RESEARCH ARTICLE

Environmental filtering of macroinvertebrate traits influences ecosystem functioning in a large river floodplain

Natalie K. Rideout[1] | Zacchaeus G. Compson[2,3] | Wendy A. Monk[4] |
Meghann R. Bruce[5] | Mehrdad Hajibabaei[6] | Teresita M. Porter[6] |
Michael T. G. Wright[6] | Donald J. Baird[2]

[1]Department of Biology, Canadian Rivers Institute, University of New Brunswick, Fredericton, New Brunswick, Canada; [2]Environment and Climate Change Canada @ Canadian Rivers Institute, Department of Biology, University of New Brunswick, Fredericton, New Brunswick, Canada; [3]Department of Biological Sciences, Advanced Environmental Research Institute, University of North Texas, Denton, Texas, USA; [4]Environment and Climate Change Canada @ Canadian Rivers Institute, Faculty of Forestry and Environmental Management, University of New Brunswick, Fredericton, New Brunswick, Canada; [5]Canadian Rivers Institute @ University of New Brunswick, Fredericton, New Brunswick, Canada and [6]Centre for Biodiversity Genomics and Department of Integrative Biology, University of Guelph, Ontario, Canada

Correspondence
Natalie K. Rideout
Email: nrideout@unb.ca

Handling Editor: Alexandra Wright

Abstract

1. The biodiversity–ecosystem function hypothesis postulates that higher biodiversity is correlated with faster ecosystem process rates and increased ecosystem stability in fluctuating environments. Exhibiting high spatiotemporal habitat diversity, floodplains are highly productive ecosystems, supporting communities that are naturally resilient and highly diverse.

2. We examined linkages among floodplain wetland habitats, invertebrate communities and their associated traits, and ecosystem function across 60 sites within the floodplain wetlands of the lower Wolastoq|Saint John River, New Brunswick, using structural equation modelling and Threshold Indicator Taxa ANalysis.

3. We identified key environmental filters structuring invertebrate communities, by linking increased niche differentiation through shoreline change, flood pulse dynamics, and macrophyte bed complexity with increased taxa and functional diversity.

4. Examination of traits linked to ecosystem functions revealed that more resilient wetlands with balance between primary productivity and decomposition as carbon sources were associated with greater functional evenness and richness, while habitat patches with elevated decomposition rates had lower functional richness, reflecting a simplified, more disturbed habitat.

5. While our more complex overarching SEM model was ultimately compromised by an overspecified number of pathways, our results nevertheless are indicative of a divergence between wetland and riverine ecosystems in their relationships linking biodiversity and ecosystem function, illustrating how to define ecosystem

health in wetland habitats, and demonstrating how critical functions support healthy wetland habitats by providing increased resilience to disturbance.

1 | INTRODUCTION

In dynamic ecosystems, the ability of communities to remain resilient to natural and human-induced disturbances and support vital ecosystem functions is degraded by biodiversity loss (Tilman & Lehman, 2001). Biodiversity, which reflects taxonomic and functional variety, provides an 'insurance policy', whereby many species exhibit a range of responses to varying disturbances. Biodiversity critically also includes redundancy (or niche overlap) ensuring that ecosystem functions are maintained even as species are lost (Díaz & Cabido, 2001). In a review of 100 studies, Srivastava and Vellend (2005) found that 71% reported enhanced rates of ecosystem function with increased biodiversity. Defined by Pacala and Kinzig (2002), ecosystem function describes an ecosystem's stability, its ability to maintain energy fluxes (e.g. production and decomposition) and its stocks of energy and biomass (e.g. Loreau et al., 2002; Tilman et al., 2006). The maintenance of these functions is an indication of a healthy ecosystem. While 'ecosystem health' is often an undefined term in ecological literature, even considered controversial by some, it is defined here after Constanza and Mageau (1999) as an 'ability to maintain structure and function over time in the face of external stress'. In floodplain wetlands, vital functions include decomposition, which link terrestrial and aquatic food webs (Langhans et al., 2006), and primary production, where aquatic macrophyte and periphyton communities generate biomass to support the base of food webs (McCormick & Stevenson, 1998).

The link between biodiversity and ecosystem function (BEF) has been recognized by ecologists for decades (Tilman & Lehman, 2001); mechanisms behind this link are the subject of active research, focusing chiefly on functional traits (Díaz & Cabido, 2001). Traits are defined as the 'morphological, physiological or behavioural characteristics of a species that describe a species' physical characteristics, functional role in an ecosystem, or its ecological niche' (Baird et al., 2008). The shift in focus from taxonomy-based biodiversity to traits-based studies is important in that traits allow ecologists to compare across broader scales, where species may be interchangeable, but traits are retained, and account for species that may fill several niches depending on their life stage (Baird et al., 2011). Trait-based ecology also encompasses the fact that abiotic variables act as environmental filters primarily for traits, only secondarily filtering for the taxa that hold those traits (Bonada et al., 2007).

From a biomonitoring perspective, traits influencing key ecosystem functions are critical to conserve (Rosenfeld, 2002); equally important is the maintenance of functional redundancy to sustain

resilience to future disturbances (Díaz et al., 2013). Ecosystem vulnerability is strongly dependent on the phylogenetic similarity of groups that provide certain functions (through taxon effect traits), as environmental filtering for response traits can eradicate entire lineages with similar functional roles (Rosenfeld, 2002; Trios et al., 2014). In fact, it is response traits—those that influence a species' ability to colonize and thrive in an environment (and thus, its fitness)—that are subject to natural selection (Rosenfeld, 2002). Trios et al. (2014) proposed that under high disturbance, communities are dominated by phylogenetically similar species, while communities with low levels of disturbance tend to be more distantly related, reducing competition through niche complementarity, resulting in more efficient use of available resources (Hooper et al., 2002). This theory assumes that natural selection of species through environmental filtering of response traits will result in communities with similar sets of traits, and therefore lineages, that are more capable of withstanding disturbance (Trios et al., 2014). While much research focusing on the link between traits and BEF has centred on trophic relationships, more recently, Maureaud et al. (2020) have emphasized the need to consider wider trait responses to multiple ecosystem functions, in real-world situations with complex, varying habitat conditions.

Following from the above, as functionally diverse ecosystems with significant spatial and seasonal habitat disturbances, river floodplains provide an excellent proving ground for traits-based ecological theory, as they support mosaics of habitat patches at different successional stages with varying degrees of hydrological connectivity to the main channel (Bayley & Guimond, 2008; Tockner et al., 2010). Despite the rise in traits-based science, taxonomic resolution has imposed limitations (Vieira et al., 2006), especially in taxonomically rich floodplain wetland ecosystems (e.g. Funk et al., 2017), which are understudied compared to riverine counterparts (Tockner et al., 2010). DNA metabarcoding via high-throughput sequencing provides a powerful tool to characterize community composition in unprecedented detail (Bush et al., 2019; Gibson et al., 2015), delivering sufficient taxonomic detail to study how environmental filters affect invertebrate traits, and the consequences for maintenance of healthy ecosystem function.

The objective of this study was to elucidate the drivers of macroinvertebrate community structure and associated wetland ecosystem function. This was done by (1) using a structural equation model (SEM) framework to quantify the linkages among environmental filters, macroinvertebrate functional diversity and ecosystem function, and test the specific hypotheses outlined in Table 2 and (2)

using Threshold Indicator Taxa ANalysis (TITAN2) to compare how taxa and traits respond to gradients of function and environmental filtering. These are critical issues to address, as they can provide insights into how to improve wetland protection, and how to prioritize wetland restoration actions to restore healthy floodplain ecosystems. Maintaining diverse, functionally redundant communities that are resilient to future disturbances is particularly important in productive, service-delivering ecosystems such as floodplain wetlands, which have been, and continue to be, under threat of human development and climate change.

2 | MATERIALS AND METHODS

2.1 | Study system

The Wolastoq | Saint John River drains a catchment of 55,110 km^2 as it flows 673 km from its headwaters in northern Maine and Quebec. Each spring, ice-jams and snow melt generate flood pulses, pushing nutrient and sediment-rich water into downstream floodplain wetlands, one of the last semi-intact large-river floodplains in eastern North America. The study area focused on part of this floodplain, Atlantic Canada's largest freshwater wetland complex, the Grand Lake Meadows and Portobello Creek wetland complex (henceforth abbreviated as the 'GLM complex'; Figure 1). These wetlands are a vital reservoir for biodiversity (including rare and endangered species) and act as important nursery, flyway and nesting habitat for many migratory and transitional species,

prompting the provincial and federal governments to protect them through the Grand Lake Meadows Protected Natural Area (GLM PNA) and the Portobello Creek National Wildlife Area (PC NWA), respectively. Despite its outstanding conservation value, however, the GLM complex has experienced substantial wetland habitat change in the last few decades, with an altered hydrologic regime, and subsequent sediment and nutrient deposition, into the floodplain due to significant anthropogenic alterations within the watershed (Rideout et al., 2021).

In all, 60 sites were sampled between June 2017 and August 2017, with sites distributed across the edge of the wetland complex among three levels of protection: (1) unprotected ($n = 12$), (2) non-contiguous protection (GLM PNA; $n = 24$; Scientific Protected Natural Area Permit # SCP2016-002 granted to NR by New Brunswick Department of Energy and Resource Development) and (3) contiguous protection (PC NWA; $n = 24$; National Wildlife Area Permit # NWA3002 granted to NR by the Canadian Wildlife Service; Figure 1). All sites were characterized as aquatic wetland habitat that extended from the edge of terrestrial high marsh vegetation to open water, containing emergent and submerged macrophytes. Sites were accessed by boat from the lake edge during the time of sampling but were disconnected from the main channel of the Wolastoq | Saint John River outside of the spring freshet season. A pair of bamboo poles with fishing line between them served to suspend sampling equipment in the water column (e.g. loggers, tiles and leaf packs) and mark the midpoints of each site; all biotic and abiotic samples and surveys were taken within 50 m of these poles.

FIGURE 1 Study sites within the Grand Lake Meadow (GLM) complex relative to different protection strategies. Sites are grouped into Portobello Creek NWA sites (blue), GLM Protected Natural Area (PNA) sites (navy) and sites in areas of no known protection strategy (i.e. 'unprotected'; orange). Major water bodies are labelled, and protected areas are coloured: Portobello Creek NWA (yellow) and GLM PNA (green). Inset map shows location of sampling (black box) in relation to the Wolastoq | Saint John River watershed. Data for all open-source background layers were sourced from GeoGratis and GeoNB.
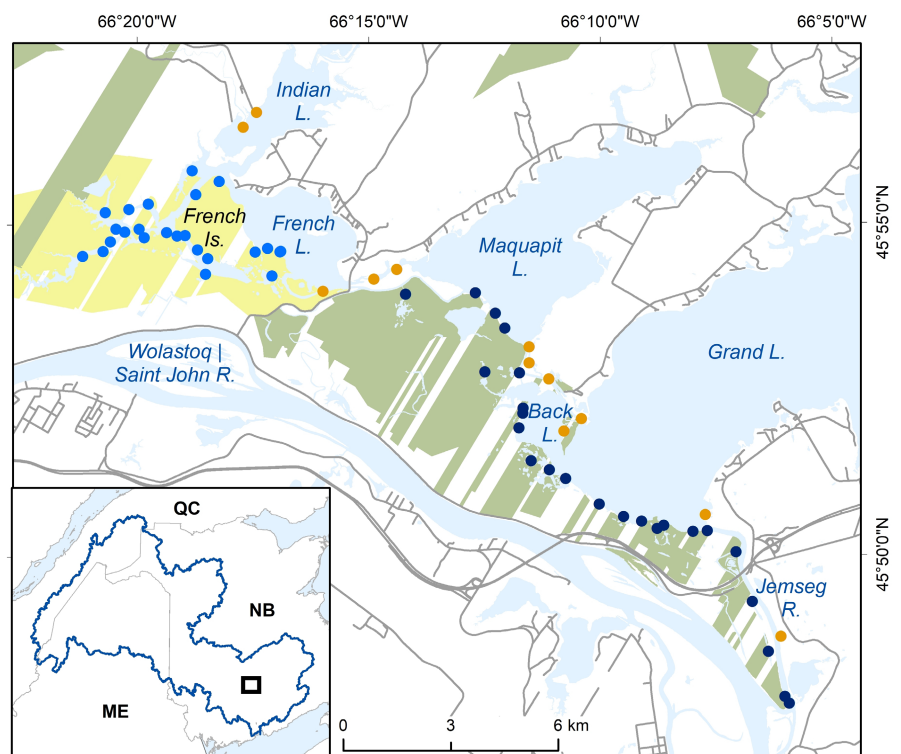
2.2 | Wetland habitat

Supporting habitat data for this work are described in detail in Rideout et al. (2021) and thus the methods employed are only summarized here.

2.2.1 | Shoreline change

Shoreline change assessed as the difference in wetland extent between 1951 and 2014 was measured from aerial photographs of the study area using ArcGIS (version 10.6.1; ESRI, 2018). Differences between the 2 years (1951 and 2014) were calculated for points along the shoreline ($n = 2500$ transects), from which the entire shoreline was interpolated. Absolute values of total change (in m) for each site were extracted from the resulting interpolated raster file.

2.2.2 | Abiotic variables

Water and sediment samples were collected following the Canadian Aquatic Biomonitoring Network (CABIN) wetland protocol standard operating procedures (Environment and Climate Change Canada, 2018) and sent to Environment and Climate Change Canada's National Laboratory for Environmental Testing and New Brunswick's provincial research organization to analyse for trace elements, nutrients, organic carbon and physical properties. HOBO loggers measured water temperature (P/N UA 001 64) every 5 min and depth (P/N 20-001-04) every hour, then summarized as descriptive variables. Hydrological metrics were calculated from water depth data using the Indicators of Hydrologic Alteration software (Richter et al., 1996).

2.2.3 | Submerged and emergent macrophyte community

Surveys for emergent and submerged macrophytes were conducted at all sites. These were categorized as (1) submerged, defined as aquatic vegetation that were either wholly submerged (e.g. water milfoil) or floating (e.g. pond lilies) and could be rooted or unrooted (e.g. duckweed) or (2) emergent, having roots in the sediment, but most of the plant out of water (e.g. arrowheads). Observers designated the top three dominant species for both emergent and submerged communities at every site and estimated percent cover for each; total macrophyte coverage at each site was estimated and recorded. Representative specimens for all emergent and submerged dominant species were collected, along with all submerged macrophyte morphotypes found, for later taxonomic identification ($n \geq 6$ per site). As identification of emergent macrophytes such as grasses can be difficult and time-consuming, particularly where reproductive structures are absent, percent cover was assigned for only the

three most common emergent macrophytes. For submerged species, the top three dominant specimens were assigned their estimated percent cover, while the difference between the total percent cover of the site and the summed dominant species was divided evenly among all other species.

2.3 | Macroinvertebrate community

Benthic macroinvertebrate samples were collected following the CABIN wetland protocol, sweeping through submerged and emergent vegetation for 2 min to dislodge invertebrates (Environment and Climate Change Canada, 2018). Samples were rinsed in the field to remove excess sediment and stored in 1 L jars with 95% ethanol. In the laboratory, all vegetation was rinsed and removed over a 250 μm sieve, and the ethanol replaced to minimize dilution. Samples were stored at −80°C and subsequently transported while frozen to the University of Guelph Centre for Biodiversity Genomics. There, DNA was extracted using a standard pipeline for metabarcoding of the cytochrome *c* oxidase subunit 1 (COI) barcoding region with BR5 and F230R amplicons (Hajibabaei et al., 2019). Taxonomic classifications were assigned using the Ribosomal Database Project classifier (version 2.12; Porter & Hajibabaei, 2018), which were then filtered for greater than 99% confidence for correct assignments at the genus level. For more information, see supplementary material (S1). Data generated from DNA metabarcoding were treated as presence/absence information (Elbrecht & Leese, 2015).

Ecologically relevant traits were chosen to describe the niches and response patterns within the wetland ecosystem; chosen traits were limited to those with information that was feasibly accessible for all taxa, totalling 13 traits and 67 modalities (Table 1). Approximately 55% of the trait information was assigned at the genus level from the USGS Database of Lotic Invertebrate Traits for North America (Vieira et al., 2006). Gaps were filled in at the genus level from first the European freshwaterecology.info database (~5%; Schmidt-Kloiber & Hering, 2015), and then from the literature (~20%); lastly, any remaining gaps (~20%), predominantly among zooplankton taxa, were completed at the family level.

2.4 | Ecosystem function measures

Primary production was estimated from the proxy of standing algal biomass by measuring chlorophyll *a* levels from unglazed tiles ($n = 3$ per site) that accumulated algae in the field for 21 days. Each 4.7 ×4.7 cm tile was scraped into de-ionized water, measured onto filter papers, and boiled for 7 min at 80°C to extract chlorophyll *a*, which was then measured using a Turner Designs Trilogy fluorometer (accuracy 0.01 μg/L).

Decomposition was assayed with litter packs deployed between June 19 and 23 and incubated for exactly 21 days. Silver maple (*Acer saccharinum* L. 1753) leaf-litter collected from the GLM complex in October 2016 was the chosen leaf type as it is the dominant species

TABLE 1 Summary of macroinvertebrate traits and their modalities that were included in analyses. All taxa were assigned either a 1 or 0 for each modality, with multiple states possible for each trait

Traits	Modality
Maximum body size	Small (<10 mm)
	Medium (10–20 mm)
	Large (>20 mm)
Body shape	Streamlined/fusiform
	Round (humped)
	Tubular
	Dorsoventrally flattened
	Bluff (blocky)
Armour	Hard shelled
	Soft
	All sclerotized
	Partly sclerotized
Voltinism	<1 generation per year
	1 generation per year
	>1 generation per year
Fecundity	<100 eggs
	100–1000 eggs
	1000–10,000 eggs
Hatch time	Days
	Weeks
	Months
Respiration	Atmospheric breathers
	Cutaneous
	Plant breathers
	Plastron
	Temporary air store
	Spiracular gills
	Tracheal gills
	Other
Feeding mode	Collector-filterer
	Collector-gatherer
	Parasite
	Piercer herbivore
	Predator
	Scraper/grazer
	Shredder
Habit	Burrower
	Climber
	Clinger
	Crawler
	Diver
	Planktonic
	Sprawler
	Miner
	Swimmer
	Other

TABLE 1 (Continued)

Traits	Modality
Microhabitat	Sand
	Silt
	Gravel
	Rocks
	Boulder
	Large woody debris
	Detritus
	Macrophytes
	Algae
	Pelagic
	Sponge
Vertical habitat position	Surface
	Macrophytes
	Pelagic
	Bed
	Hyporheic
Adult life span	Hours
	Days
	Weeks
	Months
Adult behaviour	Flying adults

in the floodplain; litter was air-dried and stored in a well-ventilated area over winter prior to leaf pack construction. Briefly, leaf litter (3.000 ± 0.010 g) was placed into 12.7 × 12.7 cm packs (n = 3 per site) made from 10 mm plastic chicken wire, allowing for the inclusion of invertebrates but exclusion of most fish. An extra set of leaf packs (n = 5) was made to account for handling loss and to determine the original percentage of organic matter present in the silver maple leaves. Harvested leaf packs were frozen until they were processed using a modification of the Benfield (2007) method. In short, packs were rinsed for excess sediment over a 250 μm sieve and invertebrates picked to reduce errors in weight measurements, then dried for 48 h at 65°C and weighed to 0.001 g. Excess suspended sediment in the water column led to many packs having excessively high weights after field collection. To account for this, the organic content of the leaf packs was burned off at 500°C for 2 h and ash-free dry mass was calculated according to standard methods (Benfield, 2007). All associated equations for calculation of ecosystem functions are found in the supplementary material (S2).

2.5 | Statistical analysis

All data manipulation, analyses and data visualization were completed in R (version 3.5.3; R Core Team, 2019).

To examine linkages among environmental filters and disturbance, macroinvertebrate community structure, and ecosystem function, an SEM was created using the *lavaan* package (version

0.6-7; Rosseel, 2012). SEM is a powerful statistical technique that infers causation between correlative variables by fitting the data to an a priori constructed model (Figure 2; Table 2), while taking all other variables into consideration; it compares the hypothesized model to a random null model to assess model fit (Grace et al., 2010). The maximum likelihood χ^2 value and its associated p-value were examined, where a non-significant result indicated that the hypothesized model was not significantly different from the data confronting the model. The root mean square error approximation (RMSEA) and the goodness of fit index (GFI) were also examined as additional measures of model fit. The model was made a priori using our best knowledge about the ecosystem, and model fit [as indicated by p-values >0.05, low χ^2 values, and GFI values close to (1) was satisfactory ($p = 0.159$; χ^2/df = 1.45; GFI = 0.963; RMSEA = 0.087)]. While this model did have fitted values within the appropriate ranges, it proved to be overspecified, with a large number of paths relative to the sample size; because of this, additional subsets of the model were made with reduced numbers of paths (available in the supplementary [S7]). These simpler SEMs were made by (i) collapsing abiotic variables (a single composite variable made with the strongest associated variables of the three PC axes) and (ii) employing summarizing macrophyte diversity metrics. As fit indices between the full and subset models differed little, the full model is presented to allow for more detailed examination of linkages, particularly for those associated with abiotic components. Furthermore, as this was an exploratory analysis, it was beneficial to examine all pathways, whether or not they were statistically significant in predicting ecosystem responses, as non-significant linkages may yet provide valuable insights, especially for understudied floodplain wetlands.

All abiotic variables entering the model were reduced for high correlations at a threshold of 0.7 Pearson correlation coefficient and condensed for analysis with principal components analysis (PCA) using the *FactoMineR* package (version 2.3; Lê et al., 2008; Table 3); three axes were chosen based on assessment of the scree plot (S3), explaining 43.6% of the variation of abiotic variables among sites: PC1 (19.9%), PC2, (14.5%) and PC3 (8.3%). Emergent and submerged macrophyte species were combined and condensed for analysis using a principal coordinates analysis with a Bray–Curtis dissimilarity matrix in *vegan* (version 2.5-4; Oksanen et al., 2019); two axes were chosen, encompassing 16.6% of the total variation. Using the *FD* package (version 1.0-12; Laliberté et al., 2014), the following multidimensional trait diversity metrics were calculated: functional richness (defined by the total trait space), functional evenness (i.e. the evenness in the distribution of traits and their relative prevalence in trait space) and functional divergence (which represents how prevalence is distributed within the trait space, relative to the centroid; Villéger et al., 2008).

To examine trait and taxa relationships with gradients of function and filters, namely decomposition and abiotic gradients, we used *TITAN2* version 2.1 (Baker et al., 2015). TITAN2 analysis assesses whether species are 'pure' (>95% have the same response direction for 999 bootstrapped runs) and 'reliable' (>95% of bootstrapped runs are significantly different than null at $p < 0.05$) indicators of the gradient, and classifies them as either positive or negative responders, as well as identifying their distribution and optimum along the gradient (Baker & King, 2010). We chose to assess trait and taxa relationships along our abiotic (i.e. abiotic PC1 axis) and decomposition gradient because they were the variables that were the most strongly associated with diversity, and the taxa and traits assessed in TITAN2 are the key components of diversity scores we calculated; in this way, the analysis
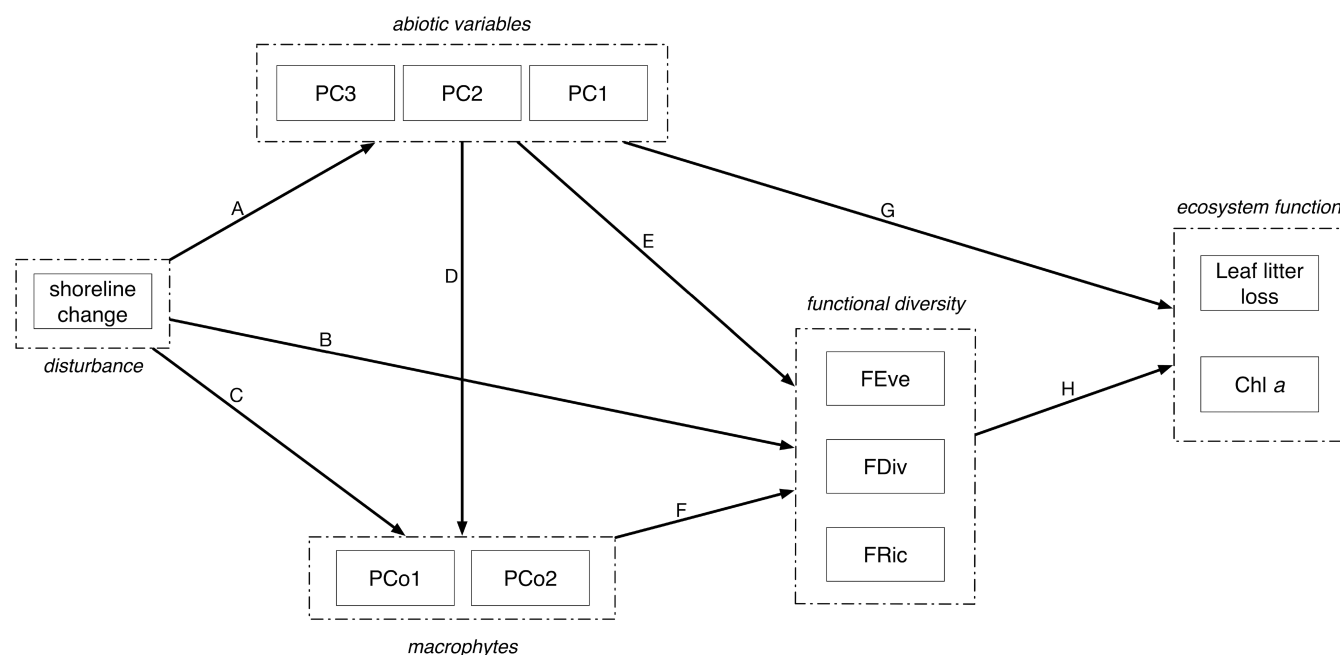

FIGURE 2 A generalized a priori conceptual model depicting hypothesized relationships between disturbance, abiotic variables, biotic components and ecosystem function. Measured input variables for the structural equation model (SEM) are shown in boxes, with dashed outlines grouping variables by type. Each path is labelled (A–H) corresponding with mechanistic hypotheses outlined in Table 2.

TABLE 2 Pathways and proposed hypotheses associated with a priori model (Figure 2)

Pathway	Code	Hypothesis
Shoreline change → abiotic variables	A	Sediment accumulation and erosion alter site hydrology and exposure, influencing accumulation of carbon, nutrients and metals.
Shoreline change → functional diversity	B	Legacy effects of shoreline change directly filtering invertebrate communities.
Shoreline change → macrophytes	C	Changes in water level with shifting shoreline alters emergent and submerged macrophyte community boundaries.
Abiotic variables → macrophytes	D	Site specific conditions needed for macrophyte community composition (e.g. exposure, nutrients, light availability through water depth).
Abiotic variables → functional diversity	E	Filtering of communities through species tolerance to water or sediment chemistry, exposure, flow, temperature, etc.
Macrophytes → functional diversity	F	Macrophytes provide niche space to invertebrates through microhabitats and resources.
Abiotic variables → ecosystem function	G	Nutrients, temperature, pH etc., directly affect levels of function.
Functional diversity → ecosystem function	H	Trait presence (richness) and dominance (evenness) in a habitat impacts decomposition and primary productivity.

TABLE 3 Variable reduction with principal component analysis (PCA) for abiotic input in structural equation models (SEMs)

Measured variable		PC1	PC2	PC3
	Eigenvalue	5.67	4.12	2.62
	% variation	19.89	14.47	9.21
	Eigenvector			
Temperature	Coefficient of variation	0.012	0.119	−0.508
	Maximum temperature	0.305	−0.535	0.390
	Minimum temperature	−0.426	0.549	−0.009
	Median diurnal range	−0.171	0.242	0.464
Hydrology	Base flow index	−0.053	0.389	−0.140
	Low pulse duration	0.187	−0.375	0.413
	High pulse duration	−0.002	0.183	−0.656
Water chemistry	Alkalinity	−0.079	0.740	−0.062
	Aluminium	0.096	−0.169	0.153
	Barium	−0.575	−0.001	0.440
	Boron	0.479	0.197	0.051
	Copper	0.629	0.037	0.100
	Manganese	0.559	−0.214	0.043
	Molybdenum	−0.055	0.620	0.135
	Total dissolved nitrogen	0.768	−0.337	−0.304
	Total phosphorus	0.642	−0.200	0.140
	Potassium	0.450	0.202	−0.047
	Sodium	−0.275	0.699	0.142
Sediment chemistry	Total organic carbon	0.367	−0.017	−0.598
	Aluminium	0.682	−0.140	0.044
	Boron	0.414	0.590	−0.052
	Iron	0.557	0.232	0.345
	Lead	0.027	0.124	−0.486
	Magnesium	0.396	0.693	0.335
	Manganese	0.336	0.010	0.335
	Molybdenum	0.790	−0.021	−0.126
	Potassium	0.691	0.392	0.028
	Zinc	0.461	0.527	0.048
Sediment composition	% Silt	0.310	0.247	0.177

provides more detailed information than the SEM, providing specific responses of key taxa and traits. This analysis allows assessment of whether ecosystem function and environmental filters show similar relationships with traits, and the taxa that express those traits.

3 | RESULTS

3.1 | DNA metabarcoding of wetland macroinvertebrates

The GLM complex is rich in aquatic invertebrate life with DNA metabarcoding identifying a total of 157 genera from 86 families across the wetlands; of those, 120 genera were from within Class Insecta. Distribution in the study area varied, with site richness ranging from 3 to 63 taxa per site (mean = 30.9, SD = 11.93). Two genera, *Amnicola* (a freshwater snail from the family Amnicolidae) and *Sida* (a water flea from the suborder Cladocera) were present at all sampled sites. Individual taxa were found at a mean of 11.81 (SD = 14.00) sites, with 77 taxa found at less than 10% of sampled sites. A total of 20 unique zooplankton and 30 Chironomidae genera were identified throughout the study area, a detection notable in that these taxa are generally difficult to identify from morphology alone.

3.2 | Relationships between environmental filters, biotic components and ecosystem function: SEMs

To gain insights into the factors that influenced this wetland diversity, an SEM was used to examine biotic components, the physical habitat and disturbance, and ecosystem function within the wetland complex (Figure 3; see Table 4 for the p-values and standardized regression weights of associated significant pathways; results of all
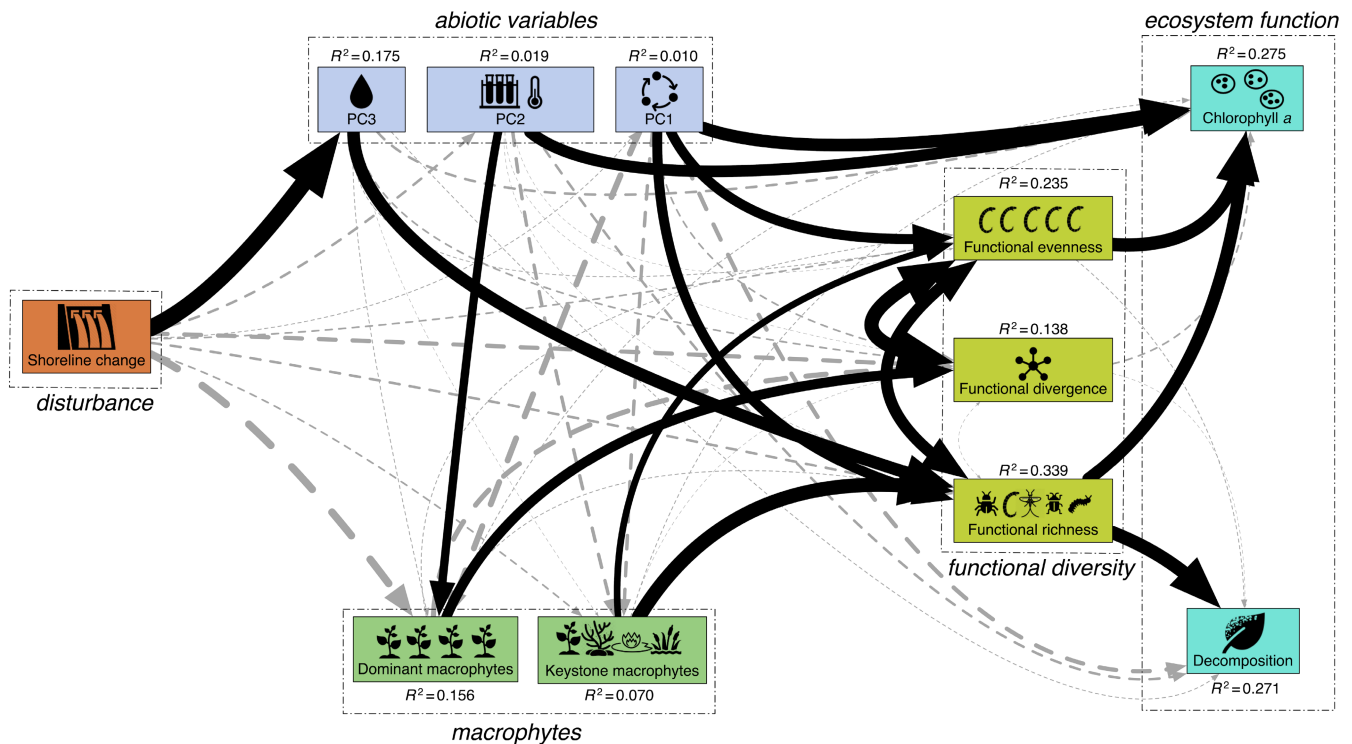
FIGURE 3 Structural equation model (SEM) assessing the role of different aspects of invertebrate functional diversity in floodplain wetland ecosystem structure. Significant paths are shown as black, solid lines, with line weights corresponding to standardized regression weights (*r*; see Table 4 for estimates of the significant pathways). R^2 values indicate the percent variation in a dataset that is explained by the correlative variables.

TABLE 4 Significant pathways from structural equation models (SEMs), corresponding to Figure 3. For statistically non-significant pathways, please refer to supplementary material (S6)

Pathway		Response	*r*	*p*[a]
Shoreline change	→	Abiotic PC3	−0.418	***
Abiotic PC2	→	Dominant macrophytes	0.252	0.035
Abiotic PC1	→	Functional evenness	−0.275	0.020
Keystone macrophytes	→	Functional evenness	0.237	0.043
Abiotic PC1	→	Functional richness	0.274	0.012
Abiotic PC3	→	Functional richness	−0.307	0.009
Diverse macrophytes	→	Functional richness	−0.335	0.002
Dominant macrophytes	→	Functional divergence	−0.273	0.036
Functional richness	→	Decomposition	−0.311	0.021
Abiotic PC2	→	Chlorophyll *a*	−0.289	0.013
Abiotic PC1	→	Chlorophyll *a*	0.302	0.016
Functional richness	→	Chlorophyll *a*	0.295	0.036
Functional evenness	→	Chlorophyll *a*	0.314	0.024
Functional evenness	←→	Functional richness	−0.295	0.028
Function evenness	←→	Functional divergence	−0.332	0.014

Note: *r* values are the standardized regression weights and indicate the strength and direction of the relationship.

[a]*p* values listed as *** are significant at *p* < 0.001.

pathways, including statistically non-significant ones, are provided in supplementary S6).

The strongest link in the model associated shoreline change with changes to abiotic PC3, namely showing a shift toward decreased low pulse duration and diurnal temperature range (positive PC3 values), and increased temperature coefficient of variation, high pulse duration and total organic carbon content of the sediment (negative PC3 values; Table 4).

Macrophytes clearly separated on two principal coordinate axes. PCo1 was associated with species which were common, but when present at a site tended to be associated with higher richness [e.g. *Brasenia schreberi* J.F. Gmel, *Pontederia chordata* L., *Nuphar lutea* L.(Sm.) and as such is labelled as *Keystone Macrophytes* in the models]. PCo2 was associated with emergent and submerged species that, when present, tended to dominate the site with high percent cover (e.g. *Myriophyllum heterophyllum* Michx., *Equisetum fluviatile* L.) and so is denoted as *Dominant Macrophytes*. The abiotic PC2 axis was significant in driving the community structure of macrophytes that were dominant forming (*Dominant Macrophytes*), with scores indicating higher concentrations of metals associated with the species. Total explained variation for both axes was low, however, at 22.6% (Figure 3).

Macrophyte community structure, in turn, had an impact on all three macroinvertebrate functional diversity metrics, with sites associated with higher macrophyte diversity (associated with keystone species) having lower evenness and higher richness, while sites being dominated by a few species were associated with lower evenness and divergence (Figure 3). All three metrics were associated with

each other; divergence and evenness were negatively associated, as were evenness and richness (Table 3).

In terms of function, the model showed that primary production ($R^2 = 0.28$), estimated from chlorophyll-*a* levels as a proxy for standing biomass levels, was driven by functional evenness (i.e. evenness was positively associated with chlorophyll-*a* content), functional richness (positive association), nutrients (positive association), metals (negative association) and temperature (positive association), as associated with principal component axes (Table 3). Decomposition rate was not affected by any variable in the model except functional richness (accounting for 27.1% of the variation), with higher decomposition rates found at lower levels of functional richness (Figure 3).

3.3 | Taxa and trait indicators: TITAN2

The SEM analyses found linkages between traits and both abiotic PC1 and decomposition rates. Extending this analysis, TITAN2 used

to identify pure and reliable taxon (Figure 4) or trait (Figure 5) responses to change along the previously established gradients of abiotic and functional change. For taxa indicators, 10.67% (10 negative and 1 positive responders) were significant indicators of change in decomposition rate, compared with 12.62% (all positive responders) along PC1 (Figure 4). Two taxa, *Hyalella*, and *Oecetis* were significant indicators for both gradients and were both positive indicators (more prevalent along the increasing gradient) for PC1 and negative responders to decomposition rate (Figure 4).

Trait modalities were better indicators of change along abiotic and functional gradients, with more pure and reliable indicators (20.90% of trait modalities for abiotic PC1, consisting of 8 negative and 6 positive responders, and 35.82% for decomposition with 16 negative and 8 positive responders; Figure 5). Again, for traits, several modalities were found to be inverse indicators of PC1 and decomposition rate. Trait modalities that were found to be significant positive indicators of nutrient change and negative indicators for changes along decomposition gradients were as follows:
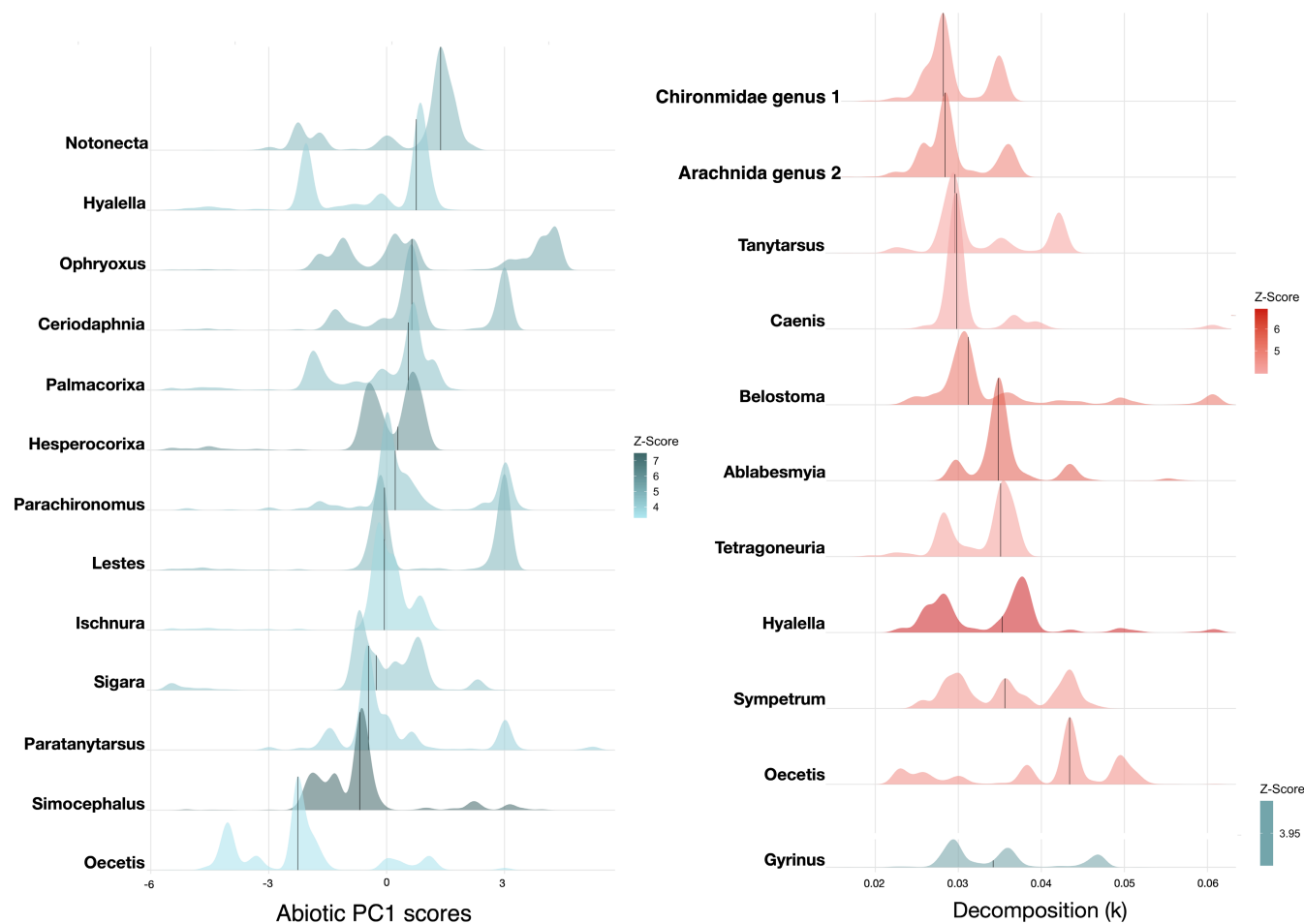

FIGURE 4 Individual response plots from Threshold Indicator Taxa ANalysis (TITAN2) comparing the response taxa modalities to changes in environmental gradients, represented by the PC1 axis, and ecosystem function, represented by decomposition. Taxa that responded positively to the gradient are shown in blue, while negative responders are shown with red. Taxa change points (across 999 bootstrapped replicates) are visualized as a probability density function with colour intensity scaled according to the magnitude of the response (i.e. its standardized *z*-score). Two taxa could not be assigned to a specific genus name, but could be associated with a lineage, and are assigned 'Chironomidae Genus 1' and 'Arachnida Genus 2', respectively, based on sequence similarity (see S1 for more details).
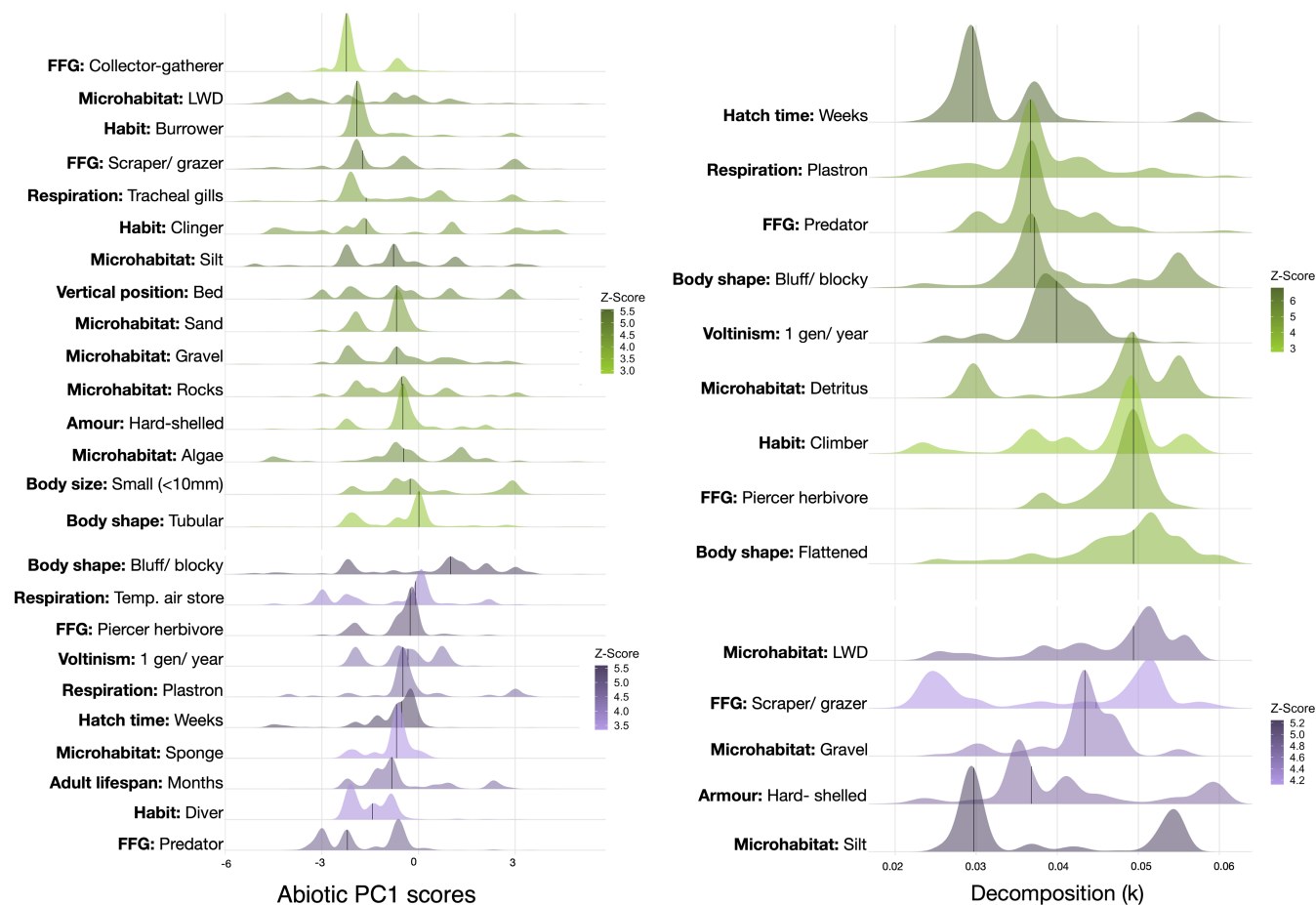
FIGURE 5 Individual response plots from Threshold Indicator Taxa ANalysis (TITAN2) comparing the response trait modalities to changes in environmental gradients, represented by the PC axis most aligned with nutrients and ecosystem function, represented by decomposition. Trait modalities that responded positively to the gradient are shown in purple, while negative responders are shown with green. Trait change points (across 999 bootstrapped replicates) are visualized as probability density functions with colour intensity scaled according to the magnitude of the response (i.e. its standardized z-score).

respiration—plastron; hatch time—weeks; body shape—bluff/blocky; voltinism—1 generation per year and feeding mode—predator. Modalities that were significant indicators for both the abiotic PC1 axis (negative) and decomposition rate (positive) were as follows: microhabitat—silt; microhabitat—large woody debris; microhabitat—gravel; feeding mode—scraper/grazer and armour—hard-shelled.

4 | DISCUSSION

4.1 | The influence of disturbance on floodplain ecosystems

Flood pulses are habitat-shaping forces within floodplain wetlands, creating oxbows, swales, levees and backwaters in their erosion and deposition of sediment, and influencing productivity by replenishing adjacent wetlands with nutrients from the main river channel (Tockner et al., 2010). Local habitat diversity of wetland patches is thus driven by flood pulse dynamics and any alteration can influence the assemblage of organisms that live there (e.g. Bayley &

Guimond, 2008). Using structural equation modelling, this study provides evidence that changes to flood pulse events in the Wolastoq | Saint John River, as seen from changes in wetland extent from 1951 to 2014, have influenced local site hydrology, leading to increased inundation during summer high flows, elevated temperature variation and increased organic carbon content of the sediment. Local-scale hydrologic variables were linked to changes in the functional richness of the aquatic invertebrate community; shoreline change may also have influenced the magnitude of this relationship, given its connection to local hydrology variables during the open water season.

The subset models made with collapsed abiotic variables (S7) did not support this link between current hydrologic metrics and historic shoreline change; however, this is not surprising as the hydrology variables that were included in the abiotic composite variable were represented most strongly on PC3, and thus likely had less weight than nutrient and temperature variables. Given the degree of complexity in floodplain ecosystems, the authors believe that utilizing the novel, highly detailed dataset to its full advantage outweighs the risk of overspecification. Nevertheless, we advisee caution in interpreting potential causal linkages. SEMs are especially useful tools in

complex environments, such as floodplain wetlands, where they can be used to examine links between flood pulse changes, fine scale (site level) hydrology and diversity, as echoed by Bino et al. (2017).

How, exactly, could habitat change indirectly increase functional diversity? We see two potential mechanistic explanations. First, as wetted meadow area shrinks, terrestrial vegetation gives way to macrophyte beds and open water (e.g. Frieswyk & Zedler, 2007), opening up habitat for more aquatic invertebrate species. The frequency and magnitude of large floods has increased over the last century, along with the likelihood that ice jam events have been altered due to increasing structures within the watershed (Canadian Rivers Institute, 2011). This has resulted in increased disturbance to habitat patches within the floodplain, potentially shifting invertebrate community dynamics from being competition driven to disturbance driven (sensu Connell, 1978; Ward et al., 1999). Our results broadly align with the conceptual model put forward by Arias et al. (2018) that combines the intermediate disturbance hypothesis (IDH; Connell, 1978) and the flood pulse concept (FPC; Junk et al., 1989) to predict how species colonize vacated niche space, shaping diversity within a spatial landscape of flooding and disturbance regimes. IDH predicts that species diversity is maximized when disturbances are neither rare nor frequent, while FPC explains how periodic inundation and drying control lateral exchange of nutrients and biodiversity between rivers and their connected floodplains. Together, these concepts predict that the flood regime controls pulses of nutrients and biotic to wetlands where species diversity peaks at intermediate stages along the natural disturbance gradient (Arias et al., 2018). Relatedly, work by Wright et al. (2015) suggests that there is a trade-off between stability and productivity under extreme disturbances, and that these relationships are mediated by community diversity.

In a previous paper focusing on disturbance regimes in the Wolastoq | Saint John River (Rideout et al., 2021), we identified connectivity and hydrology as the driving forces in the formation of floodplain wetland habitat patches, influencing shoreline change, temperature variation, nutrient and metal retention, macrophyte growth, and carbon storage. Our analysis described above has shown that habitat characteristics filter invertebrate traits, shaping the local community. The resulting community subsequently possessed traits that influenced ecosystem function. Sheltered habitats with low connectivity showed higher levels of nutrients and niche diversity, as well as significant carbon stores (Rideout et al., 2021). This resulted in reduced dependency on allochthonous carbon inputs and increased functional evenness of the invertebrate community. Habitats that were highly connected and exposed had high disturbance and low habitat heterogeneity (Rideout et al., 2021). Those habitats were dominated by generalists such as amphipods, which were associated with allochthonous carbon inputs, resulting in overall reductions in diversity and functional richness. These results are consistent with Ward et al. (1999), who stated that biodiversity within floodplains will be highest at intermediate levels of both disturbance and connectivity.

The floodplain wetlands of the Platte River show similar diversity patterns, where hydrologic regimes were key factors in shaping macroinvertebrate community structure; however, in this system, hydrology gradients were linked to community composition of vertebrate predators, like fish (Whiles & Goldowitz, 2005). Indeed, the increase in flooded aquatic wetland area also opens up habitat space for fish, which is a second mechanism that could explain how habitat change could influence functional diversity, as predators can structure invertebrate communities in a variety of other ecosystems (e.g. Diehl, 1992; Sarda et al., 1998). Our study did not include vertebrate predators, as it was assumed that their impact did not vary significantly across the study area because all sites were open and connected. This assumption, however, cannot be confirmed; thus, predator presence may be a key component of unexplained variation within the ecosystem. An increase in functional richness supports communities with multiple avoidance strategies to limit predation, as well as providing functional redundancy so that ecosystem functions can be maintained even if one group is susceptible to external disturbances (e.g. predation).

4.2 | Macrophytes as facilitators of invertebrate community structure

In this study, macrophyte community structure appeared to be an important driver of the local invertebrate community, influencing functional diversity. Functional richness increased with macrophyte diversity, tied strongly to keystone species that were associated with dense patches of submerged macrophytes. The GLM complex exhibited high richness of aquatic plants; there were a total of 37 submerged and 15 emergent macrophyte species found in the study area (note, several species ended up being counted in both emergent and submerged surveys because of growth-stage variability). The posited link between higher macrophyte diversity and invertebrate functional richness is consistent with the idea that species-rich macrophyte beds can provide a greater variety of habitat niches, and also suggest that macrophyte species-rich areas are likely to have greater niche overlap or redundancy, influencing their stability in terms of being able to continue providing vital ecosystem functions in the face of disturbances.

Despite their increased functional richness, however, the invertebrate communities that were associated with greater macrophyte diversity also showed reduced functional evenness within the invertebrate community. More taxa with a given trait modality were present in these macrophyte dominated sites, in contrast to more barren, exposed sites, where a different set of traits may be necessary to exploit the few niche spaces available. In these exposed sites, reduced habitat availability increases disturbance (e.g. via reduced physical attenuation of wave action) resulting in habitats where only a few species with select traits can thrive, contrasting to protective macrophyte beds where many species that are scrapers/grazers, climbers and plant miners can coexist. Indeed, when examining abundance and richness of macroinvertebrate taxa across different macrophyte communities, Walker et al. (2013) found that when macrophyte spatial complexity was high (e.g. *Elodea* and *Ceratophyllum* beds), total biomass and abundance of individuals was high but relatively few taxa dominated the samples, thus resulting in low evenness. Open

water sites, that is, those with no macrophytes, had the lowest richness and abundance as few macroinvertebrate taxa are specialized in pelagic feeding, except for zooplankton, which are subject to predation in open-water areas (Walker et al., 2013).

4.3 | Macroinvertebrate taxon richness and ecosystem functioning

Shredder taxa were expected to respond positively along decomposition gradients, as, by definition, they feed on and break down vascular plant tissue, including leaf litter (Cummins et al., 1989); however, the only positively responding indicator taxon was a predatory beetle (*Gyrinus*). Results from TITAN2 showed that all shredders responded negatively at different points along the decomposition gradient, likely indicating that decomposition is dominated by several species that replace each other as they compete for food. This replacement suggests functional redundancy within the shredder functional group. Results from these shredders, coupled with the negative response at the high end of the gradient of invertebrates with the 'Detritus' microhabitat, also support the idea that rapidly decomposing leaf litter does not stay in the system long enough for most shredders to utilize it (see Siders et al., 2018; and Compson et al., 2015, 2018 for examples in lotic systems); rather, element fluxes from rapidly decomposing leaf litter are expected to enter the microscopic food web (reviewed in Marks, 2019). The microbial component of leaf decomposition is likely even more important than invertebrate shredders in wetland systems, which are often warmer and have even higher rates of litter decomposition (Conner & Day, 1991; Poi de Neiff et al., 2006). The amphipod *Hyalella* had the highest range along the decomposition gradient and in preliminary sampling for morphology and abundance the previous year was found to dominate the samples in which it was present (unpublished data). Taken in accordance with SEM results, which show that decomposition decreased with increasing functional richness, this suggests that several prevalent species are likely responsible for the majority of invertebrate-mediated decomposition, outcompeting other functional groups. These results align with those of Winfree et al. (2015), who found that in local-scale studies, ecosystem function was driven by abundance of common species rather than species richness. In a follow-up study, looking at a larger, regional scale, Winfree et al. (2018) found that species turnover promotes the importance of diversity on a function. This would be consistent with what we observed in our study system, where we incorporated results from a larger, regional scale in a greater diversity of habitat types across the wider riverscape.

While decomposition was associated with negatively responding taxa, abiotic PC1 scores were only associated with positive responders. Notably, several predators responded positively to increased nutrients associated with this axis. More productive ecosystems can support a greater number and richness of predators (e.g. Malmqvist, 2002), suggesting that in the Grand Lake Meadows and Portobello Creek wetlands, increases in nutrients like nitrogen and phosphorus can be associated with apparent increases in ecosystem health indicators such as taxonomic and functional richness. Floodplains tend to be

phosphorus limited and nitrogen limited and are dependent on flood pulses to replenish these nutrients into the wetlands from the main channel, which increased algal and macrophyte productivity and support macrophyte communities (Junk et al., 1989). Our SEM analysis indicated that higher levels of nutrients were positively associated with functional richness. This suggests that wetland sites with higher nutrients support higher functional redundancy and, despite having lower local levels of decomposition, are more stable in their ability to maintain functional roles in the face of disturbance.

The inverse relationship between nutrients and decomposition is supported by the observation that multiple taxa and trait modalities were inverse indicators of decomposition and PC1. Most notable in this inverse relationship were (a) predators, which positively respond to increased nutrients, (b) microhabitat modalities associated with silt and large woody debris, which are positive indicators of decomposition and (c) scrapers and grazers, which are positive indicators of decomposition. Again, this indicates that in wetlands, healthy (sensu Constanza & Mageau, 1999) and productive sites are those with high nutrients, algal production and dense macrophyte beds, and that these sites are those associated with high invertebrate functional richness. Primary productivity, as assessed by proxy through chlorophyll-*a* content of periphyton on planted tiles, increased with increasing nutrients, as well as with functional evenness. In functionally even communities, resources are used more efficiently with no single trait modality dominating the community, which could, for example, lead to increased algal standing biomass through predatory release or competition (e.g. Rober et al., 2022). It is worth remembering, however, that chlorophyll-*a* is a static estimate of periphyton standing crop and does not necessarily reflect instantaneous primary productivity at a site; for example, a site could be highly productive, with high algal turnover due to invertebrate grazing and so have a relatively low chlorophyll-*a* value.

5 | CONCLUSION: TRAIT-BASED METRICS FOR BIOMONITORING

Employing DNA metabarcoding to provide a consistent snapshot of trait modalities revealed a more complete picture of invertebrate community composition than provided by traditional microscope-based observations (e.g. Gibson et al., 2015). This is important to highlight, as incomplete observational coverage has until now been a significant limitation for traits analysis. One drawback with DNA-based biodiversity data is that information is in the form of presence/absence, so despite knowing how many taxa hold a certain trait in a community, we are limited in that we do not know the dominance of that trait in terms of the actual abundance or biomass at each site (Elbrecht & Leese, 2015; Fonseca, 2018). In future, we would recommend employing a combination of quantitative sampling with DNA metabarcoding, where this is practical, to provide a more complete pattern of traits occurrence, while still supporting quantitative analysis of traits within key assemblages.

Healthy ecosystems—those which maximize ecosystem function and resilience (Constanza & Mageau, 1999)—can achieve stability

through balancing efficiency and completeness of resource use with functional redundancy. By providing information about the efficiency of resource use within an ecosystem and the amount of competition present, functional divergence is a potent indicator of ecosystem health; in our system, however, without abundance information, our measure of functional divergence lacks power (Villéger et al., 2008). Yet, even in the absence of functional divergence information, measures of high functional richness and evenness can indicate healthy ecosystems. Communities that show high functional richness can be resilient under environmental fluctuations, since the taxa with traits necessary to take advantage of new conditions are more likely to be present (Mason et al., 2005). Comparatively, functionally even communities are efficiently utilizing the entire range of the ecosystem's resources, reducing the opportunity for foreign invaders to occupy niche space (Mason et al., 2005). In disturbance-dominated systems, such as river floodplains, the ability to respond to and to buffer against, environmental fluctuations enable communities to support and sustain the vital ecosystem functions provided to society by floodplains and their associated wetlands.

AUTHOR CONTRIBUTIONS

ACKNOWLEDGEMENTS

CONFLICT OF INTEREST

DATA AVAILABILITY STATEMENT

ORCID

Natalie K. Rideout https://orcid.org/0000-0001-8906-4358
Zacchaeus G. Compson https://orcid.org/0000-0003-2015-3015
Wendy A. Monk https://orcid.org/0000-0001-9031-5433
Mehrdad Hajibabaei https://orcid.org/0000-0002-8859-7977
Teresita M. Porter https://orcid.org/0000-0002-0227-6874
Michael T. G. Wright https://orcid.org/0000-0002-9594-7226
Donald J. Baird https://orcid.org/0000-0003-4653-7906

REFERENCES

Arias, M. E., Wittmann, F., Parolin, P., Murray-Hudson, M., & Cochrane, T. A. (2018). Interactions between flooding and upland disturbance drives species diversity in large river floodplains. *Hydrobiologia*, *814*, 5–17. https://doi.org/10.1007/s10750-016-2664-3

Baird, D. J., Baker, C. J. O., Brua, R. B., Hajibabaei, M., McNicol, K., Pascoe, T. J., & de Zwart, D. (2011). Toward a knowledge infrastructure for traits-based ecological risk assessment. *Integrated Environmental Assessment and Management*, *7*(2), 209–215. https://doi.org/10.1002/ieam.129

Baird, D. J., Rubach, M. N., & Van Den Brink, P. J. (2008). Trait-based ecological risk assessment (TERA): The new frontier? *Integrated Environmental Assessment and Management*, *4*(1), 2–3. https://doi.org/10.1897/IEAM_2007-063.1

Baker, M. E., & King, R. S. (2010). A new method for detecting and interpreting biodiversity and ecological community thresholds. *Methods in Ecology and Evolution*, *1*(1), 25–37. https://doi.org/10.1111/j.2041-210X.2009.00007.x

Baker, M. E., King, R. S., & Kahle, D. (2015). *TITAN2: Threshold indicator taxa analysis*. R package version 2.1. https://cran.r-project.org/package=TITAN2

Bayley, S. E., & Guimond, J. K. (2008). Effects of river connectivity on marsh vegetation community structure and species richness in montane floodplain wetlands in Jasper National

Park, Alberta, Canada. *Écoscience*, *15*, 377–388. https://doi.org/10.2980/15-3-3084

Benfield, E. F. (2007). Decomposition of leaf litter. In F. R. Hauer & G. A. Lamberti (Eds.), *Methods in stream ecology* (2nd ed., pp. 711–720). Academic Press.

Bino, G., Wassens, S., Kingsford, R. T., Thomas, R. F., & Spencer, J. (2017). Floodplain ecosystem dynamics under extreme dry and wet phases in semi-arid Australia. *Freshwater Biology*, *63*(2), 224–241. https://doi.org/10.1111/fwb.13056

Bonada, N., Dolédec, S., & Statzner, B. (2007). Taxonomic and biological trait differences of stream macroinvertebrate communities between Mediterranean and temperate regions: Implications for future climatic scenarios. *Global Change Biology*, *13*, 1658–1671. https://doi.org/10.1111/j.1365-2486.2007.01375.x

Bush, A., Compson, Z. G., Monk, W. A., Porter, T. M., Steeves, R., Emilson, E., Gagne, N., Hajibabaei, M., Roy, M., & Baird, D. J. (2019). Studying ecosystems with DNA metabarcoding: Lessons from biomonitoring of aquatic macroinvertebrates. *Frontiers in Ecology and Evolution*, *7*, 424. https://doi.org/10.3389/fevo.2019.00434

Canadian Rivers Institute (2011). The Saint John River: A state of the environment report. In S. D. Kidd, R. A. Curry, & K. R. Munkittrick (Eds.). Canadian Rivers Institute.

Compson, Z. G., Hungate, B. A., Koch, G. W., Hart, S. C., Maestas, J. M., Adams, K. J., Whitham, T. G., & Marks, J. C. (2015). Closely related tree species differentially influence the transfer of carbon and nitrogen from leaf litter up the aquatic food web. *Ecosystems*, *18*(2), 186–201. https://doi.org/10.1007/s10021-014-9821-1

Compson, Z. G., Hungate, B. A., Whitham, T. G., Koch, G. W., Dijkstra, P., Siders, A. C., Wojtowicz, T., Jacobs, R., Rakestraw, D. N., Allred, K. E., Sayer, C. K., & Marks, J. C. (2018). Linking tree genetics and stream consumers: Isotopic tracers elucidate controls on carbon and nitrogen assimilation. *Ecology*, *99*(8), 1759–1770. https://doi.org/10.1002/ecy.2224

Connell, J. H. (1978). Diversity in tropical rain forests and coral reefs. *Science*, *199*(4335), 1302–1310. https://www.jstor.org/stable/1745369

Conner, W. H., & Day, J. W. (1991). Leaf litter decomposition in three Louisiana freshwater forested wetland areas with different flooding regimes. *Wetlands*, *11*(2), 303–312.

Constanza, R., & Mageau, M. (1999). What is a healthy ecosystem? *Aquatic Ecology*, *33*, 105–115. https://doi.org/10.1023/A:1009930313242

Cummins, K. W., Wilzbach, M. A., Gates, D. M., Perry, J. B., & Taliaferro, W. B. (1989). Shredders and riparian vegetation. *Bioscience*, *39*(1), 24–30. https://doi.org/10.2307/1310804

Díaz, S., & Cabido, M. (2001). Vive la différence: Plant functional diversity matters to ecosystem processes. *Trends in Ecology & Evolution*, *16*(11), 646–655. https://doi.org/10.1016/S0169-5347(01)02283-2

Díaz, S., Purvis, A., Cornelissen, J. H. C., Mace, G. M., Donoghue, M. J., Ewers, R. M., Jordano, P., & Pearse, W. D. (2013). Functional traits, the phylogeny of function, and ecosystem service vulnerability. *Ecology and Evolution*, *3*(9), 2958–2975. https://doi.org/10.1002/ece3.601

Diehl, S. (1992). Fish predation and benthic community structure: The role of omnivory and habitat complexity. *Ecology*, *73*(5), 1646–1661. https://doi.org/10.2307/1940017

Elbrecht, V., & Leese, F. (2015). Can DNA-based ecosystem assessments quantify species abundance? Testing primer bias and biomass-sequence relationships with an innovative metabarcoding protocol. *PLoS ONE*, *10*(7), e0130324. https://doi.org/10.1371/journal.pone.0130324

Environment and Climate Change Canada. (2018). *Cabin wetland macroinvertebrate protocol*. Government of Canada. https://publications.gc.ca/collections/collection_2018/eccc/CW66-571-2018-eng.pdf

Environmental Systems Research Institute (ESRI). (2018). *ArcGIS Desktop: Release 10.6.1*.

Fonseca, V. G. (2018). Pitfalls in relative abundance estimation using eDNA metabarcoding. *Molecular Ecology Resources*, *18*, 923–926. https://doi.org/10.1111/1755-0998.12902

Frieswyk, C. B., & Zedler, J. B. (2007). Vegetation change in Great Lakes coastal wetlands: Deviation from the historical cycle. *Journal of Great Lakes Research*, *33*(2), 366–380. https://doi.org/10.3394/0380-1330(2007)33[366:VCIGLC]2.0.CO;2

Funk, A., Trauner, D., Reckendorfer, W., & Hein, T. (2017). The benthic invertebrates floodplain index – Extending the assessment approach. *Ecological Indicators*, *79*, 303–309. https://doi.org/10.1016/j.ecolind.2017.04.035

Gibson, J. F., Shokralla, S., Curry, C., Baird, D. J., Monk, W. A., King, I., & Hajibabaei, M. (2015). Large-scale biomonitoring of remote and threatened ecosystems via high-throughput sequencing. *PLoS ONE*, *10*(10), 1–15. https://doi.org/10.1371/journal.pone.0138432

Grace, J. B., Anderson, M., Olff, H., & Scheiner, S. M. (2010). On the specification of structural equation models for ecological systems. *Ecological Monographs*, *80*(1), 67–87. https://doi.org/10.1890/07-1861.1

Hajibabaei, M., Porter, T. M., Robinson, C. V., Baird, D. J., Shokralla, S., & Wright, M. (2019). Watered-down biodiversity? A comparison of metabarcoding results from DNA extracted from matched water and bulk tissue biomonitoring samples. *PLoS ONE*, *14*(12), e0225409. https://doi.org/10.1371/journal.pone.0225409

Hooper, D. U., Solan, M., Symstad, A., Díaz, S., Gessner, M. O., Buchmann, N., Degrange, V., Grime, P., Hulot, F., Mermillod-Blondin, F., Roy, J., Spehn, E., & van Peer, L. (2002). Species diversity, functional diversity, and ecosystem functioning. In M. Loreau, S. Naeem, & P. Inchausti (Eds.), *Biodiversity and ecosystem functioning: Synthesis and perspectives* (pp. 195–208). Oxford University Press.

Junk, W. J., Bayley, P. B., & Sparks, R. E. (1989). The flood pulse concept in river-floodplain systems. *Canadian Journal of Fisheries and Aquatic Sciences*, *106*, 110–127. http://www.dfo-mpo.gc.ca/Library/111846.pdf

Laliberté, E., Legendre, P., & Shipley, B. (2014). FD: Measuring functional diversity from multiple traits, and other tools for functional ecology. R package version 1.0-12. https://cran.r-project.org/web/packages/FD/index.html

Langhans, S. D., Tiegs, S. D., Uehlinger, U., & Tockner, K. (2006). Environmental heterogeneity controls organic-matter dynamics in river-floodplain ecosystems. *Polish Journal of Ecology*, *54*(4), 675–680.

Lê, S., Josse, J., & Husson, F. (2008). FactoMineR: An R package for multivariate analysis. *Journal of Statistical Software*, *25*(1), 1–18. https://doi.org/10.18637/jss.v025.i01

Loreau, M., Downing, A., Emmerson, M., Gonzalez, A., Hughes, J., Inchausti, P., Joshi, J., Norberg, J., & Sala, O. (2002). A new look at the relationship between diversity and stability. In M. Loreau, S. Naeem, & P. Inchausti (Eds.), *Biodiversity and ecosystem functioning: Synthesis and perspectives* (pp. 79–91). Oxford University Press.

Malmqvist, B. (2002). Aquatic invertebrates in riverine landscapes. *Freshwater Biology*, *47*(4), 679–694. https://doi.org/10.1046/j.1365-2427.2002.00895.x

Marks, J. C. (2019). Revisiting the fates of dead leaves that fall into streams. *Annual Review of Ecology, Evolution, and Systematics*, *50*(1), 547–568. https://doi.org/10.1146/annurev-ecolsys-110218-024755

Mason, N. W. H., Mouillot, D., Lee, W. G., & Wilson, J. B. (2005). Functional richness, functional evenness and functional divergence: The primary components of functional diversity. *Oikos*, *111*, 112–118. https://doi.org/10.1111/j.0030-1299.2005.13886.x

Maureaud, A., Anderson, K. H., Zhang, L., & Lindegren, M. (2020). Trait-based food web model reveals the underlying mechanisms of biodiversity-ecosystem function relationships. *Journal of Animal Ecology*, *89*, 1497–1510.

McCormick, P. V., & Stevenson, R. J. (1998). Periphyton as a tool for ecological assessment and management in the Florida Everglades. *Journal of Phycology*, *32*, 726–733. https://doi.org/10.1046/j.1529-8817.1998.340726.x

Oksanen, J., Blanchet, F. G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P. R., O'Hara, R. B., Simpson, G. L., Solymos, P., Stevens,

H. H., Szoecs, E., & Wagner, H. (2019). *Vegan: Community ecology package*. R package version 2.5-4. https://CRAN.R-project.org/package=vegan

Pacala, S., & Kinzig, A. P. (2002). Introduction to theory and the common ecosystem model. In A. P. Kinzig, S. W. Pacala, & D. Tilman (Eds.), *The functional consequences of biodiversity: Empirical processes and theoretical extensions* (pp. 169–174). Princeton University Press.

Poi de Neiff, A., Neiff, J. J., & Casco, S. L. (2006). Leaf litter decomposition in three wetland types of the Paraná River floodplain. *Wetlands*, *26*, 558–566. https://doi.org/10.1672/0277-5212(2006)26[558:LLDITW]2.0.CO;2

Porter, T. M., & Hajibabaei, M. (2018). Automated high throughput animal CO1 metabarcode classification. *Scientific Reports*, *8*, 4226. https://doi.org/10.1038/s41598-018-22505-4

R Core Team. (2019). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. https://www.r-project.org

Richter, B. D., Baumgartner, J. V., Powell, J., & Braun, D. P. (1996). A method for assessing hydrologic alteration within ecosystems. *Conservation Biology*, *10*(4), 1163–1174. https://doi.org/10.1046/j.1523-1739.1996.10041163.x

Rideout, N. K. (2020). nata1iekat/GLM_invertebrate_traits_v1:GLM_invertebrate_traits_v1 (version v1.0.0). *Zenodo*, https://doi.org/10.5281/zenodo.3948516

Rideout, N. K., Compson, Z. G., Monk, W. A., Bruce, M. R., & Baird, D. J. (2021). The beautiful and the dammed: Defining multi-stressor disturbance regimes in an Atlantic river floodplain wetland. *Frontiers in Ecology and Evolution*, *9*, 550394. https://doi.org/10.3389/fevo.2021.553094

Rideout, N. K., Compson, Z. G., Monk, W. A., Bruce, M. R., Hajibabaei, M., Wright, M. T. G., & Baird, D. J. (2022). Data from: Environmental filtering of macroinvertebrate traits influences ecosystem functioning in a large river floodplain, Dryad, Dataset. https://doi.org/10.5061/dryad.xksn02vcm

Rober, A. R., McCann, K. S., Turetsky, M. R., & Wyatt, K. H. (2022). Cascading effects of predators on algal size structure. *Journal of Phycology*, *58*, 308–317. https://doi.org/10.1111/jpy.13235

Rosenfeld, J. S. (2002). Functional redundancy in ecology and conservation. *Oikos*, *98*(1), 156–162. https://doi.org/10.1034/j.1600-0706.2002.980116.x

Rosseel, Y. (2012). Lavaan: An R package for structural equation modeling. *Journal of Statistical Software*, *48*(2), 1–36. http://www.jstatsoft.org/v48/i02/

Sarda, R., Foreman, K., Werme, C. E., & Valiela, I. (1998). The impacts of epifaunal predation on the structure of macroinfaunal invertebrate communities of tidal saltmarsh creeks. *Estuarine, Coastal and Shelf Science*, *46*, 657–669. https://doi.org/10.1006/ecss.1997.0322

Schmidt-Kloiber, A., & Hering, D. (2015). An online tool that unifies, standardises and codifies more than 20,000 European freshwater organisms and their ecological preferences. *Ecological Indicators*, *53*, 271–282. https://www.freshwaterecology.info, https://doi.org/10.1016/j.ecolind.2015.02.007

Siders, A. C., Compson, Z. G., Hungate, B. A., Dijkstra, P., Koch, G. W., Wymore, A. S., Grandy, A. S., & Marks, J. C. (2018). Litter identify affects assimilation of carbon and nitrogen by a shredding caddisfly. *Ecosphere*, *9*(7), e02340. https://doi.org/10.1002/ecs2.2340

Srivastava, D. S., & Vellend, M. (2005). Biodiversity-ecosystem function research: Is it relevant to conservation? *Annual Review of Ecology, Evolution, and Systematics*, *36*, 267–294. https://doi.org/10.1146/annurev.ecolsys.36.102003.152636

Tilman, D., & Lehman, C. (2001). Biodiversity, composition and ecosystem processes: Theory and concepts. In A. P. Kinzig, S. W. Pacala, & D. Tilman (Eds.), *The functional consequences of biodiversity: Empirical processes and theoretical extensions* (pp. 9–41). Princeton University Press.

Tilman, D., Reich, P. B., & Knops, J. M. H. (2006). Biodiversity and ecosystem stability in a decade-long grassland experiment. *Nature*, *441*(7093), 629–632. https://doi.org/10.1038/nature04742

Tockner, K., Pusch, M., Borchardt, D., & Lorang, M. S. (2010). Multiple stressors in coupled river-floodplain ecosystems. *Freshwater Biology*, *55*, 135–151. https://doi.org/10.1111/j.1365-2427.2009.02371.xR

Trios, C. H., Petchy, O. L., & Tobias, J. A. (2014). Unraveling the interplay of community assembly processes acting on multiple niche axes across spatial scales. *The American Naturalist*, *184*(5), 583–608. https://doi.org/10.1086/678233

Vieira, N. K. M., Poff, N. L., Carlisle, D. M., Moulton, S. R., II, Koski, M., & Kondratieff, B. C. (2006). A database of lotic invertebrate traits for North America. *U.S. Geological Survey Data Series*, *187*. http://pubs.water.usgs.gov/ds187

Villéger, S., Mason, N. W. H., & Mouillot, D. (2008). New multidimensional functional diversity indices for a multifaceted framework in functional ecology. *Ecology*, *89*(8), 2290–2301. https://doi.org/10.1890/07-1206.1

Walker, P. D., Wijnhoven, S., & van der Velde, G. (2013). Macrophyte presence and growth form influence macroinvertebrate community structure. *Aquatic Botany*, *104*, 80–87. https://doi.org/10.1016/j.aquabot.2012.09.003

Ward, J. V., Tockner, K., & Schiemer, F. (1999). Biodiversity of floodplain river ecosystems: Ecotones and connectivity. *Regulated Rivers: Research and Management*, *15*(1–3), 125–139. https://doi.org/10.1002/(SICI)1099-1646(199901/06)15:1/3<125::AID-RRR523>3.0.CO;2-E

Whiles, M. R., & Goldowitz, B. S. (2005). Macroinvertebrate communities in central Platte River wetlands: Patterns across a hydrologic gradient. *Wetlands*, *25*(2), 462–472. https://doi.org/10.1672/20

Winfree, R., Fox, J. W., Williams, N. M., Reilly, J. R., & Cariveau, D. P. (2015). Abundance of common species, not species richness, drives delivery of a real-world ecosystem service. *Ecology Letters*, *18*, 626–635. https://doi.org/10.1111/ele.12424

Winfree, R., Reilly, J. R., Bartomeus, I., Cariveau, D. P., Williams, N. M., & Gibbs, J. (2018). Species turnover promotes importance of bee diversity for crop pollination at regional scales. *Science*, *359*(6377), 791–793. https://doi.org/10.1126/science.aao2117

Wright, A. J., Ebeling, A., de Kroon, H., Roscher, C., Weigelt, A., Buchmann, N., Buchmann, T., Fishcer, C., Hacker, N., Hildebrandt, A., Leimer, S., Mommer, L., Oelmann, Y., Scheu, S., Steinauer, K., Strecker, T., Weisser, W., Wilcke, W., & Eisenhaur, N. (2015). Flooding disturbances increase resource availability and productivity but reduce stability in diverse plant communities. *Nature Communications*, *6*, 6092. https://doi.org/10.1038/ncomms7092

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.