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REGULAR PAPER – ECOLOGY/ECOPHYSIOLOGY/ENVIRONMENTAL BIOLOGY

Effects of soil salinity characteristics on three habitats in inland salt marshes

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Abstract

Understanding the effect of soil salinity on the diversity and species distribution of plant communities in inland salt marsh ecosystems could provide solutions for the management of regional saline soils and the protection of salt marsh wetland vegetation. A field experiment in succulent halophyte, *Carex*, and gramineous grass habitats in Ordos, Inner Mongolia (northwest China) was conducted to study the diversity and composition of plants in different saline habitats in inland salt marsh ecosystems. Results showed that plant diversity and species richness in the *Carex* habitat were significantly higher than the succulent halophyte habitat and the gramineous grass habitat ($P < 0.05$). Further, species abundance was higher in the succulent halophyte habitat and the *Carex* habitat than the gramineous grass habitat. Similar results were obtained when considering the abundance of constructive species. No significant differences in the abundance of dominant species and companion species between the gramineous grass habitat and the *Carex* habitat were found. We concluded that species abundance, species richness, species distribution, and plant diversity together explained the response of plant communities in different habitats to soil salinity, especially Na^+ and SO_4^{2-}. This highlights the importance of soil salinity for the maintenance of plant diversity and structural composition in inland salt marsh ecosystems.

Keywords Plant diversity · Saline habitat · Species abundance · Species distribution · Species richness

Introduction

The groundwater level in inland salt marsh wetlands is low (El-Ghani et al. 2014), increasing the biodiversity in these areas under severe environmental conditions (Myers et al. 2000). Inland salt marsh wetlands play an important role in hydrological cycling (Craft 2016), regulating regional climate, carbon sequestration, and biogeochemical cycling (Brevik et al. 2015; Keesstra et al. 2012; Köchy et al. 2015; Mclaughlin and Cohen 2013). Inland salt marsh wetlands in arid and semi-arid regions have an effective role in promoting species richness; the plant communities of wetlands also increase landscape-level diversity (Minggagud and Yang 2013).

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The salinity of soil and water in inland salt marshes is strongly affected by climatic conditions, as well as the chemical characteristics of groundwater (Li et al. 2020). Halophytic species are the dominant species in these habitats (Eallonardo and Leopold 2014). The plant communities that are present in close proximity to salt marshes are characterized by a "patchy" structure, i.e., different species or one species with different levels of growth exist(s) in each "patch". Some studies have found that, on a local scale, soil factors have a greater effect on plant distribution than climactic factors do (Álvarez et al. 2001; Griffiths 2006), owing to the adaptability of the formation of their living environment (Burchill and Kenkel 1991). Halophyte plant communities are effective indicators of soil salinity and are largely determined by physical and chemical characteristics of the soil (Contreras-Cruzado et al. 2017). The structure and composition of plant communities are determined by abiotic factors such as soil characteristics and biotic factors such as interspecific competition (Nargis et al. 2010). The survival rates of plant species and consequently their distribution patterns depend on soil factors (He et al. 2009). Soil salinity and moisture affect the distribution of plants in wetlands

(Eallonardo and Leopold 2014; El-Ghani et al. 2014; Kargar et al. 2012; Koull and Chehma 2015; Minggagud and Yang 2013). The hydropedology and geomorphology of the habitat determines the variability of soil salinity and other features (Biggs et al. 2010). Plant communities around inland salt marshes generally form an obvious regional distribution, with salt-tolerant species being fixedly distributed where high soil salinity occurs (Bueno et al. 2020; Viswanathan et al. 2020). Insufficient attention has been paid to inland salt marshes, and there are fewer related studies on inland salt marshes than on coastal salt marshes (Apaydin et al. 2009; Fan et al. 2011; Lv et al. 2013; Zhang et al. 2013).

The Ordos plateau is the second largest saline-alkali lake distribution area in China. The inland salt marshes within the lake area have significant dynamics and play important ecological functions (El-Ghani et al. 2014). The area also supplies resources for the salt chemical and grazing industries in the region. The effects of climate change and anthropogenic activities have resulted in the phenomenon of fragmentation, and "patching" of salt marshes is particularly prominent in the semi-arid inland areas (Fan et al. 2011; Lv et al. 2013).

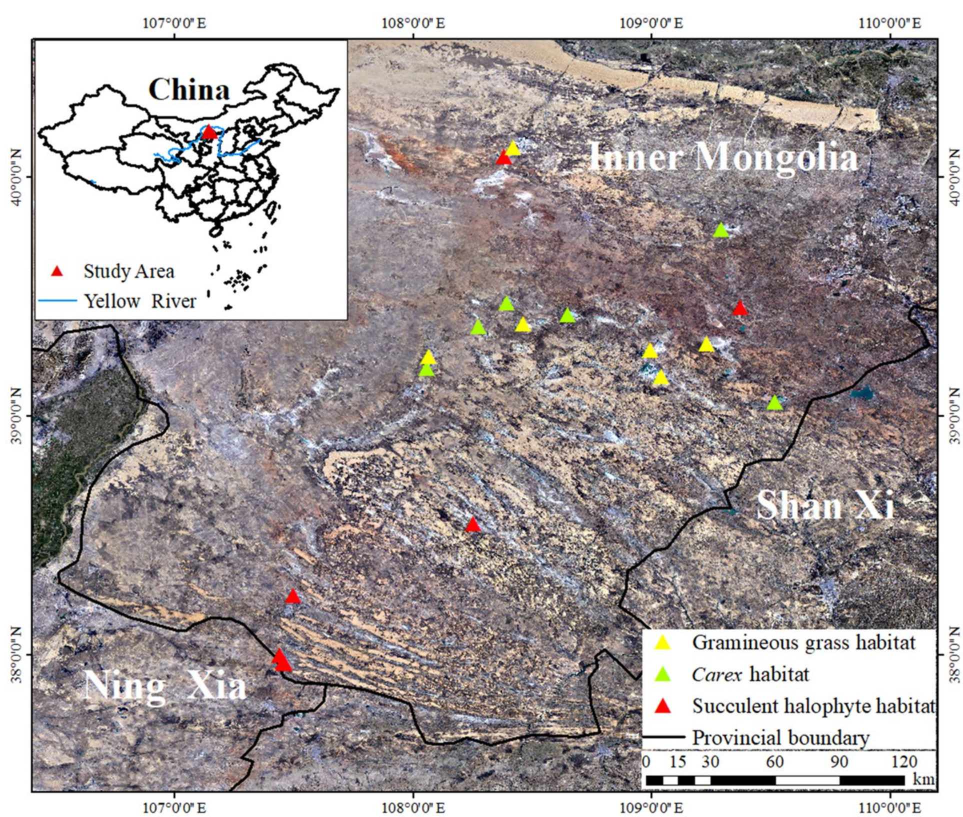
The objectives of this study were (1) to characterize the soil salinity and plant communities' composition in inland salt marshes of Ordos, Inner Mongolia; (2) to reveal the relationship between soil salinity and plant communities; (3) to provide a scientific basis for the protection and rational use of salt marsh wetland resources in the region. We hypothesized that the different concentrations of soil salinity would play a key role in the composition of plant communities, plant diversity, and species distribution. Thus, we studied the species abundance, species richness, species distribution, and Shannon index across three different habitats with varying levels of salinity. However, we did not consider seasonal vegetation changes.

Materials and methods

Study area

The study was conducted in the Ordos plateau of Inner Mongolia (NW China) (Fig. 1). The altitude of this region is 1100–1700 m above sea level, where the climate is considered "semi-arid continental". The winter climate is dry and cold, with high average temperatures in summer; however, there are considerable temperature differences between day and night. The annual mean temperature is 6.2 °C, with a daily maximum temperature of 38 °C and a daily minimum temperature of − 31.4 °C. Annual mean precipitation is 348.3 mm, with the majority of rainfall concentrated in summer, accounting for 70% of the precipitation for the year. Annual mean evaporation is 2506.3 mm. Northwest wind

Fig. 1 Study area



prevails throughout the year; the mean annual wind velocity is 3.6 m s^{-1}. The soil type is predominantly meadow soil.

There are many salt marshes distributed in the basins of the interior drainage area in the Ordos Plateau, and vegetation rings around water on lake beaches, such as halophyte plant communities. Halophyte plant communities are clearly distinguished from other community types; as a result of the isolation in their landscape, halophyte habitats have higher species richness and wetland beta diversity than other habitat types (Minggagud and Yang 2013). This research mainly studied the soil and salinized plant communities around salt marshes. Halophyte plant communities can be divided into succulent halophyte, *Carex*, and gramineous grass habitats. The plant species recorded were classified into three groups: (1) constructive species (the dominant biological species with the advantages of having the largest coverage and occupying the largest space, thereby playing the most prominent role in the construction of communities and the transformation of the environment) (Zhao et al. 2019), (2) dominant species (the biological species with the largest number of individuals in each layer of the community, large biomass, large branches, and leaves covering the ground, strong living ability, and significant effect on the habitat) (Huang et al. 2018), and (3) companion species (other minor species in the community) (Yang et al. 2019).

The selected plots of the three types of habitats, distributed representatively throughout the area, met the following conditions: (1) they were not influenced by human activities; (2) they were located close to the edge of salt marshes, as this is where halophytic vegetation is primarily distributed; and (3) they represented the typicality of the respective habitat. The three selected habitats represented the distribution characteristics of vegetation under different salt conditions in the salt marsh wetlands. The habitat characteristics of these three community types were markedly different, and the different vegetation types were reflective of the habitat soil characteristics. From the distribution of plant communities in three typical habitats, the content, type, and distribution of soil salinity in different regions of the study area could be explored, which is useful for regional saline soil management and salt marsh wetland restoration. Restoration prevents the degradation of wetlands, maintains the stability of ecosystems, and enables them to perform their ecological functions.

Experimental design

In June of 2019, three habitat types were selected as sampling sites, corresponding to the succulent halophyte habitat, the *Carex* habitat, and the gramineous grass habitat. In each habitat, there were six sampling plots, each plot having an area of 50 m × 50 m. The distance between any two plots was > 200 m, from edge to edge. Within each plot, three sampling points were set up at random. In total, there were 54 sampling points (3 sampling points per plot × 6 replicates plots × 3 habitats).

Collection of samples

At each sampling point, one 1 m × 1 m quadrat was set up to determine the composition of the plant community. Plant abundance (the number of plants in each quadrat) and plant richness (the number of plant species in each quadrat) were determined. In addition, soil at a depth of 0–20 cm (The soil layer at this depth is the rhizosphere soil, which is the area where plants are most sensitive to changes in the soil microenvironment) (Hou et al. 2019), was taken using a soil auger at the three sampling points per plot and mixed thoroughly to form a single composition sample for the soil physicochemical analyses (Gonzalez-Alcaraz et al. 2014).

Determination of soil properties

Soil moisture (SM) was measured by heating samples at 104 °C until a constant weight was reached. Soil pH was determined using a pH meter (PHS-3G, China) with a 1:5 soil–water ratio. Soil electrical conductivity (EC) was measured using a conductivity instrument (DDSJ-308F, China) with a 1:5 soil–water ratio (Aubert 1978). Na^+, K^+, Mg^{2+}, Ca^{2+}, Cl^-, and SO_4^{2-} levels were quantified using an ionic chromatographer (CIC-D100, China); CO_3^{2-} and HCO_3^- were determined by titration with H_2SO_4 (AFNOR 1999). The determination of ion concentration is important for assessing soil salinity.

Data analysis

The plant community characteristics studied were: (1) abundance; (2) richness; (3) Shannon index (to represent plant diversity). The Shannon index was calculated according to the following formula (Shannon and Weaver 1950):

$$H' = -\sum Pi \ln Pi, \tag{1}$$

where Pi is the relative abundance of the ith taxon.

A one-way analysis of variance (ANOVA), followed by LSD testing at the 95% confidence level, was used to compare the differences in the environmental factors among the three habitats. We used the Shapiro–Wilk test to check normality of residual, and Levene's tests to check homogeneity of variance, when the residual was not normally distributed, the Kruskal–Wallis non-parametric test was performed (Coleman 2008). All variances passed the normality and homogeneity tests before the ANOVA analyses. Pearson correlations and the Mantel test were used to identify any relationships between plant communities and environmental factors. The R v3.6.2 software program was used to run the above analyses.

The data were analyzed first via detrended correspondence analysis (DCA, length of gradient = 4.002), which recommended that canonical correspondence analysis (CCA) would be an appropriate approach (length of gradient > 4). Partial CCA and the Monte Carlo permutation test were used to determine the conditional effect of soil EC with other environmental variables as covariates; likewise, for SM content, with the rest of the variables as covariates. The DCA, CCA, and partial CCA were each carried out using CANOCO software for Windows 4.5.

Results

Soil characteristics

The soil EC ($F = 17.48$, $P < 0.001$) and Na^+ concentration ($F = 21.73$, $P < 0.001$) were ranked as follows: the succulent halophyte habitat > the gramineous grass habitat > the *Carex* habitat. The soil K^+ ($F = 3.46$, $P = 0.039$), Cl^- ($F = 12.56$, $P < 0.001$), and SO_4^{2-} ($F = 9.20$, $P < 0.001$) concentrations were significantly higher in the succulent halophyte habitat than in the *Carex* habitat by 0.06 g kg^{-1}, 2.50 g kg^{-1}, and 2.93 g kg^{-1}, respectively; the gramineous grass habitat presented intermediate values. The soil Ca^{2+} ($F = 9.04$, $P < 0.001$) and CO_3^{2-} ($F = 3.56$, $P = 0.036$) concentrations were significantly higher in the gramineous grass habitat than in the *Carex* habitat by 0.47 g kg^{-1} and 0.03 g kg^{-1}, respectively, with the succulent halophyte habitat having intermediate values. The SM ($F = 8.01$, $P = 0.001$) was significantly higher in the *Carex* habitat and succulent halophyte habitat than in the gramineous grass habitat by 18.82% and 6.33%, respectively. However, no significant differences in the soil pH or Mg^{2+} concentration were detected among the three habitats (Fig. 2).

Vegetation characteristics

In the three types of salinized habitat a total of 28 plant species were collected. Within these species, 8 were recorded in the succulent halophyte habitat, 14 in the *Carex* habitat, and 21 in the gramineous grass habitat. The abundance ($F = 9.06$, $P < 0.001$) in the *Carex* habitat was significantly higher than in the gramineous grass habitat and the succulent

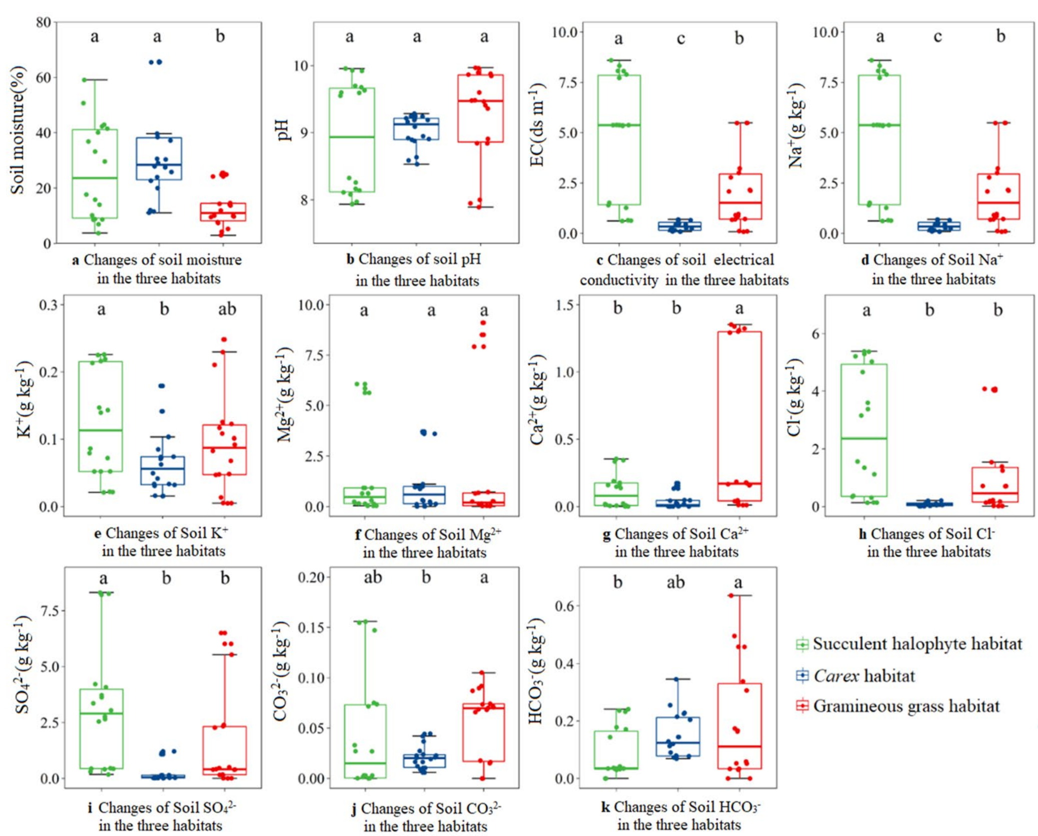


Fig. 2 Changes of soil factors in the three habitats (mean ± SE, $n = 54$). Lower-case letters indicate spatial differences among the habitats at the $P < 0.05$ level

halophyte habitat by 524 and 346, respectively. The richness ($F = 25.62$, $P < 0.001$) was significantly lower in the succulent halophyte habitat than in the gramineous grass habitat and the *Carex* habitat by 3.78 and 3.67, respectively. The Shannon index ($F = 15.95$, $P < 0.001$) was significantly lower in the succulent halophyte habitat than in the gramineous grass habitat and the *Carex* habitat by 0.70 and 0.54, respectively (Fig. 3).

The abundance ($F = 8.65$, $P = 0.001$) of constructive species in the gramineous grass habitat was significantly lower than in the *Carex* habitat and the succulent halophyte habitat by 476.05 and 297.14, respectively. The abundance of dominant species in the *Carex* habitat ($F = 5.34$, $P = 0.008$) was significantly higher than in the succulent halophyte habitat by 87.45, the gramineous grass habitat presented intermediate values. The abundance of companion species in the succulent halophyte habitat was significantly lower than in the *Carex* habitat and the gramineous grass habitat by 60.17 and 63.33, respectively ($F = 3.45$, $P = 0.039$) (Fig. 4).

This showed that abundance took the order of constructive species > dominant species > companion species in the succulent halophyte and the *Carex* habitats, but shifted to a ranking of companion species > dominant species > constructive species in the gramineous grass habitat (Table S1).

Relationship between soil conditions and species distribution

The Mantel test revealed that species distribution was significantly affected by soil salinity (Fig. 5). Pearson correlations showed that the total abundance and abundance of constructive species had a positive correlation with SM but a negative correlation with EC, Na^+, K^+, Cl^- and SO_4^{2-} and that the abundance of constructive species was negatively correlated with Ca^{2+}. The richness and abundance of dominant species had a negative correlation with EC, Na^+, Cl^- and SO_4^{2-} but was positively correlated with HCO_3^-. The Shannon index of plant communities had a negative correlation with Na^+ and SO_4^{2-}. Notably, there were no significant correlations between the abundance of companion species and any of the examined environmental factors.

CCA analysis showed that the 11 soil factors fully explained 100% variance, axis 1 explained 80.2%, and axis 2 explained 68.7% of the total variation (Fig. 5). Under the Monte Carlo permutation test, Na^+ ($F = 5.00$, $P = 0.002$), pH ($F = 3.66$, $P = 0.002$), Ca^{2+} ($F = 3.64$, $P = 0.002$), SM ($F = 3.35$, $P = 0.002$), SO_4^{2-} ($F = 3.12$, $P = 0.002$), Mg^{2+} ($F = 2.74$, $P = 0.004$), HCO_3^- ($F = 2.33$, $P = 0.010$), EC ($F = 2.39$, $P = 0.014$), and Cl^- ($F = 2.29$, $P = 0.006$) were found to be significant environmental variables, accounting for 18.68%, 9.63%, 6.29%, 6.78%, 10.78%, 3.14%, 8.19%, 12.98% and 12.31% of the total variance, respectively (Table S2). The remaining two variables (K^+ and CO_3^{2-}) were not found to be significant, accounting for 11.22% of the variance that is unexplained (Table S2). Finally, CCA showed a clear separation of sample points (Fig. 6), in which the three habitats were clearly divided into three groups in ordination space: (1) succulent halophyte habitat, (2) *Carex* habitat, and (3) gramineous grass habitat.

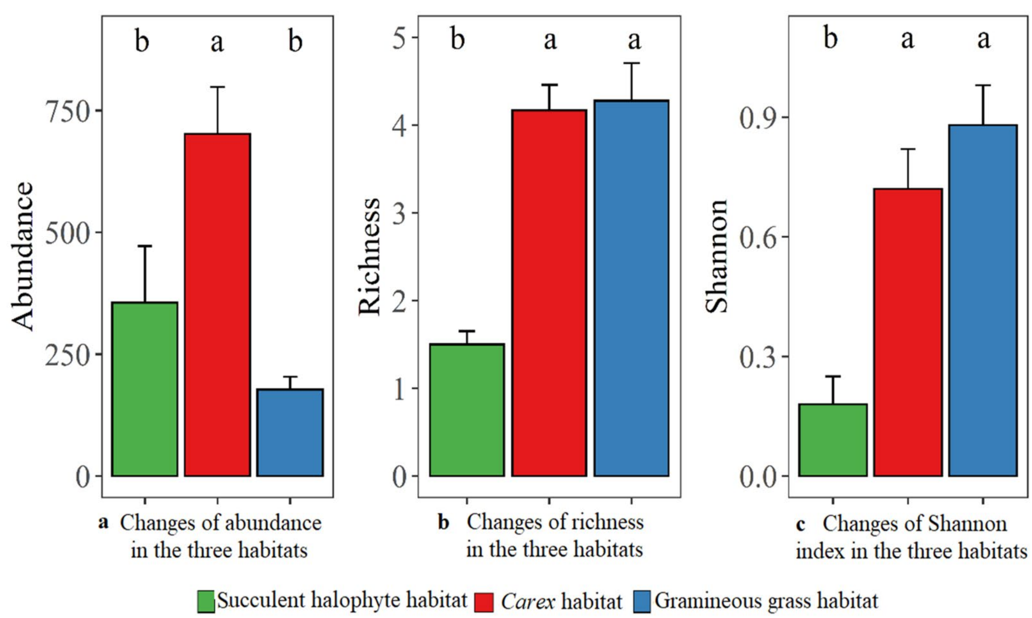


Fig. 3 Changes of plant community indices in the three habitats (mean ± SE, $n = 54$). Lower-case letters indicate spatial differences among the habitats at the $P < 0.05$ level

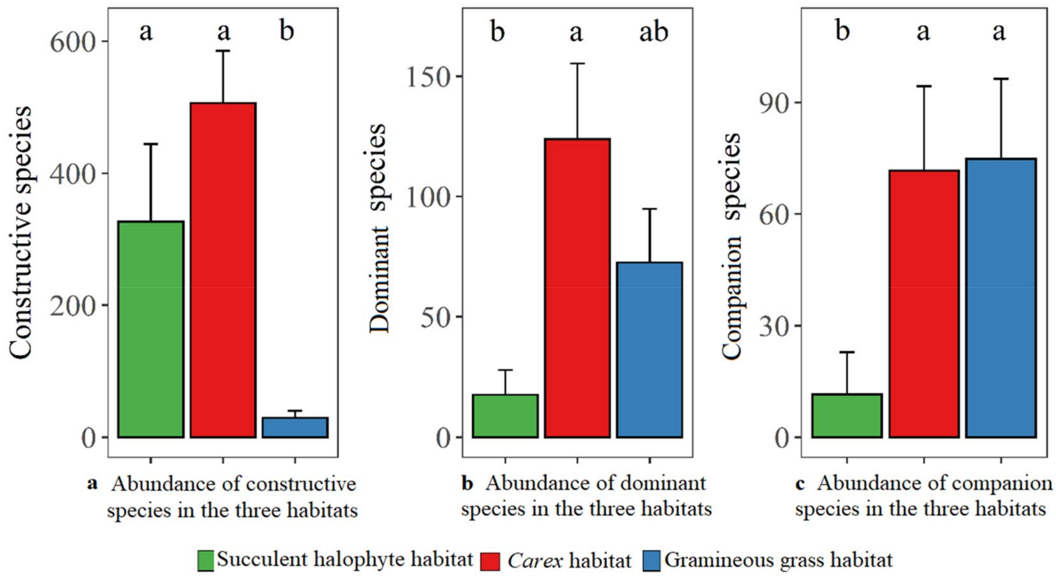


Fig. 4 Abundance of structural groups in the three habitats (mean ± SE, $n = 54$). Lower-case letters indicate spatial differences among the habitats at the $P < 0.05$ level

Discussion

Our field study indicated that the plant communities showed high variation in different saline habitats, according to their Shannon index, richness, abundance (Fig. 3) and the abundance of constructive species, dominant species, and companion species (Fig. 4). The correlation results showed that the three community indices and the abundance of constructive species and dominant species showed significant negative correlation with soil salinity factors, especially Na^+ and SO_4^{2-} (Fig. 5). Soil salinity is closely related to the distribution of species types; therefore, species can be considered effective indicators of salinity in different habitats (Veldkornet et al. 2016).

The *Carex* habitat was composed of species with high levels of SM and low salinity. The abundance of communities was significantly higher in the *Carex* habitat than in both the succulent halophyte habitat and the gramineous grass habitat; this may be attributed to dominance of competitive species in the *Carex* habitat with the lowest salinity (Dwire et al. 2004; Kluse and Diaz 2005). *C. duriuscula* formed obvious clusters with increased density, constituting their own small communities within the community—known as population patches (Wu et al. 2012). *C. duriuscula* was the species with the highest frequency on a mild salinization gradient within the *Carex* habitat. *H. ruthenica*, *T. sinicum*, and *P. anserine* appeared in the environment with less salinity, which was less harsh for the survival of these species. The succulent halophyte habitat represented species with a high salt tolerance; the soil was characterized by high levels of EC, Na^+, Cl^-, and SO_4^{2-}. Succulent halophyte leaves and stems play an important role in adapting to high-salinity environments, as they dilute the toxic salts (Khan et al. 2000). *K. cuspidatum*, *N. tangutorum*, *A. desertorum*, and *S. prostrata* are concentrated in habitats with high salinity, providing them a higher chance of survival than other species. In our study, the abundance of constructive species was significantly higher in the *Carex* habitat and the succulent halophyte habitat than in the gramineous grass habitat (Fig. 4). This could be explained by the fact that the majority of the constructive species inhabited areas where the soil salinity was the highest or the lowest. Accordingly, the findings showed that the cluster distribution of species was more obvious in the high-salinity and low-salinity habitats than in the moderate-salinity habitat, analogous to the succulent halophyte habitat and the *Carex* habitat versus the gramineous grass habitat in present study (Wu et al. 2012).

The gramineous grass habitat included species that are typically presented in soils with high pH, and high concentration of Ca^{2+}, CO_3^{2-}, and HCO_3^-. The plants distributed in the gramineous grass habitat have a wide ecological adaptation range and moderate level of tolerance to salinity; generally, they can form communities under different salt conditions (Feng et al. 2020). In the gramineous grass habitat, the species tend to be distributed in moderate-salinity conditions. *P. australis* is a species with a wide distribution range and high intraspecific variation, typically dominating saline soil. The *A. splendens* community is a typical saline plant community inhabiting arid or semi-arid region; *A. splendens*, *A. cristatum*, and *I. lacteal* are usually distributed in soils with high salinity and alkalinity; their salt tolerance is higher than that of zonal vegetation. Salt stress in

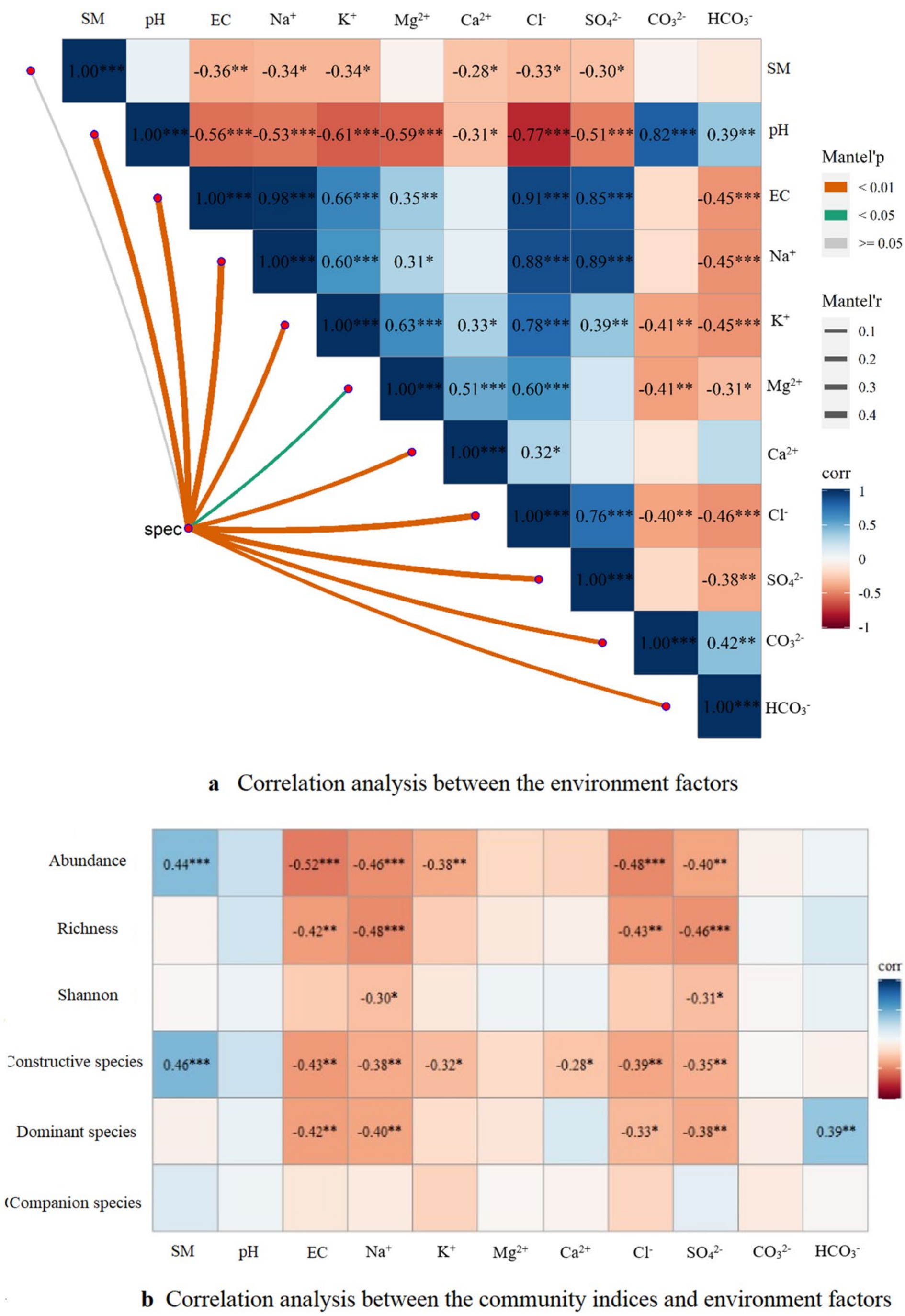
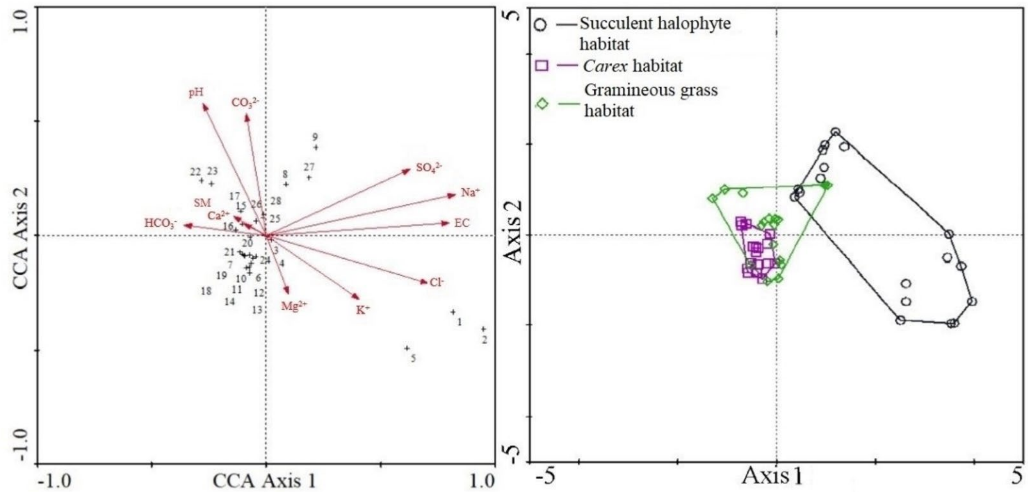


Fig. 5 Correlation analysis between the environment factors and correlation analysis between the community indices and environment factors ($n=54$). *, **, and *** indicate significant difference at 0.05, 0.01, and 0.001 levels (bilateral), respectively. *SM* soil moisture, *pH* soil pH, *EC* soil electrical conductivity

high-salinity environments could also inhibit plant growth. According to the "humped-backed" model, the biodiversity and species richness are the highest under moderate stress; therefore, the gramineous grass habitat could be considered favorable relative to the succulent halophyte habitat and the *Carex* habitat (Grime 2001; Pennings and Callaway 1992). Under moderate-salinity conditions, the abundance of the constructive species in the community was reduced. The abundance of dominant species and companion species was consistently higher in either the *Carex* habitat or the gramineous grass habitat than in the succulent halophyte habitat, indicating that the low- and moderate-salinity conditions were more conducive to the survival of dominant species and companion species than the high-salinity condition. The high-salinity habitat, which is suitable for the survival of succulent halophytes, prevented other species that cannot tolerate salt stress.

The structural composition of a community is a key indicator of ecosystem health (Werner et al. 2019). Our results have demonstrated that the plant community



a CCA ordination biplot showing the effect of soil characteristics on distribution of different species at the three habitats

b Separation of sample points at the three habitats

Fig. 6 Canonical correspondence analysis (CCA) showing the relationship between community composition and environmental variables ($n = 54$). The species groups are represented by +. *SM* soil moisture, *pH* soil pH, *EC* soil electrical conductivity. 1—*K. cuspidatum*, 2—*N. tangutorum*, 3—*P. australis*, 4—*A. splendens*, 5—*A. desertorum*, 6—*S. glauca*, 7—*C. duriuscula*, 8—*C. aculeata*, 9—*S. prostrata*, 10—*H. ruthenica*, 11—*T. sinicum*, 12—*O. racemosa*, 13—*T. palustre*, 14—*P. anserina*, 15—*I. denticulata*, 16—*P. sibiricum*, 17—*A. cristatum*, 18—*I. chinensis*, 19—*P. bifurca*, 20—*P. depressa*, 21—*T. maritima*, 22—*C. epigeios*, 23—*O. glabra*, 24—*A. frigida*, 25—*I. lactea*, 26—*G. maritima*, 27—*A. ordosica*, 28—*T. lanceolate*

composition did qualitatively change in different saline habitats (Table S1), suggesting that different habitats, in having respective edaphic characteristics, varied in how they influenced the distribution of plant communities, leading to the emergence of species-specific habitat preferences (Muchuku et al. 2020). The change in plant community composition indicates that the difference in soil salinity of the three habitats affects the abundance of different species (Castaneda et al. 2013). In heterogeneous habitats, the spatial distribution of plant species is associated with their specific niche (Valladares et al. 2015); niche reflects the status of species within plant communities (Brooker et al. 2008). Constructive species have a wider niche for specific saline habitats and occupy a larger ecological space than dominant and companion species do, thus showing that constructive species exhibit strong adaptability to changes in soil salinity and that their distribution range is large and uniform. Further, constructive species can not only efficiently utilize environmental resources but also possess important ecological status and functions (Dong et al. 2020). Conversely, companion species have a narrow niche width, poor adaptability, and weak inter-species competition (Brooker et al. 2008).

The results of the Mantel test and CCA indicate that soil salinity and moisture both influence species distribution (Figs. 5, 6), which is consistent with the finding of other researches showing that these two factors greatly influence species distribution in saline habitats (Alvarez et al. 2000; Bui 2013; Neffar et al. 2013). In our study, the SM, soil EC, Na^+, Mg^{2+}, Ca^{2+}, Cl^-, SO_4^{2-}, and HCO_3^- of habitats were found to influence the species distribution significantly, explaining 88.78% of the total variance in species distribution. Other studies have also found that the concentration of these ions are the main factors determining the distribution pattern and structure of plant communities in saline habitats of arid and semi-arid regions (Álvarez et al. 2001; Cebas-Csic et al. 1997; Chenchouni 2016; Jafari et al. 2003). Consequently, the distribution pattern essentially reflects the response of plant growth to soil salinity (Castaneda et al. 2013). Notably, the distribution of species was more significantly affected by soil salinity than by SM. This is because plants growing in salt marsh wetlands may have employed an ecological adaptation strategy to survive in the saline habitat, in order to reduce the degree of dependence on SM. Further, the distribution of plant species in saline areas depends on the type of salt rather than the soil EC, which represents the total salt content (Tug et al. 2012). The rough pattern of plant community composition depends on EC, whereas the fine scale pattern considers ionic composition to play an additional vital role in plant community composition (José et al. 1998), thus improving our understanding of the distribution of common plant species in the three plant communities. The majority of species distributed around salt lakes contain substances aiding tolerance to soil salinity, but the tolerance ranges of these species vary. The stress tolerance limit of species plays a paramount role in determining their distribution pattern in stressful habitats (Maestre et al. 2009).

Conclusion

In conclusion, soil salinity showed an inhibitory effect on the plant diversity of salt marshes, thus confirming the results of other studies in arid and semi-arid regions. Moreover, there was a significant inhibitory effect of soil salinity on the abundance, richness, and distribution of species, as well as the predominance of constructive species and dominant species in each habitat. Hence, soil salinity may influence the composition and distribution of plant communities via direct and indirect regulation of salt concentrations and ion compositions in a complex manner. We conclude that the inhibitory effect of soil salinity on salt marsh plant diversity is affected by different habitats, thus emphasizing the general importance of soil salinity in the maintenance of the stability and complexity of inland salt marsh ecosystems.

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Author contributions All authors contributed to the study conception and design. Material preparation, data collection, and data analysis were performed by TH, AZ, XQ, YF, XC and YH. The first draft of the manuscript was written by QC, and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

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Data availability The datasets used and/or analyzed during the current study are available from the corresponding author on reasonable request.

Declarations

Conflict of interest No potential conflicts of interest have been reported by the authors.

Ethics approval and consent to participate Not applicable.

Consent for publication Not applicable.

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