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# Wetland microhabitats support distinct communities of aquatic macroinvertebrates

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## ABSTRACT

The drivers of aquatic macroinvertebrate distribution in Prairie Pothole Region wetlands are not as well understood as in other aquatic ecosystems (e.g. rivers or lakes). We collected aquatic macroinvertebrates from 35 fishless prairie pothole wetlands in Alberta, including two habitat zones: the emergent zone and the open-water zone. Within each zone, we collected a vegetation sample and a water column sample, thus capturing four distinct microhabitats. We tested for community differences among these microhabitats with nested ANOVAs, looking at macroinvertebrate abundance, taxa richness, and evenness. We also visualized trends in community composition among the microhabitats with nonmetric multidimensional scaling ordination. Interestingly, we observed no difference in macroinvertebrate communities between the open-water and the emergent habitat zones. However, we found significant differences in richness and evenness between water column and vegetation sample types nested within habitat zones. Additionally, we observed high taxonomic turnover between sample types. Our results emphasize the importance of within-zone microhabitats in structuring aquatic macroinvertebrate communities in prairie pothole wetlands, and the relative insignificance of emergent and open-water habitat zone distinctions. Future analyses of macroinvertebrates in wetlands should sample both the vegetation and the water column, regardless of habitat zone, to prevent biased surveys of macroinvertebrate communities.

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## Introduction

The Prairie Pothole Region (PPR) spans over 700,000 km<sup>2</sup> crossing three central provinces in Canada and five US states. The region is characterized by small, relatively isolated depressional wetlands known as prairie potholes. The prairie potholes of the PPR do not have well-developed surface inflows and outflows (LaBaugh et al. 1998) and consequently are mainly influenced by precipitation (Euliss et al. 1999). Prairie pothole wetlands flood with snowmelt in the spring and most dry out within weeks or months due to high levels of evapotranspiration (Hayashi et al. 2016). Aquatic macroinvertebrates inhabit these productive wetland ecosystems, providing an important trophic link between macrophytes and vertebrates (Zimmer et al. 2003; Wrubleski and Ross 2011). The importance of macroinvertebrates as a food source to nesting waterfowl in the PPR (Wrubleski and Ross 2011) has prompted research into the drivers of macroinvertebrate community composition in these wetlands. Nearly two decades have passed since Euliss et al. (1999) suggested that macroinvertebrate communities in prairie pothole wetlands would be dominated by generalist taxa that can tolerate

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the dynamic environment created by natural draw-down cycles. However, since then, results of wetland macroinvertebrate studies have often been contradictory – a review by Batzer (2013) concludes that the determinants of wetland macroinvertebrate distributions remain uncertain.

One factor often cited as driving variation in wetland macroinvertebrate communities is vegetation structure (e.g. Zimmer et al. 2000). The composition and structure of vegetation influences wetland invertebrate community structure as macrophytes serve as a source of food, a refuge from predators, and an egg laying substrate (Batzer and Wissinger 1996; Keddy 2010). For example, Hanson et al. (2005) observed that aquatic invertebrates increased in abundance in shallow, heavily vegetated wetlands compared to less vegetated sites. Christensen and Crumpton (2010) agree that the presence of emergent vegetation has a significant role in determining invertebrate community structure. However, there is the potential for vegetation presence to be confounded with water depth (Zimmer et al. 2000) or fish presence (Maurer et al. 2014) and so the importance of vegetation in structuring macroinvertebrate communities is not clear.

In prairie pothole wetlands, vegetation-based habitat zones assemble along a moisture gradient, with submersed and floating vegetation typically at the wetland center and emergent vegetation surrounding it (Stewart and Kantrud 1971). The physical structure of these zones is highly distinct, with emergent cattails, sedges, and grasses providing mainly vertically oriented leaves and stems that connect the sediment to the water surface and protrude beyond the water surface, whereas submersed aquatic vegetation is typically delicate with finely divided buoyant leaves that fill the water column. These different habitat zones presumably create different microhabitats for feeding, emergence, and oviposition. Thus, we expect distinct invertebrate communities to occupy these two habitat zones.

Despite extensive evidence that microhabitat structure exerts an important influence on macroinvertebrate communities in rivers (e.g. Gregory 2005; Henshall et al. 2011; Verdonshot et al. 2016) and lakes (e.g. Weatherhead and James 2001; Bazzanti et al. 2009; Sychra et al. 2010; Cai et al. 2011), the associations between wetland invertebrates and vegetation zonation in wetlands of the Northern Prairie Pothole Region (NPPR) has received relatively little study. In lakes, for example, macroinvertebrates exhibit taxonomic turnover between the deeper open-water and the littoral zone (Sychra et al. 2010), and different lake microhabitats (benthic, macrophyte patches, open-water) are known to support distinct macroinvertebrate communities (Weatherhead and James 2001). These community differences are often attributed to the life history of particular taxonomic groups, as invertebrates with similar life histories will often exploit the same microhabitats (Vannote et al. 1980, Bazzanti et al. 2009). In lotic environments, for example, shredders will usually prefer the shelter of vegetation, whereas filter feeders and predatory invertebrates will occur in higher abundance in the water column to take advantage of pelagic resources (Wallace and Anderson 1996).

Our goal was to determine whether similar habitat partitioning of macroinvertebrate taxa among microhabitats is evident in prairie pothole wetlands. We hypothesized that there would be a significant difference in macroinvertebrate abundance, taxa richness, evenness, and community composition among the two primary habitat zones that characterize prairie potholes in the NPPR, open-water and emergent vegetation, based on macroinvertebrate functional traits. Further, nested within those zones, we expected to detect differences between invertebrate taxa using the water column and those taking refuge in or feeding on wetland vegetation. We anticipated that agile swimmers like Corixidae would occupy the open-water zone and the water column, whereas climbers like Zygoptera or grazers like Lymnaeidae would reside among the emergent vegetation (e.g. Sychra et al. 2010). Thus, we tested for differences in macroinvertebrate community among four distinct microhabitats typical of prairie pothole wetlands. We sought to control the potentially confounding effect of fish predation by sampling only fishless wetlands, which dominate Alberta's NPPR. Further, we sought to control the effect of water depth by sampling in both open-water and emergent vegetation zones across the same gradient in water depth. Our results should inform sampling protocols to ensure comprehensive and representative sample collection of wetland macroinvertebrates.

## Methods

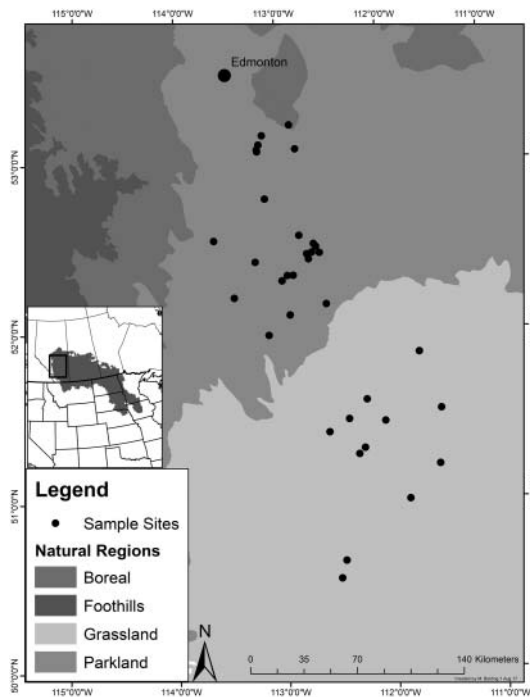
### *Wetland sites and microhabitat distinction*

We selected 35 prairie pothole wetlands for our study from the sample frame created by Alberta's provincial wetland inventory (Figure 1; Government of Alberta 2014), following a protocol described in detail in Gleason and Rooney (2017). The wetlands were all situated within either the Parkland or Grassland Natural Regions of Alberta and each included both an open-water zone and an emergent vegetation zone. Collectively, the sites spanned a range in May water depth from 0.29 to 1.02 m (see Appendix 1 (Supplemental material)).

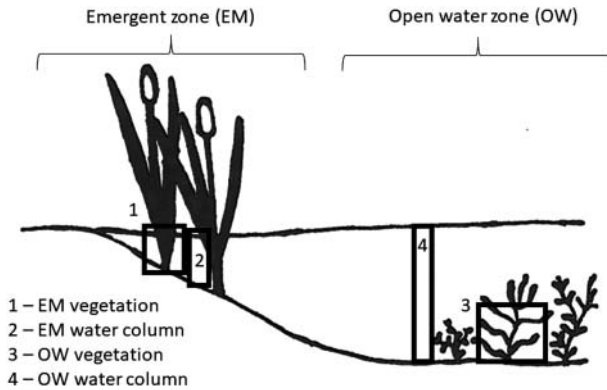
At each wetland, we first delineated the areal extent of the emergent vegetation zone, where rooted macrophytes grow and protrude beyond the surface of the water. These macrophytes were typically cattail, bulrushes, or robust *Carex* spp. Next, we delineated the extent of the open-water zone, which may have very little macrophytic vegetation growing in it or may support abundant submerged and floating aquatic plants. Commonly encountered macrophytes in the open-water zone included *Myriophyllum* spp., *Lemna* spp., and *Potamogeton* spp. Nested within each habitat zone, we collected two distinct sample types: a water column sample and a vegetation sample. This yielded four microhabitats per wetland: (1) an emergent zone, vegetation sample; (2) an emergent zone, water column sample; (3) an open-water, submerged/floating vegetation sample; and (4) an open-water, water column sample (Figure 2).

### *Macroinvertebrate collection and identification*

Sampling for aquatic macroinvertebrates took place during early May of 2014 and 2015. Macroinvertebrate sampling followed the quadrat-column-core (QCC) method described by Meyer et al. (2013) and modified by Gleason and Rooney (2017) for use in prairie pothole wetlands. In brief, we



**Figure 1.** A map of our 35 wetland sites in Alberta's Prairie Pothole Region (PPR). Our study region encompasses the two natural regions that comprise the PPR in Alberta: the Parkland and the Grassland.



**Figure 2.** The four wetland microhabitats sampled at each wetland: (1) the emergent zone, vegetation; (2) the emergent zone, water column; (3) the open-water, vegetation; and (4) the open-water, water column. Note how sample types (water column and vegetation) are nested within vegetation zones.

used a floating 0.25 m<sup>2</sup> quadrat to collect emergent or submerged vegetation. In the emergent zone, vegetation within the floating quadrat was collected by clipping within 2 cm of the substrate, whereas in the open-water zone, submersed or floating vegetation was collected with a rake into a bucket. The collected vegetation was then rinsed repeatedly in buckets of filtered water to dislodge clinging invertebrates. The rinse water was filtered through a 500- $\mu$ m mesh sieve and the collected residues preserved in 90% ethanol. A Marchant box was used to randomly sub-sample invertebrates in vegetation samples to an enumeration total of 300, based on our initial collector's curves. Water column samples were collected in clear acrylic tubes of 10 cm inner diameter to integrate across water depth. The tube was inserted vertically into the water to a depth just above the sediment. The entire contents of the tubes were emptied into a 500- $\mu$ m mesh sieve, and the residues preserved in 90% ethanol. The water column samples were enumerated in their entirety.

Collected macroinvertebrates were identified to family-level for most taxa using keys by Clifford (1991) and Merritt et al. (2008). The total number of individuals in each sample was recorded for each taxon. See Appendix 2 (Supplemental material) for details on taxonomic resolution, by order.

### Data analysis

Because there was no significant difference in richness or abundance of invertebrates between samples collected in 2014 and 2015 (Mann–Whitney  $U$  tests,  $p > 0.05$ ), the data from the two years were combined and analyzed jointly. Macroinvertebrate abundances were converted to counts per m<sup>2</sup> to relativize the different areas captured by the two sample types. Taxa richness was then a count of all taxa observed within each microhabitat at the wetland. We calculated Simpson's Dominance to measure community evenness using the following formula:  $D = \sum \left(\frac{p_i}{N}\right)^2$  (Magurran 2004).

To determine if there was a significant difference in (1) abundance (individuals per m<sup>2</sup>), (2) taxa richness (number of taxa observed), and (3) evenness among the four microhabitats sampled, we performed three nested ANOVAs using SYSTAT version 13.0 (SYSTAT Software, San Jose, CA). We used a nested model because the sample types (vegetation sample and water column sample) are embedded within the habitat zones (emergent zone and open-water zone). Prior to analysis, values for total invertebrate abundance and taxa richness were log transformed and square-root transformed, respectively, to achieve a normal distribution.

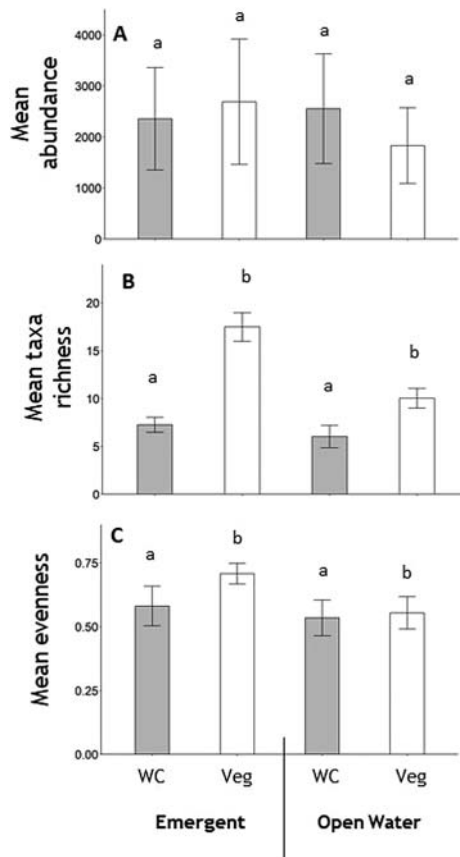
To characterize differences in macroinvertebrate community composition among microhabitats, we performed a nonmetric multidimensional scaling (NMDS) ordination on the Bray–Curtis distance measure. To do so, we used the 'metaMDS' function in the *vegan* package (Oksanen et al. 2016) in R statistical software (R Core Team 2016). Prior to ordination analysis, rare taxa (detected

in fewer than five sites) were excluded from the dataset to reduce sparsity. Taxon abundances were relativized by the maximum abundance of each taxon. Ninety percent confidence ellipses were delineated in order to visualize trends in the data, and taxa whose abundance was reasonably correlated ( $r^2 > 0.15$ ; using the function ‘*envfit*’ in the *vegan* package) to at least one ordination axis were overlaid as vectors. All graphing was performed in R statistical software (R Core Team 2016) using the package *ggplot2* (Wickham 2009).

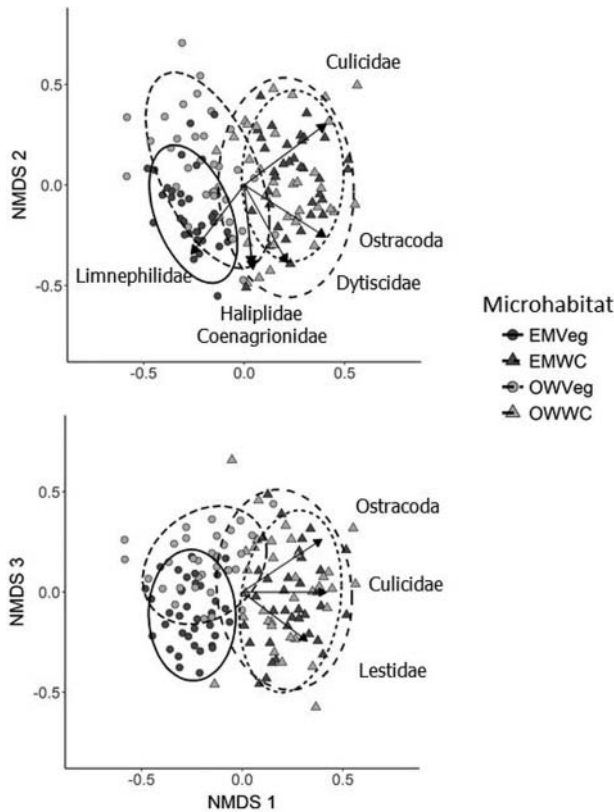
## Results

We collected 56 macroinvertebrate taxa from 35 prairie pothole wetlands in Alberta. The most abundant taxa in all microhabitats were Chironomidae and Ostracoda, which were present in every sample. In water column samples, Conchostraca and Lestidae were consistently abundant, regardless of habitat zone. Gastropod families (Planorbidae and Lymnaeidae) were abundant in the vegetation samples (Appendices 2 and 3 (Supplemental material)).

Macroinvertebrate abundance ( $F_{1,2} = 1.72, p = 0.319$ ), taxa richness ( $F_{1,2} = 0.602, p = 0.519$ ), and evenness ( $F_{1,2} = 2.44, p = 0.259$ ) did not differ significantly between open-water and emergent vegetation habitat zones (Figure 3). There was no significant difference in abundance ( $F_{2,136} = 0.75, p = 0.476$ ) between water column and vegetation sample types nested within habitat zones, but there



**Figure 3.** Average values for (A) macroinvertebrate abundance, (B) taxa richness, and (C) evenness (measured as Simpson's Dominance) for each microhabitat with standard error bars. Nested in the emergent zone is the water column sample (WC;  $n = 35$ ) and the vegetation sample (Veg;  $n = 35$ ). Nested in the open-water zone is also a water column sample (WC;  $n = 35$ ) and a vegetation sample (Veg;  $n = 35$ ). Grey bars are water column samples and white bars are vegetation samples. Lowercase letters reflect Tukey's multiple comparison results, with bars sharing a letter indicating no statistically significant differences.



**Figure 4.** An NMDS ordination of aquatic macroinvertebrate community composition in four microhabitats (EMVeg = emergent, vegetation; EMWC = emergent, water column; OWVeg = open-water, vegetation; OWWC = open-water, water column) sampled from 35 wetlands in the Prairie Pothole Region of Alberta. Symbols represent individual wetlands symbolized by microhabitat and ellipses reflect 90% confidence intervals for each microhabitat. Taxa reasonably ( $r^2 > 0.15$ ) related to the ordination solution are overlaid as vectors, with the length and direction of the vector indicative of the strength and nature of the correlation between that taxon's abundance and the ordination axes, where both larval and adult stages are aquatic (e.g. Dytiscidae), all life stages are included.

was a strongly significant difference in taxa richness ( $F_{2,136} = 92.9$ ,  $p < 0.0001$ ) and a slight but significant difference in evenness ( $F_{2,136} = 3.92$ ,  $p < 0.022$ ) between water column and vegetation subsamples nested within the two habitat zones (Figure 3). Taxa richness was higher in vegetation samples than in water column samples, regardless of wetland zone.

The optimal NMDS solution for macroinvertebrate community composition was three dimensions after 146 iterations, with a final stress of 21.71 (Procrustes RMSE = 0.0007, max residual = 0.004). Axis 1 of the ordination segregated samples of the water column from vegetation samples, regardless of habitat zone (Figure 4). Axis 2 did not differentiate among the four microhabitats. However, axis 3 provided some segregation of vegetation samples collected from the emergent and open-water zones, though water column samples overlapped substantially. Indeed, the water column samples from the emergent zone reflect a nested subset of the water column samples from the open-water zone.

As suggested by our ANOVAs and multivariate analysis, we conclude that aquatic macroinvertebrate taxa richness, evenness, and diversity differ between water column and vegetation samples, regardless of wetland habitat zone. In contrast, we see limited differentiation between habitat zones. The invertebrates collected from the water column are particularly indistinguishable between open-water and emergent habitat zones.



## Discussion

Though we observed no difference in abundance, taxa richness, or evenness between habitat zones (emergent and open-water), we detected differences in the richness and evenness of macroinvertebrates collected from the water column and vegetation microhabitats nested within habitat zones. Taxa richness was higher in vegetation samples than water column samples, regardless of habitat zone. Similarly, macroinvertebrate community composition differed significantly between water column and vegetation samples. Though differences between the open-water and emergent vegetation zone were not detected, we did observe some differentiation between macroinvertebrate communities in these zones when only the vegetation quadrat samples are considered. We conclude that vegetation exerts a strong influence on macroinvertebrate community structure, regardless of zone (e.g. emergent or submerged/floating vegetation).

There is little published work comparing macroinvertebrate distributions among wetland microhabitats, though research into the segregation of macroinvertebrates among different microhabitats in shallow lakes offers some grounds for comparison. For example, in shallow Polish lakes, invertebrate abundance and taxa richness were positively correlated with macrophyte presence and richness (Żbikowski and Kobak 2007). Similarly, research from a shallow lake in China concluded that macroinvertebrate diversity and community evenness was higher in vegetated areas compared to open-water (Cai et al. 2011). Like these studies in lakes, we observed higher taxa richness in vegetated samples; however, we also detected greater community dominance in vegetated samples, with water column samples yielding more even communities. Our vegetation samples were dominated by large numbers of Chironomidae, which led to the reduced evenness. Because richness and evenness displayed opposing relationships to sample type in our study, the difference in biodiversity between vegetated and water column microhabitats is not clear. It is possible that greater taxonomic resolution would reveal a different diversity pattern, but our study was limited to primarily family-level identifications (Appendix 2 (Supplemental material)).

### *Microhabitats support functional diversity*

We observed high taxonomic turnover between water column and vegetation quadrat sample types, regardless of which habitat zone they were collected from. We believe this is because water column and vegetation microhabitats support taxa of differing functional groups that are able to take advantage of distinct ecological niches. Sychra et al. (2010) reported that free-swimming taxa preferred open-water habitat, whereas grazing macroinvertebrates such as snails were associated with areas possessing dense macrophytes. In support of this, we observed a positive association between free-swimming taxa and water column samples. Water column samples were characterized by abundant Culicidae and Lestidae larvae, more Ostracoda, and more adult and larval Dytiscidae. Adult Dytiscidae are free-swimming predaceous diving beetles that we expect to spend more time foraging in the water column than hiding in vegetation. Both Culicidae larvae and Ostracoda are free-swimming filter feeders, likely also achieving greater foraging success in more pelagic habitat. In contrast, the Limnephilidae trichopterans dominated the vegetation samples from both open-water and emergent vegetation zones. Limnephilidae are mainly detritivores that feed on decaying plant matter that would be in abundance within the vegetation quadrats we sampled.

The association between Lestidae and water column samples challenges our functional guild framework as these predaceous odonate nymphs are typically described as vegetation climbers; however, some species within the family are categorized as climber-swimmers and will swim to hunt (Tennessen 2008). Both Weatherhead and James (2001) and Hinden et al. (2005) reported that odonate richness increased with macrophyte biomass, yet odonate families were not more common in vegetation samples from our wetlands. Interestingly, though both Lestidae damselflies and Ostracoda were more abundant in water column samples than vegetation samples, we did collect some of both taxa in our vegetation samples. Where this occurred, ostracods were more common in



vegetation samples collected from the open-water zone, whereas Lestidae nymphs were more common in vegetation samples collected from the emergent vegetation zone. This suggests that Ostracods may swim among the submersed macrophytes, but appear to avoid emergent ones. Lestidae, in contrast, will more commonly seek refuge among the robust vertical stalks of emergent plants, but avoid the thinly divided foliage of submersed aquatic vegetation. Perhaps this association with emergent macrophytes explains the discrepancy between our observations and the general descriptions of Lestidae habitat use.

### **Implications**

We highlight the great similarity in wetland macroinvertebrate community occupying the open-water and emergent vegetation zones in prairie pothole wetlands. This similarity is surprising in light of the relatively significant and consistent differences in richness, evenness, and taxonomic composition of macroinvertebrates collected from water column samples as opposed to vegetation quadrat samples, nested within those zones. Though we were able to explain many of the patterns in community composition by applying a functional guild framework, there remains unexplained variation in macroinvertebrate community composition and not all differences between invertebrates occupying the water column versus those residing in vegetation are attributable to feeding strategy or behavioral guild, perhaps due to limited taxonomic resolution.

Importantly, our results have implications for those planning to sample macroinvertebrates in wetland habitats. Whereas sampling to obtain representation from different habitat zones is often stressed in invertebrate sampling protocols, our results suggest that a comprehensive sampling of macroinvertebrate diversity depends more on the collection of different sample types than from sampling different habitat zones. For future sampling of macroinvertebrates in prairie pothole wetlands, it is integral that samples are taken from both the vegetation and the water column to adequately reflect the diversity of macroinvertebrates present. Finally, our work highlights the complexity in wetland microhabitats and the macroinvertebrate taxa they support. This may be informative for studies on waterfowl and other vertebrates that prey on vertebrates as well as inform management practices.

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### **Notes on contributors**


*Jennifer E. Gleason* was an MSc student under Dr Rooney during this study, but is now a PhD student at the University of Guelph where she studies meta-community dynamics in riverine invertebrates, as effected by agriculture.


*Jaimie Y. Bortolotti* was an undergraduate student under Dr Rooney during this study, but is now an MSc student at Queen's University in the Biology Department.

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