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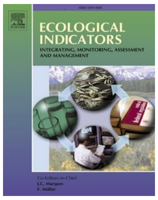

Relative importance of soil properties and functional diversity to the spatial pattern of the forest soil nitrogen

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ABSTRACT

Surface soil nitrogen (SN) is the main source of plant nutrient uptake, and its dynamic change is related to forest productivity, ecosystem carbon and nitrogen cycles, and water conservation. However, few studies have investigated the factors influencing SN. The linear mixing effect and generalized additivity model were used to investigate the spatial patterns and influencing factors of SN by collecting and measuring the total nitrogen content of forest soil samples in the middle and lower reaches of the Xijiang River Basin (XRB). We found that the total nitrogen content in broad-leaved forest soils was significantly higher than that in coniferous forest soils. Forest SN was influenced by soil properties and diversity indicators, and the full model constructed by influencing factors was more applicable to broad-leaved forests. Soil properties were the main explanatory factor for SN (53.53% in the full model, 61.02% in broad-leaved forests), with sub-surface soil nitrogen (sub SN) being the largest explanatory quantity factor (48.52% in the full model, 58.04% in broad-leaved forests). Therefore, forest management in the XRB should avoid damaging the sub-surface soils to prevent nitrogen loss. In the context of global change, the further study of the effect of nitrogen deposition on SN is warranted.

1. Introduction

Nitrogen is essential for the growth of forest trees, and it is an important component of photosynthesis in plant leaves (Raciti et al., 2008, Ohyama, 2010). Moreover, nitrogen is involved in the physiological activities of plants and the building of cellular structures (Millard et al., 2006). Studies have shown that more than half of the nitrogen plants need to grow comes from the uptake of soil by their roots (Nair et al., 2016, Jia et al., 2020b). Forest soils are major reservoirs of nitrogen and play a vital role in maintaining the carbon and nitrogen cycles of forest ecosystems and maintaining ecosystem stability (Wu et al., 2016, Deng et al., 2019). Previous studies have shown that the nitrogen content of surface soil (0–30 cm) is more important for forests than other nutrient elements (Barcena et al., 2014, Shi et al., 2016, Liu et al., 2018a). Soil nitrogen can easily enter water through the leaching process, which leads to the loss of forest soil nitrogen and may lead to surface and subsurface runoff pollution (Moldan et al., 2018, Saarnio et al., 2018).

The nitrogen content of the soil surface layer is mainly influenced by soil factors and ground cover plants. Studies have indicated that enzyme activity in soils is closely related to nitrogen content (Song et al., 2019, Liu et al., 2021a). Soil enzymes play an important role in the functional diversity and nutrient cycling of ecosystems (Sinsabaugh et al., 2002). Moreover, nitrogen content in soil may be controlled by soil-forming factors. A number of studies have discussed the relationships between topographic variation and soil element content, based on different vegetation type areas (Yang et al., 2013, Bangroo et al., 2020, Lopez-Marcos et al., 2020). Previous study found that a strong correlation exists between altitude and soil nitrogen enrichment (Zhao et al., 2017, Zhang et al., 2021, Gomoryova et al., 2022).

Changes in soil cover caused by vegetation restoration promoted the uniform distribution of nitrogen in the soil's profile (Cao et al., 2020, Liu

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et al., 2021b). This may be explained by the fact that changes in vegetation type alters the plant species, resulting in the change of litter and affecting soil properties (Yang and Luo 2011, Gavito et al., 2021). A previous study found that broad-leaved forests are more conducive to total nitrogen accumulation than coniferous forests (Guo et al., 2021). However, the results of a study on the riparian zone showed that the vegetation biomass increased significantly after vegetation restoration, and the soil nitrogen content did not change significantly (Hale et al., 2018). The influence of environmental factors on soil nitrogen was more pronounced than that of ground cover types. For example, soil properties (Liu et al., 2021b, Dai et al., 2022), altitude (Gabarron-Galeote et al., 2013, Bhandari et al., 2020), and depth of soil layer (Too et al., 2018, Paltineanu et al., 2020) were significantly correlated with soil nitrogen content.

Soil organic carbon (SOC) was an important factor affecting nitrogen content, and there was a strong coupling relationship between carbon and nitrogen (Cleveland and Liptzin 2007, Vasbieva 2019). The interactions between carbon and nitrogen are critical to ecosystem productivity and stability (Li et al., 2012, Trigalet et al., 2016, Ramesh et al., 2019). Some studies have found that carbon release from ecosystem may be closely linked to the increase of nitrogen level (Zhou et al., 2014, Wang et al., 2015), but this relationship was not stable (Jonsson and Sigurdsson 2010, Riggs and Hobbie 2016). The nonlinear relationship between soil nutrients and environmental variables was also confirmed (McBratney et al., 2000).

The Pearl River, the second largest and fourth longest river in China, is an important water source for the Guangdong-Hong Kong-Macau Greater Bay Area (Sun et al., 2008, Liu and Han 2021). The Xijiang River is the largest tributary of the Pearl River, occupying 78 % of the total water network area (Sun et al., 2015), of which the lower reaches are typical of the karst landscapes (Jiang et al., 2014, Qin et al., 2019). Therefore, the ecological security and ecosystem stability of the Xijiang River Basin (XRB) is of great importance to the development of the Pearl River Delta.

At present, the research on this area mainly focuses on hydrology, including the analysis of the impact of increased CO_2 on hydrology (Niu et al., 2013), the sources of heavy metal elements in riverbed sediments (Ru et al., 2018), and tracing the sources of particulate black carbon in the rivers of the XRB (Liu and Han 2021), among others. The XRB is rich in forest resources, and most research has been conducted on soil erosion and soil faunal communities in forested areas (Chen and Lian 2016, Ru et al., 2018). Therefore, it is highly important to study the spatial patterns of nitrogen in forest soil, the main influencing factors of such patterns, and their relative importance.

In this study, we applied linear mixed effects and generalized additive models to analyze SN from 523 soil sampling sites in XRB. Specifically, our objectives were (1) to estimate the spatial pattern of nitrogen in forest soil, and (2) to reveal the relative contributions of soil properties and diversity indices to the spatial variability in SN. The results of the study help to identify the dominant factors of SN and provide a basis for scientific forest management.

2. Materials and methods

2.1. Study area

The study area is in the middle and lower reaches of the XRB, which is the longest river in the Pearl River system (Fig. 1). The mainstem of the Xijiang River originates in the Mountain Maxiong in Yunan Province and flows into the South China Sea in Guangdong Province, with a total length of 2214 km (Pearl River Water Resources Commission, 2005). XRB has an abundance of water and flows through four provinces. The middle and lower reaches of the XRB are home to a large population and a developed economy (Wu et al., 2021). The study area exhibits a

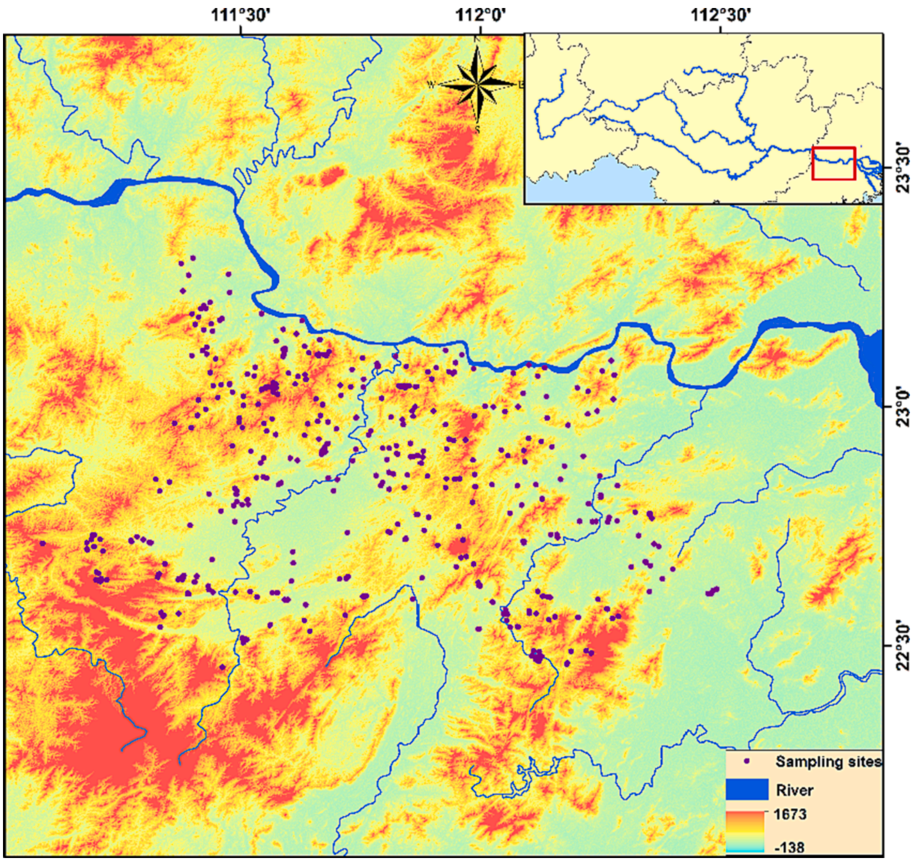

Fig. 1. Forest soil samples in middle and lower reaches of the XRB.

southern subtropical monsoon climate with dry and cold winters and hot and rainy summers (Yao et al., 2007, Zhen et al., 2016). The average annual temperature is 21.2℃, the average annual precipitation is about 1,650 mm, and the rainfall is mainly concentrated from April to October. The area is undulating and has a variety of soil types, including ruddy loam, red loam and mountainous yellow loam (Wang et al., 2019). The study area is rich in vegetation types, with 63 % forest cover, which plays an important role in water conservation and soil conservation in the XRB.

2.2. Soil properties

In order to ensure that soil samples were covered in a large enough spatial scale in the study area, a total of 523 sampling sites were selected (Fig. 1), among which 74 were coniferous forests and 449 were broad-leaved forests. In addition, topography and elevation were taken into account when selecting the sampling points. At each sampling site, we measured the thickness of litter layers and soil humus (SH) and collected soil samples from 0 to 20 cm (surface layer) and 20–40 cm (sub-surface layer). Information on the slope gradient, slope direction, soil type, and geographical location of the corresponding sample sites were recorded. Soil samples were air-dried, ground, and sieved (2 mm) for chemical analysis in the laboratory. Soil organic matter (SOM) was determined by the potassium dichromate oxidation external heating method (Nobrega et al., 2015). Total nitrogen content was determined by Kjeldahl method (Bremner 1995).

2.3. Biodiversity indicators

The remote sensing images used in this study is Landsat-8 OLI, which was downloaded from the USGS (US Geological Survey). The cloudless images from July to September in 2020 were selected for orthography correction, geometric correction, radiometric calibration, atmospheric correction, image mosaic, and cropping. The biodiversity indicators, including leaf area index (LAI), photosynthetic active radiation (PAR), nitrogen reflection index (NRI) and Normalized Difference Vegetation Index (NDVI), were obtained by interpreting remote sensing image data. LAI, which represents the degree of leaf sparsity, is an important parameter to describe vegetation growth state and canopy structure, and controls biophysical processes such as photosynthesis, respiration and transpiration of vegetation (Yasuoka et al., 2018, Nelson et al., 2020, Sinha et al., 2020). PAR is expressed as the fraction of Photosynthetically Active Radiation (FPAR), which is the ratio of the fraction of photosynthetically active radiation absorbed by the plant canopy that is involved in the accumulation of photosynthetic biomass to the radiation irradiated to the plant, reflecting the strength of the plant's photosynthetic capacity (Huemmrich et al., 2019). The NRI is an important indicator of photosynthetic efficiency and overall nutritional status of plants (Hua et al., 2019). NDVI reflects the greenness of surface vegetation, which can be calculated from remote sensing images containing near-infrared and red wavelengths (Jimenez et al., 2022).

2.4. Statistical analyses

Based on the lme function in package R “nlme”, the linear mixed effects model (LMM) was used for model fitting (Pinheiro et al., 2014). The R package ‘MuMIn’ was used to calculate the Akaike Information Criterion (AIC) and the Bayesian Information Criterion (BIC) (Anderson and Burnham 2002), and the marginal R^2 and conditional R^2 (Nakagawa and Schielzeth 2013) were used to evaluate and select models (Barton 2009). Generalized additive models (GAMs) were used to analyze the relationships between SN and influencing factors through the gam function in the ‘mgcv’ package (Wood and Wood 2015).

3. Results

3.1. Spatial pattern of soil properties and diversity indicators

High spatial variability in soil properties, the content of SOM, greatly varied across the study area (26.24 ± 13.65 g kg^{-1}, mean ± SD), with high variability in the northwest and low variability in the central and eastern regions (Fig. 2a). The vast majority of the thickness of SH in the study area was at an average level (8.23 ± 8.81 cm), and only the eastern and western parts had significant high values (Fig. 2b). However, the spatial pattern of FPAR did not change significantly, mainly concentrated around 0.78 (Fig. 2c). LAI showed a gradual increase from West to East (Fig. 2d).

The distribution of forest soil nitrogen in the middle and lower reaches of the XRB had obvious spatial variability. Although the spatial patterns of SN and sub SN were basically the same, showing high value in the northwest and low value in the middle and east, sub SN (1.19 ± 0.75 g kg^{-1}) was significantly lower than SN (1.34 ± 0.97 g kg^{-1}) (Fig. 3).

There were also significant differences in soil nitrogen content among forest categories. In coniferous forests, there was no significant difference between SN (1.22 ± 0.98 g kg^{-1}) and sub SN (1.19 ± 0.76 g kg^{-1}). However, in broad-leaved forest, SN (1.36 ± 0.97 g kg^{-1}) and sub SN (1.18 ± 0.75 g kg^{-1}) differed significantly ($p < 0.01$) (Fig. 4).

3.2. Effects of soil properties and functional diversity on SN

The results showed that soil properties and functional diversities have inconsistent effects on SN (Fig. S1). Before the model was constructed, it was found that there was no multicollinearity between the factors with a VIF (variance inflation factor) value<3.0.

Three SN content models were constructed based on different forest categories (Table 1). Linear mixed effects model (full model) showed that the SN for all forest categories in the study area could be simulated as a function of soil properties and diversity indicators, in addition to the random effects. In this model, the marginal R^2 was 0.54, and the conditional R^2 was 0.56. We differentiated forest categories at the sampling sites and found that the model performed better in broad-leaved forests, as reflected by a marginal R^2 and conditional R^2 of 0.62 and 0.62, respectively. However, the model did not fit perfectly in coniferous forests, and SN was only partially related to soil properties.

3.3. Effects of individual variables on the spatial pattern of nitrogen content

In full model, the sub SN explained 48.52 % of the variance in the SN, followed by SOM (3.47 %), SH (1.54 %), FPAR (0.44 %), and LAI (0.96 %). Moreover, the random effect of site accounted for 0.22 % of the variance. Unexplained variance was found to be 44.85 % in the study area (Fig. 5), and 58.04 % of the variance was explained by sub SN in the broad-leaved forest soil. SOM and SH accounted for lower shares of the variance (1.68 % and 1.30 %, respectively). In addition, functional diversity indicators only explained 1.03 %, with FPAR being 0.37 % and LAI 0.66 %. The random effect explained the least variance (0.12 %), and 37.83 % of the variation could not be explained (Fig. 5). In coniferous forest soils, the sub SN (27.26 %), SOM (4.19 %), and SH (1.33 %) explained 32.78 % of the variance.

4. Discussion

4.1. Soil properties and diversity indicators as explanatory factors of SN variation

In the context of global climate change, changes in soil nitrogen pools are increasingly important because of their close link to carbon cycle (Marty et al., 2017, Kou-Giesbrecht and Arora 2022). However, the

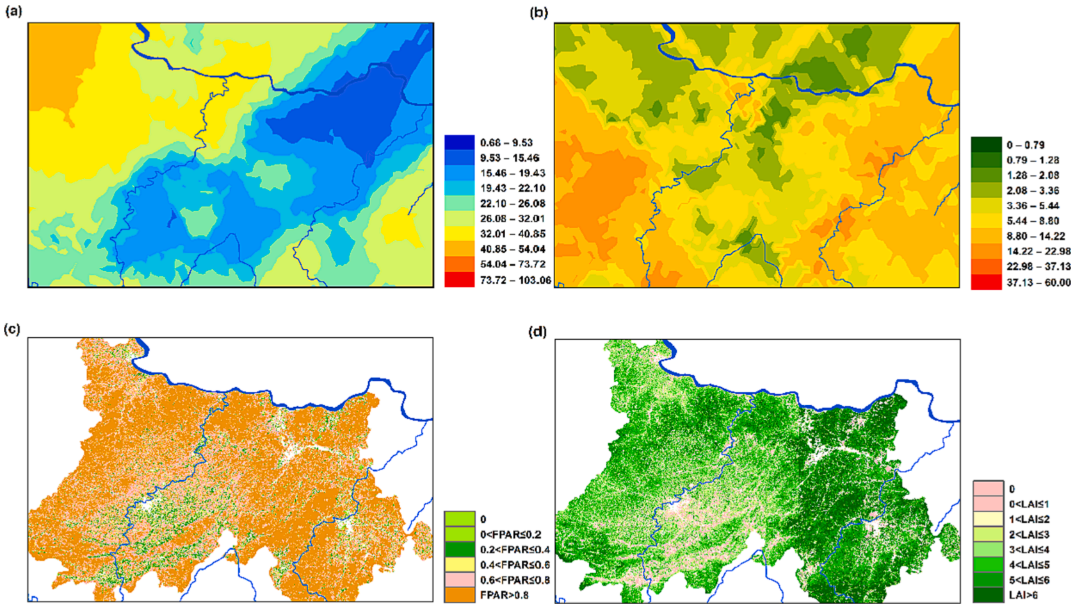

Fig. 2. Spatial pattern of SOM (a), SH (b), FPAR (c), and LAI (d) in the study area.

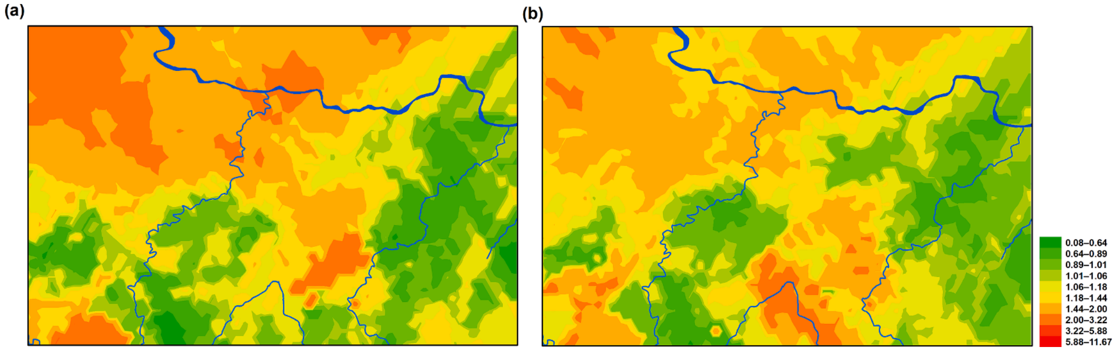

Fig. 3. Spatial pattern of SN (0–20 cm) (a) and sub SN (20–40 cm) (b) in study area.

factors affecting SN content are complex and varied. One important factor is topography, as elevation, slope, and aspect were all proved to affect SN content (Badia et al., 2016, Bayranvand et al., 2021). Changes in topography are invariably accompanied by changes in hydrothermal conditions, which, in turn, influence processes such as decomposition of the litter, microbial activity, and leaching loss (Noorbakhsh et al., 2008, Zhang et al., 2011). In the present study, the results of GAMs showed that there was no significant relationship between topographic factors and SN. This may be due to the low topographic variability in the study area, which did not produce significant environmental variability (Jia et al., 2020a). The sampling sites were investigated at an average altitude of 200 m, with small slopes.

It was found that soil surface organic matter had a significant effect on SN. Soil organic matter plays an important role in ecosystem processes and is an important source of soil nutrients (Baughman et al., 2015, Deckmyn et al., 2020). One possible explanation was that SOM supplied the energy and nutrients needed by microbes to break down and produce nitrogen (Fontaine et al., 2011, Wang et al., 2021). However, the effect of SOM on nitrogen was not consistent, and some studies have shown that the increase of SOM reduced SN content due to the coupling mechanism of carbon and nitrogen (Deng et al., 2014, Dai et al., 2022). Moreover, the thickness of the humus layer also affected the content of SN.

Humus is a black colloidal substance formed by the decomposition and transformation of fresh litter and organic matter by microorganisms (Chertov et al., 2007, Wu et al., 2020). On one hand, the humus layer increased the water absorption capacity of the soil and reduced nitrogen loss due to surface run-off (Ilek et al., 2015). Humus was also an important source of SN (Ring et al., 2001). On the other hand, humus increased the soil's buffering capacity against acidification and facilitates microbial activity. One study found that the removal of soil humus leads to a significant reduction in the nitrogen content of the soil and the plant body (Elena 2020). Sub SN had the highest amount of explanation for SN. The vertical distribution of nitrogen content correlates with soil depth (Too et al., 2018). Surface soil organic nitrogen was the main component of total nitrogen, and it decreased with the increase of soil depth. Both nitrate and ammonium nitrogen were bound to inorganic components of the soil and were adsorbed (Mgelwa et al., 2020, Soares et al., 2020). The surface soil had a higher capacity for NH_4^+ sorption than the sub-surface layer (Manirakiza and Seker 2020). Organic nitrogen undergoes nitrification to form nitrate and nitrite compounds, a process that requires sufficient oxygen and carbon sources as well as suitable temperature and humidity (Guerrieri et al., 2021, Rollinson et al., 2021). Nitrate nitrogen was more mobile in the soil and could more easily enter the sub-surface soil (Klimas et al., 2020). As a result, SN leaches into the deeper soil layers with water. Previous studies have found that vertical migration of soil nitrogen was closely related to hydrothermal conditions (Martin-Pozas et al., 2020, Zhang et al., 2020).

In this study, only two of the diversity indicators (LAI and PAR) were selected, which were based on remote sensing interpretation. Although

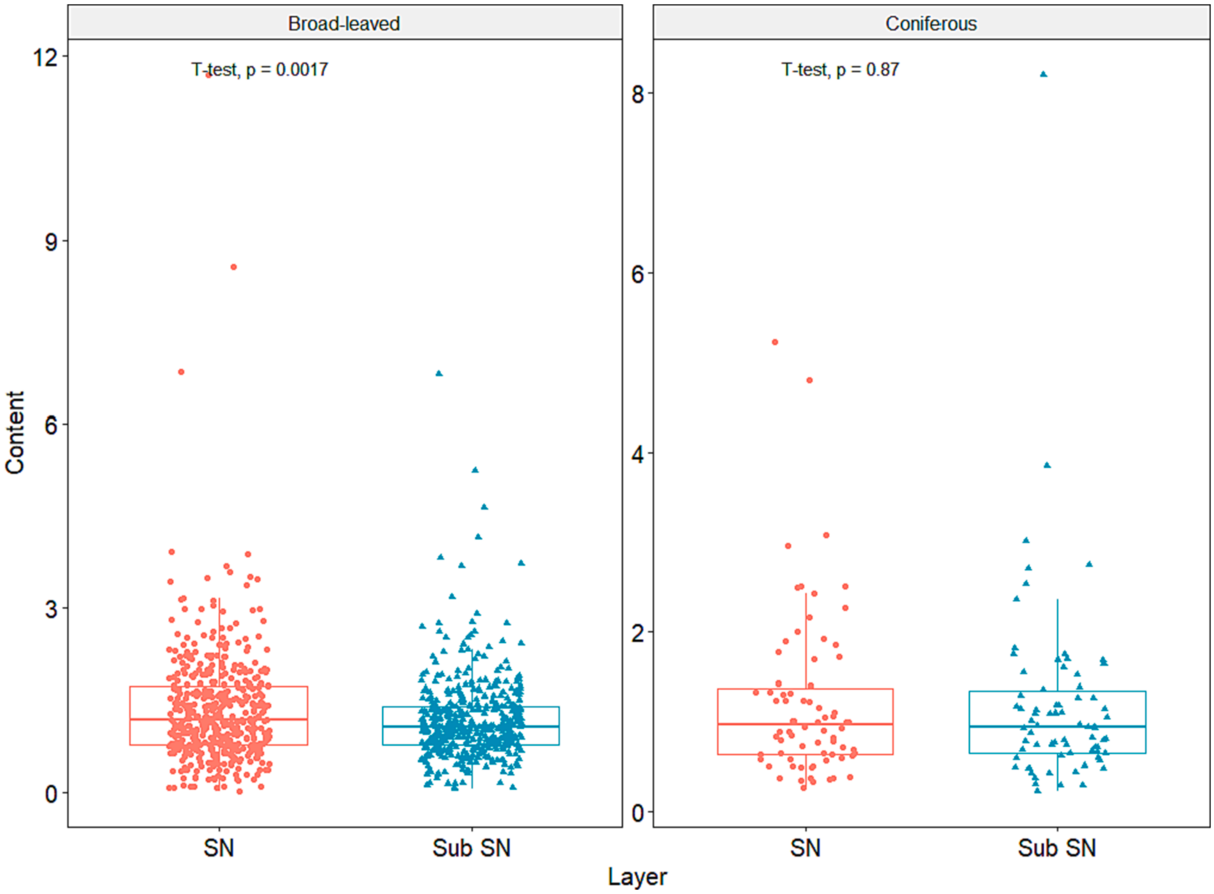

Fig. 4. Content of SN and sub SN in different forest categories.

Table 1
Statistics of models.

Model: Sub SN + SOM + SH + FPAR + LAI Variables	Standardised coefficient Full	 Broad-leaved	 Coniferous
Fixed effects			
Sub SN	0.84***	0.01***	0.01**
SOM	0.01***	1.03***	0.45***
SH	−0.01***	−0.01***	−0.01
FPAR	−0.59**	−0.53*	−0.34
LAI	0.06***	0.05**	0.08
Random effects			
SD (site)	0.12	0.03	0.00
SD (residual)	0.64	0.60	0.76
Model fit			
Marginal R^2	0.54	0.62	0.34
Conditional R^2	0.56	0.62	0.34
AIC	1086.14	869.89	202.49
BIC	1120.22	902.76	220.92

Note: For fixed effects, $^{***}p < 0.001$; $^{**}p < 0.01$; $^{*}p < 0.05$; marginal R^2 (fixed effects only); conditional R^2 (both fixed and random effects). AIC, Akaike information criterion; BIC, Bayesian information criterion.

the diversity indicators explained a low percentage of SN, they were still highly significant in the full model. LAI is a key determinant of forest productivity (Hinojo-Hinojo and Goulden 2020), which incorporates many eco-physiological processes (Liu et al., 2018b). Removal of nitrogen limitation through nitrogen addition promoted greater LAI and contributed to increased net CO_2 assimilation and increased biomass (Legros et al., 2009). Soil nitrogen affected tree photosynthesis and LAI by influencing the content and distribution of leaf nitrogen (Vose and Allen 1988, Warren et al., 2003); in turn, LAI also affected SN. The high biomass increased the amount of litter and contributed to the increase of SN content (Martins et al., 2021, Yokobe et al., 2021). High LAI significantly increased canopy interception of rainfall, significantly reduced surface runoff and soil erosion, and thus reduced surface nitrogen leaching loss (Malek 2010, Mohammed and Tarboton 2016). However, some studies also found that when LAI decreased due to thinning, the content of SN increased (Jonsson and Sigurdsson 2010, Garcia-Prats et al., 2018, Zheng et al., 2019); an explanation might be that large amounts of litter enter the soil during thinning. PAR was a source of energy for plant life activities and organic matter synthesis, and it increased transpiration in plants and allowed more soil nitrogen to be transported upwards with water to the leaves (Ward et al., 2013, Wang et al., 2022). It was found that leaf nitrogen concentration increased along with the increased PAR (Fan et al., 2022). At the same time, transpiration promoted the opening of leaf stomata, which facilitated photosynthesis and thereby increased forest biomass.

4.2. *Differences between forest categories*

The results showed that the nitrogen content of the surface layer of broad-leaved forest soils was higher than that of coniferous forest soils, with significant differences between the surface and sub-surface layers of broad-leaved forests and no significant differences of coniferous forests. The results of our study are consistent with those of other studies (Vesterdal et al., 2008, Deng et al., 2019). The nitrogen pathways into forest soils were found to be through precipitation, atmospheric nitrogen deposition and litterfall (Sayer 2006, Xu et al., 2013). Different forest categories form different soil types, and soil nitrogen effectiveness

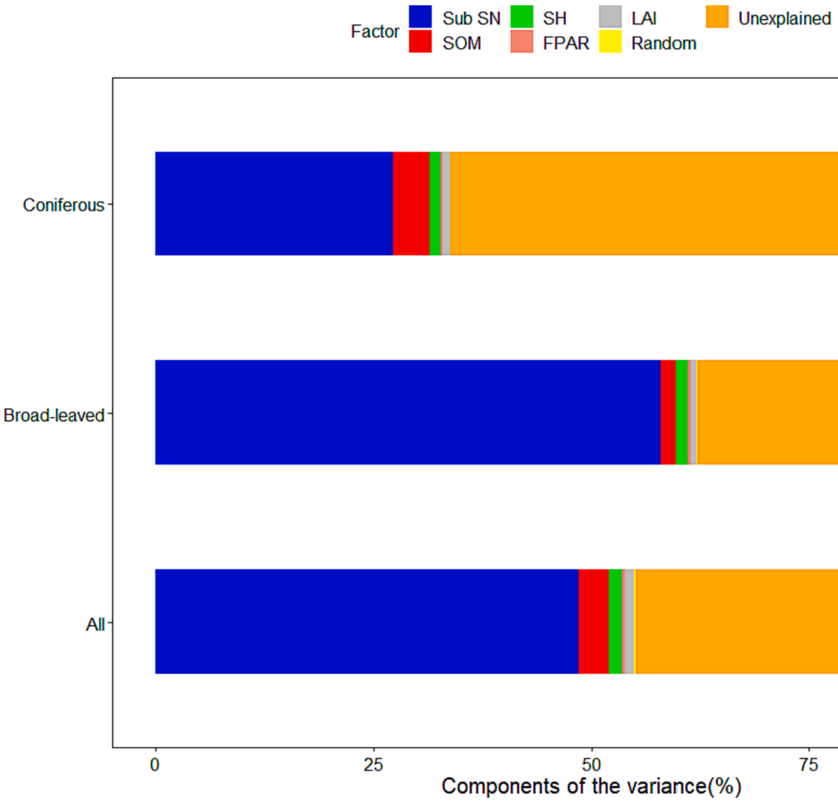

Fig. 5. Variance partition of the studied variables. Fixed variables include sub SN, SOM, SH, LAI, and FPAR. Random variables include sites.

varies greatly between forest ecosystems and soil types (Cools et al., 2014, Rennenberg and Dannenmann 2015). In general, coniferous forest soils were highly acidic and low in total nitrogen. This might be due to differences in forest categories, which may have led to differences in quality and yield of litterfall (Xu et al., 2013, Miao et al., 2019). Aboveground litterfall was the main way of the conversion from plants to soil nitrogen, mainly through the input and decomposition of organic matter into soil (Bellingrath-Kimura et al., 2015). Thus, differences in soil decomposition rates between forest categories also account for differences in N content (Rumpel and Kogel-Knabner 2011, Prescott and Vesterdal 2013, Cremer et al., 2016). However, some studies have found inconsistent results. For example, one study has shown that the litterfall fluxes in Bulgarian fir forests were significantly higher than in evergreen broad-leaved forests and that the total soil nitrogen content in fir forests was high (Michopoulos et al., 2021). In arid areas, the soil nitrogen content of coniferous forests was significantly higher than that of broad-leaved forests after afforestation (Liu et al., 2018a), a result that is likely attributable to the microclimate environment, such that the litterfall layer could regulate the soil microclimate by buffering the soil surface and the atmosphere, high soil temperatures caused by litterfall layers reduced the rate of decomposition (Sayer 2006, Teixeira et al., 2018).

The model for the SN content of forest soils based on soil properties and diversity indicators showed that the model fitted broad-leaved forests better, while coniferous forests were barely suitable. Previous studies have shown that forest type was the main explanatory factor for changes in SN (van den Berg et al., 2012, Roth et al., 2021). In our study, sub SN was the main explanatory factor for surface nitrogen, especially in broad-leaved forests. In coniferous forests, SN did not fit into the full model and remained overwhelmingly unexplained for several possible reasons. Firstly, the smaller leaf shape of coniferous forests allowed for more precipitation through the forest canopy. Secondly, the LAI of coniferous forests did not correlate significantly with transpiration and had a weaker effect on photosynthesis (Liang and Wei 2021); the small sample size in this study on coniferous forests may also have been a contributing factor. Further research is needed on the dominant factors of SN in coniferous forests.

5. Conclusion

Soil nitrogen is an important source of nutrients and its dynamic change is influenced by several factors. In this study, 523 soil samples collected from the XRB were analyzed, with the results showing that soil nitrogen was significantly higher in broad-leaved forests than in coniferous forests. The results also showed that soil properties and diversity indicators jointly influence SN content, and that the full model was more suitable for broad-leaved forests than for coniferous forests. The results of the relative importance analysis indicated that sub SN was the main explanatory factor for SN. In summary, SN was mainly influenced by soil properties, and the influence from diversity indicators was relatively weak. However, there remained a large proportion that could not be explained, highlighting the need for additional research on this topic. In order to better explain the change of forest SN content, the model needs to add soil microorganisms, mycorrhizal fungi, atmospheric nitrogen deposition, human activities and other factors, and the simulation methods should also be expanded, such as structural equation model. Moreover, the model needs more extensive coverage and more representative sampling sites data.

CRediT authorship contribution statement

Jian Kang: Conceptualization, Methodology, Data curation, Formal analysis, Writing – original draft. **Zebang Deng:** Investigation, Data curation. **Zhongrui Zhang:** Investigation, Data curation. **Shuilian Chen:** Investigation. **Jianguo Huang:** Methodology, Formal analysis. **Xiaogang Ding:** Supervision, Conceptualization, Methodology, Formal analysis, Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2022.109806.

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