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Phragmites australis meets *Suaeda salsa* on the "red beach": effects of an ecosystem engineer on salt-marsh litter decomposition

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ABSTRACT

Suaeda salsa is a pioneer species in coastal wetlands of East Asia and recently an ecosystem engineer species, *Phragmites australis*, has started to enter into *S. salsa* communities owing to either autogenic or external drivers. The consequences of this phenomenon on the ecosystem functions of coastal wetlands are still unclear, especially for decomposition processes. Here we compared the decomposition rate of *S. salsa* litter, and associated litter chemistry dynamics, between sites with and without *P. australis* encroachment. We conducted a litter transplantation experiment to tease apart the effects of litter quality and decomposing environment or decomposer community composition. Our results showed that *P. australis* encroachment led to higher carbon and phosphorus losses of *S. salsa* litter, but equal losses of total mass, lignin, hemicellulose and nitrogen. *Phragmites australis* encroachment might affect decomposition rate indirectly by making *S. salsa* produce litter with higher lignin concentrations or via increasing the fungal diversity for decomposition. Moreover, *P. australis* as an ecosystem engineer might also alter the allocation of total phosphorus between the plants and the soils in coastal

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wetlands. Our findings indicate that *P. australis* could impact aboveground and belowground carbon and nutrient dynamics in coastal wetlands, and highlight the important consequences that encroaching plant species, especially ecosystem engineers, can have on ecosystem functions and services of coastal wetlands, not only in East Asia but probably also elsewhere in the world.

Keywords: aboveground and belowground processes, carbon and nutrient cycling, ecosystem engineer, litter decomposition, plant encroachment, salt marsh

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Highlights

•*Phragmites australis* encroachment *affected the soil properties of salt marshes.*

• *Phragmites australis* encroachment *affected the litter qualities of Suaeda salsa.*

•*Decomposition of S. salsa litter was affected by P. australis encroachment.*

• Salt-marsh ecosystem functions and services could be altered by such an encroachment.

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1. Introduction

Encroachments of new species into ecosystems, which lead to dramatic changes in vegetation composition, might have significant consequences for ecosystem functions (Hibbard et al., 2001; Archer et al., 2017; Nolte et al., 2019). In particular, new species encroachments might affect the quality and quantity of primary and secondary production, decomposition and nutrient cycling, and the pools and flows of materials (Eldridge et al., 2011; Friedrich et al., 2011; Zhou et al., 2018). They might also affect the nutrient resources within biogeochemical cycles, or affect the trophic resources within food webs and on physical resource such as living space, sediment, light, or water (Vitousek, 1990; Kelleway et al., 2017). Moreover, such consequences might be particularly large if the encroached species are ecosystem engineers, i.e. they direct or indirectly modulate resources availability of ecosystems (Guy-Haim et al., 2018), e.g. nitrogen fixation by *Myrica faya* changing the nutrient status of entire islands on Hawaii (Vitousek, 1990). The consequences of new species encroachments have been widely described in many kinds of terrestrial ecosystems (Schlesinger et al., 1990; McLaren et al., 2017; Zhou et al., 2018), mainly focusing on woody plant species (Hibbard et al., 2001), but the consequences of non-woody-plant species encroachments have seldom been tested especially in coastal wetlands (but see Nolte et al., 2019).

Coastal wetlands, e.g. salt marshes, are dynamic systems with sedimentation and erosion

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causing progressive and retrogressive succession respectively. Succession-driven changes in salt marshes can lead to dramatic changes in biodiversity (Powell et al., 2011), nutrient cycling (Windham and Ehrenfeld, 2003), microorganisms (Otto et al., 1999; Ravit et al., 2003) and food webs (Belnap et al., 2005). These dynamics can be natural, e.g. as a consequence of changing spatial water and sediment flow patterns in the sea, or can be driven by external factors, e.g. fresh water inflow from higher areas, fertilization, climatic changes or human alteration of sedimentation patterns (Berendse et al., 2001; Gedan and Bertness, 2009). In temperate salt marshes worldwide, common reed, *Phragmites australis* (Cav.) Trin. Ex Steud., is often the species that defines the succession from vegetation dominated by halophytes to reed beds, in response to sedimentation or desalinization and/or by actively promoting these processes. The expansion of *P. australis* might be due to natural succession or due to environmental change such as increasing elevation and decreasing salinity (Minchinton, 2003). Indeed, *P. australis* is a true ecosystem engineer, which can enhance the sedimentation in coastal areas (Rooth and Stevenson, 2000; Hughes et al., 2016) and decrease the phosphorus availability below its stands due to high rates of phosphorus uptake (Templer et al., 1998); and it can also have either positive (Windham and Ehrenfeld, 2003) or neutral (Otto et al., 1999) effects on soil microbial activities and N mineralization rates (Ehrenfeld et al., 1997). The consequences of *P. australis* as invasive species have been documented before (Bernal et al., 2015), but as a native species in East Asia, there is a lack of empirical evidence about

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the consequences of *P. australis* encroachments on ecosystem functions and services, especially for decomposition processes.

Halophytic pioneers of salt-marshes not only are key-stone species initiating salt marsh succession, they also provide other paramount ecosystem services (sensu Díaz et al., 2007), as food crops, e.g. *Salicornia* spp. worldwide and edible oils the seed of *Suaeda salsa* (L.) Pallas (Zhao et al., 2002) or for their recreational or cultural values. In East Asia, several species have enormous recreational, cultural and economic values because of their spectacular red autumn display, for instance *S. salsa* on the east coast of China and the Japanese coast; *S. salsa* dominates stands in the salt marshes of coastal intertidal areas that turn bright red in autumn (Wu et al., 2011). The management of these areas to retain large *Suaeda* communities against the encroachments and ecosystem alteration and consequently degradation of ecosystem services (especially cultural service or ecotourism) by *P. australis* has been a real challenge (Song et al., 2011). This is mainly because the drivers of their succession are poorly understood. In particular, the role of *P. australis* therein as an ecosystem engineer in decomposition processes is still unclear. Decomposition is a fundamental process in salt marshes (McLusky and Elliott, 2004), facilitating the cycling of nutrients and other chemical elements, and supporting primary production and important food webs (Graça, 2001; Quintino et al., 2009). Other studies mostly focused on decomposition of *P. australis* itself (but see Warren et al., 2001;

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Windham and Ehrenfeld, 2003). However, as an ecosystem engineer, can it also alter the decomposition of other species in the community? If so, this could give the potential for important feedbacks to ecosystem functioning and perhaps accelerated succession.

To answer this question, we conducted a litter transplantation experiment using the litter bag method to compare the decomposition rate of *S. salsa* litter, i.e. the losses of total mass, and of biochemical compounds (lignin and hemicellulose) and elements (carbon, nitrogen and phosphorus) known to be important determinants of decomposition, between sites with and without *P. australis* encroachment. This design allows us to tease apart the aboveground and belowground drivers of litter decomposition rates between sites. We collected (whole-plant) litter of *S. salsa* from two types of sites and incubated reciprocally in both: one is the monospecific *S. salsa* community (Site S) and the other is the *S. salsa* community with the coexistence of *P. australis* (Site SP). We addressed the following three specific questions: (1) Is there a significant difference in litter decomposition rates between monospecific *S. salsa* stands and mixed *S. salsa – P. australis* stands? (2) If so, does this difference depend on where the litter comes from via litter quality or on where the litter is incubated via the decomposing environment including the decomposer community? (3) If the latter, does the decomposer community effect depend on functional diversity in terms of different groups of invertebrate and microbial decomposers (Wardle et al., 2004)? We used two kinds of mesh sizes to test the

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effect of different groups of invertebrates on the litter decomposition of *S. salsa* litter and also quantified the soil bacteria and fungal communities in both sites. This study will enhance fundamental knowledge about salt marsh succession and feedbacks and ecosystem engineering effects in general and provide useful insight for managing important ecosystem functions of coastal wetlands.

2. Materials and Methods

2.1 Study sites

The study site was located in the Liaohe Estuary National Nature Reserve (40°45′-41°08′N, 121°28′- 122°00′E) in Liaoning Province, Northeast China. This area belongs to a semi-humid temperate monsoon climate with a mean annual temperature of 8.4 °C and a mean annual precipitation of 623.2 mm (ranging from 326.6 mm to 916.4 mm). The frost-free period is about 175 days per year. The tide in this area is irregular semi-diurnal and soils of this area are classified as coastal solonchaks (FAO, 2006). The vegetation is mostly herbaceous and the prevailing vegetation types are virtually monospecific stands of the annual forb *S. salsa* and of the perennial grass *P. australis*, respectively, and their mixtures due to *P. australis* encroachment. In order to test the influence of *P. australis* encroachment into the *S. salsa* community, we selected two sites: one hosting *S. salsa* stands (site S) and the other hosting *S. salsa* coexisting with *P. australis* (site SP). Both sites had similar elevations and tidal regime with a distance of 18 km between them.

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2.2 Experimental design

We carried out a litter transplantation experiment between the two types of sites mentioned above using the litter bag method. For each type of site, fresh (whole-plant) litter of *S. salsa* was collected directly after senescence in early November, 2014 and air-dried in shade for 2 weeks before litter incubation. In order to test the effects of different soil invertebrates on litter decomposition, we used litter bags with different mesh sizes: coarse mesh with 1 mm holes and fine mesh with 0.5 mm holes. Note that the difference between two mesh sizes was small because the leaf litter of *S. salsa* was really small when air-dried, ruling out larger mesh sizes because of the risk of litter fragments falling out. For the air-dry litter, we carefully cleaned the bulk soil on the litter by hand before putting the sample into the litter bag. We put about 20 g air-dried litter in each litter bag. Besides, another five litter subsamples were also weighed and oven-dried (80 °C for 48 h) to estimate the initial water content, i.e. (air dry weight-oven dry weight)/air dry weight and in turn estimate the oven-dry weight of litter samples in the litter bags. These samples were subsequently measured for initial chemical content (see below). The litter bags were incubated in the field by vertically inserting each litter bag into the soil. The average depth from top to bottom was 30 cm, in order to keep the litter incubated at a similar soil depth and avoid exposure of the litter to the air. The distance between litter bags was around 20 cm. We incubated the plant litter reciprocally: from site S in both site

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S and site SP, and from site SP in both sites (Fig. 1). The whole experiment lasted for 9 months starting at the end of November 2014, with two harvests (one after 5 months right after the frozen season, and the other after 9 months before the start of the litter production in the following year). We had 5 replicates for each treatment per harvest and there were 80 litter bags in total. After litterbag retrieval, we cleaned and subsequently oven-dried each sample (80 °C for 48 h) and calculated % mass loss.

2.3 Measurements of the remaining litter

The remaining litter was oven dried at 80 °C overnight with subsequent grinding using a modified ball mill. An appropriate amount of material was then weighed in tin capsules prior to analysis. The samples were analyzed, along with analytical quality controls on an elemental analyzer (N1500, Carlo Erba, Milan, Italy) for the measurements of total carbon and total nitrogen concentrations, and the total phosphorus concentration was measured by inductively coupled plasma emission spectroscopy (Perkin Elmer Optima 3000 ICP Spectrometer, Waltham, MA). Moreover, the concentrations of lignin and hemicelluloses were measured by the extraction of non-ligneous compounds as described in (Freschet et al., 2010). The changes of lignin, hemicellulose, total carbon, total nitrogen and total phosphorus were then calculated as the post-exposure concentration divided by the pre-exposure concentration (fraction of the initial concentration). The loss percentages were calculated as the changes calibrated by the litter mass losses (Pan et al.,

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2015).

2.4 Soil property measurements

At each site, we randomly selected three soil samples, which we separated into different soil layers: 0-10 cm, 10-20 cm and 20-30 cm depth. Soil samples were brought into the laboratory, air dried and passed through a 1 mm-sieve before measurement. A five-gram subsample of each soil sample was shaken with 25 mL demineralized water in an Eppendorf tube for 30 min at 250 rpm and the solution was used to measure soil electrical conductivity (soil EC, μs cm^{-1}): the solution was centrifuged at 5000 rpm for 5 min, and the supernatant solution was measured for EC. In addition, we measured soil organic carbon (SOM, mg g^{-1}) by subtracting soil inorganic content from soil total carbon, which was measured by TOC analyzer (SSM 5000A; Schimadzu, Japan). All air-dry soil samples were oven-dried at 105 °C for six hours and measured for water content, and soil nutrient contents of samples were expressed per unit oven-dry mass. In addition, the soil total carbon (C) and total nitrogen (N) concentrations were analyzed on an automated elemental analyzer the same as the measurement of litter. The other soil properties, such as soil total phosphorus (P) and soil base cations (K + Ca + Mg), were analyzed by inductively coupled plasma emission spectroscopy (Perkin Elmer Optima 3000 ICP Spectrometer, Waltham, MA). For each soil variable in each site, we averaged the values of different soil layers as the mean soil property.

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2.5 Measurements of soil bacteria and fungi diversity

We also collected three soil samples in each type of site for measurements of bacterial and fungal communities in late September, and each soil sample was the mixture of three sub-samples collected from different soil layers: 0-10 cm, 10-20 cm and 20-30 cm. Soil samples were stored in an icebox for transport before being transferred into a freezer at -80 °C. Samples were freeze-dried and sieved to remove the residues of animals and plants. The DNA extraction and Illumina MiSeq sequencing of the amplified DNA were carried out at Majorbio Bio Tech Co. Ltd (Shanghai, China). The database used for OTU identification were Silva and Unite (Kõljalg et al., 2013; Quast et al., 2013). We calculated the Shannon index to represent the diversity of bacteria and fungi, and analyzed the bacterial and fungal community compositions at the phylum level. At both sites, the relative abundance of microbial taxa less than 1% of total abundance were binned into 'unclassified' group.

2.6 Statistical analysis

Firstly, in order to compare the differences of litter traits and soil properties between sites, we carried out one-way analysis of variance (ANOVA) for each variable listed in Table 1. Secondly, we tested whether the mesh size, litter incubation treatments (Fig. 1), harvest time and their (full) interactions had significant effects on the litter losses of total

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mass, lignin, hemicellulose, cellulose and nutrients using three-way ANOVAs with Tukey's multiple comparisons. Thirdly, we divided the litter incubation treatments into litter origin and litter incubation and conducted additional four-way ANOVAs for the litter losses mentioned above (Table A1), and the relative contribution of either litter origin and litter incubation can be compared based on the F-values. Fourthly, we replaced the litter origin and litter incubation by each abiotic and biotic variable separately as listed in Table 1, and included each variable together with incubation time (the number of months, i.e. 5 and 9 months for the first and the second harvest respectively) in multiple regression analyses. We used the 'lm' function in R, in order to check the relative contribution of aboveground litter traits or belowground soil and microbial properties to the decomposition rates. In the end, for microbial community data, one-way ANOVA was also conducted to compare the difference in the diversity indices of bacteria and fungi, and the relative abundances of bacteria and fungi at the phylum level. Significant difference was detected at the level of $p < 0.05$. All data were checked for homogeneity and normality before analysis and log-transformation was conducted when needed. Analyses were conducted either with SPSS 22.0 software (SPSS, Chicago, IL, USA) or with *R* software 3.5.1 (R core Team, 2014).

3. Results

Initial *S. salsa* litter collected from site S (monospecific *S. salsa*) had significantly lower

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concentrations of total C, total P and lignin than that from site SP (mixture of *S. salsa* and *P. australis*, Table 1), but there were no significant differences in total N, C/N, hemicellulose and cellulose contents of initial litter between the two sites (Table 1). For soil variables, site S had significantly higher soil concentrations of total C, total N, total P, base cations than site SP, and also had significantly higher C/N, organic matter content and electrical conductivity than site SP (Table 1). As to the soil microbes, there were ten phyla of bacteria and 12 phyla of fungi (excluding unclassified and small abundance groups) in both sites (Fig. 2). Moreover, site S had significantly lower soil fungal diversity than site SP, but there was no significant difference in soil bacteria diversity between the two sites (Table 1).

Litter incubation treatments (T1 to T4) had significant effects on the litter mass losses and on losses of total C, total N, total P, lignin and hemicellulose (Table 2, $p < 0.01$, but for total P, $p = 0.05$). Litter mass loss was the highest under T2, followed by T1 and T3; and the lowest mass loss was under T4 (Fig. 3a). The same pattern among treatments was found for litter lignin losses (Fig. 3c), but not for hemicellulose (Fig. 3e). Moreover, the highest C and N losses were observed under T2, followed by T3 and T1, and the lowest C and N losses were observed under T4 (Fig. 2b, 2d); but the highest P loss was observed under T3, followed by T2 and T4, while the lowest P loss was observed under T1 (Fig. 3e, 3f). In addition, harvest time had significant effects on litter decomposition (Table 1,

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Table A1, Fig. A1), but no significant effects of the mesh size (alone) were found on any of the decomposition variables mentioned above (Table 1).

By separating the incubation treatments into litter origin and litter incubation, we found that both litter origin and litter incubation had significant effects on the decomposition rates (Table A1, $p < 0.05$), except for the effect of litter incubation on the total phosphorus losses ($p = 0.26$). Moreover, aboveground litter traits had larger explanatory power than belowground soil and microbial properties to the decomposition rates of *S. salsa* litter based on the adjusted r^2 of regression models (Table A2).

4. Discussion

Our reciprocal litter exchange experiment between monospecific *S. salsa* stands and mixed stands of *S. salsa* and *P. australis* yielded three key findings: (1) litter from the site without *P. australis* encroachment always decomposed faster than litter from the site with *P. australis* encroachment (Fig. 3, T1 > T4; T2 > T3), no matter where litter was incubated; (2) litter also decomposed faster when incubated at the site with *P. australis* encroachment than when incubated at the site without *P. australis* (Fig. 3, T2 > T1; T3 > T4), no matter where litter had been collected; (3) C and P losses, rather than N loss, was faster at the site with *P. australis* encroachment than that without *P. australis* (Fig. 3b, 3f; T3 > T1). The encroachment of such an ecosystem engineering species might affect the

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decomposition processes of salt marshes via both aboveground and belowground processes, as will be discussed in detail in the context of our results below. Indeed, the encroachment of *P. australis* might influence the allocation of total phosphorus between soil and plants (Table 1), leading to idiosyncratic P cycling in our study system compared to C and N cycling. Note that *S. salsa* litter mass loss had reached nearly 50% after the frozen season (Fig. A1). This is likely a consequence of both leaching of soluble organic compounds and microbial decomposition shortly before and after the frozen season.

4.1 Phragmites australis as an ecosystem engineer affected the decomposition rates of S. salsa litter via aboveground processes

When in mixture with *P. australis*, *S. salsa* tended to produce litter with higher concentrations of total C, total P and lignin (Table 1). Litter decomposition rates have usually been found to be correlated with the initial chemical qualities in litter, such as total N, total P, C/N and lignin concentration (Cornwell et al., 2008; Hobbie, 2008). Our results confirmed that the *S. salsa* litter with lower initial lignin concentration had faster mass losses, and this was also shown by our multiple regression analyses, i.e. higher initial lignin concentrations led to lower decomposition rates (Table A2), except for the loss of total P. This might be due to faster release of total P from the *S. salsa* litter (Fig. A1), or due to the unique changes in phosphorus allocation between *S. salsa* litter and the soil, or due to the significantly higher concentrations of total P (nearly 1.5 fold) in the

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high lignin litter. In addition, our results did not show a positive correlation between litter decomposition rate and the initial total P in litters (Table 1: 691.97 μg g^{-1} for site S vs. 1069.13 μg g^{-1} for site SP), which was inconsistent with other decomposition studies (Cornwell et al., 2008; Pan et al., 2014). The obvious interpretation might be that total P of *S. salsa* litter was not a strong limiting factor for *S. salsa* decomposition, which is consistent with the relatively high fraction of P loss in all treatments (Fig. 3). In contrast, litter lignin concentration did play a predominant role in determining the decomposition rates of *S. salsa* litter, especially for the whole-plant litter, in this coastal wetland ecosystem. Lignin in stems of *S. salsa* could protect labile litter components such as hemicellulose and protein from microbial attack (Berg and McClaugherty, 2008) and the release of labile compounds is often assumed to drive lignin breakdown by decomposers (Talbot and Treseder, 2012). This protection by lignin was indicated by our results: at the first harvest the loss of lignin was significantly faster than that of hemicellulose, but at the second harvest the differences between lignin loss and hemicellulose disappeared (Fig. A1).

4.2 Phragmites australis as an ecosystem engineer affected the decomposition rate of S. salsa litter via belowground processes

The presence of *P. australis* always led to faster decomposition rates of *S. salsa* litter. The best explanation for the faster decomposition rate in site SP might be that *P. australis*

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brings in both oxygen (being a helophyte with aerenchyma and perhaps through its rhizomes, Armstrong and Armstrong, 1988) and fresh water (thereby reducing salinity and associated electrical conductivity). Moreover, in coastal wetlands, salinity is found to be closely linked to soil organic content and decomposition (Morrissey et al., 2014), but low electrical conductivity, indicating low salinity, might have positive, neutral or negative effects on decomposition depending on the salinity level and the ecosystem concerned (Rejmánková and Houdková, 2006; Rejmánková and Sirová, 2007). Moreover, multiple soil properties might have mixed effects on the decomposition rates of *S. salsa* litter, and our data cannot clarify the relative contribution of each soil property to the decomposition rates regrettably. However, the effects of soil properties on litter decomposition rates were considered to be relatively indirect compared to soil decomposers, such as soil fungi, which could indicate the net indirect effects of soil properties on decomposition processes.

Soil decomposers are closely linked to decomposition rates and they are usually categorized into (fragmenting) soil invertebrates and soil microbes. We did not detect the effects of soil invertebrates on the decomposition rates of *S. salsa* litter in our study site by using litter bags with different mesh sizes (Table 2, no effects of mesh size on decomposition). However, we did find a higher diversity of fungal (but not bacteria) in the mixed community of *S. salsa* with *P. australis* than in the monospecific *S. salsa*

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community, and the factors that lead to this higher fungal diversity in the mixed community - for instance doubling of litter types, higher soil oxygenation or lower soil salinity - deserve in-depth study. Moreover, higher diversities of bacteria and fungi led to higher decomposition rates of *S. salsa* litter (Table A2). The above results indicate that fungi might play the vital role in determining the decomposition rates of *S. salsa* litter in this coastal wetland, especially for the nitrogen cycling of *S. salsa* litter. Based on the multiple regression analyses, we only found the diversity of microbial organisms have a significant power in explaining the total nitrogen losses of *S. salsa* litter, which was similar to the results found in other wetland ecosystems (Gulis and Suberkropp, 2003; Meier and Bowman, 2010). In addition, we only found the 'home-field advantage' evidence with the encroachment of *P. australis* (Fig. 3a), and the 'home-field advantage' for litter decomposition mainly operate via the belowground decomposers (Ayres et al., 2009; Luai et al., 2018). This might partly infer the significant role of *P. australis* as an engineer species in altering the *S. salsa* community belowground, notably the soil fungi diversity.

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5. Conclusion

Our findings showed that *P. australis* as an ecosystem engineer might have significant consequences for the decomposition rates of *S. salsa* litter, via both aboveground and belowground pathways. Specifically, *P. australis* encroachment might affect the

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decomposition rate of *S. salsa* litter by making *S. salsa* produce litter with higher lignin concentrations, and leading to lower soil N and P availability but possibly higher oxygen availability and lower salinity as well as higher soil fungal diversity for decomposition. Moreover, *P. australis* as an ecosystem engineer might also alter the allocation of total P between plants and soils in coastal wetlands, and in turn affect the aboveground and belowground mechanisms in controlling decomposition. These results together indicated that the encroachment of *P. australis*, no matter what drives this encroachment, could lead to substantial changes in both abiotic and biotic factors, and adds to the increasing evidence that plant community shifts might be more important than the abiotic factors in controlling decomposition (Cornelissen et al., 2007; Hooper et al., 2012), especially when the shifts are caused by ecosystem engineers. Our findings also highlight the important consequences of plant encroachments in determining the carbon and nutrient cycles in coastal wetlands, as well as in evaluating the ecosystem functions and services of coastal wetlands more generally.

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Figure captions

Fig. 1 The design of the litter transplantation experiment. Treatment 1 (T1) represents *S. salsa litter* from site S (which only hosts *S. salsa* stands) incubated at site S; Treatment 2 (T2) represents *S. salsa* litter from site S incubated at site SP (which hosts *S. salsa* coexisting with *P. australis*); Treatment 3 (T3) represents *S. salsa* litter from site SP incubated at site SP; Treatment 4 (T4) represents *S. salsa* litter from site SP incubated at site S.

Fig. 2 Relative abundances of soil (a) bacterial and (b) fungal community composition at phylum level between site S (which only hosts *S. salsa* stands) and site SP (which hosts *S. salsa* coexisting with *P. australis*). Sequences that could not be classified into any known group were sorted as "others", so were the groups whose relative abundance was smaller than 1% at both sites. Error bars represent standard errors (n = 3).

Fig. 3 Effects of litter incubation treatments on litter mass loss, lignin loss, hemicellulose loss and litter nutrient losses (total C, total N and total P losses). Treatment 1 (T1) represents *S. salsa litter* from site S incubated at site S; Treatment 2 (T2) *S. salsa* litter from site S incubated at site SP; Treatment 3 (T3) *S. salsa* litter from site S incubated at site SP; Treatment 4 (T4) *S. salsa* litter from site SP incubated at site S. a-d represent the multiple comparison results among different litter incubation treatments. Significance is shown at the level of $p < 0.05$. Bars show standard errors (n = 5).

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CRediT author statement

Lijuan Cui: Conceptualization, Supervision. **Xu Pan**: Methodology, Formal Analysis, Writing – Original Draft. **Wei Li**: Resources, Investigation. **Xiaodong Zhang**: Data Curation. **Guofang Liu**: Software, Writing – Review & Editing. **Yao-Bin Song**: Validation. **Fei-Hai Yu**: Data Curation, Writing – Review & Editing. **Andreas Prinzing**: Supervision, Writing – Review & Editing. **Johannes H. C. Cornelissen**: Conceptualization, Methodology, Supervision, Writing – Review & Editing.

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Table 1 Summary and comparison of litter traits and soil properties between two sites with and without *P. australis* encroachment. Significant differences between sites are shown in bold at the level of $p < 0.05$.

Litter traits and soil properties	Site S (without *P. australis*)	Site SP (with *P. australis*)
Litter		
C (%)	**24.73 ± 1.51**	**29.12 ± 2.69**
N (%)	0.60 ± 0.04	0.70 ± 0.15
C/N	41.20 ± 4.45	43.34 ± 11.87
P (μg g^{-1})	**691.97 ± 74.60**	**1069.13 ± 184.83**
Hemicellulose (%)	5.62 ± 0.72	5.43 ± 0.10
Cellulose (%)	19.64 ± 0.32	18.75 ± 2.31
Lignin (%)	**22.39 ± 1.05**	**26.17 ± 1.75**
Soil		
C (%)	**1.020 ± 0.12**	**0.575 ± 0.04**
N (%)	**0.08 ± 0.01**	**0.05 ± 0.01**
C/N	**12.533 ± 0.205**	**11.605 ± 0.343**
P (mg g^{-1})	**757.81 ± 74.08**	**482.62 ± 97.16**
Base cations (mg g^{-1})	**49.00 ± 3.90**	**36.385 ± 0.74**
Organic matter (mg g^{-1})	**10.72 ± 0.80**	**8.01 ± 0.75**
Electrical conductivity (μs cm^{-1})	**4544 ± 1048**	**2385 ± 490**
Microbe		
Shannon index of bacteria	5.88 ± 0.39	6.54 ± 0.04
Shannon index of fungal	**3.09 ± 0.08**	**4.09 ± 0.03**

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Table 2 ANOVAs of mesh size (M, coarse mesh or fine mesh), litter incubation treatment (T: T1, T2, T3, T4), harvest time (H: two harvests) on litter mass losses, lignin and hemicellulose losses and litter nutrient losses (total carbon, total nitrogen and total phosphorus losses). The degree of freedom for the errors equals 54 throughout. Significant results at $p < 0.05$ are shown in bold. Treatment 1 (T1) represents *S. salsa litter* from site S (which only hosts *S. salsa* stands) incubated at site S; Treatment 2 (T2) represents *S. salsa* litter from site S incubated at site SP (which hosts *S. salsa* coexisting with *P. australis*); Treatment 3 (T3) represents *S. salsa* litter from site SP incubated at site SP; Treatment 4 (T4) represents *S. salsa* litter from site SP incubated at site S.

Variables	*df*	Mass loss		Carbon loss		Nitrogen loss		Phosphorus loss		Lignin loss		Hemicellulose loss	
		F	*p*	*F*	*p*	*F*	*p*	*F*	*p*	*F*	*p*	*F*	*p*
Harvest (H)	1	**42.99**	**0.0 < 1**	**59.26**	**0.0 < 1**	**37.65**	**0.0 < 1**	**11.80**	**0.0 < 1**	**11.62**	**0.0 < 1**	**17.70**	**< 0.01**
Mesh size (M)	1	0.17	0.69	1.62	0.21	0.35	0.56		0.25	0.00	0.96		
Treatment (T)	3	**23.23**	**0.0 < 1**	**16.06**	**0.0 < 1**	**5.58**	**0.0 < 1**		**0.0 < 1**	**17.69**	**0.0 < 1**		**< 0.01**
H * M	1	0.44	0.51	3.32	0.07	**5.97**	**0.01 < 8**		0.22	0.08	0.77		
		4	1	2	7		**2**	1.53	2	8	9	1.49	0.23

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					<								
		3.1	**0.0**	**9.9**	**0.0**	**4.6**	**0.0**		0.1	2.2	0.0		
H * T	3	**1**	**3**	**9**	**1**	**0**	**1**	1.68	8	7	9	**2.95**	**0.04**
		2.6	0.0	1.3	0.2	0.3	0.7		0.2	3.9	0.0		
M * T	3	5	6	3	8	8	7	1.48	3	9	1	1.25	0.30
H * M *		0.2	0.7	3.5	0.0	1.7	0.1		0.7	0.3	0.6		
T	2	6	7	4	4	8	8	0.24	9	7	9	0.83	0.44

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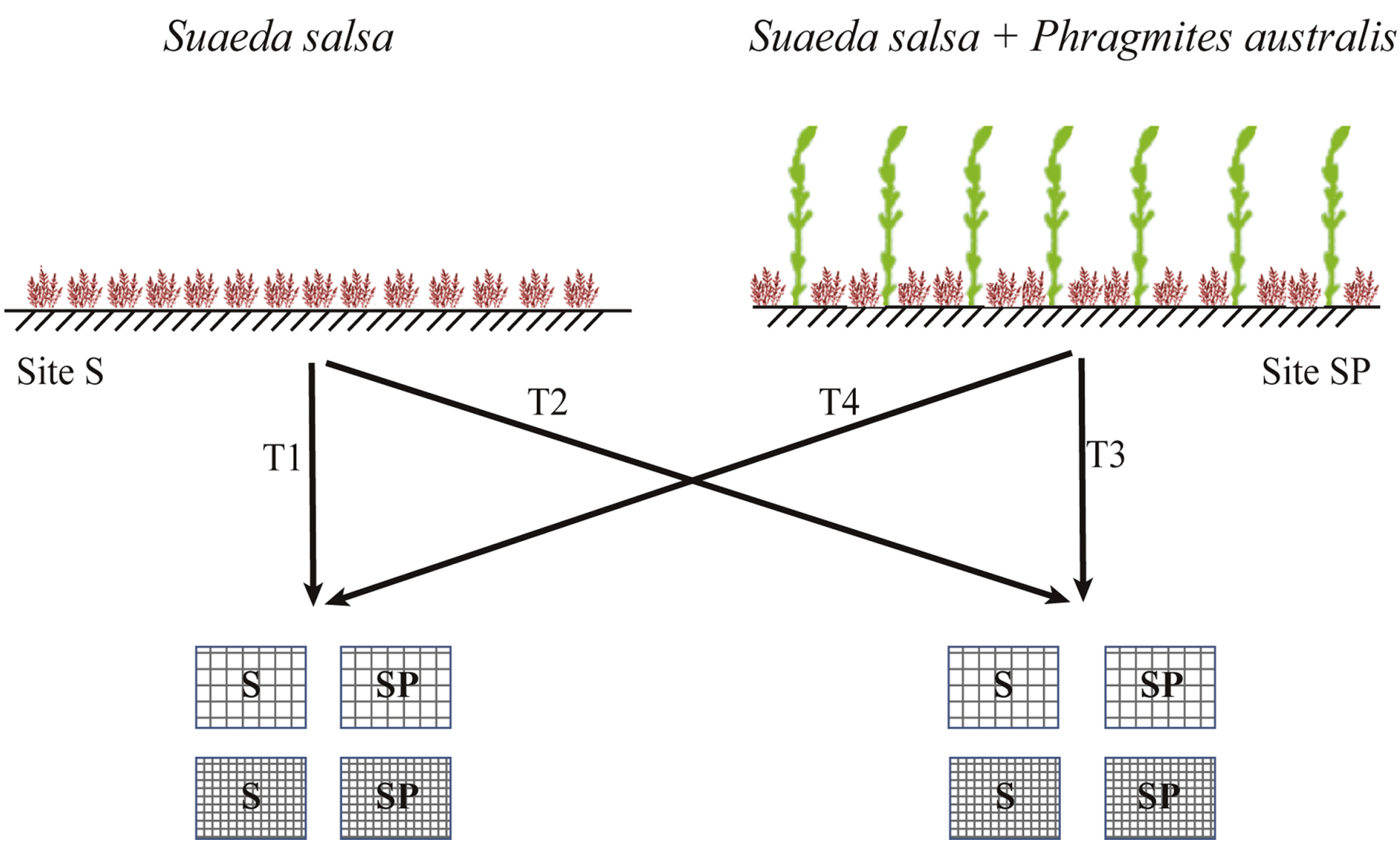
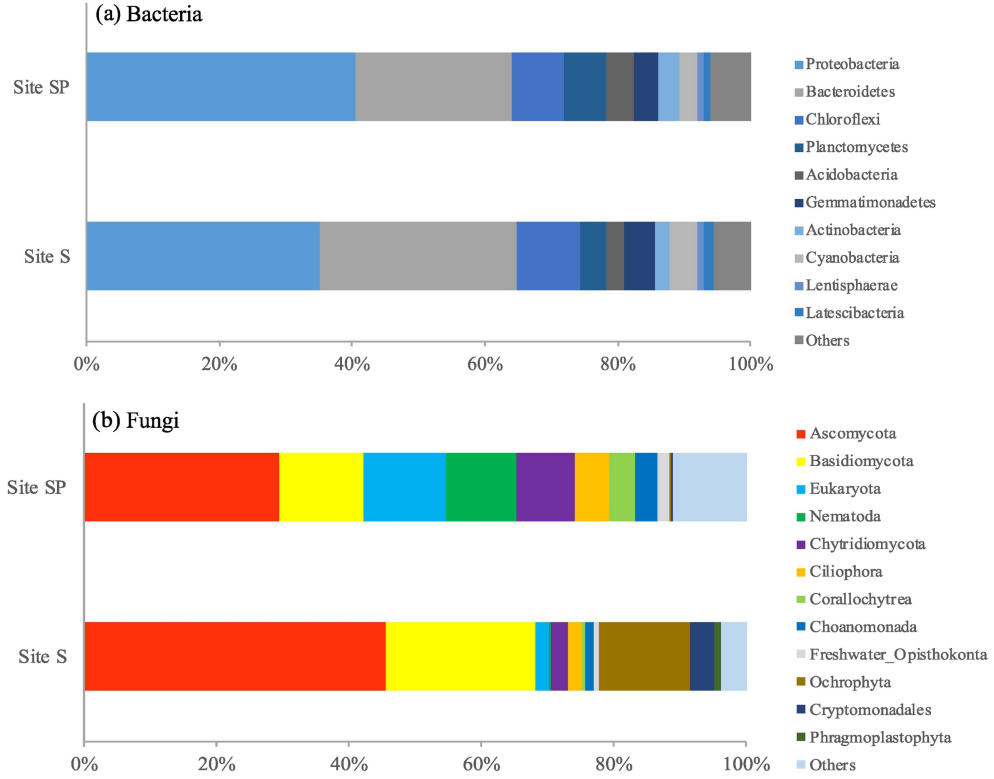

Suaeda salsa
Suaeda salsa + Phragmites australis
Site S
Site SP
T1
T2
T3
T4
S
SP
S
SP
S
SP
S
SP

Figure 1



Relative abundance of soil bacteria and fungi(%)

Figure 2

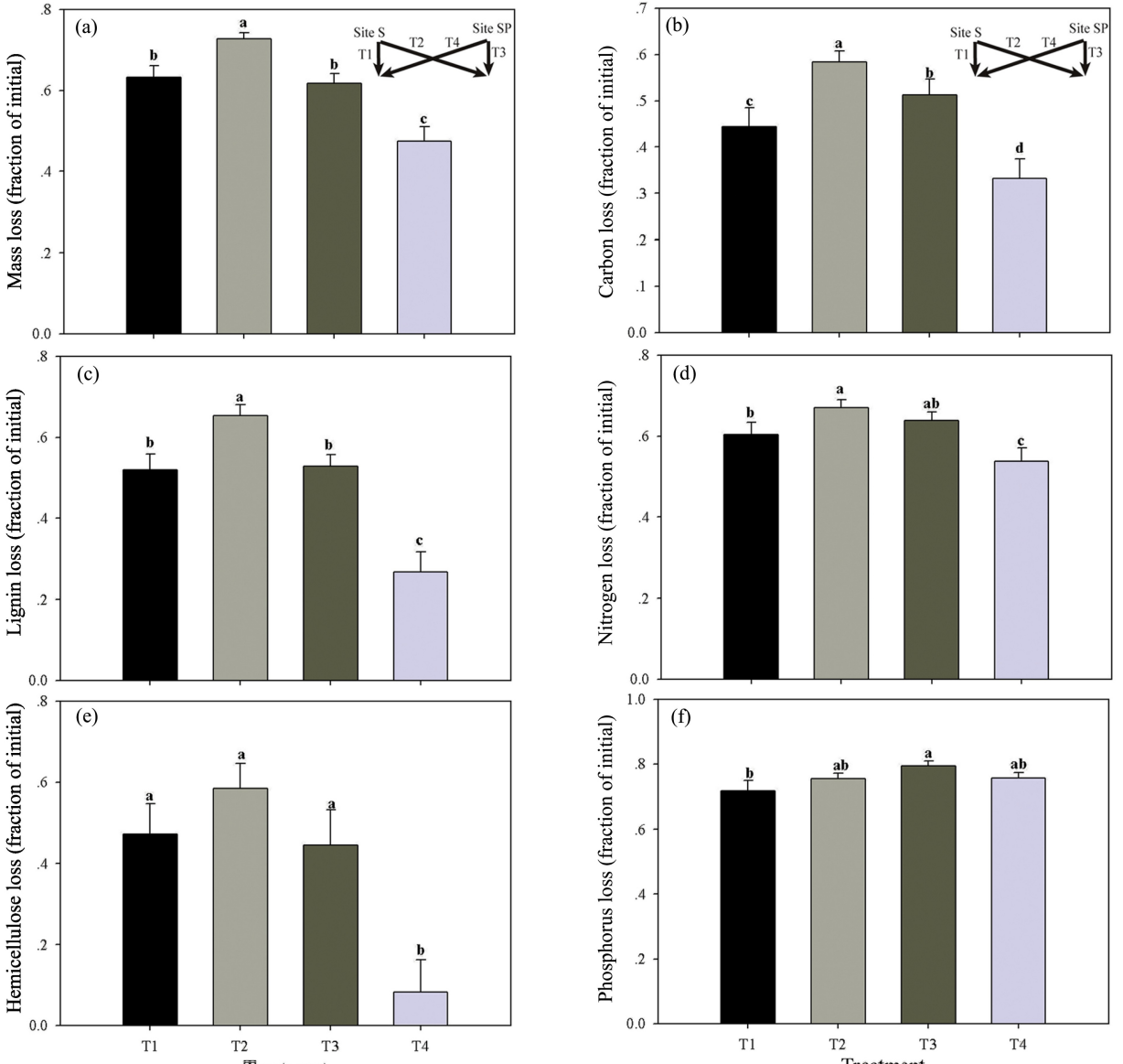

(a)
Mass loss (fraction of initial)
Site S
Site SP
T1
T2
T4
T3
(b)
Carbon loss (fraction of initial)
(c)
Lignin loss (fraction of initial)
(d)
Nitrogen loss (fraction of initial)
(e)
Hemicellulose loss (fraction of initial)
(f)
Phosphorus loss (fraction of initial)
Treatment

Figure 3