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Jack R. McLachlan

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Strong zonation of benthic communities across a tidal freshwater height gradient

1 Jack R. McLachlan¹  | Jessica M. Haghkerdar^{1,2} | Hamish S. Greig¹

¹School of Biology and Ecology, University of Maine, Orono, Maine, U.S.A.

²Centre for Biological Diversity, Scottish Oceans Institute, University of St Andrews, St Andrews, U.K.

Correspondence

Jack R. McLachlan, School of Biology and Ecology, University of Maine, Orono, ME, U.S.A.

Email: jack.mclachlan@maine.edu

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Abstract

1. Trade-offs associated with environmental gradients generate patterns of diversity and govern community organisation in a landscape. In freshwaters, benthic community structure is driven by trade-offs along generally orthogonal gradients of habitat permanence and predation—where ephemeral systems are physiologically harsh because of drying stress, but inhabitants are less likely to be under the intense predation pressure of more permanent waterbodies. However, in tidal freshwaters, these two stressors are compounding, and the trade-offs associated with them are decoupled.
2. We investigated benthic community structure in a tidal freshwater habitat. These communities experience a suite of conditions atypical for a freshwater habitat: twice-daily drying; and high predation pressure by mobile fishes. We compared benthic communities at three tidal heights (low, mid, high) and contrasted these with nearby non-tidal freshwaters that varied in their hydrology (permanent, temporary).
3. We found that communities were more strongly differentiated in tidal freshwater habitats than between permanent and temporary inland freshwaters, which was surprising given the high interconnectedness and condensed longitudinal scale of tidal habitats. The differentiation of communities in tidal habitats was probably driven by the combined gradients of desiccation risk at low tide and intense predation by fish at high tide—a combination of pressures that are novel for the evolutionary history of the regional freshwater invertebrate fauna.
4. Our study provides evidence that environmental gradients can produce stronger patterns of community zonation than would be predicted for habitats that are spatially contiguous and have little or no dispersal limitation. These results give insight into how communities might respond if drivers of community structure are altered or reorganised from their regional or evolutionary norms.

KEYWORDS

community structure, environmental gradient, tidal freshwater, trade-offs, zonation

1 | INTRODUCTION

A central tenet of community ecology is that species diversity and community organisation are governed by the trade-offs that

species face between gradients of abiotic and biological selection pressures (Kneitel & Chase, 2004; Violle, Pu, & Jiang, 2010). Trade-offs occur when the traits that increase a taxon's fitness along one axis of stress (e.g. herbivory or predation pressure)



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negatively impact fitness along another axis (e.g. shade tolerance or drought resistance) (Lubchenco, 1980; Schiesari, Peacor, & Werner, 2006). Trade-offs promote speciation and maintain diversity patterns along habitat gradients in almost all ecological systems (Connell, 1961; Kraft, Valencia, & Ackerly, 2008; McPeck, 1996), especially those where there is a strong, sustained environmental selection pressure exerted on a community that results in species with specialised functional or life history traits (Stearns, 1976). However, we know little about what happens when communities encounter novel environments or species interactions that are outside their evolutionary history—traits that were crucial for persistence in one environment may be maladaptive when conditions change. Contrasting the community organisation across hydrological gradients in non-tidal versus tidal freshwaters provides a unique opportunity to fill this knowledge gap.

Freshwater communities are often structured by gradients of habitat permanence and predation pressure. Ephemeral pools that dry frequently are physiologically harsh environments that do not support large-bodied top predators (Vanschoenwinkel, Buschke, & Brendonck, 2013; Wiggins, Mackay, & Smith, 1980); abiotic stress therefore drives community structure and species traits in temporary freshwaters. Ponds or lakes that do not dry up are more likely to support top predators, which exert a strong selective pressure on lower trophic levels and supplant environmental variability as the main driver of community structure. This trade-off between habitat permanence and predation pressure is the key driver of community structure and function in freshwaters (Batzer & Wissinger, 1996; Schriever, 2015; Wellborn, Skelly, & Werner, 1996) and has led to adaptive radiation (within families and genera) to fill vacant niches along the gradient (Stoks & McPeck, 2003; Wellborn et al., 1996; Wissinger, Whissel, Eldermire, & Brown, 2006).

In contrast to most freshwater systems, tidal freshwaters experience considerable water-level fluctuations daily (and seasonally) and are important forage areas for predatory fish (Le Pichon et al., 2017; Mclvor & Odum, 1988; Nellis et al., 2007). Tidal freshwaters occur in estuaries with riverine flows that are sufficiently strong to maintain salinity levels below 0.5‰ while still permitting upstream tidal movement and fluctuations in water height (Odum, Smith, Hoover, & Mclvor, 1984). The denser salt water of the incoming tide is forced downwards by strong freshwater flows, and the incoming tide pushes large volumes of freshwater upwards—creating uniquely freshwater intertidal zones. These intertidal areas usually host a diverse suite of freshwater wetland plants and associated fauna (Barendregt, Whigham, & Baldwin, 2009; Barendregt, Ysebaert, & Wolff, 2009; Swarth & Kiviat, 2009; Van den Bergh et al., 2009). Tidal freshwaters have a global distribution, but the hydrological conditions that create these areas are less likely to be maintained in tropical or Mediterranean climates, where precipitation patterns and river discharge values vary greatly by season (Barendregt and Swarth, 2013). The benthos in tidal freshwater wetlands are subjected to high environmental variability and desiccation stress

generated by twice-daily fluctuations in water level among zones of different tidal heights.

Additionally, because fish can move with the tides, predation pressure in tidal freshwaters is likely to be consistently high. These mobile predators are not subject to the same physiological limitations as their benthic prey, as fish can always return to the refugium of the subtidal river during low tide. The trade-offs associated with key drivers of community structure—desiccation risk and fish predation—are therefore decoupled and novel compared with the evolutionary history of nearly all freshwater invertebrate colonists in the landscape. Understanding how communities are structured in tidal freshwaters could shed light on how communities organise in novel ecosystems, or when the main drivers of community structure are altered or reorganised; for example, through climate-driven changes in species' ranges (Alexander, Diez, Hart, & Levine, 2016) or changes in the frequency or timing of natural disturbance regimes (Turner, 2010). Furthermore, despite their global distribution and known conservation importance for rare wetland plant species, anadromous fishes, and waterfowl (Barendregt, Whigham et al., 2009; Barendregt, Ysebaert et al., 2009), little has been done to investigate the ecology of benthic invertebrate communities of tidal freshwaters (but see Yozzo & Diaz, 1999).

The primary aim of this study was to investigate how benthic communities are organised under a suite of associated abiotic and biological pressures that are atypical for freshwater habitats—tidal hydrology. We predicted the combination of physiological stress (twice-daily drying) and predation pressure (twice-daily fish predation) would create some level of distinction in community structure and differences in richness between different tidal heights due to variation in the tolerances of benthic taxa to these compounding environmental pressures. Given that the trade-offs associated with drying and predation that generated the regional freshwater fauna are decoupled in tidal freshwaters, we also predicted that the fauna of tidal freshwaters would be a depauperate subset of the benthic communities found in nearby non-tidal freshwater habitats. Lastly, given the dearth of basic information on the composition of tidal freshwater benthic communities, we also assess and discuss their potential importance for landscape-level biodiversity.

2 | METHODS

2.1 | Field study site

Swan Island (44°3'55"N, 69°47'41"W) is an island in the upper Kennebec estuary, in Sagadahoc County, Maine. The island is c. 6 km long and 1.25 km wide and is surrounded by c. 200 hectares of freshwater tidal flats that are vegetated seasonally and are typically dominated by wild rice (*Zizania palustris*), three-square bulrush (*Schoenoplectus pungens*), and pickerelweed (*Pontederia cordata*). The island experiences semidiurnal tides between 1.5 m and 2.1 m in height, which vary seasonally with river discharge. The limit of

1 saline intrusion during seasonal lowest riverine flows (September) is
 2 just downstream of the most southerly point on the island (Kistner
 3 & Pettigrew, 2001); the salinity of the tides experienced by the is-
 4 land never exceeds 0.5‰ and can thus be considered truly fresh-
 5 water (McLusky, 1993). Summer electrofishing found that the tidal
 6 freshwaters around Swan Island support high densities of preda-
 7 tory fish across a range of body sizes and 18 species (Yoder, Kulik,
 8 Audet, & Bagley, 2006; see Supporting Information Table S1). There
 9 are eight man-made ponds on the island, some of which have been
 10 stocked with brown trout (*Salmo trutta*), as well as numerous natu-
 11 ral seasonal wetlands and vernal pools. The island has not been in-
 12 habited since 1936 (Kennedy, Farrar, Reynolds, & Bond, 2012), and
 13 receives around 2,000 visitors per year, so, with the exception of
 14 yearly management of the grasslands that surround the man-made
 15 ponds, there are few ongoing human impacts (J. Pratte, personal
 16 communication).

2.2 | Sampling design

Four intertidal wetlands, four ponds deemed hydrologically stable (*permanent*), and four pools that experience significant seasonal dry-down (*temporary*) were chosen for sampling sites. Inland sites were subjectively assigned to either group based on local knowledge (J. Pratte, personal communication) and by looking at historical aerial photography to see which sites varied greatly in their surface area, or disappeared seasonally (i.e. suggestive of significant dry-down). The mean distance between inland sites was $1,127 \pm 153$ m (range: 245–2,286 m). Sampling occurred at three tidal heights (low marsh, mid marsh, and high marsh) of intertidal wetland, and in the littoral zones of the inland sites. As the slope differed between tidal sites, distances between tidal height zones within a wetland were varied (range: 39–106 m, $\bar{x} = 68.3 \pm 9.7$ m) to ensure similar hydrological conditions between sites. Twice a

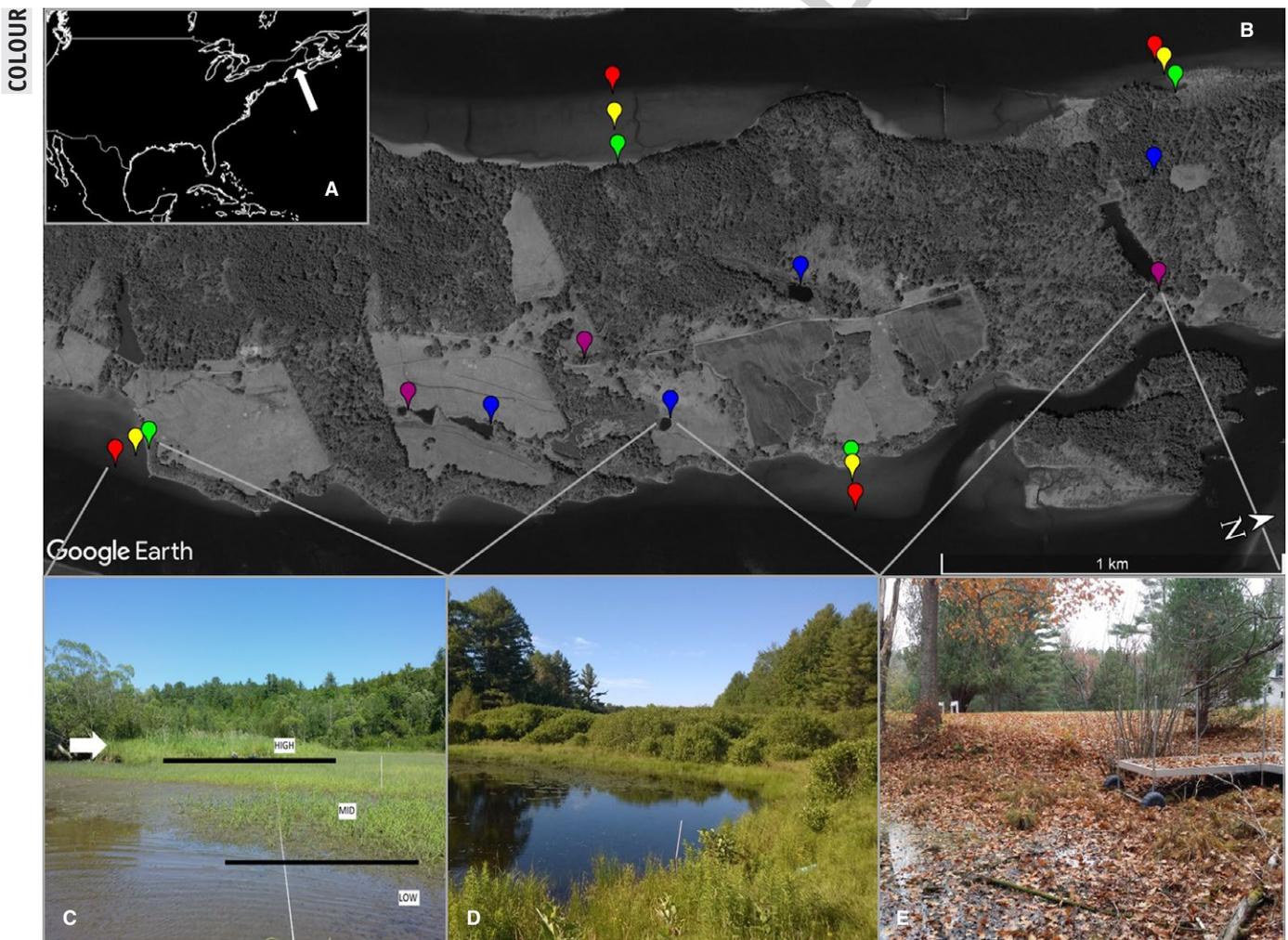


FIGURE 1 (a) Geographic location of Swan Island, Maine (arrowed). (b) Aerial photograph of Swan Island, Maine with sampling locations marked. High (closest to land), mid, and low tidal sites are marked by green, yellow, and red pins, respectively. Permanent ponds ($n = 4$) are marked with blue pins and temporary pools ($n = 3$) with purple pins. River flow is from north to south. Photograph was taken at low tide on 5 May 2018 and accessed from Google Earth on 2 June 2018. (c) A typical tidal freshwater wetland site. Black bars highlight sites of different tidal height. Here, the distance between low and high sites was 106.2 m. Photo was taken during the floodtide. The arrow denotes the approximate high tide line. (d) A typical permanent pond site. Sampling occurred in the littoral vegetation at the bottom of the photo. (e) A typical temporary wetland site that has experienced significant dry-down

day, high, mid, and low tidal heights were inundated for <3, c. 6, and c. 9 hr at a time, respectively. Sampling occurred within a 1-week window at three time-points during the summer of 2015 (May, June, and August) to account for seasonal changes in the environment and benthic invertebrate communities. A map of the sampling locations and photographs of each of the three habitat types can be seen in Figure 1.

2.3 | Physicochemical sampling

Water temperature data were recorded at 30-min intervals during the season using HOBO pendant dataloggers (Onset Computer Corporation, Bourne, MA, U.S.A.) attached to a staging post at the sediment-water interface. These dataloggers were deployed at both high and low tidal heights in tidal sites. Staging posts were also installed in inland sites to record water height changes between sampling occasions.

2.4 | Biological sampling

Benthic communities of tidal and non-tidal habitats were characterised by sweeping four replicate 0.33 m² plots with a D-frame net (1-mm mesh-size) for 30 s to collect large-bodied macroinvertebrates. A modified stovepipe sampler (ø 0.01 m section of PVC pipe) was pushed into the substrate next to each area swept by the D-frame net and an aquarium net (0.35-mm mesh-size) was repeatedly swept inside the stovepipe for 30 s to collect smaller-bodied invertebrates. These complementary sampling methods enabled the detection of rare large-bodied macroinvertebrates and the quantification of small-bodied, highly numerous taxa, respectively (method following Wissinger, Greig, & McIntosh, 2009). Samples were collected on the incoming tide, where applicable, and always at a water depth of 10 cm. Samples were stored in 95% ethanol for transport back to the laboratory.

2.5 | Laboratory sample processing

Benthic macroinvertebrate samples were washed over a 500-µm Endecott sieve, transferred to a white picking tray, and all invertebrates were removed and identified to the lowest possible taxonomic level (typically genus or family) using Peckarsky, Fraissinet, and Penton (1990), Merritt, Cummins, and Berg (2008) and other taxon-specific keys, where appropriate. Invertebrates were placed in a petri dish with graph paper for scale and photographed using a tripod-mounted Canon EOS Rebel DSLR camera (Canon Inc., Tokyo, Japan). Adobe Acrobat X Pro (Adobe Systems, San Jose, CA) was used to enumerate invertebrates using a method that followed Galatowitsch and McIntosh (2016a).

2.6 | Data analysis

Invertebrate abundance data were pooled across the four replicate samples and sampling date and converted to densities (number of

individuals per m²) by dividing by the total area sampled. Invertebrate density data were then natural-log transformed before analysis. Larval and adult forms of the same taxon were treated as separate taxa, to reflect differences in dispersal ability and tolerances to stressors. Taxa that were obligately terrestrial and would experience inundation as a stressor (non-aquatic adults, terrestrial beetles, spiders, etc.) were not included in analyses.

Taxonomic richness, quantified as the number of unique taxa found at each site, was the simplest measurement of diversity calculated, but is highly dependent on sampling effort and number of individuals collected (Magurran, 2004). Margalef's index was used in lieu of taxonomic richness to aid in site comparison of richness as invertebrate abundances often varied greatly between sites.

These univariate responses of log_e-invertebrate density and untransformed values for the normally-distributed Margalef's index were analysed using analyses of variance (ANOVA) in which habitat type (High, Mid, Low, Permanent, Temporary) was treated as a fixed effect. Tukey's honest significance difference test was performed post hoc to determine significant differences among treatment levels. Data were analysed using R 3.3.0 (R Core Team, 2016).

2.7 | Community structure and dissimilarity

Bray-Curtis dissimilarity index, which incorporates relative abundances of taxa (Magurran, 2004), was used to characterise variation in abundances and community composition between sites. Invertebrate density data were square-root transformed for Bray-Curtis calculations to dampen the effect of hyper-abundant taxa.

The resulting dissimilarity matrix was visualised using non-metric multidimensional scaling (NMDS). To test whether communities at different habitats are significantly different from each other in multivariate space, a permutational multivariate analysis of variance (PERMANOVA) was performed on the matrix of dissimilarity values. Although PERMANOVA is generally robust to heterogeneity of dispersions (Anderson & Walsh, 2013), homogeneity of dispersions was tested using PERMDISP to aid in interpretation of PERMANOVA results (Anderson et al. 2006). Diversity index calculation and all multivariate analyses were performed in R using the package *vegan* (Oksanen et al., 2016).

Sites were identified and selected for this study in April during the spring freshet. This meant that one site that was classified as a temporary inland site was in fact in the floodplain of the Kennebec River and was tidally influenced. Data from that site were not included in analyses. Additionally, one of the remaining temporary sites had dried completely by August was therefore not sampled in August.

3 | RESULTS

3.1 | Temperature

The greatest variation in daily water temperature was evident in high tidal sites, where temperatures often surpassed

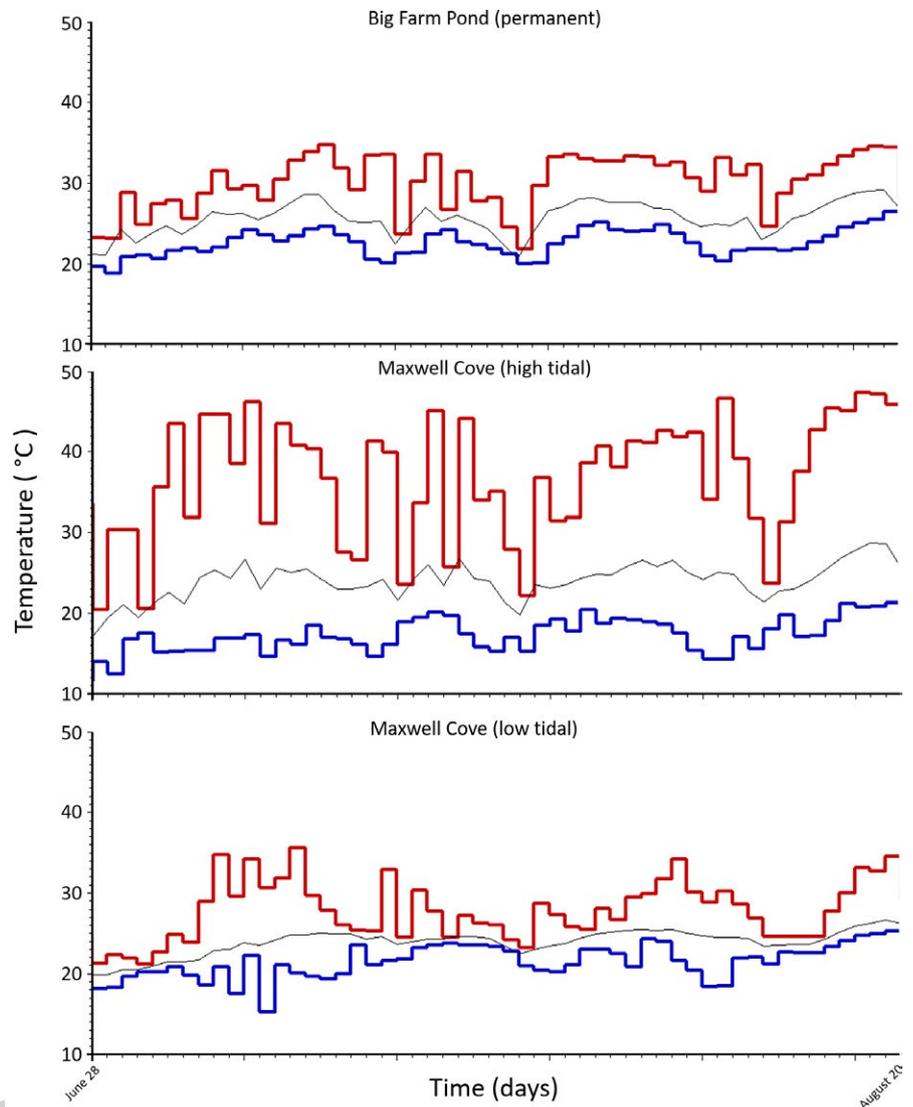


FIGURE 2 Representative temperature profiles for a permanent pond, and the high and low water lines of a tidal freshwater wetland on Swan Island, Maine. Red bars are daily maxima, blue bars are daily minima, and the grey line is the daily mean

42°C and could rapidly fall by as much as 32°C in a single day (Figure 2) due to a combination of reinundation and time of day. Low tidal sites were less warm (infrequently reaching 35°C), but still experienced rapid fluctuations in temperature. Inland permanent and temporary sites experienced a similar range of daily temperatures as low tidal sites but appeared to change more gradually. Ponds that exhibited significant dry down had more rapid increases in temperature later in the season.

3.2 | Univariate community responses

Mean invertebrate density did not differ significantly between habitats ($F_{4,14} = 2.803$, $p = 0.067$), but was generally lower in tidal sites than non-tidal sites. Taxon richness was significantly lower in tidal sites than in non-tidal sites ($F_{4,14} = 5.697$, $p = 0.006$, $R^2 = 0.51$), even when differences in total invertebrate densities were accounted for with Margalef's index. Within tidal sites, Margalef diversity decreased with tidal height, although not significantly (Figure 3).

3.3 | Multivariate community responses

Multivariate dispersion did not differ significantly between habitats (PERMDISP: Pseudo- $F_{4,14} = 2.468$, $p = 0.11$, $n = 999$). However, PERMANOVA indicated that invertebrate community structure differed significantly between habitats (Pseudo- $F_{4,14} = 5.124$, $p = 0.001$, $n = 999$, $R^2 = 0.59$). A NMDS plot based on a distance matrix of Bray-Curtis dissimilarity values (Figure 4) suggested that invertebrate communities in tidal habitats (high, mid, low) were more strongly differentiated than between the two inland habitat types (permanent and temporary), which overlapped considerably in their community structure. Overall, these analyses provided evidence that tidal and non-tidal habitats differed greatly in their community structures (Figure 4). Data on the taxa that drove these differences are presented in Supporting Information Figure S1.

3.4 | Taxonomic composition

A total of 33,560 individual invertebrates were enumerated in this study, representing 113 taxa Supporting Information (Table S2). Of

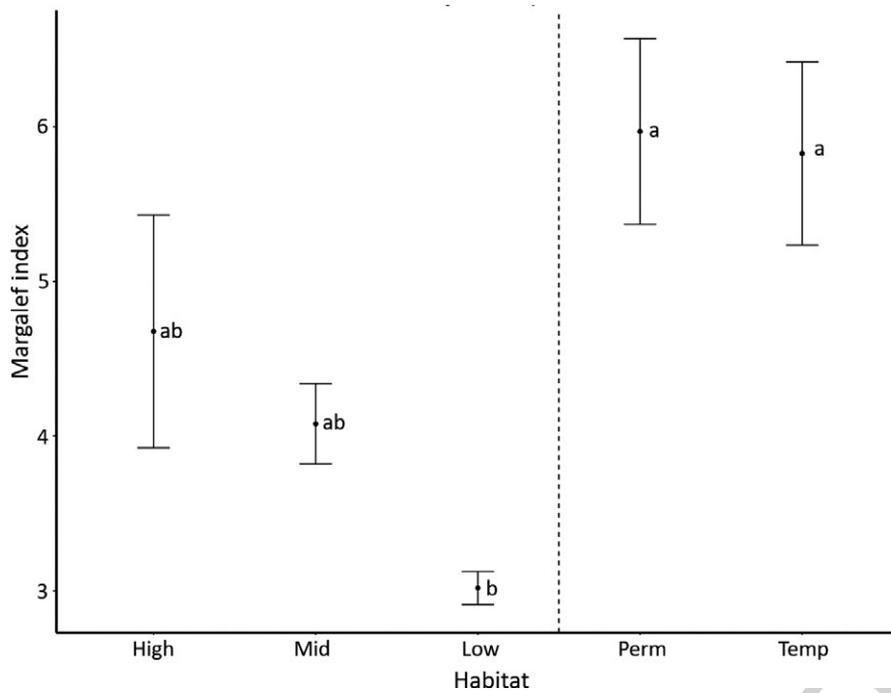


FIGURE 3 Mean Margalef diversity index values for tidal and non-tidal freshwater habitats of Swan Island, Maine. Means are plotted with one standard error and lowercase letters refer to post-hoc pairwise comparisons (Tukey's honest significance difference method). In tidal habitats, diversity decreased as a function of tidal height. Inland habitats had higher diversity on average

LOW RESOLUTION COLOUR FIG

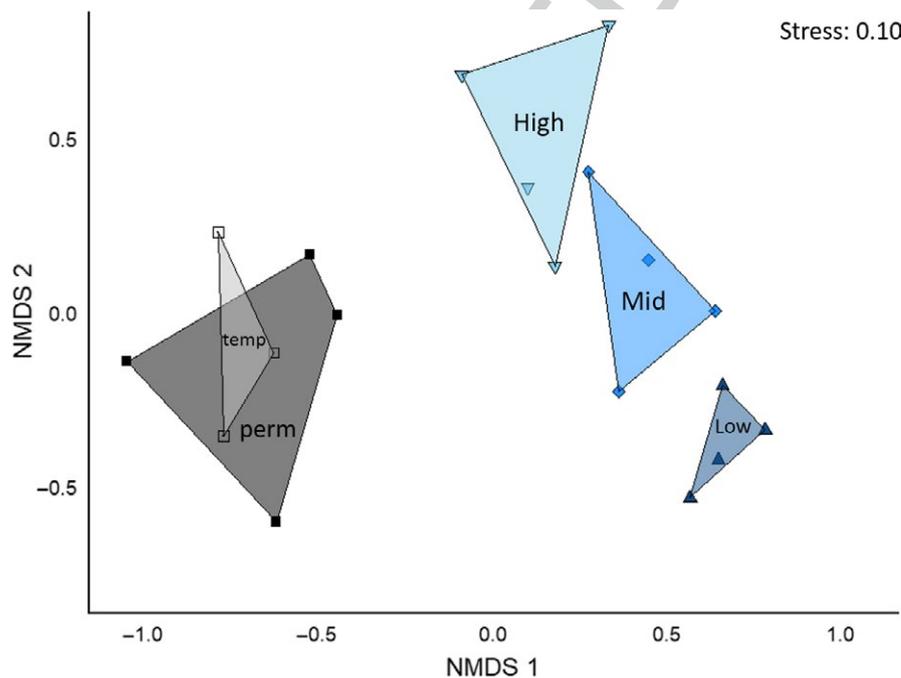


FIGURE 4 Non-metric multidimensional scaling (NMDS) ordination plot of benthic macroinvertebrate communities based on Bray-Curtis dissimilarities of square-root-transformed abundance in freshwater habitats of Swan Island, Maine. Points represent sites, and polygons are drawn to encompass all sites of a given habitat type. Communities were more greatly differentiated between different tidal height zones (High, Mid, Low) in a contiguous wetland habitat than between isolated discrete inland habitats that varied in their hydrology (Permanent, Temporary). Inland and tidal communities were also strongly differentiated from each other. A stress value of 0.10 suggests that the two axes accurately represent the multivariate data

these 113 taxa, almost a quarter were only found in tidal freshwaters, nine were restricted to permanent inland freshwaters, and eight were unique to temporary inland freshwaters (Figure 5). Of the 28 taxa found only in tidal freshwaters, 10 were unique to high marsh sites, and five and three taxa were found only at mid and

low marshes, respectively. Approximately 60% of taxa were found in more than one habitat (Figure 5). A total of 74 taxa were found at permanent inland sites, 72 taxa were found at temporary inland sites, and 70 taxa were found in tidal freshwaters (across all tidal heights).

1 Mud snails (Hydrobiidae) and nonbiting midge larvae
 2 (Chironomidae) were either dominant or abundant at all tidal heights.
 3 At low tidal heights, oligochaetes were also abundant. Taxa that were
 4 unique to low tidal sites were those generally considered lotic (e.g.
 5 the hydropsychid caddisfly, *Cheumatopsyche* sp., and the gomphid
 6 dragonfly, *Stylurus* sp.). At mid tidal heights the mayfly *Caenis*, wa-
 7 terboatmen (Corixidae), and the amphipods *Gammarus* and *Hyaella*
 8 were abundant. High densities of corixids were also observed at
 9 high tidal sites. Other abundant taxa at high tidal heights were cer-
 10 atopogonid midges (in particular *Atrichopogon*), *Caenis*, and the bee-
 11 tles *Haliplus* and *Berosus*.

12 Tidal sites also supported a unique assemblage of beetles that
 13 was not seen in inland freshwaters, including lotic taxa, such as el-
 14 mids (four genera), and taxa that are considered *semi-aquatic* or litto-
 15 ral specialists like the families Lampyridae (fireflies), Heteroceridae
 16 (variegated mud-loving beetles), Staphylinidae (rove beetles), and
 17 Tenebrionidae (darkling beetles)—all of which were found exclusively
 18 at high tidal heights.

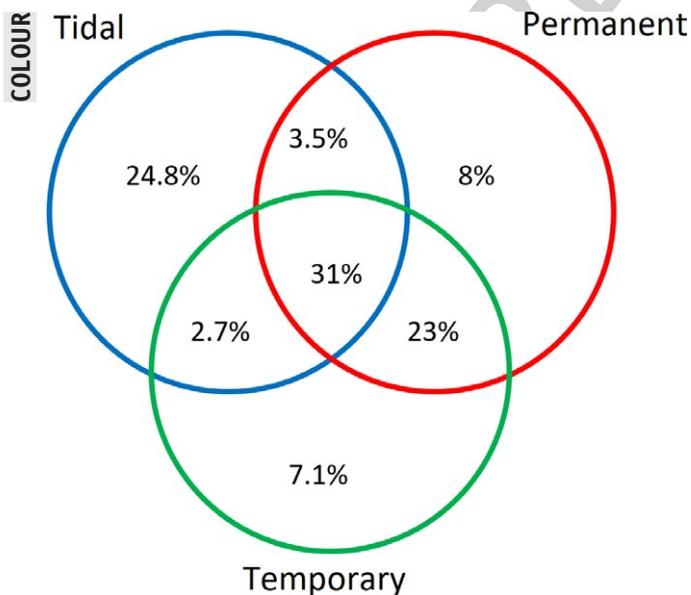
19 Inland, chironomids and *Caenis* were dominant or abundant at
 20 both permanent and temporary inland sites. Odonates from the
 21 families Coenagrionidae, Lestidae, and Libellulidae, and the isopod
 22 *Caecidotea* also ranked among the dominant taxa at both inland sites
 23 but were rare or absent from tidal sites. Adult dytiscid beetles and
 24 hemipterans were common in inland sites, but rare or absent from
 25 tidal sites.

26 27 28 4 | DISCUSSION

29 Our study provides evidence that environmental gradients can pro-
 30 duce strong changes in community structure in habitats that are
 31

spatially contiguous and have little or no dispersal limitation. We pre-
 32 dicted that benthic communities in tidal freshwaters would exhibit
 33 some level of community zonation between different tidal heights
 34 due to compounding pressures from drying and fish predation. In
 35 fact, our community sampling revealed greater differentiation in
 36 community structure between tidal heights in a contiguous wet-
 37 land habitat than between isolated wetland habitats that differed in
 38 their hydrological conditions. In the tidal freshwater habitats, com-
 39 munities were distinct in their structure despite high connectivity
 40 between the three tidal heights. There was significant overlap in
 41 the invertebrate communities of permanent and temporary ponds.
 42 These results suggest that the trade-offs that structure communities
 43 (e.g. Wellborn et al., 1996) are sufficiently strong in tidal freshwater
 44 habitats to produce greater community differentiation than would
 45 be predicted given the highly condensed longitudinal scale and high
 46 habitat connectivity.

47 In tidal freshwaters, communities are subjected to highly-
 48 predictable alternating abiotic and biological stressors. Temperatures at upper tidal heights at low tide can reach 42°C in the middle of the day and fall to around 15°C when re-inundated at high tide in the night (Figure 2). Desiccation risk and heat stress are correlated with tidal height, much like in marine intertidal areas (e.g. Dayton, 1975). When this physiological stressor is relaxed by re-inundation during the flood tide, the benthos is then subjected to predation by foraging fishes which follow the wetting front of the incoming tide (personal observation). Of the 18 spp. found by Yoder et al. (2006) in tidal freshwater habitats (see Supporting Information Table S1), 13 spp. are demersal or benthopelagic feeders on invertebrates (Froese & Pauly, 2018) and represent a broad range of body and gape sizes, and thus can exert strong top-down control on the benthos. Predation risk is likely to be greater at lower tidal heights that are inundated for longer, as fish have more time available to forage (Ellis & Bell, 2008; Kneib & Wagner, 1994; Le Pichon et al., 2017). In tidal freshwaters, the stresses of fish predation pressure and physiological stress may be compounding rather than the orthogonal contrasts that are well known to structure inland freshwater communities (Batzler & Wissinger, 1996; Schriever et al., 2015; Wellborn et al., 1996). For tidal heights that are inundated for a short period of time, benthic invertebrates will have limited time available for foraging, a period that also corresponds with the highest risk of predation. In non-tidal freshwaters, especially in hydrologically isolated waterbodies (ponds, lakes, etc.), vertebrate predators, especially fish, are subject to the same abiotic constraints as lower trophic levels (e.g. Walls, Barichivich, & Brown, 2013; Wellborn et al., 1996; Werner & Anholt, 1993) and so their ability to depress invertebrate community structure is limited (but see Greig, Wissinger, & McIntosh, 2013). The strength of predation effects in tidal freshwaters is likely to be far higher than in ponds or lakes, if fish mobility across foraging areas allows them to exploit many resource patches in a short period of time. As tidal freshwaters are connected to a subtidal refugium, a larger number of predators can be supported that can *spillover* from subtidal areas during the flood



49 **FIGURE 5** Venn diagram of percent taxonomic overlap between
 50 benthic macroinvertebrate communities in tidal (blue), permanent
 51 (red), and temporary (green) freshwater habitats of Swan Island
 52 (113 taxa in total)
 53

1 tide and move between patches (sensu Casini et al., 2012; Frost,
2 Didham, Rand, Peralta, & Tylanakis, 2015). The environmental fil-
3 ters that act on predators, determining their spatial and temporal
4 distribution, can also have knock-on effects on prey; for example,
5 dispersal-limited predators in some systems can create the illu-
6 sion of dispersal limitation in prey communities (Livingston et al.,
7 2017). In tidal freshwaters, faster-dispersing fish predators can
8 move between patches on the scale of a twice-daily tide, while
9 more dispersal-limited prey species are constrained by the tidal
10 cycle—where relief from predation at low tide is accompanied by
11 physiological stress and dispersal limitation. In isolated non-tidal
12 wetlands, the abundance of predators is more likely to be limited
13 by the availability of prey that can be supported by the wetland,
14 as predators are subject to the same environmental constraints
15 as their prey (sensu lato Rosenzweig & MacArthur, 1963), and are
16 unable to move between patches.

17 While we predicted that compounding abiotic and predation
18 pressure would limit invertebrate community diversity in tidal fresh-
19 waters, taxonomic richness generally increased with increasing tidal
20 height. High tidal freshwater wetlands may represent a *peak* in ec-
21 otonal diversity, which is commonly observed in aquatic–terrestrial
22 transition zones (Décamps & Naiman, 1990; MacKenzie, Dionne,
23 Miller, Haas, & Morgan, 2015; Tonkin, Stoll, Jähnig, & Haase, 2016),
24 and at the nexus of other adjoining ecosystem types (Grytnes,
25 Heegaard, & Ihlen, 2006; Magura, 2002), as many taxa were found
26 only at these sites. These taxa included many semi-aquatic or littoral
27 specialists (sensu Merritt et al., 2008) that may use these sites during
28 the ebb tide and may experience prolonged inundation as a stressor.
29 Few semi-aquatic or littoral taxa were collected at lower tidal
30 heights, although it is possible that these taxa (which were mostly
31 beetles) forage in these areas at low tide and can retreat to higher
32 ground with the incoming tide (Barendregt, 2005). Additionally,
33 some aquatic taxa with closed tracheal systems that are unable to
34 respire atmospheric oxygen and would therefore be susceptible to
35 prolonged drying (for instance mayflies and caddisflies), were rare
36 or not observed at upper tidal heights. However, some traditionally
37 lotic taxa that would be intolerant of drying (and require flowing
38 water), such as *Cheumatopsyche* caddisflies and *Stylurus* dragonflies,
39 were able to penetrate into lower intertidal areas.

40 Many larger bodied taxa were only found in the non-tidal habi-
41 tats. These taxa, adult beetles and hemipterans, have high tolerances
42 for desiccation (Pallarés, Velasco, Millán, Bilton, & Arribas, 2016) and
43 are highly mobile, but their larger body size makes them more sensi-
44 tive to fish predation (Antón-Pardo & Armengol, 2016; Blumenshine,
45 Lodge, & Hodgson, 2000; Zimmer, Hanson, Butler, & Duffy, 2001).
46 Also, large-bodied and susceptible to fish predation (Morin, 1984),
47 odonate larvae respire using a closed tracheal system and are even
48 less likely to inhabit tidal habitats, where hydrological conditions are
49 constantly changing. The combination of physiological stress and
50 high predation pressure in tidal habitats probably hindered the col-
51 onisation of odonates.

52 There was a substantial proportion (c. 37%) of the regional
53 invertebrate fauna that were found in both tidal and non-tidal

habitats. While it is possible that some patterns of species' segre-
gation by habitat may be obscured by a coarse level of taxonomic
resolution, especially in speciose groups such as chironomids and
oligochaetes, several taxa appear to be true *hydrological generalists*—
being able to tolerate a wide variation in physiological or predation
pressures. While highly mobile taxa can move between habitats to
reduce risks, taxa such as snails, *Caenis* mayflies, *Gammarus* am-
phipods, and the larvae of *Haliplus* and *Dubiraphia* beetles, which
were abundant at all tidal heights and inland, have low dispersal
ability and mobility (Merritt et al., 2008). The presence of these
less-mobile taxa across the range of habitats suggests that they
may share some other traits that allow persistence despite vari-
able and high abiotic and predation stress, such as predator avoid-
ance or refugium use. Invertebrate traits like these can be flexible
within species along hydrological gradients in inland freshwaters
(Crowl, 1990; Galatowitsch & McIntosh, 2016b), and apparently
contrasting selection pressures (such as desiccation risk and pre-
dation) can facilitate the development of specialised strategies that
allow generalists to persist across environmental gradients (Greig
& Wissinger, 2010). While these flexibilities have been observed
for life-history strategies, the same could be true for feeding mode
or other short-term adaptations. For instance, *Caenis* mayflies have
operculate gills for ventilation in low-oxygen environments and are
biofilm feeders (Eastman, 1932). Here, their highly-benthic nature
may confer co-tolerance to both abiotic stress and predation pres-
sure, perhaps allowing persistence and foraging in very shallow
pools or wetted areas while the tide is out, or during seasonal dry-
ing. Further work is needed to discern the importance of traits that
confer co-tolerance to opposing selection pressures.

Some previous work has suggested that the benthic commu-
nities of tidal freshwaters are species depauperate (Barendregt,
2016; Swarth & Kiviat, 2009; Yozzo & Diaz, 1999), made up of a few,
highly dominant taxa, especially chironomids and oligochaetes. In
this study, while tidal freshwater habitats were less diverse (lower
Margalef's index values) than nearby non-tidal freshwaters and did
share c. 37% of their fauna with non-tidal habitats, almost a quar-
ter of the regional species pool was restricted to tidal freshwater
wetlands. Tidal freshwater areas are often overlooked in surveys of
estuarine and riverine biotas alike (Rundle, Attrill, & Arshad, 1998;
Yozzo & Diaz, 1999), which is unfortunate as we here present evi-
dence that they contribute unique taxa to the regional species pool.
While this study did not directly investigate the faunas of the adja-
cent terrestrial or subtidal riverine habitats, our results indicate that
tidal freshwaters may be important nexus of diversity, as they sup-
ported taxa that could potentially inhabit both adjacent habitats as
well as a broad range of hydrological generalists, and taxa not found
in other freshwater habitats locally.

5 | CONCLUSION

The trade-offs that structure communities in tidal freshwaters are
sufficiently strong to create greater differentiation in community

structure than would be predicted given the condensed longitudinal scale and habitat connectivity. While we observed the greatest differentiation in community structure between different tidal heights, greater differentiation between inland habitat types may have been observed if more ephemeral habitat types were considered (ditches, rain-puddles, etc.), or if better information on their vertebrate predators were available. Nevertheless, it is surprising that community differentiation was so strong in a contiguous habitat. Hydrology, as a function of tidal height, appears to drive this differentiation, through the interactive effects of desiccation and predation risk. In contrast to many freshwater systems, hydrological changes occur on a daily scale, and the mobility of predators in tidal freshwaters means they are not subject to the same environmental constraints as lower trophic levels. Thus, habitat conditions in tidal freshwaters are offset from the evolutionary trade-offs that structure communities in non-tidal freshwaters. However, to fully understand the relative roles of abiotic and biological forces in structuring tidal freshwater communities, manipulations of hydroperiod, predation, basal resources, and habitat complexity are required. Understanding the mechanisms that structure communities in tidal freshwaters provides valuable insight into how taxa can persist in environments to which they have not been specifically adapted and can help predict how communities might respond to novel environmental conditions or species interactions driven by climate change.

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ORCID

Jack R. McLachlan  <https://orcid.org/0000-0002-4287-5644>

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