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Plant diversity and species turnover co-regulate soil nitrogen and phosphorus availability in Dinghushan forests, southern China

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Abstract

Aims The interaction between plants and soil is an important internal driver of ecosystem evolution. Many studies have reported the unidirectional effects of soil nutrients on plant diversity and species turnover. However, there are still many gaps in our knowledge about how plant diversity and species turnover feedback to soil nutrients.

Methods In the present study, three forest plots with different species composition and diversity were created through artificial disturbance in the same stand origin forest, and their long-term dynamics were observed. We identified underlying mechanisms of how plant diversity (Shannon-Wiener index) and species turnover (Bray-Curtis dissimilarity) affect soil total nitrogen (TN), total phosphorus (TP), available nitrogen (AN), and available phosphorus (AP).

Results Plant diversity was associated with soil TN, TP, AN, and AP concentrations ($P < 0.01$). Species turnover was negatively correlated with the log-response ratio of TP (*LRR* TP) ($P < 0.001$), but not correlated with *LRR* AP. Species turnover had significant positive correlations with *LRR* TN and *LRR* AN ($P < 0.001$). The structural equation model supports hypotheses that plant diversity and species turnover influenced soil N and P availability by affecting forest community growth (total tree basal area, TBA), litter quantity and quality, and soil physical and chemical properties (soil organic carbon, SOC; soil exchangeable base cations).

Conclusions Collectively, our results highlighted the co-regulation of plant diversity and species turnover on soil N and P availability by "complementary" and "mass" effects during the long-term dynamics of forest ecosystems.

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Introduction

Ecological interactions can change the pace and direction of ecological processes, which may lead to different dynamics in communities and ecosystems. Thus, understanding the relationships and feedbacks between

ecological interactions and processes is important for investigating the relationship of ecosystem ecology with evolution (Caplan et al. 2019). Plant-soil interactions play a vital role in ecosystem succession and evolutionary dynamics (Teste et al. 2017; Van Nuland et al. 2019), and many studies have investigated the effect of soil properties on plant diversity (Sellan et al. 2019). For example, soil heterogeneity can promote plant species coexistence and diversity through increasing niche availability and creating shelters and refuges (Sellan et al. 2019; Xue et al. 2019), while soil acidification caused by atmospheric nitrogen (N) deposition leads to plant diversity loss (Lu et al. 2010). However, the feedback mechanisms between plant and soil remain uncertain, and few studies have explored the mechanisms involved in the effect of plant diversity on soil properties (Leuschner et al. 2009; Lu et al. 2019; Wu et al. 2019). Therefore, how plant diversity and community compositional shifts affect soil properties has not been well studied.

Nitrogen (N) and phosphorus (P) are generally considered to be the two most limiting elements for the development of terrestrial vegetation (Borer et al. 2015), and they play an essential role in maintaining ecosystem productivity and functional stability. Additionally, plant diversity has a positive relationship with ecosystem functions (Duffy et al. 2017), but its internal mechanisms have not been fully explored. In subtropical forests, the increase in soil nutrient availability has recently been considered to be one of the underlying mechanisms for the positive effects of plant diversity on ecosystem biomass and productivity (Li et al. 2014; Wu et al. 2019). Thus, understanding feedback mechanisms between plant diversity and soil N and P availability may facilitate the development of sustainable strategies for maintaining ecosystem productivity (Wu et al. 2019). However, how plant diversity regulates soil nutrient availability has not been well investigated.

In theory, plant diversity can affect soil nutrient availability through the "complementary" or "mass" effects (Ge et al. 2019). The "complementarity effect" refers to the situation in which different plants living in the same community are able to fully and adequately take up and utilize soil nutrients through various and compatible strategies (Baxendale et al. 2014; Both et al. 2019; Turner et al. 2018; Van Nuland et al. 2019) or through the interactions among diverse plants that facilitate soil nutrients availability or other related environmental conditions (Chen et al. 2019; Hiiesalu et al.

2017; Lange et al. 2015; Liu et al. 2018; Wu et al. 2019). Furthermore, plant diversity can also affect soil nutrient availability indirectly by changing the quality and quantity of plant production, which is called the "mass effect" (De Groote et al. 2018; Haghverdi and Kooch 2019; Hobbie et al. 2006). For example, many recent studies have reported that plant composition significantly influences litter quality and turnover time (Kooch and Bayranvand 2017; Scherer-Lorenzen et al. 2007), leading to changes in soil nutrients (Cordova et al. 2018; Kooch et al. 2017; Lyu et al. 2019). Although the influence of plant diversity on soil nutrients may be shaped by these two ecological processes, only a few studies placed them into one framework for systematic research (Wu et al. 2019).

Changes in plant diversity and soil nutrients with natural succession are not consistent. For example, plant diversity increases during succession from the primary stage to the climax stage (Odum 1969). However, the availability of P increases in the early stage of succession (Coomes et al. 2013; Laliberte et al. 2012; Raven 2012), but declines after the middle stage of succession. In the early stage of succession, N-fixing species generally have a competitive advantage over other species because they can obtain N from the atmosphere and hence improve N and P availability (Coomes et al. 2013; Laliberte et al. 2012; Raven 2012). After the middle stage of succession, soil P begins to decrease owing to the rapid growth of plants and leaching (Deng et al. 2017; Sullivan et al. 2019). Thus, compared to those in previous stages, N-fixing species are less favored owing to the high P cost associated with their symbiotic N fixation (Kitayama 2012; Lambers et al. 2008; Walker et al. 2010). Contrastingly, the diversity of plants with a variety of P acquisition strategies increases during the late stage of succession compared to that in the earlier stages (Kitayama 2012; Lambers et al. 2008; Walker et al. 2010). Therefore, these shifts in species composition and number of individuals, i.e., species turnover, may also regulate the availability of soil nutrients, but this has rarely been studied.

It is difficult to separate the effects of plants on the soil versus the effects of the soil on the plants themselves, as the synchronization of plant-soil interaction occurs on both temporal and spatial scales, which brings challenges when investigating how plant diversity and species turnover affect soil nutrients. In the present study, we conducted long-term observations of three forests with different species composition and diversity

at Dinghushan Biosphere Reserve in South China. As these three forests originated from the same forest (pine forests (PF) and mixed pine and broadleaf forests (MF) were formed after monsoon evergreen broadleaf forests (BF) were destroyed decades ago), they have the similar initial soil properties and consistent climatic conditions but different species composition and diversity. We used long-term observational data (2004–2015) to explore the effects of plant diversity and species turnover (including the number of species and individuals) on soil N and P availability. Specifically, we identified potential pathways by which plant diversity and species turnover may have influenced soil N and P using linear mixed-effects (LME) models, and formulated a framework involving direct and indirect interactions. Then, we used structural equation modelling (SEM) to empirically evaluate this framework. As different plant species have varied N and P requirements and nutrient-acquisition strategies, the soil nutrient return rate is uneven (De Groote et al. 2018; Haghverdi and Kooch 2019; Hobbie et al. 2006). We hypothesized that: *i)* plant diversity has a positive effect on soil nutrient availability through direct and indirect pathways; *ii)* species turnover (the shifts of species and individuals) may alter the pace and direction of soil nutrient change along ecosystem succession, and *iii)* soil N and P may have different response mechanisms to species turnover.

Materials and methods

Study site

This study was conducted at Dinghushan Biosphere Reserve (23°09' 21" to 23°11'30" N, 112°30' 39" to 112°33' 41" E) in Zhaoqing city, Guangdong Province, southern China. The Dinghushan Biosphere Reserve was established in 1956 in order to protect a remnant of undisturbed natural BF in the subtropics. The climate type of the study site is subtropical monsoon. The Dinghushan Biosphere Reserve has a mean annual precipitation of 1900 mm and mean annual temperature of 22.3 °C. The rainfall during the wet season (from April to September) accounts for nearly 80% of the total annual rainfall. The soil of the area is classified in the Ultisol group and Udult subgroup according to the USDA soil classification system (Buol et al. 2003). The bedrocks are made of sandstone and shale belonging to the Devonian Period. The forest soil pH at the

Dinghushan Biosphere Reserve ranges between 4.0 and 4.9.

There are three types of forests at the Dinghushan Biosphere Reserve: PF, MF, and BF (~60, ~100, and > 400 years old, respectively). The PF was planted after BF was clear cut about 60 years ago, and *Pinus massoniana* Lamb. is currently the dominant species in this forest type. The MF developed from previously growing PF after 90 years of natural succession, and the dominant species currently are *Pinus massoniana*, *Schima superba* Gardner. et Champ., and *Castanopsis chinensis* (Sprengel) Hance. The BF has existed for more than 400 years without human interference, with the main species currently being *Schima superba*, *Cryptocarya concinna* Hance, *Castanopsis chinensis*, *Cryptocarya chinensis* (Hance) Hemsl., and *Aporosa yunnanensis* (Pax &K. Hoffm.) F. P. Metcalf. In 1978, one permanent sample plot of 1 ha was randomly selected and established in each forest type (PF, 23° 09′ 59.04″ N, 112° 33′ 21.24″ E; MF, 23° 10′ 25.32″ N, 112° 32′ 54.24″ E; and BF, 23° 10′ 8.4″ N, 112° 32′ 21.84″ E), and the distance between them is very close (<1.7 km, Fig. S1), and had similar conditions of soil parent material, light, temperature, and precipitation. Therefore, the differences in soil nutrients among the three forest types were likely caused by differences in plant composition and species turnover. Although it would be more precise to carry out experiments on different plant diversities in the same soil matrix, we believe that the design of this study was appropriate to test our stated hypotheses.

We chose these three forests at different succession stages for the analysis because they provide a wide range of species richness and have the same initial soil properties and consistent climatic conditions. Each permanent plot in each forest type was divided into 100 subplots of 10×10 m. In October 2004, 2010, and 2015, we investigated all trees with a diameter at breast height (DBH) larger than 1 cm in these plots, and collected soil and litter samples. TBA (cm^2) was calculated as the sum of π (DBH / 2)^2 of trees in each subplot (DBH ≥ 1 cm, height ≥ 1 m). Because litter traps were randomly distributed in each plot, not all subplots had both soil and litter samples. Therefore, we selected a total of 49 subplots with complete sample information for analysis, which included 12, 12, and 25 subplots in PF, MF, and BF, respectively.

Soil and litterfall collection

Soil sample collection and vegetation surveys were conducted simultaneously. In each selected subplot, soil from the 0–20 cm soil layer (topsoil) was collected according to a five-point mixed sampling method using soil corers with an inner diameter of 5 cm (Huang et al. 2013). These five points included the center of the subplot and four points more than one meter away from the surrounding subplot boundary. In each subplot, all soil was mixed, placed into plastic preservation bags, and brought back to the laboratory. Before analysis, all soil samples were air-dried and sieved through a 2 mm screen to remove plant roots, large stones, and debris. Three litter traps were set up in each plot to collect the newly generated forest litterfall. A nylon net (1 mm mesh) with a horizontal trapping area of 1×1 m was placed over a PVC frame, 0.8 m above the ground. Litterfall was collected every month and its weight was measured after drying at 60 °C for 48 h. The annual litterfall was calculated by adding the litterfall of all 12 months.

Chemical and physical analysis of samples

Soil pH was measured using a pH meter after shaking the soil:water suspension (1:5 w/V) for 30 min. SOC was determined using the $K_2Cr_2O_7$ oxidation method (Walkley 1947), TN was determined using an elemental analyzer (Vario MACRO cube CN; Germany), and TP was determined colorimetrically (using a UV spectrophotometer) after wet digestion with $HClO_4$-H_2SO_4 (Liu 1996). Soil AN (the sum of NH_4^+-N, NO_3^--N, amide-N, amino-acid-N, and hydrolysable-protein-N) was determined by oxidation hydrolysis to ammonia nitrogen, extracted with 2% (m/V) H_3BO_3 solution, and then titrated with H_2SO_4 (Liu 1996). Soil AP was extracted with a solution containing 25 mM HCl and 30 mM NH_4F (soil to extractant ratio = 1:7) and measured using an ultraviolet spectrophotometer. Soil exchangeable base cations (Ca^{2+}, Mg^{2+}, Al^{3+}) were extracted with 100 ml of 0.5 M NH_4Cl solution, filtrated, and measured by ICP-OES (Spectro Genesis, Spectro, Kleve, Germany) (Liu 1996). Litter carbon (C) concentration was determined following the Walkley-Black's wet digestion method. Litter N concentrations were measured using the Kjeldahl method. Litter P concentrations were measured spectrophotometrically after the

samples were digested with H_2SO_4-H_2O_2 (Dong et al. 1996).

Quantifying plant diversity and species turnover

For the analysis of plant diversity and species turnover, we selected trees with DBH ≥ 1 cm and height ≥ 1 m because the litter traps used were 0.8 m above the ground and mainly collected litterfall from trees with height ≥ 1 m. To analyze plant diversity, we calculated the Shannon-Wiener index as follows:

$$Shannon-Wiener\ index = -\sum_{i=1}^{k} p_i \ln p_i \qquad (1)$$

where k is the number of species in the subplot species matrix, and p_i represents the proportion of individuals belonging to i^{th} species in the subplot.

To analyze species turnover, we calculated Bray-Curtis dissimilarity using the "vegdist" function in the vegan package (Dixon 2003) in R (version 3.6.1) in the same subplot at different sampling times (2004, 2010, and 2015). Bray-Curtis dissimilarity has the advantage of not only considering the difference in the number of tree species among subplots, but also that in the number of individuals of each tree species. Bray-Curtis dissimilarity was calculated as follows:

$$Bray-Curtis\ dissimilarity = \frac{\sum_{i=1}^{k} |y_{i,k} - y_{j,k}|}{\sum_{i=1}^{k} |y_{i,k} + y_{j,k}|} \qquad (2)$$

where k is the number of species in the subplot species matrix, y is the species abundance, and i and j indicate the two plots that are being compared.

Statistical analysis

To reduce collinearity among variables, principal component analysis was used to calculate soil exchangeable base cations and litter quality by extracting the principal components of soil exchangeable cations (Ca^{2+}, Mg^{2+}, and Al^{3+}; Table S1) and litter C, N, and P concentration (Table S2), respectively. PCAs were conducted using the "principal" function from the psych package (Revelle 2018) in R (version 3.6.1), which rotated matrices by varimax.

LRR were used to calculate the responses of soil TN, TP, AN, and AP to species turnover and other parameters. We selected LRR to calculate species turnover effects because (1) it allows simple comparison between the responses of functional groups comprising various

plant species with different initial conditions (e.g., TN) and different species components to species turnover, and (2) the natural logarithmic transformation of the response parameters (e.g., TN, TP, AN, and AP) ratio values enables the calculation of effect values which are proportional to the original effect sizes, enabling accurate comparisons among different response directions. *LRR* were calculated as follows:

$$LRR = \ln\frac{B_m}{B_n}, \tag{3}$$

where B is the parameter of response to species turnover in each subplot, and m and n are the different survey years in the same subplot.

First, we determined the relationships between TN, TP, AN, AP, and Shannon-Wiener index, as well as the relationships between *LRR* of TN, TP, AN, AP, and Bray-Curtis dissimilarity, using Pearson correlation coefficients. Second, LME models were used to identify the effect of forest types, Shannon-Wiener index, annual litterfall, litter quality, TBA, and soil factors (pH, SOC, and soil exchangeable base cations) on soil nutrients (TN, TP, AN, and AP), as well as to identify the effect of Bray-Curtis dissimilarity and the changes in annual litterfall, litter quality, TBA, and soil factors on *LRR* of soil nutrients in all forest types. Before the LME analysis, all data were logarithmically transformed. All fixed-effect terms in the model were fitted together, using subplot and sampling year as random-effect terms. The LME analyses were conducted using the "lme()" function (Pinheiro 2012) from the in R (version 3.6.1), and restricted maximum likelihood was used to produce unbiased estimates of the model parameters.

Finally, based on the known effects and the relationships among the driving variables, a SEM was constructed to analyze the direct and indirect relationships of soil nutrients with forest type, plant diversity, species turnover, annual litterfall, litter quality, TBA, and soil factors. In our model, we investigated the influence of plant diversity, species turnover and forest type on TN, TP, AN, and AP considering the abovementioned soil factors. The data from all sampling years was transformed to natural logarithmic values before SEM analysis to mitigate departure from normality and linearity. Mplus software (version 8) was used to analyze SEMs, which were developed from the fully conceptual model using the χ^2 test, with P usually >0.05, and considering the root mean square error of approximation (RMSEA;

the model has a good fit when RMSEA <0.05). Insignificant paths ($P > 0.05$) were eliminated gradually until all links significantly contributed to the final model.

Results

Plant diversity and species turnover

Shannon-Wiener index differed significantly among the three forest types ($P < 0.05$, Table 1), following the order: BF > MF > PF (Table 1). The Shannon-Wiener index increased along succession in PF, while it increased significantly at first, and then decreased non-significantly in MF and BF (Table 1).

Bray-Curtis dissimilarity in PF, MF, and BF was 0.42, 0.52, and 0.60 between 2004 and 2010 and 0.38, 0.20, and 0.14 between 2010 and 2015, respectively (Table 2).

Soil nutrient concentrations

Soil nutrient concentrations were significantly different among the three forest types ($P < 0.05$; Table 3). TN and AN concentrations followed the following order: BF > MF > PF. The highest concentration of TP was recorded in MF, and it was significantly higher than those in PF and BF (Table 3). Furthermore, TN, TP, and AN concentrations were significantly different among succession stages ($P < 0.05$). Soil TN and AN concentrations significantly increased with time ($P < 0.05$). Meanwhile, TP concentrations in 2015 increased by 11% in PF but decreased by 15% and 11% in MF and BF, respectively, compared with those in 2004 (Table 3).

Relationships of Shannon-wiener index and bray-Curtis dissimilarity with TN, TP, AN, and AP

A positive relationship between the Shannon-Wiener index and soil nutrients was observed in the topsoil of subtropical forests (Fig. 1, Table S3). With the increase in Shannon-Wiener index, soil TN ($R = 0.0.56$, $P < 0.001$; Fig. 1a), TP ($R = 0.29$, $P < 0.001$; Fig. 1c), AN ($R = 0.54$, $P < 0.001$; Fig. 1b), and AP ($R = 0.28$, $P < 0.01$; Fig. 1d) significantly increased. Moreover, the fixed effect of Shannon-Wiener index on soil TN, TP, AN, and AP was still significant after isolating the influence of subplots on soil nutrients (Table 4).

Table 1 Forest characteristics, including species richness, annual litterfall, litter C, litter N, litter P, individuals, TBA, for PF, MF and BF. Different capital letters within a forest indicate significant differences between years. Different small letters in the same year indicate significant differences between forest types. Mean ± SE in the bracket ($n = 12$ for PF and MF, $n = 25$ for BF). TBA: total tree basal area; PF: pine forest; MF; mixed pine and broadleaf forest; BF: monsoon evergreen broadleaved forest

Year	Forest types	Species richness	Annual litterfall (t·hm^{-2}·a^{-1})	Litter C (g·kg^{-1})	Litter N (g·kg^{-1})	Litter P (g·kg^{-1})	Total Individuals	TBA (cm^2)	Shannon-Wiener index
2004	PF	7.3 ± 2.3^{Aa}	3.07 ± 0.40^{Aa}	438 ± 7^{Bb}	13.9 ± 1.6^{Aa}	0.47 ± 0.16^{Aa}	27.5 ± 14.3^{Aa}	205 ± 133^{Aa}	0.72 ± 0.42^{Aa}
	MF	9.8 ± 1.7^{Ab}	4.98 ± 0.86^{Ab}	505 ± 13^{Ba}	14.1 ± 0.9^{Ab}	0.38 ± 0.04^{Aa}	19.2 ± 5.9^{Ab}	78 ± 48^{Ab}	1.05 ± 0.28^{Ab}
	BF	15.5 ± 2.7^{Ac}	2.68 ± 0.97^{Ac}	483 ± 7^{Ba}	19.3 ± 1.0^{Ac}	0.70 ± 0.04^{Ab}	31.1 ± 14.9^{Ac}	220 ± 179^{Ac}	1.74 ± 0.37^{Ac}
2010	PF	8.0 ± 2.17^{Ba}	4.77 ± 0.55^{Ba}	508 ± 10^{Bb}	16.0 ± 1.9^{Ba}	0.48 ± 0.06^{Ba}	26.3 ± 14.0^{Ba}	202 ± 134^{Aa}	1.02 ± 0.17^{Ba}
	MF	9.4 ± 2.5^{Bb}	5.75 ± 1.13^{Bb}	450 ± 13^{Ba}	16.5 ± 0.54^{Bb}	0.56 ± 0.04^{Bb}	16.0 ± 9.5^{Bb}	59 ± 44^{Ab}	1.15 ± 0.32^{Bb}
	BF	17.6 ± 3.4^{Bc}	4.16 ± 1.75^{Bc}	508 ± 12^{Ba}	18.2 ± 0.9^{Bc}	0.72 ± 0.06^{Bb}	55.3 ± 22.7^{Bc}	294 ± 149^{Ac}	1.91 ± 0.24^{Bc}
2015	PF	7.8 ± 2.9^{Aa}	6.12 ± 0.88^{Ca}	483 ± 14^{Ab}	12.2 ± 1.2^{Ca}	0.31 ± 0.05^{Ca}	16.4 ± 9.0^{Ba}	86 ± 47^{Aa}	1.04 ± 0.28^{Ba}
	MF	8.2 ± 2.8^{Ab}	5.96 ± 0.84^{Cb}	393 ± 16^{Aa}	16.9 ± 0.9^{Cb}	0.37 ± 0.03^{Ca}	14.6 ± 8.0^{Bb}	51 ± 38^{Ab}	1.02 ± 0.35^{Ba}
	BF	15.2 ± 3.2^{Ac}	5.56 ± 1.07^{Cc}	303 ± 11^{Aa}	16.4 ± 1.6^{Cc}	0.44 ± 0.04^{Cb}	51.7 ± 23.0^{Bc}	324 ± 157^{Ac}	1.83 ± 0.27^{Bb}

Moreover, the response of TN, TP, and AN were significantly correlated with Bray-Curtis dissimilarity, but with differing response directions (Fig. 2, Table S4). *LRR* TN and *LRR* AN were significantly positively correlated with Bray-Curtis dissimilarity ($R^2 = 0.74$, $P < 0.001$ for TN; $R = 0.41$, $P < 0.001$ for AN), while *LRR* TP was significantly negatively correlated with Bray-Curtis dissimilarity ($R = 0.28$, $P < 0.01$). In all surveyed subplots, the proportion of total subplots with positive TN and AN response to Bray-Curtis dissimilarity ($LRR > 0$) was 90% and 86%, respectively, while the proportion of total subplots with negative TP response to species turnover ($LRR < 0$) was 67%. Moreover, the fixed effect of Bray-Curtis dissimilarity on *LRR* TN, *LRR* TP, and *LRR* AN was still significant after isolating the influence of subplots on soil nutrients (Table 5).

Effect of plant diversity, species turnover, and other factors on soil nutrients

LME results showed that explanatory variables varied among soil TN, TP, AN, and AP (Tables 4 and 5). Soil TN, AN, TP, and AP were prominently related to soil exchangeable base cations ($P < 0.001$). Meanwhile, SOC and pH was associated with soil TN, AN, and AP ($P < 0.05$) but had no effect on TP. Moreover, annual litterfall was related to soil TN and AN ($P < 0.05$), while litter quality was significantly associated with soil AN and TP ($P < 0.05$). Additionally, TBA was significantly related to soil TN and TP ($P < 0.05$). The *LRRs* of TN, AN, TP, and AP were clearly related to litter quality and soil exchangeable base cations ($P < 0.05$). Furthermore, annual litterfall and TBA remarkably affected

Table 2 The Bray-Curtis dissimilarity and the *LRR* TN, *LRR* AN, *LRR* TP and *LRR* AP in PF, MF and BF. Mean ± SE in the bracket ($n = 12$ for PF and MF, n = 25 for BF). *LRR* TN: log-response ratios of total nitrogen; *LRR* AN: log-response ratios of available nitrogen; *LRR* TP: log-response ratios of total phosphorus; *LRR* AP: log-response ratios of available phosphorus; PF: pine forest; MF; mixed pine and broadleaf forest; BF: monsoon evergreen broadleaved forest

		Bray-Curtis dissimilarity	*LRR* TN	*LRR* AN	*LRR* TP	*LRR* AP
2004–2010	PF	0.42 ± 0.12	0.55 ± 0.14	0.67 ± 0.21	−0.19 ± 0.07	−0.10 ± 0.13
	MF	0.52 ± 0.09	0.53 ± 0.13	0.42 ± 0.17	−0.26 ± 0.05	−0.16 ± 0.29
	BF	0.60 ± 0.11	0.58 ± 0.14	−0.08 ± 0.06	−0.32 ± 0.20	0.10 ± 0.34
2010–2015	PF	0.38 ± 0.16	0.38 ± 0.10	−0.09 ± 0.10	0.26 ± 0.10	0.52 ± 0.08
	MF	0.20 ± 0.04	0.14 ± 0.12	0.14 ± 0.14	0.09 ± 0.07	0.29 ± 0.23
	BF	0.14 ± 0.05	−0.10 ± 0.12	0.17 ± 0.19	−0.03 ± 0.07	−0.04 ± 0.48

Table 3 Soil properties for the PF, MF and BF. Different capital letters within a forest indicate significant differences between years. Different small letters in the same year indicate significant differences between forest types. Mean ± SE, (n = 12 for PF and MF, n = 25 for BF). SOC: soil organic carbon; TN: soil total nitrogen; TP: soil total phosphorus; AN: soil available nitrogen; AP: soil available phosphorus; PF: pine forest; MF: mixed pine and broadleaved forest; BF: monsoon evergreen broadleaved forest

Year	Forest types	SOC (g·kg⁻¹)	TN (g·kg⁻¹)	TP (g·kg⁻¹)	AN (mg·kg⁻¹)	AP (mg·kg⁻¹)	pH	Ca²⁺ (mmol·kg⁻¹)	Mg²⁺ (mmol·kg⁻¹)	Al³⁺ (mmol·kg⁻¹)
2004	PF	13.1 ± 2.1^{Aa}	0.45 ± 0.06^{Aa}	0.19 ± 0.01^{Aa}	44 ± 7^{Aa}	1.23 ± 0.13^{Aa}	4.31 ± 0.30^{Ba}	5.40 ± 0.46^{Aa}	0.46 ± 0.02^{Aa}	3.5 ± 2.4^{Aa}
	MF	29.4 ± 8.3^{Ab}	0.84 ± 0.10^{Ab}	0.34 ± 0.02^{Ab}	69 ± 6^{Ab}	1.27 ± 0.33^{Ab}	3.83 ± 0.08^{Bb}	3.43 ± 0.59^{Ab}	0.54 ± 0.06^{Ab}	18.9 ± 15.2^{Ab}
	BF	34.1 ± 6.5^{Ac}	1.02 ± 0.05^{Ac}	0.28 ± 0.01^{Ac}	87 ± 7^{Ac}	1.46 ± 0.23^{Ac}	3.74 ± 0.04^{Bb}	3.94 ± 0.39^{Ac}	0.66 ± 0.03^{Ac}	29.4 ± 5.1^{Ac}
2010	PF	19.5 ± 3.0^{Ba}	0.77 ± 0.08^{Ba}	0.16 ± 0.02^{Ba}	85 ± 9^{Ba}	1.11 ± 0.09^{Aa}	4.03 ± 0.06^{Ba}	2.48 ± 0.27^{Ba}	1.18 ± 0.09^{Ba}	43.8 ± 3.8^{Ba}
	MF	35.6 ± 5.2^{Bb}	1.43 ± 0.17^{Bb}	0.26 ± 0.02^{Bb}	107 ± 19^{Bb}	1.07 ± 0.23^{Ab}	3.89 ± 0.06^{Bb}	1.69 ± 0.46^{Bb}	1.36 ± 0.13^{Bb}	86.6 ± 22.5^{Bb}
	BF	43.3 ± 10.2^{Bc}	1.83 ± 0.27^{Bc}	0.26 ± 0.02^{Bc}	120 ± 16^{Bc}	1.76 ± 0.69^{Ac}	3.85 ± 0.03^{Bb}	2.05 ± 0.33^{Bc}	1.66 ± 0.14^{Bc}	90.1 ± 11.1^{Bc}
2015	PF	22.1 ± 2.8^{Ca}	1.13 ± 0.11^{Ca}	0.21 ± 0.01^{Ca}	77 ± 7^{Ca}	1.87 ± 0.18^{Ba}	3.46 ± 0.02^{Aa}	4.37 ± 0.82^{Ca}	1.12 ± 0.19^{Ca}	58.2 ± 3.5^{Ba}
	MF	35.0 ± 3.8^{Cb}	1.59 ± 0.15^{Cb}	0.28 ± 0.02^{Cb}	117 ± 10^{Cb}	1.41 ± 0.23^{Bb}	3.17 ± 0.02^{Ab}	2.15 ± 0.39^{Cb}	1.39 ± 0.26^{Cb}	86.9 ± 11.5^{Bb}
	BF	36.5 ± 4.2^{Cc}	1.79 ± 0.15^{Cc}	0.25 ± 0.01^{Cc}	145 ± 21^{Cc}	1.51 ± 0.13^{Bc}	3.26 ± 0.04^{Ab}	2.10 ± 0.37^{Cc}	1.44 ± 0.25^{Cc}	88.4 ± 6.7^{Bc}
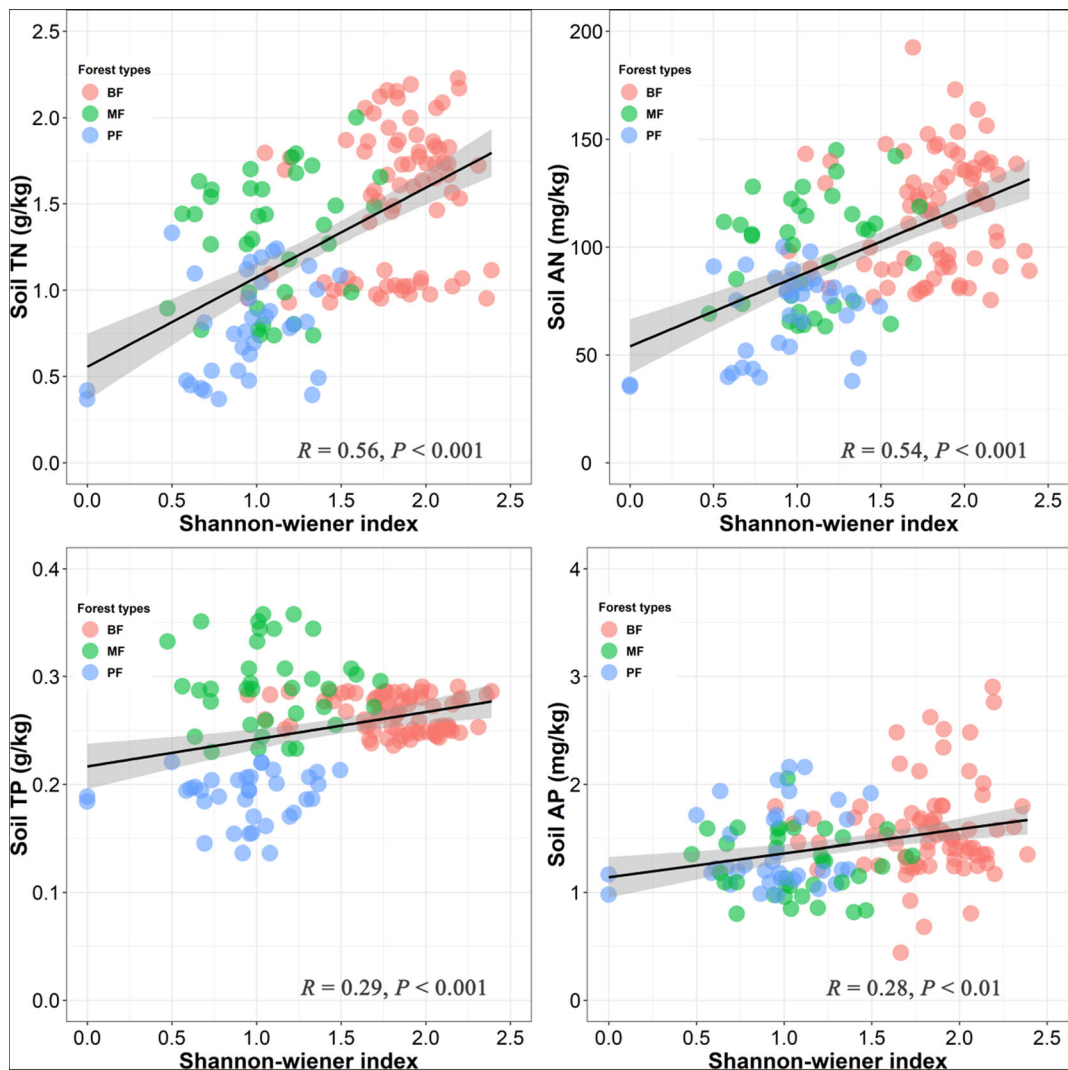
Fig. 1 Correlations of plant diversity (Shannon-Wiener index) with TN (a), AN (b), TP (c), and AP (d). Colored points present different vegetation types. The black lines are the fitted regression lines across all points (n = 147). The black shading indicates a 95% confidence interval. Only significant fitted lines are shown. TN: total nitrogen; AN: available nitrogen; TP: total phosphorus; AP: available phosphorus; PF: pine forest; MF; mixed pine and broadleaf forest; BF: monsoon evergreen broadleaved forest

LRR TN and *LRR* AN ($P < 0.05$), and SOC had an impact on *LRR* TN and *LRR* AP ($P < 0.05$).

SEM results indicated that plant diversity and species turnover had both direct and indirect effects on soil TN, TP, AN, and AP (Figs. 3 and 4). The total effects of plant diversity explained 65.2%, 65.0%, 60.8%, and 20.5% of the variation in TN, TP, AN, and AP, respectively (Fig. 3). When combined, the direct and indirect effects of species turnover explained 70.0% of the variation in TN, 49.6% in TP, and 23.8% in AN (Fig. 4). Plant diversity had a positive direct effect on soil TN and AN, but no direct effect on soil TP and AP (Fig. 3). The

indirect effects of plant diversity on soil TN, TP, AN, and AP were mediated by annual litterfall, litter C/N, TBA, SOC, and soil exchangeable base cations (Fig. 3). Species turnover had a significantly positive direct effect on *LRR* TN and *LRR* TP (Fig. 4a and c), but had no direct effect on *LRR* AN (Fig. 4b). Species turnover had indirect effects on the *LRRs* of TN, TP, and AN via litter N/P, SOC, and soil exchangeable base cations (Fig. 3). Moreover, forest type affected plant diversity through both direct and indirect paths (Fig. 3). However, it only affected species turnover through an indirect path (Fig. 4).

Table 4 Summary of the linear mixed-effect models for the effects of forest types, Shannon, AL, LQ, TBA, and soil factors (pH, SOC, EBC) on TN, AN, TP and AP in surface soil (0–20 cm) at subplot level (n = 147). The forest types are divided into PF, MF and BF according to the succession stage. Subplot and year were included as the random effect in the models. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$. Shannon: Shannon-Wiener index; AL: annual litterfall; LQ: litter quality; TBA: tree basal area; SOC: soil organic carbon; EBC: soil exchangeable base cation; TN: soil total nitrogen; TP: soil total phosphorus; AN: soil available nitrogen; AP: soil available phosphorus; PF: pine forest; MF; mixed pine and broadleaf forest; BF: monsoon evergreen broadleaved forest

TN			AN			TP			AP		
Fixed terms	Coefficient	F-value	Fixed terms	Coefficient	F-value	Fixed terms	Coefficient	F-value	Fixed terms	Coefficient	F-value
Forest types	0.032	592.83***	Forest types	0.085	406.00***	Forest types	0.035	147.58***	Forest types	−0.147	17.72**
Shannon	0.035	34.19***	Shannon	0.098	31.13***	Shannon	−0.015	18.58***	Shannon	0.111	2.78*
AL	0.036	298.04***	AL	0.055	189.71***	AL	0.030	6.57*	AL	−0.056	3.89
LQ	< 0.001	3.18	LQ	−0.026	17.69***	LQ	0.006	26.56***	LQ	−0.001	1.66
TBA	0.008	6.16*	TBA	0.016	0.56	TBA	−0.010	27.15***	TBA	0.044	1.80
pH	−0.487	57.72***	pH	−0.764	36.89***	pH	−0.017	0.00	pH	−0.545	15.19***
SOC	0.187	175.94***	SOC	0.066	53.31***	SOC	0.049	3.30	SOC	0.451	103.36***
EBC	0.109	146.14***	EBC	0.194	130.54***	EBC	−0.021	54.47***	EBC	−0.059	21.87***
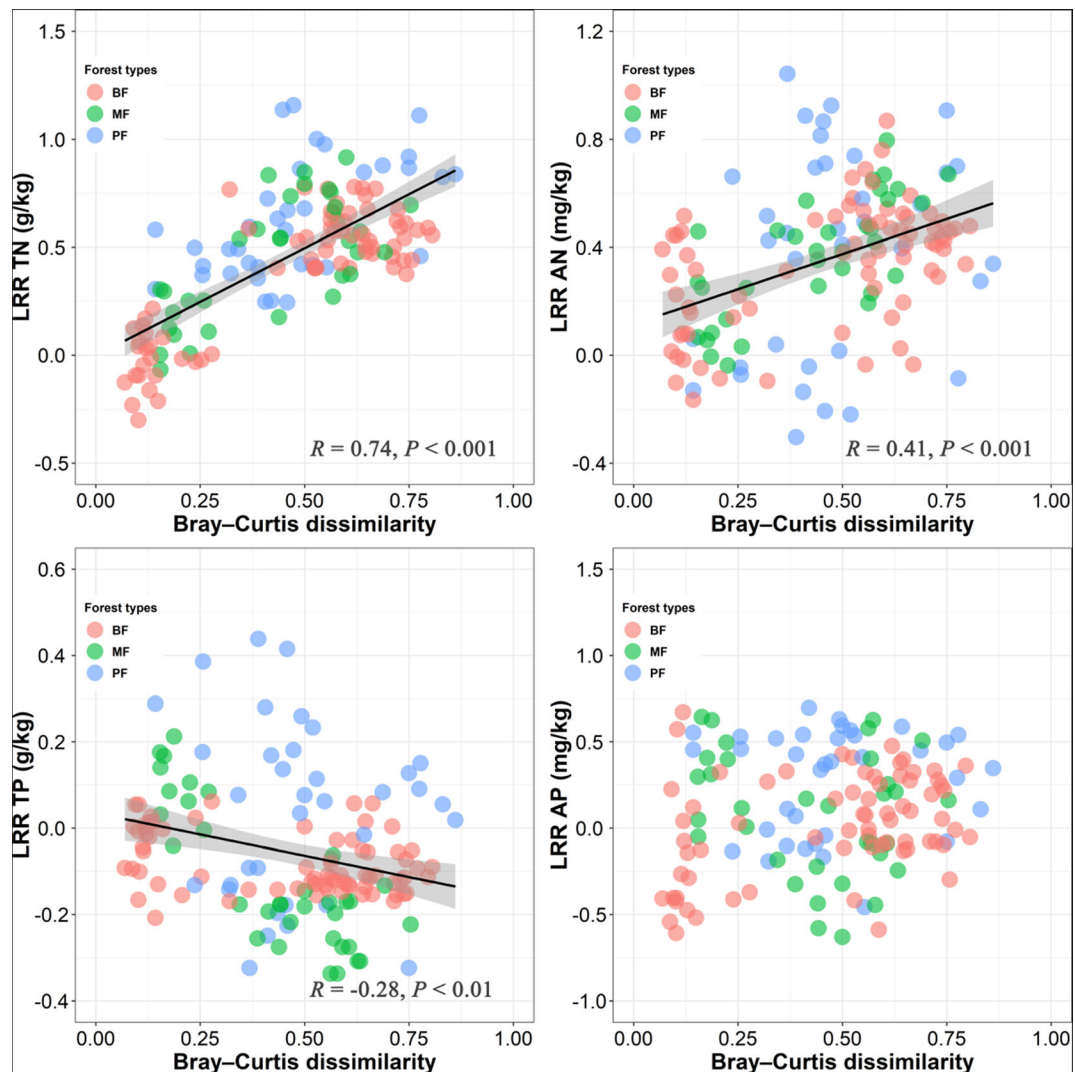
Fig. 2 Correlations of species turnover (Bray-Curtis dissimilarity) with *LRR* TN (a), *LRR* AN (b), *LRR* TP (c), *LRR* AP (d). Colored points present different vegetation types. The black lines are the fitted regression lines across all points (*n* = 147). The black shading indicates a 95% confidence interval. Only significant fitted lines are shown. *LRR* TN: log-response ratios of total nitrogen; *LRR* AN: log-response ratios of available nitrogen; *LRR* TP: log-response ratios of total phosphorus; *LRR* AP: log-response ratios of available phosphorus; PF: pine forest; MF; mixed pine and broadleaf forest; BF: monsoon evergreen broadleaved forest

Discussion

### Effect of plant diversity on soil nutrients

In accordance with our first hypothesis, plant diversity was associated with increases in soil TN, TP, AN, and AP concentrations, which is also consistent with the results of previous studies (De Groote et al. 2018; Hobbie et al. 2006; Kooch et al. 2017; Scherer-Lorenzen et al. 2007; Wu et al. 2019; Zhou et al. 2019b). Together, "complementarity" and "mass"

effects played an important role in the effect of plant diversity on soil nutrients. The "complementary" effects were reflected in two aspects. First, plant diversity promoted tree growth (Fig. 3), which is associated with increasing the demand for nutrients (Caplan et al. 2019; Duffy et al. 2017; Kooch and Bayranvand 2017; Zemunik et al. 2015) and which may lead to the use of various nutrition strategies in plants (e.g., root exudation) to increase soil nutrient availability (Baxendale et al. 2014; Sun and He 2019; Wang and Lambers 2019). Secondly, the combination of litter

Table 5 Summary of the linear mixed-effect models of *LRR* TN, *LRR* AN, *LRR* TP and *LRR* AP to forest types, species turnover and the changes of AL, LQ, TBA, soil factors (pH, SOC, EBC) (n = 147). The forest types are divided into PF, MF and BF according to the succession stage. Subplot was included as the random effect in the models. *LRR* TN: log-response ratios of total

nitrogen; *LRR* AN: log-response ratios of available nitrogen; *LRR* TP: log-response ratios of total phosphorus; *LRR* AP: log-response ratios of available phosphorus; AL: annual litterfall; LQ: litter quality; TBA: tree basal area; SOC: soil organic carbon; EBC: soil exchangeable base cation; PF: pine forest; MF; mixed pine and broadleaf forest; BF: monsoon evergreen broadleaved forest

LRR TN			*LRR* AN			*LRR* TP			*LRR* AP		
Fixed terms	Coefficient	*F*-value	Fixed terms	Coefficient	*F*-value	Fixed terms	Coefficient	*F*-value	Fixed terms	Coefficient	*F*-value
Forest types	−0.057	69.61***	Forest types	0.004	1.57	Forest types	−0.073	35.69***	Forest types	−0.030	21.92***
Species turnover	0.605	344.36***	Species turnover	−0.157	45.15***	Species turnover	0.176	29.44***	Species turnover	0.409	2.01
AL	0.042	10.53**	AL	0.053	8.24**	AL	0.038	3.85	AL	−0.050	0.25
LQ	−0.012	18.18***	LQ	0.001	21.89***	LQ	−0.032	82.42***	LQ	−0.104	19.07***
TBA	0.036	9.12**	TBA	0.029	4.60*	TBA	0.000	0.70	TBA	−0.014	1.08
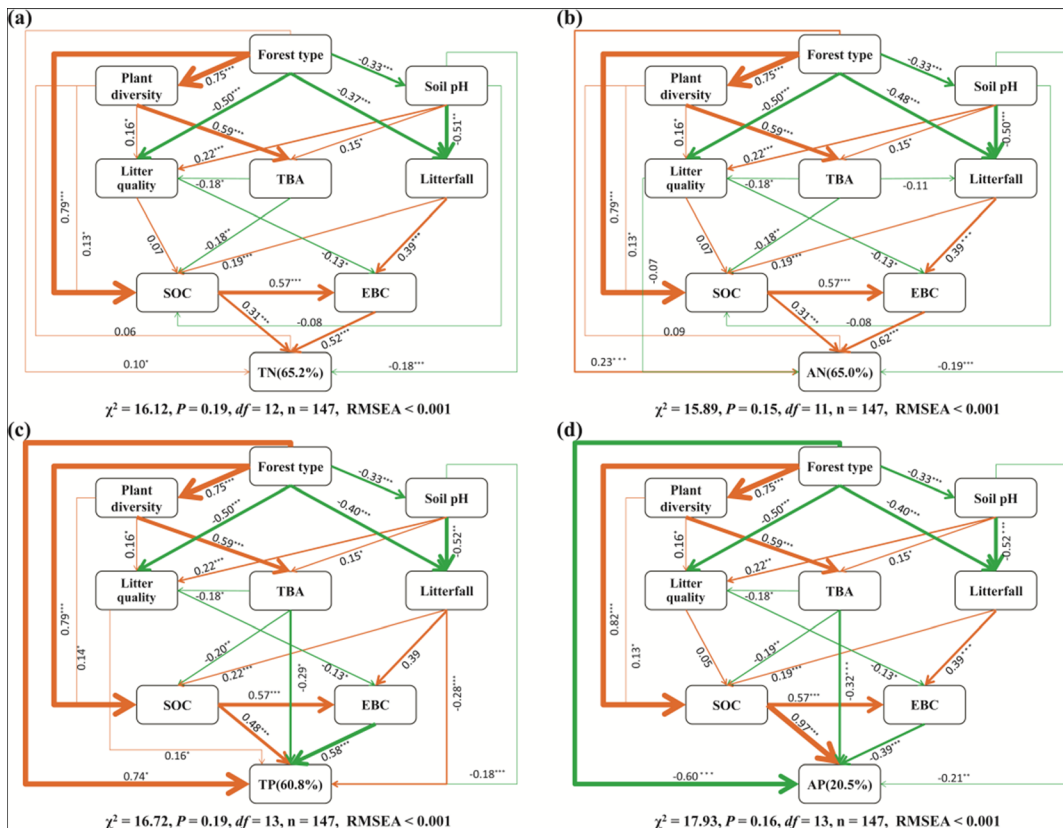
Fig. 3 Structural equation models of the effects of forest type, Shannon-Wiener annual litterfall, litter quality, TBA, and soil factors (pH, SOC, EBC) on TN (a), AN (b), TP (c), and AP (d) in surface soil (0–20 cm) at subplot level (n = 147). The numbers for the endogenous variables indicate the explained variance (R^2). The numbers on the arrows indicate standardized path coefficients.

The arrow width is proportional to the strength of the path coefficients. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$. TBA: tree basal area; SOC: soil organic carbon; EBC: soil exchangeable base cation; TN: soil total nitrogen; TP: soil total phosphorus; AN: soil available nitrogen; AP: soil available phosphorus
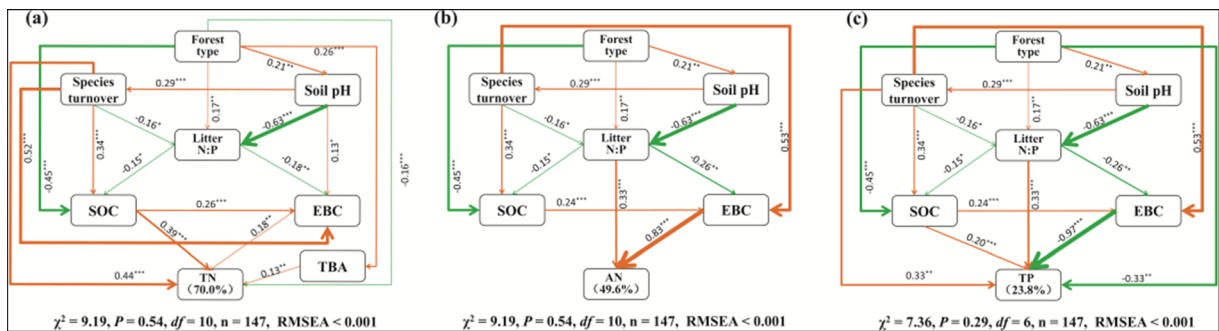
Fig. 4 Structural equation models of the effects of forest type, species turnover, *LRR* of litter N: P, *LRR* of TBA, and *LRR* of soil factors (pH, SOC, EBC) on *LRR* TN (a), *LRR* AN (b) and *LRR* TP (c), in surface soil (0–20 cm) at subplot level (n = 147). The numbers for the endogenous variables indicate the explained variance (R^2). The numbers on the arrows indicate standardized path coefficients. The arrow width is proportional to the strength of the path coefficients. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$. TBA: tree basal area; SOC: soil organic carbon; EBC: soil exchangeable base cation; *LRR* TN: log-response ratios of total nitrogen; *LRR* AN: log-response ratios of available nitrogen; *LRR* TP: log-response ratios of total phosphorus

from different species can result in faster decomposition than that of individual species (Maisto et al. 2011), thus increasing soil nutrient contents. The "mass" effect was also reflected in the relationships between plant diversity and soil TN, TP, AN, and AP (Fig. 3). Specifically, plant diversity can promote the return of N and P to the soil (Cordova et al. 2018; Hobbie et al. 2006; Kooch et al. 2017) by regulating litter quantity and quality (Zhou et al. 2019a). In addition, we found that SOC played an important role in maintaining the availability of soil N and P, and plant diversity can promote the accumulation of SOC (Chen et al. 2018; Wang and Lambers 2019). Moreover, SOC can compete with soil exchangeable base cations (i.e., Ca^{2+}, Mg^{2+}, and Al^{3+}) for adsorption sites to reduce the adsorption of N and P (Schreeg et al. 2013) and enhance the activity of soil microorganisms by providing energy, potentially promoting soil N and P mineralization (Chen et al. 2019; Hiiesalu et al. 2017; Lange et al. 2015; Liu et al. 2018; Wu et al. 2019).

In addition, soil microorganisms also play an important role in soil nutrient availability through decomposition of litter (leaves and roots), root exudates, and mineralization of organic matter (Lange et al. 2015; Wu et al. 2019). Moreover, increasing plant diversity generally increases soil microbial diversity (Hiiesalu et al. 2017; Lange et al. 2015), with many case studies on this topic carried out in tropical forests (Hiiesalu et al. 2017). Therefore, although they were not investigated in this study, soil microorganisms are one of the potential drivers for plant diversity impacts on soil nutrient availability. Thus, we suggest that soil microbial factors

should be included in future studies of plant-soil interactions.

In this study, different regulation patterns of plant diversity affecting soil TN, TP, AN, and AP were observed (Table 4, Fig. 3), which may be related to different cycling processes of N and P, including plant uptake, nutrient return by litter decomposition, nutrient source, and soil conditions (Caplan et al. 2019; Lange et al. 2015; Lu et al. 2019; Wu et al. 2019). Soil P mainly originates from the decomposition of plant tissues and weathering of parent material (Lawrence and Schlesinger 2001). In subtropical forests, the decomposition of plant tissue mediated by microbes is the dominant factor influencing soil P changes on a short time scale. In addition, there are numerous N-fixing species in subtropical forests (Ding et al. 1993), which can fix N from the atmosphere through associations with microorganisms (Png et al. 2019; Vitousek et al. 2013), thereby increasing soil N content.

Effect of species turnover on soil nutrients

Our second hypothesis was not fully supported by the results of this study. The linear response of AP to species turnover was not observed, but we found that the response degree of TN, TP, and AN to species turnover increased with species turnover (Fig. 2). Generally, the relationship between nutrient use efficiency and species composition is strong, with nutrient utilization efficiency increasing with the increase in interspecific complementarity (Lambers et al. 2008; Zemunik et al. 2015; Zhan et al. 2019). A shift in species composition is associated with changes in abiotic and biotic

processes (Wu et al. 2019), which affects the nutrient cycle and leads to the change in soil nutrient contents (Zhou et al. 2019b). Zhou et al. (2019b) found that soil quality declined significantly, especially soil available P, after the experimental changes in species composition. Our results suggested that species turnover plays an important role in regulating soil nutrient availability. However, in contrast to the results of Zemunik et al. (2016), we found that species turnover had different effects on N and P. This difference may be caused by different community composition, given that our study only assessed subtropical forests. For this reason, we suggest that more community types and regions need to be studied worldwide.

As indicated in previous studies, different community composition implies different nutrient utilization strategies. P is usually considered as a limiting nutrient in tropical and/or subtropical forests (Huang et al. 2013; Huang et al. 2012; Turner et al. 2018; Zemunik et al. 2016), and previous studies at our research site have shown that soil AP concentration was very low at all stages of succession (Huang et al. 2013; Huang et al. 2012). Turner et al. (2018) found that pervasive P limitation was detected at tree species level in tropical forests, but it was difficult to detect at the community level, which suggests that the fierce competition for soil AP might widely exist at the species scale. Therefore, the lack of significant correlation between *LRR* AP and species turnover may be a consequence of the low AP concentration and universal competition for P at the investigated site. In the process of species turnover, N-fixing species can fix a lot of N with high P cost (Laliberte et al. 2012; Raven 2012), which complicates N-fixing when P is not readily available. This may explain the different directions of soil N and P responses to species turnover.

Consistent with our third hypothesis, soil N and P responses to species turnover were different (Figs. 2 and 4). Species modify soil nutrient pools through specific or similar traits (Baxendale et al. 2014; Both et al. 2019; Caplan et al. 2019). The shift in species and plant individuals represents the fitness of tree species with different nutrition strategies, which might alter the ecosystem structure and functions and affect the nutrient cycle processes. For example, Caplan et al. (2019) found that species that reached their peak abundance in the early stage of succession usually had fine-root traits corresponding to resource acquisitive strategies (i.e., thinner and less dense roots), while species

peaking in the late stage of succession had increasing conservative strategies. Zhang et al. (2018) also found that the percentage of legumes can affect the soil nutrient contents during secondary succession. Furthermore, the pace and direction of species turnover regulates the duration and direction of a combination of ecosystem nutrition strategies. Therefore, the direction and degree of soil nutrient responses to species turnover may vary depending on vegetation, ecosystem type, and climate. Although some results in our study may not be applicable to other sites, it seems likely that the changes in soil nutrients caused by species turnover may occur in most ecosystems worldwide.

Our study highlighted the co-regulation of plant diversity, species turnover on soil nutrient availability, which can explain the inconsistency between plant diversity and soil nutrient availability during succession. In the early stages of succession, low availability of soil N limits the productivity of an ecosystem (Laliberte et al. 2012; Vitousek et al. 2013). Along with the colonization and increase in number of N-fixing species, soil N availability increases (Vitousek et al. 2013), which promotes the ecosystem evolution by supporting a higher number of species. Diverse species have associations with microbes and improve soil P availability through "complementarity" and "mass" effects (Wang et al. 2019; Wu et al. 2019). Considering the heterogeneity of biotic and abiotic conditions, our results in a single site may not be fully applicable to other forests. Thus, additional sites need to be researched in forests worldwide to corroborate these results.

Overall, our research has important implications for the conservation, management, and restoration of forest ecosystems, as well as for predicting the stability of forest functions under climate change, as it highlights the importance of considering species turnover and diversity effects on soil characteristics. Moreover, sustainable ecosystem development can be maintained under moderate changes in species composition and turnover in forests (Liu et al. 2018).

Conclusions

To the best of our knowledge, this is the first study to explore mechanisms relating to plant diversity and species turnover effects on soil N and P availability via a long-term continuous observation in a forest ecosystem. Plant diversity and species turnover increased with

forest succession, and both altered the availability of soil N and P. High plant diversity can both improve soil N and P availability as a result of increased productivity, altered litter quantity and quality, and changed soil physical and chemical properties (i.e., SOC). However, soil N and P each responded to species turnover differently. Soil TN and AN were positively related to species turnover, while soil TP was negatively correlated with species turnover, indicating that species turnover may lead to an imbalance of soil N and P supply during forest succession. Our results highlight that plant diversity and species turnover can co-regulate soil N and P availability. As climate change affects plant diversity and species turnover, this may alter the existing balance of soil N and P. Future studies on different ecosystems are urgently needed to better understand the effects of plant diversity and species turnover on soil N and P.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s11104-021-04940-x.

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