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Mitigation of nitrogen inputs causes native Phragmites australis recovery following Spartina alterniflora invasion

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Article

Keywords:

Posted Date: October 11th, 2022

DOI: https://doi.org/10.21203/rs.3.rs-2064699/v1

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Abstract

Plant invasions driven by global environmental change increasingly threaten natural ecosystems. Whether reducing nitrogen (N) input can help mitigate plant invasions remainsunclear. We used ongoing N reductions in the Yangtze River to explore how N reductions affect native community recovery in estuarine marshes degraded by plant invasions. Using Google Earth images, we mapped native *Phragmites australis* patches and assessed changes in theirabundance in *Spartina alterniflora*-invaded marshes, showing that *P. australis* gradually recovered following reduced N input. To identify the underlying mechanisms, we transplanted N-fertilized and unfertilized *S. alterniflora* populations into plots with ambient and enriched N conditions and co-planted them with *P. australis*, respectively; the competitive advantage of *S. alterniflora* over *P. australis*decreased with N reductions, regardless of fertilized population history, shifting the marsh from *P. australis*exclusion to species coexistence. Thus, nutrient reductions can shift ecosystems from being susceptible to invasion to successional recovery, offering an effective strategyfor mitigating plant invasions and facilitating landscape-scale native community recovery.

Introduction

The introduction, establishment, and spread of invasive plants have caused biodiversity declines and substantial losses in global ecosystem services[1,2]. Plant invasions have long been considered to be exacerbated by environmental changes[3,4] because invasive plants possess broad environmental tolerance, high phenotypic plasticity, and an intrinsically high growth rate, which allow them to adapt to varying environments more effectively than native plants (e.g., increased temperature, atmospheric CO_2, and nitrogen (N))[5–8]. Global environmental change has been partially responsible for the limited worldwide implementation of efficient, coordinated control and mitigation strategies (e.g., utilization of herbicides, mowing, and prescribed fire) because invasive plants are likely to recolonize restored areas after control measures have been taken[9–11]. While there have been many calls for mitigating global environmental change and for controlling exotic species invasions[12–15], whether these activities can help abate plant invasions and restore native ecosystems remains unclear.

Nitrogen enrichment is an environmental change that can facilitate plant invasion[16–18]. Over the past century, annual N inputs into the biosphere resulting from human activities (e.g., fossil fuel burning and crop fertilization) have reached 2.1×10^8 tons worldwide, creating eutrophic conditions across terrestrial, aquatic, and marine ecosystems[19]. As N is one of the most limiting nutrients for plant growth[20], invasive plants can often outcompete their native counterparts for N resources, conferring invasive species greater growth capabilities under increased N availability and potentially resulting in the competitive exclusion of native plants[21–23]. Therefore, native communities are often more susceptible to plant invasions after N enrichment[24–26]. When invasive plants have a higher capacity for N use than native plants, lowering N availability can theoretically provide effective control and mitigation of invasions[25,27]. Policies for sustainable N management[28] have been implemented in many locations around the world[29–34]. However,

whether the altered competitive hierarchy between exotic and native plants under N enrichment will be reversed following N reduction and in turn facilitate the control or mitigation of plant invasions and the restoration of native communities remains unknown.

The Yangtze River is one of the world's largest rivers, and its basin is home to 459 million people[34]. Urbanization and the rising demand for food caused by population growth have contributed to substantial increases in N inputs, reaching as high as 1.7×10^6 tons in the estuary in 2014 (Fig. 1a). With continuously increasing N inputs, the invasive plant *Spartina alterniflora* has rapidly spread in the Yangtze estuary, causing reductions in populations of native *Phragmites australis* and *Scirpus mariqueter*[35]. Starting in 2017, we conducted a long-term field N-enrichment experiment (called the *Spartina* Invasion and Nitrogen Enrichment (SINE) experiment) to investigate whether the success of *S. alterniflora* is driven by N inputs in the Yangtze estuary. The results showed that *S. alterniflora* has a higher capacity for nitrogen uptake and utilization than native species (e.g., *Phragmites australis*)[23], conferring *S. alterniflora* a competitive advantage over native species; therefore, *S. alterniflora* can successfully invade tidal areas by excluding native species or pre-empting niches[36,37].

In 2015, to combat nutrient pollution in the Yangtze River, the Chinese government enacted new policies, including increasing sewage treatment capacity, reducing the use of fertilizers, and closing industrial factories[34], which collectively reduced N discharges from 1.7×10^6 tons in 2014 to 1.4×10^6 tons in 2017 and, subsequently, to less than 0.2×10^4 tons after 2018 (Fig. 1a). Such a dramatic reduction in N inputs at the watershed scale offered us a unique opportunity to assess changes in the invasiveness of *S. alterniflora* and the resulting effects on the native plant community in Yangtze estuarine marshes that were invaded by *S. alterniflora*.

Here, we conducted a landscape-scale analysis (Fig. 1b) to determine the responses of the *P. australis*-dominated native community in an *S. alterniflora*-invaded marsh before and after the N input reductions in the Yangtze estuary in 2014 using satellite images from Google Earth (see Methods and Supplementary Fig. 1). To uncover the mechanisms driving this temporal response of *P. australis* patches, we investigated how the growth performances of *S. alterniflora* and *P. australis* responded to decreased N inputs by calculating the maximum normalized difference vegetation index (NDVI) at landscape scales and monitoring aboveground biomass in ambient N plots in the SINE experiment. In addition, we determined how the competitive impacts of *S. alterniflora* on *P. australis* responded to decreased N conditions by transplanting previously N-fertilized and unfertilized *S. alterniflora* from the SINE experiment into plots with ambient N and enriched N conditions and co-planting it with *P. australis* (see Methods). We further evaluated niche and fitness differences (i.e., how competing species differ in their use of nutrient resources and space and differences in species' growth rates and sensitivity to competition[38]); the study compared *P. australis* and *S. alterniflora* to characterize their competitive outcomes in the mixed stands under enriched N or ambient N conditions within a large *P. australis* patch in the *S. alterniflora*-invaded marsh (see Methods). Our study showed that the ability of *S. alterniflora* to

outcompete *P. australis* decreased with decreasing N availability, which facilitated the recovery of *P. australis* over time at the landscape scale.

Results

Increasing density and size of **P. australis** patches over time.

We conducted a landscape-scale analysis using satellite images from Google Earth to estimate the density and size of *P. australis* patches in 20 *S. alterniflora*-invaded marshes in the northern inlet of the Yangtze estuary from 2014 to 2020 (i.e., before and after the reduction in N inputs, which began in 2015) (Fig. 1b and Supplementary Fig. 1). We found that both the density ($p = 0.04$; Fig. 1c) and size ($p = 0.03$; Fig. 1d) of *P. australis* patches increased significantly over time. From 2014 to 2020, although the distributed area of the *S. alterniflora*-invaded marsh increased by spreading to mudflats (Fig. 1b), the density and size of the *P. australis* patches inside this invaded marsh also increased 3.5 and 2.5 times from 14 ± 6 patches/km^2 and 64 ± 23 m^2/patch in 2014 to 49 ± 9 patches/km^2 and 164 ± 37 m^2/patch in 2020, respectively (Fig. 1c and d). Moreover, the density and size of *P. australis* patches did not vary significantly across marsh elevation in 2020 (R^2=-0.04, $p = 0.643$ for density; $R^2 = 0.03$, $p = 0.227$ for size; Supplementary Fig. 2).

Decreasing growth performance of **S. alterniflora** over time.

To compare the growth performance of *S. alterniflora* and *P. australis* after the reduction in N inputs, we calculated the maximum NDVI (the most widely used remote-sensing vegetation index) from 2014 to 2020 in *P. australis* patches and monoculture stands of *S. alterniflora* in the marshes using GIS analyses. The maximum NDVI of *S. alterniflora* showed a different temporal pattern from that of *P. australis* (species × year: $F_{1,201} = 15.19$, $p < 0.001$; Fig. 1e), with the maximum NDVI for *S. alterniflora* decreasing significantly over time ($p = 0.04$; Fig. 1e) and that of *P. australis* increasing over time ($p = 0.03$; Fig. 1e).

Similar differences in growth performance (species × year: $F_{1,28} = 56.53$, $p < 0.001$ for aboveground biomass; $F_{1,28} = 82.59$, $p < 0.001$ for stem density; $F_{1,28} = 9.70$, $p = 0.004$ for height) were observed between *S. alterniflora* and *P. australis* under ambient N conditions in the SINE experiment (Fig. 2a-c). The growth performances of *S. alterniflora* (all $p < 0.001$) and *P. australis* (all $p > 0.05$) decreased and increased over time, respectively, resulting in decreasing growth advantages of *S. alterniflora* over *P. australis* (Fig. 2a-c). Multivariate regression analysis showed that the growth performance of *S. alterniflora* was positively correlated with only soil N availability (all $p < 0.05$; Supplementary Table 1; Fig. 2d-f), suggesting limitation mainly by reduced N availability. This was further supported by the increased allocation of root biomass ($p < 0.001$; Supplementary Fig. 3a, b) and reduced leaf N availability ($p = 0.009$; Supplementary Fig. 3c) of *S. alterniflora* over time.

The competitive advantage of **S. alterniflora** decreases with decreased N availability

To explore whether the increased density and size of *P. australis* patches over time were associated with the decreased competitive advantage of *S. alterniflora* over *P. australis* after the reduction in N inputs, we collected fertilized and unfertilized *S. alterniflora* populations (from 2017 to 2020) from outside the SINE experiment (Fig. 1b) and planted them with *P. australis* under enriched N (150 g N m^{-2} yr^{-1}, similar to the SINE experiment) and ambient N (the N conditions in the Yangtze estuary after the reduction in N inputs) conditions in 2021; this experiment was intended to simulate the effects of reduced N inputs on the competitive advantage of *S. alterniflora* over *P. australis*. In the transplant experiment, the interaction between N treatment and species was significant ($F_{1,20}$ = 100.41, p < 0.001), with the aboveground biomass of previously fertilized *S. alterniflora* decreasing and that of *P. australis* increasing as N availability decreased from N-enriched to ambient N conditions (Fig. 3a), which was consistent with the results of the maximum NDVI in the landscape analysis (Fig. 1e) and aboveground biomass obtained by ground monitoring (Fig. 2a). These results led to a significant increase in the dominance of co-planted *P. australis* within only a single growing season (N enrichment: $F_{1,8}$ = 35.52, p < 0.001; Fig. 3b). These effects on the aboveground biomass of both species (N enrichment × species × population history: $F_{1,20}$ = 2.61, p = 0.122; Fig. 3a) and the dominance of co-planted *P. australis* (N enrichment × population history: $F_{1,8}$ = 0.05, p = 0.826; Fig. 3b) were consistent across fertilized and unfertilized *S. alterniflora* populations, suggesting that the ability of *S. alterniflora* to outcompete *P. australis* was affected by N levels rather than by population history (i.e., a population historically exposed to a eutrophic environment).

Considering that the competitive ability of *S. alterniflora* may decrease with age[39], we determined whether the effects of N on the competitive impact of *S. alterniflora* in mixed stands were confounded by population age. *S. alterniflora* populations of different ages (2, 5, and 10 years). The *S. alterniflora* populations from both the N-fertilized and unfertilized plots in the SINE experiment were approximately 10 years old in 2020, as determined by historical images on Google Earth. Using this identification method, we also collected *S. alterniflora* turf at 2 and 5 years from *S. alterniflora* populations near the SINE experiment. The interval of population ages (2, 5, and 10 years) was similar to the period of fertilization (4 years) experienced by *S. alterniflora* populations in the N-fertilized plots. Supporting the results found in the first part of the experiment, the aboveground biomass of both species and the dominance of co-planted *P. australis* in the mixed stand were mainly affected by N levels rather than by the population age of *S. alterniflora* (N enrichment: $F_{1,17}$ = 33.36, p < 0.001; N enrichment × population age: $F_{1,37}$ = 0.10, p = 0.752; Supplementary Fig. 4).

Reduced N availability shifts competitive outcomes from exclusion to coexistence

As the competitive impact of *S. alterniflora* on co-planted *P. australis* was primarily affected by N levels (Fig. 3), the competitive dynamics between *S. alterniflora* and *P. australis* after the reductions in N inputs could then be simulated using an N fertilization experiment. Therefore, to further clarify the mechanisms by which reduced N inputs increased the *P. australis* patches in the *S. alterniflora*-invaded marshes, we conducted another N fertilization experiment (150 g N m^{-2} yr^{-1}, as in the SINE experiment) around a large patch of *P. australis* (diameter, ~ 40 m) in the *S. alterniflora*-invaded marsh in 2021 (Fig. 4a). To

characterize the changes in competitive outcomes between *S. alterniflora* and *P. australis*, we evaluated the niche and fitness differences by quantifying changes in their aboveground biomass before (2020) and after (2021) N enrichment in the mono- and mixed stands. The results showed that N enrichment increased the difference in fitness but decreased the difference in niche between *S. alterniflora* and *P. australis* (Fig. 4b), suggesting that the competitive interactions were weaker in the mixed stands under lower than under higher N levels.

N enrichment had different effects on temporal changes in plant survival between *S. alterniflora* and *P. australis* (N enrichment × species × growing time: $F_{1,127} = 12.81$, $p < 0.001$; Fig. 4c). Specifically, the survival of *P. australis* decreased significantly with growing time under N enrichment ($p = 0.001$; Fig. 4c) to 21 ± 14% during the peak biomass season, which was 3 times lower than that of *S. alterniflora* (83 ± 5%; species: $F_{1,8} = 17.91$, $p = 0.003$; Fig. 4c). Accordingly, the stem density and aboveground biomass of *P. australis* significantly decreased from levels similar to or higher than those of *S. alterniflora* before N enrichment in 2020 to lower than those of *S. alterniflora* after N enrichment in 2021 (all $p < 0.001$; Fig. 4d and e). Therefore, *P. australis* could be competitively excluded by *S. alterniflora* after N enrichment (Fig. 4b). However, under ambient N conditions, interspecific competition decreased the survival of both *S. alterniflora* and *P. australis* to similar levels (81 ± 6% vs. 73 ± 8%; species: $F_{1,8} = 0.619$, $p = 0.454$; Fig. 4c), allowing their coexistence (Fig. 4b).

Discussion

Our results revealed that nutrient pollution control was an effective strategy for mitigating *S. alterniflora* invasions and facilitating the subsequent recovery of native communities at the landscape scale. We draw this conclusion based on four lines of evidence across different spatial scales. First, multiyear monitoring analyses showed that the decreased growth of *S. alterniflora* (the maximum NDVI at the landscape scale and aboveground biomass in ambient N plots in the SINE experiment) might be caused mainly by reductions in N availability after the decrease in N inputs in the Yangtze estuary (Figs. 1e and 2). Second, the decreased growth of *S. alterniflora* in turn diminished its competitive advantage over *P. australis* following reductions in N availability, and this N effect was not affected by population history (i.e., a population historically exposed to a eutrophic environment) or population age (Fig. 3 and Supplementary Fig. 4). These results suggest that the competitive ability of any *S. alterniflora* population (< 10 years) in this study area would increase and decrease rapidly in response to increasing and decreasing N availability, respectively. Third, the decreased competitive ability of *S. alterniflora* shifted the competitive outcomes from *S. alterniflora* exclusion of *P. australis* to their coexistence (Fig. 4). Finally, this shift in competitive outcomes appeared to have caused the recovery of *P. australis* at the invaded marsh landscape following the dramatic reductions in N inputs in the Yangtze estuary (Fig. 1). These results highlight how reducing nutrient pollution can beneficially shift the altered state of an ecosystem[40,41] backwards from vulnerability to invasions to successional recovery.

Reducing nutrient pollution may decrease the growth advantages of invasive plants over native plants that once gained from nutrient pollution and reverse the competitive hierarchy between invasive and

native plants[11]. Consistently, our results showed that the higher growth advantages of *S. alterniflora* over *P. australis* in the mixed stands decreased from N-enriched to ambient N conditions (Fig. 3). Although exotic plants can invade low-resource ecosystems by optimizing their strategies (e.g., increasing root biomass allocation) to acquire and use resources[25,42], the long-lasting effects of nutrient enrichment on plants (e.g., decreasing their nutrient acquisition efficiency) may compromise their ability to absorb nutrients[42–44]. Moreover, invasive plants can increase soil N by stimulating the decomposition of their nutrient-rich litter in fertile soils of terrestrial ecosystems[45,46], but these oxic decomposition processes are largely limited in the water-saturated, anoxic sediments of wetlands[47,48]. Therefore, *S. alterniflora* populations might not be able to acquire sufficient nutrients to maintain their growth and invasiveness following a substantial reduction in N availability (as indicated by the decreasing leaf N availability in Supplementary Fig. 3c). Besides of nutrient availability, decreased plant growth can be also contributed by biotic effects (e.g., herbivores)[49,50]. *Spartina alterniflora* invasions often led to a drastic increase in herbivorous crab populations[23,51], which in turn might reduce plant growth due to the increased food demand especially when plant abundance decreases following N reduction. Collectively, *P. australis* might then be released from the high competition pressures exerted by *S. alterniflora* (Fig. 4b). These results are in agreement with those results from woodlands[52,53], wetlands[54], and agricultural lands[55], highlighting that high nutrient loss rates can limit the ability of invasive species adapted to high nutrient availability to compete with native species adapted to low nutrient availability under low-nutrient conditions.

Although increases and decreases in nutrient availability regulate plant invasions through similar mechanisms (as discussed above), the consequences might be quite different. Nitrogen enrichment can promote the landward invasion of *S. alterniflora* in both native and introduced ranges[56,57]; however, N subsidies were mainly supplied by the enriched tidal water[58], and thus, the competitive ability of *S. alterniflora* gradually decreases with decreasing nutrient availability at higher elevations less inundated by the tide[59]. Therefore, *S. alterniflora*-invaded areas were mainly converted from unvegetated mudflats rather than landward, excluding native species in coastal China[60]. In contrast, the decreased competitive ability of *S. alterniflora* after the reductions in N inputs triggered an explosive recovery of native communities throughout the entire invaded marshes even at lower elevations (Supplementary Fig. 2), where *S. alterniflora* has a stronger competitive ability[54,55]. This was probably because *S. alterniflora*, as an ecosystem engineer, can ameliorate environmental stresses (e.g., decrease flooding frequency and salinity) by increasing marsh elevation via siltation[61] and may therefore provide suitable habitats for the colonization of native species (e.g., *P. australis*) less tolerant of environmental stresses. These results highlight that reducing nutrient pollution is indeed beneficial for successional recovery in ecosystems degraded by plant invasions. Invasive *S. alterniflora* is an aggressive plant around global coastal wetlands, and its expansion is being promoted by N enrichment[57,58]. Through the lens of *S. alterniflora* in the Yangtze River estuary, our findings have important implications for managing invasive plant species in coastal wetlands in many other regions of the world as well as in other ecosystems that experience high levels of N enrichment.

Reinstating historical environmental conditions to restore invaded ecosystems along successional trajectories is time-consuming (ranging from decades to half-centuries)[41,62,63]. However, the density and size of *P. australis* patches in the invaded marshes increased immediately in response to the reduction in N inputs since 2015 without a time lag (Figs. 1b-d). This was probably because changes in the alternative state of an invaded ecosystem are largely determined by the distinctive responses of invasive plants to historical environmental conditions[41,64]. In this study, the growth performance (e.g., aboveground biomass, stem density and plant height) of *S. alterniflora* decreased rapidly under lower N levels (Figs. 2–4), which might provide more growing space and greater light availability for *P. australis* to grow under the canopy (as indicated by our previous study[65]), increasing the survival rate of *P. australis* (Fig. 4c). Moreover, *S. alterniflora* might not resist the recovery of *P. australis* patches as strongly as invasive plants in terrestrial ecosystems by reinforcing themselves[45,66] due to the limited N mineralization in wetlands (as discussed above). Furthermore, *S. alterniflora* might not resist the recovery of *P. australis* patches by pre-emptively vacating soil nutrients as other invasive plants do[53,67], because *P. australis* has a lower nutrient requirement than *S. alterniflora*[23]. and the growth of *P. australis* was not limited by lowered N availability (Figs. 2–4). Therefore, native *P. australis*, rather than other aggressive invaders (e.g., N fixer[53]), could be re-established rapidly through its propagules (both seeds and clonal tissues) that pre-expanded to the invaded marshes. These results highlight that the successional recovery of degraded ecosystems after reinstating historical environmental conditions could be more rapid than generally assumed.

However, natural succession driven by resident competitors makes it difficult to completely repel plant invasions[68,69]. Therefore, effective control of invasive species in restoration requires long-term investments[70,71]. Future efforts to reduce N input are needed to maintain the stability of coexistence between *S. alterniflora* and *P. australis* or even shift species coexistence to the exclusion of *S. alterniflora* by *P. australis* when *P. australis* becomes competitively superior. Considering that native plants (e.g., *P. australis*) have often been considered candidates to outcompete *S. alterniflora* under certain environmental conditions (e.g., low salinity and N availability) in coastal China[72], planting native plants in invaded marshes of the brackish estuary is expected to fill the vacant niche handed over by *S. alterniflora* after its growth performance decreases under lowered N levels (Figs. 2–4). These restoration efforts may not only resist the recolonization of *S. alterniflora* or new invasions but also boost the successional recovery of native communities.

Our study empirically demonstrates how practices that reduce nutrient availability to levels existing before nutrient pollution may facilitate the control of global invaders such as *S. alterniflora* and the subsequent recovery of native communities. The implementation of policies reducing nutrient pollution should thus be an important component of plant invasion control and native ecosystem recovery efforts worldwide[25,31]. Integrated approaches, for example, combining the long-term reduction in nutrient pollution and establishment of native species, can be used to facilitate the successional recovery of native communities in invaded ecosystems. Considering that multiple global environmental changes (e.g., elevated atmospheric CO_2 concentrations, climate warming, and N enrichment) can also interact to

facilitate plant invasions[73,74], multidisciplinary collaborations and integrated approaches are also needed to ensure the implementation of successful management and restoration strategies[75]. Such efforts would mitigate biodiversity loss in plant-invaded ecosystems in the context of global environmental change.

Methods

Study site and species

The study area is in a brackish marsh in the northern inlet of the Yangtze estuary, China (31°41'N, 121°41'E; Fig. 1b). This site is characterized by a subtropical monsoonal climate. The mean annual temperature (MAT) is 15.3°C, and the mean annual precipitation (MAP) is 1,022 mm. Tides are regularly semidiurnal, with an average tidal height ranging from 2 to 6 m. The brackish marshes at the study site exhibit clear shifts in the dominant plant species along an elevation gradient, with the low marsh dominated by *Sc. mariqueter* and the middle and high marshes dominated by *P. australis*[35]. *Spartina alterniflora* is native to North America and has now successfully invaded many of the world's coastal ecosystems[76]. In the Yangtze estuary, *S. alterniflora* has altered the species composition of native marshes by invading the communities of *Sc. mariqueter* and *P. australis*, forming new plant communities composed exclusively of *S. alterniflora* in the low and middle marshes and exclusively *P. australis* in the high marsh, with striking zonation or a total conversion to *S. alterniflora* alone (Fig. 1b).

In the Yangtze estuary, *S. alterniflora* and *P. australis* have different phenologies. Although *S. alterniflora* and *P. australis* sprout from clonal ramets at the same time in March, *P. australis* green up (from April to May) and senescence approximately one month earlier than *S. alterniflora* (from December to January), respectively[77,78]. *S. alterniflora* and *P. australis* also have different morphologies. The ramets of *S. alterniflora* are denser (316 ± 17 ramets m^{-2}) but shorter (115 ± 8 cm) than those of *P. australis* (50 ± 6 ramets m^{-2} and 298 ± 17 cm)[23]. These morphological differences between *S. alterniflora* and *P. australis* are particularly evident during their peak biomass season in October. Thus, *P. australis* patches in the *S. alterniflora*-invaded marshes can then be easily identified from the satellite images on Google Earth and high-resolution images taken with a drone (Supplementary Fig. 1 and see following methods).

Increasing density and size of **P. australis** patches over time.

The density and size of *P. australis* patches in an *S. alterniflora*-invaded marsh in the Yangtze estuary were estimated from 2014 to 2020 (i.e., before and after the reduction in N inputs that started in 2015). Before outlining *P. australis* patches, we determined the distribution area of *S. alterniflora* in the Yangtze estuary by using a pixel- and phenology-based mapping algorithm, time series Landsat 5/7/8 images, and the Google Earth Engine cloud computing platform. The pixel- and phenology-based algorithm was developed based on the differences in phenological characteristics among *S. alterniflora* and other native saltmarsh plants in two temporal windows (April-May and December-January) through the threshold

values and frequencies of two vegetation indices (NDVI and enhanced vegetation index (EVI)) and one water index (land surface water index, LSWI) (for detailed information, please see[78]).

When evaluating high-resolution images (ca. 1 m) taken with a DJI Phantom 3 drone during low tide on clear, cloud-free days in December 2021, we found that *P. australis* appeared as blurry fungus-like spots when it flowered (Supplementary Fig. 1). These spots were outlined in an *S. alterniflora*-invaded marsh (up to ~ 14 km^2 in 2020) from Google Earth during the flowering period of *P. australis* (from October to December). In 2020, we selected sixty areas (~ 330 × 420 m) in the invaded marsh, and then five hundred *P. australis* patches out of a total of 965 in these areas were validated with the high-resolution images taken with the drone in 2021 by determining the repeated presence of these patches at given locations between images of different resolutions (part of the validation is shown in Supplementary Fig. 1). The accuracy of the outlined *P. australis* patches reached 90.6% (± 1.4), with confounding caused mainly by omission errors. This high accuracy suggested that this approach was suitable for analysing the temporal dynamics of *P. australis* patches in the *S. alterniflora*-invaded marsh at an annual resolution.

We then outlined the *P. australis* patches within the distribution area of *S. alterniflora* on the historical satellite images in reverse chronological order (i.e., from 2020 to 2014), which made it less likely to miss *P. australis* patches when they were smaller in earlier years. The results for 2015 and 2017 were not obtained because of the lack of available satellite images during the *P. australis* flowering period. The satellite images with outlined *P. australis* patches were used to estimate the density and size of *P. australis* in the *S. alterniflora*-invaded marsh. Then, twenty 90,000 m^2 areas (300 × 300 m) with more than 40% plant cover were randomly selected in the marsh at least 500 m apart to estimate the density and size of *P. australis* patches. Considering that the competitive ability of *S. alterniflora* and *P. australis* decreases and increases with marsh elevation[56], the density and size of *P. australis* patches may increase significantly with marsh elevation. We further determined the spatial patterns in the density and size of *P. australis* patches across marsh elevation by randomly picking 20 grids (300 × 300 m) in this study area in only 2020 due to the lack of available marsh elevation data. Marsh elevation data in 2020 were obtained from the Enterprise Edition 91 Weitu Assistant.

We evaluated the temporal changes in the density and size of the *P. australis* patches in the invaded marsh using LME models, with year included as a fixed effect. Considering that both *S. alterniflora* and *P. australis* are perennial plants, we also included year as a random effect to account for the interannual impact. We further analysed the relationships between the density and size of *P. australis* patches and marsh elevation using simple linear regression. All analyses were conducted in *R* (v4.1.2) using the “nlme” package.

Decreasing growth performance of **S. alterniflora** over time.

To monitor the temporal effects of decreasing N availability on plant growth, we calculated the maximum NDVI of both plants over time at the landscape scale and measured plant biomass, stem density, plant height, and leaf N availability over time under ambient N conditions in the SINE experiment. We

calculated the maximum NDVI from 2014 to 2020 following the methods of[78,79]. Briefly, Landsat ETM+/OLI images were taken at low tide on clear, cloud-free days in the fast-growing phase (June–August) of *S. alterniflora* and *P. australis* and then were used to calculate the NDVI of 15 randomly picked sites in the monospecific stands of *S. alterniflora* and the large *P. australis* patches (diameter, > 40 m) that were present throughout the period from 2014 to 2020.

In the SINE experiment, twenty 4 × 4 m plots were established in 2017. Each set of 10 plots, spaced 20 – 30 m apart, was established at similar elevations in monospecific stands of *S. alterniflora* and *P. australis* and assigned alternately to two treatments (n = 5 replicates): ambient N or N enrichment. To simulate the eutrophic conditions in the Yangtze estuary, the N enrichment plots were enriched using a dissolved inorganic N solution (NH_4^+-N:NO_3^--N = 4:1 by weight) at a rate of 150 g N m^{-2} yr^{-1} monthly from March through December starting in 2017. Nitrogen was applied during neap tides to reduce nutrient removal by the tides and to ensure that plants had enough time to absorb the nutrients. For more details, please see[23].

We deployed three small quadrats (20 × 20 cm for *S. alterniflora* and 50 × 50 cm for *P. australis*, different quadrat sizes due to large differences in their density and height (Fig. 2a-c)) in each plot to quantify plant growth performance from 2017 to 2020, as described in previous studies[80,81]. In the peak biomass season (October), fresh and healthy leaves of both *S. alterniflora* and *P. australis* were collected, oven-dried and ground to measure carbon (C) and N concentrations and the N:C ratio using a nutrient analyser (vario MACRO cube; Elementar, Hanau, Germany). We harvested aboveground biomass, counted stem density, and measured plant height for both *S. alterniflora* and *P. australis* at ground level in each quadrat. We then collected one soil block (10 × 10 cm) from each quadrat by carefully excavating to a depth of 30 cm to determine root biomass. The soil blocks were gently washed to remove soils and adhering materials, and belowground tissues were then sorted into roots and rhizomes or other plant material.

To determine the edaphic factors, we collected three soil cores (diameter, 4 cm; depth, 30 cm) from each quadrat. The soil samples were then pooled and mixed thoroughly, cleaned to remove stones and plant materials by hand, and weighed before and after being air-dried to determine the water content. The samples were then ground and sieved (mesh size < 0.2 mm) to measure the dissolved inorganic nitrogen (DIN) concentration and salinity. Soil DIN was extracted with 0.5 mol/L K_2SO_4 (1:5, w:v) and analysed colorimetrically for NH_4^+-N and NO_x^--N on a microplate reader (Synergy 2; BioTek, Winooski, Vermont, USA). Soil salinity (1:5, w:v) was measured with a conductivity metre (SevenExcellence S479-uMix; Mettler-Toledo, Greifensee, Switzerland). We also compiled MAT from 2017 to 2020 from the Climatic Data Center of the National Meteorological Information Center in China (https://data.cma.cn/).

We evaluated the temporal changes in the maximum NDVI of each species using LME models, with year included as a fixed effect. In this model, year was also treated as a random effect to account for the interannual impact. We compared temporal patterns of growth performance (aboveground biomass, belowground biomass, root:shoot ratio, stem density, plant height, and leaf N availability) between *S. alterniflora* and *P. australis* using LME models, in which species, year, and their interactions were included

as fixed effects, and year and plot ID were included as random effects. Multivariate regression analyses were performed separately for *S. alterniflora* and *P. australis* with LME models to assess relationships between growth performance and environmental variables (MAT, soil salinity, DIN, and water content).

The competitive advantage of **S. alterniflora** decreases with decreasing N availability.

Beginning in March 2021, we conducted a field experiment to compare the competitive advantage of *S. alterniflora* on co-planted *P. australis* under ambient N and N-enriched conditions. Eight plots (2 × 1 m, spaced > 2 m apart) were established in *S. alterniflora*-dominated marshes outside of the SINE experiment at similar elevations. We transplanted 8 *S. alterniflora* turfs with similar plant heights (~ 10 cm) from N-fertilized and unfertilized plots in the SINE experiment, which has run for 4 years since 2017, using PVC pipes (diameter, 10 cm; depth, 30 cm) and then deployed the turf randomly into each 2 m^2 plot, with the top edges of the PVC pipes flush with the marsh substrate. The pipes were predrilled with 42 holes (diameter, 1 cm) into their walls to allow the soil pore water to flow in and out. The stem densities of these turfs were also counted separately before the experiment.

Four of the 8 plots were randomly assigned to each of two treatments: ambient N and N enrichment. N enrichment plots were fertilized with N monthly from March through December 2021 at a rate of 150 g N m^{-2} yr^{-1} following the method used in the SINE experiment to simulate the severe level of eutrophication in the Yangtze estuary that occurred before 2017. The ambient N plots without fertilization were used to represent the decreased N availability in the Yangtze estuary after 2017.

Considering that the competitive ability of *S. alterniflora* may decrease with age[39], we determined the confounding effect of population age on the effects of N levels on the competitive ability of *S. alterniflora* in this transplant experiment. The *S. alterniflora* populations from both the N-fertilized and unfertilized plots in the SINE experiment were approximately 10 years old in 2020, as determined by historical images on Google Earth. Using this identification method, we also collected *S. alterniflora* turf of different ages (2 and 5 years) from *S. alterniflora* populations near the SINE experiment (100 ~ 300 m apart). The interval of population ages (2, 5, and 10 years) was similar to the period of fertilization (4 years) experienced by *S. alterniflora* in the N-fertilized plots. Finally, 32 *S. alterniflora* turfs (4 populations of different ages × 2 N levels × 4 replicates) in total were transplanted into these 2 m^2 plots.

As N fertilization had no significant effect on the aboveground biomass of *P. australis* in the SINE experiment[23], three disconnected clonal ramets of *P. australis* of similar height (~ 10 cm) were transplanted carefully from the unfertilized plots in the SINE experiment into each of the 32 turfs without harming the roots of *S. alterniflora*. Any ramets of *P. australis* that died within 1 month after being transplanted were replaced with healthy ramets. Considering that the aboveground parts of *S. alterniflora* occurring outside the PVC pipes in the marsh may affect the growth of plants inside the PVC pipes through light competition, we cleared them all to ground level within 1 m away during the growing season (from March to October). In October, the plants in each PVC pipe were harvested at ground level and sorted by species (*S. alterniflora* or *P. australis*). Their aboveground biomass was weighed separately

after oven drying at 70°C to a constant mass. We analysed the effects of N enrichment, species, and population age on aboveground biomass and the effect of N enrichment and population age on *P. australis* dominance (represented by the proportion of aboveground biomass in the mixed stand) using LME models with the initial density of *S. alterniflora* in the transplanted turf as a random effect.

Reduced N availability shifts competitive outcomes from exclusion to coexistence

As the competitive advantage of *S. alterniflora* was primarily affected by N levels (Fig. 3), the competitive advantage of *S. alterniflora* before and after the reduction in N inputs could then be simulated in N-enriched (150 g N m^{-2} yr^{-1}, as in the SINE experiment) and ambient N conditions, respectively. To assess the mechanisms by which N levels affect the competitive advantage of *S. alterniflora* over *P. australis*, we conducted another N-enrichment field experiment using three plant groups: monospecific stands of *P. australis* (blue quadrat); monospecific stands of *S. alterniflora* (orange quadrat); and mixed stands with both *P. australis* and *S alterniflora* (black quadrat) (see Fig. 4a). The three plant population quadrats were grown under N-enriched conditions (solid quadrat) or lower N ambient conditions (open quadrat), and the various quadrats were arranged along radial transects in a large, approximately circular patch of *P. australis* (diameter, ~ 40 m) in an *S. alterniflora*-dominated marsh in the Yangtze estuary in 2021 (n = 5 replicates of 3 group arrangements and 2 N conditions, for a total of 30 quadrats). The transects were established inside, outside, and at the margin of the *P. australis* patch (i.e., monospecific stands of *P. australis* or *S. alterniflora* and a mixed stand of both species). Ten sets of 3 quadrats (1 × 1 m) were established along each transect, with adjacent quadrats spaced 10 m apart. In each quadrat of the mixed stands, *S. alterniflora* and *P. australis* had similar stem densities (Fig. 4d). There were 5 replicates of each treatment, and all plots along each transect were assigned alternately to one of two treatments: ambient N or N enrichment.

In 2021, N was applied to the plots in the enrichment treatment following the method of the SINE experiment[23,65]. Plant survival was recorded separately for each species in a randomly positioned quadrat (50 × 50 cm) established in each plot during the growing season (from March through October) in the same year. Aboveground biomass and stem density were monitored in both the mono- and mixed stands during the peak biomass season (October) before (2020) and after N enrichment (2021). To quantify aboveground biomass, the plants in each quadrat were harvested at ground level and sorted into *S. alterniflora* and *P. australis*. Stem density was quantified, and aboveground biomass was determined after oven drying at 70°C to a constant mass. We then evaluated niche and fitness differences by using the aboveground biomass of *S. alterniflora* and *P. australis* in both the monospecific and mixed species stands in October 2020 and 2021 (for detailed calculation, please see the following subsection). A series of ANOVAs were performed with LME models to estimate the effects of N enrichment on niche and fitness differences between the two species separately, in which case plot ID was included as a random effect; to estimate the effects of N enrichment, species, and sampling time on plant survival in the mixed stands during the growing season, in which case sampling time and plot ID were included as random effects; and to estimate the effects of N enrichment and species on stem density and aboveground biomass during the peak biomass season, in which case plot ID was included as a random effect.

Measurement of the mechanisms of coexistence

The growth rates of *S. alterniflora* and *P. australis* before (2020) and after (2021) N enrichment in the monospecific ($\mu_{i,0}$) and mixed stands ($\mu_{i,j}$) were calculated as follows[38]:

$$\mu_{i,x} = \frac{1}{T} \cdot \frac{AGB_{2021}}{AGB_{2020}}$$

where $x = 0$ or j, T is 365 d, and AGB_{2020} and AGB_{2021} are the aboveground biomass of the focal species (i.e., *S. alterniflora* and *P. australis*) in the monospecific and mixed stands in 2020 and 2021, respectively.

We estimated niche differences (NDs) and relative fitness differences (RFDs) based on species sensitivity to competition as previously described[38,82]. We calculated the sensitivity of each species to competition for each replicate, which was defined as the amount by which the per-individual growth rate for each species was reduced when grown in the mixed species treatment ($\mu_{i,j}$) relative to the growth rate that each species achieved in the respective monospecific stands ($\mu_{i,0}$):

$$S_{i,j} = \frac{\mu_{i,0} - \mu_{i,j}}{\mu_{i,0}}$$

When $S_{i,j} < 1$, i can outcompete j, and when $S_{i,j} > 1$, i cannot invade j. The ND was then calculated as one minus the geometric mean of the species' sensitivities:

$$ND = 1 - \sqrt{s_{i,j} s_{j,i}}$$

An RFD causes species sensitivities to diverge. For two species indexed such that $S_{i,j} \geq S_{j,i}$, the RFD is given as follows:

$$RFD = \sqrt{S_{i,j} / S_{j.i}}$$

Declarations

Data availability statement

Data are not yet provided. Should the manuscript be accepted, the data supporting the results will be archived in Figshare, and the data DOI will be included at the end of the article.

Acknowledgements

This work was supported by the National Natural Science Foundation of China (32030067, 41630528, and 91951112), the Program of Shanghai Academic/Technology Research Leader (21XD1420700), the "Shuguang Program" supported by Shanghai Education Development Foundation and Shanghai Municipal Education Commission (21SG02), the Science and Technology Department of Shanghai

(21TQ004 and 21DZ1201902) and the China Postdoctoral Science Foundation (BX20200094 and 2020M681164).

Author contributions

M.N. conceived the idea of the work; X.X. and S.L. conducted the field experiment and measurements with the assistance from Y.Z., X.Z., H.L., H.G. and J.M.; X.X. and S.L. analyzed the data with the assistance from M.N. and B.L.; X.X. and S.L. wrote the paper with input from all the other authors.

Competing interests

The authors declare no competing interests.

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Figures

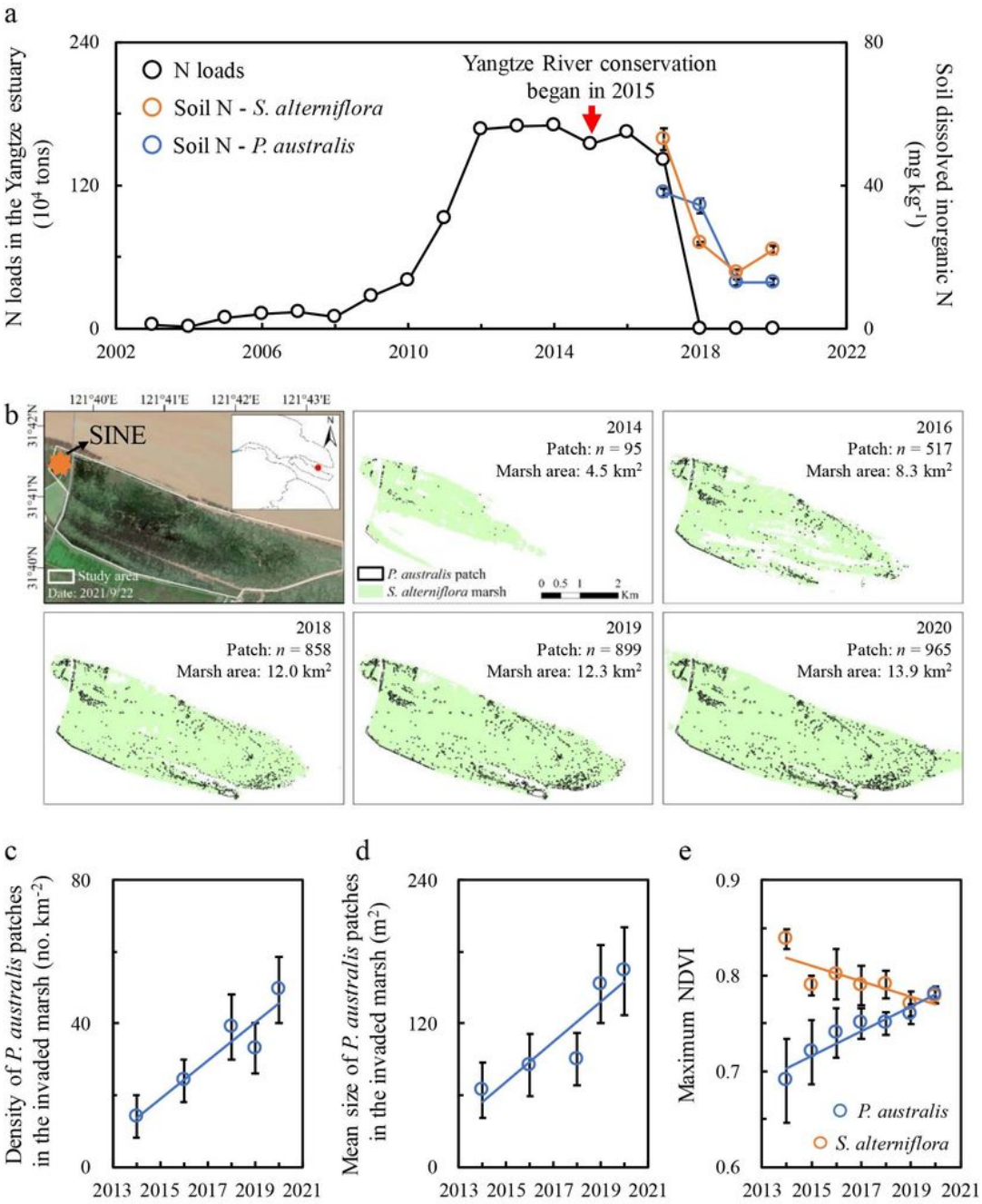


Figure 1

Temporal patterns of N inputs and *P. australis*-dominated native community recovery in an *S. alterniflora*-invaded marsh. (a) Temporal changes in the N loads in the Yangtze estuary and ambient soil dissolved inorganic nitrogen concentration in the SINE experiment. The red arrows indicate the start time of the Yangtze River conservation efforts (when the reductions in N inputs took place in 2015 and 2017). Data on the amounts of N discharged into the Yangtze estuary were obtained from the Ministry of Ecology and

Environment of the People's Republic of China (https://www.mee.gov.cn/). Soil dissolved inorganic nitrogen concentrations were measured within the top 30 cm of soil in the monospecific stands of both *P. australis* and *S. alterniflora* in the SINE experiment (n = 5 independent plots). (b) The satellite images obtained from 2014 to 2020 showed *P. australis* patches in the *S. alterniflora*-invaded marsh. *P. australis* patches were first outlined on satellite images from Google Earth, and their densities and sizes were then estimated using GIS analyses (see Methods). The dynamic areas of the *S. alterniflora*-invaded marsh were obtained from our previous study[55]. Temporal changes in the (c) density and (d) size of *P. australis* patches distributed in *S. alterniflora*-invaded marsh from 2014 to 2020 (i.e., before and after the reduction in N inputs began in 2015; data were not collected for 2015 or 2017 due to the lack of available satellite images for the entire study area). The data are shown as the mean ± standard error (n = 20). (e) Temporal changes in the maximum NDVI of *S. alterniflora* in the invaded marsh and that of *P. australis* in the patches present throughout the period 2014 to 2020. A higher positive NDVI value indicates better plant performance. The data are shown as the means ± standard errors (n = 15). The solid lines are significant linear regression lines obtained by using linear mixed-effect (LME) models with year as a random effect.

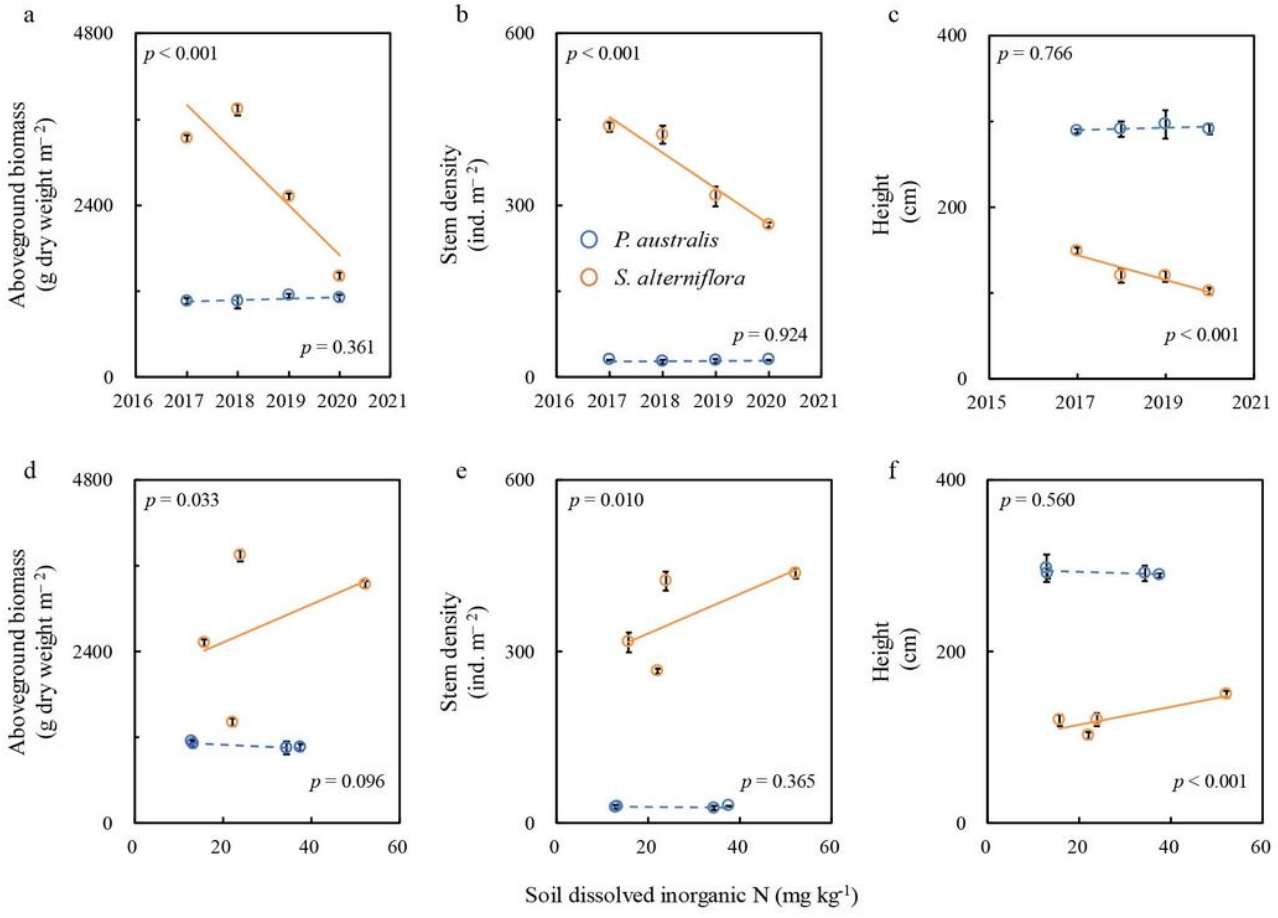


Figure 2

Plant growth dynamics under ambient N conditions in the SINE experiment after the reduction in N inputs in the Yangtze estuary. Temporal changes in growth performance. The relationships between growth performance and soil N availability. Shown are (a, d) aboveground biomass, (b, e) stem density and (c, f)

plant height. For detailed results of multivariate regression analysis, please see Supplementary Table 1. The data are shown as the means ± standard errors (n = 5). The solid lines are significant linear regression lines obtained by using linear mixed-effect (LME) models with year and plot ID as random effects.

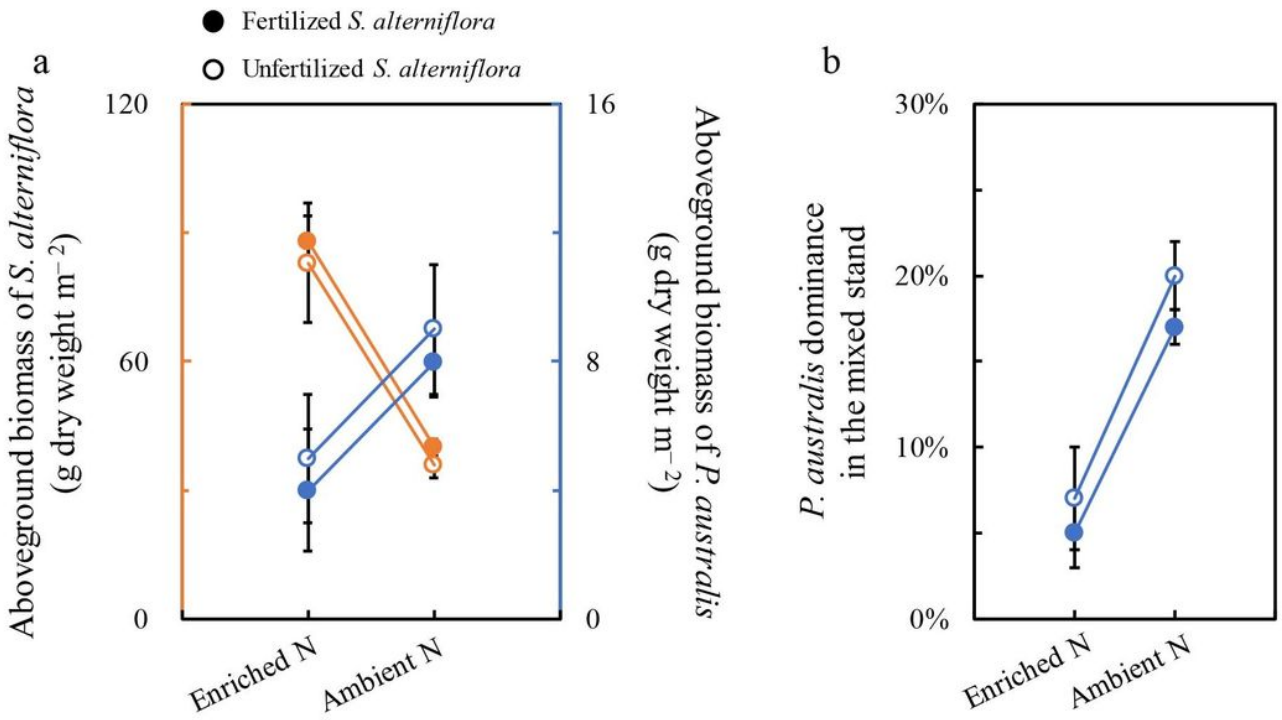


Figure 3

Effects of N on plant growth performance in the transplant experiment. (a) Effects of N on the aboveground biomass of previously fertilized and unfertilized *S. alterniflora* and co-planted *P. australis* in the mixed stands. (b) Effects of N on the dominance of *P. australis* (as represented by the proportion of aboveground biomass) in the mixed stands co-planted with previously fertilized and unfertilized *S. alterniflora*. The data are shown as the means ± standard errors (n = 4).

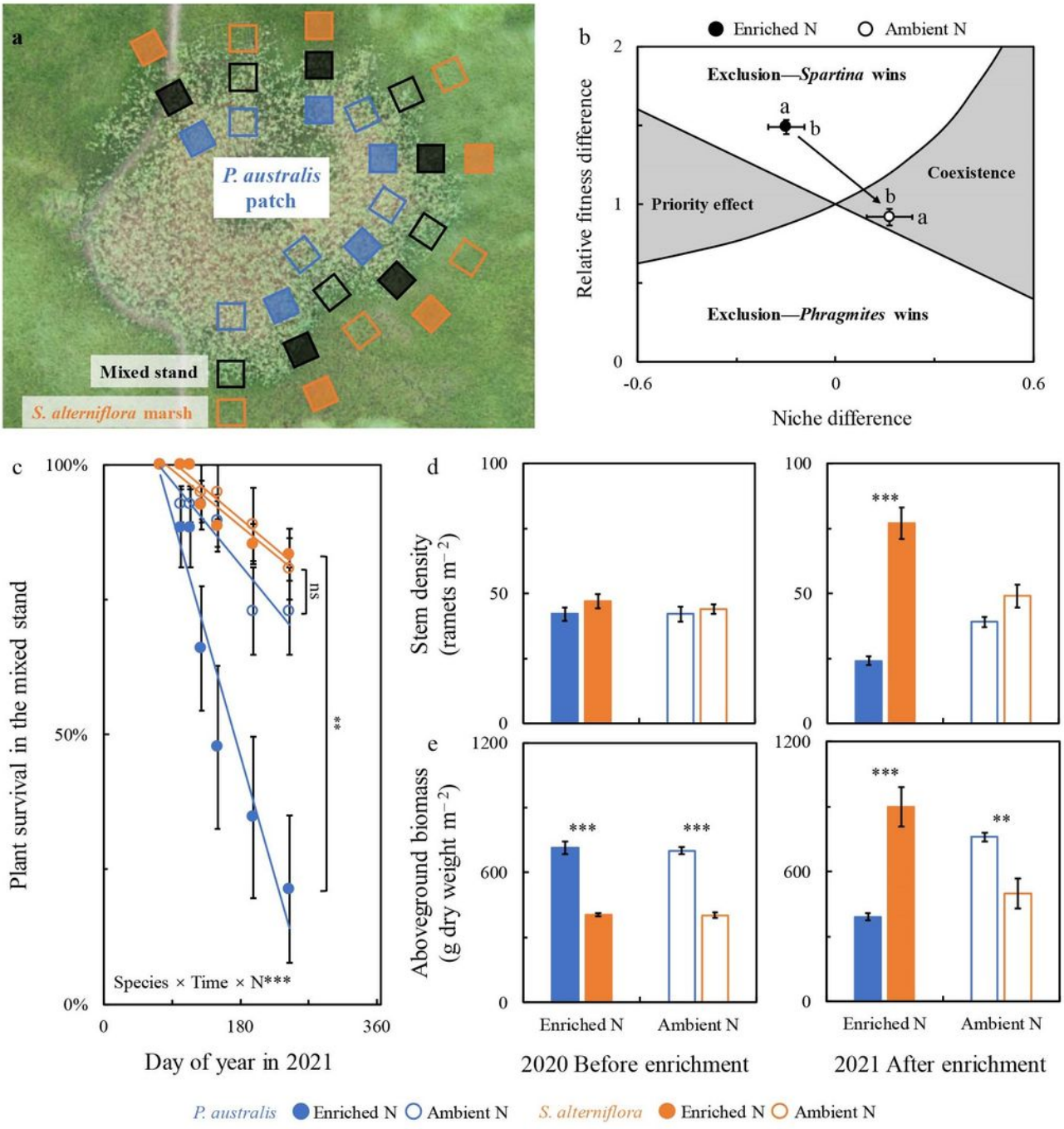


Figure 4

Mechanisms driving the temporal response of *P. australis* patches. (a) Plant performance was monitored using three plant groups: monospecific stands of *P. australis* (blue quadrat); monospecific stands of *S. alterniflora* (orange quadrat); and stands of mixed *P. australis* and *S alterniflora* (black quadrat). The three plant groups were grown under N-enriched conditions (solid quadrat) or lower N, ambient conditions (open quadrat), and the various quadrats were arranged along radial transects in a large, approximately

circular patch of *P. australis* (diameter, ~40 m) in the *S. alterniflora*-invaded marsh in 2021 (n = 5 independent sets of plots, with 3 group arrangements and 2-N conditions for a total of 30 quadrats). The annual rate of N enrichment was similar to that in the SINE experiment (150 g N m^{-2} yr^{-1}). (b) Niche and fitness differences between *S. alterniflora* and *P. australis* under ambient and enriched N conditions. The competitive outcomes in the mixed stands shifted from the exclusion of *P. australis* by *S. alterniflora* under enriched N conditions to coexistence under ambient N conditions (as indicated by the arrow). The magnitude of the fitness difference relative to the niche difference determines whether species exhibit coexistence and competitive exclusion or priority effects. Strong fitness differences promote competitive exclusion (upper and lower portion), whereas weak fitness differences lead to either coexistence (right side) or priority effects (left side)[39]. Different letters indicate a significant difference at the level of $p < 0.05$. (c) Temporal changes in plant survival in the mixed stand across two N treatments during the growing season (from March to October) in 2021. The solid lines are significant linear regression lines. (d) Stem density and (e) aboveground biomass of each species in the mixed stand before (2020) and after (2021) N enrichment. ns indicates nonsignificant, *$p < 0.05$, **$p < 0.01$, ***$p < 0.001$.

Supplementary Files

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- SupplementaryInformation.pdf