Leaf nitrogen resorption is more important than litter nitrogen mineralization in mediating the diversity–productivity relationship along a nitrogen-limited temperate forest succession chronosequence

Peng Zhang [a,b], Xiao-Tao Lü [c], Guangze Jin [a,d,e,*], Zhili Liu [a,d,e], Mai-He Li [b,f,g]

[a] *Center for Ecological Research, Northeast Forestry University, Harbin, 150040, China*
[b] *Forest Dynamics, Swiss Federal Institute for Forest, Snow and Landscape Research WSL, CH-8903, Birmensdorf, Switzerland*
[c] *Erguna Forest-Steppe Ecotone Research Station, CAS Key Laboratory of Forest Ecology and Management, Institute of Applied Ecology, Chinese Academy of Sciences, Shenyang, 110016, China*
[d] *Key Laboratory of Sustainable Forest Ecosystem Management, Ministry of Education, Northeast Forestry University, Harbin, 150040, China*
[e] *Northeast Asia Biodiversity Research Center, Northeast Forestry University, Harbin, 150040, China*
[f] *Key Laboratory of Geographical Processes and Ecological Security in Changbai Mountains, Ministry of Education, School of Geographical Sciences, Northeast Normal University, Changchun, 130024, China*
[g] *School of Life Science, Hebei University, Baoding, 071000, China*

ARTICLE INFO

ABSTRACT

The resorption of nutrients by plants before litter fall and the mineralization of nutrients from plant litter by soil processes are both important pathways supporting primary productivity. While the positive relationship between plant biodiversity and primary productivity is widely accepted for natural ecosystems, the roles of nutrient resorption and mineralization in mediating that relationship remains largely unknown. Here, we quantified the relative importance of nitrogen (N) resorption and N mineralization in driving plant community N investment and the correlation between species diversity and community productivity along an N-limited successional chronosequence of the mixed broadleaved–Korean pine (*Pinus koraiensis*) forest in northeastern China. Leaf N resorption efficiency (NRE) at the community level increased significantly along the successional chronosequence, whereas litter N mineralization rate decreased significantly. Leaf NRE was more important than litter N mineralization rate in driving the diversity–productivity relationship. However, higher leaf NRE led to less N mineralization as succession progressed along the chronosequence. Our results highlight the importance of the N resorption pathway rather than the N mineralization pathway for forest N acquisition with community succession, and they provide mechanistic insights into the positive effects of biodiversity on ecosystem functioning. In future forest management practices, we recommend appropriate application of N fertilizer to mitigate the adverse effects of N-poor soil on seedling regeneration during late succession and thus maintain the sustainable development of temperate forest ecosystems.

1. Introduction

The relationship between biodiversity and ecosystem functioning has received increasing attention from ecologists over the past three decades (Grime, 1998; Hooper et al., 2005; Lasky et al., 2014; Liang et al., 2016; Garcia-Palacios et al., 2017). In numerous studies, higher plant diversity has been reported to have positive impacts on primary productivity, due to the niche complementarity effect and the selection probability effect (Loreau and Hector, 2001; Fornara and Tilman, 2009). Forest carbon sequestration plays an important role in mitigating the anthropogenic

rise in atmospheric carbon dioxide concentrations and global warming, but this positive effect only emerges slowly as forests develop (Canadell and Raupach, 2008). An in-depth understanding of how plant diversity drives productivity over time is critical to predict potential changes in forest ecosystem functions. Forest succession is a continuous temporal process with progressive changes in plant diversity and ecosystem functioning (Odum, 1969; Lasky et al., 2014), providing an ideal natural gradient for exploring the relationships between diversity and ecosystem functioning. The relationship between diversity and productivity with forest succession is well documented (Morin et al., 2011; Lasky et al.,

2014; Ouyang et al., 2016), but the underlying mechanisms are far from understood.

The production of plant biomass depends on the ecosystem nutrient supply (Hessen et al., 2004; Wieder et al., 2015; Lü et al., 2019), which involves a trade-off between two main pathways: nutrient resorption by plants before litter fall and nutrient mineralization by soil processes after litter fall (Aerts, 1997; Deng et al., 2018). Plant diversity has positive effects on nutrient resorption and nutrient mineralization (Hooper et al., 2005; Garcia-Palacios et al., 2017; Lü et al., 2019; Kou et al., 2020), with important implications for nutrient cycling in forest ecosystems. Higher nutrient resorption efficiency by plants has been observed to be correlated with slower nutrient release from plant material, due to lower litter quality (Wardle et al., 1997; Gartner and Cardon, 2004). Conversely, fast nutrient mineralization has been reported to reduce nutrient resorption by increasing soil nutrient availability. However, such findings are mainly based on empirical evidence from a spatial perspective, while less is known about the temporal variations in their trade-offs and correlations.

Nutrient limitation increases along a forest succession chronosequence, as a result of increasing nutrient immobilization in plant biomass (Luo et al., 2004; Finzi et al., 2006; Zhang et al., 2020). In contrast to nutrient mineralization, nutrient resorption by plants during leaf senescence increases as succession progresses and plant diversity increases, as it offers a lower risk of nutrient loss and a lower energetic cost (Aerts, 1996; Wang et al., 2014). Thus, nutrient resorption may increase while nutrient mineralization may decrease in response to increasing diversity during succession, resulting in a greater role of nutrient resorption in community nutrient acquisition. To date, however, the trade-off between nutrient resorption and mineralization with forest succession and the roles of these two pathways in supporting community productivity have rarely been examined, limiting the understanding of the relative importance of nutrient cycling in the diversity–productivity relationship.

Two mechanisms could help explain the positive effects of plant diversity on nutrient resorption (Hooper et al., 2005; Fornara and Tilman, 2009; Lü et al., 2019). First, soil nutrient availability generally decreases in response to increasing diversity, as a result of resource depletion in a diverse community, leading to higher nutrient resorption efficiency, a mechanism termed the niche complementarity effect. Second, *K*-strategists (slow-growing tree species) gradually predominate over *r*-strategists (fast-growing tree species) with succession, causing an increasing ratio of *K*-strategists to *r*-strategists (Odum, 1969). Such a change in community composition can lead to a slower rate of nutrient cycling (Deng et al., 2018), even though *K*-strategists need more nutrients to support greater biomass production. Therefore, slower nutrient mineralization could cause plants to adopt a conservative resorption strategy, contributing to a higher nutrient resorption efficiency. This mechanism is known as the selection probability effect. However, there is an apparent lack of studies on the response of community-level nutrient resorption to increasing diversity, as past studies were largely carried out at the species level. Further, given that subordinate species play a critical role in community assembly (Boeken and Shachak, 2006; Zhang et al., 2018), comprehensive investigations of more or all species, considering their dominance within the community, might improve our understanding of the importance and mechanisms of nutrient cycling in the relationship between diversity and primary productivity.

The primary productivity of forest ecosystems is greatly limited by nitrogen (N) and phosphorus (P). N availability is more limited in younger higher-latitude soils, while P availability is more limited in older equatorial soils (Reich and Oleksyn, 2004). In addition, biological N fixation and N mineralization are found to decrease from tropical forests to temperate forests (Houlton et al., 2008; Menge et al., 2017; Deng et al., 2018). Primary productivity in higher-latitude temperate forests is therefore primarily limited by N availability (Reich and Oleksyn, 2004; Du et al., 2020). Consequently, plants in temperate regions rely more on the conservative N resorption pathway than the N mineralization pathway (Yuan and Chen, 2009; Vergutz et al., 2012; Deng et al., 2018).

More importantly, N resorption efficiency (NRE) increases with forest succession, owing to progressive N limitation (Luo et al., 2004; Finzi et al., 2006; Johnson, 2006; Zhang et al., 2020). While such efficient resorption may have positive consequences for forest productivity, it could result in lower litter quality (Aerts, 1997; Lü et al., 2019). Therefore, it is valuable to explore the trade-off between N resorption and mineralization in N-limited temperate forests. In this study, we examined the main drivers of changes in the plant leaf N pool and community productivity along a succession chronosequence of the mixed broadleaved–Korean pine (*Pinus koraiensis* Siebold. & Zucc.) forest in northeastern China. We aimed to address the following two questions: (1) How do successional changes in diversity, N resorption, and N mineralization affect leaf N content and community productivity? (2) Is there a trade-off between N resorption and mineralization along the succession chronosequence? We hypothesized that: (H1) species diversity mediates community leaf N pools and productivity through NRE rather than N mineralization rate across the successional stages because resorption is more likely to conserve N in plants at a lower cost than mineralization; and (H2) NRE increases, whereas N mineralization rate decreases due to the poor decomposability of the litter, with increasing diversity and community productivity as forest succession progresses. Thus, the N resorption pathway predominates over the N mineralization pathway for plant N acquisition and investment under more N-limited conditions.

2. Material and methods

2.1. Site description and sample collection

We conducted the study in the Liangshui National Nature Reserve located in Heilongjiang Province in northeastern China (47°10′50″ N, 128°53′20″ E). This natural reserve comprises diverse successional stages of the mixed broadleaved–Korean pine forests that grow naturally (without anthropogenic management) from an area of bare land. Small rolling hills with a relatively gentle slope (10°–15°) characterize the research area. This region has a temperate continental monsoon climate with a mean annual temperature of −0.3 °C. The mean annual precipitation is 676 mm, mainly occurring in summer. The soil type belongs to Humaquept or Cryoboralf following the American Soil Taxonomy (dark brown forest soil in the Chinese soil classification).

We studied four sites, each representative of a different forest type in different successional stages across the succession chronosequence: 60-year-old white birch forest (WBF) representing an early successional stage, 100-year-old broadleaved mixed forest (BMF) representing a middle successional stage, 160-year-old coniferous broadleaved mixed forest (CBMF) representing a middle-to-late successional stage, and 220-year-old primary mixed broadleaved–Korean pine forest (BKPF) representing a late successional stage (Table 2). These four sites were undisturbed and had a similar elevation, slope, aspect and historical land-use intensity. For each forest type, we established 3 independent replicate 20 m × 20 m plots for the community survey and woody vegetation sampling, resulting in a total of 12 plots. The distance between adjacent plots

Table 1

The hypotheses for the examined pathways presented in Fig. 1, with the corresponding literature references.

Pathway	Hypothesis	Reference
Succession → diversity	Positive	Odum (1969); Lasky et al. (2014)
Diversity → N resorption	Positive	Lü et al. (2019)
N resorption → N mineralization	Negative	Aerts (1997); Deng et al. (2018)
N resorption → productivity	Positive	Yuan and Chen (2009); Vergutz et al. (2012); Deng et al. (2018)
Diversity → N mineralization	None	Wardle et al. (1997); Gartner and Cardon (2004)
N mineralization → productivity	None	Deng et al. (2018)

Table 2
Stand characteristics of the four studied forest types.

	WBF	BMF	CBMF	BKPF
Successional stage	Early	Middle	Middle-late	Late
Stand age (year)	60	100	160	220
Stand density (woody stems per m^2)	0.35 ± 0.12 a	0.38 ± 0.06 a	0.42 ± 0.13 a	0.34 ± 0.08 a
Community weighted mean DBH (cm)	24.42 ± 2.50 c	27.81 ± 4.64 bc	39.03 ± 7.90 ab	43.87 ± 4.57 a
H'	1.83 ± 0.06 d	2.03 ± 0.05 c	2.27 ± 0.12 b	2.66 ± 0.10 a
N resorption efficiency (%)	37 ± 6 b	44 ± 5 b	55 ± 2 a	57 ± 5 a
N mineralization rate	0.65 ± 0.11 a	0.62 ± 0.04 a	0.31 ± 0.07 b	0.33 ± 0.05 b
Soil total N (g·kg^{-1})	6.72 ± 0.53a	9.34 ± 2.84 a	7.75 ± 0.76 a	6.79 ± 2.23 a
Leaf N pool (g)	740.97 ± 307.36 c	1575.29 ± 421.62 bc	2933.85 ± 910.54 ab	4023.95 ± 1706.72 a
Community productivity (Mg·ha^{-1}·year^{-1})	5.14 ± 1.60 b	4.74 ± 0.89 b	8.00 ± 0.35 a	7.57 ± 0.49 a

WBF: white birch forest; BMF: broadleaved mixed forest; CBMF: coniferous–broadleaved mixed forest; BKPF: mixed broadleaved–Korean pine forest. Different letters denote significant differences ($P \leq 0.05$) among the different forest types.

was large enough (>50 m) to minimize spatial autocorrelation effects. All stems ≥1 cm diameter at breast height (DBH) were taxonomically identified and measured.

In July and August 2020, we collected current-season, completely developed and sun-exposed canopy leaves from at least three average individuals of each species within each plot. The average individuals of each species were determined based on the average DBH of the species in a given plot. These leaves sampled from several individuals of each species were pooled and homogenized for nutrient analysis. For species that only had one or two individuals in a plot, we sampled additional individuals near the plot border to complete the sample.

We set up five 1 m × 1 m litter traps at 1-m height to collect newly senesced leaves (litterfall) in each plot in August. The litterfall was retrieved monthly from each plot during August to November 2020. We acknowledge that it is possible that nutrient leaching in litter traps results in an overestimation of resorption. In this study, however, most of the senesced leaves were shed during the dry season without noteworthy rainfall events before collection. Thus, the bias from leaching loss was not taken into account in the calculation of nutrient resorption. Further, as leaf litter from the shrubs rarely fell into the litter traps, senesced leaves of shrubs that had formed an abscission layer were collected directly from the plants in autumn by gently flicking branches or leaves, rather than from litter traps.

Soil sampling was performed at the same time as plant sampling. In each of 12 plots, 5 soil samples from the 0–20 cm depth layer were collected using a 5-cm-diameter soil auger from 5 randomly selected locations and then fully mixed as one composite soil sample per plot.

2.2. Litter decomposition experiment

A one-year field litter decomposition experiment was conducted to estimate N mineralization rates. We separated the collected leaf litter into two parts, one for the litter decomposition experiment and the other for chemical analysis. Leaf litter was sorted into species after being taken to the laboratory and air-dried for 2–4 weeks. Litter samples were then placed inside nylon litterbags (mesh size 1 mm) and sealed. Additional litter samples of each species were oven-dried at 75 °C for 48 h to determine the species-specific ratio of the air-dried and oven-dried mass, which was applied to convert the initial mass of the litter per bag. The proportion of leaf litter for each species was derived from the dominance of the corresponding species in each plot, which was expressed by the

relative biomass of each species in the community. A total of 216 litterbags (12 plots × 3 replicates × 6 sampling dates) containing an initial dry mass of 10 g of fully mixed leaf litter were incubated in each plot from November 2020 to November 2021. Eighteen litterbags were distributed evenly across each plot in each of the four successional stages. After carefully removing all existing forest floor litter, the litterbags were gently fastened to the ground using 10-cm-long metal stakes, with at least 50 cm between them to prevent a mutual effect. Litterbags were retrieved after 60, 120, 180, 240, 300 or 360 days of decomposition in the field, with three replicates per plot at each time point. After retrieval, the litter remaining in the bags was carefully brushed clean and oven-dried to a constant weight to determine its dry mass and N concentration.

2.3. Chemical measurements

Leaf and litter samples were oven-dried at 75 °C for 72 h. All samples were finely crushed with an MM400 ball mill (Retsch, Haan, Germany) and then sieved through a 0.25-mm mesh for the determination of element concentrations. A Multi CN/3000 analyzer (Analytik Jena AG, Jena, Germany) was applied to measure leaf C concentrations. The total N and P concentrations of the plant samples were assayed by acid digestion and colorimetric analysis on an automated discrete analyzer (AQ400, Seal Analytics, Norderstedt, Germany). Fresh soil samples were sieved through a 2-mm mesh and then analyzed for ammonium (NH_4^+) and nitrate (NO_3^-) concentrations. Soil available nitrogen (AN), defined as the sum of the concentrations of soil NH_4^+ and NO_3^-, was measured through colorimetric analysis on a continuous flow analyzer (AA3, Seal Analytical) after extraction with a 2 mol·L^{-1} solution of KCl.

2.4. Data calculations

We calculated the community-weighted mean (CWM) of the maximum tree height in each plot to quantify the dominance of species with a large body size during succession. The maximum height that each species can reach was extracted from the Flora of China website (http://www.iplant.cn/).

The CWM of maximum tree height was calculated based on the biomass-weighted mean approach (He et al., 2019):

$$\mathrm{MH_{community}} = \sum \frac{\mathrm{MH} \times B}{B_{\mathrm{community}}} \tag{1}$$

where $MH_{community}$ is the CWM of maximum height (m) in a plot, MH is the maximum height (m) that each species can reach, B is the total biomass (kg) of the corresponding species, and $B_{community}$ is the total community biomass (kg). The biomass of specific organs of each species was estimated using the allometric equations presented in Table S1.

N mineralization rates based on the litter decomposition experiment were calculated using the following equation (Bragazza et al., 2007):

$$\mathrm{N\ mineralization\ rate} = (M_1 N_1 - M_{12} N_{12}) / M_1 N_1 \tag{2}$$

where M_1 is the litter dry mass and N_1 is the litter N concentration before the litter decomposition experiment. M_{12} and N_{12} are the litter dry mass and litter N concentration after the last litter retrieval (360 d of litter decomposition), respectively. Positive values indicate N mineralization, whereas negative values mean N immobilization. We also calculated N mineralization rates for the other five retrieval times (60, 120, 180, 240 and 300 d) to determine if one year of litter decomposition was a continuous process of increasing N mineralization.

We defined the community-level leaf NRE as the weighted average of leaf NRE of all woody species occurring in each plot.

$$\mathrm{NRE_{community}} = \sum \frac{\mathrm{NRE} \times B}{B_{\mathrm{community}}} \tag{3}$$

where NRE$_{community}$ is the CWM of leaf N resorption efficiency of all woody species in a plot, NRE is the leaf N resorption efficiency of each species, and B and $B_{community}$ are defined as in Eq. 1.

For each species, leaf NRE was calculated as the proportion of N resorbed from the senescent leaves out of the N concentration in green leaves, using the following equation (Vergutz et al., 2012).

$$NRE = \left[1 - \left(MLCF \times E_{senesced} \big/ E_{green}\right)\right] \times 100\% \qquad (4)$$

where NRE is the species-specific N resorption efficiency and $E_{senesced}$ and E_{green} represent the N concentrations of senesced leaves and green leaves, respectively, for a given species. The mass loss correction factor (MLCF) is 0.784 for the deciduous broadleaved species and 0.745 for the conifer tree species.

Simultaneously, we used the community-level N resorption proficiency (i.e. N concentration in leaf litter; Killingbeck, 1996) to characterize the decomposability of litter, which mediates the effect of NRE on N mineralization rate. The equation is as follows:

$$Litter\ N_{community} = \sum \frac{Litter\ N \times B_s}{B_{litter}} \qquad (5)$$

where Litter N$_{community}$ is the CWM of the litter N concentration of all woody species in a plot, and Litter N is the litter N concentration of each species. B_s is the biomass (kg) of freshly fallen litter of the corresponding species, and B_{litter} is the total biomass (kg) of freshly fallen litter of all species in the plot.

The community-level leaf N pool was derived by summing the leaf N pools (product of leaf N concentration and biomass) of all woody species in each plot. Forest productivity was expressed as the sum of the annual increase in aboveground biomass and litterfall, following the method of Zhang et al. (2022).

2.5. Statistical analysis

We quantified the diversity in each plot using the Shannon-Wiener index (H') based on all woody plants with DBH ≥ 1 cm, calculated with the R package "vegan" (Oksanen et al., 2018). H', NRE, N mineralization rate, leaf N pool and community productivity were log-transformed before analysis to meet assumptions of normality and homoscedasticity. First, one-way analysis of variance (ANOVA) was performed to compare the differences in stand characteristics among four successional forest types. We performed multiple analyses, using H', NRE, and N mineralization rate as predictor variables in each analysis, and leaf N pool or community productivity as the dependent variable. The relationships between the predictor variables and dependent variable were estimated using linear regressions. Meanwhile, we estimated the effects of H', NRE and N mineralization rate on leaf N pool and on community productivity across successional stages using linear mixed-effects models. In both models, diversity index, NRE and N mineralization rate were included as fixed factors and successional forest type was included as a random factor. The variance inflation factor (VIF) was calculated to diagnose multicollinearity problems among these predictor variables. A model is generally considered reliable when the VIF between any two predictor variables in the model is < 10 (Chatterjee and Hadi, 2006). We found that all VIFs were <10 (Table S2), so multicollinearity was considered negligible here. The mixed-effects models were carried out using the *lme* function in the R package "nlme" (Pinheiro et al., 2021). We also calculated the marginal R^2 (proportion of variance exclusively explained by fixed factors) and conditional R^2 (proportion of variance explained by fixed factors and random factors combined) using the *r.squaredGLMM* function of the "MuMIn" package (Nakagawa and Schielzeth, 2013; Bartón, 2022). Additionally, the relative importance of each predictor in the two linear mixed-effects models was quantified by summing the Akaike weights of all possible models containing the predictor, using the R package "glmulti" (Calcagno, 2020).

Finally, we performed piecewise structural equation modeling (SEM) to examine the direct and indirect effects of diversity and nutrient cycling on the leaf N pool and community productivity, and further to test whether nutrient resorption is the main pathway through which diversity regulates community productivity. We also used piecewise SEM to examine whether diversity enhances NRE through changes in soil N availability and community composition, and to examine whether increasing NRE reduces N mineralization rate by influencing litter N concentration. Our conceptual priori model was constructed based on the existing knowledge in the literature (Table 1 and Fig. 1). The linear mixed-effects models were used as the constituent models of the piecewise SEMs. Fisher's C was employed to assess the goodness of fit of the whole SEM, and a well-fitting model was denoted by a non-significant P-value ($P > 0.05$). Piecewise SEMs were implemented using the "piecewiseSEM" (Lefcheck, 2016) package in R. All data analyses were carried out using R v. 4.0.4 (R Development Core Team, 2021).

3. Results

Forest community weighted mean (CWM) of DBH, Shannon-Wiener index (H'), NRE, leaf N pool and productivity increased significantly with succession, while N mineralization rate decreased significantly. Stand density and soil total N remained relatively constant (Table 2). H' showed a positive correlation with leaf N pool and community productivity along the succession chronosequence (Figs. 2 and 3a). NRE was positively correlated with leaf N pool and community productivity ($P < 0.05$; Figs. 2 and 3b), while N mineralization rate was negatively correlated with leaf N pool and community productivity (Figs. 2 and 3c). A significant positive correlation was detected between leaf N pool and community productivity, while there was a significant negative correlation between NRE and N mineralization rate (Fig. 4).

Linear mixed-effects models indicated that NRE had significant positive effects on leaf N pool and community productivity ($P < 0.05$; Table 3), while no significant effect of H' or N mineralization rate was observed in either model ($P > 0.05$; Table 3). NRE was also the most important predictor in determining leaf N pool and community productivity relative to the other two predictors based on the analysis of relative importance (Figs. 2 and 3d).

The piecewise SEM results showed that all predictor variables together explained 88% and 96% of the total variation in leaf N pool and
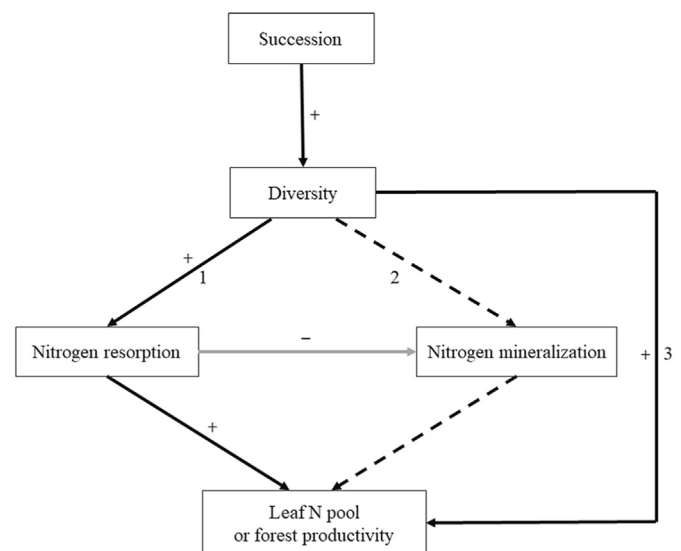

Fig. 1. The conceptual model used to test the link between diversity and ecosystem functioning, and the three alternative hypothetical pathways representing the three key processes tested in this study. 1, Indirect effects via nitrogen resorption; 2, Indirect effects via nitrogen mineralization; 3, Direct effects of diversity.
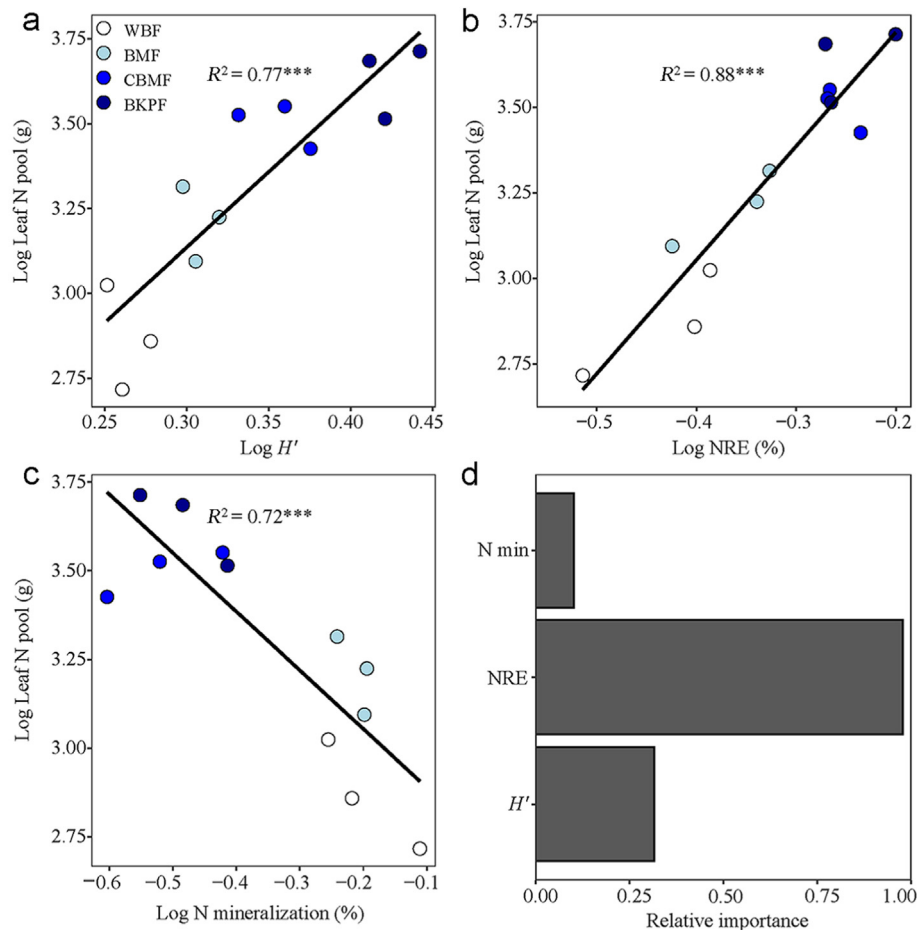
Fig. 2. Effect of diversity and nutrient cycling on leaf N pool. (**a**) Diversity and leaf N pool; (**b**) leaf N resorption efficiency (NRE) and leaf N pool; (**c**) N mineralization rate and leaf N pool; (**d**) model-averaged importance of these three predictor variables in determining leaf N pool.

community productivity, respectively (Fig. 5a and b). As succession progressed along the chronosequence, H' had significant positive indirect effects on leaf N pool and community productivity by affecting NRE (Fig. 5a and b). Further analysis indicated that select models including species diversity, soil inorganic N concentration, CWM of maximum tree height and NRE accounted for 87% of the variation in NRE (Fig. S1), and that diversity indirectly positively influenced NRE through its negative effect on soil inorganic N concentration and positive effect on CWM of maximum tree height (Fig. S1). There was no significant direct effect of diversity or indirect effect of diversity through N mineralization rate on leaf N pool or community productivity (Fig. 5a and b), whereas N mineralization rate was negatively influenced by NRE via litter N concentration (Figs. S2 and S3).

4. Discussion

We found that NRE was the most important factor influencing leaf N pools and community productivity along the forest succession chronosequence (Table 3). The diversity effects on leaf N pools and community productivity were mediated by NRE (Fig. 5a and b), which supports our hypothesis (H1). However, no significant direct effect of diversity on community productivity was found over succession, which may be ascribed to the fact that the effect of diversity on productivity is largely dependent on nutrient acquisition (Hooper et al., 2005; Fornara and Tilman, 2009; Lü et al., 2019). Complementary and selection effects can reduce nutrient losses from the ecosystem and increase total ecosystem nutrient retention (Hooper and Vitousek, 1997), so they may be more closely associated with plant nutrient uptake strategies than

with productivity. The stress gradient hypothesis suggests that facilitation and complementarity may be more beneficial than competition in harsh environmental conditions (Wright et al., 2017). To coexist within the same community under nutrient-poor soil conditions, each species needs to differentiate its resource acquisition strategy from those of other species. This differentiated resource use could occur in space, such as differences in root depth; in time, such as phenological differences in plant resource requirement; or in nutritional preference, e.g. for different present forms of N. This resource partitioning is known as niche complementarity, which is considered a crucial driver of productivity under resource-deficient environments (Hooper and Vitousek, 1998; Lohbeck et al., 2015). In this study, the leaf N:P ratio decreased significantly as stand age increased, with a range of 8.56 ± 0.21 to 6.53 ± 0.27, whereas NRE increased significantly from 37% ± 6% – 57% ± 5% and phosphorus resorption efficiency (PRE) remained constant (Table 2; Figs. S4a–c). These findings indicate a progressive shortage of N with advancing succession, based on the prevailing nutrient limitation diagnostic criteria (Koerselman and Meuleman, 1996; Vergutz et al., 2012; Yuan and Chen, 2015). This is mainly because niche differentiation may cause more complete resource use as succession progresses and species diversity increases, leading to depletion of the limited soil inorganic N (Figs. S1 and S5a).

On the other hand, our results provide new insights that the N-use strategy of the plant community may be closely related to the community composition during succession. Differences in plant community composition (the presence of a particular species or functional group) may have a significant influence on ecosystem processes if the species or functional group predominates in the community (Hooper and Vitousek, 1997). For
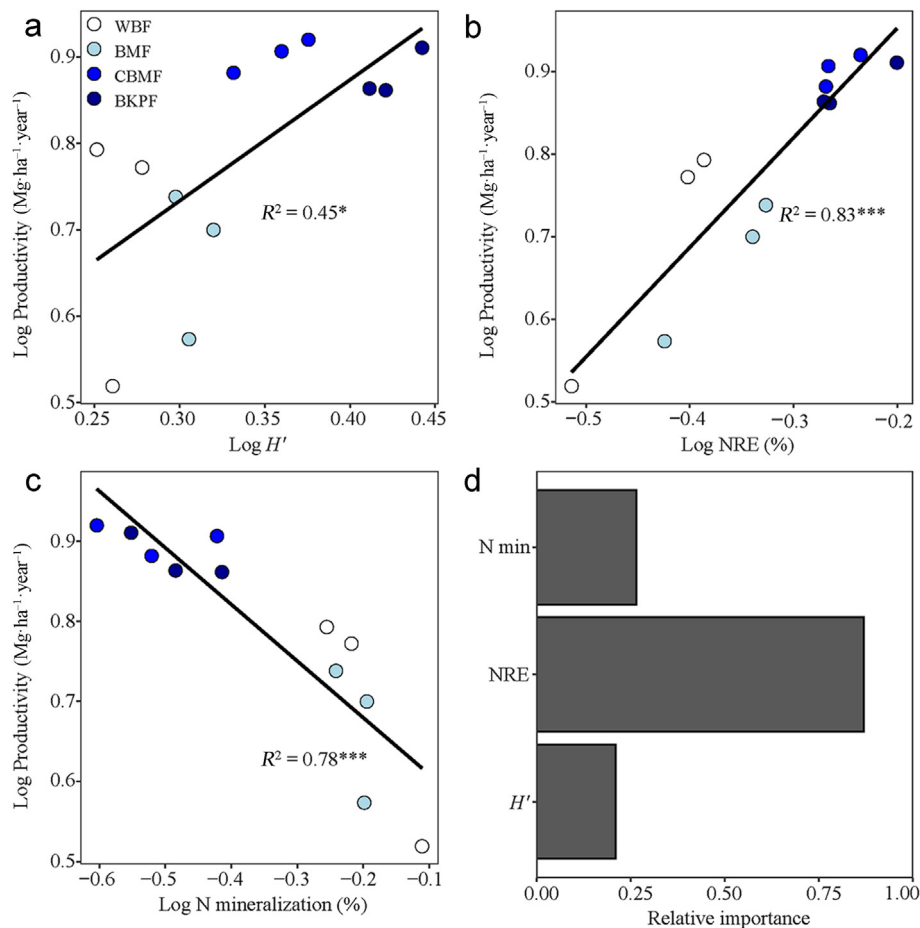
Fig. 3. Effect of diversity and nutrient cycling on productivity. (**a**) Diversity and productivity; (**b**) leaf N resorption efficiency (NRE) and productivity; (**c**) N mineralization rate and productivity; (**d**) model-averaged importance of these three predictor variables in determining productivity.
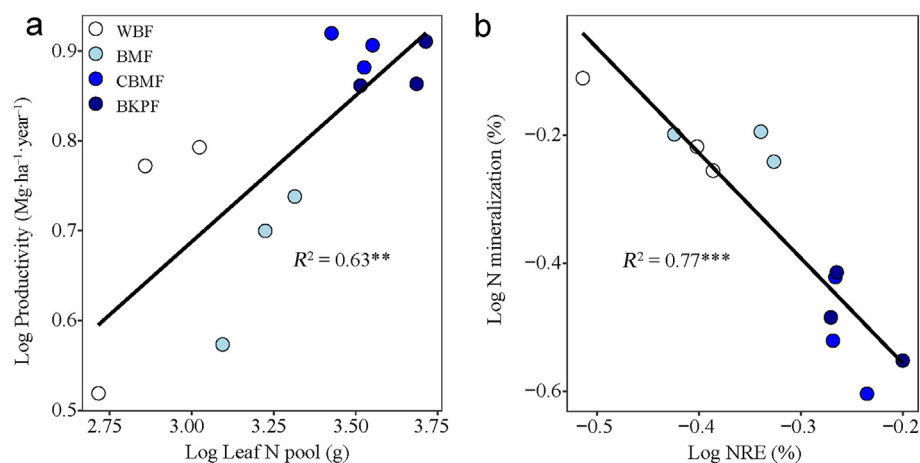

Fig. 4. Correlations between the four ecosystem processes. (**a**) Leaf N pool and productivity; (B) leaf N resorption efficiency (NRE) and N mineralization rate.

example, if the plant mixture containing a particular species or functional group has a lower rate of litter N mineralization than the plant mixture without it, this species or functional group may dominate litter N mineralization in mixtures. According to Odum's theory of succession, fast-growing *r*-strategists predominate in the early stages of succession (Odum, 1969), which leads to faster N turnover but lower N resorption in the ecosystem (Deng et al., 2018). In contrast, slow-growing *K*-strategists predominate in late succession because a plant community with higher diversity has a higher probability of containing these stress-resistant and long-lived *K*-strategists, contributing to a slower N cycling rate but higher NRE within the plant–soil system (Deng et al., 2018). Thus, as succession proceeds, the plant N-use strategy shifts from an acquisitive mineralization pathway to a conservative resorption pathway. This "conservative consumption" strategy can produce poor-quality litter that decomposes slowly, probably resulting in low soil N availability in the ecosystem. This long-term slow N release during late succession does not support the colonization of fast-growing species depending on high soil N availability, which might be advantageous for those *K*-strategists inhabiting the

Table 3
Results of linear mixed-effects models, where leaf N pool or community productivity is the response variable and the Shannon-Wiener diversity index (H'), N resorption efficiency and N mineralization rate are the predictors. SE = standard error. Significant P values ($P \leq 0.05$) are given in bold. $R^2_{marginal}$ and $R^2_{conditional}$ represent the proportion of variance explained by the fixed effects and both the fixed and random effects, respectively.

Variable	Estimate	SE	t-value	P value	$R^2_{marginal}$	$R^2_{conditional}$
Leaf N pool						
Intercept	3.66	0.65	5.67	**<0.01**	0.68	0.88
H'	1.57	1.00	1.58	0.18		
N resorption efficiency	2.61	1.00	2.62	**0.04**		
N mineralization rate	0.13	0.49	0.26	0.81		
Community productivity						
Intercept	1.68	0.23	7.36	**<0.001**	0.78	0.96
H'	0.75	0.47	1.58	0.17		
N resorption efficiency	1.89	0.29	6.44	**0.0013**		
N mineralization rate	0.08	0.19	0.40	0.71		

ecosystem with low fertility. This may also be one of the reasons why *K*-strategists are dominant over *r*-strategists in late succession. Collectively, the complete resource utilization and the greater proportion of *K*-strategists in the community contribute to a higher NRE with more advanced succession (Fig. S1).

We also found no significant effect of diversity on community productivity via litter decomposition, which could be due to the trade-off between NRE and N mineralization rate. Our results are experimental evidence of the trade-off between NRE and N mineralization rate with succession, supporting our hypothesis (H2). Diversity has been documented to have a positive effect on litter decomposition and nutrient release, potentially as a result of dispersion and complementation of litter quality and changes in environmental conditions associated with succession (Schimel and Hättenschwiler, 2007; Lummer et al., 2012; Trogisch et al., 2016). At the same time, however, increasing NRE caused by higher diversity may have a negative effect on N mineralization rates by reducing leaf litter quality (Figs. S2 and S3), considering that initial litter quality predominantly controls the litter decomposition process (Garcia-Palacios et al., 2017; Bhatnagar et al., 2018; Liao et al., 2022). Essentially, the positive effect of diversity on N mineralization may be neutralized by the negative effect of proficient N resorption on litter quality, i.e. a trade-off.

The increase in NRE and decrease in N mineralization rate with succession observed in our study indicates an increase in N use efficiency. Previous studies have also found that higher plant diversity (as occurs with succession) enhances plant N use efficiency, not only by increasing C sequestration per unit of N uptake, but also by extending the residence time of N in plants via resorption (Fornara and Tilman, 2009; Lü et al., 2019). Here, while higher diversity increased NRE at the community level, the C:N ratio in leaves was negatively correlated with species diversity (Fig. S5b), which is inconsistent with previous findings. This discrepancy may be ascribed to the different research scale. Previous studies have focused on the effect of diversity on inter- and intraspecific variations in plant stoichiometry within a community (Guiz et al., 2018; Lü et al., 2019), and thus the cause of these variations is often considered to be nutrient competition by niche overlap and interaction with neighboring plants. In the present study, however, we conducted a comprehensive investigation at the community level, including both dominant and subordinate species. Compared with single species, increases in N uptake and then in N retention in biomass may be more important than the biomass produced per unit of N in supporting community productivity as succession progresses and there is an increasing depletion of soil resources. The most acknowledged ecological mechanisms explaining greater N uptake and retention by increasing productivity under higher diversity are greater fine-root production, to improve the ability of plants to acquire N from the soil, and increased NRE from senescing leaves. Specifically, increasing fine-root production is usually accompanied by greater carbon allocation to mycorrhizal fungi in more diverse communities (Finzi et al., 2007; Parrent and Vilgalys, 2007; Hagenbo et al., 2021). Mycorrhizal fungi can help plants obtain N by

releasing enzymes that participate in the decomposition of soil organic matter and the capturing of organic and inorganic N from the soil (Leigh et al., 2009; Castaño et al., 2022), resulting in the depletion of soil N. Subsequently, lower soil N availability stimulates long-term N retention in plant biomass by enhancing NRE (Deng et al., 2018). Together, these strategies result in plant N accumulation.

It should be noted that the N release rates presented here refer to N loss during the first year of litter decomposition only, and thus we do not know how the rates of N release change after one year. Thus, the longer-term N release dynamics of litter decomposition still need to be observed. Additionally, given the climate-dependent nutrient use strategy across global terrestrial ecosystems, more attention needs to be paid to nutrient cycling processes with succession in other biomes. Further, the relative importance of nutrient resorption and mineralization in mediating the diversity–primary-productivity relationship needs to be evaluated on a global scale in future research.

5. Conclusion

In line with our hypotheses, we found that community-level NRE increased significantly, whereas N mineralization rate decreased significantly, with increasing community diversity and productivity along the forest succession chronosequence in an N limited area, and NRE was more important than N mineralization in driving the diversity–productivity relationship. These results provide robust empirical evidence that diversity significantly indirectly facilitates community productivity through its positive effect on the community-level leaf NRE in this N-limited forest succession chronosequence. This nutrient conservation strategy gives plants an advantage in adapting to low N availability. However, in the present study increased NRE also inhibited N turnover, indicated by a lower N mineralization rate, preventing the settlement of species with a low resource use efficiency that are dependent on high N availability, resulting in a harmonized community composition. Our results suggest that the trade-off between resorption and mineralization should be considered when analyzing the effects of diversity on forest ecosystem functioning. This finding has important implications for incorporating nutrient cycling into terrestrial C cycle models to improve the accuracy of predictions of the C sink capacity as nutrient limitation increases across forest ecosystems globally.

Data availability

The datasets used and/or analyzed during the current study are available from the corresponding author on reasonable request.
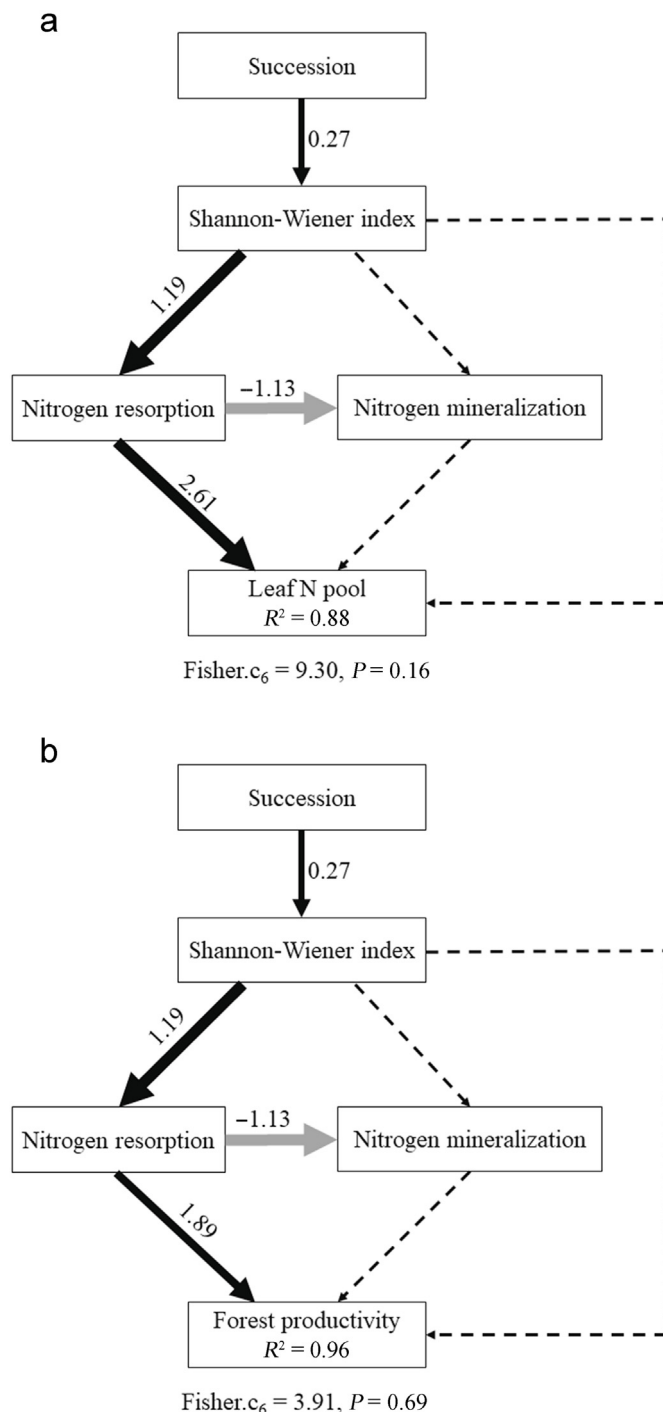
Fig. 5. Structural equation model relating leaf N pool and productivity to diversity (Shannon Wiener index, *H′*), N resorption efficiency (NRE), and N mineralization rate during the temperate forest succession. (**a**) Leaf N pool was explained by *H′*, NRE and N mineralization rate; (**b**) productivity was explained by *H′*, NRE and N mineralization rate. The numbers are standardized regression coefficients for each causal path. The solid black arrows represent significant ($P \leq 0.05$) positive paths; the solid gray arrows represent significant ($P \leq 0.05$) negative paths; and dashed arrows indicate non-significant paths ($P > 0.05$). The test results for each model are shown underneath each plot.

Authors' contributions

PZ and GZJ conceived the idea for the study. PZ performed the experiments, analyzed the data and wrote the initial manuscript. XTL, GZJ, ZLL and MHL contributed substantially to subsequent versions.

References

Aerts, R., 1996. Nutrient resorption from senescing leaves of perennials: are there general patterns? J. Ecol. 84, 597–608.
Aerts, R., 1997. Nitrogen partitioning between resorption and decomposition pathways: a trade-off between nitrogen use efficiency and litter decomposibility? Oikos 80, 603–606.
Bartón, K., 2022. MuMIn: Multi-Model Inference. R Package Version 1.46.0.
Bragazza, L., Siffi, C., Iacumin, P., Gerdol, R., 2007. Mass loss and nutrient release during litter decay in peatland: the role of microbial adaptability to litter chemistry. Soil Biol. Biochem. 39, 257–267.
Bhatnagar, J.M., Peay, K.G., Treseder, K.K., 2018. Litter chemistry influences decomposition through activity of specific microbial functional guilds. Ecol. Monogr. 88, 429–444.
Boeken, B., Shachak, M., 2006. Linking community and ecosystem processes: the role of minor species. Ecosystems 9, 119–127.
Calcagno, V., 2020. Glmulti: Model Selection and Multimodel Inference Made Easy. R package version 1.0.8.
Canadell, J.G., Raupach, M.R., 2008. Managing forests for climate change mitigation. Science 320, 1456–1457.
Castaño, C., Hallin, S., Egelkraut, D., Lindahl, B.D., Olofsson, J., Clemmensen, K.E., 2022. Contrasting plant–soil–microbial feedbacks stabilize vegetation types and uncouple topsoil C and N stocks across a subarctic–alpine landscape. New Phytol. https://doi.org/10.1111/nph.18679.
Chatterjee, S., Hadi, A.S., 2006. Regression Analysis by Example. John Wiley & Sons, Inc., Hoboken, New Jersey.
Deng, M.F., Liu, L.L., Jiang, L., Liu, W.X., Wang, X., Li, S.P., Yang, S., Wang, B., 2018. Ecosystem scale trade-off in nitrogen acquisition pathways. Nat. Ecol. Evol. 2, 1724–1734.
Du, E.Z., Terrer, C., Pellegrini, A.F.A., Ahlström, A., van Lissa, C.J., Zhao, X., Xia, N., Wu, X.H., Jackson, R.B., 2020. Global patterns of terrestrial nitrogen and phosphorus limitation. Nat. Geosci. 13, 221–226.
Finzi, A.C., Moore, D.J.P., DeLucia, E.H., Lichter, J., Hofmockel, K.S., Jackson, R.B., Kim, H.-S., Matamala, R., McCarthy, H.R., Oren, R., Pippen, J.S., Schlesinger, W.H., 2006. Progressive nitrogen limitation of ecosystem processes under elevated CO2 in a warm-temperate forest. Ecology 87, 15–25.
Finzi, A.C., Norby, R.J., Calfapietra, C., Gallet-Budynek, A., Gielen, B., Holmes, W.E., Hoosbeek, M.R., Iversen, C.M., Jackson, R.B., Kubiske, M.E., Ledford, J., Liberloo, M., Oren, R., Polle, A., Pritchard, S., Zak, D.R., Schlesinger, W.H., Ceulemans, R., 2007. Increases in nitrogen uptake rather than nitrogen-use efficiency support higher rates of temperate forest productivity under elevated CO2. Proc. Natl. Acad. Sci. U.S.A. 104, 14014–14019.
Fornara, D.A., Tilman, D., 2009. Ecological mechanisms associated with the positive diversity: productivity relationship in an N-limited grassland. Ecology 90, 408–418.
Garcia-Palacios, P., Shaw, E.A., Wall, D.H., Hättenschwiler, S., 2017. Contrasting mass-ratio vs. niche complementarity effects on litter C and N loss during decomposition along a regional climatic gradient. J. Ecol. 105, 968–978.
Gartner, T.B., Cardon, Z.G., 2004. Decomposition dynamics in mixed-species leaf litter. Oikos 104, 230–246.
Grime, J.P., 1998. Benefits of plant diversity to ecosystems: immediate, filter and founder effects. J. Ecol. 86, 902–910.
Guiz, J., Ebeling, A., Eisenhauer, N., Hacker, N., Hertzog, L., Oelmann, Y., Roscher, C., Wagg, C., Hillebrand, H., 2018. Interspecific competition alters leaf stoichiometry in grassland species. Oikos 127, 903–914.
Hagenbo, A., Piñuela, Y., Castaño, C., de Aragón, J.M., de-Miguel, S., Alday, J.G., Bonet, J.A., 2021. Production and turnover of mycorrhizal soil mycelium relate to variation in drought conditions in Mediterranean Pinus pinaster, Pinus sylvestris and Quercus ilex forests. New Phytol. 230, 1609–1622.
He, N.P., Liu, C.C., Piao, S.L., Sack, L., Xu, L., Luo, Y.Q., He, J.S., Han, X.G., Zhou, G.S., Zhou, X.H., Lin, Y., Yu, Q., Liu, S.R., Sun, W., Niu, S.L., Li, S.G., Zhang, J.H., Yu, G.R., 2019. Ecosystem traits linking functional traits to macroecology. Trends Ecol. Evol. 34, 200–210.
Hessen, D.O., Ågren, G.I., Anderson, T.R., Elser, J., Ruiter, P.D., 2004. Carbon sequestration in ecosystems: the role of stoichiometry. Ecology 85, 1179–1192.
Hooper, D.U., Chapin III, F.S., Ewel, J.J., Hector, A., Inchausti, P., Lavorel, S., Lawton, J.H., Lodge, D.M., Loreau, M., Naeem, S., Schmid, B., Setälä, H., Symstad, A.J., Vandermeer, J., Wardle, D.A., 2005. Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. Ecol. Monogr. 75, 3–35.
Hooper, D.U., Vitousek, P.M., 1997. The effects of plant composition and diversity on ecosystem processes. Science 277, 1302–1305.

Hooper, D.U., Vitousek, P.M., 1998. Effects of plant composition and diversity on nutrient cycling. Ecol. Monogr. 68, 121–149.

Houlton, B.Z., Wang, Y.P., Vitousek, P.M., Field, C.B., 2008. A unifying framework for dinitrogen fixation in the terrestrial biosphere. Nature 454, 327–330.

Johnson, D.W., 2006. Progressive N limitation in forests: review and implications for long-term responses to elevated CO$_2$. Ecology 87, 64–75.

Killingbeck, K.T., 1996. Nutrients in senesced leaves: keys to the search for potential resorption and resorption proficiency. Ecology 77, 1716–1727.

Koerselman, W., Meuleman, A.F.M., 1996. The vegetation N:P ratio: a new tool to detect the nature of nutrient limitation. J. Appl. Ecol. 33, 1441–1450.

Kou, L., Jiang, L., Httenschwiler, S., Zhang, M.M., Niu, S.L., Fu, X.L., Dai, X.Q., Yan, H., Li, S.G., Wang, H.M., 2020. Diversity-decomposition relationships in forests worldwide. Elife 9, e55813.

Lasky, J.R., Uriarte, M., Boukili, V.K., Erickson, D.L., Kress, W.J., Chazdon, R.L., 2014. The relationship between tree biodiversity and biomass dynamics changes with tropical forest succession. Ecol. Lett. 17, 1158–1167.

Lefcheck, J.S., 2016. piecewiseSEM: piecewise structural equation modelling in R for ecology, evolution, and systematics. Methods Ecol. Evol. 7, 573–579.

Leigh, J., Hodge, A., Fitter, A.H., 2009. Arbuscular mycorrhizal fungi can transfer substantial amounts of nitrogen to their host plant from organic material. New Phytol. 181, 199–207.

Liang, J.J., Crowther, T.W., Picard, N., Wiser, S., Mo, Z., Alberti, G., Schulze, E.-D., McGuire, A.D., Bozzato, F., Pretzsch, H., de-Miguel, S., Paquette, A., Hérault, B., Scherer-Lorenzen, M., Barrett, C.B., Glick, H.B., Hengeveld, G.M., Nabuurs, G.-J., Pfautsch, S., Viana, H., Vibrans, A.C., Ammer, C., Schall, P., Verbyla, D., Tchebakova, N., Fischer, M., Watson, J.V., Han, Y.H.C., Xiandong, L., Schelhaas, M.-J., Huicui, L., Gianelle, D., Parfenova, E.I., Salas, C., Lee, E., Lee, B., Hyun, S.K., Bruelheide, H., Coomes, D.A., Piotto, D., Sunderland, T.C.H., Schmid, B., Gourlet-Fleury, S., Sonké, B., Tavani, R., Jun, Z., Brandl, S., Vayreda, J., Kitahara, F., Searle, E.B., Neldner, V.J., Ngugi, M.R., Baraloto, C., Frizzera, L., Balazy, R., Oleksyn, J., Zawila-Niedzwiecki, T., Bouriaud, O., Bussotti, F., Finér, L., Jaroszewicz, B., Jucker, T., Valladares, F., Jagodzinski, A.M., Peri, P.L., Gonmadje, C., Marthy, W., O'Brien, T., Martin, E.H., Marshall, A.R., Rovero, F., Bitariho, R., Niklaus, P.A., Alvarez-Loayza, P., Chamuya, N., Valencia, R., Mortier, F., Wortel, V., Engone-Obiang, N.L., Ferreira, L.V., Odeke, D.E., Vasquez, R.M., Lewis, S.L., Reich, P.B., 2016. Positive biodiversity-productivity relationship predominant in global forests. Science 354, 6309. https://doi.org/10.1126/science.aaf8957.

Liao, C., Long, C.Y., Zhang, Q., Cheng, X.L., 2022. Stronger effect of litter quality than micro-organisms on leaf and root litter C and N loss at different decomposition stages following a subtropical land use change. Funct. Ecol. 36, 896–907.

Lohbeck, M., Poorter, L., Martínez-Ramos, M., Bongers, F., 2015. Biomass is the main driver of changes in ecosystem process rates during tropical forest succession. Ecology 96, 1242–1252.

Loreau, M., Hector, A., 2001. Partitioning selection and complementarity in biodiversity experiments. Nature 412, 72–76.

Lü, X.T., Hu, Y.Y., Wolf, A.A., Han, X.G., 2019. Species richness mediates within-species nutrient resorption: implications for the biodiversity-productivity relationship. J. Ecol. 107, 2346–2352.

Lummer, D., Scheu, S., Butenschoen, O., 2012. Connecting litter quality, microbial community and nitrogen transfer mechanisms in decomposing litter mixtures. Oikos 121, 1649–1655.

Luo, Y.Q., Su, B., Currie, W.S., Dukes, J.S., Finzi, A., Hartwig, U., Hungate, B., McMurtrie, R.E., Oren, R., Parton, W.J., Pataki, D.E., Shaw, M.R., Zak, D.R., Field, C.B., 2004. Progressive nitrogen limitation of ecosystem responses to rising atmospheric carbon dioxide. Bioscience 54, 731–739.

Menge, D.N.L., Batterman, S.A., Hedin, L.O., Liao, W.Y., Pacala, S.W., Taylor, B.N., 2017. Why are nitrogen-fixing trees rare at higher compared to lower latitudes? Ecology 98, 3127–3140.

Morin, X., Fahse, L., Scherer-Lorenzen, M., Bugmann, H., 2011. Tree species richness promotes productivity in temperate forests through strong complementarity between species. Ecol. Lett. 14, 1211–1219.

Nakagawa, S., Schielzeth, H., 2013. A general and simple method for obtaining R^2 from generalized linear mixed-effects models. Methods Ecol. Evol. 4, 133–142.

Odum, E.P., 1969. The strategy of ecosystem development. Science 164, 262–270.

Oksanen, J.F., Blanchet, G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H., Szoecs, E., Wagner, H., 2018. Vegan: community ecology package. R package v. 2.5.2. https://cran.r-project.org (Accessed 15 October 2022).

Ouyang, S., Xiang, W.H., Wang, X.P., Zeng, Y.L., Lei, P.F., Deng, X.W., Peng, C.H., 2016. Significant effects of biodiversity on forest biomass during the succession of subtropical forest in south China. For. Ecol. Manag. 372, 291–302.

Parrent, J.L., Vilgalys, R., 2007. Biomass and compositional responses of ectomycorrhizal fungal hyphae to elevated CO$_2$ and nitrogen fertilization. New Phytol. 176, 164–174.

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., R Core Team, 2021. Nlme: Linear and Nonlinear Mixed Effects Models. R package version 3.1–152.

Reich, P.B., Oleksyn, J., 2004. Global patterns of plant leaf N and P in relation to temperature and latitude. Proc. Natl. Acad. Sci. U.S.A. 101, 11001–11006.

Schimel, J.P., Hättenschwiler, S., 2007. Nitrogen transfer between decomposing leaves of different N status. Soil Biol. Biochem. 39, 1428–1436.

Trogisch, S., He, J.S., Hector, A., Scherer-Lorenzen, M., 2016. Impact of species diversity, stand age and environmental factors on leaf litter decomposition in subtropical forests in China. Plant Soil 400, 337–350.

Vergutz, L., Manzoni, S., Porporato, A., Novais, R.F., Jackson, R.B., 2012. Global resorption efficiencies and concentrations of carbon and nutrients in leaves of terrestrial plants. Ecol. Monogr. 82, 205–220.

Wang, M., Murphy, M.T., Moore, T.R., 2014. Nutrient resorption of two evergreen shrubs in response to long-term fertilization in a bog. Oecologia 174, 365–377.

Wardle, D.A., Bonner, K.I., Nicholson, K.S., 1997. Biodiversity and plant litter: experimental evidence which does not support the view that enhanced species richness improves ecosystem function. Oikos 79, 247–258.

Wieder, W.R., Cleveland, C.C., Smith, W.K., Todd-Brown, K., 2015. Future productivity and carbon storage limited by terrestrial nutrient availability. Nat. Geosci. 8, 441–447.

Wright, A.J., Wardle, D.A., Callaway, R., Gaxiola, A., 2017. The overlooked role of facilitation in biodiversity experiments. Trends Ecol. Evol. 32, 383–390.

Yuan, Z.Y., Chen, H.Y.H., 2009. Global-scale patterns of nutrient resorption associated with latitude, temperature and precipitation. Global Ecol. Biogeogr. 18, 11–18.

Yuan, Z.Y., Chen, H.Y.H., 2015. Negative effects of fertilization on plant nutrient resorption. Ecology 96, 373–380.

Zhang, J.H., Zhao, N., Liu, C.C., Yang, H., Li, M.L., Yu, G.R., Wilcox, K., Yu, Q., He, N.P., 2018. C:N:P stoichiometry in China's forests: from organs to ecosystems. Funct. Ecol. 32, 50–60.

Zhang, K.R., Cheng, X.L., Dang, H.S., Zhang, Q.F., 2020. Biomass:N:K:Ca:Mg:P ratios in forest stands world-wide: biogeographical variations and environmental controls. Global Ecol. Biogeogr. 29, 2176–2189.

Zhang, J.H., Hedin, L.O., Li, M.X., Xu, L., Yan, Y., Dai, G.H., He, N.P., 2022. Leaf N:P ratio does not predict productivity trends across natural terrestrial ecosystems. Ecology 103, e3789.