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The spatial overlapping regulated by nitrogen promotes the *Spartina alterniflora* potential regenerated invasion in coastal wetlands

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Abstract The mechanisms that link the aboveground plant community structure with soil seed bank is crucial for predicting the potential regeneration direction. However, the spatial structure of invasive clonal plants should be reasonably quantified. We assume that the selection effect of *Spartina alterniflora* community spatial structure on soil seed bank composition would affect the seed reproduction invasion intensity. We set the native species of *Phragmites australis* in Dongtan wetland as a reference object, to explore the nitrogen regulation on the soil seed bank formation processes after *S. alterniflora* became the dominant species. The results showed that the *S. alterniflora* growth tended to be stable in summer and autumn, and its height change trend and peak height under different coverage was relatively consistent. The seasonal variation trend of *P. australis* height is opposite to that of *S. alterniflora*. In the autumn community structure at mature stage, the dominance index of *S. alterniflora* and *P. australis* showed a downward trend from low to high aboveground coverage after the soil seed bank germination, and the dominance index of *S. alterniflora* was higher than that of *P. australis*. The overlapping resistance structure of *S. alterniflora* community was synergistically affected by soil ammonium nitrogen, leaf total nitrogen and soil microbial biomass nitrogen, and the effect of this structure on the soil seed bank formation under different soil depth showed an opposite trend. Our results suggest that the overlapping complementarity between *S. alterniflora* plays a positive regulatory role between functional trait plasticity and sexual reproduction advantage.

Keywords Coastal wetland· Invasion advantage· Nitrogen regulation· Overlapping resistance structure· *S. alterniflora*· Soil seed bank

1. Introduction

Soil seed bank is vital to maintain and promote the plant community diversity. It could be used as a temporary buffer carrier to hinder plant survival and reduce seed yield (Devictor et al. 2007; Wang et al. 2013). A strong soil seed bank is conducive to the community regeneration process and the functional persistence stability (Bezemer, van der Putten 2007). In coastal salt marshes, due to the simple community species composition or the lack of vegetation coverage in some habitats, they are vulnerable to be invaded by alien species. Since the *S. alterniflora* was introduced into China in the 1970s, due to its high ecological adaptability to the environment and strong sexual and asexual reproduction capabilities, it has promoted its rapid expansion and reduced native species habitat (Li et al. 2009). The special environment of Dongtan coastal wetland be beneficial to the survival and maintenance of native species (*P. australis*, *Scirpus mariqueter* and *Scirpus triqueter*, etc.) community, and the soil seed bank has made great contributions to community stabilization (Jia et al. 2022). Although the invasion of alien species has been widely studied (Nie et al. 2023), the exact way of seed dispersal and its related effects are still unclear. Therefore, in order to more effectively protect, restore and manage coastal salt marsh wetlands, it is necessary to understand the specificity and formation process of soil seed banks in wetland plant communities.

At present, most of the research on vegetation spatial structure focuses on forests, grasslands and shrubs. Williams (2017) study on the relationship between crown complementarity and stem biomass in young plantation stand opened a new direction

for the impact of crown-based spatial niche differentiation on ecosystem productivity (Williams et al. 2017). Subsequently, this method was applied to the relationship between canopy complementarity and forest productivity represented by litters in natural forests (Zheng et al. 2019). The process of seed maturation and entering the soil is similar to the litter formation process. However, wetland vegetation is different from forest vegetation (with diverse canopy structures and very different appearance shapes) (Rodrigues et al. 2016). Therefore, it is not appropriate to quantify the effect of spatial niche differentiation of wetland vegetation on the soil seed bank formation by using the method of crown spatial complementarity. During the process of seed falling, vegetation which own unique spatial structure could capture seeds through physical resistance, and then form a soil seed bank (Mamede, de Araújo 2008). Some studies have found that the shrubs shape characteristics will affect the seeds capture or accumulation. For example, the higher the plant, the more seeds will be intercepted. The denser the branches, the more obvious the lateral creeping state, and the more seeds can also be retained. But this is only from a single dimension (plant height-horizontal direction; branch creeping-horizontal direction) to explain vegetation structure on the seed capture capacity and cumulation effect (Ellsworth et al. 2004). Recent studies have combined measurements of species coverage and height into the spatial resource utilization index (SRU) to predict changes in grassland productivity and species diversity (Zhang et al. 2019a; Zhang et al. 2015). However, SRU is closely related to species dominance, and compared with wetland salt marsh vegetation, the niche formed by spatial volume of grassland vegetation is relatively simple, which cannot well

characterize the wetland vegetation diversified physical resistance screening structure. Therefore, it is necessary to explore suitable niche differentiation methods to evaluate the wetland vegetation spatial structure. It can not only be used as the main barrier for wetland seed sources, but also provide convenient conditions for seed accumulation in soil.

In this study, we explored the differences in the spatial structure of wetland vegetation with different aboveground coverage and seasonal changes, and analyzed the effects of the resistance levels formed by overlapping plants in the wetland community on the accumulation effect of the soil seed bank (**Figure 2**). Here, we use the dominance index to measure the accumulation effect of the target species seeds in the soil seed bank germination seedling. By combining biomass and height, the physical structure of overlapping resistance was constructed to evaluate the ability of wetland community spatial structure to capture seeds. The biomass of plants is an effective indicator of the spatial model system, which can organically combine the leaf-based horizontal space with the stem-based vertical space, and avoid invalid estimation of redundant gaps (Battude et al. 2016). The plant assemblages with the same height will form same layers, and the multiple layers formed by different plant assemblages with different heights could reflect the diverse community spatial structures. The analysis of the relationship between community spatial structure and the underneath soil seed bank is helpful to understand the influence of the diverse community structure on the soil seed bank formation and potential regeneration intensity.

We assume that plant biomass and height are different among wetland

communities, which leads to changes in the resistance structure of overlapping spaces. We predict that the more diverse the spatial resistance structure of wetland plant communities, the greater the seed density contained in the soil seed bank. Our previous studies have found that the nitrogen-regulated resource utilization strategy of *S. alterniflora* invasion process is to preferentially allocate resources to the aboveground parts (height, biomass and chlorophyll) and weaken the underground parts. Therefore, in this study, the external environmental nitrogen and plant internal nitrogen content were used as the basic nitrogen sources affecting the formation of soil seed bank, and the invasive species *S. alterniflora* and the native species *P. australis* with similar morphological characteristics in Dongtan wetland were used as the comparison object. The structural equation model was used to study the multiple relationships between soil environmental nitrogen (total nitrogen, ammonium nitrogen and nitrate nitrogen), soil microbial biomass nitrogen, plant internal total nitrogen, vegetation overlapping resistance index and species dominance index. This study is aim to analyze: (1) the difference in the spatial resistance structure formed by the invasive species *S. alterniflora* and the native species *P. australis*; (2) whether the spatial resistance structure plays an important mediating role in the relationship between nitrogen regulation and species dominance maintenance; (3) how different types of nitrogen sources have direct or indirect effects on the accumulation process of soil seed bank by affecting the overlapping spatial resistance structure.

2. Materials and Methods

2.1 Study area

Dongtan coastal wetland is the easter area of Chongming island in Shanghai which is characterized by rapid siltation, vast tidal flats, rich wetland vegetation and benthic animals. It is an important migratory bird habitat and water bird habitat. It has been included in the Ramasar International Convention on Wetland Protection. This region is a typical subtropical monsoon climate, with high temperature and rainy in summer and low temperature and dry in winter. The annual average temperature varies from 15.3 °C to 16.2 °C. The precipitation season is mainly concentrated in April to September, and the annual rainfall range is between 900-1050 mm. The annual sunshine hours are about 2104 hours. The sunshine hours in February are the least, and in August are the most.

In this study, the invasive species *S. alterniflora* and the native species *P. australis* were research for comparison, and different aboveground community coverage (high: 60 % -100 %; medium: 30 % -60 %; low: 0-30 %). Since seasonal changes may affect the soil seed bank, we set up different sampling seasons (summer, autumn and spring).

2.2 Vegetation investigation and soil samples collection

The abundance, height, coverage and biomass of *S. alterniflora* communities and *P. australis* communities were measured. At the same time, soil samples were collected for soil seed bank germination experiment and soil physical and chemical properties determination.

2.3 Construction process of plant overlapping resistance structure

The height and abundance of plants in each plot were measured. Based on Williams (2017) calculation method of canopy overlapping, we improved the calculation method

suitable for the shape characteristics of wetland plant *S. alterniflora* and *P. australis* (**Figure 2a**). For two plants with height difference, the height overlapping index OH_{xy} is recorded as the ratio of two times the lowest plant height to the sum of the two plant heights (formula 1). For the two plants with the same height, the height overlapping coefficient is recorded as zero. And so on, multiple wetland plants with the same height can form a plant height level belonging to this height (**Figure 2b**).

In order to facilitate understanding, the biomass of each plant is quantified into small quality balls. Therefore, each plant with the same height can be aggregated to form a level with a screening function for seeds (such as $\sum OR_a$ and $\sum OR_b$). Due to the interlacing of $\sum OR_a$ and $\sum OR_b$, the structure $\sum OR_{ab}$ with screening function is formed. Therefore, different plants growing in the field will form different types of overlapping resistance layers (**Figure 2c**). The mean value of the height overlapping index and the average biomass of the plot were recorded as the overlap resistance index *ORI* (formula 2).

$$OH_{xy} = \frac{2H_{min_{xy}}}{H_x + H_y} \quad \text{.....(1)}$$

$$ORI = \frac{\sum OH_{xy}}{n} \times \text{AB} \quad \text{.....(2)}$$

Here, OH_{xy} is the overlapping height index; $H_{min_{xy}}$ is the minimum height between the two plants; H_x is the height of plant *x*; H_y is the height of plant *y*; *ORI* is the overlapping resistance index; $\sum OH_{xy}$ is the overlapping height index of all paired plants; n is the number of paired plants ; AB is the average biomass of each plot.

2.4 Germination experiment of the soil samples for investigating soil seed bank

The plant species and number in the soil seed bank were identified by germination

method. The germination experiment continued until to the October. If there were no new seedlings in the pot for 1 month, the germination experiment was ended.

2.5 Measurement of different source of nitrogen

Nitrate nitrogen (NO_3^--N), total nitrogen (TN), ammonium nitrogen (NH_4^+-N) and microbial biomass nitrogen (MBN) in soil samples were measured. Leaf total nitrogen (LTN) and stem total nitrogen (STN) were measured (**Supplementary material in materials and methods for details**).

2.6 Statistical methods

In order to study the effect of different nitrogen sources on the cumulation effect of soil seed bank, we classified different nitrogen sources into 3 types. Soil TN, NO_3^--N and NH_4^+-N were used as soil nitrogen sources, soil MBC was used as soil microbial nitrogen source, plant LTN and STN were used as plant nitrogen sources. The potential regeneration of soil seed bank was evaluated by species richness, Sørensen similarity index and dominance index. Species richness (R) is the number of species contained in the sampling plot (formula 3). The Sørensen similarity index (CC) was used to calculate the similarity between the species contained in the soil seed bank and the aboveground community (formula 4). The dominance index (D) was used to measure the distribution of biological individuals contained in the community among species, the D can effectively represent the biodiversity (formula 5).

$$R=S \quad \text{(3)}$$

$$cc = \frac{2c}{s_1+s_2} \quad \text{(4)}$$

$$D= N_{max}/N \quad \text{(5)}$$

Here, *CC* refers to the Sørensen similarity index; *c* refers to the number of species between the aboveground vegetation and soil seed bank in common; s_1 refers to the species number in the aboveground vegetation; s_2 refers to the species number in the soil seed bank. *D* refers to the dominance index; N_{max} refers to the number of dominant species; *N* refers to the number of all species contained in the functional group.

The effects of different seasons, different aboveground vegetation coverage and different soil depth on soil seed bank dominance index and nitrogen source were estimated by single factor analysis of variance and *LSD* method ($p < 0.05$). The general linear mixed model was used to estimate the single factor effect and multi-factor mixed effect of soil seed bank dominance index in different seasons, different aboveground vegetation coverage and different soil depth. A structural equation model (SEM) was used to evaluate the direct and indirect effects of different nitrogen sources and overlapping resistance index on the dominance index of soil seed banks under the *S. alterniflora* and *P. australis* communities (**Figure S8 & Table S1**).

All data were analyzed using R (version 4.0.5)(Shake, Throw 2021). The 'lme4' package was used for mixed linear model (Bates et al. 2021); the 'lavaan' package (Rosseel 2012) was used for SEM; 'agricolae' package (Verdooren 2021) was used for multiple comparisons, and the 'ggplot2' package (Wickham 2009) and software Origin 2018 was used for plotting figures.

3. Results

3.1 Species composition of soil seed bank under different types of communities

The species of soil seed bank germination under different communities of *P. australis*

and *S. alterniflora* were identified. It was found that the species richness of seed bank in 0-5cm soil depth was higher than that in 5-10cm soil depth. There were 3 species (belonging to 2 families) in 0-5cm soil depth soil seed banks under *S. alterniflor*a community, and 2 species (belonging to 1 family) in 5-10cm soil depth. There were 5 species (belonging to 3 families) in 0-5cm soil depth soil seed banks and 3 species (belonging to 2 families) in 5-10cm soil depth under *P. australis* community. The common families of the soil seed bank under the *P. australis* and *S. alterniflora* communities were Gramineae and Asteraceae, and only one common species *Tripolium pannonicum* of the two types of communities were found in 0-5cm soil depth soil seed bank. In addition, the results showed that the similarity of seed bank and aboveground plant community structure in 0-5cm soil depth under *S. alterniflora* community was higher than that in *P. australis* community, and the seed bank in 5-10cm soil depth showed the same trend (**Table S2**).

Height structure stratification of different types of communities

In order to better reflect the differences in the spatial structure formation process between the *S. alterniflora* community and the *P. australis* community, we measured all heights of plants in each filed community plot and their corresponding numbers. In summer, the plant height structure of the *S. alterniflora* community was mainly concentrated at about 1.0m-1.5m under low coverage, and the plant height was mainly concentrated at about 1.5m under medium and high coverage (**Figure 3a**). The plant height structure of the *S. alterniflora* community in autumn is relatively consistent under different coverage conditions, mainly concentrated in the range of 1.5m-1.8m

(**Figure 3b**). The plant height structure of the *S. alterniflora* community in spring was relatively dispersed under different coverage. The plant height structure was mainly concentrated at about 0.4 m under low and medium coverage, and mainly concentrated between 0.6m-0.7m under high coverage (**Figure 3c**). In addition, the height of the main plant concentration layer in autumn community was higher than that in summer and spring community under low coverage (**Figure 3a&b**).

The plant height structure was mainly concentrated at about 0.6 m in summer *P. australis* community of low coverage, and it was mainly concentrated at about 1.2 m and 1.8 m under medium coverage and high coverage, respectively (**Figure 3d**). The plant height structure was mainly concentrated at about 0.8 m in autumn *P. australis* community of low coverage, and it was mainly concentrated at about 1.2 m and 1.9 m under medium coverage and high coverage, respectively (**Figure 3e**). For the height structure of spring *P. australis* community, the abundance of different heights was relatively uniform under low coverage, and the height structure was mainly concentrated at about 0.3m under medium coverage and high coverage (**Figure 3f**).

By comparing the height structure of *S. alterniflora* and *P. australis*. It was found that the height structure of *S. alterniflora* community was basically the same in summer and autumn under different coverage, however, it was relatively dispersed in spring under different coverage. The height structure of *P. australis* community is the opposite to *S. alterniflora* community. The range of the main plant height is relatively dispersed in summer and autumn under different coverage, while the plant height is relatively concentrated in spring under different coverage.

3.2 The dominance index trend of soil seed bank under *S. alterniflora* and *P. australis* communities

In the soil seed bank germination experiment, we found that the dominant species of soil seed bank under *S. alterniflora* community was species *S. alterniflora*. The soil seed bank dominance index of the two soil depths (0-5cm and 5-10cm) was equal in summer under the low and medium coverage, respectively. The dominance index of soil seed bank in 5-10cm soil depth under high coverage community was higher than that in 0-5cm soil depth (**Figure 4a**). The dominance index in autumn soil seed bank from the low coverage to high coverage showed a decreased trend, and that of 5-10 cm soil depth was higher than that in 0-5 cm soil depth (**Figure 4b**). The dominance index in spring soil seed bank from the low coverage to high coverage showed a decreased trend under 0-5cm soil depth. The dominance index in spring soil seed bank of 5-10 cm soil depth under low coverage and medium coverage was equal, while the dominance index of soil seed bank under high coverage was the lowest, and the dominance index of 5-10 cm soil depth soil seed bank was higher than that in 0-5 cm soil depth (**Figure 4c**).

In the seedlings germinated from the summer soil seed bank under the *P. australis* community, it was found that the dominance index of soil seed bank in the two soil depths (0-5cm and 5-10cm) from low to high coverage showed a gradual downward trend, and which in the 5-10cm soil depth was higher than that in the 0-5cm soil depth (**Figure 4d**). The dominance index in autumn soil seed bank of 5-10 cm soil depth decreased from low coverage to high coverage, while the dominance index of soil seed

bank in 0-5 cm soil depth was the lowest under medium coverage. In addition, the dominance index of soil seed bank in 5-10 cm soil depth was higher than that in 0-5 cm soil depth (**Figure 4e**). The dominance index in spring soil seed bank of 0-5cm soil depth decreased from low coverage to high coverage (**Figure 4f**).

The dominance index in autumn soil seed bank of 0-5cm and 5-10cm these two soil depths under *S. alterniflora* community was higher than that under *P. australis* community. The soil seed bank dominance index of *S. alterniflora* community was higher than that of *P. australis* community except that in summer soil seed bank of 0-5cm soil depth under low coverage.

The effects of different seasons, coverage and soil depth on the soil seed bank dominance index were tested by multivariate analysis of variance. It was found that the dominance index of soil seed bank under *S. alterniflora* community, as a single factor of season, coverage and soil depth, had significant effects respectively, and the interaction of the three factors also had significant effects. For the dominance index of soil seed bank under *P. australis* community, as a single factor, season, coverage and soil depth all had significant effects on it, respectively. The interaction between season and coverage, season and soil depth, coverage and soil depth also had significant effects on it, and the interaction of three factors also had significant effects on it (**Table S3 & Table S4**).

3.3 The direct and indirect factors affecting soil seed bank dominance under *S. alterniflora* and *P. australis* communities

After stepwise regression by comparing the AIC values, the structural equation model

(SEM) of soil ammonium nitrogen in 0-10 cm (NH_4^+-N1) and 10-20 cm soil depth (NH_4^+-N2), soil nitrate nitrogen in 10-20 cm soil depth (NO_3^--N2), leaves total nitrogen content (LTN) of *S. alterniflora*, soil microbial biomass nitrogen in 0-10 cm soil depth (MBN1) and aboveground community overlapping resistance index (*ORI*) was constructed. The fitness effect of the soil seed bank dominance index in the 0-5 cm soil depth under the *S. alterniflora* community was good (x^2=8.792，*p*=0.118，*df*=5，*CFI*=0.969), and the interpretation of this index was 90.3 %. The model showed that the NH_4^+-N1, MBN1 and NO_3^--N2 had significant direct negative effects on the dominance index of 0-5 cm soil depth soil seed bank under *S. alterniflora* community. The NH_4^+-N2 and *ORI* had a significant direct positive effect on the dominance index of 0-5 cm soil depth soil seed bank under *S. alterniflora* community. The LTN, NH_4^+-N2 and MBN1 had an indirect positive effect on the dominance index of soil seed bank in 0-5 cm soil layer under *S. alterniflora* community by affecting *ORI* (**Figure 5a**).

After stepwise regression by comparing the AIC values, the SEM constructed by soil total nitrogen in 0-10 cm soil depth (TN1), soil ammonium nitrogen (NH_4^+-N2) and total nitrogen (TN2) in 10-20 cm soil depth, leaves total nitrogen (LTN) of *S. alterniflora*, soil microbial biomass nitrogen in 0-10 cm soil depth (MBN1) and overlap resistance index (*ORI*) had a good fitness effect on the dominance index of 5-10 cm soil depth soil seed bank under *S. alterniflora* community (x^2=9.461，*p*=0.092，*df*=5，*CFI*=0.939), and the interpretation of the dominance index was 33.8 %. The model showed that NH_4^+-N2 and TN1 had a significant direct positive effect on the dominance index of soil seed bank in 5-10 cm soil depth under *S. alterniflora* community, while

TN2, MBN1, LTN and *ORI* had a direct negative effect on the dominance index of soil seed bank. The LTN, NH_4^+-N2 and MBN1 had an indirect negative effect on the dominance index of soil seed bank in 5-10 cm soil depth by affecting the *ORI* (**Figure 5b**).

After stepwise regression by comparing the AIC values, the factors affecting the dominance of 0-5 cm soil depth soil seed bank under *P. australis* community were screened for constructing SEM, but the fitness effect was poor (**Figure S9**). And the soil nitrate nitrogen in the 0-10 cm soil depth (NO_3^--N1), the soil microbial biomass nitrogen in the 0-10 cm soil depth (MBN1), the stem total nitrogen content (STN) of the *P. australis* and the overlap resistance index (*ORI*) were well fitted for the soil seed bank dominance index of the 5-10 cm soil depth under *P. australis* community (x^2=3.190，p=0.363，df=3，CFI=0.993), and the interpretation of the dominance index was 68.9 %. We found that the NO_3^--N1 and STN had a direct positive effect on the soil seed bank dominance index in the 5-10 cm soil depth under *P. australis* community. The MBN1 and *ORI* had a direct negative effect on the dominance index of soil seed bank in 5-10 cm soil layer under *P. australis* community. In addition, NO_3^--N1 had an indirect negative effect on the soil seed bank dominance index in the 5-10 cm soil depth under the *P. australis* community by affecting *ORI* (**Figure 5c**).

4. Discussion

4.1 Differences in species composition of soil seed bank between *S. alterniflora* community and *P. australis* community

After *S. alterniflora* invaded into Dongtan wetland, it gradually expanded and formed a community with *S. alterniflora* as the dominant species. Compared with the soil seed

bank under *P. australis* community, the species richness and native species abundance decreased under *S. alterniflora* community. One of the threats of invasive species to native ecosystems is their competitive effects on native plants, which may lead to a decrease in the number of native species or even extinct in local area (Zheng, Liao 2017). Since *S. alterniflora* was introduced into Dongtan wetland, it has produced a large number of seeds through sexual reproduction due to its high adaptability to the environment, which provides convenient conditions for the long-distance transmission of *S. alterniflora* (Yuan et al. 2017). The *S. alterniflora* invasion process has coevolution with native species. The coexistence of seeds depends not only on the life characteristics of seeds themselves, but also on the external environmental conditions. The transformation of environmental conditions by *S. alterniflora* and symbiotic species is a key step to consolidate the results of invasion (Ning et al. 2019; Shang et al. 2015). The soil seed bank structure under *S. alterniflora* community in Dongtan wetland was highly similar to that of aboveground community, indicating that the soil seed bank had similar environmental requirements with aboveground vegetation, which ensured the potential dominant status of *S. alterniflora* in the community formed by soil seed bank (Jia, et al. 2022).

4.2 Differences of natural and potential regeneration ability between *S. alterniflora* community and *P. australis* community

The difference of vegetation height in different seasons is the embodiment of its time heterogeneity. The height change trend of *S. alterniflora* community in summer and autumn was consistent, and the peak height was relatively concentrated. Summer and

375 autumn are basically the relatively stable periods of plant community structure changes.
376 The 'self-steady state' structure is conducive to maximum utilization of resources for *S.*
377 *alterniflora* in the community (Wang et al. 2006). The change trend of the aboveground
378 height of the native species *P. australis* was opposite to that of the *S. alterniflora*.
379 Compared with C_4 plant *S. alterniflora*, the photosynthesis rate of *P. australis* as C_3
380 plant was significantly lower. Therefore, in the early spring of *P. australis* growth, the
381 aboveground vegetation under different coverage has low demand for resources as a
382 whole, and the relatively consistent peak height is sufficient to meet the coexistence of
383 species in the community (Emery et al. 2001; Vasquez et al. 2006).

384 The dominance index of seedlings germinated from the soil seed bank under *S.*
385 *alterniflora* community was higher than that of seedlings germinated from the *P.*
386 *australis* community. It is indicated that the number distribution of different species
387 was not uniform in the coexisting seedlings germinated from the soil seed bank under
388 the *S. alterniflora* community, and the ecological function of *S. alterniflora* in the
389 community was significantly higher than that of *P. australis* in the community (Reich
390 et al. 1998; Zhang et al. 2019b). Seeds are concentrated in the 0-5 cm soil depth, and
391 different aboveground community coverage has different ability to capture seeds. The
392 number of plants per unit area gradually increased with the increase of aboveground
393 community coverage, and the ability to capture different types of seeds gradually
394 increased, thus reducing the dominance index of dominant species in the soil seed bank
395 (He et al. 2023; Khalaj et al. 2023). Compared with the 0-5 cm soil depth seed bank,
396 the trend of dominance index in the two communities is not consistent in the 5-10 cm

soil depth, and the dominance index of germination seedlings under medium coverage *P. australis* community is the lowest. The dominance index of germination seedlings in 5-10 cm soil depth seed bank was not only affected by the aboveground community, but also by the internal structure of underground structure (such as rhizome). The rhizome of *P. australis* was thinner than that of *S. alterniflora*, and distributed in deeper soil depth. When the community coverage increased gradually, the roots of *P. australis* extended to the surface layer and resulting in less space occupied for the seeds (Xiao et al. 2010).

4.3 Effects of overlapping resistance regulated by different types of soil nitrogen source on soil seed bank potential regeneration

SEM analysis showed that soil NH_4^+-N in 0-10 cm and 10-20 cm soil depth had negative and positive effects, respectively, on the dominance index of germination seedlings in 0-5 cm soil depth under *S. alterniflora* community. The soil seed bank mainly exists in 0-10 cm soil depth. Soil NH_4^+-N is a requirement type of effective nitrogen for plant growth and development, and its content will affect the plant community structure and species coexistence (Kant et al. 2010; Liu, von Wirén 2017). It has been found that the change of soil NH_4^+-N could adjust the ratio of other types of soil nitrogen, which causes the preference transfer of nitrogen types to the coexisting species with *S. alterniflora*, resulting in the increase of interspecific competition intensity of *S. alterniflora* and the decrease of its dominance index in the community (Huang et al. 2019). In addition, soil NH_4^+-N in the 10-20 cm soil depth had a significant positive effect on the dominance index of soil seed bank germination

seedlings in the 0-5 cm soil depth, but soil NO_3^--N in the 10-20 cm soil layer had a negative effect on the dominance index. Nitrogen forms can affect the species and quantity of coexisting species (Midolo et al. 2019). In the deeper 10-20 cm soil depth, the salt content was lower than that in the 0-10 cm soil depth. Some studies have shown that under low salt conditions, an appropriate increase in NH_4^+-N is beneficial to the growth of *S. alterniflora*, while interfering with the NO_3^--N absorption of *S. alterniflora* and is not conducive to its growth (Sheng et al. 2022). The deep soil depth NH_4^+-N in 10-20 cm has low availability for *S. alterniflora* in soil seed bank, and low content of NH_4^+-N is beneficial to the salt gland function of *S. alterniflora* and promote the construction of *S. alterniflora* community (Qing et al. 2012).

For the soil seed bank in the 5-10 cm soil depth, the soil TN in the 0-10 cm soil depth had a significant positive effect on the soil seed bank under *S. alterniflora* community, while the soil TN in the 10-20 cm soil depth had a significant negative effect on it. The TN in the 0-10 cm soil depth was significantly higher than that in the 10-20 cm soil depth in sample site (**Figure S2**), and the excessive TN would further increase the invasion ability of *S. alterniflora* (Chen et al. 2020). In different *S. alterniflora* invasion stages and vertical distribution patterns, the change trend of soil TN was also similar, indicating that the change of *S. alterniflora* distribution and soil TN was a coordinated process. The invasion of *S. alterniflora* promoted the increase of the species and number of nitrogen-fixing bacteria in the soil, and transforming the soil nitrogen into a form which more conducive to the absorption of *S. alterniflora* (Gao et al. 2019; Sheng et al. 2022). In addition, more than 50 % of the roots of *S. alterniflora*

441 are concentrated in the soil surface. *S. alterniflora* also absorbs the nitrogen brought by
442 the tide along with absorbing the organic matter of seawater, so that the nitrogen
443 accumulates in the soil surface (Wang et al. 2018; Zhang et al. 2010). With the
444 deepening of the invasion time and degree of *S. alterniflora*, the TN in soil will
445 gradually increase, but the increase is not continuous (Yang et al. 2016; Yang et al.
446 2017). Therefore, regulating the nitrogen content is of important to the species
447 coexistence of germination seedlings in the deep soil depth seed bank under *S.*
448 *alterniflora* community.

449 The overlapping resistance structure formed by *S. alterniflora* had a significant
450 positive effect on the 0-5 cm soil depth soil seed bank, but a significant negative effect
451 on the 5-10 cm soil depth soil seed bank. Overlapping resistance index (*ORI*) is a
452 comprehensive reflection of vegetation in vertical and horizontal space, so it is vital to
453 study the formation and potential regeneration of soil seed bank. The species richness
454 and abundance of germinated seedlings in the 0-5 cm soil seed bank were higher than
455 those in the 5-10 cm soil seed bank. Soil seed bank is an important stage to ensure the
456 community potential regeneration niche. After screening by the overlapping resistance
457 structure of *S. alterniflora* community, the gravitational potential energy of seeds from
458 the external environment will be significantly reduced. As a result, it is difficult to enter
459 the deep soil and a large number of seeds are concentrated in the 0-5 cm soil depth. The
460 seeds of *S. alterniflora* are larger than the seeds of *P. australis*, and the resistance during
461 the falling process is large, and the gravitational potential energy falling to the surface
462 will decrease. The *ORI* of *S. alterniflora* and *P. australis* communities had a significant

463 negative effect on the dominance index of seed bank germination seedlings in the 5-10
464 cm soil depth, but had no significant effect on the *P. australis* dominance index of seed
465 bank germination seedlings in the 0-5 cm soil depth, indicating that the overlapping
466 resistance structure formed by *P. australis* was not enough to have a significant effect
467 on the surface (0-5 cm) soil seed bank under the *P. australis* community as a small seed
468 plant.

469 The main purpose of this study is to explore the effects of different types of soil
470 nitrogen on the formation of overlapping resistance structures formed by aboveground
471 communities, and then to understand the effects of this structure on soil seed banks.
472 Any species with invasive advantage has its specific invasion strategy (Perkins, et al.
473 2011, Masson, et al. 2016). Combined with the seasonal changes of *S. alterniflora*
474 height with different coverage, it can be seen that once *S. alterniflora* enters the invasion
475 stable stage, its community height structure is not affected by the aboveground
476 community coverage. The similar appearance characteristics ensure the *S. alterniflora*
477 competitive advantage, while different types of soil nitrogen maintain the overlapping
478 resistance structure of *S. alterniflora* community. Some studies have found that the
479 nitrogen fixation of *S. alterniflora* litter is high, which has an activation effect on soil
480 nitrogen fixation organisms, and the high proportion of leaf biomass in *S. alterniflora*
481 litter is conducive to the nitrogen fixation of *S. alterniflora* (Zhang et al. 2022). The
482 N_2O emission rate of *S. alterniflora* was higher than that of native species, indicating
483 that the *S. alterniflora* invasion increased the richness of denitrifying bacterial
484 functional groups, and promoted the utilization of NH_4^+-N and the accumulation of *S.*

alterniflora biomass (Gao et al. 2019; Jin et al. 2017). *S. alterniflora* community had obvious 'fertile island effect' on soil microbial biomass carbon, while soil microbial biomass had weak ability to absorb and redistribute soil nitrogen, which was not conducive to the growth of *S. alterniflora* (Zhang et al. 2021). In general, different types of soil nitrogen in Dongtan wetland have a clear division of labor on *S. alterniflora* invasion, which makes *S. alterniflora* show a strong reproductive capacity, resulting in a decrease in wetland biodiversity and a change in service function.

5. Conclusion

The soil seed bank under *S. alterniflora* community is an effective carrier to maintain its potential competitive advantage and overcome the limitations of clonal reproduction. The community overlapping resistance structure constructed by combining height and biomass can scientifically quantify the spatial structure formed by large invasive clonal plants. The plant traits of the invasive species *S. alterniflora* and the native species *P. australis* tend to adopt 'convergent adaptation' and 'divergent adaptation' strategies during seasonal changes. At the seed mature stage, the spatial structure formed by the S. *alterniflora* community has a better ability to capture its own seeds than the *P. australis* community, and the spatial structure of the community with the high coverage *S. alterniflora* could increase the proportion of its own seeds in the soil seed bank. In the process of community construction and spatial structure formation, *S. alterniflora* can make full use of various types of soil nitrogen to maintain its dominant position and potential regeneration by soil seed bank.

Therefore, reasonable quantification of the screening mechanism by the

overlapping resistance structure of the invasive species *S. alterniflora* on the soil seed bank could provide a new implementation direction for removing the seed reproduction advantage of *S. alterniflora* by mechanical means.

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Conflict of interest statement

The authors declare no conflict of interest.

Author contributions

Peng Jia conceived the ideas, designed methodology, collected the data, analyzed the data and wrote original draft. Dezhi Li conceived the ideas, designed methodology, collected the data, analyzed the data and wrote original draft and wrote review & editing. Guojuan Qu collected the data and analyzed the data. Jing Jia collected the data and revised original draft.

Open Research: Data are available in https://figshare.com/s/cb412c21bc032fd1747d

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Figures:

Figure 1 The location of the study area and sampling sites (bule triangle: *S. alterniflora*; orange triangle: *P. australis*)

Figure 2 Conceptual diagram for calculating the overlapping resistance index (*ORI*), which was used to explain the effect of spatial structure of the community formed by the plant combinations with different heights on seed entry into soil. (a) The overlapping height index of different types of paired plants (OH_{ab} represented the overlapping of plants with different heights; OH_{bc} represented the overlapping of plants with the same height, and the height overlap index was zero). (b) Spatial network resistance structure formed by different plant combinations ($\sum OR_a$ represented the spatial network resistance layer formed by all plants with height a; $\sum OR_b$ represented the spatial network resistance layer formed by all plants with height b; $\sum OR_{ab}$ represented their overlapping spatial structure in the sample plot; the black ball represented that the biomass of the plant was quantified as a ball with a certain height; the black line represented the plant height). (c) The overlapping visualization structure formed by the plant communities with different heights.

Figure 3 Statistics and distribution of the number of plant heights in the community of *Spartina alterniflora* and *Phragmites australis*, respectively. (a-c) was *S. alterniflora* height in summer, autumn and spring, respectively; (d-f) was *P. australis* height in summer, autumn and spring, respectively (blue: high coverage; green: medium coverage; orange: low coverage)

683 **Figure 4** The soil seed bank dominance index of *S. alterniflora* and *P. australis*
684 community, respectively. (a-c) was the soil seed bank dominance index under the *S.*
685 *alterniflora* community in summer, autumn and spring, respectively; (d-f) was the soil
686 seed bank dominance index under the *P. australis* community in summer, autumn and
687 spring, respectively (blue circle: 0-5cm soil depth seed bank; orange triangle: 5-10cm
688 soil depth seed bank)
689 **Figure 5** Structural equation model based on the soil nitrogen (TN1, TN2, NH_4^+-N1,
690 NH_4^+-N2, NO_3^--N1 and NO_3^--N2) and the plant leaf total nitrogen (LTN) and stem total
691 nitrogen (STN), microbial biomass nitrogen (MBN1 and MBN2) and overlapping
692 resistance index (*ORI*) to test the direct and indirect effects on the variations of the
693 dominance index in soil seed banks. Solid and dashed arrows indicated significant
694 (p<0.05) and non-significant relationships (p>0.05) between the initial variables and
695 the terminal variables, respectively. R^2 represented the proportion of variance explained
696 for the dominance index in each soil seed bank in the model. Numbers at arrows
697 represented the correlation coefficient. The arrow size represented the significance
698 strength (a-b: the SEM for the dominance index in soil seed bank under *S. alterniflora*
699 community at 0-5cm and 5-10cm soil depth; c: SEM for the dominance index in soil
700 seed bank under *P. australis* community at 5-10cm soil depth). The number 1 and 2
701 after soil nitrogen and microbial biomass nitrogen variables were 0-10cm and 10-20cm
702 soil depths, respectively
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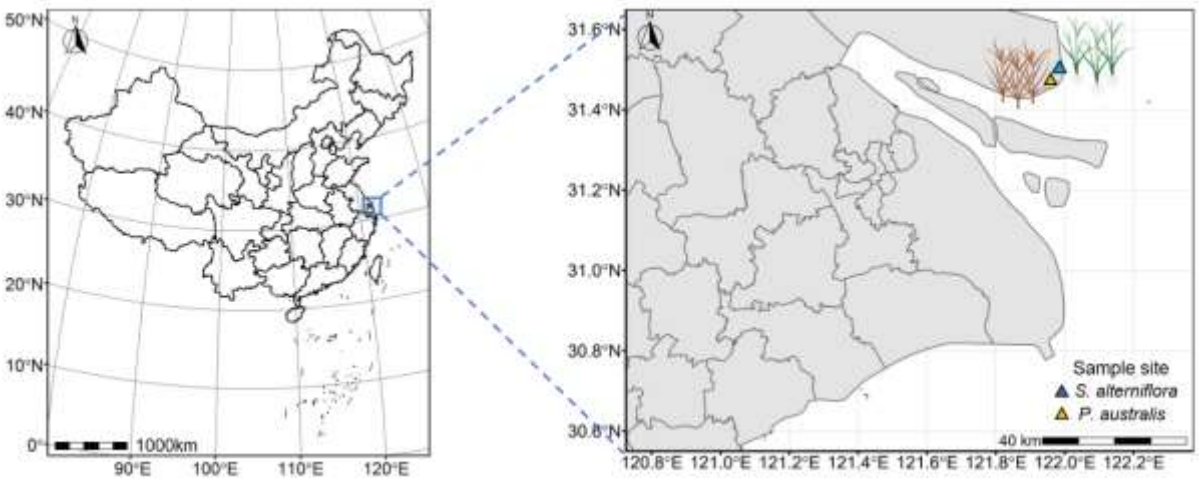

50°N
40°N
30°N
20°N
10°N
0°
1000km
90°E
100°E
110°E
120°E
31.6°N
31.4°N
31.2°N
31.0°N
30.8°N
30.6°N
Sample site
S. alterniflora
P. australis
40 km
120.8°E 121.0°E 121.2°E 121.4°E 121.6°E 121.8°E 122.0°E 122.2°E

Figure 1

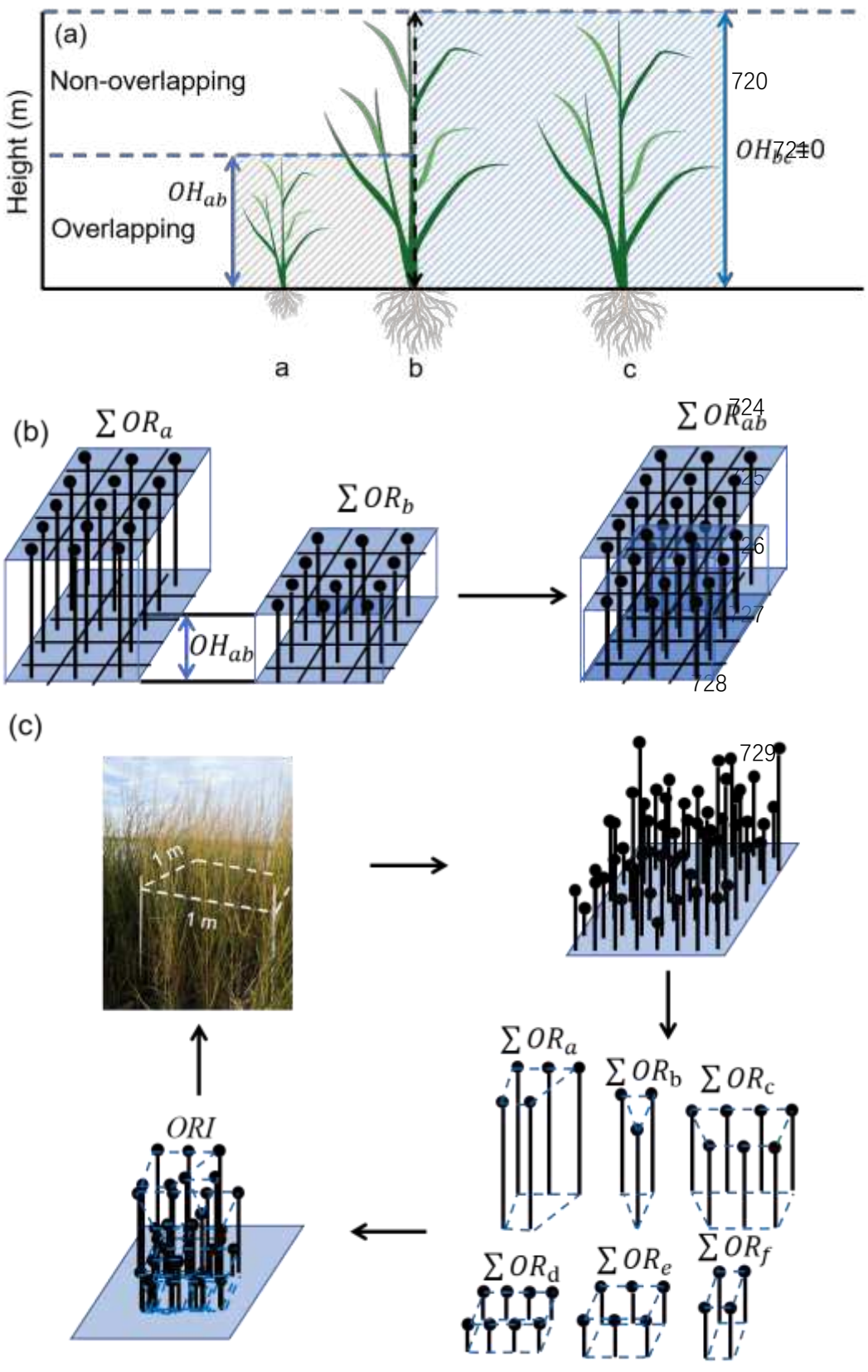
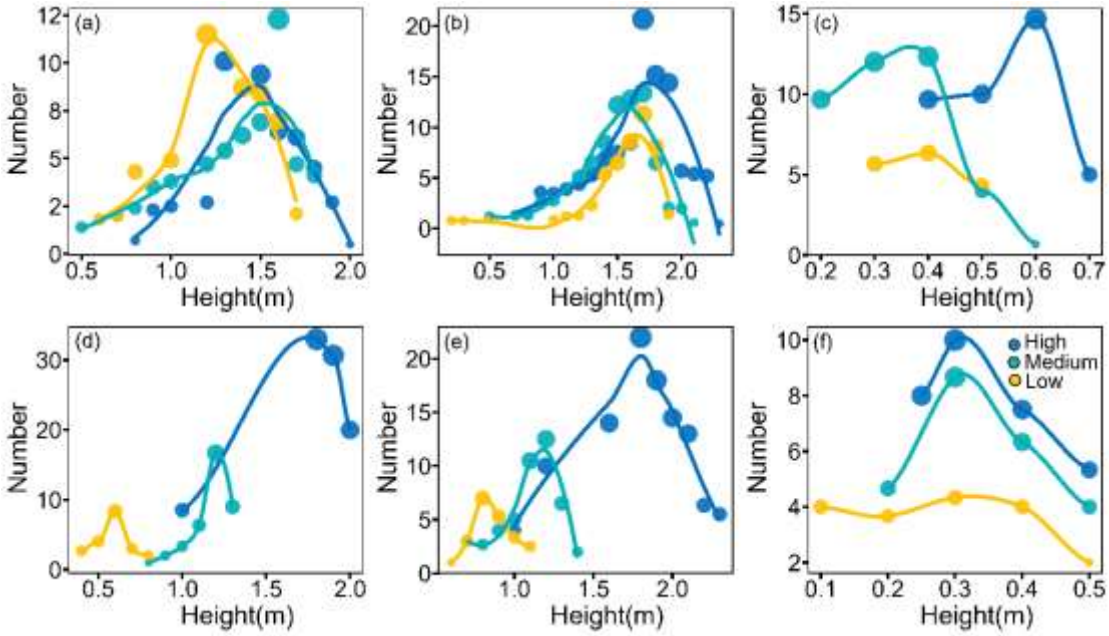

(a)
Non-overlapping
Height (m)
OH_{ab}
Overlapping
a
b
c
(b)
$\sum OR_a$
$\sum OR_b$
OH_{ab}
$\sum OR_{ab}$
(c)
1 m
1 m
ORI
$\sum OR_a$
$\sum OR_b$
$\sum OR_c$
$\sum OR_d$
$\sum OR_e$
$\sum OR_f$

Figure 2



741 **Figure 3**

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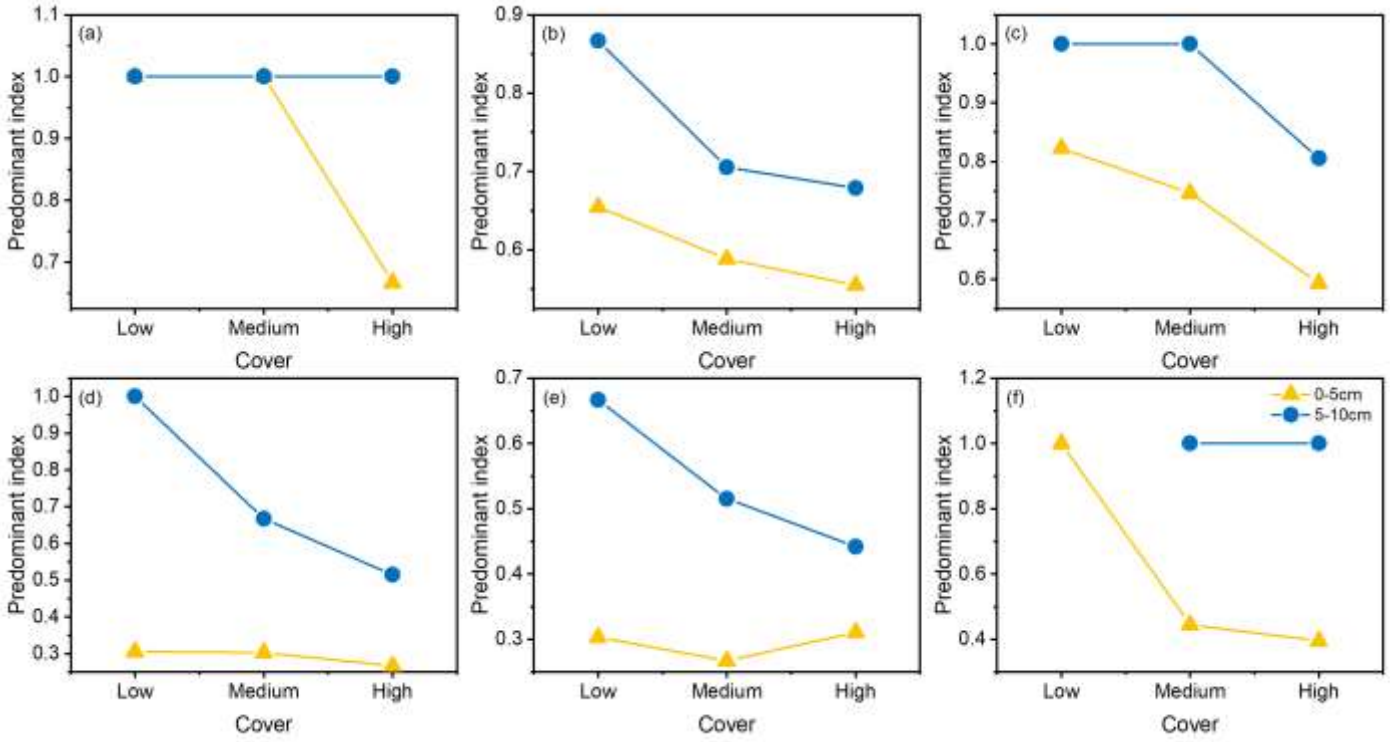
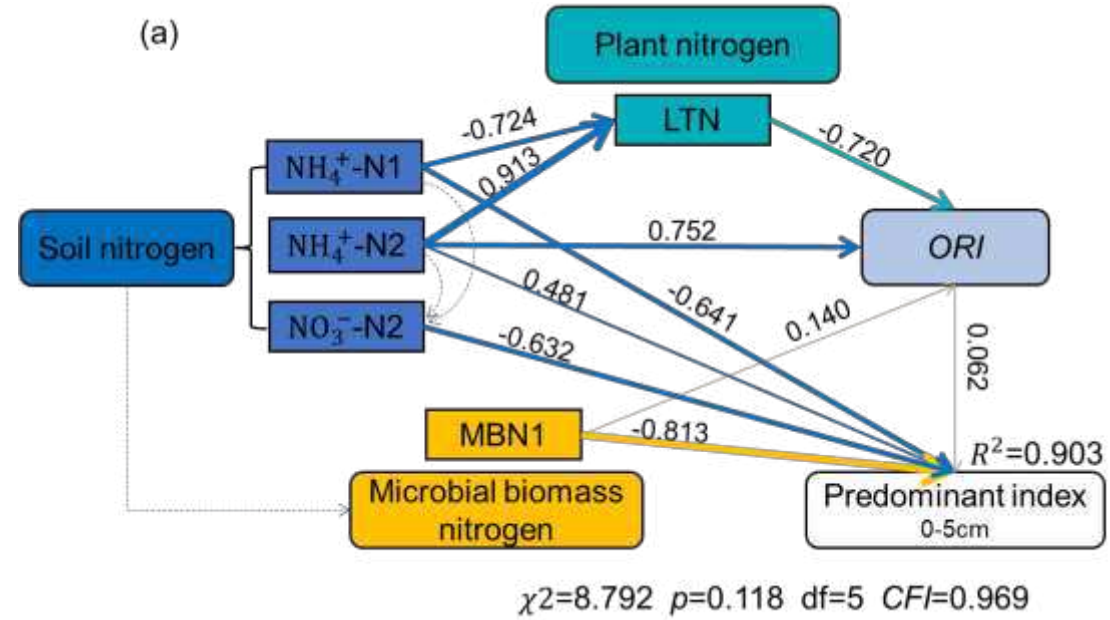
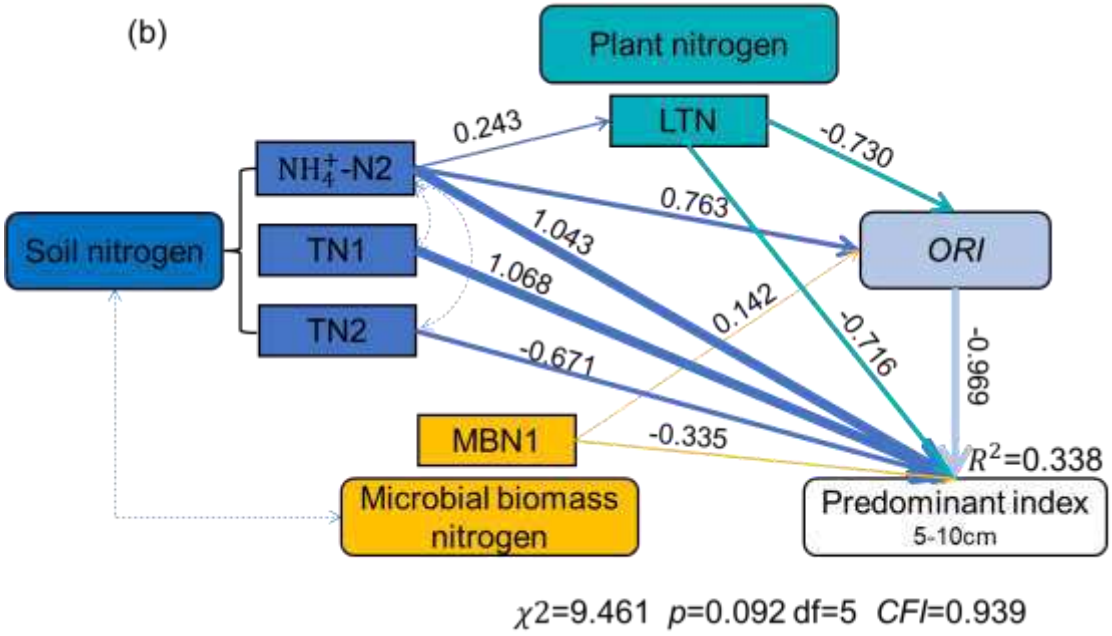


Figure 4


(a)
Plant nitrogen
LTN
-0.724
0.913
-0.720
NH_4^+-N1
Soil nitrogen
NH_4^+-N2
0.752
ORI
0.481
-0.641
0.140
NO_3^--N2
-0.632
0.062
MBN1
-0.813
R^2=0.903
Microbial biomass nitrogen
Predominant index
0-5cm
χ2=8.792 p=0.118 df=5 CFI=0.969


(b)
Plant nitrogen
0.243
LTN
-0.730
NH_4^+-N2
0.763
Soil nitrogen
TN1
1.043
ORI
1.068
0.142
-0.716
TN2
-0.671
-0.969
MBN1
-0.335
R^2=0.338
Microbial biomass nitrogen
Predominant index
5-10cm
χ2=9.461 p=0.092 df=5 CFI=0.939

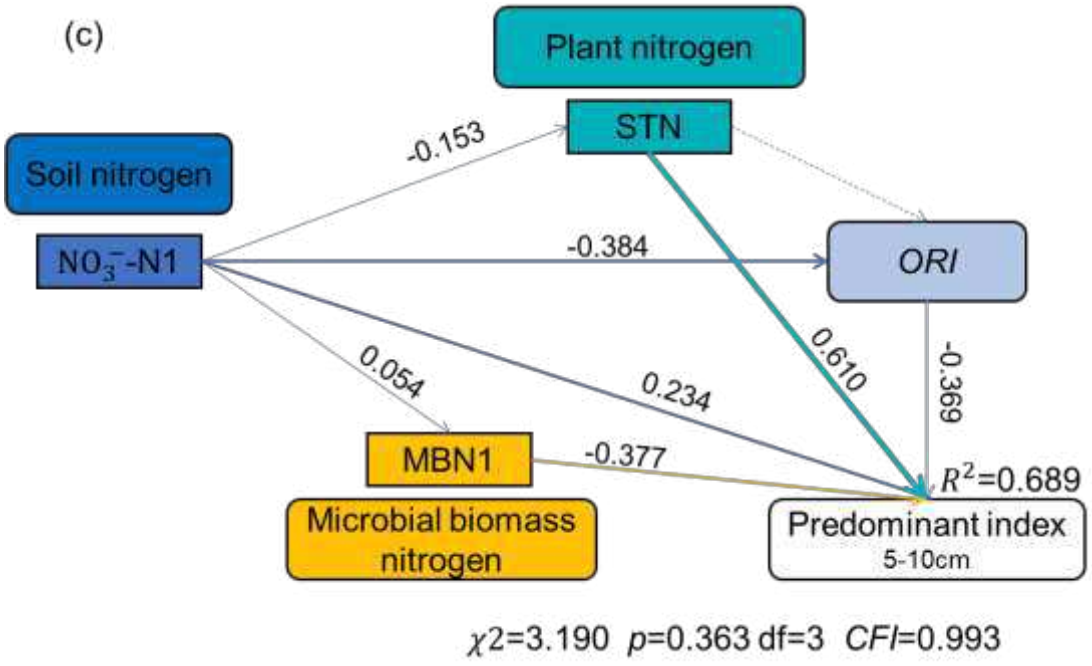

(c)
Plant nitrogen
STN
-0.153
Soil nitrogen
NO_3^--N1
-0.384
ORI
0.610
-0.369
0.054
0.234
MBN1
-0.377
R^2=0.689
Microbial biomass nitrogen
Predominant index
5-10cm
χ2=3.190 p=0.363 df=3 CFI=0.993

Figure 5

Supplementary Files

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