Research article

Revealing biogeographic patterns in genetic diversity of native and invasive plants and their association with soil community diversity in the Chinese coast

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Within-species genetic diversity is shaped by multiple evolutionary forces within the confines of geography, and has cascading effects on the biodiversity of other taxa and levels. Invasive species are often initially limited in genetic diversity but still respond rapidly to their new range, possibly through 'pre-adapted' genotypes or multiple sources of genetic diversity, but little is known about how their genetic structure differs from that of native species and how it alters the genetic-species diversity relationship. Here, we selected a widespread native species *Phragmites australis* and its co-occurring invasive competitor *Spartina alterniflora* as our model plant species. We investigated the genetic structure of *P. australis* using two chloroplast fragments and ten nuclear microsatellites in 13 populations along the Chinese coastal wetlands. We discovered a distinct geographical differentiation, showing that the northern and southern populations harbored unique genotypes. We also found a significant increase in genetic diversity (allelic richness and expected heterozygosity) from south to north. Combined with previous studies of *S. alterniflora*, the Mantel tests revealed a significant correlation of genetic distances between *P. australis* and *S. alterniflora* even when controlling for geographic distance, suggesting that the invasive species *S. alterniflora* might exhibit a phylogeographic pattern similar to that of the native species to some extent. Furthermore, our results suggest that the *S. alterniflora* invasion has altered the relationship between the genetic diversity of the dominant native plant and the associated species richness of soil nematodes. The reason for the alteration of genetic-species diversity relationship might be that the biological invasion weakens the environmental impact on both levels of biodiversity. Our findings contribute to understanding the latitudinal patterns of intraspecific genetic diversity in widespread species. This work

on the genetic diversity analysis of native species also provides significant implications for the invasion stage and ecological consequences of biological invasions.

Introduction

Genetic diversity, as a basic level of biodiversity, is critical for population persistence, species evolution and ecosystem functioning (Hughes et al. 2008, Ellegren and Galtier 2016, Abbott et al. 2017). Although geographic patterns of genetic diversity are shaped by many evolutionary mechanisms, the genetic structure of many invasive species is profoundly influenced by a bottleneck effect (Estoup et al. 2016). Such species can possess low genetic diversity and weak spatial genetic structure in the early and middle stages of their introduction (Qiao et al. 2019, Smith et al. 2020). High migration rates, repeated introductions, and hybridization with native species are among the factors identified in different systems that have been proposed to resolve this lack of diversity (Uller and Leimu 2011, Estoup et al. 2016). In both native and invasive species, geographical and environmental changes contribute to genetic divergence in spite of some differences in the life history, reproductive mode and genome characteristics (Bock et al. 2015, Mounger et al. 2021). Therefore, similar geographical patterns of genetic diversity may eventually emerge between native and invasive species (Avise et al. 1987, Avise 1992, Miraldo et al. 2016).

Latitude is one of the most predictive factors of biodiversity gradients (Gaston 2000). A variety of studies ranging from the tropics to the poles have demonstrated species diversity and total genetic diversity across species at both neutral and functional loci tend to decrease with increasing latitude (Adams and Hadly 2013, Miraldo et al. 2016, Guo et al. 2021, Li et al. 2021). However, intraspecific genetic diversity tends to increase with latitude (Lawrence and Fraser 2020), implying a negative correlation between species-specific diversity and associated species diversity along latitudinal gradients. These patterns suggest that the response of these two levels of biodiversity to the environmental gradient is in opposite directions. Intraspecific genetic variation of dominant plant species can also affect the structure and dynamics of associated biotic communities such as arthropods, nematodes and microbes by releasing oxygen and root exudates below ground and providing leaf litter above ground (Hersch-Green et al. 2011, Bowen et al. 2017, Yan et al. 2021). Furthermore, invasive species can have different dispersal abilities, ecological preferences and biological interactions than native species, which impacts biodiversity at many levels (Young et al. 2017, Stotz et al. 2019, Zhang et al. 2019). A lack of genetic data, particularly over large latitudinal ranges, limits our understanding of latitudinal biodiversity gradients at different levels and further assessment of ecological consequences of invasion.

Phragmites australis is a worldwide foundation plant growing mainly in wetlands. The species has high genetic diversity and plays a significant role in maintenance of biodiversity and ecosystem functioning (Eller et al. 2017). The distinct phylogenetic divergences of *P. australis* were found in North America (Saltonstall 2003, Lambertini et al. 2012a), Europe (Lambertini et al. 2012b) and China (An et al. 2012, Liu et al. 2022) as well as over the world (Saltonstall 2002, Lambertini et al. 2006, Liu et al. 2018). Functional traits of *P. australis* in common gardens display a remarkable clinal adaption (Ren et al. 2020). Genotypic identity and diversity of *P. australis* have been shown to shape soil biota communities (Bowen et al. 2017, Yan et al. 2021). Therefore, in its native regions, *P. australis* is useful as native counterpart in ecological assessments of biological invasions in wetlands. This is especially true on the eastern coast of China, where the exotic grass *Spartina alterniflora* is heavily invading native *P. australis* communities.

Across Chinese coastal wetlands, *S. alterniflora*, native to North America, has become widespread along the coastal wetlands of China following its first introduction in 1979 (Xia et al. 2020). Due to genetic admixture occurring in Luoyuan Bay of China among three populations isolated from the native range (Morehead City in North Carolina, Sapelo Island in Georgia and Tampa Bay in Florida), the introduced populations in China have very high levels of genetic diversity (Qiao et al. 2019, Shang et al. 2019). However, the native populations of *S. alterniflora* have strong phenotypic, haplotypic and genotypic structure that is associated with latitude while the invasive ones only have such structure in some reproductive traits (Liu et al. 2020a, b, Chen et al. 2021). The invasion of *S. alterniflora* has resulted in biotic homogenization of soil biota communities (Zhang et al. 2019, 2020). *Phragmites australis* and *S. alterniflora* are wind pollinated grasses that share similar coastal wetland habitats over a wide latitudinal range (approx. 20°) in China. However, it remains unknown to what extent the biological invasion (dominant vegetation species turnover from *P. australis* to *S. alterniflora*) has changed the pattern of genetic diversity within *P. australis* populations or the association of genetic diversity with species diversity.

Here, we analyzed the biogeographical patterns of haplotype composition, genetic diversity, and genetic structure of *P. australis* across coastal saltmarshes of China. We also assessed the ecological consequences of *S. alterniflora* invasion into *P. australis* communities, by comparing our study with the published genetic data of *S. alterniflora* as well as associated soil nematode diversity data. In our framework, we hypothesized that: 1) the native *P. australis* has a stronger genetic structure along the coast than the invasive *S. alterniflora*; 2) there is a weak correlation of genetic structure between the two species along a large latitudinal range; 3) the *S. alterniflora* invasion

alters the relationship between genetic and species diversity in coastal wetlands. This study provides novel insights into the evolutionary mechanisms and ecological consequences of genetic diversity of native and invasive species.

Material and methods

Sampling, genotyping and sequencing of *Phragmites australis*

We collected 194 individuals of *P. australis* from 13 sites along the Chinese coast (Table 1, Fig. 1). To avoid collecting the same clone and to get enough genetic variation, we selected five *P. australis* reed populations within each site, with a distance of at least 1 km between stands. We collected three individuals from each population. All individuals were transplanted with rhizomes in a common garden at Jiangwan Campus of Fudan University in Shanghai (31°16′48″N, 121°28′48″E). After the plants regrew, we collected and dried young leaves from all individuals, and stored them in zip-lock plastic bags with silica gel at room temperature until DNA isolation. We extracted total DNA from the dried leaves according to a modified cetyltrimethylammonium bromide (CTAB) method. We examined the quality and quantity of extracted DNA with 1% agarose gels and a microscope spectrophotometer, and stored DNA at −20°C until later genotyping and sequencing.

To measure genetic variation, we used 10 microsatellite primer pairs previously designed for *P. australis* (Saltonstall 2003, Yu et al. 2013) (Supporting information). Forward primers were labeled at the 5′ end with the fluorescent dyes FAM, HEX or TAMRA. We performed polymerase chain reaction (PCR) as described by Liu et al. (2022), and separated the PCR products by capillary electrophoresis using an ABI 3730XL DNA capillary sequencer (Applied Biosystems) after confirming the PCR product on a 2% agarose gel. We scored fragment profiles and carefully check the stutter peaks and the low-frequency alleles with GeneMarker ver. 2.2.0 to reduce the potential effect of null allele. We did not discover the null alleles with Hardy–Weinberg equilibrium-based method, since there is no reliable approach to elimination of allele dosage for our polyploid data. The same clones were detected by the function *assignClones* in R package 'polysat' (www.r-project.org, Clark and Jasieniuk 2011). The duplicated genotypes were removed for the further genetic estimates.

To determine the haplotype, we amplified two non-coding chloroplast regions by PCR in one sample of each stand, using the primer pairs [*trn*T (UGU) 'a'-*trn*L (UAA) 'b' and *rbc*L-*psa*I] as described previously (Saltonstall 2002). We sequenced the PCR products in both directions on an ABI 3730XL DNA sequencer (Applied Biosystems). We assembled and checked the sequencing with SeqMan ver. 7.7.0 (Lasergene) and identified haplotypes to the naming scheme of *P. australis* described by Saltonstall (2016).

Data analysis of genetic diversity and structure of *Phragmites australis*

To estimate the genetic diversity level of *P. australis*, we calculated the number of alleles per locus or allelic richness (Na), and the expected heterozygosity (He) with R package 'polysat' (Clark and Jasieniuk 2011). We assessed the relationship between genetic diversity and latitude using linear regression.

To assess the genetic structure of *P. australis*, we calculated genetic differentiation (Fst) with the R package 'polysat'. We also calculated Pairwise Bruvo distances based on microsatellite variation, and used the genetic distance matrix for principal coordinates analysis (PCoA) and hierarchical cluster analysis using the unweighted pair-group method with arithmetic means (UPGMA). We applied Bayesian clustering with Structure ver. 2.3.4 (Pritchard et al. 2000) to detect the genetic structure of *P. australis*. We performed 20 replicates of the clustering analysis at each value of K from 1 to 10 under the admixture model with 50 000 burn-in steps and 500 000 Markov chain Monte Carlo repeats. We calculated Delta K using the online program Structure Harvest (Earl and vonHoldt 2012) to determine the most likely cluster number (K value) for our genetic data, grouped replicates in CLUMPP ver. 1.1.2b (Jakobsson and Rosenberg 2007) and visualized in DISTRUCT ver. 1.1 (Ramasamy et al. 2014).

Table 1. Sampling sites and sample sizes of *Phragmites australis* in Chinese coastal marshes

| Latitudinal gradient	Site	Site ID	Sample size	Latitude (N)	Longitude (E)
High	Panjin	PJ	15	40°53′52″	121°47′21″
	Tangshan	TS	15	39°01′31″	118°20′8″
	Dongying	DY	13	37°49′19″	119°05′18″
	Lianyungang	LYG	15	34°49′52″	119°11′25″
Middle	Yancheng	YC	15	33°38′11″	120°34′2″
	Shanghai	SH	16	31°41′4″	121°39′8″
	Cixi	CX	15	30°22′5″	121°13′52″
	Taizhou	TZ	15	28°42′13″	121°25′15″
	Wenzhou	WZ	15	28°00′19″	120°47′1″
Low	Fuzhou	FZ	15	26°01′45″	119°37′34″
	Zhangzhou	ZZ	15	23°56′2″	117°24′5″
	Zhuhai	ZH	15	22°25′51″	113°37′24″
	Beihai	BH	15	21°34′47″	109°07′52″
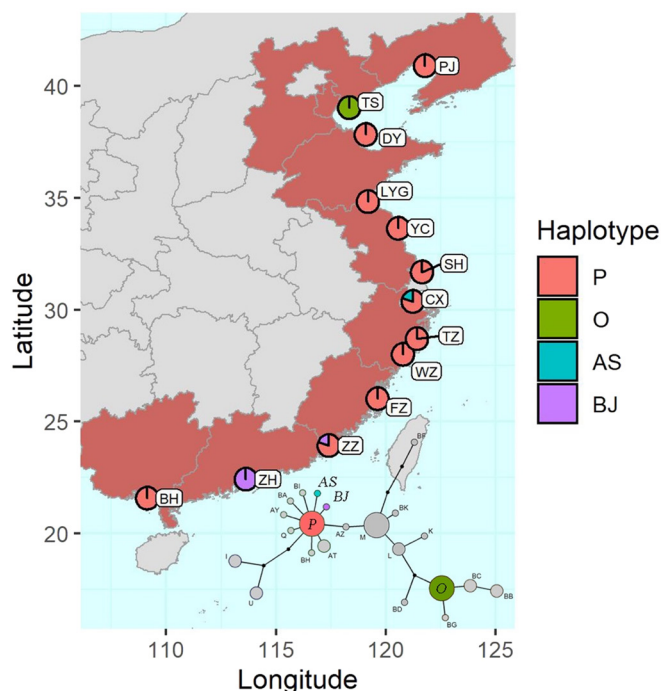
Figure 1. Sampling sites of *Phragmites australis* along the east coast of China, and their haplotype compositions. The haplotype network of *P. australis* in China was from Liu et al. (2022).

Correlation analysis between geographical and genetic distances of *Phragmites australis* and *Spartina alterniflora*

We used the previously published nuclear microsatellites and chloroplast sequences data of *S. alterniflora* in China (Qiao et al. 2019, Shang et al. 2019, Xia et al. 2020). We extracted the geographical coordinates (Supporting information) and the diversity indices (i.e. allele number, Na; expected heterozygosity, He) of surveyed populations of *S. alterniflora* from Shang et al. (2019) and Xia et al. (2020) for further comparisons. For genetic analysis of *S. alterniflora*, we used the raw data of 11 nuclear microsatellites from Qiao et al. (2019). We removed three loci from the raw dataset because there were many missing values or null alleles in loci 5, 7 and 9. We calculated geographic distances using the function *distm* in R package 'geosphere' and used pairwise Fst for genetic distance.

We used Mantel test and multiple matrix regression with randomization (MMRR) (Wang 2013) to examine relationships between geographic and genetic distance matrices at the site level. We ran correlation analyses between geographical and genetic distance matrices using the function *mantel* in R package 'vegan', and regression analyses using the function *MMRR* written by Wang (2013) with genetic distance as the dependent matrix and geographical distances as the independent (predictor) matrices with 9999 permutations. The correlation of genetic distances between the two species were also performed with partial Mantel test while controlling the geographical distance for seven common sites.

Correlation between genetic variation and nematode community

We used the geographic records of nematode genera from a published work (Zhang et al. 2019). These nematode data were investigated to reveal the biotic homogenization of nematode communities by exotic *S. alterniflora* in China. This study found a clear latitudinal cline (nematode diversity increased with increasing latitude) and a strong correlation of nematode diversity to environmental variables in soils for *P. australis*, but weak for *S. alterniflora* (Zhang et al. 2019). Because the TJ and TS sites were located within a very short distance (approx. 54 km; see the northernmost red circles in the Supporting information) around the same bay, we considered them as one site when comparing the variation in geography, genetics and community. Thus, we had seven common sites with both genetic and nematode information. We estimated the Jaccard distances between nematode communities using the function *dist* with a method binary parameter. We used these Jaccard distances to perform PCoA of nematodes. Matrix correlation analyses between geographic, genetic and nematode distance matrices for seven common sites were performed using both Mantel test using the function *mantel* in R package 'vegan' and MMRR using the function MMRR written by Wang (2013) with nematode distance matrices as the dependent variable using 9999 permutations.

Results

Latitudinal pattern of genetic diversity

We found a moderate diversity of *Phragmites australis* populations in the saltmarsh wetlands of China (He = 0.68), slightly lower than our previous results of the riverine wetlands in China (e.g. He = 0.71 in the Ningxia Plain; He = 0.79 in the Xiaoqing River; He = 0.73 in the riverine habitats of the Yellow River Delta), but similar to the previous survey in the saltmarsh of the Yellow River Delta (He = 0.67) (Liu et al. 2021). The averaged Na across all ranged from 3 in BH to 9.2 in PJ, and the He ranged from 0.55 in BH to 0.78 in PJ. The linear model analysis displayed that the genetic diversity of *P. australis* decreased significantly with decreasing latitude (Fig. 2, Na: slope = 0.17, R^2 = 0.48, p = 0.01; He: slope = 0.01, R^2 = 0.40, p = 0.02). There was no significant relationship between the genetic diversity of *Spartina alterniflora* and latitude for any diversity indices in any applied dataset (all p values > 0.05) (Fig. 2). The Pearson's tests showed no significant correlation of genetic diversity between *P. australis* and *S. alterniflora* (Na: r = 0.16, p = 0.57; He: r = 0.59, p = 0.16).

Spatial similarity of genetic structure

We found four haplotypes in *P. australis*, of which haplotype P was found in eleven sites, BJ in two (ZZ and ZH), O in one (TS) and AS in one (CX) (Fig. 1). In PCoA of *P.*
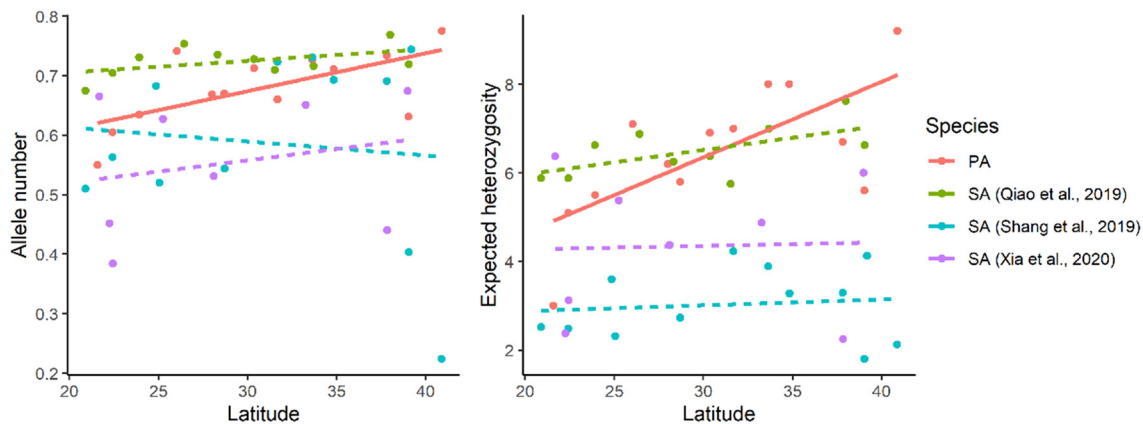
Figure 2. The latitudinal variation of genetic diversity based on nuclear microsatellite data of *Phragmites australis* (PA) and *Spartina alterniflora* (SA). Solid lines indicate a significant correlation, while dashed lines are non-significant.

australis, increasing values of the first coordinate were associated with decreasing latitude except for BH which had the lowest latitude but was found on the far left. The second axis showed that this same population (BH) separated from the rest (Fig. 3A). In the UPGMA tree, the sites BH, TS, ZH and ZZ were divided into new branches in sequence (Supporting information). According to delta K statistics, the optimal K value for Bayesian clustering was five (Supporting information), and BH, TS and ZH were clustered as three distinct groups at K = 5 (Fig. 3C). Specifically, TS, BH and ZH were separated from K = 2, 3 and 4, respectively (Fig. 3C).

Among all surveyed populations of *S. alterniflora*, we found a positive correlation between geographic and genetic distances (Mantel test: r = 0.37, p = 0.01; MMRR: R^2 = 0.14, p = 0.02), while this was not significant in *P. australis* (Mantel test: r = 0.26, p = 0.07; MMRR: R^2 = 0.07, p = 0.13) (Fig. 3B). However, there was a significant correlation of genetic distances between *P. australis* and *S. alterniflora* (Mantel test: r = 0.63, p = 0.01; MMRR: R^2 = 0.63, p = 0.02) (Supporting information) even when accounting for geographic distances (partial Mantel test: r = 0.53, p = 0.03).

Correlation between genetic variation and nematode community

In the PCoA of the nematode community, the first coordinate was generally associated with latitude, and the second with plant species identity. The exceptions were the two southern sites (SH and ZH) (Fig. 4). The nematode communities were not correlated with geographical or genetic distances in habitats of *P. australis* or *S. alterniflora*, regardless of whether all surveyed sites or the seven common sites were used (all p values > 0.10; Supporting information). The nematode richness was not significantly correlated to the genetic diversity (He) of *S. alterniflora* (Pearson test: r = 0.15, p = 0.75), but it was negatively correlated to *P. australis* (Pearson test: r = −0.78, p = 0.05) (Fig. 4). Among feeding groups of nematodes, the carnivore richness was most correlated to genetic diversity of *P. australis* (Pearson test: r = −0.81, p = 0.02).

Discussion

Lower latitudes have been reported to have higher species diversity (Schluter and Pennell 2017, Guo et al. 2021) and total genetic diversity across animal species (Adams and Hadly 2013, Miraldo et al. 2016, Li et al. 2021) than higher latitudes. However, this latitudinal gradient of biodiversity may result from shorter generation times, higher mutation rates and higher metabolic rates under higher temperature in animals living at the lower latitudes (Rohde 1992, Allen et al. 2006, Lawrence and Fraser 2020), while plants may have different characteristics. Here, we found a positive association between latitude and nuclear genetic diversity in *P. australis* (Fig. 2). This suggests that conclusions drawn from animal haplotypic information, such as mitochondrial sequences, is not appropriate for polyploid plants with frequent hybridization between intraspecific lineages and even among species. Stressful environments (e.g. drought) are often associated with increased levels of genetic diversity in plant populations (De Kort et al. 2021). Compared with wild grasses in the tropics, the same or related species at higher latitudes usually have early flowering dates, high seed fecundity and high shoot density, typical of a 'weedy' or r-strategy, which could contribute to higher genetic diversity (Qiao et al. 2019, Ren et al. 2020, Liu et al. 2020b). This strategy is congruent with the higher genetic diversity in *P. australis* populations from the higher latitudes. On the other hand, strong selection in higher latitudes (e.g. low temperature) may reduce the genetic diversity in some species (Thomas et al. 2017).

The spatial genetic structure of native species could generally reflect the geography, including physical barriers and habitat conditions. For *P. australis*, we found strong genetic structure in the coastal saltmarshes of China. We found that haplotype P was the most common and made up the majority of our samples while O and AS were mostly found in a single population and BJ was found in two. Our previous research unveiled the existence of two major chloroplast haplotypes (O and P) within temperate China (An et al. 2012), and this divergence was further substantiated by
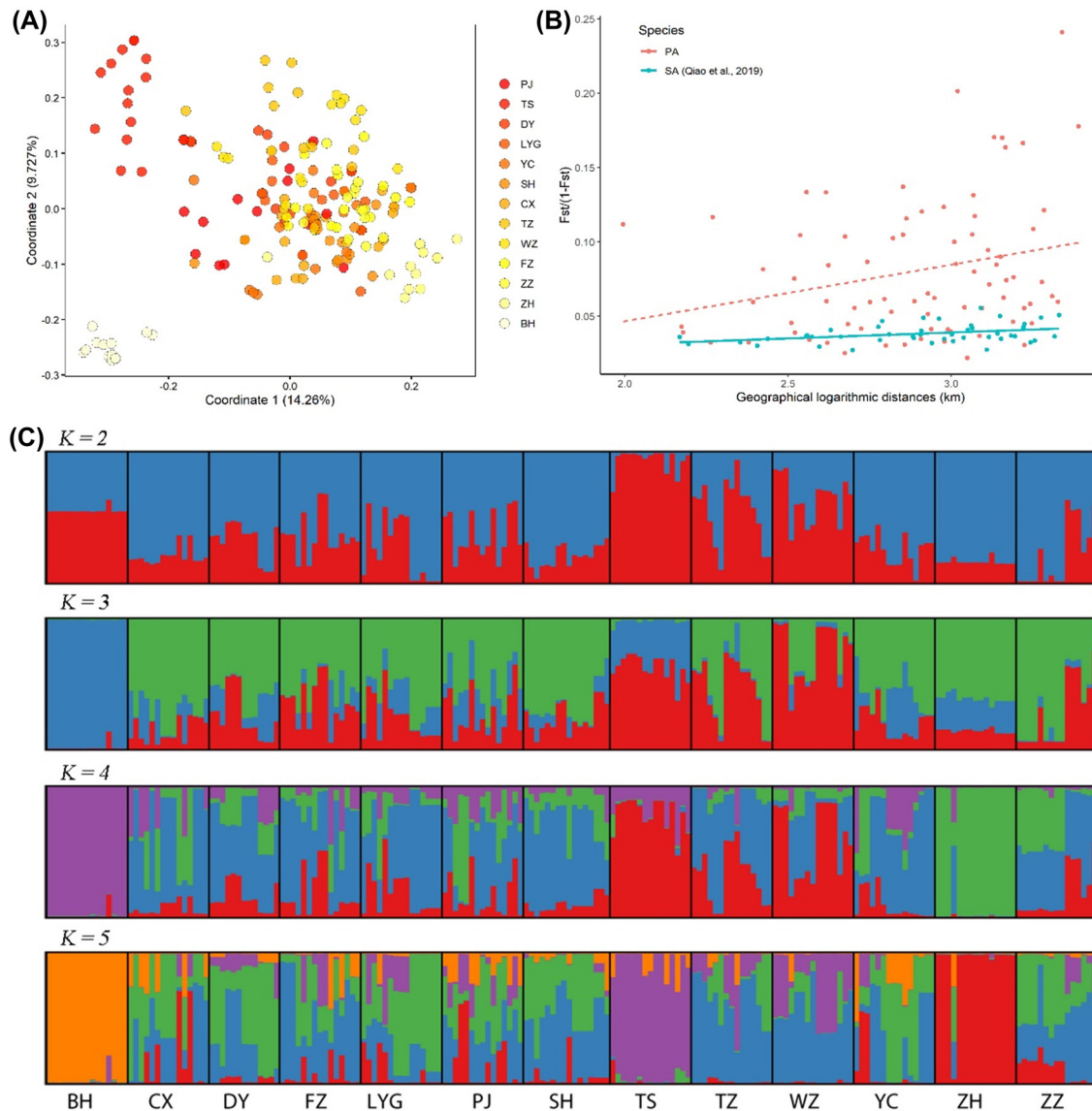
Figure 3. The genetic structure of *Phragmites australis*. (A) Principal coordinates analysis (PCoA) of microsatellite data for *P. australis*. Color depths indicate latitudes for each site, with darker colors indicating higher latitudes. (B) Genetic isolation patterns by geographic distances. PA denotes *P. australis* and SA denotes *Spartina alterniflora*; solid lines indicate a significant correlation, while dashed lines are non-significant. (C) Genetic admixture inferred from microsatellites of *P. australis* by STRUCTURE at K = 2–5. Each individual is represented by a thin line (y-axis), which is partitioned into five colored segments representing the individual's membership fractions of the distinguished genetic clusters. Regions are separated by bold lines.

nuclear microsatellites where each haplotype was assigned to a separate group according to STRUCTURE (Liu et al. 2022). This concordance between chloroplast and nuclear variation is common in *P. australis* (Saltonstall 2003, 2016, Lambertini et al. 2012b, Liu et al. 2022). Haplotype P signifies an octoploid lineage and exhibits wide distribution in eastern China (Liu et al. 2022), particularly prevalent in coastal salt marshes as indicated by this study. Conversely, haplotype O represents a tetraploid lineage predominantly found in the inland regions of northern China (Liu et al. 2022). The introduction of haplotype O from inland areas to the coastal regions might account for the presence of

haplotype O in coastal salt marshes, including the TS population. The haplotypes AS and BJ were derived from the haplotype P by one nucleotide substitution and one repeat insertion, respectively (Liu et al. 2022), but we found that the individuals with haplotype BJ in our studies were genetically differentiated from those with haplotype P. Unexpectedly, we found that the haplotype P from the southernmost site (BH) was extremely different in nuclear variation from the other individuals. We suspect the individuals from BH might be related to the subtropical lineage of *P. australis* in southwest China (e.g. the haplotypes U and I) or the congeneric species *P. karka* (Lambertini et al. 2006, Liu et al. 2022, Tanaka et al.
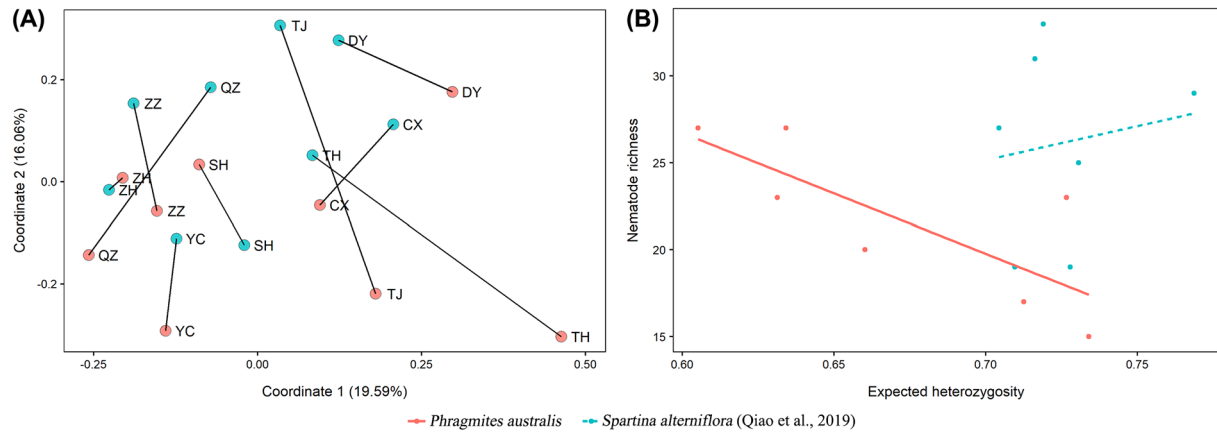
Figure 4. Soil nematode diversity associated with *Phragmites australis* and *Spartina alterniflora*. (A) Principal coordinates analysis (PCoA) of nematode data from Zhang et al. (2019). (B) Correlation between nematode richness and plant genetic diversity (expected heterozygosity). Genetic data of *S. alterniflora* is from Qiao et al. (2019). Solid line indicates a significant correlation, while dashed lines are non-significant.

2017). In general, it seems that the Chinese coast supports strong genetic structure of native *P. australis*.

Human activities promote long-distance dispersal, repeated introductions, and habitat disturbance of invasive species. Therefore, some invasive plant species can simply mix genetics from multiple populations, gain an adaptive advantage, and develop genetic structure (Smith et al. 2020). For *S. alterniflora*, the current genetic structure might be the consequence of the recent rapid population expansion from a single origin (Luoyuan) but high genetic diversity due to the intentional genetic mixture among three native populations from North America (Shang et al. 2019, Xia et al. 2020). In addition, the initial introductions and subsequent long-distance dispersal might also contribute to the current genetic structure (Xia et al. 2020). In our analysis, we found isolation by distance in both *P. australis* and *S. alterniflora*, and there was a significant correlation in genetic differentiation (Fst) between *P. australis* and *S. alterniflora* even when accounting for the effects of geographic distance. The spatial similarity of genetic structure implied the invasion of *S. alterniflora* might have been restricted by some geographical or environmental factors, which also play a significant role in the evolution of *P. australis*. Our results demonstrate the potential to gain insight into the evolutionary processes of native species through the study of biological invasion.

The biotic community (e.g. soil nematode) associated with the vegetation of an ecosystem is shaped by the plant species (or genotypic) identity and plant species (or genetic) diversity, as well as the abiotic conditions (Hersch-Green et al. 2011, van den Hoogen et al. 2019, Zhang et al. 2019, Yan et al. 2021). Among the nematode communities along the Chinese coast, we identified two geographic clusters (the northern cluster: TJ, TH, DY and CX; the southern cluster: YC, SH, QZ, ZZ and ZH) by PCoA (Fig. 4), but we did not detect isolation by distance for the nematode communities in the habitats of either *P. australis* or *S. alterniflora* (Supporting information). Our results indicated that environmental factors instead of dispersal limitation, were the major drivers of community assembly of soil nematodes, consistent with previous analyses (Yan et al. 2021) and a global scale study (van den Hoogen et al. 2019). Plant species identity also affected the nematode community, but the effect might depend on the environmental context. For example, the effect of species identity in SH and ZH was very different from that in other sites (Fig. 4), and we found no geographical correlations of related nematode communities between two plant species (NT (PA) versus NT (SA) in the Supporting information). Therefore, the geographic pattern in nematode species diversity is explained more by environmental effects than neutral processes (e.g. long-distance dispersal), which is very different from the driving mechanisms of plant genetic diversity discussed above. Opposite impacts by environmental factors on different biodiversity levels could contribute to the negative correlation between genetic and species diversity (Marchesini et al. 2018). Our study suggests that plant invasion can alter the genetic-species diversity relationship by impairing these environmental impacts on both biodiversity levels.

Previous analyses revealed a clearer latitudinal cline in nematode diversity and a stronger correlation with the abiotic environment in *P. australis* communities than in *S. alterniflora*, which was attributed to the biotic homogenization by the *S. alterniflora* invasion (Zhang et al. 2019, Yan et al. 2021). We found that a negative correlation between *P. australis* genetic diversity and nematode species diversity, but no correlation for *S. alterniflora* (Fig. 4). A meta-analysis showed that variation in genotypes within species (including plants and animals) is an important positive driver of community and ecosystem dynamics (Raffard et al. 2019). This is not consistent with our results. It is possible to speculate that our observed pattern is more due to the variation in the background environment along latitude, rather than pure ecosystem processes (i.e. the interaction between *P. australis* genetic diversity and nematode species diversity in the context of our study ecosystem). Furthermore, our results suggest that *S. alterniflora* genetic diversity has a stronger effect on soil

nematode diversity than native *P. australis*, homogenizing the latitudinal pattern of nematode diversity. Therefore, our evidence did not support that the effect of *S. alterniflora* is much more homogeneous due to less genetic variation among sites, and the stronger effect of *S. alterniflora* than native counterpart *P. australis* could be the main reason for the biotic homogenization. However, some plant functional traits associated with nematode diversity might not be conserved in the phylogeographic history inferred from neutral DNA markers, due to local adaptation (Zerebecki et al. 2021) or rapid evolution (Qiao et al. 2019). Hence, the phenomenon of biotic homogenization should be further tested by correlation analysis with relevant adaptive traits by combining the field survey and the common garden experiment.

Conclusion

In this study, we found a strong genetic structure of *P. australis* with four haplotypes (P, O, AS, PJ) across the coastal saltmarshes of China. The results indicated a significant positive association of genetic diversity with increasing latitude in *P. australis* while such an association was only weak or absent in *S. alterniflora*. However, we observed isolation by distance in both species, and discovered a significant correlation of genetic variation between the two species even when controlling for the geographical distance. This suggests that the genetic diversity of the invasive *S. alterniflora* has been shaped by both dispersal limitation and natural selection in a similar way that variation across this environmental gradient affecting *P. australis*. It could be that the invasion of *S. alterniflora* has already begun to evolve in a way that recapitulates the patterns found in the native. Finally, we found a negative genetic-species diversity correlation (i.e. the negative association of genetic diversity in plant species with species diversity of soil community) in the native species but not in the invasive one. Our finding suggests that biotic homogenization resulting from biological invasion might be due to stronger effects of the invasive species than latitudinal factors, rather than homogeneous effects due to less intraspecific genetic variation among populations.

Author contributions

Lele Liu and **Yaolin Guo** share first authorship. **Lele Liu**: Conceptualization (lead); Funding acquisition (lead); Project administration (equal); Writing – original draft (lead); Writing – review and editing (lead). **Yaolin Guo**: Conceptualization (equal); Methodology (lead); Project administration (lead); Resources (lead); Writing – original draft (equal); Writing – review and editing (lead). **Yiming Wu** Methodology (supporting); Writing – original draft (supporting). **Meiqi Yin**: Methodology (supporting); Writing – original draft (supporting). **Xiao Guo**: Writing – original draft (supporting). **Franziska Eller**: Writing – original draft (supporting); Writing – review and editing (equal). **Christina L. Richards**: Writing – original draft (equal); Writing – review and editing (equal). **Hans Brix**: Writing – original draft (equal); Writing – review and editing (equal). **Rui-Ting Ju**: Conceptualization (equal); Funding acquisition (equal); Writing – original draft (equal); Writing – review and editing (equal). **Weihua Guo**: Conceptualization (equal); Funding acquisition (equal); Project administration (equal); Writing – original draft (equal); Writing – review and editing (equal).

Data availability statement

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.9zw3r22mt (Liu et al. 2023).

Supporting information

The Supporting information associated with this article is available with the online version.

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