



Geographic variation of litter chemistry and palatability in an invasive plant versus its native competitor

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Abstract

Aim: Latitudinal variation in biotic interactions is recognized as a driver underlying variation in plant invasion success and therefore an important issue in conservation biogeography. However, previous studies have mainly focused on interactions between living plants and herbivores, whereas litter traits and detritivory have been hardly studied along latitude or compared between native and invasive plants. Our aim was to compare latitudinal variation in leaf litter chemistry and palatability to detritivores between invasive and native plants, and investigate which chemical traits determine detritivory and whether they are climate-driven.

Location: China.

Taxa: *Spartina alterniflora*, *Phragmites australis*, *Porcellio laevis*, *Chiromantes dehaani*.

Methods: We combined field surveys with laboratory experiments to compare latitudinal variation in litter chemistry between the widespread invasive *Spartina alterniflora* and its native competitor *Phragmites australis* across their co-occurring range (20.9–40.7° N, ~2200 km). For both species, we examined litter palatability to two common detritivores (*Porcellio laevis* and *Chiromantes dehaani*) along the same latitude. We also analysed relationships among climate, litter traits and detritivory.

Results: In five of nine litter traits, we found latitudinal clines, with little difference between the two plant species in how they responded across the gradient. Litter palatability decreased with increasing latitude, but was generally higher in *Spartina* than *Phragmites*. Two key litter traits (C:P ratio and flavonoid content) were significantly associated with temperature of origin and with detritivory.

Main Conclusions: There were geographic clines in litter traits and palatability, with strong links between climate, litter chemistry and detritivory, in both *Spartina* and

Phragmites. *Spartina* litter, however, was more rapidly decomposed by detritivores, which could create positive feedbacks, and contributes to the successful *Spartina* invasion along China's coast. Future ecological restoration projects should therefore dispose *Spartina* plant tissue or litter off-site, to reduce the competitiveness of *Spartina* and support the conservation of native *Phragmites*.

KEYWORDS

biogeography, biological invasion, biotic interactions, detritivory, litter decomposition, litter palatability, *Phragmites australis*, *Spartina alterniflora*

1 | INTRODUCTION

One well-supported biogeographical paradigm is that species diversity declines from low to high latitudes (Hillebrand, 2004). This paradigm helps explain the stronger biotic interactions that sometimes exist at lower latitudes, and variation in species traits along latitudinal gradients (Ollerton & Cranmer, 2002; Schemske et al., 2009). A specific biogeographic hypothesis related to biotic interactions is the latitudinal herbivory defence hypothesis (LHDH), which postulates that plants from low latitudes are under higher herbivory pressure than those from high latitudes (Cronin et al., 2015; Pennings et al., 2001; Schemske et al., 2009), leading to a greater investment in defence and lower palatability of plants at lower latitudes (Pennings et al., 2009). Accordingly, bioassays under controlled conditions have found that herbivores prefer plant tissues from high over low latitudes (Pennings et al., 2007; Siska et al., 2002). In addition to herbivory, abiotic environmental factors such as temperature, precipitation and solar radiation can also contribute to latitudinal variation in plant traits, and this variation can affect plant interactions with other trophic groups along latitudinal gradients (Abdala-Roberts et al., 2016; Moles et al., 2011; Moreira et al., 2018). Such abiotic constraints are subject of the resource availability hypothesis (RAH), which states that poorer resource availability at high versus low latitudes should lead to higher plant growth cost, so plants will increase their defences or decrease palatability to reduce tissue loss by herbivores at high latitudes (Hahn & Maron, 2016). Hence, the interaction between biotic and abiotic pressures impinges on predictions of plant palatability.

Plants interact with other organisms not only through their living tissues but also through their litter. Not surprisingly, the traits of leaf litter are strongly influenced by those of the living leaves that produce the litter. For instance, low-quality leaves generally produce low-quality litter (Pennings et al., 2007). Latitudinal variation in the traits of living leaves can therefore create similar geographical variation in the traits of leaf litter, which will influence biotic interactions with litter detritivores at different latitudes (Quadros et al., 2014). Like microbial decomposers, macro- and mega-detritivores (e.g. earthworms, arthropods and molluscs) greatly affect decomposition in ecosystems (Marks, 2019; McCary & Schmitz, 2021). These animals shred and feed on litter, assimilate part of the ingested material and excrete the largest part as organic fragments which are then

further decomposed by microbiota (Gessner et al., 2010). Litter detritivory is geographically ubiquitous, but its intensity can vary locally, depending on climate, litter type and detritivore taxa (Quadros et al., 2014). So far, however, biogeographic studies of litter detritivory have been scarce (but see Boyero et al., 2017, 2021 for aquatic detritivory in streams). A recent global analysis summarized biotic interactions along latitudinal gradients based on 119 publications, but the vast majority of these were concerned with herbivory, carnivory and parasitism (Zvereva & Kozlov, 2021).

Besides their general importance for ecosystem processes, litter traits may play a key role in the ecosystem impacts of many invasive plants. Several previous studies found higher litter decomposability for invasive than native plants (Quadros et al., 2014; Zhang et al., 2021; Zhang, Li, et al., 2019), but whether this is related to litter palatability to detritivores has not yet been tested. If both detritivory and decomposability are governed by litter traits, it should be possible to predict decomposition and its feedbacks to invasion by comparing the litter traits of invasive versus native plants (Zhang, Li, et al., 2019). Although previous studies have already used litter traits to predict decomposability (Cornwell et al., 2008; Pérez-Harguindeguy et al., 2000; Zhang et al., 2021), the links between litter traits and litter palatability to detritivores are so far poorly understood.

Latitudinal clines in leaf traits that determine detritivory or herbivory may differ between invasive and native plants. For example, recent common-garden experiments have found that latitudinal clines in leaf palatability to herbivores and related traits are not parallel between co-occurring invasive and native genotypes of *Phragmites australis*, possibly because of insufficient time for the coevolution between local herbivores and invasive genotypes (Bhattacharai et al., 2017). If this is true for native versus invasive genotypes, it should also apply to native versus invasive species. Given the relationship between living leaves and their litter, we also expect that latitudinal clines in litter palatability to detritivores, and their related litter traits, should differ between invasive and native plants. These differences may result in geographical variation in detritivory between plant species and ultimately affect the decomposition and growth of invasive versus native plants, which can have implications for the management of invasive plants.

Here, we report a large-scale study of latitudinal variation in litter traits and litter palatability to detritivores of an invasive plant

species (i.e., *Spartina alterniflora*, hereafter *Spartina*) versus a native plant species (i.e., *P. australis*, hereafter *Phragmites*). Both species have been used as model organisms for studying plant invasions (Ainouche et al., 2009; Guo et al., 2013; Kettenring et al., 2012; Liu, Chen, Strong, et al., 2020; Liu, Zhang, Chen, et al., 2020). *Spartina* is native to the Atlantic coast of the Americas and has become widely invasive along the coast of China following its introduction in 1979 (Meng et al., 2020). *Phragmites* is a native species of China and is equally widely distributed along the Chinese coast (Zhang, Pennings, et al., 2019). The two species are dominant in the coastal saltmarshes of China, with very similar latitudinal ranges from approximately 20°N and 40°N. However, *Phragmites* is rapidly being displaced by *Spartina* (Meng et al., 2020). Zhang et al. (2021) found that litter decomposition was faster for *Spartina* than for *Phragmites*, but they did not examine detritivory. In this study, we collected leaf litter of *Spartina* and *Phragmites* from saltmarshes across their 20° distribution ranges on the coast of China, and we measured litter traits related to detritivory. Furthermore, we tested the litter palatability of both species to two detritivores that are common in our collection sites: a macro-detritivore (the isopod *Porcellio laevis*) and an omnivore (the crab *Chiromantes dehaani*). We considered *C. dehaani* to be a mega-detritivore, although it also feeds on living leaves (Pennings et al., 2007). We used these data to analyse relationships between climate, litter traits and litter detritivory. Based on previous studies (Bhattarai et al., 2017; Zhang et al., 2021; Zhang, Pennings, et al., 2019), we hypothesized that: (1) latitudinal clines in litter traits and palatability to detritivores differ between *Spartina* and *Phragmites*; (2) across a broad latitudinal range in China, *Spartina* litter is generally more palatable than *Phragmites* litter to both detritivores (because of faster litter decomposition by microorganisms for *Spartina* than for *Phragmites*, Zhang et al., 2021). Combined with previous findings (Zhang et al., 2021; Zhang, Pennings, et al., 2019), support for this hypothesis would suggest that litter decomposition is faster in *Spartina* habitats than in *Phragmites* habitats, and this could generate positive feedbacks to *Spartina* invasion across coastal habitats; (3) some litter traits like nutrients and secondary metabolites are strong determinants of litter palatability to detritivores; and (4) latitudinal variation in litter traits are closely related to climatic factors.

2 | MATERIALS AND METHODS

2.1 | Study species

To compare latitudinal patterns in leaf litter traits and consumption by detritivores, we focused on the invasive *Spartina* and the native *Phragmites* for the following reasons: (1) Both species are widespread (Figure S1), well studied in many ecological contexts and serve as models for the study of saltmarsh ecology and plant invasions (Ainouche et al., 2009; Cesarino et al., 2020; Eller et al., 2017; Ju et al., 2019; Li et al., 2009; Meyerson et al., 2016); (2) the distributions of both species overlap along latitudinal gradients in China (Figure S1; Zhang, Pennings, et al., 2019; Zhang et al., 2021), and the species compete when they co-occur (Ju et al., 2017; Li et al., 2009);

and (3) both species are members of the Poaceae and share several herbivores and detritivores (Chen, 2000; Qin et al., 2010; Sun et al., 2020; Xu et al., 2022), which provides a good framework for comparison of plant-animal interactions between invasive and native plants (Sun et al., 2020). We selected the isopod *Porcellio laevis* and the crab *Chiromantes dehaani* as relevant detritivores in this system. In saltmarshes, *P. laevis* is a typical macro-detritivore, while *C. dehaani* is an omnivore (and mega-detritivore) that consumes both living and dead plant tissues (Pennings et al., 2007). The two animal species occur in all of the coastal wetlands in China, including *Spartina*- and *Phragmites*-dominated saltmarshes (Chen, 2000; Chu et al., 2014). Both detritivores consume *Spartina* and *Phragmites* litter by physical shredding and chemical digestion. In addition, the excrements of both detritivores are rich in microbes that can further accelerate litter decomposition (Zimmer et al., 2004). Thus, *P. laevis* and *C. dehaani* play an important role in decomposition and nutrient cycling in saltmarsh ecosystems. More detailed background information on the two plant species and two detritivores used in our study is provided in Appendix S1.

2.2 | Litter collection and litter traits

We collected leaf litter of *Spartina* and *Phragmites* from 12 sites between 20.89°N and 40.68°N (~2200 km) along the eastern coast of China between November 2015 and February 2016. Half of the sites have only *Phragmites* or *Spartina*; hence, we had nine collection sites for each plant species (Figure 1; Table S1). At each site, we randomly selected five subsites (i.e., latitudinal replicates, separated by ~1 km) and marked a 5 m × 5 m plot at each subsite. In each plot, we selected five 1 m × 1 m quadrats and collected all dead leaves (i.e., leaf litter) from stands of *Phragmites* and/or *Spartina*. These leaves were completely senescent but were still attached to the plant. Within each subsite, we pooled the leaves of different quadrats for each plant species. All leaves were oven-dried and ground to powder for subsequent trials (see Appendix S2 for more methodological details).

To assess litter traits for the different species and collection sites, we measured a range of nutrient contents/ratios and secondary compounds: the total carbohydrate and protein contents of each sample, as well as the ratios of C:N, C:P and N:P, and the concentrations of alkaloids, terpenoids, saponins and flavonoids. All of these traits have been found to strongly correlate with the performances of herbivores (Ju et al., 2019; Sun et al., 2020), and we therefore expected them to also affect litter palatability to detritivores. For each plant species and collection site, there were five replicate samples from the five subsites. For more details on the chemical analyses, see Appendix S3.

2.3 | No-choice feeding trials

As a first assessment of litter palatability, we conducted no-choice feeding trials with *P. laevis*. We purchased commercial *P. laevis* individuals from Chunzhe Company (Anhui, China), initially reared

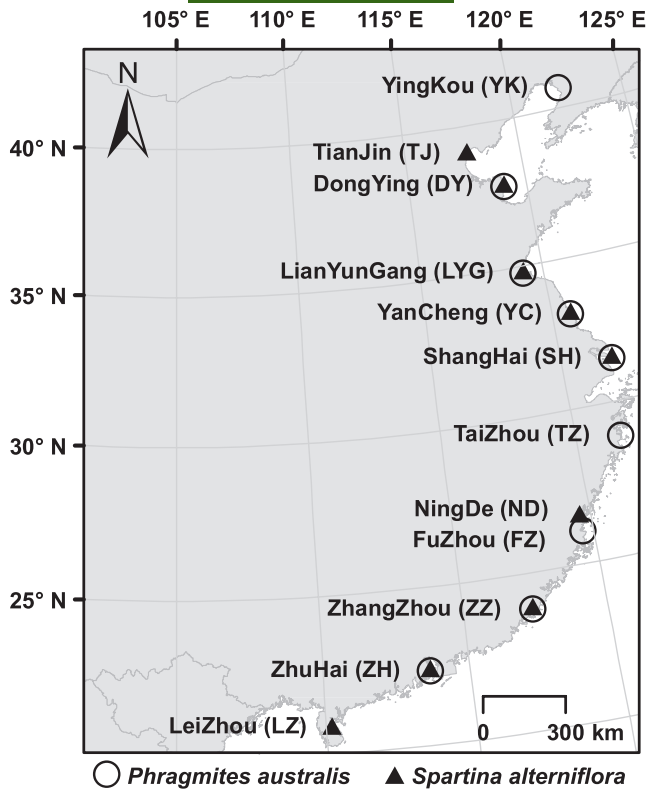


FIGURE 1 Collection sites for leaf litter of *Phragmites australis* and *Spartina alterniflora* on the eastern coast of China's mainland. The map projection used: Lambert.

them in the laboratory at 25°C with a relative humidity (RH) of 60% and a 12h:12h (L:D) photoperiod and selected adults for trials (see Appendix S4). As in Pennings et al. (2007), we conducted the feeding trials with artificial diets based on agar, water and litter powders, with a weight ratio of agar:water:dry litter = 1:25:5 (see Appendix S4). For each individual trial, we first weighed a sample (~1.5 g) of each diet and determined its dry mass, placed the diet in a 9 cm Petri dish and added five *P. laevis* individuals that had been starved for 24 h. We closed the dish and maintained it under the same conditions as for *P. laevis* rearing. After 72 h, we weighed the remaining diet (dry mass) to obtain the quantity of diet consumed by the isopod (Pennings et al., 2007). We analysed only Petri dishes in which all five *P. laevis* individuals survived and in which the diets were not completely consumed. For each plant species and geographic collection site, we had five replicates, each based on the litter collected from a different subsite. For each subsite, we tested 10 Petri dishes (i.e. total $2 \times 9 \times 5 \times 10 = 900$ individual trials) and calculated the average dry mass of diet consumed across the 10 replicates.

For the second round of no-choice feeding trials, we collected *Chiromantes dehaani* individuals from the Shanghai Chongming Dongtan wetlands in China (31.65°N, 121.73°E). We reared them in the laboratory at 25°C with a 12h:12h (L:D) photoperiod, and selected vigorous males for trials. We conducted the crab feeding trials using a horizontal template, that is, a 10 cm \times 10 cm \times 3 mm plate with ~700 wells (1.5-mm-diameter) filled with 6–7 g of fresh diet (the dry mass was calculated) of leaf litter of *Spartina* or *Phragmites* (see Appendix S4) in a plastic

box (19 cm \times 12.5 cm \times 7.5 cm). We maintained each individual box under the same crab-rearing conditions. After a 24-h starvation treatment, we placed one crab in a box, and removed it again after 72 h of feeding. We considered a trial valid if the diet within the box was not completely consumed, and if the crab survived. We quantified the amount of diet consumed (dry mass) by the fraction of wells in a template that still contained diet, that is, had not been consumed by the crab (Pennings et al., 2007). As for the feeding trials with the isopods, we conducted trials for each species and collection site, except that there were only five replicates per subsite (i.e. total $2 \times 9 \times 5 \times 5 = 450$ individual trials), from which we then calculated the average consumption per subsite. After all feeding trials finished, we returned all the surviving crabs to the collection sites.

2.4 | Paired-choice feeding trials

To determine whether the differences in diet consumption observed in the no-choice trials with *Spartina* versus *Phragmites* litter were due to feeding preferences of the detritivores, we conducted additional paired-choice feeding trials with each detritivore species. For the paired-choice trials with *P. laevis*, we used a similar approach as in the no-choice trials, except that each Petri dish contained two diets (1.5–2 g each, determining its dry mass), that is, one made with *Spartina* litter and one made with *Phragmites* litter. We placed the two types of litter diets on each side of the Petri dish. At the same time, we recorded the information of plant species and collection site of the litter diet at the bottom of the Petri dish to avoid confusion. Based on our observations, we did not observe any mixing of the two types of litter diet during the experiment. For each trial, we used the litter from the same latitude or the closest latitudes. After the trial, we dried and reweighed the remaining diets to calculate the dry mass consumed by the five *P. laevis* individuals per dish. We conducted this trial for 10 latitudinal sites, with 7–10 paired-choice Petri dishes for each site.

The paired-choice feeding trials with *C. dehaani* were also similar to their no-choice feeding trials, except that half of the template wells in each template were filled with the *Spartina* litter diet, and the other half with the *Phragmites* litter diet. Again, we used the litter from the same latitude or the closest latitudes for the paired-choice trials. Since the colour of both diet types was indistinguishable, we did not randomly distribute the two diet types among the wells in each template, but kept all *Spartina* litter on one side and all *Phragmites* litter on the other side, so that the amounts consumed could be easily determined at the end of the trial. We quantified the dry mass of each type of diet before and after the trial to obtain the dry masses of diets consumed by a crab in each template. We conducted this trial for 10 latitudinal sites, with each represented by 8–10 templates.

2.5 | Data analyses

All analyses were performed with R version 3.6.2 (R Core Team, 2019). To determine whether litter traits and litter consumption of the no-choice trials differed between plant species and among latitudes, we

TABLE 1 AICc best models ($\Delta_i < 2$) for the effects of latitude (L), plant species (S) and their interaction (L×S) on leaf litter traits and the quantity of litter consumed by detritivores.

Dependent variable	Model	AIC _c	Δ_i	w_i	R ²
Litter traits					
C: N	L	71.34	0.00	1.00	0.19
C: P	L+S	108.74	0.00	0.65	0.57
	S	110.01	1.26	0.35	0.52
N: P	L+S+L×S	116.26	1.18	0.64	0.63
	L+S	117.44	0.00	0.35	0.58
Carbohydrates	L+S+L×S	-53.27	0.00	1.00	0.30
Proteins	S	98.17	0.00	1.00	0.60
Alkaloids	S	207.75	0.00	1.00	0.00
Flavonoids	L+S	7.75	0.00	1.00	0.36
Terpenoids	S	74.04	0.00	1.00	0.37
Saponins	S	-629.87	0.00	1.00	0.10
Litter consumption					
<i>Porcellio laevis</i>	L+S	23.88	0.00	1.00	0.78
<i>Chiromantes dehaani</i>	L+S	32.20	0.00	1.00	0.49

used the *lme4* package for linear mixed models (LMMs) to analyse the data from the litter trait measurements and the no-choice feeding trials. Each model included plant species (*Phragmites* versus *Spartina*), latitude and their interaction as fixed effects, and collection subsite nested within latitude as a random effect (Bates et al., 2015). To normalize the distribution of residuals, we ln-transformed all dependent variables except for saponins. For each response variable, we used the Akaike's information criterion corrected (AIC_c) for finite sample size to select the most parsimonious model (see Appendix S5). If the plant species was included in this model, this indicated differences between the two species. Likewise, if the selected model included latitude, this indicated that the response variable varied by latitude. Finally, if the best model included a plant species × latitude interaction, this indicated species differences in their relationship with latitude (Bhattarai et al., 2017). The significance of fixed effects in the most parsimonious model was assessed by Type II Wald chi-squared test using the CAR package (Fox & Weisberg, 2019). If latitude was part of the best model, we further examined latitudinal gradients through linear regression testing the relationship between the response variable and latitude, separately for each species.

We used the data from the paired-choice trials to test feeding preferences of detritivores, comparing the consumption of the two diets (*Spartina* litter vs. *Phragmites* litter) across the 10 sites with a paired Wilcoxon test (as the data were not normally distributed).

To understand the direct and indirect relationships between climate (data from <http://cdc.nmic.cn/>), litter traits and litter palatability to the detritivores, we conducted path analyses that connected the climatic conditions at the collection sites with litter traits and the diet consumption by each detritivore. To simplify explanatory variables, we used linear and stepwise regressions to identify the key litter traits that affected diet consumption. For the full stepwise model, we used only litter traits that had significant relationships with consumption in simple univariate linear regressions (see Appendix S6). We identified four traits as significant predictors of consumption

and used the stepwise backward model to select the best model with the smallest AIC value using multiple regression in the *stat* package (Burnham & Anderson, 2002). We found that C:P ratio and flavonoid content were the strongest drivers of diet consumption by both detritivores (see Appendix S6; Table 2). In addition, we considered both temperature variables and solar radiation as potential drivers, mainly because these factors are known to affect the studied plant traits (Abdala-Roberts et al., 2016; Moreira et al., 2018). We did not consider precipitation because previous work demonstrated that it hardly affects the studied plant traits in saltmarshes due to the regular tides (Liu, Xu, Zhou, et al., 2020). We extracted multiple temperature and radiation variables (see Appendix S6) for our collection sites in 2015 from the Sharing Service System of Climate Information for China (<http://data.cma.cn>). To simplify the variables, we conducted separate principal component analyses for temperature and radiation variables and found that the temperature PC1 had a latitudinal gradient but the radiation PC1 had a humped-curve latitudinal pattern. We therefore excluded radiation from our subsequent analyses and only included the effects of temperature on litter traits. In summary, we included the temperature PC1, the two key litter traits and the diet consumptions by two detritivores in the path analyses (Moreira et al., 2018). We carried out separate analyses for each plant species.

3 | RESULTS

3.1 | Litter traits

The AICc best models based on LMMs analyses showed that for five of the nine litter traits (C:N, C:P, N:P, carbohydrates and flavonoids), latitude was included in the most parsimonious model, indicating relationships with latitude. In seven of the nine traits (C:P, N:P, carbohydrates, proteins, flavonoids, terpenoids and saponins), the

model included species, indicating significant differences between the two plant species (Table 1; Figure 2). Only for two traits (N:P, total carbohydrates), did the best model include a latitude \times plant species interaction (Table 1; see Appendix S5 for the full statistical results). In both plant species, C:P, N:P and the flavonoid content of litter increased with latitude. In addition, the carbohydrate content increased and the C:N ratio of litter decreased with latitude only in *Phragmites* (Figure 2). Across all latitudes, C:P, N:P and the contents of flavonoids, terpenoids and saponins were significantly lower in *Spartina* litter than in *Phragmites* litter, whereas the opposite was true for the contents of carbohydrates and proteins (Figure 2).

3.2 | Consumption of litter diets by detritivores

In the no-choice feeding trials, the best AIC_c models included both plant species and latitude, indicating that the quantity of litter diet consumed by both *P. laevis* and *C. dehaani* was significantly associated with collection latitude and differed between the two plant

species (Table 1; Figure 3). In both plant species, the quantity of diet consumed by each detritivore significantly decreased with increasing latitude (Figure 3). The most parsimonious models did not include a species \times latitude interaction, that is, the pattern of consumption of litter diet from each of the two plant species across latitude tended to be similar. Overall, both detritivores consumed significantly more *Spartina* than *Phragmites* litter (+60% for *C. dehaani*, $p < 0.001$, Figure 3c, and +110% for *P. laevis*, $p < 0.001$, Figure 3a). In the paired-choice feeding trials, *P. laevis* consumed significantly more *Spartina* than *Phragmites* litter diet in seven out of the 10 comparisons of specific litter collection sites (Figure 3b), and for *C. dehaani*, this was true for nine out of 10 comparisons (Figure 3d).

3.3 | Relationships among climate, litter traits and the quantity of litter diet consumption

The stepwise multiple regression models indicated that the C:P ratio and flavonoid content were the two litter traits most strongly associated

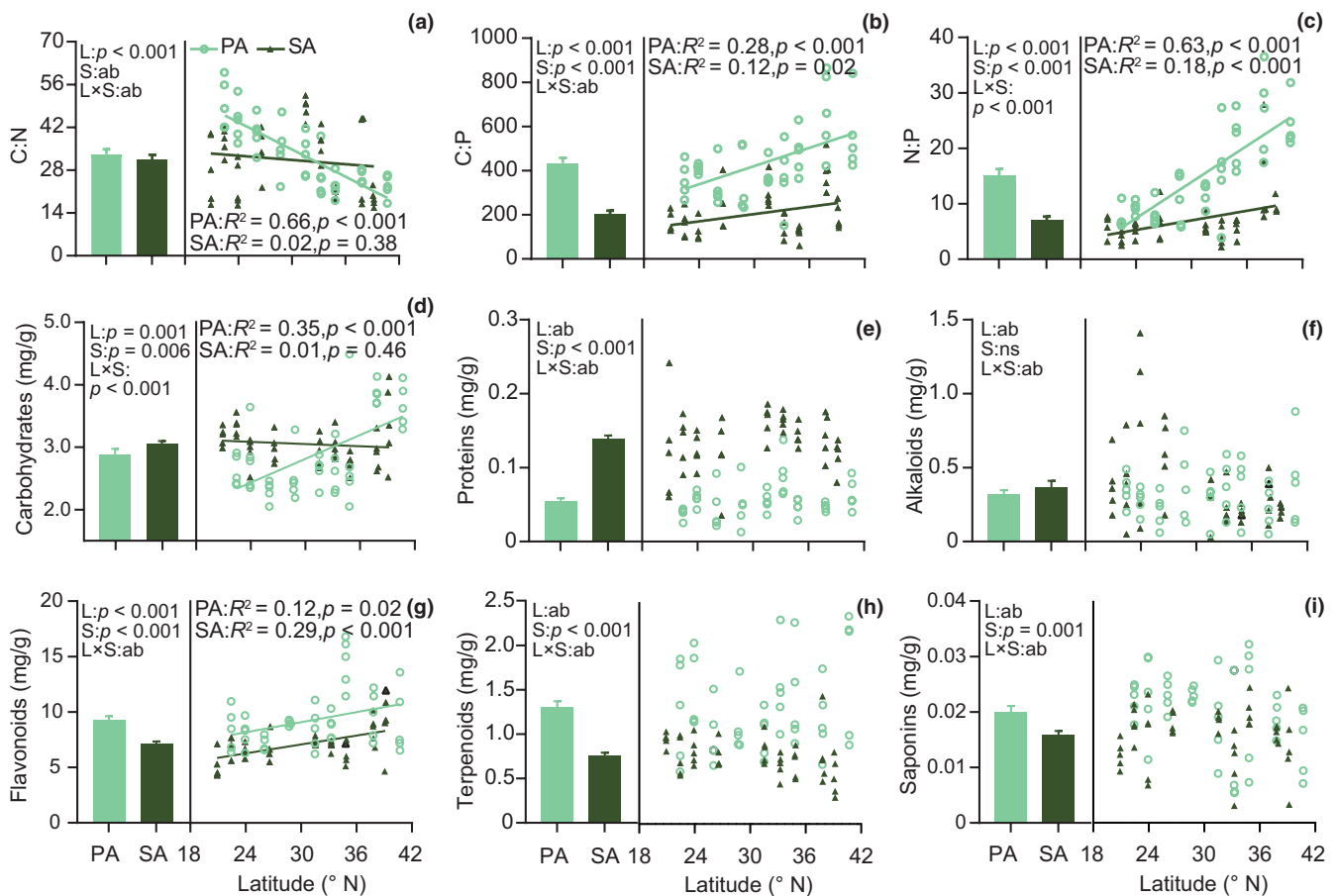


FIGURE 2 Leaf litter traits of *Phragmites australis* (PA) and *Spartina alterniflora* (SA) as affected by plant species and collection latitude. In each panel, the p -values were reported for the effects of latitude (L), plant species (S) and their interactions (L \times S) as tested in the most parsimonious models determined by AIC_c; ab=absent (i.e. this factor is absent in the best model); ns=not significant (i.e. the effect of a factor is not significant in the best model); $p < 0.05$ indicates a significant effect. The left side of each panel shows the means (± 1 SE) of litter traits for the two plant species across all collection sites. The right side of each panel shows the relationships between litter traits and collection latitude, separately for each species. In the cases of significant latitude effects, we plotted the regression lines for each plant species and reported their associated R^2 - and p -values.

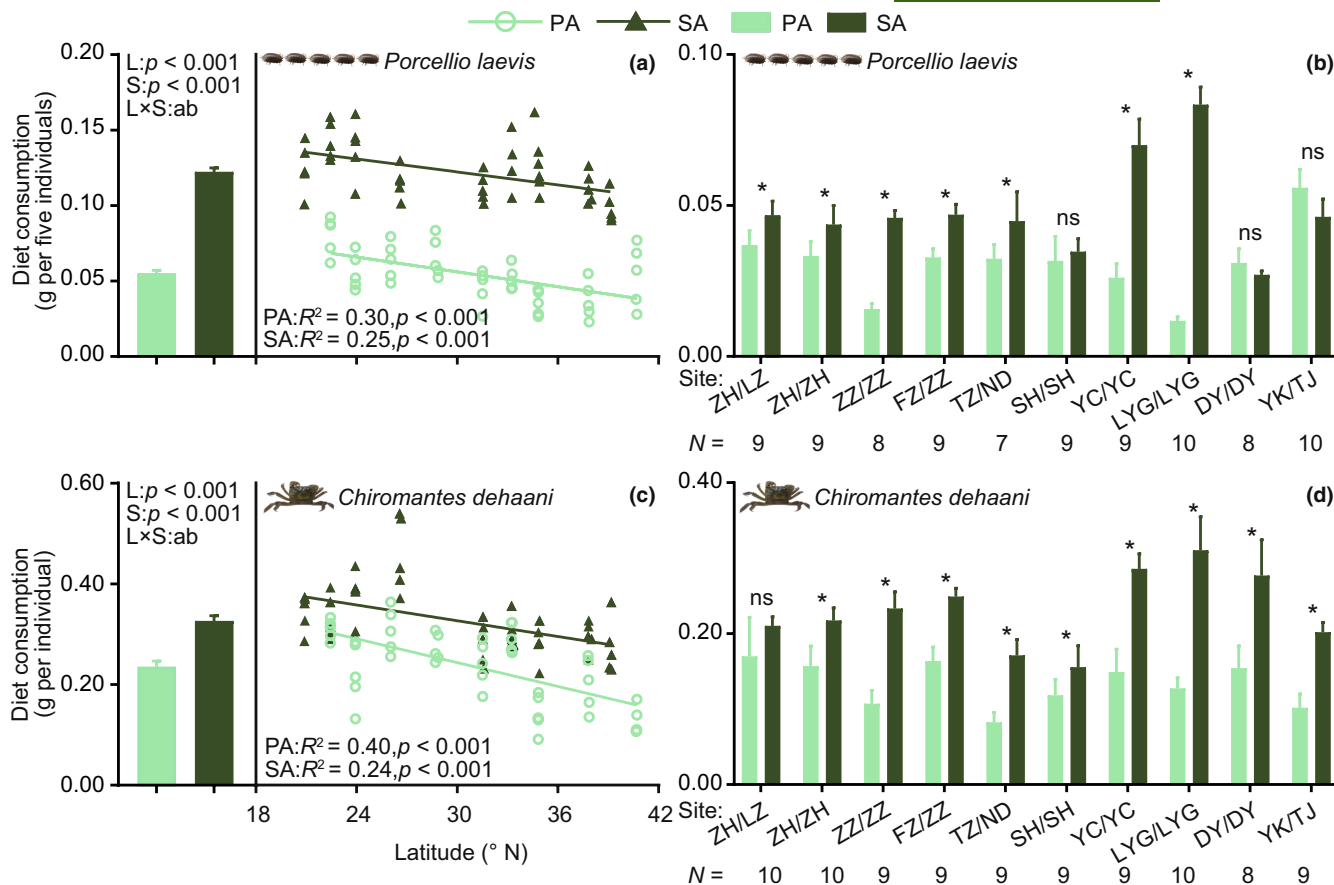


FIGURE 3 Consumption of the artificial diets made with the leaf litter of *Phragmites australis* (PA) and *Spartina alterniflora* (SA) by the isopod *Porcellio laevis* and the crab *Chiromantes dehaani* across different latitudes of origin in the no-choice feeding trials (a,c) and in the paired-choice feeding trials (b,d). In panels a and c, the *p*-values were reported for the effects of latitude (L), plant species (S) and their interactions (L×S) as tested in the most parsimonious models selected through AICc; ab=absent (i.e. this factor is absent in the best model); *p* < 0.05 indicates a significant effect. The left side of each panel shows the mean (±1SE) quantity of consumed diet for the two plant species across all collection sites. The right side of each panel shows relationships between the litter collection latitude and litter consumption. In the case of significant latitude effects, we plotted the regression lines for each plant species, and reported their associated *R*²- and *p*-values. In panels b and d, the bars display the mean (±1SE) quantity of consumed diet for each plant species in one paired feeding trial, with the codes of litter collection sites below the bars. The sites are ordered from the lowest to the highest latitude. ‘*’ and ‘ns’ indicate significant and not significant differences at *p* < 0.05.

with the quantity of litter diet consumed by both detritivores (Table 2). The subsequent path analyses showed that the first principal component related to temperature (PC1) was significantly associated with the C:P ratio and flavonoid content in both plant species (see Appendix S6; Figure 4). Both C:P ratio and flavonoid content increased with the decreasing temperatures at higher latitudes, and the two litter traits, in turn, were negatively associated with litter detritivory (although the correlation between flavonoid content and the consumption of *Spartina* litter by *C. dehaani* was not significant). Altogether, the path analyses suggested a causal sequence from climate to litter quality/palatability, and to litter consumption by the two detritivores.

4 | DISCUSSION

Several studies have demonstrated that latitudinal variation in biotic interactions is a driver of plant invasion success, but this work

has mainly focused on interactions between living plants and herbivores. In our study, we assessed variation in leaf litter traits considering that characteristics of living leaves can also be reflected in their litter, and affect palatability to detritivores and decomposition (Kurokawa et al., 2010). Although we found a cline of increasing palatability with decreasing latitude, we did not find support for our prediction that latitudinal clines in litter traits and palatability to detritivores would differ between invasive *Spartina* and native *Phragmites* that co-occur. Instead, we found evidence supporting that *Spartina* litter is generally more palatable than *Phragmites* litter to two detritivores. In addition, we found associations between two litter traits (C:P ratio and flavonoid content) with litter palatability to detritivores, and that these traits were associated with variation in temperature.

The latitudinal herbivory defence hypothesis (LHDH) provides a context for interpreting the patterns we discovered for each trait. The LHDH posits that stronger biotic interactions at low

Detritivores	Models	AIC	Δ AIC	R^2	p	N
<i>P. laevis</i>	(-) C:P***, (-) flavonoids***, (-) terpenoids, (-) saponins	-78.13	0.00	0.62	<0.001	90
	(-) C:P***, (-) flavonoids***, (-) terpenoids	-78.00	0.13	0.61	<0.001	90
	(-) C:P***, (-) flavonoids***	-76.51	1.62	0.60	<0.001	90
<i>C. dehaani</i>	(-) C:P***, (-) flavonoids**, (-) terpenoids	-45.97	0.00	0.45	<0.001	90
	(-) C:P***, (-) flavonoids**	-44.83	1.14	0.43	<0.001	90
	(-) C:P***	-39.07	6.90	0.38	<0.001	90

Note: In the second column, ‘*’, ‘**’ and ‘***’ indicate that the explanatory variables are significant at $p < 0.05$, $p < 0.01$, and $p < 0.001$, respectively, in the whole models, and ‘+’ and ‘-’ in the parentheses indicate positive and negative associations with litter consumption respectively.

TABLE 2 Best multiple regression models for the effects of leaf litter traits (regardless of plant species) on the quantity of litter-based diet consumed by *Porcellio laevis* and *Chiromantes dehaani*.

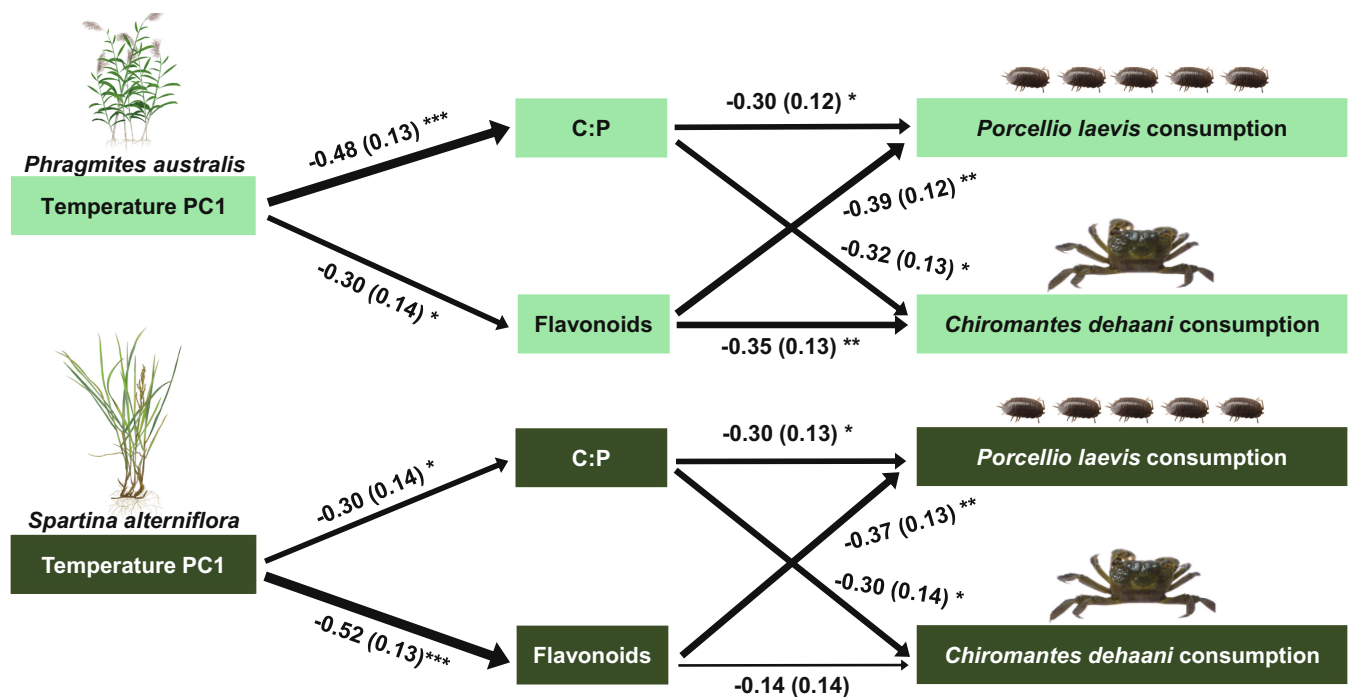


FIGURE 4 Path diagrams showing the relationships between the climate at latitudes of collection (temperature PC1) and the litter traits of *Phragmites australis* and *Spartina alterniflora*, as well as the relationships between litter traits and the quantity of litter-based artificial diet consumed by *Porcellio laevis* and *Chiromantes dehaani*. The values next to each arrow are path coefficients (i.e. standardized regression coefficients), with their standard errors. The thickness of arrows corresponds to the magnitudes of their path coefficients. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

compared to high latitudes can induce foliar traits that reduce palatability which would be indicated by high ratios of C:N or C:P, low levels of nutrients and high rate of synthesis of secondary metabolites (Anstett et al., 2016). Our results provided mixed evidence for the LHDH. We found that C:N decreased and the content of carbohydrates increased with increasing latitude in *Phragmites* litter (Figure 2a,d), indicating better quality of *Phragmites* at higher latitudes that is consistent with the LHDH. However, we found that C:P and the content of flavonoids indicate better palatability of *Spartina* and *Phragmites* at lower latitudes (Figure 2b,g), which is inconsistent with the LHDH. In addition, P may be a more critical limiting nutrient than N for detritivores (Danger et al., 2013;

Kurokawa et al., 2010), we found lower N:P ratio at low compared to high latitudes (Figure 2c), suggesting that litter quality is higher at low latitudes for both plant species, which is also inconsistent with the LHDH.

Our results indicate that the difference in the litter-diet consumption between plant species was caused by the feeding preference of the detritivores for *Spartina* litter (Figure 3b,d). This finding is consistent with our observation of higher palatability of *Spartina* compared to *Phragmites* in the no-choice trials. One caveat is that we ground leaf litter into powder in the feeding trials, which eliminated the differences in some physical traits (e.g., litter toughness), and might also result in the volatilization or degradation of secondary

metabolites (Siska et al., 2002). We must therefore be conservative in interpreting the results and recognize that the difference in the palatability of *Spartina* and *Phragmites* litter for detritivores may be more complex in nature than in our laboratory.

We found that C:P ratio and the flavonoid content of litter were strongly associated with litter consumption, suggesting that these may be pivotal traits determining litter palatability to both detritivores (Table 2). The low C:P ratio and the low content of flavonoids in litter (reflecting high litter quality) from low compared to high latitudes and in *Spartina* compared to *Phragmites* (Figure 2b,g), therefore, appeared to contribute to the latitudinal variation and the interspecific difference in litter palatability to both detritivores (Figure 4). Such differences can generate latitudinal heterogeneity in litter detritivory of *Spartina* and *Phragmites* (see discussion later). In a previous common-garden investigation, Zhang et al. (2021) found that the rates of litter decomposition by microbes and microfauna increased with increasing latitude for both *Spartina* and *Phragmites*, which was mainly mediated by the contents of C, tannin, total phenols and trace elements. These previous results and those of the current study suggest that the change in litter decomposition along a latitudinal gradient mediated by micro-decomposers differs or is even opposite from that mediated by macro- and mega-detritivores, and that the two types of litter decomposition are also driven by different litter traits.

One explanation for the increases in C:P ratio and flavonoid content in litter with increasing latitude is that both traits are driven by climate independent of the herbivory on living leaves (Abdala-Roberts et al., 2016). According to the resource availability hypothesis (RAH), plants at high latitudes grow slowly, and the construction cost of tissue is high due to the limitations imposed by climate (e.g., low temperature, less photosynthetically active radiation and low precipitation). As a consequence, plants at high latitudes have traits that provide high resistance to abiotic or biotic pressures (Coley et al., 1985). In our study, we found that among climate characteristics, temperature was most closely associated with C:P ratio and the content of flavonoids in leaf litter (see Appendix S6). In addition, both C:P ratio and the flavonoid content increased as temperature decreased with increasing latitude (Figure 4). Because high C:P ratio indicates high construction costs but a low palatability of plant tissue (Abdala-Roberts et al., 2016), and because the increased flavonoid content in plant tissue can contribute to resistance of both abiotic and biotic pressures (Harborne & Williams, 2000), our results are consistent with the RAH. Perhaps the low palatability of *Spartina* and *Phragmites* litter produced at high latitudes is simply an indirect result of plants coping with low temperature, which results in litter traits that also affect palatability. Determining whether this possibility is correct will require additional research.

In contrast to the previous findings of dissimilarity in latitudinal patterns in leaf traits related to herbivory between native and invasive lineages of *Phragmites* (Bhattarai et al., 2017), we found that all litter traits except N:P and carbohydrates behaved similarly between invasive *Spartina* and native *Phragmites* across latitude (i.e. no significant plant species \times latitude interaction, Table 1). Similarly, Zhang et al. (2021) found that the litter decomposition caused by

microdecomposers and several related traits (e.g. total phenols and hemicelluloses) were comparable in *Spartina* and *Phragmites* across a latitudinal gradient along China's coast. So, the overall result that the two species did not differ in their latitudinal patterns of litter traits appears to be robust. Further studies are needed to address additional questions that compare aboveground herbivory and related traits between both plant species.

The parallel latitudinal patterns in most litter traits of *Spartina* and *Phragmites* suggest that both plants have similar responses across the latitudinal gradient. Other studies have found that invasive and native lineages of some exotic plants (e.g., *Hypericum perforatum*, *Microstegium vimineum* and *Ambrosia artemisiifolia*) also have parallel latitudinal gradients in their traits (Li et al., 2015; Novy et al., 2013). Along China's coast, *Spartina* and *Phragmites* are sympatric species that encounter similar geographical variation in environmental conditions (Xu et al., 2020). Under these conditions (e.g., temperatures, as discussed earlier), both *Spartina* and *Phragmites* have been found to generate latitudinal clines (Liu et al., 2016; Liu, Chen, Strong, et al., 2020; Liu, Xu, Liu, et al., 2020; Liu, Zhang, Chen, et al., 2020), which is a possible explanation for the consistent latitudinal patterns in litter traits between both plant species. This type of phenotypic variation in response to environmental gradients has been well established in native populations of *Spartina* along the eastern coast of North America (Pennings & Bertness, 2001; Richards et al., 2005; Zerebecki et al., 2021) and invasive populations along the eastern coast of China (Liu et al., 2016; Liu, Chen, Strong, et al., 2020; Liu, Zhang, Chen, et al., 2020). While some of these responses are due to phenotypic plasticity (Liu et al., 2016), recent studies suggested that at least some of the clinal variation could be the result of genetic differentiation (Qiao et al., 2019; Zerebecki et al., 2021).

Although invasion success in *Spartina* is largely seen to be linked to physical properties of this plant facilitating the silting up and raising levels of saltmarshes (Meng et al., 2020), changes in the rate of nutrient cycling are also an important contributor to promote invasion (Zhang et al., 2021; Zimmer et al., 2004). Litter consumption by detritivores is an important component of nutrient cycling in ecosystems (Coulis et al., 2016). In our study, both detritivores consumed greater quantities of diet made with litter obtained from *Spartina* and *Phragmites* collected from low latitudes than from high latitudes (Figure 3a,c). This result suggests that the litter of both plant species has a greater potential for preliminary decomposition (i.e., the first step of decomposition, which provides food fragments and faeces for other decomposer taxa) at low than at high latitudes (Gessner et al., 2010). The speed by which detritivory contributes to nutrient cycling and plant growth may therefore be greater at low than at high latitudes for both *Spartina* and *Phragmites*. Litter detritivory, however, also depends on the abundance of detritivores and on the effect of climate on their feeding performance in the field (Bradford et al., 2016; Waring, 2012), which were not evaluated in the current investigation, and should be considered in further studies.

In our study, both detritivores consumed more diet made with litter of the invasive *Spartina* than made with litter of the native

Phragmites across latitude (Figure 3). This result indicates that litter detritivory, and consequently the initial rates of decomposition, may be greater in *Spartina* communities than in *Phragmites* communities along the eastern coast of China. Previous studies have demonstrated that plant leaf palatability is positively correlated with litter decomposition rate (Grime et al., 1996), and that the direct positive effect of detritivores on soil nutrient availability can change into benefits for plant growth and soil nutrition (Setälä & Huhta, 1991; Winck et al., 2020). Huang et al. (2016) found that biomass of invasive *Spartina* exhibited a stronger response to increased soil nutrition compared to that of native *Phragmites* in saltmarshes. Therefore, it could be that *Spartina* can benefit more from strong detritivory than *Phragmites*. If so, the invasive community would experience a faster rate of nutrient cycling than the native community in their co-occurring regions. In addition, previous studies have shown that herbivory has more positive effects for *Spartina* than for *Phragmites* on soil nutrient availability and compensatory growth (Xu et al., 2022; Zhou et al., 2017). This could generate more positive feedbacks from both detritivory and herbivory on *Spartina* growth and ultimately facilitates its invasion across coastal habitats.

Our study combined with previous findings provides a new hypothesis for why *Spartina* has successfully invaded Chinese coastal wetlands. We suggest that the invasive *Spartina* has a stronger positive feedback effect mediated by herbivory, decomposition, detritivory than the sympatric native *Phragmites*, which may be a common phenomenon for widespread invaders.

In the context of many other studies that demonstrate how increased nutrient cycling accelerates the invasion success of *Spartina* (Xu et al., 2020; Zhang et al., 2021; Zhang, Pennings, et al., 2019), our results have implications for the management of native saltmarshes. In all Chinese coastal wetlands, *Spartina* is a notorious invasive plant. It outcompetes and replaces native plants due to fast growth, high tolerance to salt and great reproductive capacity (An et al., 2007; Li et al., 2009). Since *Spartina* has become the dominant plant and spread rapidly along the entire coast of China (Hu et al., 2021), it is crucial to include the response of detritivores to leaf litter palatability in saltmarsh management and improve our protection of saltmarsh wetlands. In general, many *Spartina* management projects have harvested the aboveground plant tissues of *Spartina* to reduce their growth and invasion (An et al., 2007). Then, they leave the plant tissues in place or bury them in the soil. However, this allows the plant tissues to continue to be part of the food web and contribute to the nutrient cycle which contributes to the positive feedback effect of litter decomposition on *Spartina* invasion. Hence, management practices that involve leaving unwanted plant debris to decay in the field can have unintended consequences on nutrient cycling (Carson et al., 2018; Holdredge & Bertness, 2011). Our study recommends that *Spartina* plant tissue be disposed of off-site after harvesting, thereby reducing the competitiveness of *Spartina* and the positive feedback effect on *Spartina* invasion. Moreover, to protect the native *Phragmites* saltmarshes, strict measures and valid management methods to prevent and control invasive *Spartina* should be implemented throughout the coast of China.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interests.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in Dryad Digital Repository at <https://doi.org/10.5061/dryad.3xsj3txhz>.

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BIOSKETCHES

Yaolin Guo, Christina L. Richards, Oliver Bossdorf, Bo Li and Rui-Ting Ju are interested in biogeographical patterns and mechanisms underlying plant invasions. **Youzheng Zhang and Jihua Wu** are interested in the interaction between plants and soil organisms.

Authors' contributions: R.T.J., Y.G. and Y.Z. designed and performed the experiments. R.T.J. and Y.G. analysed the data, and drew the figures. All authors contributed to writing the paper.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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