

Trait-based approach of aquatic insects to track recovery of wetland ecosystems in Northeast China

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ABSTRACT

Wetland restoration has received increasing attention to compensate for the continuing loss of natural wetlands and revive biodiversity and associated ecological functions. The development of methods for assessing the effectiveness of restoration measures is important for wetland management. However, most studies assessing restoration success in freshwater ecosystems are based on taxonomic biodiversity; trait-based approaches remain limited, particularly in wetland ecosystems. Here, we assess the effectiveness of wetland restoration in the Sanjiang Plain, Northeast China, based on the trait composition and functional diversity of aquatic insect assemblages. We found that functional richness in restored wetlands was significantly higher than impacted wetlands but lower than natural wetlands. Compared to natural wetlands, functional beta diversity of impacted wetlands was higher. In terms of dissimilarity between wetland types, trait composition of aquatic insects in restored wetlands showed a higher similarity to natural wetlands compared to those in impacted wetlands. Trait compositions of aquatic insect assemblages in restored wetlands were more similar to impacted wetlands in May but showed a greater similarity to natural wetlands in October. Our study shows that restoration measures have facilitated the partial recovery of functional diversity and trait composition of aquatic insect assemblages in the Sanjiang Plain wetlands. Our study confirms the potential of using trait-based approach to assess the effectiveness of wetland restoration. Given that assessments based on taxonomic and trait data can provide complementary information, we recommend incorporating both taxonomic and functional metrics and considering seasonal dynamics of wetlands in post-restoration monitoring and assessment in wetlands.

1. Introduction

Wetlands are highly diverse ecosystems and provide important contributions to human well-being, including food supplies, flood regulation, water purification, carbon sequestration, and recreational activities (Keddy et al., 2009; Junk et al., 2013; Mitsch and Gosselink, 2015). However, they are often not formally protected from human impacts and are subject to multiple stressors (Reis et al., 2017). Since 1700, 3.4 million km² of inland wetlands have been lost due to extensive

anthropogenic activities, including agricultural expansion and intensification, urbanization, and drainage (Fluet-Chouinard et al., 2023). Wetland loss and degradation are pressing environmental challenges, leading to severe declines in biodiversity and associated ecological functions (Albert et al., 2020).

In recent decades, wetland restoration has received increasing attention worldwide (Montoya et al., 2012; O'Brien et al., 2022) and have been emphasized in various environmental initiatives, including the US Department of Agriculture's (USDA) Wetland Reserve Program

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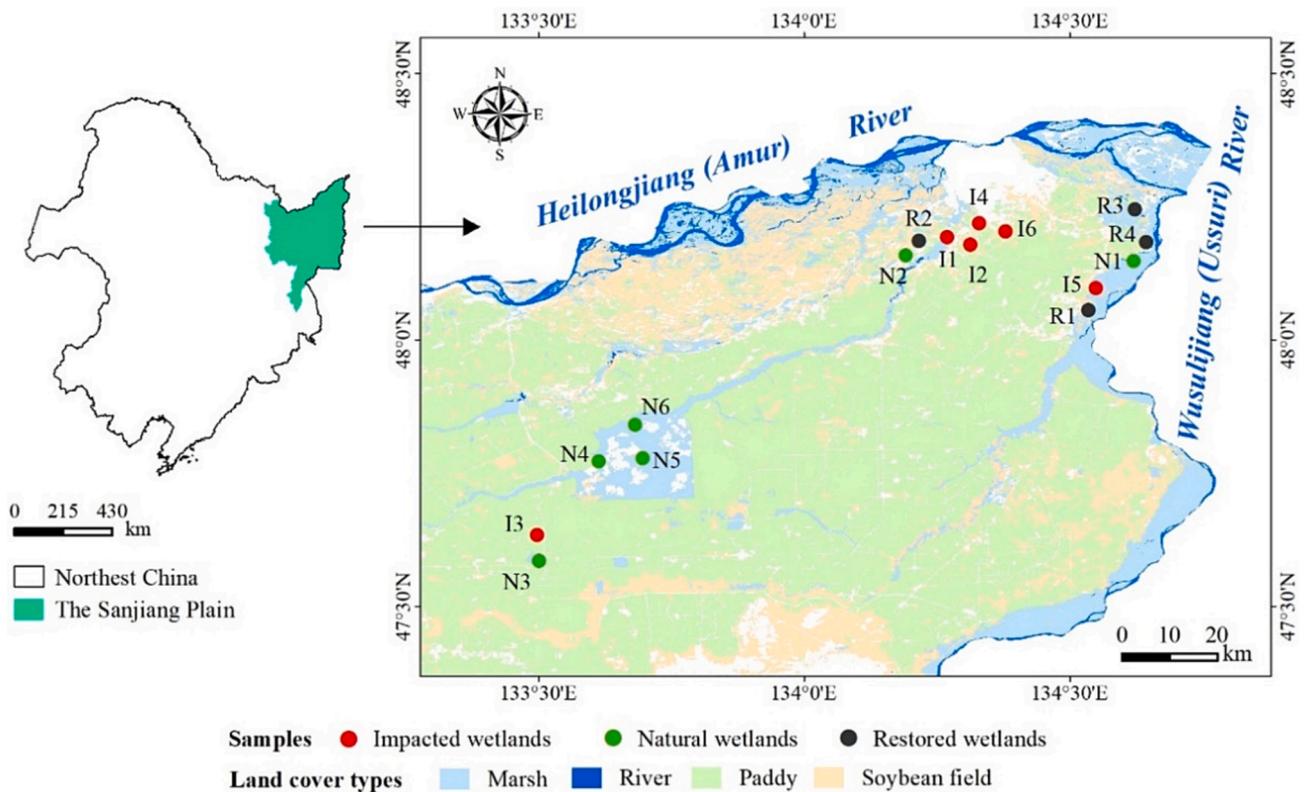


Fig. 1. Geographic locations of the sampling sites in the Sanjiang Plain, Northeast China. Six natural wetlands (N1-6), four restored wetlands (R1-4), and six impacted wetlands (I1-6) were included in the study.

and Conservation Reserve Program (Yeppen et al., 2014), and China's Red Line for Wetland Conservation (Wang et al., 2015). Many projects aim to offset the continuing loss of natural wetlands and restore biodiversity (Perring et al., 2015). Nonetheless, few studies have documented the recovery of ecosystem functions after restoration efforts, particularly in wetlands (Jones et al., 2018; He et al., 2023). Given the growing number of wetland restoration projects, it is important to assess the ecosystem function of restoration by comparing it with both natural and impacted biological communities (Almeida et al., 2020).

Aquatic insects are an essential component of wetland ecosystems and support key ecological processes, including nutrient cycling, bioturbation, and linking primary producers to higher trophic levels (Boix and Batzer, 2016; Schmera et al., 2017; Eisenhauer et al., 2019). In addition, aquatic insects are highly diverse and broadly distributed in wetlands (Dalu et al., 2022; Epele et al., 2022). They have relatively short generation times and diverse life histories and respond rapidly to environmental change (Batzer and Wissinger, 1996). Therefore, aquatic insects have been widely used for biomonitoring in wetlands (e.g., Menetrey et al., 2011; Lunde and Resh, 2012; Lu et al., 2019), including assessments on the effectiveness of wetland restoration (e.g., Batzer et al., 2015; Swartz et al., 2019; Lu et al., 2021).

To date, most studies assessing the effectiveness of wetland restoration are based on taxonomic biodiversity (e.g., Suding, 2011; Kail et al., 2015; Swartz et al., 2019; Lu et al., 2021). Other diversity dimensions (e.g., functional diversity), which can provide complementary insights into ecosystem status (Cadotte et al., 2011; Perez-Rocha et al., 2018; Wu et al., 2021), are often not considered. Compared to traditional taxonomy-based metrics, trait composition and functional diversity metrics consider differences in morphological, physiological, or behavioral characteristics of species. They not only reveal shifts in taxonomic composition but also reflect changes in associated ecological processes (Petchev and Gaston, 2006; Villéger et al., 2008; Moretti and Legg, 2009). These trait-based approaches also allow researchers to

establish causal relationships between stressor exposure or removal of stressors and ecological functions (Violle et al., 2007; Mouchet et al., 2010; Ricotta and Moretti, 2010; Nock et al., 2016). A trait-based approach to restoration can aid interpretation of restoration progress through insights into community assembly and ecosystem functioning (Carlucci et al., 2020). In the last two decades, trait-based approaches have been increasingly employed to evaluate the effectiveness of restoration projects in rivers and lakes (e.g., Cadotte et al., 2011; Frainer et al., 2018; Josué et al., 2021), but received limited attention in wetlands (Coccia et al., 2021).

The Sanjiang Plain supports one of the largest freshwater wetland complexes in China (Liu and Ma, 2002). Since 1950, more than 80 % of its wetland areas has been drained for agriculture (Wang et al., 2011). Since 2000, large scale restoration programmes have been implemented (Wang et al., 2019). Previous studies have observed a recovery in taxonomic composition of aquatic insects in restored wetlands compared to impacted wetlands (Lu et al., 2021). However, the responses of trait composition and functional diversity of aquatic insects to wetland restoration have yet to be investigated. In this study, we evaluate the effectiveness of wetland restoration in the Sanjiang Plain, Northeast China using a trait-based approach. We compare the trait composition and functional diversity of aquatic insect assemblages in restored wetlands to those in natural and impacted wetlands, considering both alpha and beta dimensions. Restoration measures in wetlands create new habitats and enhance natural variability, which increases habitat heterogeneity and promotes the recovery of species with different niches (Ruhf et al., 2016). Hence, we hypothesize that restored wetlands have a higher functional diversity than impacted wetlands (H1). In addition, we expect that aquatic insect assemblages in restored wetlands have trait compositions more similar to those in natural wetlands and less similar to those in impacted wetlands (H2).

Table 1
Trait categories of aquatic insects used in the study. Trait categories were adapted from Poff et al. (2006).

| Grouping feature | Trait group | Trait Categories |
|-----------------------|--------------------------------|----------------------------------------------------------------------------------------------------------------------------------------------------|
| Life history | Volitinism | Semivoltine (<1 generation per year) Univoltine (1 generation per year) Bi- or multivoltine (>1 generation per year) |
| | Development | Fast seasonal Slow seasonal Non seasonal |
| | Adult life span | Very short (<1 week) Short (<1 month) Long (>1 month) |
| | Adult ability to exit | Absent (not including emergence) Present |
| | Ability to survive desiccation | Absent |
| | Mobility | Female dispersal |
| Adult flying strength | | Weak (e.g., cannot fly into light breeze) Strong |
| Swimming ability | | None Weak Strong |
| Morphology | | Attachment |
| | Armoring | None (soft-bodied forms) Poor (heavily sclerotised) Good (e.g., some cased caddisflies) |
| | Shape | Streamlined (flat, fusiform) Not streamlined (cylindrical, round, or bluff) |
| | Respiration | Tegument Gills Plastron, spiracle (aerial) |
| | Size at maturity | Small (<9 mm) Medium (9–16 mm) Large (>16 mm) |
| | Ecology | Thermal preference |
| Habit | | Burrower Climber Sprawler Clinger Swimer Skater |
| Trophic habit | | Collector-gatherer Collector-filterer Herbivore (scraper, piercer, and shedder) Predator (piercer and engulfer) Shredder (detritivore) |

2. Materials and methods

2.1. Study area

This study was conducted in the Sanjiang Plain (45°01'–48°28' N, 130°13'–135°05' E), Northeast China in May (Spring) and October (Autumn) in 2017 (Fig. 1). The region is characterized by a temperate continental monsoon climate with a mean annual air temperature of 2.7 °C in the past ten years. The mean annual precipitation is 550 mm, with more than 60 % of which occurs between July and September. The Sanjiang Plain is formed by the Heilong (Amur) River and its two major tributaries, the Songhua and Wusuli (Ussuri) Rivers. It covers a total area of 1.09×10^5 km² and supports one of the largest freshwater wetland

complexes in China (Liu and Ma, 2002). Freshwater sedge marsh is the major vegetation type of natural wetlands in the Sanjiang Plain (Wu et al., 2017). Since 1950, more than 80 % of the wetland area has been drained for agriculture, with some relatively pristine wetlands remaining in a few nature reserves (Wang et al., 2011). From 2000 to 2014, more than 100 km² of wetlands have been restored in the Sanjiang Plain (Wang et al., 2019). Wetland restoration in the Sanjiang Plain follows a nature-based approach (e.g., using natural hydrological disturbance to facilitate the recovery of habitats and diversity), complemented by human-assisted measures (e.g., reconstruction of habitats). The main restoration measures include reconnecting isolated wetlands to rivers and reconstructing diverse habitat types such as islands and pools (Figure S1; Table S1). Detailed information on the wetland restoration strategies used has been described in an earlier study (Lu et al., 2019).

2.2. Sampling of aquatic insects in wetlands

We investigated aquatic insect assemblages in 16 wetlands distributed across the Sanjiang Plain, including natural (n = 6), impacted (n = 6), and restored (n = 4) wetlands (Fig. 1; detailed descriptions of each wetland can be found in Table S1). Among them, six wetlands located within a nature reserve were best-protected and were therefore categorized as the natural group to provide baseline information. Many wetlands in the Sanjiang Plain are subject to multiple stressors, such as draining, grazing by domestic animals, and levee constructions (Wu et al., 2017). We selected six wetlands that were under the influence of human activities as the impacted group. Four wetlands that received intervention measures to improve their ecological conditions were selected as the restored group. Of the restored wetlands sampled, three wetlands had been restored for 4 years and the other restored for 1 year.

Aquatic insects were sampled with a D-shaped sweep net (1-mm mesh, 35-cm diameter). Four one-meter horizontal sweeps were performed in each wetland. As the nets sieved the water column, scraped the bottom, and swept submersed and emergent plant surfaces, a representative sample was collected at each site (Batzer et al., 2001). In the field, the sweeps were combined into a single representative sample (0.35 m × 1 m × 4 sweeps) of the aquatic insects for each wetland. Overall, we collected a total of 32 samples from 16 wetlands over two seasons. The samples were preserved with 95 % alcohol and transported to the laboratory for identification.

2.3. Identification and traits of aquatic insects

All taxa were identified to the genus level following taxonomic keys (Clifford, 1991; Morse et al., 1994) except for Chironomidae (Diptera), which were identified to subfamily (Tang, 2006). We collected information on 16 traits for each taxon (Table 1). These traits describe their morphological and life-history characteristics and are related to their ecological roles in wetland ecosystems. Following Ao et al. (2022b), we determined the trait categories of each taxon based on the information collected from the literature (Poff et al., 2006; Vieira et al., 2006; Tachet et al., 2010; US EPA, 2012; Sarremejane et al., 2020; Twardochleb et al., 2021; Ao et al., 2022b) and an online database (<https://www.freshwaterrecology.info>). If the trait information of a genus was not reported in our study region (e.g., *Somatochora*, *Fabria*), we adopted the published trait information of this genus reported in regions with a similar climate and/or sharing the same zoogeographic zone. If a certain trait for a genus in our dataset was not reported in the published literature, we used information from other genera from the same family with similar life histories. Detailed information on trait determination is described in Figure S2.

2.4. Data analysis

To investigate the response of functional diversity of aquatic insect assemblages to restoration measures, we calculated functional alpha and

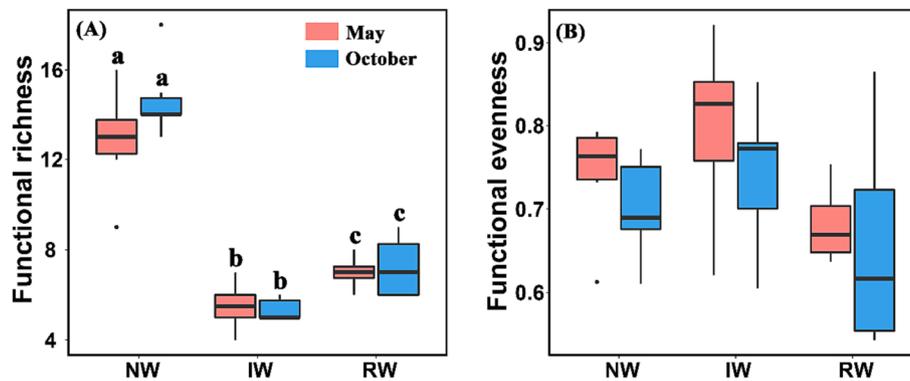


Fig. 2. Functional richness (A) and functional evenness (B) of each wetland type (NW: natural wetlands; IW: impacted wetlands; RW: restored wetlands). Different letters above boxes indicate significant differences between wetland types ($P < 0.05$; ART-ANOVA).

beta diversity in different wetlands for each sampling season. Functional richness, which represents the size of the functional space occupied by an assemblage, and functional evenness, which represents the regularity of the distribution of species' abundances in functional space (Villéger et al., 2008), were used to measure functional alpha diversity. Functional richness and functional evenness were calculated using the *dbFD* function in the “FD” package of R (Laliberté et al., 2014). To evaluate whether there were differences in trait compositions between wetland types, we calculated Community-Weighted Means (CWMs, Garnier et al., 2004) of each trait category. The CWMs quantifies the weighted mean of a functional trait within a given taxa assemblage (Ricotta and Moretti, 2011; Coccia et al., 2021). This metric considers the traits of the most abundant taxa to determine ecosystem processes (Ricotta and Moretti, 2011). CWMs were calculated using the *cwm* function in the “BAT” package of R (Cardoso et al., 2015).

For functional beta diversity, we calculated functional pairwise beta diversity using the Sørensen dissimilarity index (Baselga, 2010; Villéger et al., 2011). For each season, we generated a dissimilarity matrix. Then, we tested for differences in the dispersions of functional beta diversity between wetland types using the multivariate dispersion analysis (Anderson, 2006). Functional pairwise beta diversity was calculated with *functional.beta.pair* function in the “betapart” package of R (Baselga et al., 2017), while multivariate dispersion analysis was performed with *betadisper* function in the “vegan” package (Anderson et al., 2006; Oksanen et al., 2018).

To test the differences in functional alpha and beta diversity metrics and CWMs between wetland types, we applied an aligned rank transformation (ART) (Mansouri et al., 2004) to data followed by an Analysis of Variance (ANOVA) using adjusted sums of squares (Wobbrock et al., 2011) with the *art* function in the “ARTool” package (Elkin et al., 2021). We used the biological metrics (i.e., functional alpha and beta diversity and CWMs) as the response variables separately, while wetland types was used as treatments. All data analyses were performed in R version 4.2.1 (R Core Team, 2022).

3. Results

3.1. Alpha diversity

Functional richness and functional evenness were significantly different between wetland types ($P < 0.001$, $P = 0.034$; ART ANOVA test; Table S2) in May and October. Functional richness was significantly higher in natural wetlands than in restored wetlands and impacted wetlands ($P < 0.05$; ART ANOVA test; Fig. 2A). Restored wetlands also had a significantly higher functional richness than impacted wetlands. However, we did not detect any significant differences in functional evenness between wetland types (Fig. 2B). Functional evenness showed a decline trend, albeit not significantly, from May to October in all

wetland types (Fig. 2B).

3.2. Community-weighted mean trait value

In both sampling months, we observed clear differences in trait compositions between wetland types (Table 2). Moreover, natural wetlands had more aquatic insects with univoltine life cycles, long adult life spans, slow seasonal growth, strong flying and swimming abilities, and poor armoring compared to impacted wetlands. Impacted wetlands had fewer climbers, swimmers, herbivores, shredders, tegument-breathing taxa, and taxa that prefer cold stenothermal/eurythermal or warm eurythermal environments than natural wetlands. There were more burrowers, sprawlers, collector-gatherers, predators, gill-breathers, and cool/warm eurythermal taxa in impacted wetlands than in natural wetlands. In October, restored and natural wetlands had fewer taxa with fast life cycles (e.g., two or more generations per year, very short adult life spans), sprawlers, collector-gatherers, but more climbers and herbivores than impacted wetlands. In general, trait compositions of aquatic insect assemblages in restored wetlands were more similar to impacted wetlands in May but showed a greater similarity to natural wetlands in October (Table 2).

3.3. Beta diversity

We observed similar results in the two sampling seasons regarding functional beta diversity. A significant difference was detected in within-group and between-group functional beta diversity between wetland types ($P < 0.001$; ART ANOVA test; Table S3). There was a significantly lower dissimilarity of trait composition between natural wetlands than impacted wetlands (Fig. 3A). Functional beta diversity between restored wetlands did not show any significant differences with either natural or impacted wetlands (Fig. 3A). In terms of dissimilarity between wetland types, trait composition of aquatic insects in restored wetlands showed a higher similarity to natural wetlands compared to those in impacted wetlands (Fig. 3B).

Although we did not detect a significant difference in functional beta diversity between wetland types with the permutation test of multivariate homogeneity of group dispersions ($P > 0.05$; Fig. 4 and Table S4), multivariate dispersion analyses showed that natural wetlands were clearly separated from impacted and restored wetlands. The separation was more evident in October than in May. In addition, restored wetlands were more separated from impacted wetlands in October than in May.

4. Discussion

Trait-based assessments have been widely conducted to assess the effectiveness of restoration in rivers and lakes (e.g., White et al., 2017;

Table 2

F- and P-values of ART-ANOVA tests for differences in Community-Weighted Mean (CWM) trait values (standard deviation of each CWM value was shown in parenthesis) P-values < 0.05 are marked in bold.

| Trait group | Trait categories | May | | | Wetland types | | October | | | Wetland types | |
|--------------------------------|-----------------------------------|----------------|----------------|----------------|---------------|----------|----------------|----------------|----------------|---------------|----------|
| | | NW | IW | RW | F-values | P-values | NW | IW | RW | F-values | P-values |
| Voltinism | Semivoltine | 0.11 (0.07) | 0.12 (0.16) | 0.02 (0.04) | 2.060 | 0.167 | 0.09 (0.11) | 0.05 (0.06) | 0.01 (0.01) | 3.401 | 0.065 |
| | Univoltine | 0.37 (0.17) | 0.34 (0.17) | 0.17 (0.07) | 3.371 | 0.066 | 0.33 (0.17) | 0.25 (0.09) | 0.40 (0.31) | 0.260 | 0.775 |
| | Bi-or multivoltine | 0.52 (0.18) | 0.55 (0.20) | 0.81 (0.07) | 5.581 | 0.018 | 0.58 (0.20) | 0.70 (0.11) | 0.59 (0.32) | 0.290 | 0.753 |
| Development | Fast seasonal | 0.40 (0.27) | 0.58 (0.19) | 0.74 (0.13) | 3.485 | 0.061 | 0.49 (0.08) | 0.70 (0.10) | 0.54 (0.38) | 2.808 | 0.097 |
| | Slow seasonal | 0.59 (0.26) | 0.28 (0.15) | 0.23 (0.09) | 4.204 | 0.039 | 0.49 (0.07) | 0.23 (0.13) | 0.46 (0.38) | 3.422 | 0.064 |
| | Non seasonal | 0.01 (0.02) | 0.14 (0.12) | 0.03 (0.06) | 2.004 | 0.174 | 0.02 (0.03) | 0.07 (0.12) | — | 2.698 | 0.105 |
| Adult life span | Very short | 0.27 (0.22) | 0.56 (0.16) | 0.65 (0.22) | 4.956 | 0.025 | 0.27 (0.17) | 0.60 (0.13) | 0.31 (0.32) | 5.553 | 0.018 |
| | Short | 0.13 (0.10) | 0.08 (0.07) | 0.07 (0.06) | 0.596 | 0.566 | 0.11 (0.08) | 0.07 (0.07) | 0.27 (0.34) | 0.774 | 0.481 |
| | Long | 0.60 (0.19) | 0.36 (0.22) | 0.28 (0.23) | 3.414 | 0.064 | 0.62 (0.17) | 0.33 (0.16) | 0.41 (0.25) | 2.939 | 0.089 |
| Adult ability to exit | Absent | 0.41 (0.15) | 0.30 (0.13) | 0.25 (0.16) | 3.250 | 0.072 | 0.29 (0.11) | 0.20 (0.10) | 0.32 (0.33) | 0.467 | 0.637 |
| | Present | 0.59 (0.15) | 0.70 (0.13) | 0.75 (0.16) | 3.250 | 0.072 | 0.71 (0.11) | 0.80 (0.10) | 0.68 (0.33) | 0.467 | 0.637 |
| Ability to survive desiccation | Absent | 0.71 (0.13) | 0.67 (0.11) | 0.76 (0.18) | 0.372 | 0.696 | 0.64 (0.21) | 0.72 (0.16) | 0.71 (0.21) | 0.265 | 0.771 |
| | Present | 0.29 (0.13) | 0.33 (0.11) | 0.24 (0.18) | 0.372 | 0.696 | 0.37 (0.21) | 0.28 (0.16) | 0.29 (0.21) | 0.265 | 0.771 |
| Female dispersal | Low | 0.40 (0.11) | 0.16 (0.09) | 0.19 (0.12) | 8.943 | 0.004 | 0.26 (0.07) | 0.13 (0.07) | 0.40 (0.37) | 2.228 | 0.147 |
| | High | 0.60 (0.11) | 0.84 (0.09) | 0.81 (0.12) | 8.943 | 0.004 | 0.75 (0.07) | 0.87 (0.07) | 0.60 (0.37) | 2.228 | 0.147 |
| Adult flying strength | Weak | 0.42 (0.21) | 0.67 (0.21) | 0.73 (0.26) | 2.750 | 0.101 | 0.39 (0.16) | 0.69 (0.13) | 0.59 (0.26) | 5.597 | 0.018 |
| | Strong | 0.58 (0.21) | 0.33 (0.21) | 0.27 (0.26) | 2.750 | 0.101 | 0.61 (0.16) | 0.31 (0.13) | 0.41 (0.26) | 5.597 | 0.018 |
| Swimming ability | None | 0.28 (0.22) | 0.47 (0.15) | 0.60 (0.21) | 3.880 | 0.048 | 0.33 (0.14) | 0.56 (0.14) | 0.31 (0.32) | 3.261 | 0.071 |
| | Weak | 0.22 (0.17) | 0.12 (0.08) | 0.14 (0.14) | 0.453 | 0.646 | 0.10 (0.08) | 0.07 (0.07) | 0.35 (0.37) | 0.643 | 0.542 |
| | Strong | 0.50 (0.17) | 0.42 (0.21) | 0.26 (0.26) | 1.914 | 0.187 | 0.58 (0.18) | 0.38 (0.16) | 0.35 (0.25) | 2.015 | 0.173 |
| Attachment | None | 0.88 (0.08) | 0.82 (0.15) | 0.99 (0.02) | 3.767 | 0.051 | 0.91 (0.05) | 0.87 (0.12) | 0.95 (0.07) | 0.783 | 0.478 |
| | Some | 0.12 (0.08) | 0.18 (0.15) | 0.01 (0.02) | 3.767 | 0.051 | 0.09 (0.05) | 0.13 (0.12) | 0.05 (0.07) | 0.783 | 0.478 |
| Armoring | None | 0.35 (0.21) | 0.52 (0.17) | 0.66 (0.23) | 2.658 | 0.108 | 0.34 (0.16) | 0.60 (0.12) | 0.55 (0.28) | 3.257 | 0.071 |
| | Poor | 0.54 (0.16) | 0.42 (0.12) | 0.31 (0.20) | 2.048 | 0.169 | 0.56 (0.24) | 0.36 (0.15) | 0.38 (0.27) | 1.185 | 0.337 |
| | Good | 0.12 (0.07) | 0.06 (0.09) | 0.03 (0.04) | 2.503 | 0.120 | 0.10 (0.13) | 0.04 (0.06) | 0.07 (0.11) | 1.038 | 0.382 |
| Shape | Streamlined | 0.33 (0.14) | 0.23 (0.10) | 0.27 (0.21) | 0.996 | 0.396 | 0.42 (0.17) | 0.23 (0.14) | 0.55 (0.28) | 3.250 | 0.072 |
| | Not streamlined | 0.67 (0.14) | 0.77 (0.10) | 0.73 (0.21) | 0.996 | 0.396 | 0.58 (0.17) | 0.77 (0.14) | 0.45 (0.28) | 3.250 | 0.072 |
| Respiration | Tegument | 0.17 (0.16) | 0.04 (0.06) | 0.09 (0.06) | 3.372 | 0.066 | 0.10 (0.07) | 0.02 (0.05) | 0.14 (0.12) | 4.948 | 0.025 |
| | Gills | 0.45 (0.18) | 0.69 (0.15) | 0.66 (0.22) | 3.440 | 0.063 | 0.48 (0.05) | 0.69 (0.10) | 0.57 (0.30) | 3.312 | 0.069 |
| | Plastron, spiracle | 0.38 (0.18) | 0.28 (0.18) | 0.25 (0.25) | 1.077 | 0.369 | 0.42 (0.10) | 0.29 (0.14) | 0.30 (0.24) | 1.913 | 0.187 |
| Size at maturity | Small | 0.65 (0.18) | 0.69 (0.16) | 0.89 (0.08) | 2.724 | 0.109 | 0.63 (0.12) | 0.77 (0.10) | 0.63 (0.36) | 0.875 | 0.440 |
| | Medium | 0.15 (0.09) | 0.08 (0.09) | 0.05 (0.07) | 1.875 | 0.193 | 0.16 (0.13) | 0.05 (0.06) | 0.05 (0.07) | 1.710 | 0.219 |
| | Large | 0.20 (0.14) | 0.24 (0.12) | 0.07 (0.05) | 2.724 | 0.103 | 0.21 (0.16) | 0.18 (0.12) | 0.32 (0.34) | 0.008 | 0.992 |
| Thermal preference | Cold stenothermal/ eurythermal | 0.11 (0.21) | — | — | 7.675 | 0.006 | 0.04 (0.08) | — | — | 3.980 | 0.045 |
| | Cool/warm eurythermal | 0.44 (0.15) | 0.78 (0.09) | 0.70 (0.14) | 11.037 | 0.002 | 0.48 (0.23) | 0.74 (0.13) | 0.59 (0.26) | 1.840 | 0.198 |

(continued on next page)

Table 2 (continued)

| Trait group | Trait categories | May | | | Wetland types | | October | | | Wetland types | |
|---------------|--------------------|----------------|----------------|----------------|---------------|----------|----------------|----------------|----------------|---------------|----------|
| | | NW | IW | RW | F-values | P-values | NW | IW | RW | F-values | P-values |
| Habit | Warm eurythermal | 0.45 (0.18) | 0.22 (0.09) | 0.31 (0.14) | 3.304 | 0.069 | 0.48 (0.26) | 0.26 (0.13) | 0.41 (0.26) | 0.908 | 0.428 |
| | Burrow | 0.18 (0.23) | 0.36 (0.14) | 0.50 (0.17) | 5.036 | 0.024 | 0.22 (0.16) | 0.47 (0.16) | 0.24 (0.30) | 2.395 | 0.130 |
| | Climb | 0.40 (0.13) | 0.20 (0.11) | 0.27 (0.18) | 3.577 | 0.058 | 0.38 (0.18) | 0.24 (0.13) | 0.63 (0.28) | 4.585 | 0.031 |
| | Sprawl | 0.13 (0.10) | 0.29 (0.21) | 0.13 (0.10) | 1.405 | 0.280 | 0.05 (0.03) | 0.15 (0.18) | 0.08 (0.06) | 0.561 | 0.584 |
| | Cling | 0.09 (0.05) | 0.02 (0.04) | 0.04 (0.06) | 6.202 | 0.013 | 0.01 (0.06) | 0.02 (0.05) | 0.02 (0.04) | 6.946 | 0.009 |
| | Swim | 0.21 (0.09) | 0.14 (0.16) | 0.06 (0.07) | 2.563 | 0.115 | 0.25 (0.13) | 0.10 (0.11) | 0.04 (0.03) | 6.649 | 0.010 |
| | Skate | — | — | — | — | — | 0.01 (0.01) | — | — | 2.019 | 0.172 |
| Trophic habit | Collector-gatherer | 0.38 (0.26) | 0.48 (0.21) | 0.76 (0.05) | 3.467 | 0.062 | 0.44 (0.10) | 0.63 (0.10) | 0.50 (0.37) | 1.560 | 0.247 |
| | Collector-filterer | 0.04 (0.05) | 0.08 (0.08) | 0.03 (0.02) | 0.723 | 0.504 | 0.04 (0.07) | 0.05 (0.06) | 0.02 (0.04) | 0.050 | 0.951 |
| | Herbivore | 0.06 (0.08) | — | 0.04 (0.06) | 6.539 | 0.011 | 0.03 (0.04) | — | 0.07 (0.11) | 3.399 | 0.065 |
| | Predator | 0.43 (0.21) | 0.44 (0.21) | 0.17 (0.04) | 4.567 | 0.031 | 0.36 (0.16) | 0.32 (0.10) | 0.41 (0.32) | 0.021 | 0.979 |
| | Shredder | 0.10 (0.14) | — | 0.01 (0.02) | 2.514 | 0.119 | 0.12 (0.11) | — | 0.01 (0.02) | 9.610 | 0.003 |

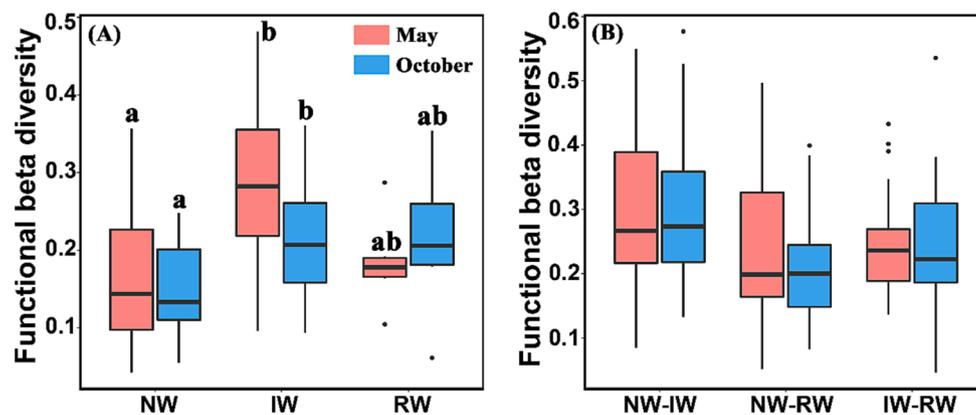


Fig. 3. Functional beta diversity based on Sørensen dissimilarity between sites (A) within each wetland type (NW: natural wetlands; IW: impacted wetlands; RW: restored wetlands) and (B) between different wetland types. Different letters above boxes indicate significant differences between wetland types ($P < 0.05$; ART-ANOVA).

England and Wilkes, 2018; Josué et al., 2021), it has received relatively limited attention in wetland ecosystems (but see Coccia et al., 2021). Our study evaluate restoration success of wetland in the Sanjiang Plain, Northeast China using a trait-based approach.

In line with the first hypothesis, we found that both natural and restored wetlands had higher functional richness than impacted wetlands in both May and October. In line with functional richness, higher taxonomic richness was previously observed in both natural and restored wetlands compared to impacted wetlands (Lu et al., 2021), and functional richness is often positively associated with taxonomic richness (Mason et al., 2005). Compared to impacted wetlands, the increases in both taxonomic and functional richness of aquatic insects indicate that wetland restoration after 1–4 years has provided habitats for more taxa and increased the functional space occupied by aquatic insects (Villéger et al., 2008). Indeed, restoration measures in the Sanjiang Plain include re-establishment of hydrological connections and creating diverse habitats (e.g., elevated islands, ecological ditch-pool mosaics, and corridors that connects previously isolated wetland patches, Figure S1). Restored hydrological connections enhanced the frequency of flood disturbances in restored wetlands. The recovery of hydrological

disturbances in restored wetlands provides a wider range of habitat types for aquatic insects with different ecological niches, which in turn increases their functional richness (Heino, 2008). In addition, restored hydrological connection and the creation of diverse habitat types facilitate the re-colonization of some aquatic plants in restored wetlands (Wang et al., 2019). Aquatic vegetation offers multiple benefits to aquatic insects, including enhanced food availability and habitats to hide from predators (Clynick et al., 2013; Culler et al., 2014). In restored wetlands, taxa with fast life cycles and strong dispersal abilities were abundant. These organisms possess traits that allow them to use a wide range of resources, disperse over long distances and reproduce quickly (Ruhf et al., 2014). These taxa are often called “pioneer species” in habitats recovering from disturbances (Gallardo et al., 2012; Coccia et al., 2016; Lu et al., 2021).

Both functional richness and between-group functional beta diversity confirmed the partial recovery of aquatic insect assemblages in restored wetlands, which stands in line with our second hypothesis. It is interesting that functional richness and within-group functional beta diversity showed an opposite pattern. The high within-group functional beta diversity in impacted wetlands is likely caused by the variation in

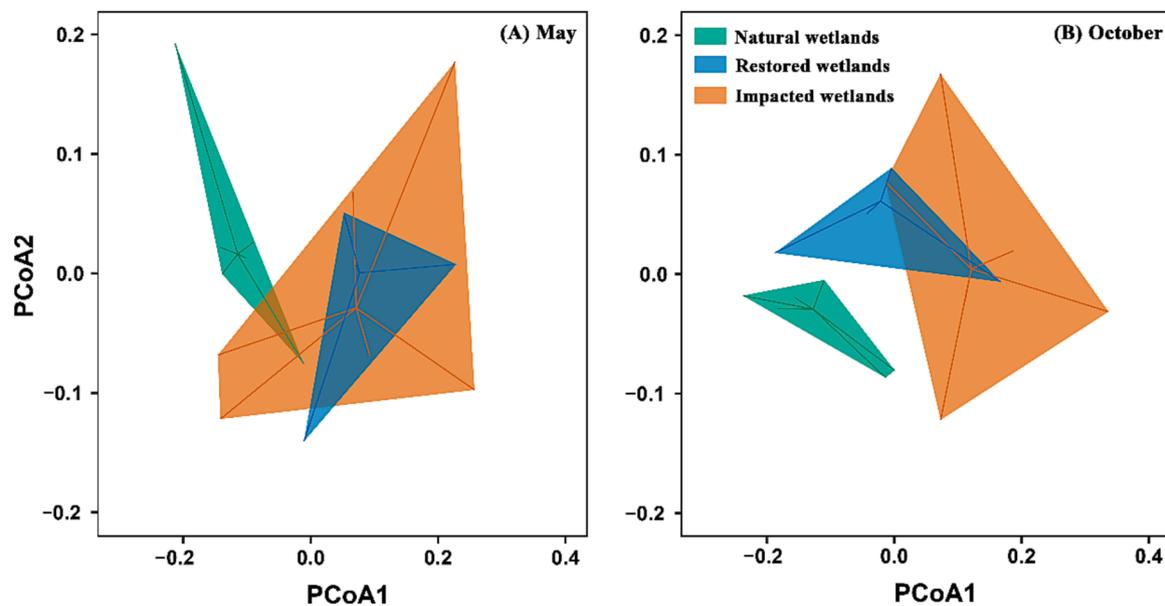


Fig. 4. Multivariate dispersion analyses showing the median position and distances between each site for natural (green), impacted (orange), and restored wetlands (blue) in different seasons in May (A) and October (B). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

anthropogenic influence in these wetland habitats. Some impacted wetlands are subject to stressors from agricultural activities (e.g., rice paddy fields), while others are influenced by grazing activities of domestic animals and draining. These activities often lead to distinct changes in the abiotic environment of wetlands (Bartzen et al., 2010; Wu et al., 2017). Taxa with traits that do not benefit their persistence in these altered environmental conditions are eliminated (Ribera et al., 2001). Consequently, due to strong environmental filtering, remaining taxa share similar traits across impacted wetlands. However, taxonomic assemblages of aquatic insects are dissimilar among impacted wetlands because local sites are subject to different anthropogenic influences. Hence, impacted wetlands are characterized with low functional richness at local sites but high functional beta diversity between sites.

The CWMs of restored wetlands does not yet match the CWMs of natural wetlands. This may be related to the time required for restoration. Studies suggest that the recovery of functional diversity may be slow and needs a longer time than the recovery of taxonomic diversity (O'Brien et al., 2022), and the investigated wetlands in our study have just been restored for only 1–4 years. If given sufficient time, the conditions in the restored wetlands may approximate those in natural wetlands. Therefore, active restoration is needed to maintain positive wetland recruitment and biodiversity. Moreover, based on the observed patterns in trait composition and functional diversity, our results indicate that aquatic insect assemblages in restored wetlands in Sanjiang Plain have not yet recovered to natural status. A previous study showed a greater progress of recovery in restored wetlands when only taxonomic diversity was considered (Lu et al., 2021). Hence, there may be a time lag between the recoveries of taxonomic and trait compositions of aquatic insects after restoration is implemented, which has also been observed in other regions (Baker et al., 2021).

In the Sanjiang Plain, strong seasonal dynamics exist in wetland ecosystems. In winter, wetlands are often frozen, and most agricultural activities stop (Liu and Ma, 2002). On one hand, a harsh environment in winter can suppress the growth and movement of aquatic organisms (Hurst, 2007) and affect their survival and distribution (Sakai and Larcher, 2012). The influences of cold winter on different wetland types in the Sanjiang Plain are similar. On the other hand, winter limits the ongoing anthropogenic activities on impacted wetlands. Hence, the influence of restoration measures on wetlands may not be readily evident

when impacted wetlands are assessed soon after thawing. Indeed, the differences in trait compositions between restored and impacted wetlands were minor in May and more pronounced in October.

The summer period allows natural and restored wetlands to recover from the harsh winter. For example, increased ecosystem productivity, including the growth of aquatic vegetation, provides more habitats and food resources for aquatic insects as the growing season progresses (Marklund et al., 2001; Swartz et al., 2019). Indeed, we observed a major increase in the abundance of climbers, which are adapted to climb on aquatic plants (Hershey et al., 2010), in restored wetlands from May to October. Although impacted wetlands benefit from enhanced primary productivity as well as temperature increases, the intensity of anthropogenic stressors on them also increases dramatically compared to winter. The effects of anthropogenic activities likely accumulate over the summer and lead to changes in trait compositions of aquatic insect assemblages. For example, agricultural activities often result in increased surface runoff and soil erosion, leading to more fine particle input from surrounding areas to wetlands (Xie et al., 2019). Those fine particles flushed into wetlands provide may more food resources for collector-gatherers (Ao et al., 2022a), which explains the increased abundance of that group in impacted wetlands over the summer. Moreover, we observed a declining trend in functional evenness, albeit not statistically significant, from May to October in all wetlands. It indicates that functional space in the Sanjiang Plain wetlands was less occupied in summer than in winter (Mouchet et al., 2010), particularly in restored wetlands which had the lowest functional evenness among all wetland types.

Although we did not observe significant differences between wetland types in multivariate dispersion analyses in either May or October (Table S4), the separation between natural and restored wetlands from impacted wetlands was more evident in October than in May. It is likely caused by the selective exclusion of aquatic insects in impacted wetlands due to intensified human disturbance in summer (Si et al., 2016; Barnum et al., 2017) and recovery colonization of taxa in natural and restored wetlands. The reduced overlap between restored wetlands and impacted wetlands from May to October reflects the influence of restoration measures in the summer. However, overlap between natural wetlands and restored wetlands was not detected in either May or October, suggesting major differences in functional space occupied by aquatic insects

in these two wetland types. Although our results showed clear differences in trait compositions and functional diversity between Spring and Autumn, each season was sampled only once. Future studies are warranted to investigate whether impacted wetlands also experienced a certain progression of recovery in winter due to reduced anthropogenic activities.

Overall, our study showed that trait-based approaches provide valuable information for the understanding of wetland restoration in addition to traditional evaluation criteria such as species diversity. We recommend incorporating both taxonomic and functional diversity in post-restoration monitoring, to detect trajectories towards a comprehensive recovery of biodiversity following restoration. We also highlight the value of the trait-based approaches for assessing restoration success, thereby facilitating the management planning and implementation in future wetland restoration projects.

5. Conclusions

Our study shows that restoration measures have facilitated a partial recovery of trait composition and functional diversity of aquatic insect assemblages in the Sanjiang Plain wetlands. However, the trait composition and functional diversity of aquatic insects in restored wetlands have not recovered to the level of natural wetlands. Compared to the recovery in taxonomic composition and diversity shown in a previous study (Lu et al., 2021), the recovery of trait composition and functional diversity was slower. Trait-based approaches thus provide complementary information to the assessments based on taxonomic diversity alone. Our study highlights the importance of combining taxonomic and trait-based approaches for comprehensively evaluating the effectiveness of wetland restoration, which provides insights into the recovery of both the community structure of aquatic insects and associated ecological functions. In the future, long-term monitoring that combines taxonomic and trait-based approaches is needed to comprehensively understand the recovery trajectory of aquatic insect assemblages in wetlands.

CRedit authorship contribution statement

Kangle Lu: Conceptualization, Methodology, Funding acquisition, Investigation, Writing – original draft, Writing – review & editing. **Sonja C. Jähnig:** Writing – review & editing. **Haitao Wu:** Supervision, Conceptualization, Methodology, Funding acquisition, Writing – review & editing. **Zhijing Xie:** Writing – review & editing. **Xing Chen:** Writing – review & editing. **Fengzhi He:** Supervision, Conceptualization, Methodology, Writing – original draft, Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecolind.2023.111012>.

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