationships (all $p < 0.05$; Figure 3b,c). Regarding soil microbial N limitation, soil pH emerged as the most significant moderator, positively influencing N limitation ($p < 0.05$; Figure 3d,e). Furthermore, soil microbial P limitation exhibited a negative relationship, while N limitation demonstrated a positive relationship with increasing levels of soil microbial C limitation (all $p < 0.05$; Figure 4).

4 | Discussion

4.1 | Pervasive P Limitation Worldwide

Our observation of worldwide microbial P limitation in terrestrial ecosystems is, to the best of our knowledge, the first of its kind. This widespread occurrence of soil microbial P limitation can be elucidated through several ecological theories-growth rate hypothesis (Sterner and Elser 2002; Zechmeister-Boltenstern et al. 2015), the stoichiometry of consumer-driven nutrient recycling theory (Sterner and Elser 2002), and the soil microbial substrate preference (McGill and Cole 1981; Zechmeister-Boltenstern et al. 2015). First, according to the growth rate hypothesis, soil microorganisms are inherently prone to P limitation (Sterner and Elser 2002). Given their rapid growth rates, microorganisms require substantial amounts of P to maintain the dynamic population stability by synthesising P-rich ribosomal RNA and adenosine triphosphate (Elser et al. 2000). Second, the stoichiometry of consumer-driven nutrient recycling theory suggests that the elemental composition of microorganisms, as consumers, tends to remain relatively stable (Evans-White and Lamberti 2006). Soil microorganisms play a crucial role in decomposing plant detritus, leading to a decline in the N:P ratio from 45:1 in litter to 17:1 in soil, ultimately converging to 6:1 for microorganisms (Sinsabaugh et al. 2008; Xu, Thornton, and Post 2013). This trend suggests that soil microorganisms are more likely to be limited in P, as more N is involved in the detrital biogeochemical processes. Conversely, our results could verify the phenomenon of the global N limitation for plants due to their acquisition of N and P mainly from soils. Furthermore, studies have indicated that certain microbial taxa exhibit a preference for utilising C sources such as organic polymers and humus rich in organic N (Zechmeister-Boltenstern et al. 2015). This substrate preference may enhance the availability of N to soil microorganisms. However, the availability of soil P is predominantly governed by the slow weathering process of soil parent material (Augusto et al. 2017), resulting in P being relatively less available and thus contributing to pervasive P limitation in terrestrial ecosystems worldwide.

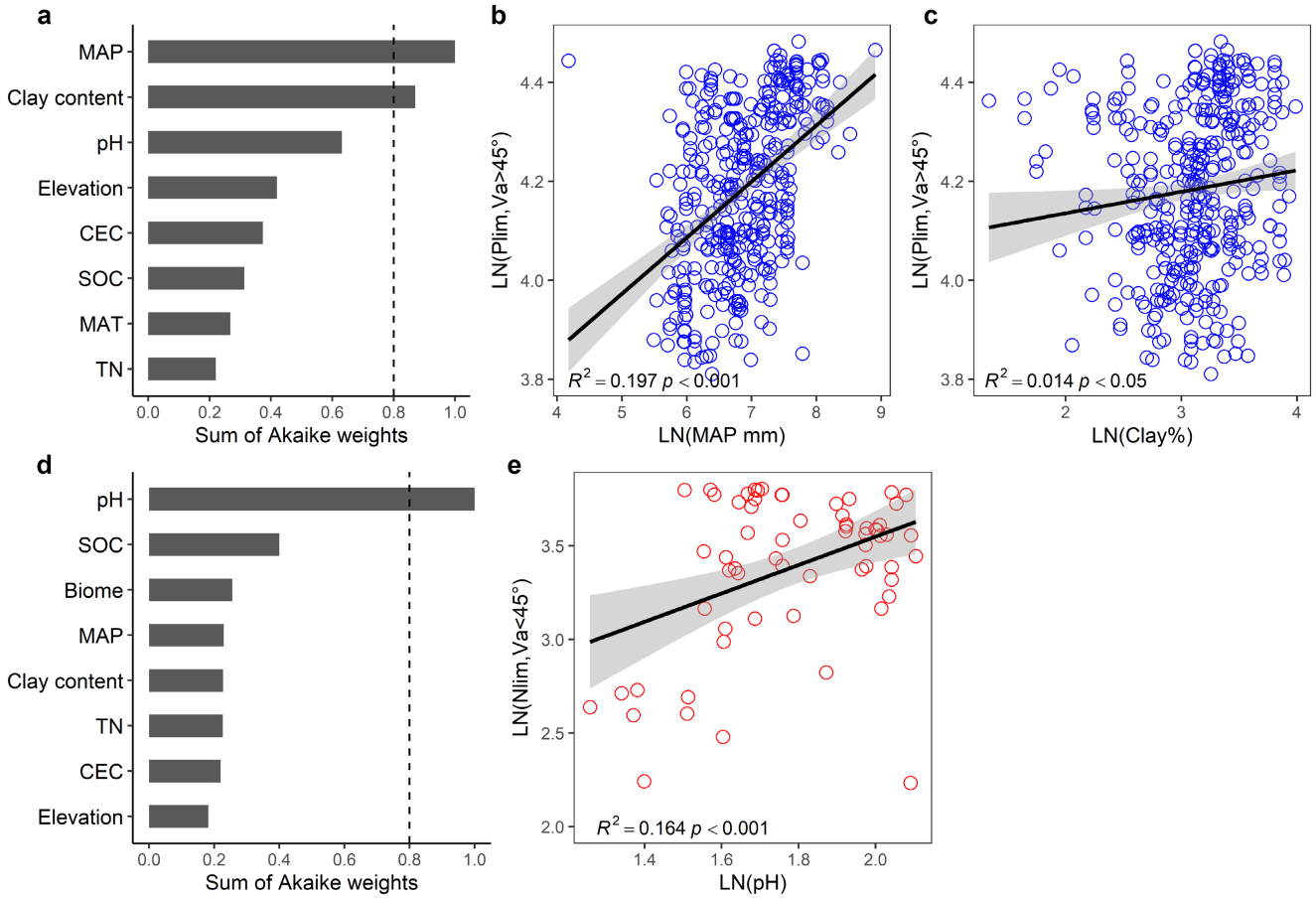

FIGURE 3 | Model-averaged importance of predictors on soil microbial P (a) and N (d) limitation and relationship of P limitation with mean annual precipitation (MAP) (b) and clay content (c) and that of N limitation with soil pH (e). The cutoff is set at 0.8 (dashed line) to distinguish essential predictors from non-essential predictors. The light grey area around the regression line indicates a 95% confidence interval. P_{lim} and N_{lim} denote soil microbial P and N limitation, respectively. N_{lim} increases as the vector angle decreases, whereas P_{lim} increases as the vector angle increases (see Figure S3). P_{lim} was positively correlated with MAP and clay ($y = 0.113x + 3.406$; $y = 0.043x + 4.049$); N_{lim} was positively correlated with soil pH ($y = 0.759x + 2.033$). Abbreviations of the soil properties and environmental factors are: Mean annual temperature (MAT), soil organic carbon (SOC), total nitrogen (TN) and cation exchange capacity (CEC).

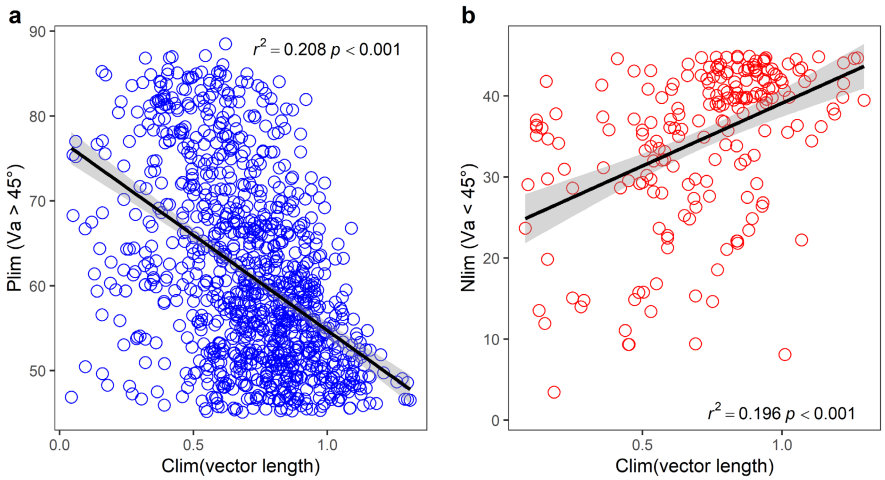

FIGURE 4 | Relationships of soil microbial C limitation with P (a) and N limitation (b). The light grey area around the regression line indicates a 95% confidence interval. P_{lim} and N_{lim} represent soil microbial P and N limitations, respectively. P_{lim} was negatively correlated with C_{lim} ($y = -22.439x + 77.197$); N_{lim} was positively correlated with C_{lim} ($y = 15.029x + 24.053$). N_{lim} increases as the vector angle decreases, whereas P_{lim} increases as the vector angle increases (see Figure S3).

4.2 | P Limitation Among Climatic Zones

Our results revealed higher soil microbial P limitation in tropical and cold zones compared to that in temperate zones. The elevated P limitation observed in the tropics may predominantly stem from the low bioavailability and high leaching of P, whereas in cold zones, it is primarily driven by the low accessibility of P and reduced soil microbial activity (Mori et al. 2018). In tropical regions, soil P is often chemically protected but susceptible to loss through physical processes such as leaching. Chemically, soil P is adsorbed by oxides and hydroxides of aluminium, iron or a combination of both, forming complexes that effectively sequester P and render it inaccessible to microorganisms (Vitousek and Farrington 1997; Hou et al. 2020). Physically, the combination of high rainfall and temperature in tropical regions promotes the continuous loss of dissolved inorganic P and organophosphorus through leaching, as well as the depletion of native minerals during long-term soil development (Hou et al. 2020). Additionally, the high N deposition in tropical regions stimulates soil phosphatase activity, suggesting that soil microorganisms are more susceptible to P limitation (Brookshire et al. 2012).

The substrate age hypothesis posits that high-latitude soils, which have undergone cycles of glaciation, are relatively young and thus possess a greater capacity to release P compared to older tropical soils that have experienced prolonged P leaching (Hou et al. 2021). However, our findings reveal high soil microbial P limitation in cold zones. This unexpected result may stem from the inhibitory effects of cold climates on the processes that typically release mineral P into a bioavailable form. Specifically, the cold climate hampers the conversion of mineral P to available P through abiotic weathering, desorption and biophosphate solubilisation (Darcy et al. 2018). Moreover, low temperatures and dry conditions in cold zones substantially suppress the activity of soil microorganisms (Cruz-Paredes, Tájmel, and Rousk 2021), hindering their ability to mine P and physically impeding microbial access to available P in soil profiles (Viereck et al. 1983; Vitousek et al. 2010; Segura et al. 2017). Overall, the low temperatures prevalent in cold zones likely impede the mobilisation of mineral P, thereby exacerbating soil microbial P limitation. In contrast, we noted that soil microbial N limitation was predominantly restricted to temperate regions. This observation may be attributed to the fact that soils in old-growth tropical zones are typically rich in available N (Vitousek et al. 2010), as tropical forests could accumulate N through rapid biological N fixation. In cold regions, the lower temperature makes the activity of soil microorganisms weaken and the demand for N is minimal according to the temperature-biogeochemical hypothesis (Post et al. 1985; Reich and Oleksyn 2004). These findings highlight the complexity of the relationship between soil N cycles and soil microorganisms on a global scale. To further enrich our understanding of microbial nutrient limitations, future research should focus on acquiring data on the structure and function of soil microbial communities.

4.3 | Predictors of P and N Limitation

We identified MAP and soil clay content as the two primary factors regulating soil microbial P limitation on a global scale. The observed increase in P limitation with increasing MAP can be attributed to several factors. First, increased precipitation tends to inhibit soil organic P mineralisation by enhancing P adsorption processes. High water availability stimulates the reduction of iron (Fe) and the reprecipitation of amorphous iron (Fe)/aluminium (Al) oxides (Nordt and Driese 2009), resulting in greater binding of soil organic P to the surface of these amorphous metal oxides. Soil organophosphorus bounded to Fe/Al oxides typically exhibits low solubility and can transform into intermediate or recalcitrant forms, which are difficult to decompose (Jiang et al. 2015). Second, our data showed that high precipitation is generally associated with high temperatures in most regions of the globe (Figure S7a). Moreover, high temperature accelerates the transformation of soil-available P and secondary mineral P to occluded forms, while high precipitation may lead to the loss of secondary mineral P or occluded P. Additionally, hypoxic conditions induced by high precipitation may restrict soil microbial activity, further limiting microbial P mining. Consistent with previous regional studies (Jian et al. 2022), we found that P limitation increased with higher clay content. This is likely due to the fact that soils with a high clay fraction are typically strongly weathered and have relatively poor P availability (Vitousek et al. 2010). Moreover, clay particles in soils serve as important P-binding components, providing numerous interfaces for P adsorption. This phenomenon reduces the mobility of P in the soil, further contributing to soil microbial P limitation (Gérard 2016). In general, precipitation and soil clay directly or indirectly influence P-related soil processes, leading to alterations in P forms and availability to microorganisms. These factors positively mediate soil microbial P limitation.

For soil microbial N limitation, we observed a decrease with increasing soil pH, suggesting a negative relationship. This phenomenon may be attributed to several factors. First, soils with low pH reduced microbial biomass and activity, leading to weak soil N mineralisation and subsequent N accumulation (Kemmitt et al. 2006; Zhao et al. 2017; Chen et al. 2024b). As a result, there is less substrate (ammonia N) available for soil microbial nitrification (Li et al. 2020) (Figure S7b). Second, increasing soil pH enhances nitrification activity among soil microorganisms, leading to higher N availability (Zhang et al. 2017; Wang et al. 2019; Li et al. 2020). Third, soil pH negatively affects enzyme activity involved in the N cycle (Li et al. 2019). For instance, a global-scale meta-analysis has shown that NAG decreases significantly with increasing pH (Sinsabaugh et al. 2008). Additionally, other studies have noted that certain protease and urease activities are highest under acidic conditions (Kamimura and Hayano 2000; Li et al. 2019).

4.4 | Implications and Limitations

Globally, microbial energy–nutrient limitation exhibits an inverse coupling, as indicated by our finding that microbial C limitation increased with decreasing microbial N or P limitation. Microbial activity plays a crucial role in mediating soil nutrient cycling, facilitating the decomposition of organic matter and releasing soil C into the atmosphere. Our results suggest that the availability of N and P in terrestrial ecosystems may profoundly affect the decomposition or sequestration of SOC.

Biogeochemical constraints, such as N and P limitations, exert significant influence on catabolic processes within soil, thereby affecting soil respiration rates and the accumulation of organic C (Cui et al. 2022a). Conversely, the substantial alterations in N and P inputs to terrestrial ecosystems, particularly the increased deposition of N and P, have the potential to reshape current microbial N and P limitation patterns. These changes could lead to shifts in biogeochemical processes, potentially resulting in greater C emissions into the atmosphere (Zhu et al. 2016; Wang et al. 2017; Pan et al. 2021). Our findings underscore the importance of investigating the roles of microbial nutrient limitation in mediating the global C cycle.

There are several limitations in this global synthesis of microbial nutrient limitation. First, experimental data from cold zones are largely underrepresented, and more studies from these ecosystems are needed for a more comprehensive understanding of terrestrial ecosystems. Second, some potential predictors, such as soil N and P availability, were not included in our analysis. Lastly, while we base our interpretation on orthodox ecological theory, we acknowledge the contrast between ecological theory and biochemical reality in soil ecology. For example, microorganisms often adopt a conservative recycling strategy under nutrient limitation, retaining and efficiently reusing N and P intracellularly whenever molecular adaptations are needed (Frossard et al. 2000; Chen et al. 2024a). Despite these limitations, our study is the first comprehensive evaluation of soil microbial nutrient limitations and their driving factors in natural ecosystems. It underscores the importance of explicitly integrating microbial nutrient limitation into biogeochemical models to improve predictions of the global C cycle.

Author Contributions

All authors contributed to the intellectual content, research procedures and/or manuscript preparation. X.X. conceived the idea and designed the study. L.G. collected and complied the data set. L.G., C.J. and X.X. analysed the data and wrote the first draft of the manuscript with input from all authors.

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Data Availability Statement

The data that support the findings of this study are openly available in figshare at https://figshare.com/s/688a4d49d6865498cb8d.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.