Framework of multidimensional macrobenthos biodiversity to evaluate ecological restoration in wetlands

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Abstract

Sustaining biodiversity is a priority for ecological restoration in degraded wetlands, and biodiversity is an inherently multidimensional ecosystem property, as it includes genetic, taxonomic, functional, and other types of diversity. However, most restoration projects have only employed taxonomic diversity to assess restoration, and given the multidimensional nature of biodiversity, this may partially describe the true situation. In this paper, we constructed a multidimensional macrobenthos biodiversity framework (for genetic, taxonomic, and functional diversity), developed a holistic biodiversity index that accounted for these dimensions, and explored the consequences of freshwater restoration in a case study of this index. We found that freshwater restoration increased genetic and taxonomic diversity, but had no significant effect on functional diversity, and that the functional traits of the macrobenthos appeared to have converged on homogeneous functional traits. On the other hand, freshwater restoration had a significant positive effect on the holistic biodiversity. The relationship between ecosystem function (in macrobenthos biomass) and holistic biodiversity in the restoration areas was unimodal, with the highest biomass found at intermediate levels of holistic biodiversity. The multidimensional framework challenged the utility of using any one dimension of biodiversity as a surrogate for other dimensions. The holistic biodiversity index provided more comprehensive and holistic insights into the management of freshwater restoration projects.

1. Introduction

Wetland ecological restoration is increasingly a focus of ecosystem management, and has been undertaken in many inland and coastal regions in recent years (Zedler 2000, Cui et al 2009, Robson et al 2011). The ultimate goals of wetland restoration are to systematically maintain ecosystem biodiversity, and to improve the delivery of ecosystem services and functions (Zedler 2000, Heller and Zavaleta 2009, Palmer and Filoso 2009, Kaiserbunbury et al 2017). Several freshwater restoration projects have been implemented by regulating the environmental flow regimes to re-establish a wetland’s hydrology and re-construct the links between biotic and abiotic components in degraded wetland ecosystems (Alexander and Dunton 2002, Cui et al 2009, Yang et al 2016). This has become an urgent task due to the intensifying anthropogenic and natural stressors in most wetlands (Cui et al 2009, Poff and Zimmerman 2010). Previous studies showed that ecological restoration has been effective based on the evaluation of various indicators in the wetlands, including water quality, vegetation succession, and macrobenthos (Aldous et al 2005, Li et al 2016a, Marshall 2017, Yang et al 2017). In recent decades, the macrobenthos has been regarded as a particularly important indicator of wetland ecosystem health because these organisms respond sensitively to environmental conditions in wetlands as a result of living in direct contact with the sediment, and transfer energy and materials through the ecosystem (Alves et al 2015, Li et al 2016b).
Previous studies showed that ecological restoration through long-term implementation of restoration measures can improve ecosystem biodiversity, but this result was normally obtained through an analysis of taxonomic diversity (Rey Benayas et al. 2009, Yang et al. 2016). However, biodiversity is inherently multidimensional, as it refers to multiple scales and dimensions, including genetic, phylogenetic, taxonomic, functional, and trophic dimensions, which vary among organisms in complex ways (Devictor et al. 2010, Dreiss et al. 2015, Naeem et al. 2016, Nakamura et al. 2017). Relying only on taxonomic diversity to evaluate restoration effects, as a surrogate for other dimensions of biodiversity, might therefore produce limited and misleading insights into the success of ecological restoration.

Research with two, three, or more dimensions of biodiversity examined simultaneously is a growing trend and a hot topic in biodiversity research. These studies can provide novel and more comprehensive insights into biodiversity responses to environmental changes that differ from the empirical understanding gained from traditional single-dimension biodiversity research (Thompson et al. 2015, Naeem et al. 2016). Nakamura et al. (2017) found that the functional and phylogenetic dimensions were more important than the taxonomic dimension for capturing variation in the biodiversity space formed by simultaneous examination of these three dimensions. What’s more, each dimension of biodiversity might respond at different rates to environmental changes (Lyashevska and Farnsworth 2012). Therefore, each dimension may have a greater or lesser value in different contexts, and the different dimensions may respond differently, even within the same region. For example, Muscarella et al. (2016) found that functional diversity decreased during succession in a tropical forest, whereas phylogenetic diversity increased. Devictor et al. (2010) identified cases of congruence and mismatch among the responses of taxonomic, phylogenetic and functional diversity of birds in protected areas of France. Thompson et al. (2015) used a structural equation model to develop a solution that synthesized phylogenetic, functional, and taxonomic diversity, and found more pronounced positive relationships between diversity and ecosystem function for functional and phylogenetic diversity than for taxonomic diversity. However, given the inconsistency in the relative strengths of the different biodiversity dimensions in these previous studies, it is difficult to provide an appropriate suggestion for restoration management based on multidimensional biodiversity. In specific cases, it may be necessary to focus on a single type of diversity (e.g. genetic diversity for a critically endangered species), but holistic metrics are necessary when managers must protect multiple types of diversity simultaneously, leading to tradeoffs among the types. Holistic metrics that integrate two or more metrics to produce a multidimensional metric are therefore becoming increasingly necessary, but no studies have employed a truly holistic metric.

To provide some of the missing knowledge, we designed the present study to examine the response of wetland macrobenthos to restoration. We chose these organisms due to their ecological importance and value as indicator species, constructed a multidimensional biodiversity framework, and developed a holistic biodiversity index to evaluate their responses to ecological restoration. To demonstrate our framework, freshwater restoration areas within China’s Yellow River Delta were selected as a case study. The effects of the restoration were evaluated based on the genetic, taxonomic, and functional diversity and based on the holistic biodiversity index for the macrobenthos, and we examined the relationships between holistic biodiversity and ecosystem function for the macrobenthos, and we examined the relationships between holistic biodiversity and ecosystem function for the macrobenthos.

2.2. Materials and methods

2.1. Development of a multidimensional biodiversity framework

The framework developed in this study provides a more comprehensive understanding of the effects of ecological restoration on the multidimensional macrobenthos biodiversity in a wetland. Different environmental gradients (including but not limited to water quality, water depth, and sediment salinity) can be used to represent the abiotic effects of ecological restoration on environmental conditions. We focused on three dimensions of macrobenthos biodiversity: genetic, taxonomic, and functional diversity. Each of these dimensions emphasized a different scale of the responses to ecological restoration. A holistic biodiversity index was developed to support restoration management based on the three dimensions of diversity. The index can be used to identify the relationship between each dimension of biodiversity and abiotic environment by means of linear or non-linear regression, as well as the relationship between the holistic biodiversity index and abiotic environment. All of these relationships illustrate the responses to ecological restoration more systematically and holistically than single-dimensions indices.

Genetic diversity was represented by the observed heterozygosity (Het_{obs}), expected heterozygosity (Het_{exp}), and nucleotide polymorphism index (P_i). Het_{obs} is the proportion of homozygous individuals for each single-nucleotide polymorphism (SNP), averaged over an individual chromosome or an entire genome. Het_{exp} was calculated using the formula provided by Nei (1978) based on the frequency of the allelic forms. All the metrics were calculated using
version 3.2 of the POPGENE software (https://sites.ualberta.ca/~fyeh/pogene_download.html).

Four indices of taxonomic diversity were calculated: the Shannon–Weiner index ($H'$; Magurran 1988), Pielou’s evenness index ($J$; Pielou 1975), Simpson’s diversity index ($D$; Magurran 1988), and Margalef’s richness index ($d$; Margalef 1968). The four indices were chosen because each diversity metric reflects a different aspect of the macrobenthos, and the different aspects cannot be adequately described using only one index (Shah and Pandit 2013). Taxonomic diversity was analyzed using version 3.4.3 of the R software (www.r-project.org) with version 2.5-4 of the Vegan package (Oksanen et al. 2019).

Four independent functional diversity indices were used to capture different components of functional diversity: functional richness ($FRic$), functional evenness ($FEve$), and functional divergence ($FDiv$) (Villéger et al. 2008, Laliberté and Legendre 2010), and Rao’s quadratic entropy ($RaoQ$) (Botta-Dukát 2005). $FRic$ characterizes the total volume of a multidimensional space defined by the functional traits of a community, whereas $FEve$ represents the regularity with which species are distributed throughout a multidimensional functional space. $FDiv$ also describes the distribution of species throughout a multidimensional space, but focuses on the proximity of the species to the center or the edges of the functional space (Naem et al. 2016). $FDiv$ and $FEve$ cannot be calculated for single traits within a community. $RaoQ$ measures the average difference among species based on multiple characteristics and reflects the degree of multivariate dispersion. The functional diversity indices were calculated using the FD package (Laliberté et al. 2014) in the R software.

### 2.2. Improvement of indicator values

The methods of Ricotta (2005) and Nakamura et al. (2017), were used to develop an improved multidimensional indicator that accounts for the importance value, which represents the relative contribution of a given dimension of biodiversity to capturing the variation present in a community. A single matrix was assembled that summarized the values of the three dimensions of biodiversity in the macrobenthos at a given sampling site, and then principal-components analysis (PCA) was used to obtain the axes (principal components) that represented significant variation in the 11-dimensional biodiversity space created by the 11 biodiversity metrics that were used to represent the three biodiversity dimensions. Using the selected PCA axes that accounted for at least 80% of the total variation in the biodiversity space, the importance value of each dimension could be calculated as follows:

$$IV_i = \sum_{j=1}^{n} (r_{ij} \times R_j^2),$$

where $IV_i$ is the importance of biodiversity metric $i$, $n$ is the total number of axes selected by the PCA, $r_{ij}$ is...
the correlation value between metric $i$ and principal component $j$ (for $j$ axes), and $R_j$ is the proportion of the total variation explained by principal component $j$. We used four principal components in this calculation. $IV$ is a dimensionless value from 0 to 1, with higher $IV$ values representing a greater proportion of the variation captured by that biodiversity dimension.

2.3. Holistic biodiversity

Holistic biodiversity of the macrobenthos simultaneously considered the three selected dimensions of biodiversity (genetic, taxonomic, and functional diversity) and their importance values to capture the variation in a community. The multiple metrics of macrobenthos biodiversity were standardized using the min-max normalization method, then combined with the importance values and summed to produce a dimensionless holistic biodiversity index ($HB$):

$$SM_i = \frac{BM_i - \min(BM_i)}{\max(BM_i) - \min(BM_i)}$$

$$HB = \sum_{i=1}^{n} SM_i IV_i$$

where $SM_i$ is the standardized value of biodiversity metric $i$, $BM_i$ is the biodiversity metric $i$ (i.e. $Het_{Obs}$, $Het_{Exp}$, $P_0$, $H'$, $J$, $D$, $d$, $FRic$, $FEve$, $FDiv$, or $RaoQ$), and $n$ is the total number of biodiversity metrics ($n = 11$), and $HB$ is the holistic biodiversity of macrobenthos with dimensionless.

3. Case study

3.1. Study area

The Yellow River Delta wetland is located in China’s Shandong Province (37.58°N–38.20°N, 118.55°E–119.35° E), facing the Bohai sea (figure 2). The Yiqianer National Nature Reserve was established in 1992 in the wetlands around the river’s old channel. From 1964 to 1976, the Yellow River flowed through the old channel to the sea, and migrated to the modern channel in 1976. As a result, the reserve region has no natural freshwater inflows and its original freshwater ecosystems have been adversely affected by water erosion, salinization of the wetland, and habitat degradation; for example, there were nearly 12.52 and 52.03 km² of $Phragmites australis$ and Marsh plants in 1998, respectively, and these areas decreased greatly, to 6.98 and 19.49 km² in 2008 (table S1, figure S1 is available online: stacks.iop.org/ERL/14/054003/mmedia).

The Yiqianer National Nature Reserve has played an essential role in protecting, re-establishing, and restoring the wetlands through the implementation of freshwater releases (Cui et al 2009). Freshwater restoration in the wetlands has been conducted by environmental flow releases from upstream reservoirs. The restoration project has released $1.3 \times 10^7$ to $3.6 \times 10^7$ m³ of freshwater annually into the reserve since 2010 or 2012 in different parts of the reserve (Yang et al 2017a). The areas of $Phragmites australis$ and Marsh plants in 2012 increased after freshwater restoration compared with the areas in 2008 (table S1).

The study region can be divided into three sub-areas based on its restoration histories and elevation. Areas I and II have received freshwater releases since 2010, whereas area III has received these releases since 2012. Areas I, II, and III normally receive freshwater releases in July of each year, during water and sediment regulation work for the upstream Xiaolangdi Reservoir, which is in the middle reaches of the Yellow River. There is an intertidal area located between the freshwater restoration area and the Bohai, and the
3.2. Fieldwork and sampling
Fieldwork was performed in the autumn of 2014, 2015, and 2016 to sample the sediments and macrobenthos. Four sites were sampled in each area (figure 2). In total, there were 12 samples in each area. Sediment samples were collected to a depth of 5.0 cm using a soil core, and the salinity was measured in a 1:5 v/v sediment to water solution using an Hq30d multi-meter (Hach, Loveland, CO, USA). Macrobenthos samples were collected at three random locations (each 0.3 m × 0.3 m × 0.3 m) at each sampling site. The sediment was passed through a 0.5 mm sieve to obtain the macrobenthos organisms, which were then cleaned and preserved in 75% alcohol until they could be counted, identified under a stereomicroscope (ideally to the species level; if not, to the family level), and weighed.

Restriction-site-associated DNA sequencing was used to examine the natural population of Chironomids (a dominant and common species in the freshwater restoration areas) by developing genome-wide SNP molecular markers, and the SNP markers were used for our population genetics research. A total of 17 Chironomid samples (6, 7, and 4 samples obtained from areas I, II, and III, respectively) were genotyped using the Illumina BovineHD Genotyping BeadChip system (Neogen, Lincoln NE, USA), which contained 419,431 SNPs. DNA was isolated from the organisms using a standard proteinase K digestion followed by phenol/chloroform extraction and ethanol precipitation (Campana et al. 2010), and then the DNA concentrations were measured using a NanoDrop2000 spectrophotometer (ThermoFisher Scientific, Waltham, MA, USA). The integrity of the genomic DNA was confirmed by means of 1% agarose gel electrophoresis. The genomic sequence of Chironomus tentens (http://ftp.ncbi.nlm.nih.gov/ genomes/all/GCA/000/786/525/GCA_000786525.1_CT01/GCA_000786525.1_CT01_genomic.fna.gz) was used as a reference; the reference genome size was 213 Mbp and the GC content was 33.3%. We compared all SNPs from the sequenced reads with the reference genome sequence, and used the Picard tools software (https://broadinstitute.github.io/picard/) to remove sequencing reads generated by PCR-duplication in the BWA software (Li et al. 2009). The SNPs were filtered by removing the sites with minor allele frequencies (<0.05) and including selected screening genotypes that covered at least 70% of all samples. This resulted in a total of 4457 SNPs. Based on the results of the SNP analysis, the abovementioned genetic diversity indices were calculated and the genetic differentiation among the populations (Fst) was used to represent genetic diversity and genetic differentiation. Fst is an important indicator of genetic differentiation among the sub-populations of a species (Rousset 1997). The larger the Fst value, the greater the genetic differentiation among the sub-populations.

The taxonomic and functional diversity indices in the framework were also calculated. Here, the functional diversity indices were calculated using seven macrobenthos traits (voltinism, size at maturity, habit, trophic habit, swimming ability, respiration, and salinity preference; supplementary materials 1 and table S2), as these factors were important in previous studies (Usseglio-Polatera et al. 2000, Poff et al. 2006, Vieira et al. 2006, Archaibault et al. 2010).

3.3. Statistical analysis
The sediment properties were tested for significant differences among the three freshwater restoration areas in the taxonomic and functional biodiversity dimensions and in the functional traits of the macrobenthos using one-way ANOVA. When the ANOVA result was significant, Tukey’s HSD test was used to identify significant differences between pairs of sites (p < 0.05). All the tests were performed using version 20.0 of the SPSS software (www.ibm.com/analytics/us/en/technology/spss/). Nonlinear regression was used to describe the relationships between the three dimensions of biodiversity, the holistic biodiversity index, and freshwater restoration, and to describe the relationship between ecosystem function and holistic biodiversity. The regression analyses were performed using version 9.0 of the Origin software (http://originlab.com/).

4. Results
4.1. Variation of sediment salinity and water content in the restoration areas
As a result of the freshwater restoration, sediment salinity and sediment water content both differed significantly among the three freshwater restoration areas (for salinity, F2,35 = 8.125, p = 0.001; for water content, F2,35 = 7.322, p = 0.002; figure 3). Sediment salinity in area III was significantly higher than that in area I (p = 0.001) and area II (p = 0.024), but areas I and II (which have both received freshwater releases since 2010) did not differ significantly (p = 0.487). In contrast, sediment water content in area I was significantly higher than that in area II (p = 0.043) and area III (p = 0.002), but areas II and III (which
have received freshwater releases since 2010 and 2012, respectively) did not differ significantly \((p = 0.441)\).

### 4.2. Multidimensional macrobenthos biodiversity

#### 4.2.1. Genetic diversity

The genetic diversity metrics \((\text{Het}_{\text{Obs}}, \text{Het}_{\text{Exp}}, \text{and } P_i)\) produced similar patterns among the three freshwater restoration areas (table 1). The genetic diversity of the macrobenthos was highest in area I, followed by area II, and was lowest in area III, except for a lower \(\text{Het}_{\text{Obs}}\) value in area II. Consistent with these results, the population divergence \(\left(\text{F}_{\text{st}}\right)\) was lowest between areas I and II and much higher between areas I and III and between areas II and III (table 2).

#### 4.2.2. Taxonomic diversity

We collected a total of 32 taxa in the three areas during the study period, including 4 classes and 3 phyla (table S3). Of these, we collected 22 taxa in area I: 4 Crustacea, 17 Insecta, and 1 Gastropoda (table S4). We collected a total of 21 taxa in area II, including 1 Polychaete, 5 Crustacea, and 15 Insecta (table S5). In area III, we collected a total of 16 taxa, including 2 Polychaetes, 4 Crustacea, and 10 Insecta (table S6).

Taxonomic diversity differed among the freshwater restoration areas based on differences in their typical species. The Shannon–Weiner index \((H')\) differed significantly among the areas \((F_{2,35} = 5.563, p = 0.008, \text{figure } 4)\). \(H'\) was significantly higher in area I than in areas II and III (for area II, \(p = 0.016\); for area III, \(p = 0.021\)), but did not differ significantly between areas II and III \((p = 0.993)\). Pielou’s evenness index \((J)\) did not differ significantly among the three areas \((F_{2,32} = 1.727, p = 0.195, \text{figure } 4)\). Simpson’s diversity index \((D)\) differed significantly among the areas \((F_{2,32} = 3.820, p = 0.033, \text{figure } 4)\). \(D\) was significantly higher in areas I and III than in area II \((p = 0.031)\). Margalef’s richness index \((d)\) differed significantly among the areas \((F_{2,34} = 5.364, p = 0.010, \text{figure } 4)\), with a significantly higher value in area I than in area II \((p = 0.049)\) and area III \((p = 0.011)\); however, \(d\) did not differ significantly between areas II and III \((p = 0.782)\).

#### 4.2.3. Functional diversity

Figure 5 illustrates the PCA results for the macrobenthos functional traits. PC1 explained the largest proportion of the variation in ecological traits among areas I, II, and III, with values ranging from 86.7% for habitat to 97.9% for voltinism. There was no statistically significant difference among the three areas in the ecological traits of the macrobenthos (for voltinism, \(F_{2,58} = 1.840, p = 0.168\); for size at maturity; \(F_{2,58} = 1.004, p = 0.373\); for habit, \(F_{2,58} = 0.354, p = 0.704\); for trophic habit, \(F_{2,58} = 0.404, p = 0.669\); for swimming ability, \(F_{2,58} = 0.179, p = 0.837\); for respiration, \(F_{2,58} = 0.504, p = 0.607\); and for salinity preference, \(F_{2,58} = 1.662, p = 0.199\) ). Most macrobenthos were correlated with bi- or multivoltine voltinism (figure 5(a)), small size at maturity (figure 5(b)), burrow habit (figure 5(c)), and a collector-gatherer or

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**Table 1.** Genetic diversity of the macrobenthos communities in areas I, II, and III.

| Freshwater restoration areas | Observed heterozygosity \((\text{Het}_{\text{Obs}})\) | Expected heterozygosity \((\text{Het}_{\text{Exp}})\) | Nucleotide diversity \((P_i)\) |
|-----------------------------|------------------|------------------|------------------|
| I                           | 0.2329           | 0.2703           | 0.0037           |
| II                          | 0.0648           | 0.1725           | 0.0023           |
| III                         | 0.0705           | 0.0770           | 0.0004           |

**Table 2.** Genetic differentiation \((\text{F}_{\text{st}})\) of the macrobenthos communities sampled in areas I, II, and III.

| Area | I     | II    |
|------|-------|-------|
| II   | 0.1702|       |
| III  | 0.5829| 0.6771|

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![Figure 3](image-url)  
*Figure 3. Sediment salinity (mean ± SE) in freshwater restoration areas I, II, and III. Bars for a parameter labeled with different letters differ significantly.*
Figure 4. Taxonomic diversity of the macrobenthos sampled in areas I, II, and III (mean ± SE). Indices: $H'$, Shannon–Weiner index; $J$, Pielou’s evenness index; $D$, Simpson’s diversity index; $d$, Margalef’s richness index. Bars for an index labeled with different letters differed significantly.

Figure 5. Results of the principal-components analysis for the ecological traits of the macrobenthos in areas I, II, and III: (a) volitionism, (b) size at maturity, (c) habit, (d) trophic habit, (e) swimming ability, (f) respiration, and (g) salinity preference.
predation trophic habits (figure 5(d)). Macrobenthos collected in area I tended to have no or weak swimming ability, whereas macrobenthos from areas II and III tended to have strong swimming ability (figure 5(e)), which corresponded with the higher water levels in areas II and III. The macrobenthos collected in area I were significantly positively correlated with the respiration trait (by plastron or spiracle (aerial); figure 5(f)), whereas macrobenthos in areas II and III were significantly correlated with respiration by gills and tegument (figure 5(f)). The macrobenthos collected in area I were clustered with fresh water, whereas sites in areas II and III were clustered with brackish water (figure 5(g)).

Further analysis showed no significant difference in functional diversity of the macrobenthos among the three areas (figure 6; $F_{2,58} = 0.082$, $p = 0.922$ for FRic; $F_{2,50} = 0.526$, $p = 0.594$ for FEve; $F_{2,44} = 1.080$, $p = 0.349$ for FDiv; $F_{2,58} = 2.319$, $p = 0.108$ for RaoQ).

4.3. Importance values for macrobenthos multidimensional and holistic biodiversity

In the PCA, PC1 and PC2 together accounted for 69% of the total variation of multidimensional biodiversity, versus 89% for the cumulative proportion explained by PC1 to PC4 (figure S2). Therefore, we used the first four axes to calculate the importance values. The $J$, $D$, RaoQ, $d$, and $H'$ values were negatively correlated with PC1 and positively correlated with PC2. In contrast, HetObs, HetExp, $P_i$, FRic, FDiv, and FEve were negatively correlated with both PC1 and PC2 (figures 7(a) and S2). Our results showed that the RaoQ metric was significantly correlated with all of the taxonomic diversity indices, whereas the other functional metrics
tended to be weakly and non-significantly correlated with all the taxonomic diversity indices (table S7). IV differed greatly among the three dimensions of biodiversity (figure 7(b)). IV ranged from 0.20 to 0.33 for the taxonomic indices, from 0.09 to 0.21 for the functional indices, and from 0.25 to 0.28 for the genetic indices. Overall, IV for all taxonomic diversity indices except J were higher than those of the genetic diversity indices, and functional diversity had the lowest IV.

The holistic biodiversity index for the macrobenthos differed significantly among the three freshwater restoration areas (figure 8; $F_{2,35} = 28.652$, $p < 0.001$). Holistic biodiversity of the macrobenthos in area I was significantly higher than those in area II ($p < 0.001$) and area III ($p < 0.001$). However, there was no significant difference in holistic biodiversity between areas II and III ($p = 0.111$).

4.4. Relationship between sediment salinity, sediment water content, ecosystem function, and holistic biodiversity

The exponential regression results showed a statistically significant inverse relationship between the holistic biodiversity index for the macrobenthos and sediment salinity (figure 9(a)), but a statistically significant positive relationship between the index and sediment water content (figure 9(b)). The holistic biodiversity decreased obviously with increasing sediment salinity (figure 9(a), Adj $R^2 = 0.21$, $p < 0.05$), but increased greatly with increasing sediment water content (figure 9(b), Adj $R^2 = 0.22$, $p < 0.05$). Overall,
this means that holistic biodiversity increased as a result of the freshwater restoration program. The patterns of the regression relationship between sediment salinity, sediment water content, and holistic biodiversity were consistent with the relationships between genetic and taxonomic diversity and sediment properties (figures S3 and S4, table S8). However, the regression relationships between taxonomic biodiversity and sediment properties were relatively weak. In contrast, there were inconsistent patterns for the regression relationships between holistic biodiversity, the functional diversity indices, and sediment salinity or water content (figure S5, table S9).

Holistic biodiversity explained a moderate proportion of the variation between sites, and showed a unimodal polynomial regression relationship with the ln-transformed macrobenthos biomass. The highest biomass was found at sites with intermediate (from 0.4 to 1.25) holistic biodiversity (figure 10, Adj $R^2 = 0.50$, $p < 0.001$). The macrobenthos biomass decreased greatly at high holistic biodiversity in the freshwater restoration areas.

5. Discussion

5.1. Inconsistency among the multidimensional macrobenthos biodiversity metrics and necessity for a holistic biodiversity index

Historically, species richness and taxonomic diversity have been the most common metrics in restoration projects whose goals were to measure and protect biodiversity (Pacini et al 2009, Campbell et al 2011). In our study, focusing on the effect of ecological restoration on multidimensional biodiversity provided valuable insights compared with focusing on individual dimensions of biodiversity, which produced inconsistent results. Recent papers have stated that biodiversity should be recognized as being multidimensional, and highlighted the different outcomes for analyses based on two or more indices compared with a single-dimension approach (Korb et al 2016, Naeem et al 2016). The inconsistent results for our individual dimensions mainly resulted from the fact that different dimensions respond differently to environmental gradients or pressures (Wilsey et al 2005, Gallardo et al 2011, Nakamura et al 2017). Although an index for a single dimension of biodiversity may be more useful for managers who must focus on optimizing only that dimension, the holistic index is more useful when managers must manage multiple dimensions simultaneously, which involves trade-offs among the dimensions.

A controlled restoration experiment showed that restoration techniques could maintain genetic diversity by importing transplants or seeds which have high genetic diversity (Reynolds et al 2012). In our study, we found that genetic diversity could be improved by restoration, and that genetic diversity was higher in areas with longer restoration histories, which is consistent with the results of Suji et al (2017). Genetic diversity of the macrobenthos in areas I and II was much higher than that in area III, possibly because areas I and II had been restored for longer than area III.

As we hypothesized, positive relationships between freshwater restoration and biodiversity emerged most clearly when measures of taxonomic diversity were used, which is consistent with previous experimental evidence and theory (Poff and Zimmerman 2010, Yang et al 2016). Li et al (2016b) found that macrobenthos communities had the highest species richness in a freshwater restoration area with a 16 year restoration history than in areas with shorter restoration histories. We found complex relationships between taxonomic diversity and freshwater restoration (the opposite relationships for sediment salinity and sediment water content) in the present...
study, with different patterns for the four taxonomic diversity metrics. This is consistent with the findings of Shah and Pandit (2013). Such relationships were unimodal in the present study, but nearly a saturating function between sediment salinity and $H^\prime$ or $D$, and between $d$ and sediment salinity or water content. Previous studies have attempted to define a generalized relationship between taxonomic diversity and environmental heterogeneity, with highly modified and semi-natural ecosystems characterized by the dominance of positive and negative relationships, respectively, whereas natural ecosystems show mixed responses, as in the present study (Tews et al. 2004, Seifering et al. 2014).

Despite the increases in genetic and taxonomic diversity in response to the freshwater restoration, functional diversity showed no significant difference among the three areas with different durations of restoration. In previous research, functional diversity was used to quantify the range of organismal traits (Diaz and Cabido 2001, Petchey and Gaston 2006). In contrast, we found that the traits of the macrobenthos tended to be homogenous and dominated by freshwater species characteristics because of the freshwater restoration. This is because the environmental conditions that result from this restoration are more suitable for freshwater species (Zedler 1983, Yang et al. 2017b), which have become more dominant as the inflows of freshwater have continued. Changes in the functional traits of the macrobenthos represent the consequences of succession that results from their adaptations to the environmental stress created by restoration (De Juan et al. 2007).

The relationships among the combinations of the three biodiversity dimensions were complex; for example, the genetic diversity of the macrobenthos in area II was obviously higher than that in area III, whereas the taxonomic diversity of the macrobenthos did not differ significantly between areas II and III. Some sampling sites had high genetic and taxonomic diversity and low functional diversity, and this is consistent with the results of Lindgren et al. (2018). However, it remains difficult to provide appropriate suggestions for restoration management based on the multidimensional biodiversity index owing to the inconsistent responses of the three dimensions of biodiversity; that is, because the individual dimensions changed in different directions rather than all changing in the same direction, this weakened the strength of the relationship between ecosystem function and the holistic index. Holistic biodiversity nonetheless provides a good compromise solution because it integrates multiple dimensions of biodiversity and their importance values, thereby representing a good compromise between the dimensions. What’s more, holistic biodiversity is a useful indicator for restoration management because it is a dimensionless parameter, which means that it can be compared with the values in other restoration periods or areas, and possibly even in other restoration ecosystems.

5.2. Suggestions for freshwater restoration in wetlands

The purpose of freshwater restoration project in the Yellow River Delta was to restore the degraded wetlands and their ecological structure and functions (Cui et al. 2009). Based on the insights obtained using our holistic biodiversity index, we can provide some suggestions for management of freshwater restoration in these wetlands. Although the regression analysis revealed relatively weak correlations between holistic biodiversity and the sediment salinity and water content, freshwater restoration nonetheless had positive effects on holistic biodiversity. The weak regression results result from the fact that the holistic biodiversity index simplified the extremely complicated relationships among the three dimensions of biodiversity, which responded inconsistently to the restoration. In addition, the changes in the abiotic environment caused by freshwater restoration would interact with changes in the available ecological niches and interactions among species in the macrobenthos community, and this, in turn, might affect holistic biodiversity (Crain et al. 2004, Mor et al. 2018).

The pattern was inconsistent with the duration of freshwater restoration, especially for areas I and II. This is might be because area II is closer to ocean, which makes it more vulnerable to infiltration of saltwater during high tides. This is consistent with Li et al. (2016b). Therefore, in addition to the duration of freshwater restoration, future analysis should consider whether other factors such as the elevation and distance from the sea will affect the optimal way to maintain, restore, and improve the study area’s degraded wetland ecosystems.

Biomass is a useful indicator of ecosystem function in natural communities, such as forests and zooplankton communities (Chisholm et al. 2013, Thompson et al. 2015). Previous studies usually focused on the relationship between ecosystem function and taxonomic diversity, and most experiments and field investigations revealed that ecosystem function is significantly positively related to taxonomic diversity, represented by species richness, but with high variability (Cardinale et al. 2011). The high variability in the relationship between taxonomic diversity and ecosystem function motivated ecologists to look for relationships between other dimensions of biodiversity and ecosystem function (Reiss et al. 2009, Thompson et al. 2015). Some studies showed that functional diversity can explain the variation in ecosystem function better than species richness and other taxonomic diversity measures (Cadotte et al. 2011, Flynn et al. 2011). In our study, we found that holistic biodiversity explained 50% of the total variation of ecosystem function. The relationship between biodiversity and ecosystem function (both the slope of the regression and the $R^2$) had high variation and could be scale-dependent. This may be because differences in the community composition within a site would influence this relationship.
framework in a case study in China. We then demonstrated the use of this biodiversity framework, and used it to develop a holistic approach to improve restoration of the wetland ecosystem, it will be necessary to manage and conserve biodiversity; that is, the macrobenthos in our three restoration areas appears to have converged on the most suitable approach for the wetland ecosystem that we studied.

6. Conclusions

In this study, we constructed a multidimensional biodiversity framework, and used it to develop a holistic biodiversity index to evaluate the effects of freshwater restoration. We then demonstrated the use of this framework in a case study in China’s Yellow River Delta wetland. Our analysis revealed that freshwater restoration maintained or increased genetic and taxonomic diversity among the three restoration areas had different restoration histories and different community composition, genetic diversity, and taxonomic diversity among the three areas. These differences may explain the relatively low proportion of the total variation in ecosystem function explained by the holistic biodiversity index.

In our present study, the relationship between the holistic biodiversity index and ecosystem function was unimodal, and not the saturating function observed in most research on the relationship between biodiversity and ecosystem function (Cardinale et al 2011). We found the highest macrobenthos biomass at intermediate levels (from 0.4 to 1.25) of the holistic biodiversity index, and ecosystem function decreased with increasing holistic biodiversity beyond this point. This is consistent with the relationship between species richness and zooplankton community biomass (Thompson et al 2015).

Our findings provide valuable guidance for management of the freshwater restoration. Generally, freshwater restoration improved species richness, but in previous research, macrobenthos biomass in freshwater restoration areas was normally lower than that in areas that had not undergone restoration or in intertidal areas (Li et al 2016a, 2016b, Yang et al 2017b). Therefore, the macrobenthos in freshwater restoration areas tended to be r-selected species (Chiu and Kuo 2015), which are normally small and have many offspring. This means that there will be trade-off between biodiversity and ecosystem function, and that the ecosystem state will depend on what managers consider to be the optimal state. Therefore, adaptive freshwater restoration to achieve this trade-off will be the most suitable approach for the wetland ecosystem that we studied.

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