Chin. Geogra. Sci. 2020 Vol. 30 No. 2 pp. 217–232
https://doi.org/10.1007/s11769-020-1109-0

Springer Science Press
www.springerlink.com/content/1002-0063

Spatiotemporal Variation of Plant Diversity Under a Unique Estuarine Wetland Gradient System in the Yellow River Delta, China

SUN Jingkuan[1], CHI Yuan[2], FU Zhanyong[1], LI Tian[1], DONG Kaikai[1]

(1. *Shandong Key Laboratory of Eco-Environmental Science for Yellow River Delta*, *Binzhou University*, *Binzhou* 256603, *Shandong*, *China*; 2. *First Institute of Oceanography*, *Ministry of Natural Resources*, *Qingdao* 266061, *China*)

Abstract: Multiple natural and human factors in estuarine wetlands result in complicated land surface characteristics with distinct spatial and temporal heterogeneities, thereby contributing to the difficulty in identifying spatiotemporal variations and influencing factors of plant diversity. A unique estuarine wetland gradient system (UEWGS) consisting of soil, vegetation, heat, distance, landscape, and anthropogenic gradients was established based on the ecological features of estuarine wetland through remote sensing and field investigation methods. It resolved the complicated land surface characteristics, covered all aspects of factors influencing plant diversity, and possessed distinct spatiotemporal heterogeneities. The Yellow River Delta, the largest estuarine wetland in the northern China, was selected as the study area to demonstrate UEWGS in four seasons in 2017. A total of 123 species were recorded with considerable seasonal difference. *Phragmites australis*, *Suaeda salsa*, and *Tamarix chinensis* were the dominant species, and crop species also played important roles. In single effect, all aspects of gradients exerted significant influences, yet only vegetation gradient possessed significant influences in all seasons. In comprehensive effect, soil, vegetation, heat, and distance gradients showed significant gross influences. Moisture content in soil gradient and net primary productivity in vegetation gradient possessed significant net influences in all seasons and can be considered as the main driving factor and indicator, respectively, of plant diversity. The results validated the significance of UEWGS in revealing the plant diversity spatiotemporal characteristics and influencing factors, and UEWGS possessed universal applicability in the spatiotemporal analysis of plant diversity in estuarine areas.

Keywords: plant diversity; spatiotemporal variation; single effect; comprehensive effect; Yellow River Delta

Citation: SUN Jingkuan, CHI Yuan, FU Zhanyong LI Tian, DONG Kaikai, 2020. Spatiotemporal Variation of Plant Diversity Under a Unique Estuarine Wetland Gradient System. *Chinese Geographical Science*, 30(2): 217–232. https://doi.org/10.1007/s11769-020-1109-0

1 Introduction

Estuarine wetlands possess distinct ecological vulnerability to various natural and anthropogenic disturbances, including climate change, sea level rising, seawater intrusion, flooding, environmental pollution, and urban construction (Chust et al., 2013; Kong et al., 2015; Prandle and Lane, 2015; Mansur et al., 2016; Bárcena et al., 2017; Chi et al., 2018a). Estuarine plants are essential to maintain ecosystem and functions as protecting the shore from erosion, purifying pollution, sequestrating carbon, and providing bird habitats and migration stops (Barbier et al., 2008; Du et al., 2011; Chen et al., 2018; Chi et al., 2018b; c). Plant diversity

Received date: 2019-01-02; accepted date: 2019-04-09

Foundation item: Under the auspices of the National Natural Science Foundation of China (No. 41871089), the Basic Scientific Fund for National Public Research Institutes of China (No. 2018Q07), the National Natural Science Foundation of China (No. 41971119), the Natural Science Foundation of Shandong Province (No. ZR2019MD024), Shandong Province University Youth Innovation Team（No. 2019KJD010）and the Open Research Fund Program of Shandong Provincial Key Laboratory of Eco-Environmental Science for Yellow River Delta (No. 2019KFJJ01)

Corresponding author: CHI Yuan. E-mail: chiyuan@fio.org.cn

plays a fundamental role in regulating the material and energy cycling and maintaining the ecosystem stability (Hooper et al., 2005; Tilman et al., 2006; Ma, 2013; Chi et al., 2016). Revealing the spatiotemporal characteristics and main influencing factors of plant diversity in estuarine wetland is important for grasping the plant diversity variations and providing reference for biodiversity and ecosystem conservation. Plant diversity in estuarine wetland is influenced by multiple natural and human factors. Land-sea interactions, including large amounts of sediment input, coastal erosion, and sea level rising, render the natural conditions unique (Tian et al., 2010; Li et al., 2014; Chi et al., 2018b). Meanwhile, various human activities, such as unban construction, farming, transportation, and sea reclamation, are attracted due to the important geographical positions, abundant natural resources, and good ecological conditions (Huang et al., 2008; Chi et al., 2018a). *Phragmites australis*, *Suaeda salsa*, and *Tamarix chinensis* are the dominant wetland plant species in the Yellow River Delta (Xue et al., 2017). Their distributions are driven by the natural conditions, including soil moisture, salinity, and heat. They are also influenced by human activities, such as sea reclamation and vegetation restoration (Ding et al., 2015; Chi et al., 2018b). Agriculture activities are common in the estuarine areas because of the fertile land and flat terrain (Huang et al., 2008). Thus, crop species are widespread and replace the native wetland species, accompanying with other alien species. Crop species are artificial species, and their growth is affected by natural conditions (Chi et al., 2018c). All these conditions contribute to the complicated factors influencing plant diversity, making it difficult to accurately identify the spatiotemporal variations of plant diversity.

Gradient effect analyses are important means to explain plant diversity variations (Austrheim, 2002; Watt and Scrosati, 2013; Arias et al., 2016). The multiple natural and human factors in estuarine wetland result in complicated land surface characteristics with distinct spatial and temporal heterogeneities, which can be resolved in different aspects of gradients. In microscopic aspects, soil is the base of the ecosystem, and soil properties are crucial to plant diversity (Chi et al., 2018b); and heat condition influences water cycling and plants (Qin et al., 2001; Urqueta et al., 2018). In macroscopic aspects, distances to the river and sea indicate the influence generated by them and plant diversity always show regular distributions along the distances (Xue et al., 2017); landscape pattern is always reported to substantially influence plant diversity (Ramalho et al., 2014); and human activities generate anthropogenic gradient due to their differences in intensity and influence on natural ecosystem (Michelsen et al., 2014; Chi et al., 2018a). Therefore, six 'micro to macroscopic' aspects of gradients, namely, soil, vegetation, heat, distance, landscape, and anthropogenic gradients, are considered to resolve the complicated land surface characteristics in estuarine wetland; the gradients consist of various gradient factors, possess distinct spatiotemporal heterogeneities, and constitute the unique estuarine wetland gradient system (UEWGS). Whether and how UEWGS influences the spatiotemporal characteristics of plant diversity are topics worth exploring.

In this study, the Yellow River Delta, the largest estuarine wetland in the northern China, was selected as the study area. A UEWGS was established based on the typical features of the estuarine wetland ecosystem by using field and remote sensing data in four seasons in 2017. The spatiotemporal characteristics of plant diversity were revealed, and the single and comprehensive effects of UEWGS were analyzed to identify the main influencing factors of plant diversity. We aim to solve the following concerns: 1) how UEWGS for plant diversity can be established to resolve the complicated land surface characteristics and cover all aspects of gradients with spatiotemporal heterogeneities in estuarine wetland; 2) does UEWGS possess universal applicability in the spatiotemporal analysis of plant diversity in estuarine areas; and 3) how and what are the spatiotemporal variations and main influencing factors of plant diversity in the Yellow River Delta.

2 Materials and Methods

2.1 Study area

The Yellow River Delta is located at 37°31′N–38°09′N and 118°34′E–119°16′E, and in the estuarine area of the Yellow River (Huanghe River), south to Bohai Bay and west to Laizhou Bay, which are in the Bohai Sea (Fig. 1). It possesses the largest newly formed wetland in north China and a large number of water and sediment input via the river (Cui and Li, 2011; Chi et al., 2018b). The Yellow River Delta has various ecological functions

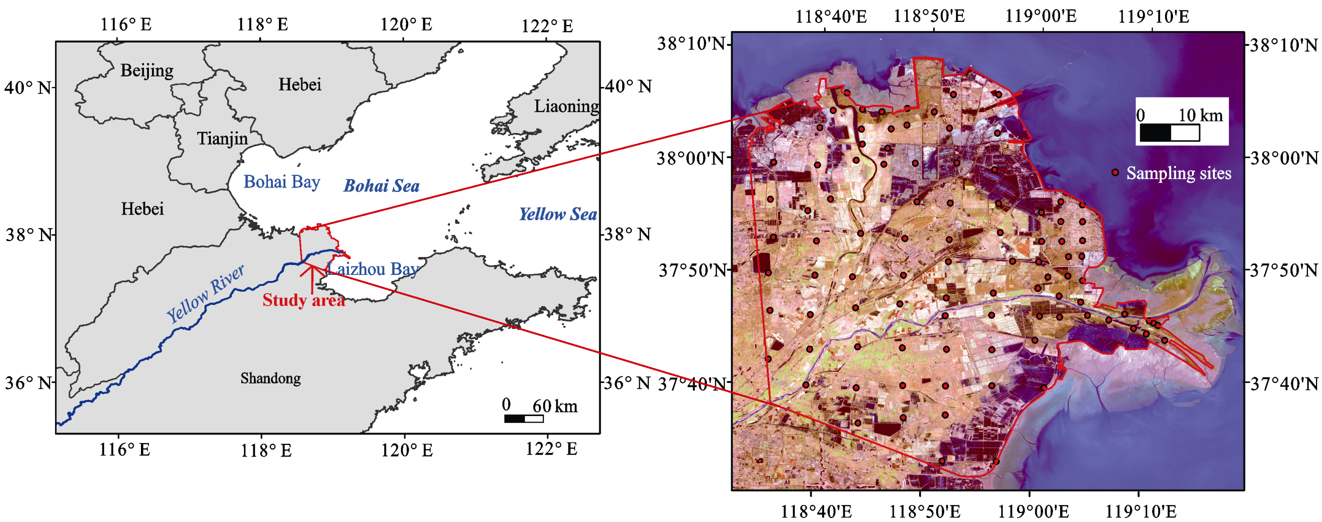

Fig. 1 Location and sampling sites of the study area

and provides key bird habitats and migration stopover sites, but it exhibits evident vulnerability (Kong et al., 2015; Chi et al., 2018a). Various plants cover the delta and are influenced by multiple gradient effects. Land surface characteristics possess distinct heterogeneity caused by the aforementioned natural and human factors (Fan et al., 2012; Chi et al., 2018a). The components of the land surface characteristics, including soil, vegetation, heat, distances to typical land features, landscape pattern, and human disturbance, vary considerably in space. Meanwhile, seasonal differences in some components result in temporal variations. All these conditions result in UEWGS and the multiple effects of UEWGS on plant diversity in both spatial and temporal aspects. However, the spatiotemporal characteristics of plant diversity under UEWGS are unclear.

2.2 Data sources

2.2.1 Field investigation

Field investigations were conducted in February, May, August, and October 2017, thereby representing different seasons of winter, spring, summer, and autumn, respectively. Sampling sites were set on the basis of distribution, representativeness, and accessibility, and 95 sampling sites were finally investigated, of which 77 sites were wetland vegetation and 18 sites are other vegetation (Fig. 1). The latitude and longitude of each sampling site were measured using a handheld GPS device, and land cover types and plant community were recorded. In each season, plant data, including species, abundance, and height of tree, shrub, and herb layers, were recorded. Surface soil samples (0–30 cm) were collected. Then, moisture content (MC), salinity (Sa), and pH were measured in the Shandong Provincial Key Laboratory of Eco-Environmental Science for Yellow River Delta, Binzhou University. MC was measured using an oven drying method, Sa was measured using a gravimetric method, and pH was measured using a potentiometric method.

2.2.2 Remote sensing data

Remote sensing images were acquired from satellite LANDSAT 8, which was launched at 2013 with an operational land imager and a thermal infrared sensor. The data are open source and provided by U.S. Geological Survey (https://www.usgs.gov/land-resources/nli/landsat). For scenes of images in February, May, August, and October, which are in accordance with the time of field investigation and have minimal or no clouds with a resolution of 30 m × 30 m, were adopted. Radiometric calibration and band fusion were conducted via ENVI 5.3 and ArcGIS 10.0. The spectral radiance and reflectance were obtained. Land cover types were classified as wetland vegetation, bare land, water area, farmland, saltern, and construction land through visual interpretation on the basis of fused remote sensing data and then modified by field investigation. The latter three were typical exploitation types in the study area. The classification accuracy was assessed based on the corresponding Google Earth map, and the Kappa coefficient was 0.91, which achieved a good performance (Chi et al., 2018d).

2.3 Plant diversity assessment

2.3.1 Plant diversity determination

Plant diversity refers to α diversity and was determined using biodiversity indices on the basis of the important value (*IV*) of species. *IV* was calculated using the following Equation (1) (Zhang, 2004; Fang et al., 2009; Chi et al., 2016):

$$IV_{s,i} = \left(\frac{Ab_{s,i}}{Ab_s} + \frac{Co_{s,i}}{Co_s} + \frac{He_{s,i}}{He_s}\right)/3 \quad (1)$$

where $IV_{s,i}$, $Ab_{s,i}$, $Co_{s,i}$, and $He_{s,i}$ are *IV*, abundance, coverage, and height of species *i* in sample site *s*, respectively; and Ab_s, Co_s, and He_s are the total abundance, total coverage, and total height in sample site *s*, respectively. The species with the highest *IV* was considered as the dominant species in a site, and the maps of dominant species in different sampling sites in different seasons were obtained. Ten species with the highest *IVs* were considered as the dominant species in the entire study area. Although most of the investigated sample points were wetland vegetation, due to the development of agriculture, few sampling points were transformed to farmland. The crops in these sampling points were included in the biodiversity evaluation to show the impact of agricultural development on wetland biodiversity.

The common used biodiversity indices, namely, species number (*N*), Shannon-Wiener index (*H'*), and Pielou index (*E*), were adopted. *N* directly refers to species richness, *H'* reflects species complexity, and *E* indicates species evenness. The equations are as follows:

$$H'_s = -\sum_{i=1}^{n} IV_{s,i} \mathrm{Ln} IV_{s,i} \quad (2)$$

$$E_s = H'_s / \mathrm{Ln}(N_s) \quad (3)$$

where N_s, H'_s, and E_s are the species number, Shannon-Wiener index, and Pielou index of site *s*, respectively.

2.3.2 Spatiotemporal analysis of plant diversity

The spatial distributions of plant diversity were exhibited using ArcGIS 10.0, the maps of plant diversity in different seasons were directly obtained using *N*, *H'*, and *E* values in each site. To further reveal the spatiotemporal analysis of plant diversity, we analyzed *N*, *H'*, and *E* in different nature reserves, and plant communities in different seasons.

2.4 Estuarine wetland gradient effects assessment

2.4.1 Establishment of unique estuarine wetland gradient system (UEWGS)

UEWGS was established based on the ecological features of estuarine wetland through remote sensing and field investigation methods. It consists of six aspects of gradients and comprises 12 gradient factors (Table 1).

(1) Soil gradient. Soil properties in estuarine wetland including MC, Sa, and pH are the crucial factors for the ecosystem and plant diversity (Chi et al., 2018b). Vegetation species are always distributed regularly along the soil gradients in estuarine areas (He et al., 2011; Xue et al., 2017). Soil MC is an important water source, and wetland damage and degradation are closely related to water (Wang et al., 2011). Soil Sa, which is related to the salinization, considerably affects soil quality, plant community, and crop yield and severely influences ecosystem health (Aragüés et al., 2014; Cassel et al., 2015; Wang et al., 2018). Soil pH is also a restricting factor for vegetation condition, and limitations to crop production may emerge when soil is excessively acidic or alkaline (Filippi et al., 2018). The data of soil gradient factors were derived from field data with season differences.

(2) Vegetation gradient. Vegetation gradient refers to the vegetation growth state, which are presented by biomass or productivity. Many studies indicate high correlations between plant diversity and productivity (Zhang and Zhang, 2003). Normalized difference vegetation index (NDVI) and net primary productivity (NPP) were adopted to represent vegetation gradient. NDVI

Table 1 The estuarine wetland gradient system for plant diversity

Gradient classification	Gradient factors	Gradient type	Data source
Soil gradient	MC, Sa, pH	Seasonal	Field sampling
Vegetation gradient	NDVI, NPP	Seasonal	Remote sensing
Heat gradient	LST	Seasonal	Remote sensing
Distance gradient	DTY, DTS	Unseasonal	Remote sensing
Landscape gradient	VC, ED, PD	Unseasonal	Remote sensing
Anthropogenic gradient	HII	Unseasonal	Remote sensing

Notes: MC: soil moisture content; Sa: soil salinity; pH: soil pH; NDVI: normalized difference vegetation index; NPP: net primary productivity; LST: land surface temperature; DTY: distance to Yellow River; DTS: distance to shoreline; VC: vegetation coverage; PD: patch density; ED: edge density; HII: human interference index. Gradient type: seasonal gradients vary across seasons, and unseasonal gradients stay the same in different seasons can rapidly reflect the vegetation condition through the band calculation of remote sensing data (Chi et al., 2018a). NPP refers to the remaining part of the organic matter produced by plant photosynthesis minus the consumption by respiration. It represents the efficiency and quality of an ecosystem and is fundamental for the survival and reproduction of each member of the ecosystem (Chi et al., 2018c). In contrast to NDVI directly representing the growth condition without considering the differences in vegetation types, NPP also focuses on vegetation types and meteorological condition. The data of vegetation gradient factors were derived from remote sensing with season differences. The calculation methods for NDVI and NPP can be found in the study of Chi et al. (2018c).

(3) Heat gradient. Heat condition is important for water cycling, energy flow, and other ecological processes in estuarine ecosystem, thereby influencing the plant diversity (Qin et al., 2001; Li et al., 2018; Urqueta et al., 2018). Heat condition is influenced by natural and human factors, including solar radiation, atmospheric condition, and land surface characteristics (Li et al., 2018; Hadria et al., 2018). At one point in time in an area, land surface characteristics become the main factor of heat gradient (Bertoldi et al., 2010). Human activities considerably affect heat conditions. Urban and rural constructions always result in the increase in heat, and vegetation planting and saltern reclamation lead to the decrease in heat (Chi et al., 2015). Heat condition was represented by land surface temperature (LST) by using the following equations:

$$LST = T_{10} + A\,(T_{10} - T_{11}) + B \tag{4}$$

where T_{10} and T_{11} are the at-satellite brightness temperatures (K) of bands 10 and 11, respectively, which are calculated using the radiance and metadata; and A and B are the intermediate parameters. The detailed calculation method can be found in the study of Chi et al. (2015). The data of heat gradient factor were derived from remote sensing with season differences.

(4) Distance gradient. Distance gradient refers to the distances to the typical land features involving plant diversity. The sea and the Yellow River are the most distinct land features in the study area. Sediment input via the Yellow River is the fundamental force of delta formation and extension, and the freshwater of the river provides an important water source for vegetation growth and relieving soil salinization (Fan et al., 2012; Chi et al., 2018d). Seawater intrusion and coastal erosion from the sea considerably threaten plant community and ecosystem stability (Yue et al., 2003; Xing et al., 2016). Thus, the sea and the Yellow River were selected as the typical land features, and distances to them generated distance gradient. The distances to the Yellow River (DTY) and sea (DTS) were obtained through Euclidean Distance tool in ArcGIS10.0. The data of distance gradient factors were derived from remote sensing with no season differences.

(5) Landscape gradient. Landscape gradient factors indicate the outcome of natural conditions and human activities on the space and substantially affects estuarine ecological processes (Strohbach and Haase, 2012; Ramalho et al., 2014). Landscape fragmentation considerably threatens biodiversity (Cook, 2002; Ramalho et al., 2014). Three factors, namely, vegetation coverage (VC), patch density (PD), and edge density (ED) were selected to represent the landscape gradient. VC, PD, and ED were calculated using the proportion of vegetation area, patch number, and total edge length in the analysis unit. Unit size was determined by the buffer effect and a 300 m × 300 m size was adopted. The data of landscape gradient factors were derived from remote sensing with no season differences.

(6) Anthropogenic gradient. Anthropogenic gradient directly represents the human activity intensity and its negative influence on plant diversity (Michelsen et al., 2014; Chi et al., 2018a). Human activities have spread all over the world and deeply affect the natural ecosystem, and plant diversity always varies clearly along the human activity intensity gradient (Moffatt et al., 2004; McKinney, 2008; Chi et al., 2016). We used human interference index (HII) to reflect the anthropogenic gradient, and the calculation methods are as follows:

$$HII = \begin{cases} \sum_{i=1}^{5} [EA_i \times IC_{i,min} + EA_i \times (IC_{i,max} - IC_{i,min}) \times (1 - EV_i)] / TA & D_i = 0 \text{ m} \\ \sum_{i=1}^{5} \frac{200 - D_i}{200} \times [EA_i \times IC_{i,min} + EA_i \times (IC_{i,max} - IC_{i,min}) \times (1 - EV_i)] / TA & 0 < D_i \le 200 \text{ m} \end{cases} \tag{5}$$

where EA_i is the occupied or adjacent area of exploitation type i, and i = 1, 2, and 3 are construction land, saltern, and farmland, respectively, in the land cover types. IC_i is the influence coefficient of exploitation type i; $IC_{i,\min}$ and $IC_{i,\max}$ are the minimum and maximum values of IC_i, respectively; EV_i is the ecological value of exploitation type i; TA is the total area of the analysis unit; and D_i is the distance from exploitation type i. High HII indicates considerable human interference. Detailed calculation method and process are provided in the study by Chi et al. (2018a). The data of anthropogenic gradient factor were derived from remote sensing with no season differences.

2.4.2 Estuarine wetland gradient effects on plant diversity

The effects of UEWGS on plant diversity were analyzed from single and comprehensive perspectives, respectively. For single perspective, each gradient factor was divided into five equal percentile intervals [0, 20%], (20%, 40%], (40%, 60%], (60%, 80%], and (80%, 100%] according to the value, and one-way ANOVA and line chart were adopted to identify the differences and change characteristics of plant diversity along the gradient based on the intervals through SPSS 18 and Excel, respectively.

For comprehensive perspective, due to the existence of 12 gradient factors that may be correlated with one another, canonical correspondence analysis (CCA) ordination was adopted to reveal the influence process and degree of each gradient factor on plant diversity through Canoco 4.5 (Jiang et al., 2007). The matrices of 'sampling sites × species' and 'sampling sites × gradient factors' were species and environmental data, respectively. Data from four seasons were analyzed. Monte Carlo permutation test was used to test the significances of axes. We identified the influence degrees of the gradient factors through the following procedures. CCA was conducted using each gradient factor as an independent variable to analyze its gross influence. Partial CCA was performed using each gradient factor as an independent variable and the others as covariates to analyze its net influence. Significance tests were also conducted through Monte Carlo permutation test, and canonical characteristics values were adopted to evaluate the influence degrees of the factors (Chi et al., 2016).

3 Results

3.1 Spatiotemporal characteristics of plant diversity

3.1.1 Species composition and dominant species

We recorded 123 species in four seasons, 76, 91, 74, and 27 of which were recorded in spring, summer, autumn, and winter, respectively. The 123 species belonged to 98 genera and 45 families. At the family level, Compositae possessed the highest number of species (28), followed by Gramineae and Chenopodiaceae (22 and 10, respectively). At the genus level, *Artemisia* had the highest number of species (eight), followed by *Sonchus* and *Chenopodium* (five and four, respectively).

The dominant species in the whole year were *P. australis*, *S. salsa*, and *T. chinensis* in descending order of their *IVs*. In different seasons, dominant species that possessed the highest 10 *IVs* in each season are shown in Table 2. Except for the aforementioned three species, *Triticum aestivum*, which is crop species, occupied the top three species in spring and autumn.

Table 2 Dominant species in different seasons in study area

Rank	Spring	Summer	Autumn	Winter
1	*Phragmites australis*	*Phragmites australis*	*Phragmites australis*	*Phragmites australis*
2	*Tamarix chinensis*	*Suaeda salsa*	*Suaeda salsa*	*Suaeda salsa*
3	*Triticum aestivum**	*Tamarix chinensis*	*Triticum aestivum**	*Tamarix chinensis*
4	*Suaeda salsa*	*Zea mays**	*Tamarix chinensis*	*Triticum aestivum**
5	*Apocynum venetum*	*Suaeda glauca*	*Imperata cylindrica*	*Setaria viridis*
6	*Imperata cylindrica*	*Setaria viridis*	*Triarrhena sacchariflora*	*Aeluropus sinensis*
7	*Artemisia capillaris*	*Artemisia capillaris*	*Sonchus brachyotus*	*Triarrhena sacchariflora*
8	*Cynanchum chinense*	*Echinochloa crusgalli*	*Suaeda glauca*	*Aster subulatus*
9	*Triarrhena sacchariflora*	*Nelumbo nucifera**	*Artemisia capillaris*	*Artemisia capillaris*
10	*Gossypium hirsutum**	*Cynanchum chinense*	*Gossypium hirsutum**	*Suaeda glauca*

Notes: the dominant species in different seasons were determined by their *IVs* and ranked following a descending order of *IVs*. * The species is artificial crop species

3.1.2 Spatiotemporal characteristics of N, H′, and E

The spatiotemporal characteristics of *N*, *H*′, and *E* in site and regional scales are shown in Fig. 2, respectively. In spring, the central parts of the study area possessed high *N*, *H*′, and *E*. Other areas, including the alongshore areas and western and southern parts, exhibited low *N* and *H*′.

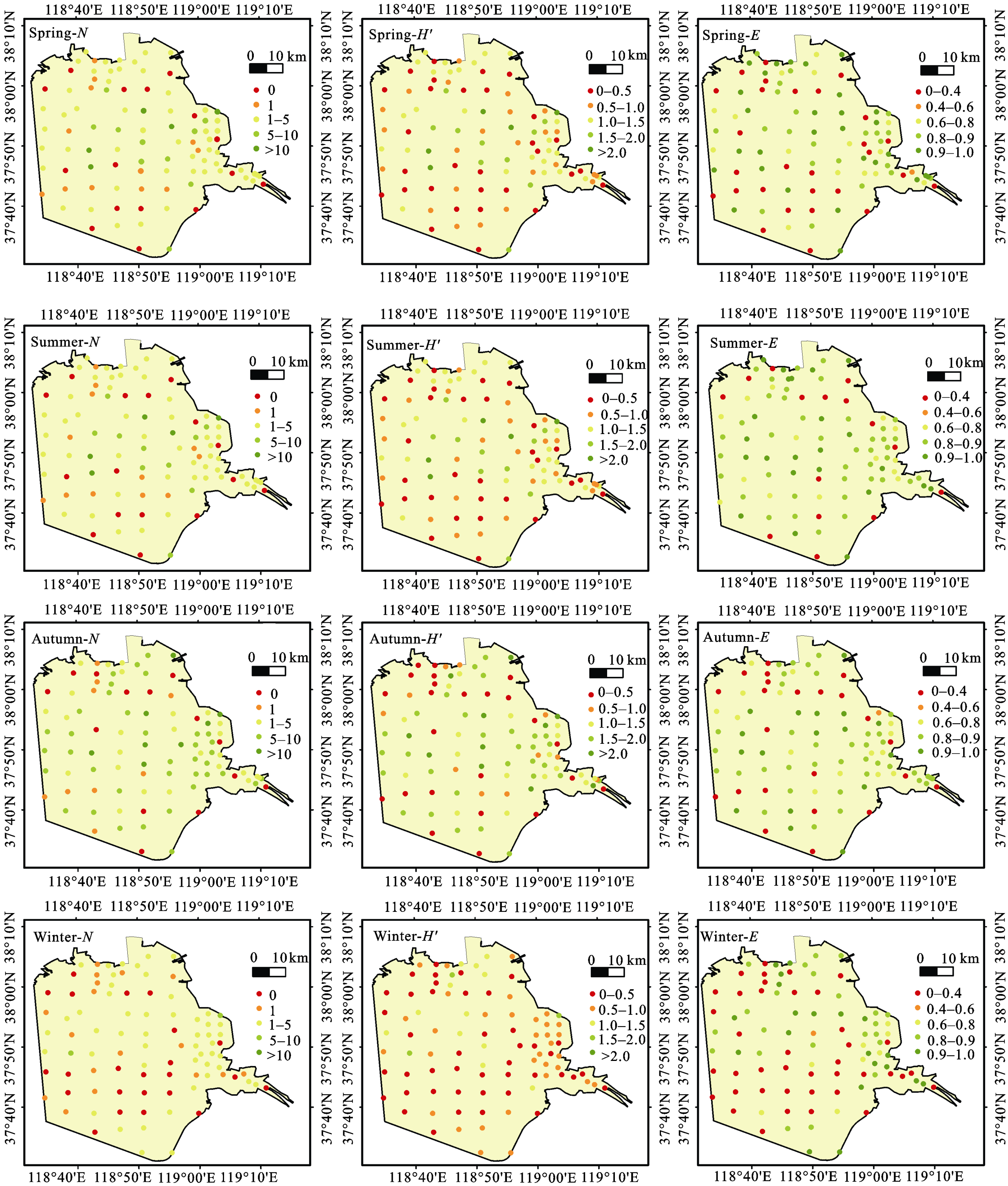

Fig. 2 Plant diversity in site scale: *N*, species number; *H*′, Shannon-Wiener index; *E*, Pielou index

Small areas with high E were scattered in the study area. In summer, the indices showed significant increase in the entire study compared with those in spring. The northwestern and northeastern corners, estuarine mouth areas, and scattered areas in southern parts possessed low index values, whereas other areas had high index values. In autumn, indices were similar to and slightly lower than those in summer, and low index value areas increased scattering in the central parts. In winter, indices reached the lowest of all the seasons; high index value areas occupied a small part in the study area.

N, H', and E in different nature reserves, and plant communities are shown in Fig. 3. Indices were slightly higher in nature reserve than those outside it except in winter. Old estuary possessed lower H' and E in summer and autumn, higher values in winter, and similar values in spring compared with those of new estuary. E value in old estuary was generally higher than that in new estuary. For plant community, *S. salsa* and crop communities generally possessed low indices; *T. chinensis* and other species communities possessed high indices, especially in summer and autumn. Meanwhile, the indices of *P. australis* were intermediate.

3.2 Estuarine wetland gradient effects on plant diversity

3.2.1 Single effect

(1) Effect of soil gradient. For MC, only N and E in spring exhibited significant differences along the gradient ($P < 0.05$). They showed fluctuating decreasing characteristics as a whole and reached the highest in the 2nd interval. For Sa, the three indices at spring, summer, and autumn showed significant differences along the gradient ($P < 0.05$ or 0.01), but no significant differences existed in winter. They showed fluctuating decreasing characteristics and were the highest in the 1st or 3rd interval as a whole. For pH, no significant differences existed along the gradient.

(2) Effect of vegetation gradient. All three indices showed significant differences along the NDVI and NPP gradients in all seasons ($P < 0.01$). Except for winter, they generally increased along the gradients and slightly decreased when reaching the 5th interval.

(3) Effect of heat gradient. Along the LST gradient, the three indices in spring, summer, and autumn showed significant differences ($P < 0.05$ or 0.01). These indices generally first increased and then decreased.

(4) Effect of distance gradient. Only H' and E in winter and only E in winter showed significant differences along the DTY and DTS gradients, respectively ($P < 0.05$). For DTY, H' and E in winter generally increased and reached the highest in the 5th interval. For DTS, E in winter first increased and then decreased and was the highest in the 2nd interval.

(5) Effect of landscape gradient. The three indices showed significant differences along the VC gradient in spring, summer, and autumn ($P < 0.05$ or 0.01) and exhibited initial increasing and then decreasing characteristics. No significant differences existed along PD and ED gradients.

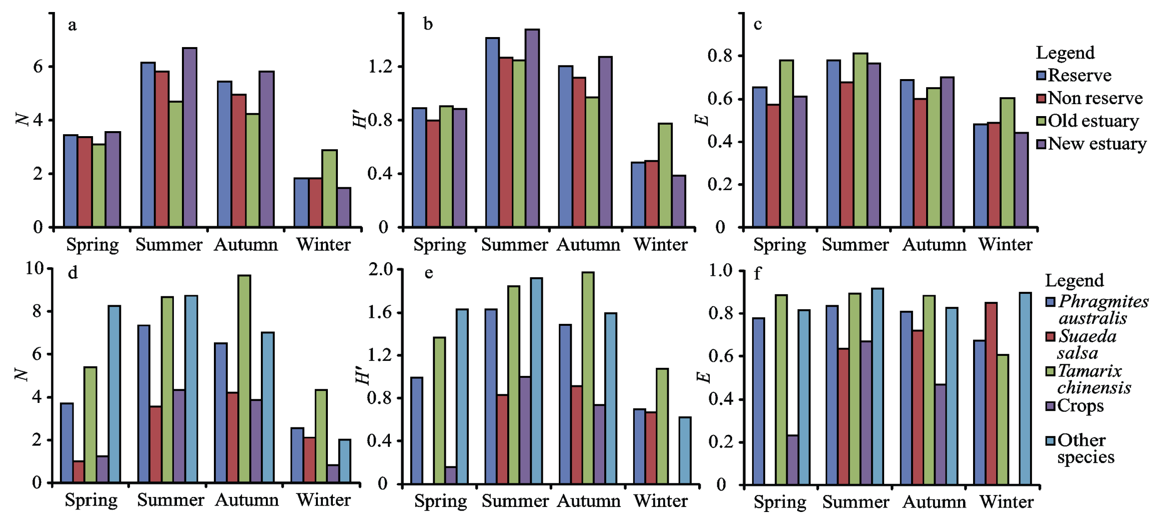

Fig. 3 Plant diversity in different nature reserves (a, b, c), and plant communities (d, e, f): N, species number; H', Shannon-Wiener index; E, Pielou index

(6) Effect of anthropogenic gradient. The *N*, *H'*, and *E* in summer, *H'* and *E* in spring, and *E* in autumn showed significant differences along the *HII* gradient ($P < 0.05$ or 0.01). These indices exhibited fluctuating decreasing characteristics and reached the highest in the 2nd interval as a whole.

3.2.2 Comprehensive effects

(1) Summary of CCA ordination. CCA results revealed that all canonical axes were statistically significant in all seasons ($P < 0.05$ or 0.01). The cumulative percentage variances of species-environment relations were 65.1%, 67.1%, 70.4%, and 80.5% in spring, summer, autumn, and winter, respectively. Axes 1 and 2 accounted for the most proportions.

(2) CCA ordination diagrams. The two-dimensional CCA ordination diagrams were drawn based on Axes 1 and 2 (Fig. 4 and Fig.5). The projected position and length of each gradient factor on the axis represented the nature and degree of its correlation with the axis (Chi et al., 2016). In spring, from left to right on Axis 1, DTS significantly increased, and NDVI slightly increased; meanwhile, MC, Sa, and DTY considerably decreased, and pH and NPP slightly decreased. From bottom to top on Axis 2, NDVI and NPP considerably increased, and ED slightly increased; meanwhile, Sa considerably decreased. In summer, from left to right on Axis 1, MC and Sa considerably increased, while NDVI and DTS substantially decreased, and *LST* and *HII* slightly decreased. From bottom to top on Axis 2, Sa considerably increased; meanwhile, MC, pH, NDVI, and NPP substantially decreased. In autumn, from left to right on Axis 1, DTS considerably increased, and *LST* slightly increased; meanwhile, MC and NPP significantly decreased, and DTY slightly decreased. From bottom to top on Axis 2, MC substantially increased, and pH slightly increased; meanwhile, PD and ED considerably decreased. In winter, from left to right on Axis 1, NDVI, *LST*, and DTS substantially increased; meanwhile, MC and NPP considerably decreased, and Sa, pH, and DTY slightly decreased. From bottom to top on Axis 2, Sa and DTY substantially increased; meanwhile MC, NDVI, and NPP significantly decreased, and pH, LST, and DTS slightly decreased.

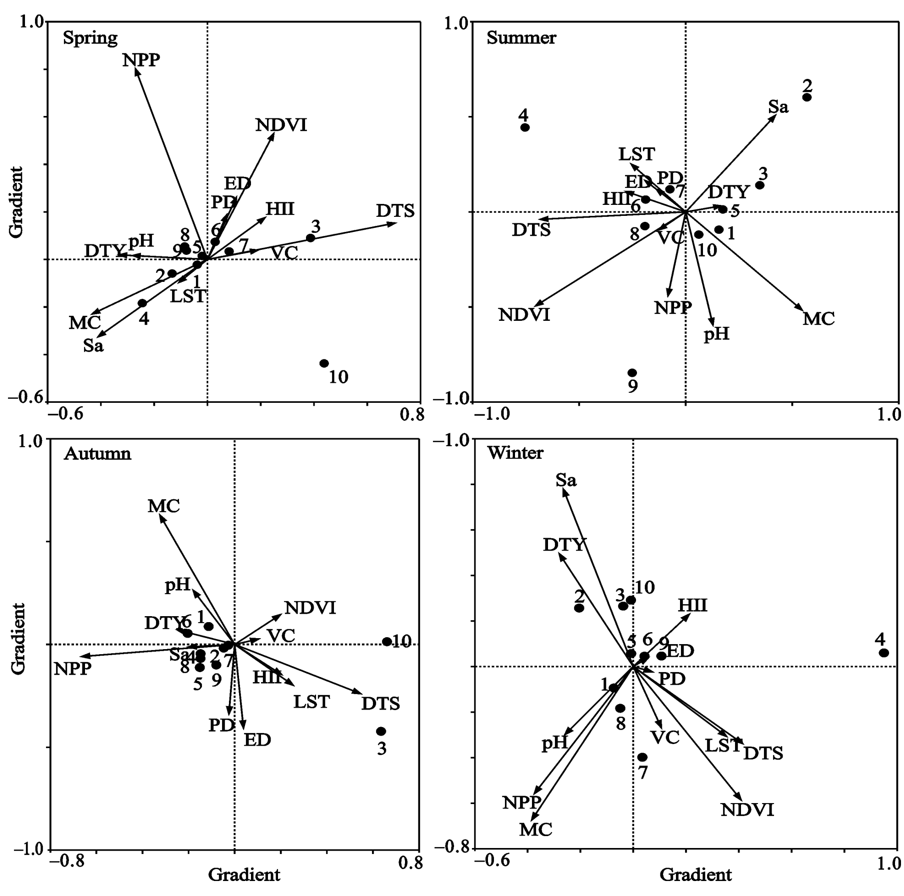

Fig. 4 CCA ordination diagrams of dominant species based on Axes 1 and 2: The species numbers of 1–10 indicate the corresponding dominant species in Table 2; abbreviations for gradient factors are the same as for Table 1

The CCA ordination diagrams of dominant species are shown in Fig. 4. Species sequence numbers 1–10 indicated different dominant species in different seasons (Table 2). In spring, most of the dominant species were distributed near the origin except for species 3, 4, and 10, indicating most of the dominant species are wide distribution without distinct spatial inclinations. Species 3 was mainly distributed in positions with high NDVI and DTS and low MC, Sa, pH, and DTY; species 4 was generally on the contrary. Species 10 was mainly distributed in positions with high DTS and low pH, NDVI, NPP, and DTY. In summer, species 1, 5, 6, 7, 8, and 10 were near the origin. Species 2 was mainly distributed in positions with high Sa and low pH, NDVI, *NPP*, DTS. Species 3 was mainly in positions with high MC and Sa and low NDVI, NPP, *LST*, DTS, and HII. Species 4 was mainly in positions with high NDVI, LST, DTS, and HII and low MC and pH. Species 9 was mainly in positions with high MC, pH, NDVI, NPP, and DTS and low Sa, LST, and HII. In autumn, most of the dominant species were close to the origin except for species 3 and 10. Species 3 was generally in positions with high LST, DTS, PD, ED, and low MC, pH, NPP, and DTY. Species 10 was mainly in positions with high LST and DTS and low MC, pH, NPP, and DTY. In winter, species 1, 5, 6, 8, and 9 were near the origin. Species 2, 3, and 10 were mainly in positions with high Sa and DTY and low MC, pH, NDVI, NPP, LST, and DTS; species 7 was on the contrary. Species 10 was mainly in positions with high NDVI, LST, and DTS and low MC, Sa, pH, DTY, and NPP.

The CCA ordination diagrams of the sampling sites are shown in Fig. 5. The different colors of sampling sites represented different index values, and colors from red to orange, yellow, light green, and then dark green indicated increasing index values. In spring, N and H' exhibited similar distribution characteristics, that is, dark green sites were mainly located in the upper positions of Axis 2, orange sites for N and red sites for H' were mainly in the 4th quadrant, and other sites were evenly distributed in the diagram. For E, red ones were mainly in the 4th quadrant, and other sites were evenly distributed. In summer, for N, dark green sites were mainly in the 2nd and 3th quadrants, and the others were evenly distributed. For H' and E, all the colors of sites were evenly distributed. In autumn, three indices showed similar characteristics, that is, light and dark green sites were mainly in the 2nd and 3th quadrants, orange sites for N and red sites for H' and E were mainly in the 4th quadrant, and the other sites were evenly distributed. In winter, nearly all colors of the sites for three indices were evenly distributed in the diagrams.

(3) Influence degrees of gradient factors. The gross and net influences of gradient factors on plant diversity in different seasons are shown in Table 3. Gradient factors exhibited different influences in different seasons. In spring, MC, Sa, NDVI, NPP, and DTS possessed significant gross influences; MC, NPP, and DTS exhibited significant net influences. In summer, MC, Sa, NDVI, NPP, and DTS possessed significant gross influences; MC and DTS exhibited significant net influences. In autumn, MC, Sa, NDVI, NPP, *LST*, and DTS possessed significant gross influences; MC, NDVI, NPP, *LST*, and DTY exhibited significant net influences. In winter, MC, Sa, NDVI, NPP, DTY, DTS, and *HII* possessed significant gross influences; only MC and NPP exhibited significant net influences.

4 Discussion

4.1 Significance of UEWGS

UEWGS possessed the following significances: 1) unique gradients in estuarine wetland, namely, soil, vegetation, heat, distance, landscape, and anthropogenic gradients, resolved the complicated land surface characteristics and covered all aspects of the factors influencing plant diversity; 2) UEWGS represented both spatial and temporal heterogeneities; all gradients showed spatial heterogeneities; soil, vegetation, and heat gradients exhibited evident seasonal differences; 3) the required data for UEWGS establishment can be easily obtained through conventional field work and remote sensing, and the identification of the single and comprehensive effects of UEWGS can be conducted using the widely used Excel, SPSS, and Canoco software, rendering UEWGS highly applicable to plant diversity study in estuarine areas. Application in the Yellow River Delta demonstrated that UEWGS can accurately reveal plant diversity spatiotemporal characteristics, influencing factors, and their influencing processes and degrees.

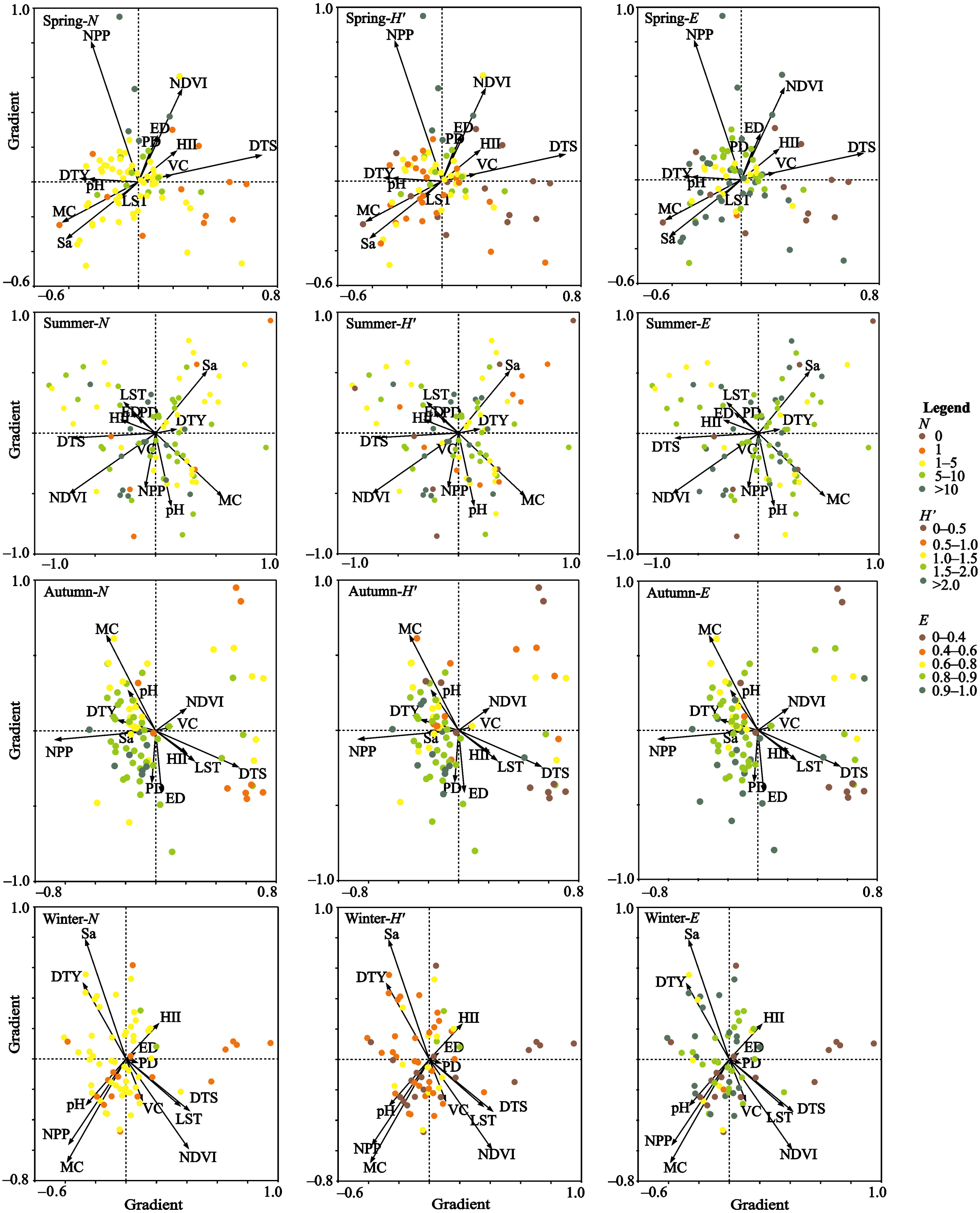

Fig. 5 CCA ordination diagrams of all sampling sites based on Axes 1 and 2: Different colors of sampling sites indicate different plant diversity values as for Fig. 2; abbreviations for gradient factors are the same as for Table 1; abbreviations for the diversity indexes are the same as for Fig. 2

Table 3 Gross and net influences of gradient factors on plant diversity in different seasons

Factor	Spring				Summer				Autumn				Winter			
	Gross influence	*P* value	Net influence	*P* value	Gross influence	*P* value	Net influence	*P* value	Gross influence	*P* value	Net influence	*P* value	Gross influence	*P* value	Net influence	*P* value
MC	0.294**	0.002	0.251**	0.010	0.363**	0.002	0.254*	0.012	0.395**	0.002	0.338**	0.002	0.294**	0.002	0.166*	0.040
Sa	0.340**	0.002	0.224	0.062	0.251*	0.032	0.092	0.912	0.219*	0.048	0.107	0.664	0.251**	0.006	0.122	0.168
pH	0.232	0.07	0.204	0.088	0.214	0.058	0.149	0.432	0.151	0.330	0.154	0.182	0.096	0.520	0.061	0.890
NDVI	0.326**	0.004	0.199	0.128	0.419**	0.004	0.215	0.088	0.312**	0.002	0.350**	0.002	0.245**	0.004	0.113	0.250
NPP	0.393**	0.002	0.397**	0.002	0.270**	0.004	0.261**	0.002	0.436**	0.002	0.507**	0.002	0.226*	0.016	0.261**	0.002
LST	0.207	0.096	0.246*	0.014	0.194	0.158	0.186	0.150	0.225*	0.026	0.225**	0.008	0.163	0.088	0.077	0.720
DTY	0.218	0.100	0.192	0.144	0.182	0.170	0.150	0.436	0.208	0.058	0.204*	0.032	0.185*	0.040	0.090	0.534
DTS	0.378**	0.002	0.238*	0.028	0.340**	0.002	0.135	0.622	0.334**	0.002	0.145	0.248	0.207*	0.024	0.055	0.900
VC	0.135	0.504	0.090	0.920	0.070	0.980	0.151	0.422	0.077	0.896	0.113	0.594	0.061	0.718	0.070	0.752
PD	0.097	0.726	0.100	0.820	0.121	0.630	0.104	0.838	0.128	0.382	0.124	0.474	0.079	0.512	0.062	0.772
ED	0.147	0.460	0.142	0.476	0.147	0.486	0.098	0.920	0.181	0.168	0.153	0.218	0.103	0.374	0.054	0.864
HII	0.142	0.574	0.111	0.752	0.132	0.728	0.119	0.800	0.152	0.346	0.128	0.426	0.217*	0.014	0.162	0.096

Notes: Abbreviations for gradient factors are the same as for Table 1. ** $P < 0.01$, * $P < 0.05$

4.2 Plant diversity variations under UEWGS in the Yellow River Delta

The recorded species in the Yellow River Delta was 123 in 95 sampling sites and showed an intermediate species diversity compared with similar study areas, as follows: the Yangtze River Delta, which is also an important estuarine wetland, had 198 species in 171 sampling sites (Sun, 2013); five southern islands of Miaodao Archipelago, which are in the coastal areas with similar latitude to that of the Yellow River Delta but consist of bedrocks, possessed 114 species in 50 sampling sites (Chi et al., 2016); Hejiagou Basin in northern Shanxi Province, which is in western China with similar latitude to that of the Yellow River Delta, had 57 species in 84 sampling sites (Zheng et al., 2009). In different seasons, plant diversity reached the highest in summer, followed by autumn and spring, and was lowest in winter. This result is determined by substantial seasonal differences of climate conditions in northern China (Chi et al., 2018c). *P. australis*, *S. salsa*, and *T. chinensis*, which are all natural species, were the top three dominant species in the whole year. *P. australis* possessed *IV* much higher than those of the other species, thereby reconfirming its strong adaptability and wide distribution in northern China (Chen et al., 2017; Xue et al., 2017). All these results indicated that the plant species in the Yellow River Delta were generally natural but controlled by human transformation in certain areas.

Plant diversity in the Yellow River Delta exhibited distinct spatiotemporal variations, which was controlled by UEWGS. For soil gradient, MC and Sa exerted significant influences in both single and comprehensive effects, and plant diversity tended to decrease with the increase in MC and Sa, but pH did not show significant influence. These results reconfirmed the importance of MC and Sa in plant community in estuarine wetland and revealed that high MC and Sa were the limiting factors of plant diversity (Wang et al., 2011; Gao et al., 2015; Chi et al., 2018b). For vegetation gradient, NDVI and NPP played the most important roles in both single and comprehensive effects, and plant diversity generally increased with the increase in NDVI and NPP. These results reconfirmed that the good vegetation growth resulted in the high plant diversity (Wang et al., 2016). However, indices showed first increasing and then decreasing characteristics. The flourishing *P. australis* and crops may influence the survival of other species by occupying sunlight and soil water, thereby leading to the decrease in plant diversity (Oindo and Skidmore, 2002). For heat gradient, LST also exerted a significant influence on plant diversity in both effects, and sites with an intermediate LST always possessed high plant diversity. For distance gradient, DTY and DTS showed significant influences mainly in comprehensive effects, and sites with low DTY and high DTS always possessed low plant diversity. Areas near the Yellow River and far from the sea were always occupied by farmland due to their suitability for agriculture (Chi et al., 2018c). Thus, plant diversity was low. Sites with certain DTS showed higher plant diversity than those with the lowest DTS because the latter ones were severely influenced by the sea (Chi et al., 2018d). For landscape gradient, plant diversity was generally insensitive; only VC possessed significant influence in single effect, and PD and ED did not show any significant influences. The reason may be that landscape fragmentation was generally indistinct in the study area. For anthropogenic gradient, HII exerted significant influences mainly in single effect. It indicated that a mild human interference may result in high plant diversity, which was in accordance with the intermediate disturbance hypothesis (Connell, 1979; Molino and Sabatier, 2001).

Gradient factors were correlated with each other, and some gradient factors may exert influences on plant diversity by influencing other factors (Chi et al., 2016). The gross and net influences of each gradient factor in Table 3 showed that the number of gradient factors with significant net influences drastically decreased compared with the gross ones in all seasons. MC in soil gradient and NPP in vegetation gradient exhibited significant net influences in all seasons, thereby indicating their fundamental roles in the spatiotemporal variations of plant diversity. MC and NPP can be considered as the main driving factor and indicator, respectively, of the plant diversity. Meanwhile, MC and NPP were closely related to the other gradient factors that possessed significant gross influences, including Sa, NDVI, *LST*, DTY, DTS, and *HII*; and these factors were all determined by natural conditions (climate, river input, seawater intrusion, etc.) and human activities (farming, urban construction, ecological restoration, etc.) in the Yellow River Delta (Fig. 6).

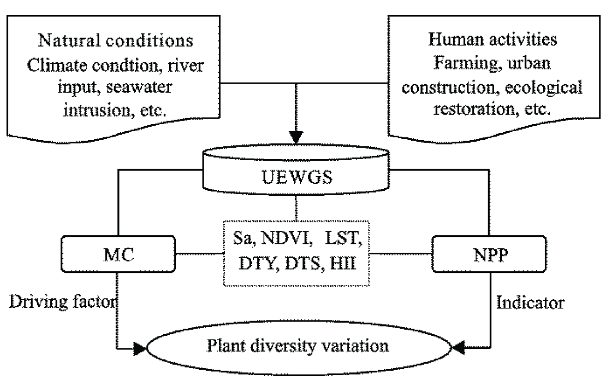

Fig. 6 Main influencing factors of plant diversity variation in the Yellow River Delta: Abbreviations for gradient factors are the same as for Table 1

In summary, for plant diversity variations under UEWGS, in spring, sites with high NDVI and NPP and low Sa possessed high *N* and *H'*; sites with high DTS and low MC, Sa, pH, and DTY displayed low *N*, *H'*, and *E*. In summer, sites with high NDVI, NPP, and DTS and low Sa possessed high *N*. In autumn, sites with high NPP and DTY and low *LST* and DTS generally exhibited high *N*, *H'*, and *E*; sites with high *LST*, DTS, PD, and ED and low MC, pH, NPP, and DTY showed low index values. In winter, the spatial distributions of plant diversity were insensitive to gradient factors in general.

5 Conclusions

We established a UEWGS for plant diversity in estuarine wetland with multiple natural and human factors. UEWGS effectively resolved complicated land surface characteristics, comprehensively covered all aspects of the influencing factors of plant diversity, and possessed distinct spatiotemporal heterogeneities. Application in the Yellow River Delta validated the significance of UEWGS in revealing plant diversity spatiotemporal characteristics and influencing factors. The required data for UEWGS can be obtained through conventional field work and remote sensing, and the establishment and analysis processes were characterized by simple operation and high repeatability. Therefore, UEWGS possessed universal applicability in the spatiotemporal analysis of plant diversity in estuarine areas.

The results in the Yellow River Delta indicated that 123 species were recorded in four seasons in 2017, and season difference was distinct. *P. australis*, *S. salsa*, and *T. chinensis*, which are all natural species, were the top three dominant species. Artificial crop species, including *T. aestivum*, *Zea mays*, and *Gossypium hirsutum*, also exhibited high *IVs*. In single effects of UEWGS, all aspects exerted significant influences, especially the vegetation gradient possessing significant influences in all seasons. In comprehensive effects of UEWGS, soil, vegetation, heat, and distance gradients showed significant gross influences; MC in soil gradient and NPP in vegetation gradient possessed significant net influences in all seasons. MC and NPP were the main driving factor and indicator, respectively, of the plant diversity. In spring, sites with high NDVI and NPP and low Sa possessed high *N* and *H'*; sites with high DTS and low MC, Sa, pH, and DTY displayed low *N*, *H'*, and *E*. In summer, sites with high NDVI, NPP, and DTS and low Sa possessed high *N*. In autumn, sites with high NPP and DTY and low LST and DTS generally exhibited high *N*, *H'*, and *E*; sites with high LST, DTS, PD, and ED and low MC, pH, NPP, and DTY showed low index values. In winter, the spatial distributions of plant diversity were generally insensitive to gradient factors.

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