The response of stocks of C, N and P to plant invasion in the coastal wetlands of China

Weiqi Wang[1,2,3,4*], Jordi Sardans[3,4*], Chun Wang[1,2], Congsheng Zeng[1,2], Chuan Tong[1,2], Guixiang Chen[1,2], Jiafang Huang[1,2], Haoran Pan[5], Guille Peguero[3,4], Helena Vallicrosa[3,4], Josep Peñuelas[3,4]

[1] Key Laboratory of Humid Subtropical Eco-geographical Process, Ministry of Education, Fujian Normal University, Fuzhou 350007, China

[2] Institute of Geography, Fujian Normal University, Fuzhou 350007, China

[3] CSIC, Global Ecology Unit CREAF-CSIC-UAB, 08913 Cerdanyola del Vallès, Catalonia, Spain

[4] CREAF, 08913 Cerdanyola del Vallès, Catalonia, Spain

[5] Guangxi Mangrove Research Center, Guangxi Academy of Sceinces, Beihai 536000, China

Correspondence

Weiqi Wang, Key Laboratory of Humid Subtropical Eco-geographical Process, Ministry of Education, Fujian Normal University, Fuzhou 350007, China, Institute of Geography, Fujian Normal University, Fuzhou 350007, China. Email: wangweiqi15@163.com;

Jordi Sardans, CSIC, Global Ecology Unit CREAF-CSIC-UAB, 08913 Cerdanyola del Vallès, Catalonia, Spain, CREAF, 08913 Cerdanyola del Vallès, Catalonia, Spain. Email: j.sardans@creaf.uab.es

Abstract

The increasing success of invasive plant species in wetland areas can threaten their capacity to store carbon, nitrogen, and phosphorus (C, N, and P). Here we have investigated the relationships between the different stocks of soil organic carbon (SOC), and total C, N, and P pools in the plant-soil system from eight different wetland areas across the South-East coast of China, where the invasive tallgrass *Spartina alterniflora* has replaced the native tall grasses *Phragmites australis* and the mangrove communities, originally dominated by the native species *Kandelia obovata* and *Avicennia marina*. The invasive success of *Spartina alterniflora* replacing *Phragmites australis* did not greatly influence soil traits, biomass accumulation or plant-soil C and N storing capacity. However, the resulting higher ability to store P in both soil and standing plant biomass (approximately more than 70 and 15 kg P by ha, respectively) in the invasive than in the native tall grass communities suggesting the possibility of a decrease in the ecosystem N:P ratio with future consequences to below- and above-ground trophic chains. The results also showed that a future advance in the native mangrove replacement by *Spartina alterniflora* could constitute a serious environmental problem. This includes enrichment of sand in the soil, with the consequent loss of nutrient retention capacity, as well as a sharp decrease of the stocks of C (2.6 and 2.2 t C ha^{-1} in soil and stand biomass, respectively), N, and P in the plant-soil system. This should be associated with a worsening of the water quality by aggravating potential eutrophication processes. Moreover, the loss of carbon and nutrient decreases the potential overall fertility of the system, strongly hampering the re-establishment of woody mangrove communities in the future.

KEYWORDS

Active carbon, plant invasion, soil organic carbon, nutrient stoichiometry

INTRODUCTION

The world contains an estimated 2011 Pg organic carbon of soil (IPCC, 2000). The importance of soil as a carbon sink is, therefore, crucial for the ability of the Earth to buffer the increasing levels of atmospheric CO_2 as a consequence of human activities (Joiner et al., 1999; Smith, 2004; Bonan & Van Cleve, 2011). Wetlands are one of the most sensitive ecosystems to global climate change. Despite accounting just for 4 to 6% of the land area (Howe et al., 2009), wetlands accumulate between 20 to 30% of the whole terrestrial soil C stock (Smith et al., 2004), thus playing a disproportionate role in the global C cycle. As the ecosystems with the world's highest productivity per unit of area, wetlands combine the dual function of being a "C source" and a "C sink" (Andreetta et al., 2016). Therefore, even minor changes in the dynamics of wetland areas will affect global greenhouse gas emissions, which in turn will influence global warming (Tian et al., 2010). Among wetland areas, estuarine wetland soils, due to their location at the river-ocean interface, have a particularly large potential to act as sediment sinks, thus accumulating C (Bianchi et al., 2013; Burden et al., 2013; Mitsch et al., 2013). In this context, the changes occurred in the last decades in China coastal wetlands, such as the reduction in area because of sea level rise (Wang et al., 2015b) and land use change (Wang et al., 2014) are especially important. Despite this reduction, coastal wetlands in China currently still cover 5.80×10^4 km^2 (Wetland China, 2014) and provide many ecosystem services and products (Liu et al., 2006; Wang et al., 2015a). We know that increases in tropical storms and ocean levels have altered flooding intensities, which together with increased pollution and nutrient loads have impacted sedimentary processes and the capacity of wetlands to store and release C and nutrients (Schewe et al., 2011; Mendelsohn et al., 2012; Sardans et al., 2012; Ramsar, 2013; Piecuch & Ponte, 2014;

Sardans & Peñuelas, 2014). In this context, the success of invasive plant species can also have an impact on the capacity of wetlands to store and release C, N and P (Wang et al., 2014; Wang et al., 2015b).

Invasive plant species can change the capacity to accumulate N and P in biomass and soil (Wang et al., 2015a). The impacts of successful invasive plants on the concentrations and stoichiometry of soil nutrients have been widely studied (Funk & Vitousek, 2007; Sardans & Peñuelas, 2012), and some general trends have emerged (González et al., 2010; Matzek, 2011; Sardans & Peñuelas, 2012; Sardans et al., 2017). The impacts of invasive plants can differ and even be opposite depending on the natural availability levels of soil nutrients and, generally, on the capacity of a site to sustain low or high plant production in accordance with the soil and climatic conditions (González et al., 2010; Matzek, 2011; Sardans & Peñuelas, 2012; Sardans et al., 2017).

The active C from the total soil organic carbon, is highly susceptible to oxidation and decomposition and is strongly influenced by plants and microorganisms (Kimura et al., 2004; Chen et al., 2010) and includes dissolved organic carbon (DOC), labile organic carbon (LOC), and soil microbial biomass organic carbon (MBC). Differently, the total content of soil organic carbon (SOC) changes over a long-time scale, and their fluctuations are not easily discerned within a short time period (Wissing et al., 2011). Therefore, distinguishing between the active-C fraction from the total SOC pool is important to assess the effect of plant invasion on soil C dynamics. Different forms of active SOC have different sensitivities to environmental change (Gu et al., 2004), but few studies have examined the relationships between the different forms of active SOC and changes in other environmental parameters (Xu et al., 2011; Zhao et al., 2014), and especially of soil properties. Active SOC is a major source of CO_2 and CH_4 produced by microbes, so properly managing this pool of active C is important for mitigating global climate change (Knoblauch et al., 2011; Hanke et al., 2013). This C:nutrient stoichiometry is a good indicator of changes in soil C dynamics in wetlands due to changes in the environment, thereby providing information of the impacts on nutrient cycling and status and, thus, is informative about the potential capacity of these ecosystems to fix C and reduce the impact of the emissions of C-source greenhouse gases (Peñuelas et al., 2012 and 2013).

The impacts of plant invasion on total soil C accumulation in the various soil fractions and the further relationships of these impacts on C with other soil traits, such as C:N:P ratios, are also unresolved (Sardans & Peñuelas, 2012). Most available data generally suggest that the low costs of foliar construction and high phenotypic plasticity in taking up available nutrients frequently contribute to invasive species success in nutrient-rich environments (Daehler, 2003; González et al., 2010; Sardans & Peñuelas, 2012), whereas in nutrient-poor soils the success of invasive plants would depend on more conservative strategies, such as a higher nutrient-use efficiency (Funk & Vitousek, 2007; González et al., 2010; Matzek, 2011; Sardans et al., 2017), especially on short timescales (Funk & Vitousek, 2007). The existence of numerous exceptions, however, prevent this question from being totally resolved (Sardans & Peñuelas, 2012).

Some studies have discussed soil C dynamics and nutrient stoichiometry (Tian et al., 2010; Schipper & Sparling, 2011), but few have distinguished them at a fine scale in soil profiles. Studies addressing the relationships of species invasive success with soil C and nutrient status has been mainly focused on the first centimeters of soil (Sardans & Peñuelas, 2012). However, there is little available information about the impact of plant invasive success on soil depth. The different soil textures and soil organic matter decomposition observed in superficial soil layers linked to plant alien success, can thereafter produce a shift in the accumulation of some organic carbon fractions along soil deep layers (Senga et al., 2011; Xiang et al., 2015). The impacts of plant invasion on the distribution of total soil C accumulated among the various soil fractions and the further relationships of these impacts on C dynamics with other soil traits, such as C:N:P ratios, are also unclear (Sardans & Peñuelas, 2012). We hypothesized that changes in soil C storage along the soil profile could be related to different plant species dominating above-ground. The knowledge of the variation in C accumulation along the vertical soil profile and its causes is crucial for understanding the capacity of wetlands to act as carbon sinks in absolute amounts (Craft, 2007).

We aimed (i) to determine whether the success of plant invasion of the same invasive species at different sites was based on a similar strategy of C, N, and P use, and (ii) to compare the differences of soil traits and plant-soil system C, N, and P stocks between successful recently established invasive communities of *Spartina alterniflora* in two very different native communities: native tallgrass and mangrove communities with respect pure non-invaded native communities in different areas along subtropical and tropical coastal wetlands of China.

MATERIALS AND METHODS

Study area

We studied the coastal wetlands of central-south China, where today plant invasion effect is one of the most important problems (Figure 1). In 1979, *Spartina alternifolia* was introduced into China from the United States for the purpose of accumulating silt, thereby protecting beaches and berms. However, *S. alterniflora* was identified as an efficient invasive plant, decreasing the area of indigenous vegetation communities, transforming the habitat, and jeopardizing the survival of the animal species in the intertidal zone, and ultimately producing a series of ecological and economic hazards to the area (Yang et al., 2009). *S. alterniflora* is the only coastal wetland invasive plant identified by the State Environmental Protection Administration of China since 2003. *S. alterniflora* has an apparently superior breeding ability and adaptability than several native wetland species. Thus, it has spread wildly and invaded and replaced coastal native plant communities where it forms mono-species communities. Today, *S. alterniflora* grows from the North of China from the Yalu River estuary to the South in Guangxi Beibu Gulf. The distribution area accounts for about 2% of the wetland area in China (Lu & Zhang, 2013). China is the country with the largest outbreak of *S. alterniflora* in the world, especially in its subtropical coastal wetland. The distribution area of *S. alterniflora* reaches more than 92.44% of the total invaded areas in the subtropical coastal wetland (Lu & Zhang, 2013). Therefore, the subtropical coastal wetland is an ideal area for the study of *S. alterniflora* invasion.

Sample collection and measurements

Soil samples were collected during the plants' main growing season (June to August) in 2015 from eight locations in China's subtropical and tropical coastal wetlands (Figure 1). We sampled soils in well stablished *Spartina alterniflora* communities in sites originally dominated by *Phragmite australis* (grass), *Kandelia obovata* (mangrove), *Avicennia marina* (mangrove), *Spartina alterniflora* (invaded from 7 to 15 years ago), and also collected soils form native plants communities growing at these sites for more than 30 years. In our study, for the *S. alterniflora*-invaded *Phragmite australis* site, the native plants were completely replaced by *S. alterniflora*. However, for the *S. alterniflora*-invaded mangrove site, the invasion has begun in mangrove community margins and empty spaces within the mangrove community, and it is currently spreading its cover by all the mangrove community space. Three plots were randomly established in each community type, and soil profiles (width, 1 m; length, 0.6 m; depth, 0.4 m) were excavated. The samples were collected with a small sampler (length, 0.4 m; diameter, 0.1 m) from each of four soil layers (0–10, 10–20, 20–30, and 30–40 cm) at the center and both ends of the soil pits. These three samples from each layer were bulked to form one composite sample per layer. A total of 240 soil samples (ten sampling site × two communities × three plots × four soil layers) were thus collected. The core samples were divided into two parts, with one part unprocessed for the measurement of soil MBC and DOC, and the other part air-dried and finely grounded in a ball mill after the removal of all roots, and visible plant remains used for the determination of total SOC and LOC. Total SOC was measured with a Vario EL III Elemental Analyzer (Elementar Scientific Instruments, Hanau, Germany), DOC by extracting the soils with deionized water (1:5 ratio) and measuring the C concentration using a TOC-V CPH total C analyzer (Shimadzu Scientific Instruments, Kyoto, Japan), MBC by fumigation-extraction (Lu, 1999), and LOC by digestion with 333 mM $KMnO_4$ (Xu et al., 2011; Wang et al., 2015c).

Bulk density was measured for the three bulked cores (5 cm diameter, 3 cm depth) collected from each soil layer. Soil salinity, pH, and particle-size distribution were measured by a DDS-307 salinity meter (Boqu Scientific Instruments, Shanghai, China), an 868 pH meter (Orion Scientific Instruments, Minnesota, USA), and a Master Sizer 2000 Laser Particle Size Analyzer (Malvern Scientific Instruments, Suffolk, UK), respectively. Soil total N concentration was determined with a Vario EL III Elemental Analyzer (Elementar Scientific Instruments, Hanau, Germany), and total soil P concentration was determined by perchloric-acid digestion followed by ammonium-molybdate colorimetry and measurement using a UV-2450 spectrophotometer (Shimadzu Scientific Instruments, Kyoto, Japan).

Tallgrass above-ground biomass in each plot was collected from a randomly selected quadrat (10 × 10 m), and the above-ground biomasses were collected from a selected center sub-quadrat (1 × 1 m). For the mangrove, we only collected some above-ground materials, not all of the above-ground biomass. At the same time, we determined the mangrove diameter at the breast height and the height and density of all plants. Also, the above-ground mangrove biomass of each plant population was calculated by a previously reported equation (Tam et al., 1995).

All plant material was gently washed with deionized water and then oven-dried to a constant mass (80 °C for 24–36 h) and weighed. The concentrations of C and N of the plants were determined using a Vario EL III Elemental Analyzer (Elementar Scientific Instruments, Hanau, Germany). Total plant P concentrations were all determined by the method of colorimetrically using a UV-2450 spectrophotometer (Shimadzu Scientific Instruments, Kyoto, Japan) at a wavelength of 700 nm (Lu, 1999). C, N, and P stocks in the plant were calculated by the biomass multiplied by the nutrient concentration.

Statistical analyses

We performed general mixed models (GLM) with plant type (invasive versus native) as an independent fixed categorical variable, site as an independent random factor, and soil traits plant above-ground biomass, and C, N, and P stocks in plant above-ground biomass as continuous dependent variables. We used the "*nlme*" (Pinheiro et al., 2016) R package with the "*lme*" function. If the variable was not normally distributed, it was log-transformed. We chose the best model for each dependent variable based on the Akaike information criterion.

We used the MuMIn (Barton, 2012) R package in the mixed models to estimate the percentage of the variance explained by the mixed models. We conducted Tukey's post hoc tests to detect significant differences in the analyses for more than two communities using the "*multcomp*" (Hothorn et al., 2013) R package with the "*glht*" function.

We also performed other multivariate statistical analyses. We determined the overall differences in the changes of the soil C fractions, N, and P concentrations, stoichiometric ratios, salinity, pH, and temperature in the species-specific plant communities using general discriminant analysis (GDA), including the component of the variance due to the different soil layers as an independent categorical variable. Discriminant analyses consist of a supervised statistical algorithm that derives an optimal separation between groups established a priori by maximizing between-group variance while minimizing within-group variance (Raamsdonk et al., 2001). GDA is thus an adequate tool for identifying the variables most responsible for the differences among groups, while controlling the component of the variance due to other categorical variables. The GDAs were performed using Statistica 6.0 (StatSoft, Inc. Tulsa, USA).

RESULTS

Spartina alterniflora invasion of tallgrass wetlands

Compared to the original native communities of *Phragmite australis*, the *Spartina alterniflora* communities that currently occupy wetland areas previously inhabited by the native tallgrass *P. australis* had higher soil C in microbial biomass, total soil C and P content, soil C:N ratio, and P content in above-ground biomass, but lower soil N:P ratio and C stocks in above-ground plant biomass (Table 1, Figures 2 and 3). Our data analyses provide evidences of higher soil C (approx. 18.8 versus 17.5 t C ha^{-1}) in the invaded than native community but smaller C stocks in aboveground biomass (approx. 6 versus 8 t C ha^{-1}) in the invaded than in native communities, thus resulting in a trend to less total C stored in the plant-soil system, irrespective of the C stored in below-ground biomass. Additionally, our data indicate higher amounts of P stored in soil (approx. 0.07 t P ha^{-1}) and in aboveground biomass (approx. 1.5 g m^{-2}, that is 0.015 t P ha^{-1}) in invasive than in native communities. Therefore, without knowing the P stored in the belowground biomass, the data showed a total higher P stored in the invasive than native communities.

The GDA analysis with soil data, comparing the communities dominated by *Phragmites australis* with those dominated by *Spartina alterniflora*, showed no differences in main soil features (Squared Mahanalobis = 2.46, F = 1.01, P = 0.46) between the *Phragmites australis* and *Spartina alterniflora* communities.

***Spartina alterniflora* invasion of mangrove**

In our study, the *Spartina alterniflora* communities that currently occupy areas in the margins of mangrove community and in the empty spaces within the mangrove community, which previously were occupied by native mangrove communities (mostly previously inhabited by *Kandelia obovata* or *Avicennia marina*), had lower soil organic carbon, total soil C and P content, and soil C:N, C:P, and N:P ratios (Table 2). Moreover, *Spartina alterniflora* communities also had lower C, N, and P stocks in the above-ground plant biomass (only compared with *Avicennia*-dominated mangroves) and lower aboveground biomass than native mangrove communities (Figures 2 and 3). Hence, data analyses indicate higher stocks of soil C (approx. 2.6 t C ha^{-1}), N (approx. 0.17 t N ha^{-1}), and P (approx. 0.05 t P ha^{-1}) and also higher stocks in the above-ground biomass of C (approx. 2.2 t C ha^{-1}), N (approx. 0.65 t N ha^{-1}), and P (approx. 0.08 t P ha^{-1}) in the native than invaded community (Figures 2 and 3).

Thus resulting in a trend to substantially less C, N, and P stored in the invaded plant-soil system relative to the native-dominated mangrove communities, irrespective of the C, N, and P stored in below-ground biomass.

In contrast, in this case, the GDA analysis of the soil data, comparing the *Spartina*-dominated with the native mangrove communities, revealed significant differences (Squared Mahalanobis = 9.84, F = 17.3, $P < 0.0001$) arising after the invasion (Figure 4).

DISCUSSION

General descriptive results

We have not observed important changes in C:N and C:P soil ratios along the soil profile. This is an interesting and particular result of these studied wetland soils, which is probably related to the sediment loadings that these soils continuously receive and the anoxic conditions that prevent a fast and complete decomposition of the litter, which is incessantly covered by new sediments and progressively buried to deeper soil layers. A trend to uniform organic carbon contents along the vertical soil profile in wetlands has been previously observed in soils receiving regular loads of sediments (Alongi et al., 2001; Senga et al., 2011), which is related to the physical protection of soil organic carbon linked to sedimentation typical from seasonally-flooded wetlands (Maynard et al., 2011).

The relationships between species invasion in tallgrass wetland communities and soil traits and plant-soil C, N, and P stocks

Our results show that the invasion of *Spartina alterniflora* replacing *Phragmites australis*, when comparing adult communities of both species, had no clear impacts on the overall C storing capacity of the plant-soil systems. Although the invaded community had more C in the soil, there was a correspondingly lower amount of C stored in the above-ground biomass. Previous studies conducted elsewhere in Chinese wetlands and investigating the impact of *S. alterniflora* on soil properties after replacing tallgrass communities dominated by other native species, such as *Cyperus malaccensis* or *Suaeda salsa*, also showed a trend to increasing soil C stocks with time since invasion (Chen et al., 2015; Jin et al., 2017; Liu et al., 2017). In light of these previous results, our data appear consistent with the general view that invasive processes in wetlands tend to maintain or even increase C stocks in the soil, as observed at the global level (Liao et al., 2008).

Reports addressing the impacts of *S. alterniflora* on soil stocks of N and P and on the stocks of C, N, and P in plant biomass are rare. After the replacement of *P. autralis* by *S. alterniflora*, we found a general increase in P stocks both in the soil and above-ground biomass, but not in N, thus resulting in a decrease in soil and plant N:P ratios. To our knowledge, so far there are very few equivalent studies with which we can compare our results. Likewise, Wang et al. (2015a) found a decrease in N:P ratios in a wetland area of the Minjiang River, where *S. alterniflora* was invading the native *Cyperus malaccensis* tall grass communities, although they did not observe any effects of invasion on soil P concentrations.

The higher P contents in soil observed after the invasion was mainly due to the higher bulk density in the invaded than in the native communities. Bulk density has been positively correlated with organic C, N, and P concentrations in similar wetland areas in the soils below *Carex* sp. and *Phragmites australis* (Peng et al., 2005). Differences and fluctuations in bulk density have also been frequently associated with the success of invasive plant species (Miller et al., 2006; Lortie & Cushman, 2007; Pande et al., 2007). Summarizing, the successful invasion of *Spartina alterniflora* replacing *Phragmites australis* in Chinese wetlands should not produce great impacts on their C storing capacity, but it could increase soil and ecosystem

P-storing ability due to the higher plant P concentrations and also due to the increase in soil bulk density, further decreasing the N:P ratios at an ecosystem level with likely consequences for the whole soil and above-ground trophic chains.

The relationships between species invasion in mangrove communities and soil traits and plant-soil C, N, and P stocks

The lower soil bulk densities in *S. alterniflora*-invaded communities relative to the native mangrove communities were mainly related to a lower sand content in the latter. The success of *S. alterniflora* was thus associated with decreases in bulk density and total soil C, N, and P contents per unit of surface area.

As in other studies that have observed differences in bulk density and elemental composition between soils in invaded and native communities (Wang et al., 2018), the causes of these differences in our study were unclear. Nevertheless, this result suggests that the scarcer root system of a tallgrass community, compared with the more consistent root system of a mangrove stand, could have a lower ability to retain small-size particles in the soil, such as clay.

In this case, the large differences in above-ground biomass between the native mangrove stands compared to the *Spartina alternifora*-dominated tallgrass community can easily explain the great losses in C, N, and P stocks in the soils after the invasion. Changes in soil traits due to plant invasion, such as SOC concentration (Zhou et al., 2015), texture (Uselman et al., 2014; Haubensak et al., 2014), and other soil parameters (Blank et al., 2015), have been correlated with differences in plant or root biomass and/or shoot:root ratio between native and invaded plant communities. In fact, soil properties such as texture can change in wetlands within 10 years, as observed in other studies (Craft et al., 1999 and 2002). Other works have also observed changes in soil bulk density (Zhang et al., 2009), C contents (Koutika et al., 2007; Koteen et al., 2011; Throop et al., 2013; Yu et al., 2014), and several other traits (Yu et al., 2014; Souza-Alonso et al., 2015) as a consequence of successful plant invasion. The similar SOC values along the vertical soil profile shown earlier suggest that these wetlands are sinks of sediments, reinforcing the idea that sites with different vegetation cover with different structure and root system size can change soil structure by favoring sedimentation of different particle size classes. Thus, our study is consistent with the observation that soil texture is a sensitive factor during plant invasion, as has been observed in several previous studies (Craft et al., 1999 and 2002; Surrette & Brewer, 2008; Zhang et al., 2009). The evidence emerging from many previous investigations generally indicates that the differences in soil properties between invaded and original native communities are associated with the distinct structural and functional traits of the invasive versus the native species; namely nutrient uptake, root system size and structure, litter production, foliar nutrient resorption, and growth rate (Lindsay & French, 2005; Titus, 2009; Sardans & Peñuelas, 2012; Novoa et al., 2014).

Nevertheless, the replacement of mangrove woody ecosystems by tallgrass formations is clearly associated with an extensive change in the physical and chemical traits of the whole ecosystem, with biomass loss, reductions in soil bulk density, and depletions of C, N, and P stocks in the plant-soil system. These findings suggest that an eventual future regeneration process would be difficult because the ecosystem has become a lot less fertile and with sandy soil, conditions that are unfavorable for the reestablishment of the original woody community, whose higher biomass requires greater resources that largely exceeds the supply capacity of the current invaded system. Additionally, the lower ability to retain N and P has negative consequences for water quality since it promotes eutrophication processes.

Moreover, these elements combined also worsen the overall C and nutrients storing capacity of these wetlands and should be considered as a general process reducing the environmental quality of the ecosystem.

FINAL REMARKS AND CONCLUSION

We show that the strong ecosystem impacts on soil characteristics, biomass accumulation, and plant-soil system C, N, and P stocks after the successful invasion of *S. alterniflora* are clearly different depending on the original native community being replaced.

When replacing the native grass *P. australis*, *S. alterniflora* did not produce a change in soil traits, biomass accumulation or plant-soil C and N storing capacity. However, a higher ability to store more P in both the soil and stand plant biomass suggests the possibility of a decrease in ecosystem N:P ratios, which may imply future consequences for the whole below- and above-ground trophic chains. Secondly, a higher efficiency to absorb P might improve the P-filtering performance by the ecosystem, thus better preventing the eutrophication of water.

However, the replacement of the native mangrove communities by *S. alterniflora* resulted in several critical impacts and involved a serious environmental problem. These included an enrichment of sand in soil with a consequent loss of nutrient retention capacity, the loss of great amounts of C, N, and P out of the plant-soil system with a general loss of plant production and decay of water quality, thereby exacerbating potential eutrophication processes. Moreover, the loss of C and nutrient decreased the overall fertility of the system, strongly hampering the future re-establishment of the original woody mangrove communities.

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CONFLICS OF INTEREST

The authors declare no conflicts of interest.

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Figure Captions

FIGURE 1 The location of the study area and sampling sites in China.

FIGURE 2 C, N, and P stocks (mean ± S.E.) in above-ground biomass of invasive tallgrass wetland communities of *Spartina alterniflora* (in black) replacing tall grass native *Phragmites australis* community wetlands (in red) and also replacing mangrove (dominated by the native species *Avicennia marina*) communities (in green).

FIGURE 3 Above-ground biomass (mean ± S.E.) of invasive tallgrass wetland communities of *Spartina alterniflora* (in black) replacing tall grass native *Phragmites australis* community wetlands (in red) and replacing mangrove (dominated by the native species *Kandelia obovata*) communities (in blue) and also replacing mangrove (dominated by the native species *Avicennia marina*) communities (in green).

FIGURE 4 Results of the general discriminant analysis (GDA) with the different studied soil variables as independent continuous variables, different sites as categorical controlling independent variable, and community types (Mangrove and *Spartina alterniflora* communities) as dependent grouping categorical variable.

TABLE 1 Results of the mixed models of sites where *Spartina alterniflora* has replaced native *Phragmites australis* tallgrass with different studied plant and soil variables as dependent factors, species invasion as fixed factor, and site and soil depth as random values in the case of soil variables. SOC = soil organic carbon, DOC = dissolved organic carbon, LOC = labile organic carbon, MBC = microbial biomass organic carbon. Significant responses ($P < 0.05$) to *S. alterniflora* invasion is highlighted in bold type

Dependent variables	Mixed model					
	lme(Dependent variable ~ invasion, data = dades, random = list(~1|site, ~1|soildepth))					
	Fixed Factor (invasion)				Model results	
	Native	Invasive	F	*P*-value	R^2m	R^2c
SOC (mg g^{-1})	21.2±0.6	20.9±0.6	0.28	0.60	0.0022	0.48
LOC (mg g^{-1})	3.69±0.24	3.63±0.17	0.055	0.82	0.00051	0.34
DOC (mg g^{-1})	118±8	121±10	1.44	0.23	0.00093	0.95
MBC (mg g^{-1})	**300±22**	**336±24**	**13.2**	**<0.0001**	0.012	0.94
Soil Total C content (t ha^{-1})	**17.5±0.6**	**18.9±0.7**	**4.36**	**0.041**	0.024	0.61
Soil Total N content (t ha^{-1})	1.21±0.05	1.22±0.06	0.016	0.90	0.0001	0.57
Soil Total P content (t ha^{-1})	**0.783±0.027**	**0.850±0.033**	**11.3**	**0.0014**	0.027	0.83
Soil C:N	**15.1±0.7**	**16.4±0.9**	**21.3**	**<0.0001**	0.014	0.95
Soil C:P	22.4±0.5	22.4±0.5	0.0009	0.98	0.0001	0.17
Soil N:P	**1.62±0.09**	**1.52±0.09**	**4.12**	**0.047**	0.0072	0.88
Plant height	**2.63±0.10**	**1.60±0.05**	**130**	**<0.0001**	0.53	0.71
Plant density (plant m^{-2})	**90.9±9.2**	**155±9**	**220**	**<0.0001**	0.20	0.93
Soil [N] (g kg^{-1})	**1.55±0.10**	**1.43±0.10**	**4.80**	**0.033**	0.0080	0.88
Soil [P] (g kg^{-1})	0.944±0.013	0.931±0.012	1.99	0.16	0.0064	0.77
Soil pH	7.32±0.19	7.40±0.18	2.77	0.10	0.00089	0.98
Soil salinity (mS cm^{-1})	1.92±0.29	1.97±0.30	0.20	0.65	0.00014	0.95
Soil water content (%)	41.9±1.5	40.8±1.6	2.29	0.14	0.0028	0.91
Soil bulk density (g cm^{-3})	**0.851±0.037**	**0.912±0.039**	**7.09**	**0.01**	0.014	0.86
Soil Clay content (%)	14.1±0.7	14.6±0.8	0.57	0.45	0.0023	0.71
Soil silt content (%)	**65.1±1.3**	**62.4±1.4**	**14.8**	**<0.0001**	0.022	0.90
Soil sandy content (%)	**20.7±1.8**	**23.0±2.1**	**5.37**	**0.024**	0.0071	0.91

TABLE 2 Results of the mixed models of sites where a *Spartina alterniflora* have replaced a native mangrove community with different studied plant and soil variables as dependent factors, species invasion as fixed factor and site and soil depth as random values in the case of soil variables. SOC = soil organic carbon, DOC = dissolved organic carbon, LOC = labile organic carbon, MBC = microbial biomass organic carbon. Significant responses (P<0.05) to *Spartina alterniflora* invasion is highlighted in bold type

Dependent variables	Mixed model					
	lme(Dependent variable ~ invasion, data = dades, random = list(~1|site, ~1|soildepth))					
	Fixed Factor (invasion)				Model results	
	Native	Invasive	F	*P*-value	R^2m	R^2c
SOC (mg g^{-1})	**16.6±0.5a**	**14.8±0.4b**	**41.9**	**<0.0001**	0.034	0.86
LOC (mg g^{-1})	4.20±0.15	4.29±0.14	0.067	0.80	0.00033	0.17
DOC (mg g^{-1})	77.3±4.1	74.2±2.6	0.55	0.46	0.0025	0.25
MBC (mg g^{-1})	337±22	305±21	3.2	0.078	0.0060	0.69
Soil Total C content (t ha^{-1})	**13.3±0.3**	**10.9±0.3**	**89.1**	**<0.0001**	0.16	0.71
Soil Total N content (t ha^{-1})	**1.20±0.03**	**1.03±0.02**	**45.8**	**<0.0001**	0.10	0.63
Soil Total P content (t ha^{-1})	**0.570±0.017**	**0.526±0.014**	**10.3**	**0.0017**	0.020	0.68
Soil C:N	**11.2±0.2**	**10.7±0.2**	**9.16**	**0.0029**	0.016	0.71
Soil C:P	**24.6±0.7**	**21.2±0.5**	**42.5**	**<0.0001**	0.072	0.72
Soil N:P	**2.30±0.10**	**2.06±0.07**	**15.2**	**<0.0001**	0.017	0.81
Plant height	**3.14±0.19**	**1.49±0.04**	**128**	**<0.0001**	0.28	0.64
Plant density (plant m^{-2})	**1.29±0.07**	**100±10**	**202**	**<0.0001**	0.35	0.71
Soil [N] (g kg^{-1})	**1.48±0.05**	**1.39±0.04**	**12.6**	**<0.0001**	0.012	0.84
Soil [P] (g kg^{-1})	0.710±0.025	0.723±0.022	1.87	0.17	0.00086	0.92
Soil pH	**6.14±0.13**	**6.65±0.13**	**24.7**	**<0.0001**	0.035	0.76
Soil salinity (mS cm^{-1})	4.21±0.22	4.29±0.25	0.11	0.74	0.00014	0.80
Soil water content (%)	**46.3±0.9**	**49.6±1.1**	**13.5**	**0.0003**	0.026	0.68
Soil bulk density (g cm^{-3})	**0.855±0.025**	**0.774±0.026**	**31.2**	**<0.0001**	0.022	0.88
Soil Clay content (%)	13.8±0.6	14.6±0.5	1.81	0.18	0.0050	0.54
Soil silt content (%)	**58.5±2.1**	**60.5±2.0**	**5.26**	**0.023**	0.0021	0.93
Soil sandy content (%)	**27.6±2.6**	**24.8±2.4**	**5.46**	**0.021**	0.0028	0.91