RELATIONSHIP BETWEEN SPECIES DIVERSITY AND PLANT BIOMASS OF UNDERSTORY FERNS IN HIGH-NITROGEN HABITAT

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Abstract. The aim of the study was to explore the relationship between species diversity of understory ferns and plant biomass in high-nitrogen habitats in China. Four species *Cyrtogonellum fraxinellum, Pteris nipponica, Humata griffithiana* and *Pteris fauriei* were chosen to set up three species richness (1, 2 and 4 species) and a total of 11 species combinations at two nitrogen habitats (control and 10 g N m^2 yr^{-1}). Plant biomass and soil physical and chemical properties were determined. The study had the following results: (1) Species richness had no significant effect on plant biomass under both nitrogen habitats. (2) Under both nitrogen habitats, species combination had a significant effect on plant biomass. (3) The presence of *P. nipponica* and *P. fauriei* significantly increased the plant biomass, and the presence of *C. fraxinellum* significantly reduced the plant biomass under two nitrogen habitats. (4) Nitrogen addition significantly increased soil nitrogen content, but plant species diversity had no significant effect on soil physical and chemical properties. (5) There was a significantly negative correlation between plant biomass (aboveground, underground, and total) and soil phosphorus content; there was also a significantly negative correlation between plant underground biomass and soil pH. Assembling specific species combinations can improve plant biomass and promote ecological restoration under high nitrogen habitat.
Keywords: *understory plant, species richness, species identity, ecosystem functioning, soil physical and chemical properties*

Introduction

Over the past century, global atmospheric nitrogen (N) deposition has increased nearly 3- to 5-fold with accelerated industrialization and increased agricultural intensification (Galloway et al., 2008; Gu et al., 2015). From 1980 to 2010, the average value of atmospheric (wet) N deposition in China increased from 11.11 kg ha^{-1} yr^{-1} to 13.87 kg ha^{-1} yr^{-1} (Liu et al., 2013). N deposition has become one of the main causes of biodiversity loss (Bobbink et al., 2010; Midolo et al., 2019). Increase of N deposition within a certain range increases ecosystem productivity (Bai et al., 2010; Isbell et al., 2013), but excessive N deposition can lead to N saturation, reducing ecosystem productivity (Tian et al., 2016). Therefore, exploring the relationship between biodiversity and ecosystem functioning in high-N habitat and its mechanism have important theoretical value and application guidance for biodiversity conservation and ecosystem functioning restoration.

Biodiversity and ecosystem functioning in different N habitats have attracted widespread attention. In low-N habitat, species richness increased plant aboveground

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biomass (Tilman et al., 2001; Palmborg et al., 2005; Roscher et al., 2008), whereas other studies showed that species richness reduced (Creed et al., 2009) or did not affect plant aboveground biomass (He et al., 2002). In high-N habitat, species richness increased or did not affect plant aboveground biomass (Fridley et al., 2002; Abalos et al., 2014; Han et al., 2018). Species composition, as an important part of plant species diversity, significantly affected plant biomass in different N habitats. In low-N habitat, the presence of legumes significantly increased plant biomass in the system (Roscher et al., 2008; Fornara and Tilman, 2009). In high-N habitat, the presence of *Coix lacryma-jobi* significantly increased plant biomass, and the presence of legume *Aeschynomene indica* significantly reduced plant biomass (Ge et al., 2015). However, most of the current research on biodiversity and plant biomass were carried out in grassland ecosystems or constructed wetland systems, and even some studies conducted in forest ecosystems only focused on the impact of woody plant diversity on ecosystem functioning, did not consider the impact of understory herbaceous plant diversity on plant biomass in forest ecosystems.

Understory herb are an important part of forest ecosystem, and its plant species richness is higher than in any other forest layer (Gillam, 2007). In addition, understory herbaceous plants are sensitive to N deposition, and excessive N deposition reduced the species diversity of understory herbaceous plants (Walter et al., 2017). Therefore, exploring the relationship between species diversity and ecosystem function of understory herbaceous plants in high-N habitat has important theoretical value and guiding significance for the protection of understory biodiversity and the function of forest ecosystems.

In this study, we conducted a microcosm experiment with three species richness (1, 2, 4) and 11 species compositions, and each species compositions were added N or not. To explore (1) the effect of plant species diversity on biomass of understory ferns in different nitrogen habitats; (2) the effect of plant species diversity on soil physicochemical properties in different nitrogen habitats; (3) the relationship between soil physicochemical properties and plant biomass.

Materials and methods

Experimental design

The study site was located at Wenzhou University in Wenzhou, Zhejiang Province, China (120°42'4'E, 27°55'46''N), the study site had a subtropical monsoon climate. In this study, a two-factors experiment was conducted. One factor was N habitats, N addition and without N addition. Considering the ambient wet nitrogen deposition (2.69 g N m^{-2} $year^{-1}$) in Zhejiang Province (Xu et al., 2015), we set up three nitrogen addition levels 10 g N m^{-2} $year^{-1}$. The other factor was plant species diversity. Three species richness levels (1, 2, 4) with 11 species combinations: four monocultures, six two-species compositions and one four-species composition, were set in each N habitats. The experiment was arranged with a completely randomized design with four replicates (*Figure 1*). Totally, 88 microcosms (30 cm×30 cm×20 cm in length, width and height) were conducted. Each microcosm was added 6 L garden soil, the soil pH, TN, and TP were 5.67±0.01, 642.74±8.24 mg kg^{-1}, and 408.68±73.24 mg kg^{-1}.

Four local common species *Cyrtogonellum fraxinellum*, *Pteris nipponica, Humata griffithiana*, and *Pteris fauriei* were selected to assemble plant species diversity. In the middle of April 2020, the seedlings with similar plant height were selected and

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transplanted to the microcosms. Each microcosm was planted with four individuals assigned to each species and uniformly distributed. According to the N treatments, the N were added once a month from April to July. At each time, 500 mL NH_4NO_3 or distilled water was added to the microcosms. During the experiment, equal amount of distilled water was added to each microcosm every week to ensure the plant growth.

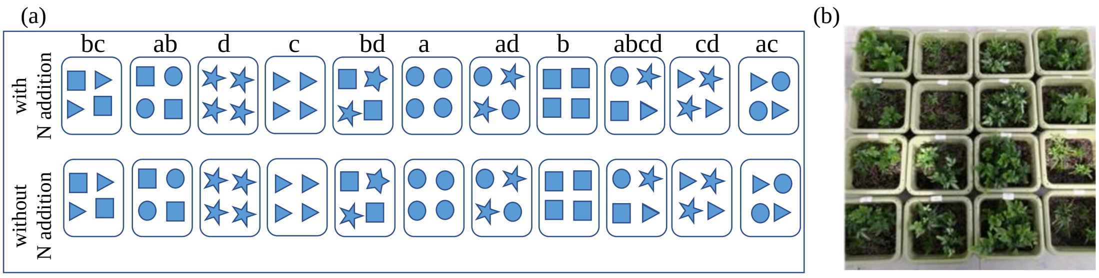

Figure 1. *Experiment design. (a) Experiment design of one block. (b)Photos of some microcosm. Different shapes represent different species*

Parameter determination and calculation

Plant biomass

The plants were harvested by species in August 2020. Each plant was clean and then divided into aboveground and underground parts. Plant samples were dried at 105 ºC for 30 minutes, then dried at 65 ºC for 72 hours, and weighed. The sum of plant aboveground biomass and underground biomass was the total biomass.

Soil physical and chemical properties

After plant harvesting, the soil of each microcosm was well homogenized, 300 g fresh soil was sampled and measured soil pH, soil available N and available phosphorus (P) concentrations. Soil pH was determined with a PHS-3C acidity meter; Soil available N concentrations were determined by diffusion uptake; Soil available P concentrations were determined by molybdenum-antimony antimony colorimetry.

Statistical analysis

In this study, two-way ANOVA was used to analyze the effects of N habitats and plant species richness, plant species identity and their interactions on various parameters (aboveground, underground, and total biomass, soil pH, soil available N and available P concentration). One-way ANOVA with Tukey’s post hoc test was used to analyze the differences in each parameter among species richness and species compositions. The simple linear regression was performed to detect the effect of plant species richness on each parameter. An independent t test was used to determine the difference between the means of each parameter when a species was present and when it was absent in the system. Simple linear regression was also used to detect the relationship between plant biomass and soil physical and chemical properties. All statistical analysis was performed with R ver 4.1.0 (R core team, 2021). The statistical significance level was set to 0.05. All values are expressed as the mean ± standard error.

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Results and analysis

Plant biomass

Plant species richness and N addition had no significant effects on plant biomass (aboveground, underground, and total biomass) (*Table 1a*, *Figure 2*). But species composition had significant effect on plant aboveground and total biomass (*Table 1b*, *Figure 3*). Among four monocultures, plant aboveground and total biomass of *P. fauriei* were significantly higher than those of *P. fauriei*. Without N addition, the presence of *P. fauriei* significantly increased plant aboveground biomass, underground biomass, and total biomass by 73.6%, 62.9% and 66.9%, respectively; the presence of *P. nipponica* significantly increased plant aboveground biomass by 34.1%, and the presence of *C. fraxinellum* significantly reduced plant aboveground biomass by 31.4% (*Table 2*). With N addition, the presence of *P. fauriei* significantly increased plant aboveground biomass, underground biomass, and total biomass by 48.8%, 41.4% and 49.5%, respectively; the presence of *P. nipponica* significantly increased plant aboveground biomass and total biomass by 53.7% and 16.1%, respectively; the presence of *C. fraxinellum* significantly reduced plant aboveground biomass and total biomass by 12.7% and 9.2%, respectively; the presence of *H. griffithiana* also significantly reduced plant aboveground biomass and total biomass by 94.6% and 34.4%, respectively (*Table 2*).

Table 1. *A two-factor variance analysis (a) effects of species richness and N habitats, (b) species compositions and N habitats on plant biomass and soil physical and chemical properties*

Variable	Aboveground biomass	Underground biomass	Total biomass	Soil pH	Soil N content	Soil P content
(a)						
Species richness	0.350	0.084	0.231	0.952	0.999	0.791
N habitats	0.622	0.173	0.534	0.500	0.038*	0.894
(b)						
Species composition	<0.001**	0.202	<0.001**	>0.999	0.949	0.923
N habitats	0.547	0.212	0.471	0.539	0.046*	0.898

Note: Significant *P*-values ($P < 0.05$), *$*P < 0.05$; $**P < 0.01$*

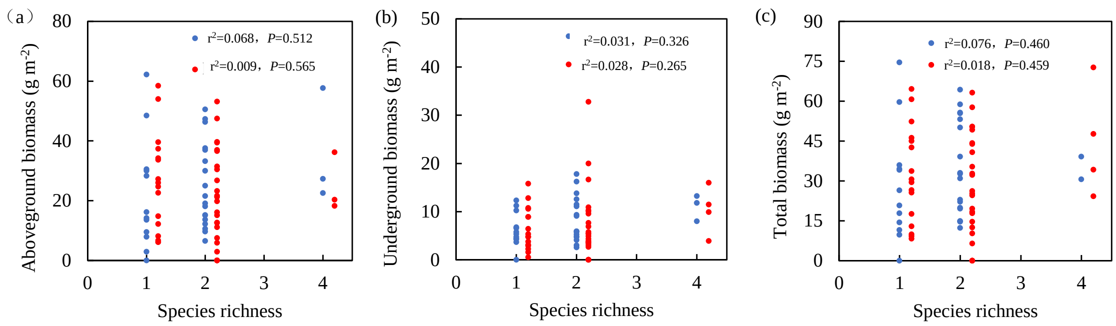

Figure 2. *Relationship between plant species richness and plant aboveground (a), underground (b) and total biomass (c). Blue dot: without N addition, red dot: with N addition*

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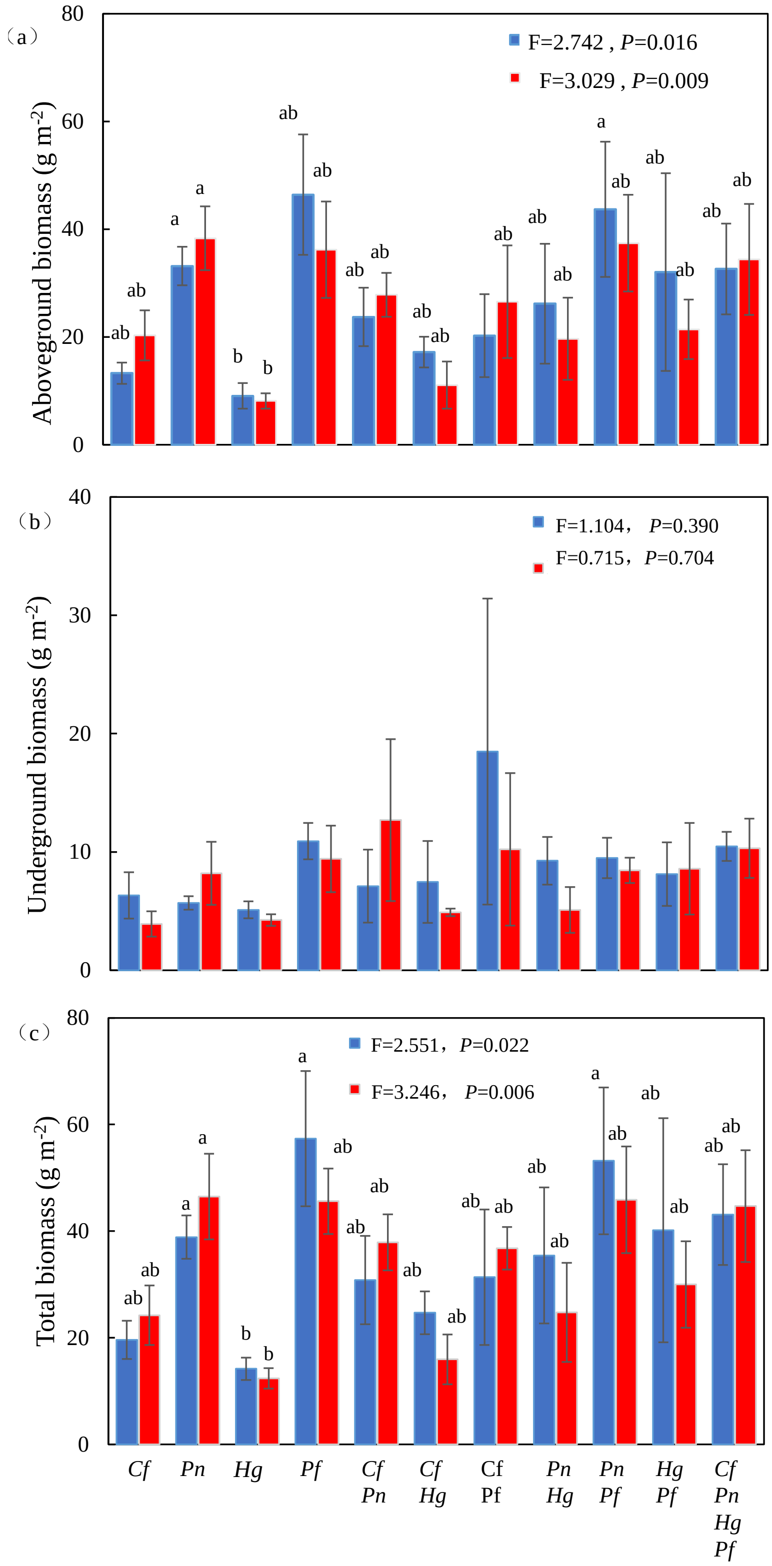

***Figure 3.** Plant aboveground (a), underground (b) and total biomass (c) in response to species compositions. Cf, C. fraxinellum; Pn, P. nipponica; Hg, H. griffithiana; Pf, P. fauriei. Blue bar: without N addition; Red bar: with N addition. Different lowercase letters above the column indicate significant differences among different species compositions. Values are mean ±SE*

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Table 2. *Effects of presence of individual species on plant biomass*

Parameter	*C. fraxinellum*		*P. nipponica*	
CK	**Presence**	**Absence**	**Presence**	**Absence**
Aboveground biomass	21.944±2.763*	32.009±3.898	32.181±3.691*	23.990±3.546
Underground biomass	9.704±2.233	8.056±0.656	8.363±0.842	9.092±1.755
Total biomass	30.420±3.627	40.065±4.410	40.544±4.236	32.121±4.171
	H. griffithiana		***P. fauriei***	
	Presence	**Absence**	**Presence**	**Absence**
Aboveground biomass	23.728±3.271	31.303±3.906	35.600±4.166**	20.510±2.464
Underground biomass	0.833±0.871	0.848±0.162	10.983±1.837**	6.742±0.854
Total biomass	31.761±3.802	39.722±4.540	45.478±4.729**	27.253±2.874
	C. fraxinellum		***P. nipponica***	
HN	**Presence**	**Absence**	**Presence**	**Absence**
Aboveground biomass	24.497±3.283*	28.051±3.353	31.522±3.363*	20.503±2.755
Underground biomass	8.399±1.808	7.504±0.942	8.95±1.504	6.656±1.074
Total biomass	32.275±3.735*	35.556±3.796	31.533±0.338*	27.159±3.260
	H. griffithiana		***P. fauriei***	
	Presence	**Absence**	**Presence**	**Absence**
Aboveground biomass	19.351±3.370**	31.515±2.889	31.710±3.724*	21.314±2.772
Underground biomass	6.719±1.071	8.687±1.447	9.302±1.188*	6.580±1.329
Total biomass	26.070±4.020**	39.722±3.094	41.012±3.748**	27.435±3.355

Note: Values are mean ± SE. The asterisk in the presence column indicates that there is a significant difference between the presence and absence of a specific species: **P < 0.05; **P < 0.01*

Physical and chemical properties of soil

N addition significantly increased soil N content by 13.2% but did not affect soil pH and soil P content (*Table 1*). Plant species richness and compositions had no significant effect on soil physical and chemical properties (*Figure 4*, *Table 3*).

Table 3. *Effects of species on soil physical and chemical properties*

Parameter	*C. fraxinellum*		*P. nipponica*	
CK	**Presence**	**Absence**	**Presence**	**Absence**
Soil N content	625.873±143.585	718.388±41.863	709.145±49.560	652.849±37.833
Soil P content	726.489±166.668	959.643±120.831	886.962±131.189	835.629±119.182
Soil pH	5.529±1.268	5.494±0.087	5.571±49.560	5.457±0.087
	H. griffithiana		***P. fauriei***	
	Presence	**Absence**	**Presence**	**Absence**
Soil N content	702.284±45.463	656.666±8.105	680.652±137.653	676.756±43.438
Soil P content	992.232±138.630	737.281±20.396	884.750±140.989	839.364±122.654
Soil pH	5.509±0.086	5.509±0.186	5.449±1.418	5.554±0.092
	C. fraxinellum		***P. nipponica***	
HN	**Presence**	**Absence**	**Presence**	**Absence**
Soil N content	738.395±42.284	803.206±36.900	740.020±33.196	804.552±42.767
Soil P content	729.462±102.520	951.675±88.771	768.487±85.651	928.413±102.409
Soil pH	5.451±0.046	5.464±0.049	5.447±0.046	5.469±0.050
	H. griffithiana		***P. fauriei***	
	Presence	**Absence**	**Presence**	**Absence**
Soil N content	831.090±42.392	767.433±41.704	831.090±46.438	728.660±31.274
Soil P content	926.425±98.700	848.727±102.200	926.425±108.120	796.798±87.541
Soil pH	5.468±0.053	5.487±0.042	5.468±0.058	5.451±0.040

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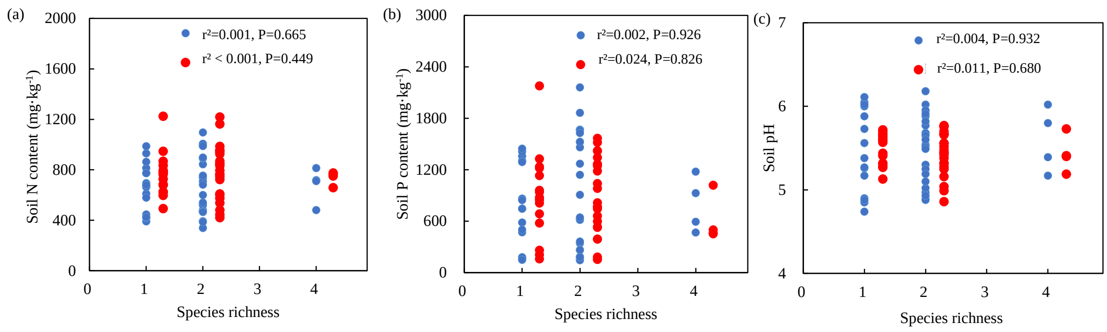

Figure 4. *Relationship between plant species richness and soil N content(a), soil P content(b), soil pH(c). White dot: without N addition, black dot: with N addition*

Relationship between soil physical and chemical properties and plant biomass

There was no significant correlation between plant biomass and soil N content (*Figure 5 a-c*). Plant aboveground, underground, and total biomass were significantly negatively correlated with soil P content (*Figure 5 d-f*); Plant underground biomass was also significantly negatively correlated with soil pH, but there was no correlation between plant aboveground biomass, total biomass and soil pH (*Figure 5 g-i*).

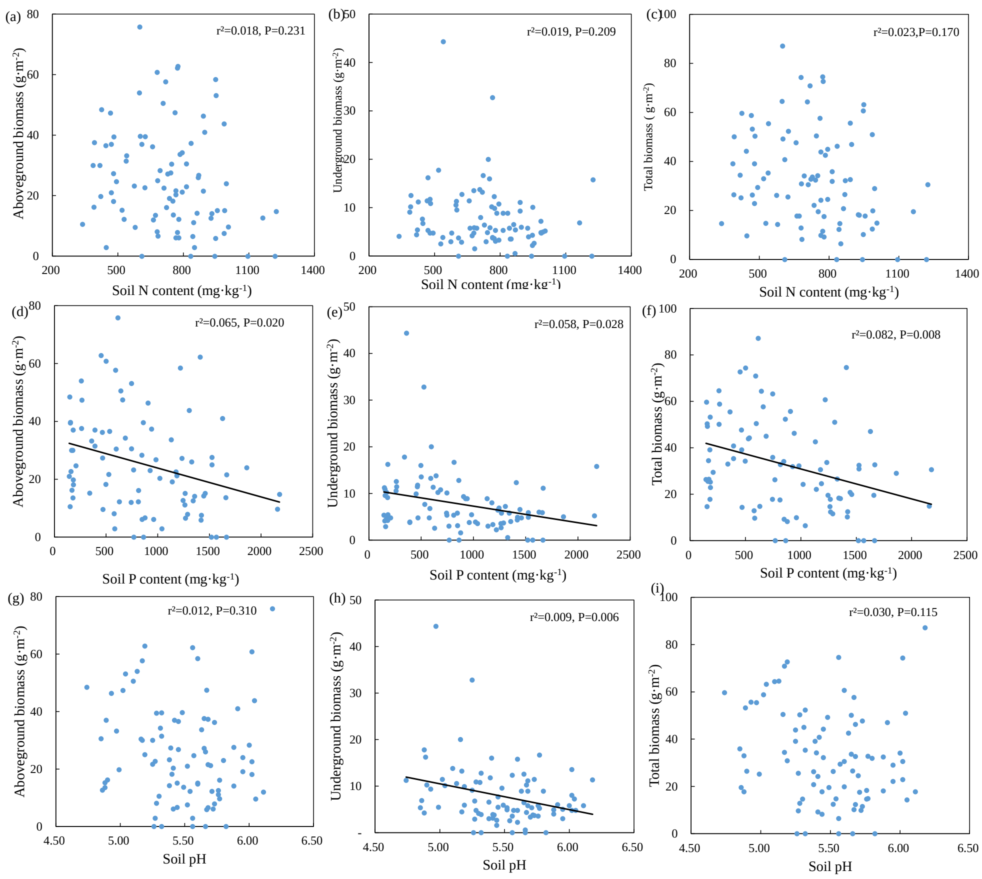

Figure 5. *The relationship between soil physical and chemical properties and plant biomass. A solid line indicates a significant correlation (P< 0.05)*

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Discussion

N is an essential resource for plant growth, previous studies have reported that the increase of N in a certain range will increase plant biomass, but too high N deposition may lead to N saturation and soil acidification, then reduced plant biomass (Bai et al., 2010; Isbell et al., 2013; Tian et al., 2016). In this study, N addition did not affect plant biomass (*Table 1*). The reason may be that previous studies conducted in N limited system (Isbell et al., 2013), in this study the soil N was 642.74 mg kg^{-1}, which was enough for plant growth. Although we found plant underground biomass was negatively correlation with soil pH (*Figure 5*), but N addition did not affect soil pH (*Table 1*), then did not affect plant biomass.

Effect of plant species richness on plant biomass in different N habitats has been widely studied (Roscher et al., 2016; Han et al., 2022). Most studies reported plant species richness had positive effect on plant biomass through enhancing resource complementarity (Barry et al., 2019). However, plant species richness did not affect plant biomass in both two N habitats (*Figure 2*). Plant species richness also did not affect soil N and P content (*Figure 4*). Some studies also reported plant species richness had no effect on plant biomass in low- and high-N habitats (He et al., 2002; Abalos et al., 2014; Han et al., 2018).

As an important part of plant species diversity, species identity has significant effect on ecosystem functioning (Tilman et al., 2014; Han et al., 2022), and the effect may even exceed species richness (Abalos et al., 2014; Han et al., 2022). In this study, we also found species identity had significant effect on plant biomass in different N habitats (*Table 1*, *Figure 3*). Under both N habitats, the presence of *P. nipponica* and *P. fauriei* increased plant aboveground biomass and total biomass (*Table 2*). This may be related to the fact that the biomass of *P. nipponica* and *P. fauriei* in the four monocultures were significantly higher than that of the other species (*Figure 3*). Species with high biomass are highly competitive and thus play a decisive role in the ecosystem functioning (Engelhardt et al., 2001). Conversely, the presence of *H. griffithiana* reduced plant aboveground biomass and total biomass (*Table 2*). The monoculture of this species was also the lowest among four monocultures (*Figure 3*). In addition, the presence of *H. griffithiana* may reduce plant biomass by altering soil physicochemical properties. In this study, soil P content was significantly correlated with plant biomass in this study (*Figure 5*). The presence of *H. griffithiana* increased soil P content by 9.1% and 34.6% in the treatment with N addition and without N addition (*Table 2*). These results showed that the effect of species identity of understory plants on plant biomass was stronger than species richness, and the rational allocation of plant species composition can promote the productivity of communities.

Conclusion

In this study, we first explored the effect of understory ferns species richness on ferns biomass in high-N habitat. The results showed that species identity excessed species richness affected plant biomass. The presence of *P. nipponica* and *P. fauriei* significantly increased plant biomass. Our results highlight the importance of understorey biodiversity for maintaining ecosystem functioning in forests, which should be considered in forest management.

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