



Hydrological connectivity shapes multiple diversity facets of snail (Mollusca: Gastropoda) assemblages in freshwater floodplain wetlands

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ABSTRACT

Hydrological connectivity is crucial for supporting aquatic biodiversity and serving ecosystem function in river floodplain wetlands. Although the effects of longitudinal connectivity in the composition of snail (Mollusca: Gastropoda) assemblages is well understood, the effects of lateral connectivity are less evaluated. Here, we evaluated the effects of lateral and longitudinal connectivity on multiple facets of alpha and beta diversity (i.e., taxonomic, functional, and phylogenetic) of freshwater snails in 38 floodplain wetlands in the Da Xing'an Mountains of Northeast China. A total of 9,784 snails subjected to 5 orders, 14 families, 24 genera, and 42 species were collected. Overall, the snail alpha diversity was higher in the nearly isolated wetlands and downstream areas. Multivariate analyses revealed that the taxonomic, functional, and phylogenetic structures of snail assemblages in floodplain wetlands differed significantly across the lateral and longitudinal gradients. Waterscape and climate variables appeared to equivalently explain a large proportion of variations in the taxonomic, functional, and phylogenetic structures of snail assemblages. Lateral connectivity and river order were paramount variables that explain the greatest variation in taxonomic, functional, and phylogenetic structures of the snail assemblages. Our study suggests that hydrological connectivity is a key factor controlling the multiple facets of snail diversity in floodplains. Attention should be paid to the effects of changing climate and waterscape on the multi-faceted diversity of snail assemblages. Due to the extant patterns in assemblage structures, floodplain restoration and management should consider the full spectrum of longitudinal and laterally connectedness to maximize aquatic biodiversity.

1. Introduction

River floodplains are one of the most widely distributed wetland habitats worldwide (Batzer et al., 2016; Reis et al., 2019). They are productive and heterogeneous ecosystem types, providing habitat for numerous aquatic organisms (Kingsford, 2015). The major driving forces within this ecosystem are fluvial deposition and lateral instability in planforms associated with flood-controlled disturbance processes (Keruzoré et al., 2013). Flood-controlled disturbances can be caused by riverine over-bank flooding and/or direct precipitation and runoff (Batzer et al., 2016; Reis et al., 2019). Such disturbances lead to a mosaic of sub-habitats (e.g., oxbow lakes, isolated depressions, abandoned channels) that occur across most floodplains (Bellmore et al., 2015), thus determining connectivity across reaches, and between rivers and adjacent floodplains (Batzer et al., 2016; Penha et al., 2017; Dube et al.,

2019; Reis et al., 2019). In these floodplains, multiple gradients (lateral and longitudinal) of hydrological connectivity, largely control the structure and diversity of the aquatic assemblages therein (Hermoso et al., 2012; Batzer et al., 2016).

The first conceptual framework of rivers and their ecology focused on The River Continuum Concept (longitudinal connectivity; Vannote et al., 1980; Reese & Batzer, 2007; Guan et al., 2017). Longitudinal connectivity allows both long- and short-distance migration of biota through a river network (Hermoso et al., 2012). Therefore, from the headwaters to the downstreams, aquatic assemblages in river channels varied predictably (Batzer et al., 2016). Invertebrate assemblages in floodplain wetlands have also been proven to change along this longitudinal gradient (Batzer et al., 2016; Guan et al., 2017). Later studies on the environmental factors controlling resident biota in floodplain wetlands focused on their lateral connectedness with main channels

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(Manfrin et al., 2020). Wetlands along lateral gradient display a wide spectrum of connectedness, from permanently connected to nearly isolated with river channels (Amoros and Bornette, 2002). These lateral floodplain waterbodies are inhabited by different representative species which contribute to the whole aquatic biodiversity of these ecosystems (Maire et al., 2015; Manfrin et al., 2020). By directly promoting the dispersal and indirectly altering the local habitat characteristics (e.g., water velocity, nutrient transport), both longitudinal and lateral hydrological connectivity between wetlands and river channels affect assemblage characteristics (Hermoso et al., 2012). Thus, examining the effects of longitudinal and lateral connectivity on aquatic assemblages of river floodplain wetlands is attracting attention (Manfrin et al., 2020).

Research on macroinvertebrates in floodplains typically focuses on a few organisms that are considered critical to these habitats. Snails (class Gastropoda, phylum Mollusca) are among the most diverse and widespread groups of aquatic invertebrates. They have been proved as useful indicators for bioassessment in floodplain wetlands (Guan et al., 2017). The world's freshwater gastropods are dominated by two main clades: Heterobranchia and Caenogastropoda (Strong et al., 2008). Caenogastropoda uses gills for breathing and requires oxygenated water to survive. They also exhibit longer maturation times, lower fecundities, and longer lifespans than Heterobranchia (Lydeard et al., 2004; Strong et al., 2008). Heterobranchia is a major gastropod subclass that includes "Lower Heterobranchia" and Euthyneura. The "Lower Heterobranchia", which was introduced by Bouchet et al. (2017) as a sister infraclass with Euthyneura, includes six superfamilies, including Valvatoidea in wetlands. Species in the superorders Eupulmonata and Hygrophila of Euthyneura are the main components of freshwater snails in wetlands (Guan et al., 2023). Pulmonate snails (Heterobranchia) breathe air, exhibit broad environmental tolerance, feature short generation times and are capable of surviving in stagnant wetland habitats. With their diversity in taxonomy, ecological niches, and dispersal capabilities (passive and poor), snails are a good model for delineating the controls of connectivity in floodplains.

The importance of multiple diversity facets (i.e., taxonomic, functional, and phylogenetic) of aquatic invertebrate assemblages has been widely recognized in recent studies (Heino and Tolonen, 2017; Li et al., 2020; Pozzobom et al., 2021; Zheng et al., 2022; Guan et al., 2023). Taxonomic diversity, a traditional measure of assemblage dependent on classification and species counts, treats all species as equivalent and independent (Gaston, 2000; Cai et al., 2018). Functional diversity is conceived to measure the ecological importance of species in assemblages based on species traits and its value and range (Petchey & Gaston, 2006; Zheng et al., 2022). Phylogenetic diversity is a measurement of the branch lengths in a phylogenetic tree and considers the evolutionary relationships among species (Cai et al., 2018; Miller et al., 2018). Relative influences of variables may differ depending on the aspect (taxonomic, functional, and phylogenetic) of diversity considered (Gerhold et al., 2015). Undoubtedly, a multifaceted assessment of diversity enhances our understanding of the mechanisms underlying biodiversity patterns in floodplain wetlands (Swenson et al., 2012; Gerhold, et al., 2015; Roa-Fuentes et al., 2018). Therefore, floodplain bioassessment, management and conservation, multiple diversity facets of aquatic assemblages should be considered (Devictor et al., 2010).

Da Xing'an Mountains support one of the largest temperate mountain river networks in China. The majority of floodplain wetlands in Da Xing'an Mountains are distributed along river channels, are wide, shallow, meandering systems. The vast floodplain wetlands extensively inundate during summer flooding and provide an expansive habitat for wetland invertebrates. In this study, snail assemblages from 39 floodplain wetlands in the Da Xing'an Mountain were randomly sampled to investigate the multiple facets of diversity along longitudinal (headwater – downstream gradient) and lateral (connected – isolated gradient) connectivity. We hypothesized that: (i) floodplain wetlands in the downstream and laterally connected areas harbor higher alpha diversity (snail species richness, abundance, functional diversity,

phylogenetic diversity; Manfrin et al., 2020; Zheng et al., 2022); (ii) the structure of snail assemblages (taxonomic, functional, and phylogenetic) differ across longitudinal and lateral connectivity (Schleuter et al., 2012; Cai et al., 2018); and (iii) among numerous environmental factors governing the three structure of snail assemblages, longitudinal and lateral connectivity are the predominant driver (Santos et al., 2020; Stenert et al., 2020).

2. Materials and methods

2.1. Study area

The Da Xing'an Mountains are located in northeast China. Due to dense river network and flat terrain, the Da Xing'an Mountains supports large floodplain wetland complexes (Fig. 1). The Da Xing'an mountains cover a total area of 43.60 million ha (Xue et al., 2021). The Da Xing'an Mountains are surrounded by the Songnen Plain and the Amur, Eerguna, and Songhua Rivers. It is divided by the Yilehuli Mountain into north and south section, the Heilong River basin in the north and the Nen River basin in the south. The climate in this region is dominated by continental monsoon conditions. The mean annual temperature of the study sites ranges from -5.2 to -2.1°C and the mean annual precipitation ranges from 430 to 507 mm based on the 38 sites.

The principal wetland types in the Da Xing'an Mountains are swamp, bog, and fen. We conducted studies at 38 pristine wetlands ($50^{\circ}15' - 53^{\circ}40' \text{ N}$) in the Da Xing'an Mountains (Fig. 1), with the altitude of the sampling sites ranging from 258 to 724 m. These floodplain wetlands are located in areas near to streams or rivers. They are flooded periodically and include continuous side channels, backwater paleo channels, river bottom flats, perennial intermittent streams, backwater swamps, oxbow lakes, and isolated depressions. We categorized these wetlands into four lateral connectedness based on previous studies (Lasne et al., 2007; Penha et al., 2017; Manfrin et al., 2020): 1) connected wetlands (permanently connected, CW); 2) regularly connected during summer flow (RC); 3) occasionally connected during high floods (OC); and 4) nearly isolated, but rarely connected during exceptionally high floods (NI; Fig. 1). The river basins were classified as the Heilong River, Emuer River, Pangu River, Huma River, Gan River or Duobukuer River. These six rivers originate in the high mountains, flow into the Heilong and Nen Rivers, and have similar geomorphic features, hydrological conditions, and vegetation compositions. The sampling location was then classified as tributary, headwater, mid-reach or downstream of each river. These wetlands were dominated by woody plants (*Larix gmelinii*, *Betula platyphylla*, *Vaccinium uliginosum* and *Ledum palustre*), emergent grassy vegetation (*Carex pseudo-curaica*, *C. meyeriana*, *C. rhynchophysa* and *C. lasiocarpa*), floating plants (*Nymphoides peltatum*) and mosses (*Sphagnum palustre*).

2.2. Snail sampling and taxonomic identification

The 38 wetlands were sampled at Autumn 2019 and Summer 2020 to incorporate temporal differences into the composition of snail assemblages. At every wetland and for each date, four sweeps, each one meter long, were conducted using a D-frame dip net (35-cm diameter) with a 1 mm mesh net. For each wetland, the sweeps covered the four dominant microhabitats, such as benthic substrate habitats, leaf litter habitats, and emergent, submerged and spongiform plants, to represent a large habitat heterogeneity. Sweeps were then combined into a single representative sample ($0.35 \text{ m} \times 1 \text{ m} \times 4$ sweeps) of the assemblage for each wetland. The representative samples (per wetland per date) were transferred in Ziplock bags and filled with 95% alcohol. Snails were sorted from sediments and plants in the laboratory under a stereo microscope. Snails were put in 20 ml glass bottles and filled with ethanol. By using standard references, keys, and guides from Vinariski et al. (2017), Sitnikova et al. (2014a,b,c, 2017), and MolluscaBase (2023), snails were identified to the lowest category in taxonomic hierarchy. We

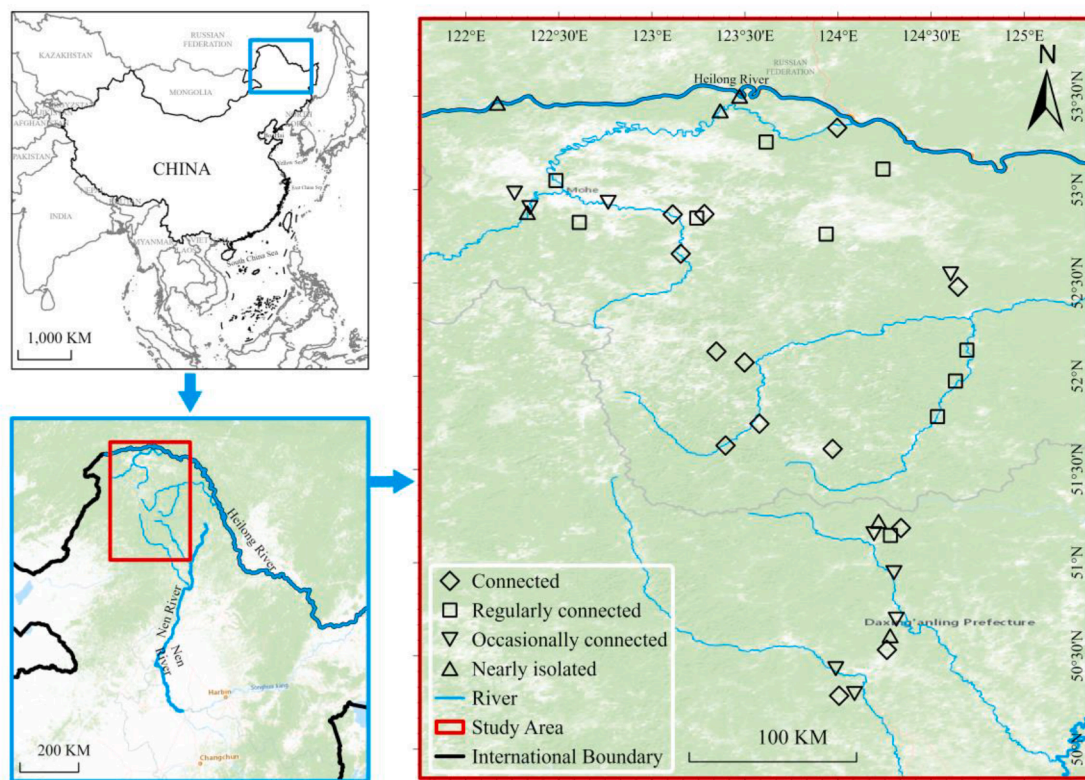


Fig. 1. Map showing the locations of floodplain wetland study sites in the Da Xing'an Mountains along lateral connectivity gradients. Connected: permanently connected wetlands; Regularly connected: regularly connected during summer flow; Occasionally connected: occasionally connected during high floods; Nearly isolated: nearly isolated, but extremely connected during exceptionally high floods.

identified Oxychilidae family to the genus level and other snail families to species.

2.3. Environmental predictors

Three groups of inter-related variables were identified, namely climate, waterscape (hydrology and connectivity), and local habitat. First, environmental predictors at the local habitat scale were measured. Before snail sampling, pH, dissolved oxygen, NO₃, total dissolved solids (g/L), turbidity, conductivity (ms/cm), total suspended solids, salinity (g/L), and chlorophyll-a concentration were measured using a portable meter (Seba KLL-Q-2, Germany). After each sampling effort, coordinates (latitude and longitude; WGS84 system), altitude (Table 1) and water depth were recorded for each location. Next, several environmental predictors at the waterscape scale were measured. The river basins were classified as the Heilong River, Emuer River, Pangu River, Huma River, Gan River or Duobukuer River. River reach was classified as headwater, mid-reach or downstream, based on the location of the floodplain wetland within the river (Table 1). Stream order was also classified as

main river (Heilong and Nen River), primary tributary, secondary tributary, third tributary or fourth tributary. The distance from the river source to each floodplain wetland location and habitat area was measured using the online program Tianditu (<https://www.tianditu.gov.cn/>). Lateral connectivity was categorized into four classes based on the previous description (Table 1). The bioclimatic attributes were downloaded from WorldClim Global Climate Data (version 2.0) at 10 min resolution. In total, 19 attributes were extracted for each wetland (1970–2000 period; Fick and Hijmans, 2017).

2.4. Taxonomic, functional and phylogenetic distances

In each sampled wetland, snail abundance was measured as the number of individuals per sample. Species richness was the summed number of species recorded in different season. The seasonal relative density data were averaged to obtain the taxonomic composition for each sampling wetland in each region. The taxonomic distance matrix was measured using Bray-Curtis similarity among wetlands. In order to reduce the contributions of quantitatively dominant species, we

Table 1

Altitude (m a.s.l.) and representative variables in different classes of longitudinal connectivity (tributaries, headwaters, mid-reaches, and downstream reaches) and lateral connectivity (CW: permanently connected wetlands; RC: regularly connected during summer flow; OC: occasionally connected during high floods; NI: nearly isolated, but extremely connected during exceptionally high floods) of floodplains wetlands. Stand errors are listed in parentheses.

Connectivity	Classes/Reaches	Number of sites	Altitude	pH	Annual Mean Temperature	Annual Precipitation	Water Depth
Lateral connectivity	CW	13	508 (29.68)	7.11 (0.12)	-3.87 (0.25)	484.69 (5.94)	26.77(3.16)
	RC	10	436 (12.73)	6.98 (0.15)	-3.26 (0.30)	478.11 (8.19)	27.89(2.12)
	OC	9	417 (27.39)	7.33 (0.12)	-3.61 (0.16)	466.50 (7.04)	27.30(2.23)
	NI	6	383 (44.30)	7.04 (0.11)	-3.70 (0.34)	459.67(12.56)	30.00(5.47)
Longitudinal connectivity	Headwater	6	528 (41.73)	7.09 (0.15)	-3.78 (0.41)	486.67 (7.07)	30.83(4.17)
	Mid-reaches	9	428 (11.20)	7.13 (0.15)	-3.61 (0.21)	465.89 (7.57)	30.56(1.94)
	Downstream	5	281 (8.67)	7.17 (0.12)	-3.68 (0.33)	441.20 (4.14)	21.40(2.18)
	Tributary	18	476 (18.13)	7.13 (0.11)	-3.57 (0.21)	483.78 (5.22)	25.94(2.07)

transformed the seasonal relative density data using square-root transform.

The functional features of the snail assemblages were characterized using eight traits: maximal body size, maximal weight, body shape, respiration strategy, feeding habits, reproduction mode, substrate relation, and habitat preference (detailed in Appendix S1). These are critical biological traits widely used to reflect ecological importance (Cai et al., 2018). Trait information was gathered primarily from the standard references, keys and guidelines used for snail identification. All snail trait groups were converted into a series of textual possibilities by scoring the categories. For a certain trait, we used 1 to the maximum number of categories to code each species. The same code (category) indicates the same trait for the snail species. According to the trait codification, a similarity type resemblance matrix was created from the information worksheet of functional traits for each species. The resemblance matrix can be thought of as describing the pattern of functional similarity of each pair of species (Clarke et al., 2014). The functional diversity for the snail assemblage of each wetland was obtained based on the resemblance matrix. The original sample data based on the Gamma + resemblance measure was used to create a resemblance matrix of functional dissimilarities among the wetlands. The Gamma + resemblance measure calculates dissimilarity between wetlands based on the resemblance matrix of functional similarity between each species (Clarke et al., 2014).

Linnaean taxonomic hierarchy approach was used to determine phylogenetic distances between pairs of species (Teichert et al., 2018). Although using Linnaean taxonomic hierarchy as a proxy for true phylogenetic relationships inevitably causes information loss, these approaches has been proved strongly correlated (Ricotta et al., 2012; Heino et al., 2015). Taxonomic assignments for every taxon were confirmed using *MolluscaBase* (2023). After the taxonomic verification, a taxonomic variable information worksheet was generated for each species, including ten taxonomic levels from species to class. For some species, certain taxonomic levels were not found in the literature; therefore, we substituted the missing information with an abbreviation of higher taxonomic levels (Heino et al., 2015). We used equal branch lengths at each taxonomic level and the distance between two adjacent taxonomic levels was set to 11.111, 22.222, 33.333, 44.444, 55.556, 66.667, 77.778, 88.889 and 100 units to genus, subfamily, family, superfamily, order, superorder, infraclass, subclass and class. The phylogenetic diversity for the snail assemblage of each wetland was obtained based on taxonomic distance. After calculating taxonomic distances, original sample data based on the taxonomic P/A (Gamma +) measure was used to create a resemblance matrix of phylogenetic dissimilarities among the wetlands (Clarke et al., 2014).

2.5. Statistical analyses

First, ANOVAs was used to evaluate the lateral and longitudinal differences in richness, abundance, functional and phylogenetic alpha diversity among the floodplain wetlands. The taxonomic, functional, and phylogenetic structure of snail assemblages was tested in response to lateral and longitudinal connectivity. The PERMANOVA (permutational multivariate analysis of variance) routine with 999 unrestricted permutations of the Monte Carlo tests was employed based on resemblance matrices. Non-metric multidimensional scaling ordination (NMDS) was applied to visualize the variations in compositions of snail assemblage (Clarke and Gorley, 2015). Next, PERMDISP (permutational analysis of multivariate dispersion) was used to access the multivariate dispersions among the four lateral and longitudinal connectivity of floodplain wetlands (Anderson et al., 2008). This procedure tested whether one group of wetlands was more “variable” (heterogeneous) than another by comparing the distances from each individual wetland (sample) to their group centroid in the full dimensional space. A distance-based linear model (DistLM) was then used to analyze the taxonomic, functional, and phylogenetic structure in response to the

climate, waterscape, and local habitat variables (Anderson et al., 2008). Before the DistLM tests, the Draftsman Plot tool was used for each set of environmental variables to identify skewness and multi-collinearity. We excluded 10 climatic and 4 local habitat variables (Pearson correlation coefficients: $r > 0.80$) and a total of 22 variables were retained. When attempting to build models in DistLM, an adjusted R^2 criterion was used to identify the fine models, and a forward selection procedure was used to pick the environmental variables. In the DistLM, environmental variables were automatically normalized. Marginal tests were performed to show how much each group of variables explained the variation when ignoring other groups of variables. Sequential tests were performed to show individual variables done in a specified order by the conditional tests.

ANOVA was conducted in IBM SPSS Statistics 27. Taxonomic, functional, and phylogenetic resemblance matrices, functional and phylogenetic diversity analyses, Shade plots, PERMANOVA, NMDS, PERMDISP, and marginal tests and sequential tests for the DistLM were created or conducted in PRIMER (Version 7.0.21).

3. Results

3.1. Effects of connectivity on multiple facets of alpha diversity

We collected 9784 individual snails belonging to 5 orders, 14 families, 24 genera, and 42 species from the 38 floodplain wetlands. Snail richness ranged from 3 to 16 taxa/wetland and abundance ranged from 37 to 734 individuals/wetland. For longitudinal connectivity, species richness of the snail assemblages did not differ across four reaches (Fig. 2). Snail abundance in downstream reaches was greater than that in the other three habitats (ANOVA, $F = 4.905$, $p < 0.001$; Fig. 2). Additionally, snail functional and phylogenetic diversity in the downstream reaches were greater than those in the headwater and tributaries, whereas snail functional and phylogenetic diversity in the mid-reach were greater than in the headwater (Fig. 2).

For lateral connectivity, the near isolated (14.17 ± 0.60 taxa) and occasionally connected floodplain wetlands (12.89 ± 1.02 taxa) presented higher snail species richness than the regularly connected and connected floodplain wetlands (ANOVA, $F = 8.699$, $p < 0.001$; Fig. 3). The near isolated wetlands presented the highest snail abundance with 575.67 ± 52.95 individuals/wetland. The snail abundance in occasionally connected wetlands exceeded that of the connected wetlands (ANOVA, $F = 31.20$, $p < 0.001$; Fig. 3). The functional and phylogenetic alpha diversity of the snail assemblages in nearly isolated floodplain wetlands were significantly higher, than in the other three habitats (Fig. 3). Finally, phylogenetic alpha diversity in occasionally connected and regularly connected wetlands exceeded that of the connected wetlands (ANOVA, $F = 10.84$, $p < 0.001$; Fig. 3).

3.2. Effects of connectivity on beta diversity

The taxonomic, functional, and phylogenetic structures of snail assemblages significantly differed between different reaches (PERMANOVA, Pseudo-F = 2.0951, $p < 0.005$, Pseudo-F = 3.1206 and $p = 0.0094$, Pseudo-F = 2.5784, $p < 0.01$, respectively; Table 2). The taxonomic, functional, and phylogenetic structures of the snail assemblages also significantly differed between classes of lateral connectivity (PERMANOVA, Pseudo-F = 4.91, $p < 0.001$; Pseudo-F = 11.07, $p < 0.001$; Pseudo-F = 7.47; $p < 0.001$; respectively, Table 3). Based on pair-wise tests, taxonomic similarity, functional dissimilarity, and phylogenetic dissimilarity decreased along lateral connectivity between the rivers and wetlands (Table 3).

Points representing wetlands in the four reaches widely overlapped in the NMDS plot generated using the taxonomic, functional, and phylogenetic structures of the snail assemblages (Fig. 4). NMDS ordination plots showed a relative clear separation across connected, regularly connected, occasionally connected, and nearly isolated wetlands

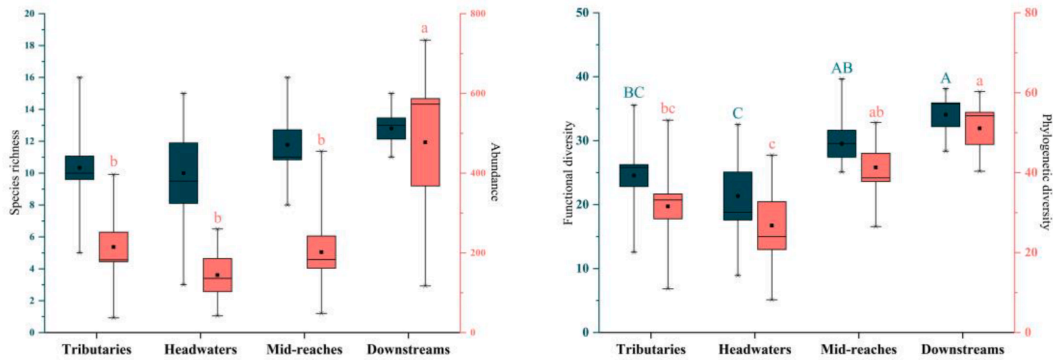


Fig. 2. Mean snail richness (species per wetland), abundance (species per wetland), functional diversity, and phylogenetic diversity in the floodplain wetlands of tributaries (18 sites), headwaters (6 sites), mid-reaches (9 sites), and downstream (5 sites) reaches. Boxes indicate the standard error. Distinct upper-case letters (right: functional diversity) and lower-case letters (left: abundance; right: phylogenetic diversity) above the box with same color indicate significant differences ($p < 0.05$) among tributaries, headwater, mid-reaches, and downstream reaches. Order from A to C based on the value from large to small.

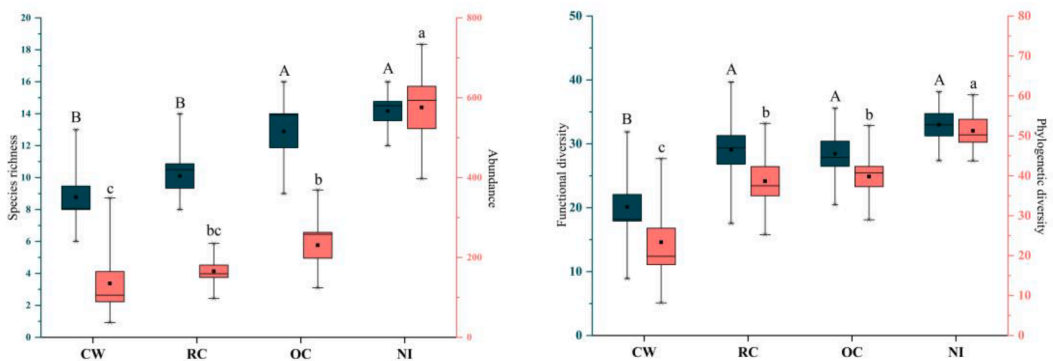


Fig. 3. Mean snail richness (species per wetland), abundance (species per wetland), functional diversity, and phylogenetic diversity in floodplain wetlands with different lateral hydrological connectivity. CW: 13 sites, permanently connected wetlands; RC: 10 sites, regularly connected during summer flow; OC: 9 sites, occasionally connected during high floods; NI: 6 sites, nearly isolated, but extremely connected during exceptionally high floods. Boxes indicate the standard error. Distinct upper-case letters (left: species richness; right: functional diversity) and lower-case letters (left: abundance; right: phylogenetic diversity) above the box with same color indicate significant differences ($p < 0.05$) among CW, RC, OC, NI. Order from A to C based on the value from largest to smallest.

Table 2

Permutational multivariate analysis of variance (PERMANOVA) for taxonomic, functional and phylogenetic structures of snail assemblages and average similarity/dissimilarity between/within longitudinal connectivity (tributaries, headwaters, mid-reaches, and downstream reaches, 999 Monte Carlo permutations).

Diversity facet	Reach	Headwater	Mid-reach	Downstream	Tributary
Species composition	Main test:				
	Pseudo-F = 2.0951**				
	Pair-wise test: Similarity				
	Headwater	26.624			
	Mid-reach	27.182	39.521		
	Downstream	19.696	33.513	31.31	
Functional structure	Main test:				
	Pseudo-F = 3.1206**				
	Pair-wise test: Dissimilarity				
	Headwater	8.4753			
	Mid-reach	7.3085	4.8607		
	Downstream	10.373	6.5637	7.6061	
Phylogenetic structure	Main test:				
	Pseudo-F = 2.5784**				
	Pair-wise test: Dissimilarity				
	Headwater	17.151			
	Mid-reach	16.689	12.047		
	Downstream	18.401	13.038	13.378	
Tributary	15.101	13.304	15.554	13.415	

Table 3

Permutational multivariate analysis of variance (PERMANOVA) for taxonomic, functional and phylogenetic structures of snail assemblages and the average similarity/dissimilarity between/within lateral connectivity (CW: permanently connected wetlands; RC: regularly connected during summer flow; OC: occasionally connected during high floods; NI: nearly isolated, but extremely connected during exceptionally high floods; 999 Monte Carlo permutations).

Diversity facet	Lateral connectivity	CW	RC	OC	NI
Species composition	Main test:				
	Pseudo-F =				
	4.912**				
	Pair-wise test:				
	Similarity				
	CW	32.292			
	RC	21.776	38.363		
	OC	29.757	36.153	44.733	
	NI	16.699	31.196	40.254	51.746
Functional structure	Main test:				
	Pseudo-F =				
	11.072**				
	Pair-wise test:				
	Dissimilarity				
	CW	5.5867			
	RC	8.0151	6.0157		
	OC	6.9514	4.9017	3.3927	
	NI	11.267	7.2876	5.696	4.9686
Phylogenetic structure	Main test:				
	Pseudo-F =				
	7.4738**				
	Pair-wise test:				
	Dissimilarity				
	CW	13.748			
	RC	18.251	13.151		
	OC	15.076	10.609	8.4914	
	NI	19.749	13.149	10.802	8.626

based on the taxonomic structure of the assemblage similarity (Fig. 5). In the NMDS plots generated by assemblage dissimilarity of functional and phylogenetic structures, wetlands with different lateral connectivity slightly overlapped (Fig. 5). For the three plots, points representing assemblage structures in the connected and regularly connected wetlands were widely scattered, indicating inter-wetland variability.

The taxonomic structure was more homogeneous in the mid-reach wetlands than in the headwater wetlands (PERMDISP, $t = 2.95$, $p < 0.01$; Table 4). The taxonomic structure was more homogeneous in the nearly isolated wetlands than in the connected (PERMDISP, $t = 4.61$, $p < 0.01$) and regularly connected wetlands (PERMDISP, $t = 3.75$, $p < 0.01$; Table 4). Occasionally connected wetlands were more homogeneous than connected wetlands (PERMDISP, $t = 3.38$, $p < 0.01$). The functional structure was more homogeneous in the occasionally connected wetlands than in the regularly connected wetlands (PERMDISP, $t = 2.51$, Table 4).

3.3. Relationships between beta diversity and environmental factors

Three groups of environmental variables explained large proportions of the variance in all facets (taxonomic, functional, and phylogenetic structures) of snail assemblages, as indicated by the DistLM results (Table 5). In all models, the fractions representing shared effects were generally large. Waterscape, climate, and habitat variables all significantly explained the variances in snail assemblage taxonomic structures. The functional and phylogenetic structures of snail assemblages, waterscape, and climate variables significantly explained the variances. Waterscape and climate variables equivalently explained the variations in taxonomic, functional, and phylogenetic structures. The marginal tests identified lateral connectivity and river order as two of the most critical variables explaining variations in taxonomic (14.6%, 11.3%, respectively), functional (33.4%, 28.9%, respectively) and phylogenetic structures (23.1%, 20.2%, respectively; Table 5). The maximum temperature of warmest month was the third critical variable explaining variations in the taxonomic and phylogenetic structures (9.3%, 14.8%,

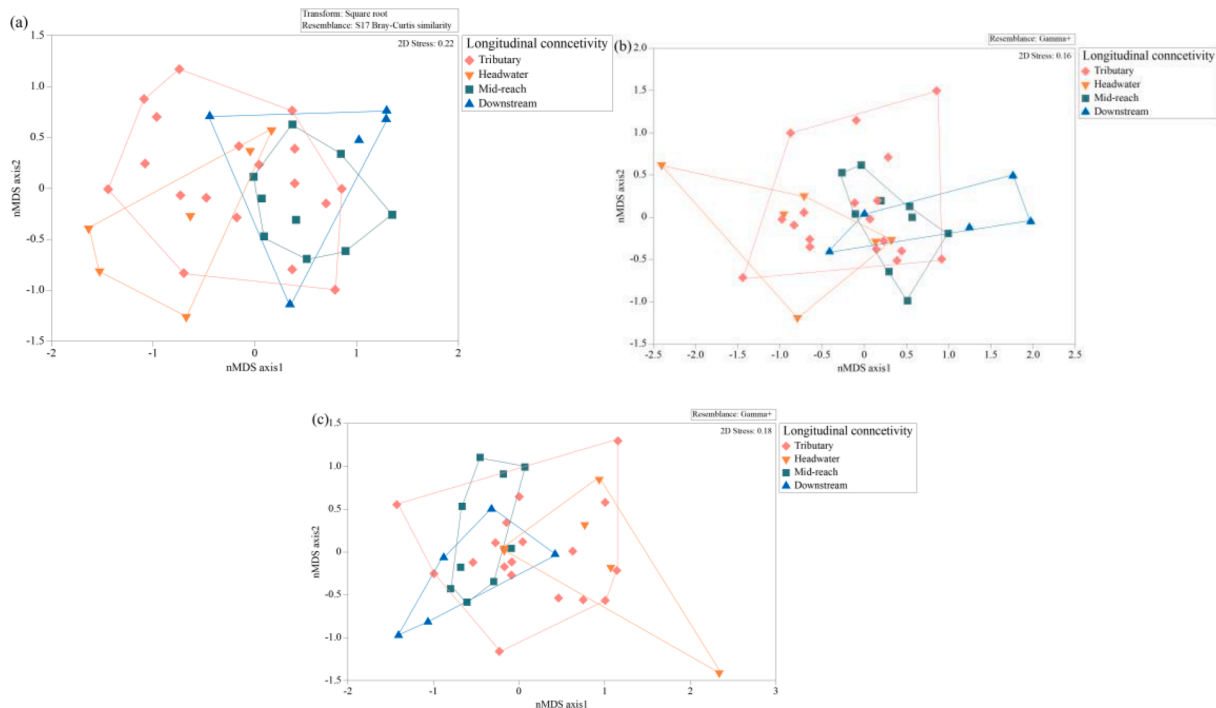


Fig. 4. Non-metric multidimensional scaling (NMDS) plots for 38 floodplain wetlands in the Da Xing'an Mountains with different classes of longitudinal connectivity (tributary, headwater, Mid-reaches, and downstream). Plots based on (a) taxonomic compositions: snail species abundance (from Bray-Curtis dissimilarities); (b) functional structure: the simple matching coefficient calculated between pairs of species using trait scores (Gamma + measure); and (c) phylogenetic structure: distances through taxonomic classification (Gamma + measure).

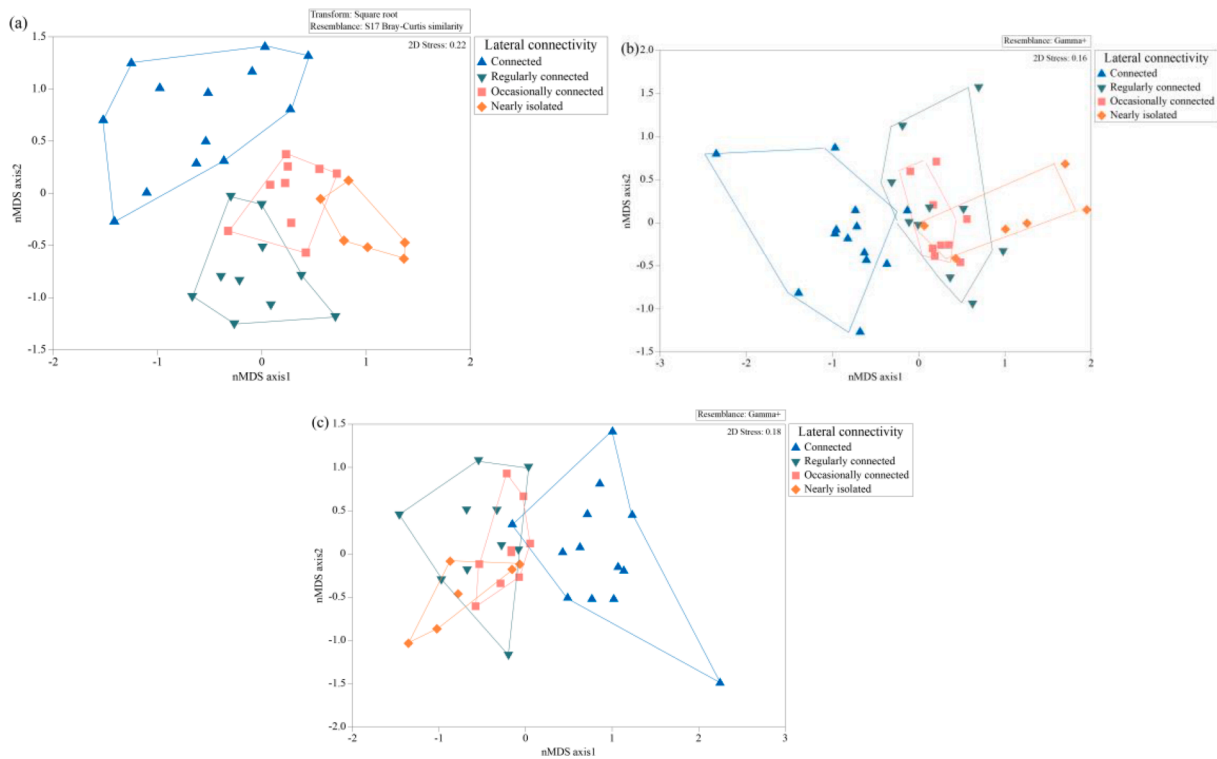


Fig. 5. Non-metric multidimensional scaling (NMDS) plots for 38 floodplain wetlands in the Da Xing’an Mountains with different classes of lateral connectivity: plots based on (a) snail species abundance (from Bray-Curtis dissimilarities); (b) the simple matching coefficient calculated between pairs of species using trait scores (Gamma + measure); and (c) distances through taxonomic classification (Gamma + measure). Connected: permanently connected wetlands; Regularly connected: regularly connected during summer flow; Occasionally connected: occasionally connected during high floods; Nearly isolated: nearly isolated, but extremely connected during exceptionally high floods.

Table 4

Results of distances to group centroids in distance-based tests for homogeneity of multivariate dispersions (PERMDISP) for taxonomic, functional and phylogenetic structures among longitudinal (tributaries, headwaters, mid-reaches, and downstream reaches) and lateral connectivity (CW: permanently connected wetlands; RC: regularly connected during summer flow; OC: occasionally connected during high floods; NI: nearly isolated, but extremely connected during exceptionally high floods), including Monte Carlo p values (9999 permutations). PERMDISP test whether one group of wetlands was more “variable” (heterogeneous) than another by comparing the distances from each individual wetland (sample) to their group centroid in the full dimensional space.

Diversity facets	Longitudinal connectivity	Distances to centroids	Lateral connectivity	Distances to centroids
Species composition	Headwater	47.57 (1.76) ^a	CW	46.16 (1.95) ^a
	Mid-reach	40.55 (1.54) ^b	RC	41.56 (1.71) ^{ab}
	Downstream	43.96 (4.55) ^{ab}	OC	37.06 (1.55) ^b
	Tributary	46.25 (1.44) ^{ab}	NI	31.26 (2.10) ^c
Functional structure	Headwater	5.29(1.47)	CW	3.39(0.91) ^{ab}
	Mid-reach	3.31(0.30)	RC	4.00(0.54) ^a
	Downstream	4.77(1.34)	OC	2.33(0.36) ^b
	Tributary	4.14(0.62)	NI	3.18(0.72) ^{ab}
Phylogenetic structure	Headwater	11.20(2.25)	CW	9.11(1.40)
	Mid-reach	8.20(0.75)	RC	8.61(1.11)
	Downstream	8.30(2.18)	OC	5.50(0.96)
	Tributary	9.18(0.95)	NI	5.82(0.74)

respectively). Alternatively, channel distance to the source was the third critical variable explaining variations in the functional structure (23.7%).

4. Discussion

This study has assessed the taxonomic, functional, and phylogenetic diversity of snail assemblages in floodplain wetlands across lateral and longitudinal gradients of connectivity simultaneously. Floodplains comprise a variety of snail species, some of which are aquatic pulmonates, some are aquatic non-pulmonates, while others are terrestrial. Both longitudinal and lateral variations contributed to heterogeneous snail assemblages due to the differences within habitat (alpha) and among habitats (beta). Beyond our first hypothesis, the alpha diversity of snail assemblages decreased along the degree of lateral connectedness between the floodplain wetlands and their adjacent channels while increased along the length of the rivers. Structural variations in snail assemblages were closely related to waterscape and climatic variables. Furthermore, lateral connectivity and river order explained large amount of the total variation in the three structures of snail assemblages. Considering the extant patterns in assemblage structures and their predictors, biodiversity conservation and restoration of river floodplain wetlands should not only consider the river length, but also pay more attention to the lateral connectedness of floodplain wetlands (i.e., from permanently connected to rarely flooded, or even to isolated wetlands).

The effects of lateral connectivity on aquatic invertebrate assemblages in general and snail assemblages in particular have been studied to a certain extent (Batzer et al., 2016). In the previous studies, lenticlotic distinguishing method in snail or aquatic invertebrate assemblage structures was spatially evident in floodplain wetlands (Batzer et al., 2016; Guan et al., 2017). Lotic snails are generally restricted to wetlands which have strong connectedness with adjacent rivers. On the other

Table 5

Results of distance-based linear models (DISTLM) was used to analyze the taxonomic, functional, and phylogenetic structure in response to the climate, waterscape, and local habitat variables, obtained using stepwise selection based an adjusted R^2 selection criterion of environmental variables. Total, each group of variables, and individual variables explained the variation were listed respectively.

Variables	Taxonomic composition			Functional structure			Phylogenetic structure		
	Prop.	Pseudo-F	p	Prop.	Pseudo-F	p	Prop.	Pseudo-F	p
Total	0.747	–	–	0.793			0.598		
Waterscape variables	0.376	2.581	0.001	0.600	6.4384	0.001	0.439	3.357	0.001
Lateral connectivity	0.146	6.159	0.001	0.334	18.053	0.001	0.231	10.814	0.001
Reach	0.091	3.608	0.002	0.158	6.758	0.0023	0.114	4.642	0.004
River order	0.113	4.597	0.001	0.289	14.625	0.001	0.202	9.0973	0.001
River basin	0.053	2.017	0.019	0.113	4.606	0.0151	0.056	2.143	0.091
Habitat area	0.040	1.501	0.097	0.042	1.589	0.2266	0.016	0.598	0.638
Channel distance to source	0.044	1.652	0.065	0.237	11.192	0.001	0.137	5.710	0.006
Minimum distance to river	0.076	2.978	0.002	0.054	2.042	0.1417	0.025	0.929	0.457
Climatic variables	0.383	1.932	0.001	0.522	3.395	0.001	0.474	2.803	0.001
AMT	0.051	1.926	0.026	0.056	2.132	0.131	0.047	1.786	0.155
MDR	0.045	1.686	0.072	0.025	0.914	0.443	0.039	1.456	0.243
ISO	0.057	2.163	0.021	0.060	2.279	0.116	0.051	1.915	0.130
MTW	0.093	3.697	0.002	0.152	6.470	0.004	0.148	6.253	0.001
MTD	0.043	1.636	0.072	0.043	1.628	0.214	0.046	1.750	0.156
AP	0.075	2.931	0.002	0.173	7.530	0.001	0.117	4.752	0.003
PDM	0.062	2.391	0.009	0.124	5.081	0.007	0.090	3.570	0.012
PS	0.046	1.727	0.071	0.069	2.668	0.076	0.038	1.431	0.250
PDQ	0.062	2.366	0.009	0.055	2.098	0.143	0.061	2.338	0.069
Habitat variables	0.251	1.434	0.009	0.238	1.335	0.250	0.156	0.794	0.698
Sal	0.062	2.369	0.011	0.082	3.2126	0.053	0.058	2.230	0.083
pH	0.035	1.313	0.184	0.031	1.170	0.352	0.007	0.244	0.853
Dissolved Oxygen	0.048	1.800	0.039	0.084	3.3182	0.058	0.045	1.682	0.171
NO ₃ ⁻	0.033	1.240	0.267	0.010	0.348	0.635	0.014	0.506	0.653
Turbidity	0.042	1.589	0.077	0.031	1.152	0.336	0.020	0.742	0.552
chlorophyll <i>a</i>	0.044	1.637	0.073	0.042	1.589	0.218	0.006	0.206	0.869
Water depth	0.042	1.571	0.085	0.017	0.612	0.575	0.029	1.057	0.388

AMT: Annual Mean Temperature; MDR: Mean Diurnal Range; ISO: Isothermality; TS: Temperature seasonality; MTW: Maximum temperature of warmest month; AP: Annual Precipitation; PDM: Precipitation of wettest month; PS: Precipitation seasonality.

hand, if the lateral connectedness of wetlands to channels is weak or the wetlands are only occasionally flooded or even nearly isolated, snail assemblages tend to be dominated by lentic species (Guan et al., 2017). Our results show that snail alpha diversities and structural similarities declined along with the river-floodplain connections. A dilution process may exist via lateral connections between floodplains with main river channels. Indicator analyses also confirmed that some lentic “obligate wetland fauna” were representative species for the nearly isolated wetlands. Higher alpha diversity in the nearly isolated wetlands indicates suitable habitats that support distinct groups of snails featuring divergent trait combinations and phylogenetic diversity. Within the set of nearly isolated wetlands, assemblages were remarkably homogeneous, which could be because these nearly isolated wetlands may occur under similar stable inundating conditions and stable physical structures, providing plenty of time for aquatic invertebrates to grow.

With the decrease of certain controlling physical factors, snail diversity increases laterally from the connected floodplains to the nearly isolated wetlands. Meanwhile, across the connected and regularly connected sites, snail assemblages are heterogeneous and show significantly increased dispersion. Increases in the flow and flood pulses usually cause higher floodplain habitat heterogeneity (Liu and Wang, 2018; Zheng et al., 2022). In more connected waterbodies, multidimensional environmental processes can occur, such as water level fluctuation, inundation, turbulence, water scouring, and drying. These habitat characteristics changes, which are led by flood connections, threaten the growth, reproduction, and survival of some snail species, resulting in the loss of inappropriate species and their possessed functional traits in the given floodplain wetlands (Raulings et al., 2010; Zhang et al., 2014). Moreover, fish predation is considered to be an important driving factor that shape snail assemblages (density, biomass, and diversity; McPeck 2004; Chase et al. 2009). In floodplain wetlands with higher lateral connectivity, fish assemblages have been proved to support higher species richness and abundance (Manfrin et al., 2020). Thus, predatory fish in more connected waterbodies may reduce the diversity of snails.

Meanwhile, flood pulse can severely change the floodplain riparian vegetation, causing regression of emergent and submerged plants. Habitats with lower vegetation cover, lower diversity of plant species, and fewer detrital decomposition would subsequently lack resources for snails (Hoverman et al., 2011).

Our research spans across six major rivers in the Da Xing’an Mountains. The conditions of floodplain wetlands differ among these sub-river basins. In general, the width and extent of flood pulse are the highest in the lower reach and lowest in the upper reach of a specific river. This work about snail assemblages in floodplains wetlands of Da xing’an Mountains also sustains the point of view that floodplain aquatic invertebrates vary along the river (Batzer et al., 2016). The structure of snail assemblages in the studied floodplain wetlands was significantly different between the headwater and mid-reaches, as well as between the headwater and downstream reaches. It was also observed that snail alpha diversity increased along the longitudinal gradient from the headwater to the downstream reaches. For the lower-lying flooded wetlands, for example the mid-reach or downstream floodplains, longer-inundated flooding generate longer water retention and greater taxonomic richness of snails. This is also likely related to the biotic dispersal among floodplains and channels. The small headwater floodplains increase the opportunity for aquatic invertebrates to floodplain wetlands. Notably, the tributaries supported a slightly higher alpha diversity than the upstream reaches. These tributaries are also located in different reaches of the river and have a relatively preferable habitat than the upstream reaches.

In this study, the linear models included climate, waterscape, and aquatic habitat variables that broadly shape patterns of snail assemblages. Since snail assemblages are strongly dependent on patterns in water availability and permanence (Guan et al., 2017; Wu et al., 2019), it was not surprising to observe that waterscape variables explained large portions of all compositional variations. Generally, lateral connectivity and river order were the significant factors that shaped multifacets of the snail assemblage beta diversity in these floodplain

wetlands. However, the overall significance of lateral connectivity for variations in snail assemblages was not surprising (Zheng et al., 2022). Meanwhile, with the decrease in river class, channel width, hydrological connectivity, habitat area, and hydroperiod showed an increasing trend (Batzer et al., 2016). This is similar to longitudinal connectivity and may cause an increase in the abundance and richness of snails. Climate variables explained a similar proportion of variance to waterscape variables. Climate influences the hydrology in floodplain wetlands by regulating the seasonality and intensity of floods, pulses, and dry periods in different ways. These variations in floods undisputed influence the assemblages of resident snails (Batzer et al., 2016). We found that the MTW explained the third largest variations in taxonomic and phylogenetic structures across the floodplain wetlands. Freshwater snails are ectotherms and need a high temperature for a set number of days to complete their reproductions, and considered particularly vulnerable to climate extremes (Woodward et al., 2010; Epele et al., 2022). Annual precipitation explained the third largest variations in the functional structure. Previous studies have shown that permanence gradient is an important factor affecting aquatic invertebrate assemblages. (Wellborn et al., 1996; Wissinger, 1999; Williams, 2006). It was expected that annual precipitation would generate a stronger ecological impact on snail functional structures (Epele et al., 2022).

Floodplain wetlands provide critical ecosystem services, including biodiversity support, nutrient retention, flood mitigation, and carbon sequestration etc. (Blake et al., 2022). The guidelines for floodplain-river complex ecosystem management and restorations implicitly state the necessity to restore the functional integrity of the river-floodplain complex. However, most of the conservation plans in floodplains are guided by longitudinal connectivity, and rarely considered the role of lateral hydrological connectedness (Manfrin et al., 2020). This study proposes to widen the focus beyond longitudinal gradient, to embrace the lateral aspects of the specific river basin, as each facet of snail assemblage diversity varies at different positions along the lateral gradient. Instead, these strategies should be formulated in an integrated viewpoint by considering the lateral and longitudinal as a unique and complementary hydrological connectivity (Tockner et al., 2010; Manfrin et al., 2020). We should acknowledge that floodplain management should consider the full spectrum of longitudinal section and lateral connectivity so that multiple facets of snail biodiversity can be maximized. Finally, differentiated strategies based on the longitudinal and lateral hydrological connectivity should be formulated to ensure the success of floodplain restoration and habitat enhancement.

CRedit authorship contribution statement

Qiang Guan: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Software, Supervision, Writing – original draft, Writing – review & editing. **Haitao Wu:** Conceptualization, Funding acquisition, Project administration, Supervision, Writing – review & editing. **Yuxiang Yuan:** Supervision, Writing – original draft. **Wenfeng Wang:** Supervision, Writing – review & editing. **Zhongsheng Zhang:** Software, Visualization, Writing – review & editing. **Lei Xu:** Formal analysis, Software. **Yujuan Kang:** Formal analysis, Writing – original draft. **Kangle Lu:** Investigation. **Dandan Liu:** Investigation. **Dandan Han:** Investigation, Data curation. **Zhen-shan Xue:** Software, Writing – review & editing

Data availability

Data will be made available on request.

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.

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Supplementary data

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