

Article

Context-Dependent Cross-Taxon Congruence Between Plants and Macrozoobenthos in Coal-Mining Subsidence Wetlands

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Abstract

Coal-mining subsidence wetlands are post-industrial landscapes whose sustainable management requires coordinated biodiversity monitoring across multiple taxonomic groups. We surveyed wetland plants and macrozoobenthos across nine coal-mining subsidence wetlands at three subsidence stages in China's Jining Coalfield over three seasons. We evaluated cross-taxon congruence in α -diversity and community composition, together with environmental associations. Results indicated that plant species richness and Shannon–Wiener diversity were lower at the middle stage than at the late stage, whereas macrozoobenthos richness was higher at the late stage than at the initial and middle stages. Overall species richness was positively correlated between taxa, whereas stage- and season-specific congruence occurred only for Pielou's evenness at the initial stage (negative) and Shannon–Wiener diversity in autumn (positive). Community composition varied among stages and exhibited significant cross-taxon congruence ($p < 0.01$). Environmental analyses indicated some shared associations but different overall response patterns between communities. Thus, the development of coal-mining subsidence wetlands involved asynchronous and context-dependent community reorganization rather than uniform cross-taxon convergence. These findings support stage-sensitive, multi-taxon monitoring to improve biodiversity assessment and provide a case-based reference for the science-based conservation, ecological restoration, and sustainable management of similar post-industrial wetland systems.

Keywords: coal-mining subsidence wetlands; post-industrial landscapes; cross-taxon congruence; biodiversity surrogacy; community composition; multi-taxon monitoring



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1. Introduction

Post-industrial landscapes are landscapes in which industrial activities have ceased, declined, or undergone substantial transformation, but which still retain the physical remnants, ecological effects, environmental damage, or cultural heritage resulting from those activities [1]. Mining activities can profoundly alter landforms, hydrological processes, and landscape structure, while exerting persistent effects on ecosystem structure, functioning, and community succession through land-use and disturbance legacies [2–4]. In the Jining Coalfield on the eastern North China Plain, China, underground coal mining has caused widespread surface subsidence across a region characterized by shallow groundwater

tables and flat terrain, transforming former cropland, land surrounding rural settlements, and other terrestrial habitats into post-industrial landscapes with a pronounced legacy of anthropogenic disturbance [4–6]. As groundwater, precipitation, and surface runoff accumulate, extensive areas of permanent or seasonal standing water develop within these post-industrial landscapes; accompanied by soil gleization and the colonization of wetland plants, these inundated areas rapidly develop into coal-mining subsidence wetlands (CMSWs) [5,7–9]. Unlike natural or semi-natural wetlands formed through long-term ecological development, CMSWs are secondary ecosystems jointly shaped by underground mining, hydrological alteration, and biotic colonization. They are characterized by their recent origin, pronounced water-level fluctuations, rapidly shifting habitat boundaries, and high environmental heterogeneity [7–9]. As time since subsidence increases, the physicochemical properties of the water, sediment conditions, and soils associated with wetland vegetation continue to change, while habitat components such as the water column, bottom sediments, and vegetated wetland zones become increasingly differentiated and structurally complex [8–10]. Consequently, CMSWs provide valuable model systems for investigating ecosystem development, community succession, and biodiversity patterns in post-industrial landscapes [6,8].

Previous ecological studies of CMSWs have primarily focused on water quality, wetland vegetation recovery, macrozoobenthos community composition, waterbird habitat use, and the effectiveness of ecological restoration [8–13]. These studies have provided an important foundation for understanding the ecological characteristics and recovery trajectories of these wetlands, yet most have focused on a single biological assemblage or ecological process [14,15]. Because taxonomic groups differ in their life-history traits, habitat use, resource-use strategies, and sensitivity to environmental change, any single group generally captures only a subset of the ecological information associated with a particular habitat component or process, limiting its ability to reveal coordinated or divergent responses among multiple taxa during wetland development [14–16]. This limitation may be particularly important in CMSWs, which are jointly shaped by natural processes and anthropogenic drivers—most notably mining-induced subsidence—and differ in their abiotic and biotic characteristics because they formed at different times [7,8,10]. Accordingly, assessments based on a single taxonomic group may not fully characterize biodiversity patterns in these wetlands, highlighting the need for a multi-taxon perspective to clarify ecological reorganization during their development [15–17].

Covariation among taxonomic groups in species richness, diversity indices, or community composition is commonly referred to as cross-taxon congruence [14,17–19]. Cross-taxon congruence is a central issue in biodiversity monitoring and conservation ecology because it determines whether one taxonomic group can serve as a surrogate for others or for biodiversity as a whole [20,21]. When congruence among groups is strong, a focal taxon may serve as a practical surrogate for other taxa or even broader biodiversity, thereby improving the efficiency of ecological monitoring and conservation assessment [22]. However, existing evidence indicates that cross-taxon congruence is neither universal nor consistently strong; its magnitude and direction vary with spatial scale, habitat type, disturbance intensity, and the dimension of biodiversity considered [14,16,17,19,23,24]. Testing cross-taxon congruence within specific ecosystems and environmental contexts can therefore not only evaluate the reliability of surrogate taxa but also help determine whether different groups are structured by similar ecological processes [17,19].

This context dependence is particularly important for evaluating ecological restoration and supporting the long-term sustainable management of CMSWs. The formation and persistence of water bodies and wetland habitats in CMSWs do not necessarily indicate that biodiversity and ecological integrity have recovered concurrently across different ecosystem

components. Reliable restoration assessment requires quantifiable biodiversity indicators and continued monitoring of the trajectories of aquatic and terrestrial taxa across different stages of wetland development [25,26]. Within this framework, cross-taxon congruence is not a direct measure of sustainability; rather, it can be used to evaluate the reliability and applicability of surrogate-based monitoring. By determining whether changes in plant communities adequately reflect changes in macrozoobenthic communities, cross-taxon congruence analysis can inform the choice between single-taxon and multi-taxon monitoring approaches. Clarifying the strength and applicability of such congruence can help prevent incomplete assessments of restoration outcomes and provide a scientific basis for developing stage-sensitive multi-taxon monitoring strategies, ecological restoration measures, and long-term sustainable management plans [25,27].

In cross-taxon congruence studies, wetland plants and macrozoobenthos are frequently used to assess wetland biodiversity and ecological condition because of their distinct ecological roles and sensitivity to environmental change [15,28,29]. In some ecosystems, plant and invertebrate diversity exhibit relatively strong congruence [15,19,29–32], leading vascular plants to be proposed as potential surrogates for invertebrate communities [31]. However, such surrogacy is not universal, and its strength and direction may vary with habitat type, environmental conditions, and differences in ecological niches among taxa [14,15,17,33]. This may be especially true in ecosystems spanning aquatic–terrestrial ecotones or subject to pronounced hydrological variation and complex disturbance regimes, where plants and macrozoobenthos may be structured by different habitat components and ecological processes [14,15]. In CMSWs, wetland plants occupy habitats ranging from relatively dry or periodically inundated soils to shallow water and open-water zones, and can influence other biological groups by modifying vegetation structure, light availability, organic matter inputs, and microhabitat heterogeneity [29,34,35]. Macrozoobenthos, in contrast, inhabit the water–sediment interface, contribute to organic matter decomposition, nutrient cycling, and energy transfer through food webs, and are sensitive to changes in water quality, sediment properties, and hydrological conditions [10,28,34–36]. The two groups may therefore respond similarly to wetland development and water-level fluctuations, but differences in their habitat associations and ecological requirements may also result in weak congruence or incongruence [15,19,29]. Examining cross-taxon congruence between wetland plants and macrozoobenthos can thus help determine whether plant communities can serve as reliable surrogates for macrozoobenthic diversity and community composition, while improving our understanding of ecological linkages between terrestrial and aquatic habitats in CMSWs [14,15].

Against this background, we investigated nine CMSWs in the Jining Coalfield on the North China Plain, China. These wetlands formed at different times following subsidence and collectively represent a developmental chronosequence, providing a space-for-time substitution framework for examining biodiversity change during wetland development [37]. By integrating observations across subsidence stages and seasons with measurements of water and soil conditions, we systematically evaluated cross-taxon congruence between wetland plants and macrozoobenthos at the levels of α -diversity and community composition and examined its associations with wetland development and local environmental conditions. During the field surveys, our research team observed that the two taxonomic groups might exhibit some degree of congruence. However, these observations were insufficient to support any a priori prediction regarding the strength or direction of this congruence across different subsidence stages. Accordingly, we formulated the following three hypotheses: (1) wetland plant and macrozoobenthic diversity would exhibit stage-dependent variation during the development of CMSWs; (2) wetland plants and

macrozoobenthos would exhibit cross-taxon congruence; and (3) this congruence would vary among subsidence stages.

By jointly analyzing wetland plants and macrozoobenthos, this study addresses the limited use of integrated multi-taxon assessments in current research on CMSWs. The results indicate that cross-taxon congruence was generally weak and strongly context-dependent. Wetland plants should therefore not be regarded as universal surrogates for macrozoobenthos; instead, stage-sensitive, multi-taxon monitoring represents a more appropriate approach. These findings provide a scientific basis for adaptive biodiversity conservation, stage-specific evaluation of ecological restoration, and the long-term sustainable management of CMSWs.

2. Materials and Methods

2.1. Study Area and Sampling Design

Based on field surveys and the interpretation of remote-sensing imagery, we selected nine CMSWs in Jining, China, spanning 1–18 years since subsidence (35.363551–35.554203° N, 116.750206–116.980776° E; Figure 1). Subsidence-stage classification was based on local subsidence histories and time since wetland formation and was further informed by field-observed characteristics, including wetland area, hydrological conditions, open-water development, aquatic–terrestrial habitat zonation, and vegetation development. Site-specific information for the nine wetlands is summarized in Table S1. Jining has a temperate monsoon climate characterized by hot, rainy summers and cold, dry winters, with a mean annual precipitation of approximately 600 mm and a mean annual temperature of 13.5–15.0 °C [5]. Long-term underground coal mining has generated extensive subsidence-induced water bodies in the region, which have progressively developed into secondary wetland ecosystems characterized by pronounced aquatic–terrestrial transitions. The study included three wetlands within each of the three subsidence stages and three sampling locations within each wetland. Wetland plants, macrozoobenthos, and environmental variables were surveyed at all nine wetlands in summer (July 2024), autumn (October 2024), and spring (March 2025). Wetland area ranged from 0.017 to 1.42 km², and hydrological connectivity also varied among sites. Water inputs were derived primarily from precipitation and groundwater, although some wetlands were connected to adjacent surface-water networks through artificial channels. The surrounding landscape was predominantly agricultural, with maize–wheat rotation as the principal cropping system; villages and planted forest belts occurred in some areas [38].

Because the spatial and temporal patterns of underground coal extraction differed across the region, surface subsidence occurred at different times. Based on local subsidence histories and time since wetland formation, the wetlands were classified into three developmental stages: initial (approximately 1–2 years since subsidence), middle (3–10 years), and late (≥ 11 years):

Initial stage. Newly formed wetlands were generally small and hydrologically vulnerable, with water availability strongly dependent on precipitation; some wetlands could dry out during prolonged droughts.

Middle stage. Continued surface subsidence maintained a dynamic phase of wetland expansion and reorganization, during which wetland area increased and hydrological conditions became relatively more persistent.

Late stage. Surface subsidence had generally slowed or ceased, and the wetlands had expanded into relatively large open-water bodies (“subsidence lakes”). Broad and clearly zoned belts of emergent vegetation, including *Phragmites australis* and *Typha angustifolia* communities, had also developed.

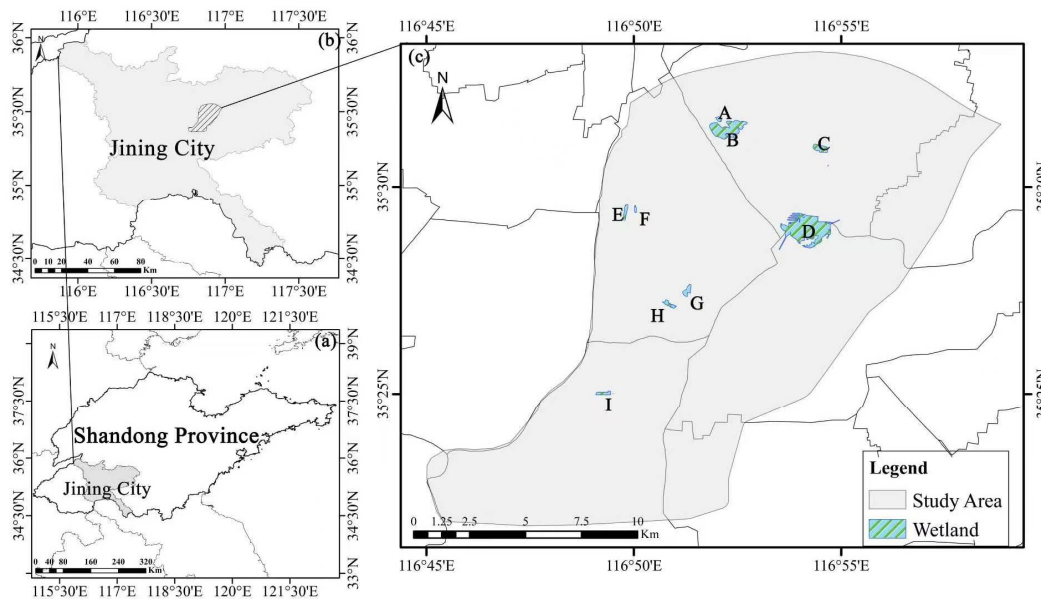


Figure 1. Location of the study area and spatial distribution of the nine surveyed CMSWs in the Jining Coalfield, Jining City, Shandong Province, China. (a) Location of Jining City within Shandong Province; (b) location of the study area within Jining City; (c) distribution of the nine study wetlands (A–I). Based on time since subsidence, wetlands B, E, and H were classified as the initial stage; wetlands F, G, and I as the middle stage; and wetlands A, C, and D as the late stage.

2.2. Field Sampling and Environmental Measurements

2.2.1. Plant Community Survey

Plant communities were surveyed using quadrat sampling [39]. At each sampling location, four 1 m × 1 m quadrats were established to survey wetland plant communities. Within each quadrat, all vascular plant species were recorded, together with the abundance, mean height, and percentage cover of each species. Plant height was expressed as the mean height of representative individuals, whereas species cover was visually estimated as the percentage of the quadrat area occupied by each species. For herbaceous plants whose individual boundaries were difficult to distinguish, identifiable aboveground ramets or relatively discrete clumps were used as the units for recording abundance. Plant species were identified primarily according to the Flora of China [40]. Specimens that could not be reliably identified in the field were collected and transported to the laboratory for further identification.

2.2.2. Macrozoobenthos Sampling

Quantitative samples of macrozoobenthos were collected using a sediment grab. Sampling locations were positioned along the waterward margin of emergent vegetation stands and distributed from shallow to deeper water. At each sampling location, three replicate sediment samples were collected using a Petersen grab with a sampling area of 1/40 m² and pooled to form one composite sample [10,41]. After collection, the sediment samples were washed through a 250-μm-mesh sieve, transferred to sealed bags, and transported to the laboratory for further processing. In the laboratory, all macrozoobenthic organisms were sorted from the retained material and preserved in 75% ethanol. Morphological identification was conducted using a stereomicroscope and a compound microscope. Aquatic oligochaetes and chironomid larvae were identified under the compound microscope, whereas leeches, gastropods, and most aquatic insects were examined and identified using a SOPTOP SZN stereomicroscope (Sunny Optical Technology Co., Ltd., Ningbo, China). Macrozoobenthos were identified using relevant taxonomic keys and identification guides [42–45]. Efforts

were made to identify all macrozoobenthic specimens to the species level using relevant taxonomic keys and identification guides [46]. All macrozoobenthic individuals collected at each sampling location were counted separately by taxon. For fragmented specimens, only fragments containing the head were counted, whereas posterior fragments were excluded. For data analysis, macrozoobenthic densities were standardized to the number of individuals per square metre (ind. m^{-2}).

2.2.3. Environmental Measurements

Environmental variables were measured concurrently with the biological surveys to characterize the aquatic and soil environments of the CMSWs. Seven variables characterizing the aquatic environment were measured: sediment organic matter (SOM-W), pH, dissolved oxygen (DO), water electrical conductivity (EC-W), total nitrogen (TN), total phosphorus (TP), and chlorophyll a (Chl-a). Water pH, DO, and EC-W were measured in situ using a DZB-718 portable multiparameter water-quality meter (Shanghai INESA Scientific Instrument Co., Ltd., Shanghai, China). Before biological sampling, a 1 L water sample was collected from each sampling location and transported to the laboratory for the determination of TN, TP, and Chl-a following standard APHA methods [47]. Sediment samples were also transported to the laboratory, and sediment organic matter was determined using the potassium dichromate oxidation method [48].

Seven soil variables were measured within the plant sampling areas: soil temperature, soil moisture, soil electrical conductivity (EC-S), soil salinity, total dissolved solids (TDSs), dielectric constant, and soil organic matter (SOM-S). Soil temperature, moisture, electrical conductivity, salinity, total dissolved solids, and dielectric constant were measured in situ using a Shunkeda TR-8D soil meter (Beijing Shunkeda Technology Co., Ltd., Beijing, China). Soil organic matter was also determined using the potassium dichromate oxidation method [48]. The formation time of each of the CMSWs was determined through visual interpretation of historical satellite imagery, and wetland area was delineated and calculated using ArcMap 10.8 software [7,49]. Environmental observations were associated with their corresponding plant and macrozoobenthos sampling units and were subsequently used to analyse environmental differences, conduct principal component analysis, and evaluate relationships between biodiversity and environmental variables.

2.3. Data Processing and Statistical Analyses

In determining the statistical strategy, we carefully balanced statistical independence against the preservation of ecological information. A single observation from each sampling location in each season was defined as the basic statistical unit, yielding a total of 81 seasonal samples (nine wetlands $\times$ three sampling locations per wetland $\times$ three seasons). The four plant quadrats and three replicate macrozoobenthos samples established at each sampling location were treated as subsamples. These subsamples were aggregated to characterize the community at the corresponding sampling location in each season and were not included in subsequent analyses as independent statistical units. Thus, neither individual plant quadrats nor replicate macrozoobenthos samples were treated as independent replicates.

For annual-scale analyses, data from the three seasons were further aggregated for each sampling location, resulting in 27 annual samples at the sampling-location level. Each subsidence stage included three wetlands, with three sampling locations established in each wetland; therefore, nine annual samples were included for each stage ($n = 3 \times 3 = 9$). All annual regression and correlation analyses were based on these aggregated values at the sampling-location level. Season-specific analyses of α -diversity were conducted separately for spring, summer, and autumn, with 27 sampling locations included in each season and 81 seasonal observations in total. Consequently, repeated observations from

the same sampling location across different seasons were not simultaneously treated as independent replicates within any individual seasonal analysis.

Through this approach, comparisons among subsidence stages based on space-for-time substitution were conducted at a consistent spatial and temporal scale. This procedure reduced the risk of pseudoreplication arising from treating quadrats or parallel samples as independent replicates, while retaining information on seasonal dynamics and ecological heterogeneity among sampling locations.

The importance value of plant species i was calculated as $IV_i = (RA_i + RH_i + RC_i)/3$, where RA_i , RH_i , and RC_i denote relative abundance, relative height, and relative cover, respectively. Importance values were averaged across the four quadrats to construct a plant species importance-value matrix. Macrozoobenthos were represented by a species-density matrix based on standardized densities (ind. m^{-2}). Species richness (S) was defined as the number of species recorded in a sample, and the Shannon–Wiener index (H') was calculated as [50]:

$$H' = -\sum_{i=1}^S p_i \ln p_i$$

Pielou's evenness index (J') was calculated to quantify the evenness of species distributions within each community [51]:

$$J' = \frac{H'}{\ln S}$$

where (H') is the Shannon–Wiener diversity index and (S) is species richness. For plants, p_i represents the mean importance value of species i ; for macrozoobenthos, it represents the proportion of total density contributed by species i . Annual and season-specific α -diversity analyses were based on 27 seasonally aggregated samples and 81 original observations, respectively.

One-way analysis of variance followed by Tukey's HSD test was used to examine differences in environmental variables and plant and macrozoobenthic α -diversity among subsidence stages [52]. Stage differences were also examined separately within spring, summer, and autumn. Principal component analysis was conducted separately on standardized soil variables (temperature, moisture, EC-S, salinity, TDSs, dielectric constant, and SOM-S) and aquatic variables (TN, TP, Chl-a, pH, EC-W, DO, and SOM-W). The first two principal component axes were retained to represent the major environmental gradients.

Cross-taxon congruence in species richness, the Shannon–Wiener index and Pielou's evenness index was evaluated using simple linear regression, and the correlation coefficient (r) and corresponding two-tailed p value were reported [53,54]. Analyses were conducted for the full dataset and separately within each subsidence stage and season. To formally test whether congruence varied among stages, general linear models including the plant diversity metric, subsidence stage, and their interaction were fitted.

For community composition analyses, the plant importance-value and macrozoobenthos density matrices were Hellinger-transformed, and Bray–Curtis dissimilarities were calculated [55,56]. NMDS was used to visualize community composition among subsidence stages, and PERMANOVA with 9999 permutations was used to test the stage effect [57,58]. Congruence between the plant and macrozoobenthos NMDS configurations was evaluated using symmetric Procrustes analysis and PROTEST with 999 permutations [59].

Second-order polynomial models containing linear, quadratic, and interaction terms were used to relate plant α -diversity to soil PC1 and PC2 and macrozoobenthic α -diversity to aquatic PC1 and PC2 [53,54]. Two-dimensional marginal response curves and three-dimensional response surfaces were generated from the model predictions. Mantel tests with 999 permutations were used to evaluate relationships between individual environ-

mental variables and community composition dissimilarities [60]. RDA was used to relate community composition to soil and aquatic variables, wetland area, and time since subsidence. Following evaluation of the full model, forward selection constrained by adjusted R^2 was used to construct a reduced model, and envfit with 999 permutations was used to assess associations between the selected variables and the community ordinations [55,61].

Data organization and α -diversity calculations were performed in Microsoft 365 Excel and PRIMER 6, respectively. All other analyses and visualizations were conducted in R 4.6.1, primarily using the vegan, linkET, ggplot2, plot3D, and emmeans packages. Unless otherwise stated, statistical significance was defined as $p < 0.05$.

3. Results

3.1. Environmental Variation Among Subsidence Stages

Several environmental variables differed significantly among subsidence stages (Table 1). Soil temperature and soil electrical conductivity (EC-S) were both highest at the middle stage and lowest at the late stage ($F_{2,24} = 5.944$, $p = 0.008$; $F_{2,24} = 3.799$, $p = 0.037$, respectively), whereas the dielectric constant increased across the three subsidence stages but did not differ significantly among them ($F_{2,24} = 2.242$, $p = 0.128$). Soil salinity did not differ significantly among stages ($F_{2,24} = 2.594$, $p = 0.095$), nor did any of the other soil variables. With the exception of TP and sediment organic matter (SOM-W), all aquatic environmental variables differed significantly among subsidence stages. TN decreased progressively from the initial to the late stage ($F_{2,24} = 9.130$, $p = 0.001$). TP and Chl-a were highest at the initial stage, decreased at the middle stage, and increased again at the late stage; however, the stage-related difference was significant only for Chl-a (TP: $F_{2,24} = 1.915$, $p = 0.169$; Chl-a: $F_{2,24} = 3.499$, $p = 0.046$). EC-W and DO were highest at the middle stage ($F_{2,24} = 10.685$, $p < 0.001$; $F_{2,24} = 23.747$, $p < 0.001$, respectively), whereas pH was lowest at the late stage ($F_{2,24} = 40.645$, $p < 0.001$). SOM-W did not differ significantly among subsidence stages ($F_{2,24} = 1.413$, $p = 0.263$).

Table 1. Environmental characteristics of CMSWs across subsidence stages.

Parameter	Initial Stage	Middle Stage	Late Stage	F	p	Total
Soil temperature (°C)	26.44 ± 1.24	28.17 ± 1.36	25.74 ± 1.93	5.94	0.008 **	26.78 ± 1.81
Soil moisture (%)	28.22 ± 4.58	27.94 ± 7.14	28.61 ± 5.22	0.03	0.97	28.25 ± 5.53
EC-S (µS/cm)	451.12 ± 130.18	563.99 ± 238.77	345.71 ± 103.51	3.80	0.037 *	453.61 ± 185.21
Salinity (mg/L)	300.90 ± 109.80	360.72 ± 149.33	237.38 ± 72.33	2.59	0.095	299.67 ± 121.71
TDSs (mg/L)	234.50 ± 75.78	289.56 ± 123.76	208.06 ± 53.06	1.96	0.163	244.04 ± 92.43
Dielectric constant	14.77 ± 2.93	16.91 ± 5.78	19.32 ± 4.52	2.24	0.128	17.00 ± 4.78
SOM-S (%)	3.54 ± 2.63	6.63 ± 7.61	4.02 ± 1.80	1.10	0.35	4.73 ± 4.78
TN (mg/L)	3.50 ± 1.42	2.21 ± 0.23	1.72 ± 0.66	9.13	0.001 **	2.48 ± 1.17
TP (mg/L)	0.42 ± 0.29	0.23 ± 0.12	0.34 ± 0.17	1.92	0.169	0.33 ± 0.21
Chl-a (mg/m ³)	50.23 ± 17.26	25.17 ± 13.64	34.65 ± 27.40	3.50	0.046 *	36.68 ± 22.15
pH	7.99 ± 0.20	7.93 ± 0.16	7.25 ± 0.22	40.65	<0.001 ***	7.72 ± 0.39
EC-W (mS/cm)	0.45 ± 0.10	1.02 ± 0.52	0.44 ± 0.05	10.69	<0.001 ***	0.64 ± 0.41
DO (mg/L)	8.30 ± 1.00	10.75 ± 1.82	5.77 ± 1.65	23.75	<0.001 ***	8.28 ± 2.54
SOM-W (%)	1.97 ± 1.01	2.49 ± 0.38	2.58 ± 0.95	1.41	0.263	2.34 ± 0.84

Note: Values are presented as means ± standard deviations (SD; $n = 9$ per stage and $n = 27$ overall). F and p values were obtained from one-way analysis of variance. Asterisks indicate statistical significance: * $p < 0.05$, ** $p < 0.01$, and *** $p < 0.001$. EC-S, soil electrical conductivity; TDSs, total dissolved solids; SOM-S, soil organic matter; TN, total nitrogen; TP, total phosphorus; Chl-a, chlorophyll a; EC-W, water electrical conductivity; DO, dissolved oxygen; SOM-W, sediment organic matter.

The first two axes of the PCA based on soil variables jointly explained 75.78% of the total variance. PC1 primarily represented variation in soil moisture and electrical properties, whereas PC2 reflected a contrast between soil temperature and both SOM-S and dielectric constant. The first two axes of the PCA based on aquatic environmental variables jointly

explained 69.24% of the total variance. PC1 primarily represented a nutrient–conductivity contrast, whereas PC2 primarily represented covariation in DO and pH (Figure 2). The complete PCA loading matrices from PC1 to PC7 are provided in Table S2.

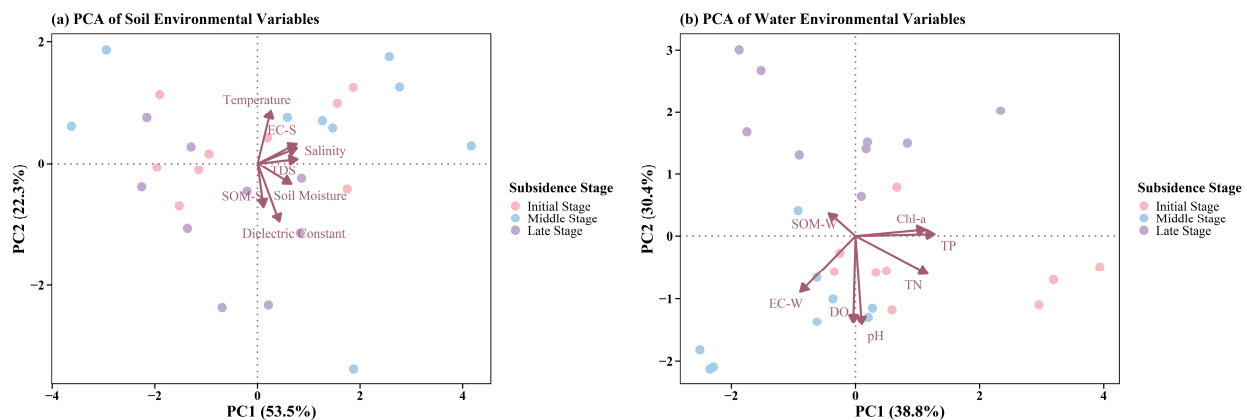


Figure 2. Principal component analysis (PCA) of soil and aquatic environmental variables across subsidence stages and seasons. Point colours represent subsidence stages and arrows indicate the direction and magnitude of environmental-variable loadings. Percentages in parentheses on the axes indicate the variance explained by each principal component.

3.2. Stage-Dependent Variation in the α -Diversity of Wetland Plants and Macrozoobenthos

When classified by subsidence stage, plant species richness (S) and the Shannon–Wiener index (H') both differed significantly among stages (both $p < 0.01$). Both indices were significantly lower at the middle stage than at the late stage, whereas the initial stage did not differ significantly from either stage (S: middle = 20.56, late = 28.00, $F_{2,24} = 6.098$, $p = 0.007$, Tukey-adjusted $p = 0.005$; H' : middle = 2.48, late = 2.85, $F_{2,24} = 7.105$, $p = 0.004$, Tukey-adjusted $p = 0.003$; Figure 3a,c). Plant Pielou evenness index (J') did not differ significantly among stages ($F_{2,24} = 2.721$, $p = 0.086$; Figure 3e). Macrozoobenthos species richness also differed significantly among subsidence stages, with a significantly higher value at the late stage than at the initial and middle stages (late = 14.33, initial = 8.56, middle = 9.44, $F_{2,24} = 6.524$, $p = 0.005$; Tukey-adjusted $p = 0.007$ and 0.024, respectively; Figure 3g). In contrast, the Shannon–Wiener and Pielou evenness indices of macrozoobenthos did not differ significantly among stages (H' : $F_{2,24} = 1.102$, $p = 0.348$; J' : $F_{2,24} = 0.438$, $p = 0.650$; Figure 3i,k).

From a seasonal perspective, plant species richness differed significantly among subsidence stages in summer ($p < 0.05$) and significantly in autumn ($p < 0.01$), whereas the plant Shannon–Wiener index showed a highly significant stage-related difference only in summer ($p < 0.01$). In summer, both plant species richness and the Shannon–Wiener index were significantly higher at the late stage than at the middle stage (S: late = 14.78, middle = 9.78, $F_{2,24} = 4.967$, $p = 0.016$, Tukey-adjusted $p = 0.012$; H' : late = 2.25, middle = 1.84, $F_{2,24} = 5.989$, $p = 0.008$, Tukey-adjusted $p = 0.006$; Figure 3b,d). In autumn, plant species richness was significantly lower at the middle stage than at the initial and late stages (middle = 9.67, initial = 13.56, late = 14.11, $F_{2,24} = 6.116$, $p = 0.007$; Tukey-adjusted $p = 0.025$ and 0.010, respectively; Figure 3b). The remaining seasonal stage effects on plant diversity, including Pielou evenness index in all three seasons, were not significant (all $p > 0.05$). For macrozoobenthos, only spring species richness differed significantly among subsidence stages ($p < 0.05$), with a significantly higher value at the late stage than at the initial stage (late = 8.44, initial = 4.22, $F_{2,24} = 4.806$, $p = 0.018$, Tukey-adjusted $p = 0.019$; Figure 3h). No other seasonal stage effects on macrozoobenthos diversity were significant (all $p > 0.05$; Figure 3h,j,l).

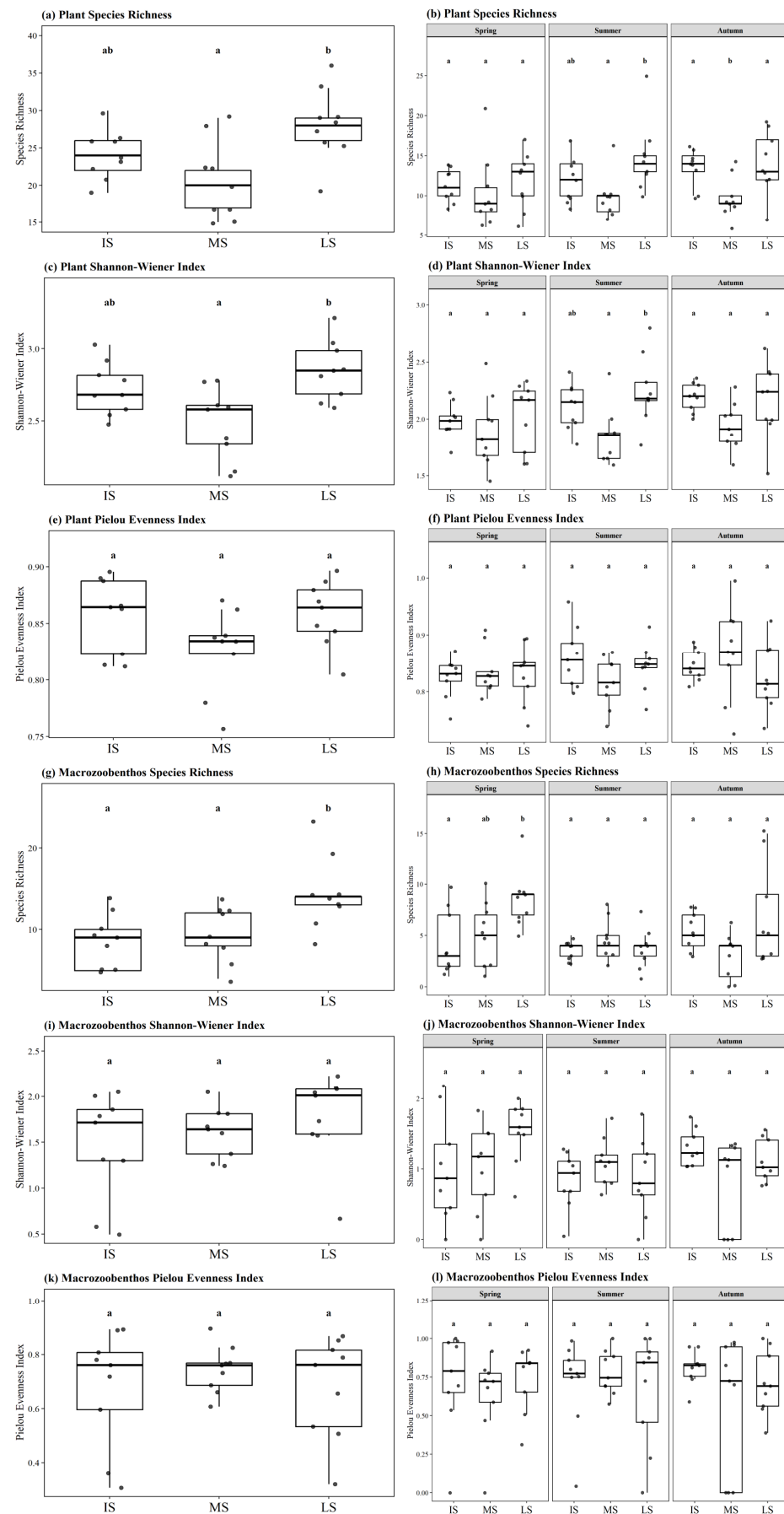


Figure 3. Species richness, Shannon–Wiener diversity, and Pielou evenness index of wetland plants and macrozoobenthos across subsidence stages and seasons. **(a,b)** Plant species richness; **(c,d)** plant

Shannon–Wiener index; (e,f) plant Pielou evenness index; (g,h) macrozoobenthos species richness; (i,j) macrozoobenthos Shannon–Wiener index; and (k,l) macrozoobenthos Pielou evenness index. Panels (a,c,e,g,i,k) show annual differences among subsidence stages, whereas panels (b,d,f,h,j,l) show stage differences within each season. Boxes represent the interquartile range, horizontal lines indicate medians, whiskers extend to 1.5 times the interquartile range, and points represent individual observations. Groups without a shared lowercase letter differ significantly among subsidence stages based on Tukey’s HSD test ($p < 0.05$). Different lowercase letters (a and b) indicate significant differences among groups, whereas groups labeled “ab” do not differ significantly from groups labeled “a” or “b”. IS, initial stage; MS, middle stage; LS, late stage.

3.3. Cross-Taxon Congruence Between Wetland Plants and Macrozoobenthos

3.3.1. Congruence in α -Diversity

When analyzed by subsidence stage, only the Pielou evenness index at the initial stage showed a significant correlation between the two groups, and this relationship was negative ($r = -0.714$, $p = 0.031$; Figure 4h). All remaining stage-specific correlations were nonsignificant (species richness—initial: $r = 0.301$, $p = 0.431$; middle: $r = 0.494$, $p = 0.176$; late: $r = 0.000$, $p = 1.000$; Figure 4b; Shannon–Wiener index—initial: $r = -0.581$, $p = 0.101$; middle: $r = 0.586$, $p = 0.097$; late: $r = 0.052$, $p = 0.895$; Figure 4e; Pielou evenness index—middle: $r = -0.477$, $p = 0.195$; late: $r = 0.391$, $p = 0.298$; Figure 4h).

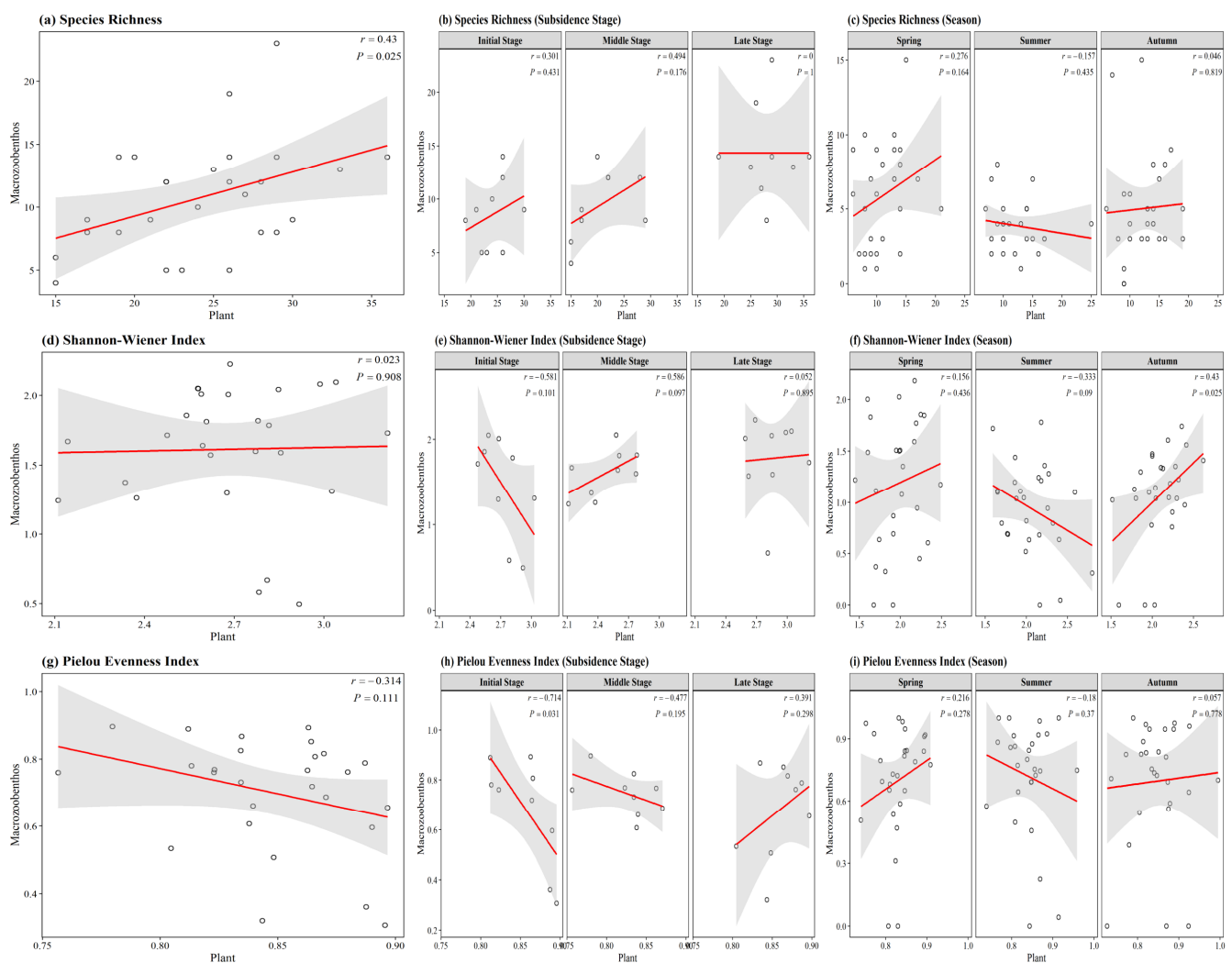


Figure 4. Cross-taxon congruence in α -diversity between wetland plants and macrozoobenthos across subsidence stages and seasons. (a–c) Relationships in species richness; (d–f) relationships in

the Shannon–Wiener index; and (g–i) relationships in the Pielou evenness index. Panels (a,d,g) show the overall relationships based on annual values for all paired sampling units ($n = 27$); panels (b,e,h) show the annual relationships separately for the initial, middle, and late subsidence stages ($n = 9$ per stage); and panels (c,f,i) show the relationships separately for spring, summer, and autumn based on seasonal observations ($n = 27$ per season). Plant α -diversity is plotted on the x-axis and macrozoobenthos α -diversity on the y-axis. Points represent paired plant and macrozoobenthos observations from the same sampling location, using annual values in panels (a,b,d,e,g,h) and seasonal values in panels (c,f,i). Red lines indicate fitted simple linear regressions, and grey ribbons represent 95% confidence intervals. Pearson's correlation coefficients (r) and corresponding two-tailed p values are displayed in each panel or facet. From an overall perspective, only species richness showed a significant positive correlation between wetland plants and macrozoobenthos ($r = 0.430$, $p = 0.025$; (a)). The remaining correlations were nonsignificant (Shannon–Wiener index: $r = 0.023$, $p = 0.908$; Figure 4d; Pielou evenness index: $r = -0.314$, $p = 0.111$; (g)).

At the seasonal scale, only the Shannon–Wiener index in autumn showed a significant correlation between the two groups, and this relationship was positive ($r = 0.430$, $p = 0.025$; Figure 4f). All remaining season-specific correlations were nonsignificant (species richness—spring: $r = 0.276$, $p = 0.164$; summer: $r = -0.157$, $p = 0.435$; autumn: $r = 0.046$, $p = 0.819$; Figure 4c; Shannon–Wiener index—spring: $r = 0.156$, $p = 0.436$; summer: $r = -0.333$, $p = 0.090$; Figure 4f; Pielou evenness index—spring: $r = 0.216$, $p = 0.278$; summer: $r = -0.180$, $p = 0.370$; autumn: $r = 0.057$, $p = 0.778$; Figure 4i).

3.3.2. Congruence in Community Composition

The NMDS ordinations indicated stage-associated shifts in both plant and macrozoobenthos community composition, although considerable overlap occurred among subsidence stages (plant: stress = 0.240; macrozoobenthos: stress = 0.216; Figure 5a,b). Plant community composition differed significantly among subsidence stages, with stage explaining 13.94% of the total variation (PERMANOVA: pseudo- $F_{2,24} = 1.944$, $R^2 = 0.139$, $p = 0.001$; Figure 5a). Pairwise comparisons indicated that the middle stage differed significantly from both the initial and late stages (both BH-adjusted $p = 0.012$), whereas the initial and late stages did not differ significantly (BH-adjusted $p = 0.222$). Thus, stage-related differentiation in plant community composition was primarily associated with the middle stage. Macrozoobenthos community composition also differed significantly among subsidence stages, with stage explaining 14.99% of the total variation (PERMANOVA: pseudo- $F_{2,24} = 2.115$, $R^2 = 0.150$, $p = 0.003$; Figure 5b). Pairwise comparisons detected a significant difference only between the initial and late stages (BH-adjusted $p = 0.009$); the initial–middle and middle–late comparisons were nonsignificant (both BH-adjusted $p = 0.069$).

Despite these differences in stage-associated compositional patterns, Procrustes analysis identified moderate but significant congruence between the ordination configurations of the plant and macrozoobenthos communities ($r = 0.536$, $p = 0.004$; Figure 5c).

3.4. Environmental Associations of α -Diversity and Community Composition

3.4.1. Relationships Between α -Diversity and PCA-Derived Environmental Axes

Plant species richness and the Shannon–Wiener index varied only weakly along soil PC1 and PC2, and neither full second-order polynomial model was significant (species richness: $R^2 = 0.167$, $p = 0.535$, Figure 6a; Shannon–Wiener index: $R^2 = 0.233$, $p = 0.311$, Figure 6c). All terms in the species-richness model were nonsignificant. Although the linear PC2 term in the Shannon–Wiener model had a significant negative coefficient ($\beta = -0.115$, $p = 0.043$), the remaining terms and the overall model were nonsignificant. In contrast, the Pielou evenness index exhibited a significant nonlinear response to the combined soil PCA axes ($R^2 = 0.510$, $p = 0.007$; Figure 6e). This response was characterized by significant negative linear and quadratic effects of PC2 (linear: $\beta = -0.0153$, $p = 0.016$; quadratic:

$\beta = -0.0080$, $p = 0.017$) and a significant negative $PC1 \times PC2$ interaction ($\beta = -0.0086$, $p = 0.012$), whereas the terms involving $PC1$ alone were nonsignificant.

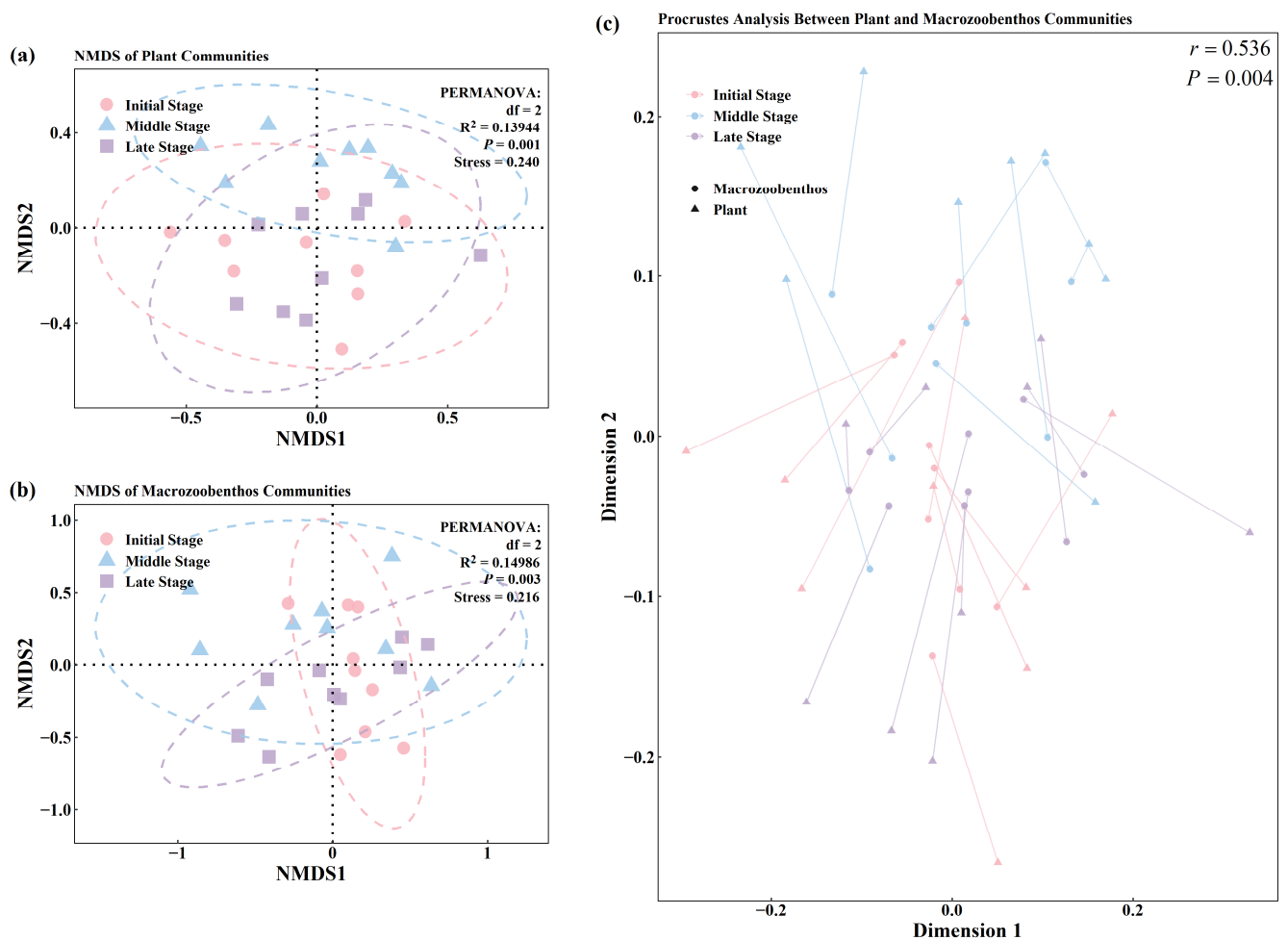


Figure 5. NMDS ordinations and Procrustes analysis of wetland plant and macrozoobenthos communities. **(a)** NMDS ordination of plant communities; **(b)** NMDS ordination of macrozoobenthos communities; and **(c)** Procrustes superimposition of the two ordination configurations. In panels **(a,b)**, point colours and shapes represent subsidence stages, and dashed ellipses indicate stage groupings. In panel **(c)**, circles and triangles represent macrozoobenthos and plant configurations, respectively; colours represent subsidence stages, and lines connect paired samples.

Macrozoobenthos species richness declined with increasing aquatic $PC1$ and exhibited a U-shaped response to aquatic $PC2$. Both single-axis models were significant ($PC1$: $R^2 = 0.289$, $p = 0.017$; $PC2$: $R^2 = 0.459$, $p < 0.001$), as was the full second-order polynomial model ($R^2 = 0.605$, $p < 0.001$; Figure 6b). In the single-axis models, the linear effect of $PC1$ was significantly negative ($\beta = -1.384$, $p = 0.012$), whereas the quadratic effect of $PC2$ was significantly positive ($\beta = 0.934$, $p = 0.009$). The Shannon–Wiener index of macrozoobenthos varied significantly along aquatic $PC1$ ($R^2 = 0.225$, $p = 0.047$), but not along $PC2$ ($R^2 = 0.041$, $p = 0.602$). Its full model was also significant ($R^2 = 0.393$, $p = 0.048$; Figure 6d), with a significant positive $PC1 \times PC2$ interaction ($\beta = 0.0797$, $p = 0.037$); all other terms were nonsignificant. In contrast, the Pielou evenness index of macrozoobenthos was not significantly related to either aquatic PCA axis, and the full model was nonsignificant ($R^2 = 0.291$, $p = 0.173$; Figure 6f), although the $PC1 \times PC2$ interaction coefficient was significant ($\beta = 0.0311$, $p = 0.038$).

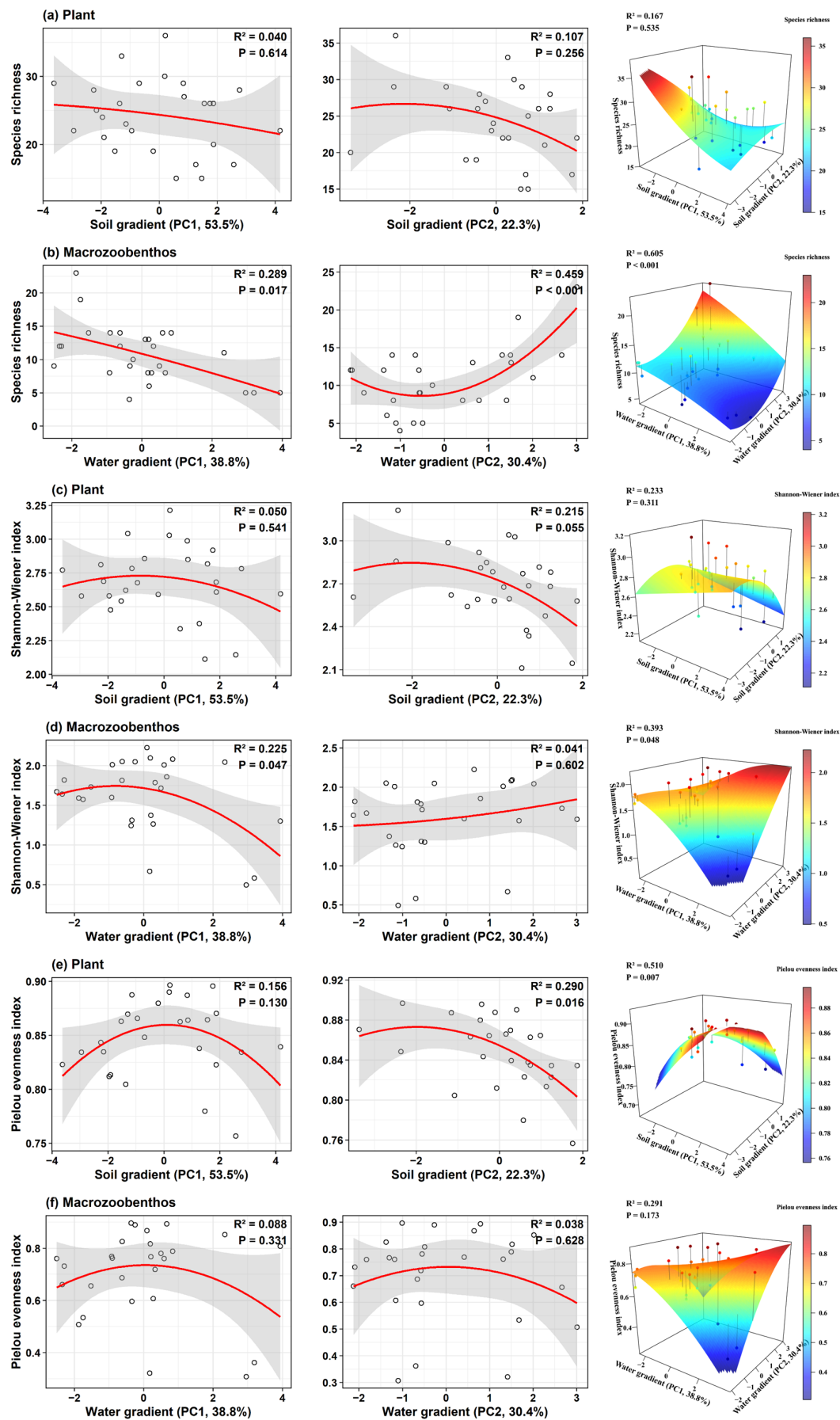


Figure 6. Responses of wetland plant and macrozoobenthos α -diversity to soil and water environmental gradients represented by the first two PCA axes, based on annual observations. Plant species richness,

the Shannon–Wiener index, and the Pielou evenness index were modeled as functions of PC1 and PC2 derived from soil environmental variables, whereas the corresponding macrozoobenthos metrics were modeled as functions of PC1 and PC2 derived from aquatic environmental variables. Within each panel, the left and middle plots show relationships with PC1 and PC2, respectively, fitted using separate second-order polynomial regression models. Red curves represent fitted relationships, and grey ribbons indicate their 95% confidence intervals. The right plot shows the joint predicted response to PC1 and PC2 from a bivariate second-order polynomial model containing the linear and quadratic terms of both axes and their interaction. Points represent annual observations ($n = 27$), and vertical lines in the three-dimensional plots connect observed values to the fitted response surfaces. The coefficient of determination (R^2) and overall p value are displayed for each model. (a) Plant species richness; (b) macrozoobenthos species richness; (c) plant Shannon–Wiener index; (d) macrozoobenthos Shannon–Wiener index; (e) plant Pielou evenness index; and (f) macrozoobenthos Pielou evenness index.

3.4.2. Environmental Associations of Community Composition

Mantel tests identified significant positive associations between plant community composition and six environmental variables: EC-W ($r = 0.319$, $p = 0.001$), TP ($r = 0.230$, $p = 0.011$), TN ($r = 0.212$, $p = 0.018$), TDSs ($r = 0.182$, $p = 0.012$), EC-S ($r = 0.149$, $p = 0.029$), and pH ($r = 0.128$, $p = 0.045$). Macrozoobenthos community composition was significantly associated with DO ($r = 0.247$, $p = 0.002$) and time since subsidence ($r = 0.137$, $p = 0.048$). All remaining Mantel associations were nonsignificant. Overall, the significant Mantel correlation coefficients ranged from 0.128 to 0.319 (Figure 7).

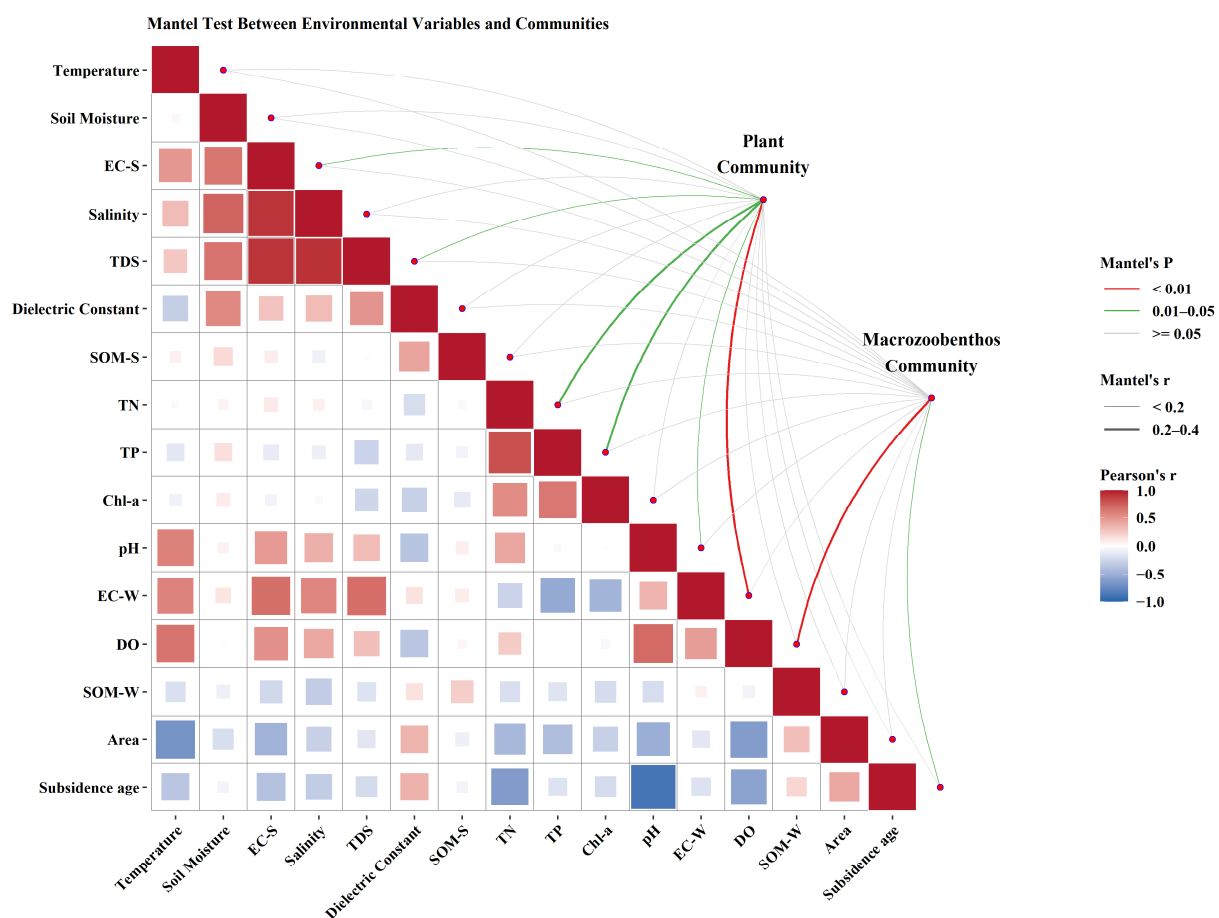


Figure 7. Associations between environmental variables and the community composition of wetland plants and macrozoobenthos based on Mantel tests. The lower-triangular matrix shows Pearson correlations among environmental variables. Square colours indicate the direction and magnitude of

Pearson's r , whereas square size represents its absolute magnitude. Curved links connect individual environmental variables to the community composition dissimilarities of plants and macrozoobenthos. Link colours indicate Mantel-test significance levels: red, $p < 0.01$; green, $0.01 \leq p < 0.05$; and grey, $p \geq 0.05$. Link widths represent the magnitude of Mantel's r (< 0.2 or $0.2-0.4$).

The full RDA model for plant community composition was significant (adjusted $R^2 = 0.204$, $p = 0.001$). Forward selection retained EC-W, TN, DO, wetland area, time since subsidence, and salinity, and the reduced model remained significant and explained 18.9% of the adjusted community variation (adjusted $R^2 = 0.189$, $p = 0.001$; Figure 8a). The first two constrained axes jointly accounted for 52.30% of the constrained variation. Envfit analysis identified DO ($r^2 = 0.283$, $p = 0.014$) and EC-W ($r^2 = 0.279$, $p = 0.016$) as the only variables significantly associated with the plant community ordination; TN, salinity, wetland area, and time since subsidence were not significant (Figure 8b).

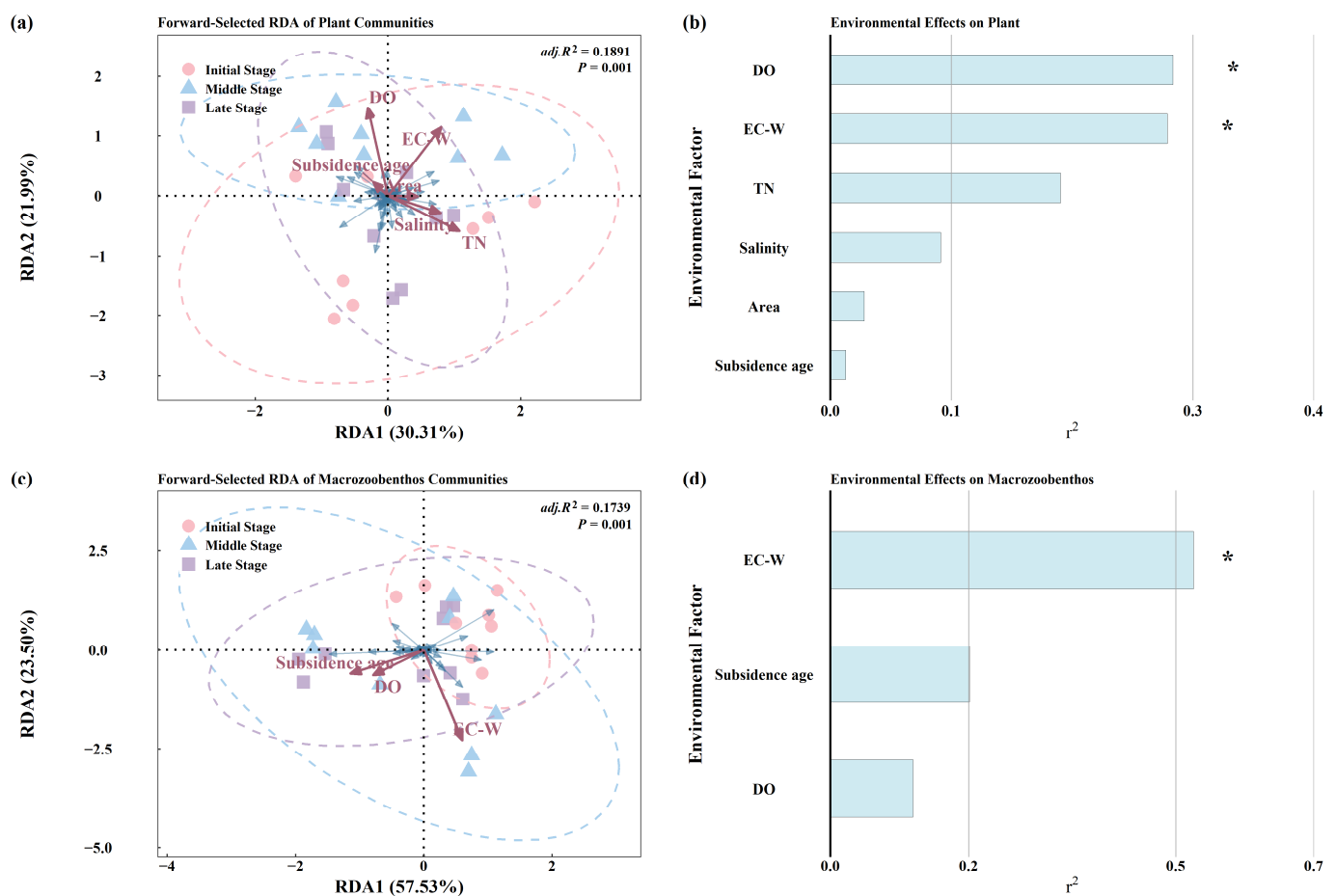


Figure 8. Environmental associations of wetland plant and macrozoobenthos communities based on forward-selected redundancy analysis (RDA) and envfit tests. Panels (a,c) show the forward-selected RDA ordinations of plant and macrozoobenthos communities, respectively. Point colours and shapes represent subsidence stages, and dashed ellipses indicate 95% confidence ellipses for the stage groupings. Blue arrows represent individual species scores, whereas red arrows represent environmental variables retained by forward selection. Percentages in the axis labels indicate the proportions of constrained variance explained by the first two RDA axes. Panels (b,d) show the corresponding envfit coefficients of determination (r^2) for the selected environmental variables. Bar lengths represent r^2 values, and asterisks indicate significant envfit associations ($p < 0.05$). Adjusted R^2 and permutation-based p values for the overall forward-selected RDA models are displayed in panels (a,c).

The full RDA model for macrozoobenthos community composition was also significant (adjusted $R^2 = 0.227$, $p = 0.012$). Forward selection retained time since subsidence, DO, and EC-W, and the reduced model remained significant and explained 17.4% of the adjusted community variation (adjusted $R^2 = 0.174$, $p = 0.001$; Figure 8c). The first two constrained axes jointly accounted for 81.03% of the constrained variation. Envfit analysis showed that only EC-W was significantly associated with the macrozoobenthos community ordination ($r^2 = 0.526$, $p = 0.001$), whereas time since subsidence and DO were not significant (Figure 8d).

4. Discussion

Cross-taxon congruence can be used to assess whether biodiversity changes correspond among different biological groups and whether one group can reliably represent another. Focusing on wetland plants and macrozoobenthos, this study examined how cross-taxon congruence in α -diversity and community composition varied among subsidence stages and seasons and evaluated its associations with environmental conditions. The results supported all three hypotheses. However, Hypothesis 2 was manifested as condition-dependent congruence, with significant congruence detected only for species richness, the Shannon–Wiener index in autumn, and community composition. Meanwhile, Pielou evenness index could serve only as a supplementary index for characterizing part of the information missing from the assessment of cross-taxon congruence in CMSWs. This also indicates that wetland plants cannot serve as a consistently reliable surrogate for macrozoobenthos diversity, although they may provide valuable supplementary information under particular subsidence stages, seasons, or diversity dimensions. Environmental analyses further showed that aquatic environmental variables exhibited more pronounced stage-related changes than the soil variables measured within the plant quadrats. However, the measured environmental variables had relatively limited explanatory power for community composition and therefore could not fully explain the observed compositional changes or patterns of cross-taxon congruence. The specific findings are as follows:

4.1. Stage-Dependent Variation in Wetland Plants and Macrozoobenthos

The results support Hypothesis 1. The α -diversity of both wetland plants and macrozoobenthos varied among subsidence stages, and the community composition of both groups also exhibited clear stage-related differences. Plant species richness and the Shannon–Wiener index both decreased at the middle stage and subsequently recovered at the late stage, indicating that plant communities responded markedly to the development of CMSWs. This pattern did not represent a simple developmental process of plant communities in natural or semi-natural wetlands, but was more likely a distinctive process of community reorganization in CMSWs under the combined effects of natural and anthropogenic processes. After land use ceased, its effects on soil properties, the propagule bank, and community composition could persist for a long period [2,62], while plant richness during the early development of newly formed wetlands may also depend on surrounding species sources and water-level fluctuations [63]. The relatively high plant diversity at the initial stage may therefore reflect the persistence of former agricultural plants, disturbance-adapted herbs, and the soil seed bank, while newly created habitats spanning different moisture and inundation regimes may have provided colonization opportunities for pioneer wetland and aquatic plants. As the inundated area expanded and the duration of flooding increased, hydrological filtering may have excluded terrestrial and mesophytic plants that were intolerant of prolonged inundation. Because inundation depth, duration, and frequency influence the germination, establishment, and community composition of wetland plants, while characteristic wetland plant communities may not yet

have been fully established, these processes may have produced the middle-stage diversity minimum [64,65]. By the late stage, water depth and inundation patterns may have become more stable, providing a wider range of suitable habitats for wetland and aquatic plants and allowing plant diversity to recover. The concentration of stage-related differences in summer and autumn further suggests that hydrological filtering and seasonal plant growth jointly contributed to community reassembly [66,67].

The stage-dependent response of macrozoobenthos α -diversity was comparatively weak, being characterized primarily by an increase in species richness at the late stage while the Shannon–Wiener index remained stable. This pattern may have resulted from the addition of low-abundance taxa. Taxa newly detected at the late stage, including *Belamya quadrata*, *Anodonta woodiana*, and large-bodied aquatic insects such as Dytiscidae sp., occurred in only a few samples. Their addition expanded the late-stage species pool but was insufficient to produce a significant change in abundance-weighted diversity. Newly formed water bodies can be rapidly colonized by aquatic insects with winged adult stages, and taxa with high dispersal capacity and short generation times, such as chironomids, can quickly establish populations under fluctuating environmental conditions [68]. During the initial and middle stages, surface subsidence and seasonal precipitation may have jointly produced substantial fluctuations in water area and physicochemical conditions, favouring opportunistic taxa with rapid turnover and high environmental tolerance. As subsidence slowed and more persistent aquatic habitats developed at the late stage, molluscs and insects with longer aquatic life stages may have acquired the conditions required for long-term persistence. Hydroperiod can strongly influence the species richness and community composition of wetland macrozoobenthos by constraining colonization, the time available for life-cycle completion, and the persistence of taxa with different levels of drought tolerance [69–71]. Previous studies have shown that seasonal life-history processes, including emergence, reproduction, and larval recruitment, can influence seasonal variation in macrozoobenthic communities [72,73]. These processes may therefore provide a possible explanation for why significant stage-related differences were detected only in spring in the present study. This seasonal pattern is consistent with previous findings from CMSWs in northern China, where macrozoobenthic diversity and community composition varied significantly among wetland types and seasons [10]. Thus, the late-stage increase in the species richness of macrozoobenthos may have primarily reflected the addition of low-abundance taxa rather than a synchronous increase in all α -diversity metrics; whether this pattern was also associated with a broader range of life-history strategies remains to be tested.

4.2. Cross-Taxon Congruence Across Diversity Dimensions

The results support Hypothesis 2. The two groups exhibited cross-taxon congruence. At the overall scale, species richness was significantly and positively correlated between wetland plants and macrozoobenthos, whereas no significant correlations were detected for the Shannon–Wiener index or Pielou evenness. A significant relationship was also detected in a specific season (Shannon–Wiener index—autumn: $r = 0.430$, $p = 0.025$; Figure 4f). These findings also indicate that the two groups can provide a certain degree of correspondence only in terms of species richness. However, this relationship was not stable across subsidence stages, seasons, or diversity dimensions. This pattern may arise because the two groups use different habitat units and are constrained by different factors: wetland plants respond relatively more strongly to soil conditions, inundation, propagule sources, and interspecific competition, whereas macrozoobenthos respond more directly to the water environment, sediment conditions, and the spatial configuration of aquatic habitats. Previous land-use types may also have persistent effects on subsequently de-

veloping wetland biological communities [2,74]. Cross-taxon congruence in freshwater ecosystems is often dependent on spatial scale, habitat context, and the diversity metric considered, and a single taxonomic group does not necessarily represent the diversity patterns of other groups [14,15,75,76]. Similar dimensional differences have been reported in river–riparian ecotones, where species richness was incongruent among taxonomic groups despite significant correspondence in multivariate community composition, and where these relationships varied with anthropogenic disturbance [32,77]. Large-scale studies of lakes have likewise found generally weak congruence among aquatic communities and substantial variation in congruence across regional environmental contexts [78]. Therefore, the near-zero and nonsignificant overall cross-taxon correlations in α -diversity do not support the use of wetland plant diversity as a reliable surrogate for macrozoobenthos diversity [79].

Nevertheless, the community composition analysis indicated that the two groups were not entirely independent. Procrustes analysis revealed significant but limited congruence between the ordination configurations of wetland plant and macrozoobenthos communities. This finding does not conflict with the weak congruence observed in α -diversity because species richness and the Shannon–Wiener index reduce community information to single values and therefore cannot fully capture species replacement, whereas Procrustes analysis preserves the overall configuration of samples in multivariate ordination space. Communities with similar species richness may nevertheless comprise different species; consequently, correspondence in community composition does not necessarily coincide with synchronous variation in α -diversity. Cross-taxon congruence may also differ among taxonomic, functional, and β -diversity dimensions [75,80–82]. Given the relatively high stress value of the plant NMDS, the Procrustes result should be interpreted as limited structural correspondence rather than completely synchronous community change. Cross-taxon congruence was therefore clearly dependent on the diversity dimension considered: it was generally weak at the α -diversity level but retained a degree of overall correspondence at the community composition level.

4.3. Stage- and Season-Dependent Variation in Cross-Taxon Congruence

The results support Hypothesis 3. Across the subsidence stages, the only significant stage-specific relationship between the two taxonomic groups was the negative correlation in Pielou evenness index at the initial stage. The $r = 0$ observed at the late stage resulted from the cancellation of positive and negative covariance contributions within the sample, producing an estimate of zero linear covariance. This result indicates only that no linear correlation was statistically detected in the current data and does not demonstrate that the two groups were completely unrelated ecologically. Nevertheless, the strength and direction of the associations for the different indices varied among subsidence stages (Figure 4), indicating that the two groups did not exhibit a stable or synchronous response. This variation may have arisen because the community assembly processes of the two groups changed dynamically during wetland development.

The two groups adopted different response strategies at different developmental stages of the newly formed CMSWs. At the initial stage, both taxonomic groups responded to the newly formed water bodies and newly available space for colonization, and numerous pioneer plant and animal species rapidly colonized the newly formed wetlands. At the middle stage, continued land subsidence and expansion of the inundated area promoted further wetland development, and both plant and animal communities were affected by these changes. However, the ways in which the two groups responded to environmental change began to diverge. Plant species composition continued to change before stable wetland plant communities became established. In contrast, the early colonizers

of macrozoobenthos mainly consisted of taxa characterized by rapid turnover and high disturbance tolerance and therefore responded less strongly to this process. Meanwhile, habitat change primarily involved the conversion of the land–water ecotone from terrestrial to wetland habitat, which directly affected plants. Macrozoobenthos, however, were mainly constrained by aquatic physicochemical conditions and the spatial configuration of aquatic habitats and were less directly affected by wetland transformation in the riparian zone. Consequently, the principal environmental domains to which the two groups responded gradually diverged, resulting in the progressive decoupling or even absence of association between their diversity patterns. Other wetland studies have similarly shown that hydroperiod exerts a stronger influence on aquatic macroinvertebrate communities than on co-occurring plant communities, suggesting that shared environmental filtering may play a greater role than direct interactions between taxonomic groups in determining cross-taxon relationships [83]. At the late stage, the rates of wetland development and changes in environmental conditions tended to moderate. As the shared disturbance weakened, differences in diversity among wetlands may have been determined increasingly by taxon-specific processes. The communities may have gradually approached saturation and become relatively stable, with each group responding to its respective niche conditions. Although plants can provide organic matter, attachment substrates, and refuges, these ecological functions depend primarily on vegetation cover, biomass, and spatial structure and do not necessarily increase synchronously with plant α -diversity. Macrozoobenthos may also exhibit time-lagged responses to changes in vegetation and hydrological conditions. However, the dual effects of vegetation and time lags in community responses were not directly examined in this study and therefore remain potential mechanisms requiring further verification.

The seasonal results further demonstrated this context dependence. The Shannon–Wiener index was the only diversity metric that showed a significant positive correlation between the two groups, and this relationship occurred only in autumn. This seasonal congruence may have been associated with relatively stable hydrological conditions, well-developed vegetation structure, and the recruitment and dispersal of macrozoobenthos in autumn [72,73]. Following the low water levels in spring and water replenishment in summer, water-level fluctuations may have moderated in autumn, and plant communities may have gradually stabilized toward the end of the growing season. Meanwhile, the expansion of aquatic areas and land–water ecotones may have increased the habitat space available to macrozoobenthos. The two groups may also have responded to partly shared microhabitat conditions, thereby promoting relatively congruent diversity responses at the local scale [35,84].

4.4. Environmental Context of Cross-Taxon Congruence

The contrasting environmental responses of the two groups provide a possible explanation for this stage-dependent variation. Among the plant diversity metrics, only Pielou evenness index responded significantly to the soil environment, whereas no significant relationships were detected for the other metrics. By contrast, macrozoobenthos species richness showed a clear response to aquatic environmental gradients, whereas the Shannon–Wiener index showed a detectable but weaker response. These results indicate that the measured soil physicochemical variables alone were insufficient to explain the stage-dependent variation in plant diversity.

Macrozoobenthos diversity exhibited different response patterns along the two aquatic environmental PCA axes. The concurrent declines in species richness and the Shannon–Wiener index along aquatic PC1 suggest that integrated changes in nutrient status and primary productivity may have excluded some macrozoobenthos taxa through environ-

mental filtering, thereby reducing overall community diversity. When considered together with the supplementary information provided by Pielou evenness, this pattern suggests that the decline in the Shannon–Wiener index was primarily associated with a reduction in species richness rather than a pronounced reorganization of community dominance structure. The PC2 gradient, which was mainly characterized by DO, pH, and EC-W, may have affected species occurrence, disappearance, or replacement. These changes may have primarily involved relatively low-abundance taxa and may therefore have been insufficient to substantially alter the overall relative-abundance distribution of the community. However, this potential turnover of low-abundance taxa was not directly examined in the present study and requires further verification.

Overall, variation in the aquatic environment may have initially affected macrozoobenthos richness through species filtering and the potential turnover of low-abundance taxa. The Shannon–Wiener index, which is jointly determined by species richness and evenness, exhibited a relatively buffered response to environmental variation. Because the PCA axes integrated multiple correlated environmental variables, these relationships should be interpreted as associations with multidimensional aquatic environmental gradients rather than as direct effects of any single water-quality variable. These findings indicate that different taxonomic groups and diversity dimensions integrate different environmental information, which may help explain the weak and context-dependent cross-taxon congruence observed in this study [85].

Although Mantel tests and RDA identified partly overlapping but taxon-specific environmental associations for wetland plants and macrozoobenthos, the overall explanatory power of these environmental variables for community composition remained relatively limited. Mantel tests indicated that plant community composition was associated with multiple environmental factors (Figure 7), whereas macrozoobenthos community composition was mainly associated with DO and time since subsidence. The Mantel correlation coefficients were generally weak to moderate, indicating that individual environmental variables exhibited only weak to moderate associations with community dissimilarity. After retaining multiple factors through forward selection (Figure 8), the plant and macrozoobenthos RDA models explained 18.9% and 17.4% of the variation in community composition, respectively. The envfit results were consistent with partially shared filtering by the aquatic environment between the two groups, which may be one factor contributing to the significant Procrustes congruence observed in their community composition. However, plants were associated with a broader range of environmental conditions, whereas the environmental associations of macrozoobenthos were more concentrated on aquatic physicochemical conditions and time since subsidence. This suggests that the pathways and sensitivities through which the two groups responded to the same process of wetland development were not entirely consistent. Collectively, the environmental analyses indicate that environmental filtering was partly shared but also clearly taxon specific.

Previous studies have shown that wetland plant community composition is jointly influenced by soil moisture, soil chemical properties, and local hydrological conditions [65,86], whereas hydroperiod, wetland area, water quality, sediment characteristics, and microhabitat structure can influence macrozoobenthos community composition [70,71,84]. Environmental changes may cause species replacement in both groups without necessarily producing synchronous changes in their species richness, Shannon–Wiener index, and Pielou evenness index [87]. This may explain why community composition exhibited some degree of Procrustes congruence in the present study, whereas α -diversity congruence varied among subsidence stages, seasons, and diversity indices.

Despite the statistical significance of these environmental associations, the plant and macrozoobenthos RDA models still left approximately 81.1% and 82.6% of the variation

in community composition unexplained, respectively. Therefore, the measured environmental variables should be interpreted as partial correlates of community composition rather than as strong controlling factors determining community change. The relative contributions of deterministic environmental filtering, dispersal limitation, biotic interactions, historical effects, and stochastic colonization processes may differ between the two groups [88]. Shared environmental responses therefore represent only one possible mechanism underlying cross-taxon congruence, and environmental filtering is unlikely to be its sole source [89]. Continuous water-level variation, inundation duration, sediment grain size, vegetation biomass and patch structure, aquatic habitat connectivity, and trophic relationships, which were not measured in this study, may also contribute to shaping community composition. Future studies should increase the temporal resolution of hydrological and environmental monitoring and incorporate analyses of spatial processes, vegetation structure, and stochastic community assembly to further distinguish the relative contributions of shared environmental filtering, taxon-specific responses, and unmeasured processes to cross-taxon congruence.

Overall, wetland plants and macrozoobenthos jointly captured community reorganization in CMSWs but reflected different ecological processes. Wetland plants responded more strongly to land-use legacies, soil conditions within the plant quadrats, and inundation conditions, whereas macrozoobenthos more directly integrated the spatial configuration of aquatic habitats, water physicochemical conditions, and seasonal life-history processes. Because the chronosequence may confound site history with spatial variation, continuous water-level records, sediment grain-size data, and information on vegetation patch structure were unavailable, and the macrozoobenthos samples primarily represented continuously inundated microhabitats, the underlying mechanisms require further verification through long-term monitoring and environment–space variation partitioning. Biodiversity assessment in CMSWs should integrate wetland plants, macrozoobenthos, and key environmental factors through joint multi-taxon monitoring, rather than relying on a single taxonomic group or treating cross-taxon congruence as a restoration indicator expected to increase continuously with time since subsidence.

5. Conclusions

This study characterized the diversity patterns of macrozoobenthos and wetland plants in CMSWs. Cross-taxon congruence between the two groups was generally context dependent, varying among subsidence stages, seasons, and diversity dimensions, with clear congruence detected only for species richness. The development of CMSW ecosystems was more consistent with asynchronous community reorganization occurring in the context of hydrological restructuring and habitat differentiation caused by mining subsidence than with a linear ecological trajectory in which different taxonomic groups converge toward a shared mature state. Accordingly, the management and biodiversity monitoring of the wetlands examined in this study should account for asynchronous community responses and differences in ecological resilience and should integrate both wetland plants and macrozoobenthos rather than relying on a single taxonomic group. Because the study area is located in the temperate monsoon region of eastern China, these findings may not be applicable to mining landscapes with different climates, hydrological conditions, or restoration histories. Future studies should evaluate whether the condition-specific relationships identified here apply to other subsidence wetlands, quantify a broader range of environmental variables, and investigate how ecosystem and community stability can be maintained under different environmental conditions.

Supplementary Materials: The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/su18199896/s1>. Table S1: Site information for the nine CMSWs; Table S2: Principal component loadings of soil and water environmental variables.

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Abbreviations

The following abbreviations are used in this manuscript:

CMSWs	coal-mining subsidence wetlands
IS	Initial stage
MS	Middle stage
LS	Late stage
EC-S	Soil electrical conductivity
TDSs	Total dissolved solids
SOM-S	Soil organic matter
TN	Total nitrogen
TP	Total phosphorus
Chl-a	Chlorophyll a
EC-W	Water electrical conductivity
DO	Dissolved oxygen
SOM-W	Sediment organic matter

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