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Title: Functional dispersion of wetland birds, invertebrates and plants more strongly influenced by hydroperiod than each other.

Authors: Jody Daniel ^{1,2} and Rebecca C Rooney ^{1,3, *}

¹B2-251, Department of Biology, University of Waterloo, Waterloo, Ontario, Canada, N2L 3G1

²ORCID: 0000-0003-3153-8164

³ORCID: 0000-0002-3956-7210

***Corresponding Author: Phone** – 519-888-4567 EXT 33820; **Email** –

rebecca.rooney@uwaterloo.ca

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Abstract:

The relative role of biological and abiotic filters on the assembly of co-occurring taxa is widely debated. While some authors point to biological interactions (e.g., competition) as the stronger driver of ecological selection, others assert that abiotic conditions are more important because they filter species at the regional level. Because communities influenced by a dominant abiotic filter, (e.g., Prairie Pothole Region (PPR) wetlands, each varying in ponded water permanence), often have strong cross-taxon relationships, we can study these communities to better understand the relative influence of abiotic vs biotic filters on community structure. Using functional dispersion as our measure of communities, we test six alternate hypotheses about the relative importance of various pathways representing influence of biological and permanence filters on birds, aquatic macroinvertebrates and wetland plants in the northwest PPR using structural equation modeling. We aimed to understand whether: 1) ponded water permanence alone explained functional dispersion; 2) the influence of permanence on functional dispersion was direct or mediated; and 3) abiotic filtering by permanence was stronger than biotic filtering by co-occurring taxa. The best model suggests that there is a direct influence of permanence on the functional dispersion of each taxonomic group and that both bird and macroinvertebrate functional dispersion are causally related to plant functional dispersion, though for invertebrates the influence of plants is much less than that of permanence. Thus, the relative importance of wetland permanence and the functional dispersion of co-occurring taxa depends on which taxon is considered in PPR wetlands.

Keywords: Structural equation model, hydroperiod, Prairie Pothole Region, biological communities, wetland, marsh, functional dispersion, permanence class

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1 Introduction

2 Though there is consensus among community ecologists that abiotic and biotic filters
3 structure communities (Azeria et al. 2009, Qian and Kissling 2010, Chase and Myers 2011,
4 Cabra-García et al. 2012, Devercelli et al. 2016), the relative role of each filter is widely debated
5 (Kraft et al. 2015, Duan et al. 2016). Poff (1997) presented a nested filter conceptual model of
6 community assembly. Poff argued that species within the regional species pool must first pass
7 through the coarse filter of abiotic conditions; species with functional traits adapted to the range
8 of conditions set by the abiotic filter would survive. Next, these surviving species would
9 influence each other's abundances through biological interactions – a more fine-scaled filter.
10 Since Poff (1997), several other authors have found support for this nested filter model (e.g.,
11 Ackerly and Cornwell 2007, Williams et al. 2009, Aronson et al. 2016). Though manipulative
12 experiments should prove useful in understanding the relative role of abiotic and biotic filters
13 (Tiunov and Scheu 2005, Wardle 2006, Maynard et al. 2018), we posit that studying taxonomic
14 groups exposed to a predominant environmental filter could help in partitioning their relative
15 role in the assembly of communities by providing a simplified but environmentally relevant
16 system.

17 Wetlands of varying ponded water permanence in the northwestern Prairie Pothole
18 Region (PPR) provide an excellent candidate for such a model system. Wetlands in the PPR
19 differ in the length of time ponded water is present (i.e., hydroperiod), some containing ponded
20 water year-round and others drying up a few weeks after spring snowmelt (Stewart and Kantrud
21 1971, Leibowitz and Vining 2003). While the diversity and community structure of birds,
22 aquatic macroinvertebrates and plants in PPR wetlands appear directly impacted by hydroperiod
23 (Casanova and Brock 2000, Ruhí et al. 2014, Gleason and Rooney 2018, Daniel et al. 2019),

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interactions are evident among these taxa: 1) birds forage, roost in and nest on plants, but also disperse their seeds (e.g., Fox et al. 2011, Ayers et al. 2015, Soons et al. 2016); 2) birds consume aquatic macroinvertebrates and can influence their egg bank (e.g., Horváth et al. 2012; van Leeuwen et al. 2017); and 4) plants provide habitat for aquatic macroinvertebrates (e.g., Gleason et al. 2018). Evaluating the relative role of these filters can be pursued using a causal framework, which requires a univariate proxy of community composition; functional dispersion – a measure of how species abundances vary in trait space (Schleuter et al. 2010) – is a reliable proxy for community structure in studying community assembly processes (Gerhold et al. 2015). Dispersion is a preferred univariate measure of composition when studying these assembly processes because it captures how abiotic and biotic filtering can influence community structure. Species with similar functional traits will “pass through” an abiotic filter, resulting in low dispersion. In contrast, interspecific competition will encourage higher functional dispersion as species with different functional traits enable niche partitioning (Gerhold et al. 2015). We would expect, therefore, that if there is support for Poff’s nested filter model, then the influence of hydroperiod on a taxon’s functional dispersion would be stronger than the correlation in functional dispersion between taxa.

We can conceive of six distinct, plausible models to describe the possible interactions in our model system. First, the functional dispersion of taxonomic groups in our wetlands may be entirely the result of the influence of ponded water permanence on each taxon, independently (Fig. 1A). For example, hydroperiod may determine which plants in the seedbank will germinate and prolonged flooding can exclude ill adapted species (van der Valk 1981, Casanova and Brock 2000, Euliss et al. 2004, Tsai et al. 2012, Mushet et al. 2018). Hydroperiod may also filter macroinvertebrates lacking desiccation adaptations from lower permanence wetlands (Hall et al.

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2004, Gleason and Rooney 2018). Birds also show sensitivity to hydroperiod; it can dictate which terrestrial birds, shorebirds and waterfowl can establish (Niemuth et al. 2006, Morissette et al. 2013), with waterbirds particularly responsive to the extent of open water (O'Neal et al. 2008). In this case, the functional dispersion of the three taxa are independent.

Alternatively, one or more taxon may be unaffected by hydroperiod directly, but its functional dispersion may be subject to indirect effects of ponded water permanence because it is directly influenced by the functional dispersion of a co-occurring taxon that itself is influenced by hydroperiod. We can conceive of three possible pathways that could yield this type of mediated effect. Our first mediated-effects model posits that hydroperiod structures the functional dispersion of wetland communities through its effect on the functional dispersion of plants (Fig. 1B). Here, we hypothesized that because plants determine whether birds can nest or forage (Klaassen and Nolet 2007, Austin and Buhl 2011, Fox et al. 2011, Ayers et al. 2015) and act as substrate for numerous aquatic macroinvertebrate families (Campeau et al. 1994, Lee Foote and Rice Hornung 2005), they shape resource availability for the other taxa. In this model, hydroperiod directly influences the functional dispersion of plants, as the moisture gradient is known to be a strong constraint on the distribution of hydrophytes (e.g., van der Valk 1981, Euliss et al. 2004), but only indirectly influences birds and macroinvertebrates.

For our second mediated-effects model (Fig. 1C), we posit that plants are independent of hydroperiod, and are rather structured by stochastic factors. Wetland plants are largely wind dispersed (Guarino et al. 2005) and plant communities are typically recruitment limited (e.g., Hurtt and Pacala 1995), hence the abundance of plants may prove random with respect to ecological selection pressures like hydroperiod. However, hydroperiod should directly structure macroinvertebrate functional dispersion, with less permanently ponded wetlands filtering out

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taxa that lack desiccation tolerance strategies (e.g., Gleason and Rooney 2018). In this model, bird functional dispersion is directly influenced by the functional dispersion of both plants and macroinvertebrates, since they structure the availability of roosting or nesting habitat and foraging opportunities for birds (e.g., Gurney et al. 2017, Vanausdall and Dinsmore 2019). More, because birds are highly mobile, they may prove the most sensitive to cross-taxon influences as they select wetlands for foraging and nesting based on the availability of preferred habitat and forage. Birds are thus indirectly influenced by hydroperiod, through its influence on aquatic macroinvertebrates.

Our final mediated model posits that hydroperiod structures both bird and plant functional dispersion, which in turn structure the functional dispersion of aquatic macroinvertebrates (Fig. 1D). For example, a study from Hungary reported that wetlands populated by waterbirds typically support smaller species of aquatic macroinvertebrates, which are less easily consumed by birds (Horváth et al. 2012). Similarly, vegetation, by providing habitat heterogeneity and refugia, is reported to influence the diversity and abundance and diversity aquatic macroinvertebrates (Davis and Bidwell 2008, Meyer et al. 2015; Gleason et al. 2018). Thus, the influence of hydroperiod on aquatic macroinvertebrates could be indirect, mediated through its effect on the functional dispersion of birds and plants in the wetland.

Yet, if Poff's nested filter model is correct, we should see both a strong, direct influence of hydroperiod on the functional dispersion of each taxon and a simultaneous but weaker cross-taxon influence of functional dispersion, at least between some taxon pairs. We conceived of two competing, but plausible models that combine direct hydroperiod effects with direct cross-taxon effects. Our first combined-influence model (Fig. 1E) is similar to Fig. 1B, but with the addition of a direct influence of hydroperiod on both aquatic macroinvertebrates and birds, as is

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depicted in Fig. 1A. Our final combined-influence model (Fig. 1F), incorporates the direct effect of hydroperiod on the functional dispersion of all taxa (like in Fig. 1A) with the cross-taxon influence of the functional dispersion of plants and aquatic macroinvertebrates on plants, birds (as visualized in Fig. 1C. posits that the functional dispersion of all communities is structured by hydroperiod, but it is bird functional dispersion that is structured by aquatic macroinvertebrates and plants (Fig. 1F). We believe that this model may explain community functional dispersion because birds are the most transient of these taxa, and they can select wetlands for foraging and nesting based on whether their preferred habitat is present.

We tested our six competing hypotheses regarding how the functional dispersion values of birds, plants, and aquatic macroinvertebrates relate to hydroperiod and the functional dispersion of co-occurring taxa. We asked 1) whether functional dispersion is driven by hydroperiod alone (Fig. 1A) or by both hydroperiod and the functional dispersion of co-occurring taxonomic groups (Fig. 1B-F), 2) whether the influence of hydroperiod on each taxonomic group was primarily direct or indirect; and 3) whether hydroperiod had a stronger influence on the functional dispersion of taxonomic groups than did the functional dispersion of co-occurring taxonomic groups (i.e., support for Poff's nested filter model; Fig. 1E,F). We used structural equation modelling and AIC to evaluate the support for our six alternative hypotheses (Fig. 1). We predicted that there would be support for Poff's nested filter model, which would be evidenced by 1) the influence of wetland hydroperiod exceeding that of the functional dispersion of co-occurring taxonomic groups, as this theory dictates that abiotic filters like hydroperiod should take precedence over biological filters and 2) a direct influence of both hydroperiod and cross-taxon interactions on community functional dispersion.

Methods

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Study Area

Our wetlands are prairie potholes in the Grassland and Parkland Natural Regions of Alberta, Canada (Fig. 1). They are depressions that fill with ponded water, which were formed in the last glacial period (Wright 1972). Also in this region, the climate is semi-arid, as the rate of potential evapotranspiration exceeds that of annual precipitation (Hayashi et al. 2016). In the Grassland Natural Region, the dominant vegetation is mixed-grass prairie. Conversely, in the Parkland Natural Region, deciduous trees and grasses dominate (Downing and Pettapiece 2006).

Study Design

We surveyed 96 wetlands that ranged in pond permanence class (sensu Stewart and Kantrud 1971) from temporary with a hydroperiod on the order of weeks to permanent with ponded water year round, even in dry years. We selected sites to mirror the frequency distribution of permanence classes in the Alberta Merged Wetland Inventory (Government of Alberta 2014), and so included an unequal number of wetlands per permanence class category. Generally, most of our wetlands were small (mean size 0.81 ± 0.12 SE ha), reflecting the dominance of small prairie pothole wetlands in the region, independent of their permanence class.

Biological Surveys

Birds

We used visual and auditory point counts to survey birds twice during the peak breeding season (May-June in either 2014 or 2015) to record the presence of birds actively foraging or breeding (singing, nesting, territorial displays) in the study wetlands. Fly-overs were excluded from data analyses. In summary, visual surveys commenced first; they lasted for 10 minutes and were carried out from a vantage that allowed a clear view of the open water zone. We next

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conducted an 8-minute auditory survey. These surveys were 100-m, fixed-radius point counts, occurring at the center of the wetland. When a wetland was larger than 3 ha, we conducted multiple auditory surveys; each point-count location was at least 100 m from the wetland edge and 200 m from any other point-count location. We summed abundances across the multiple auditory point counts to account for differences in wetland size. For both visual and auditory counts, we recorded the identity and abundance of species (species list in Appendix S1A). Importantly, species abundances were summed across visits, rather than averaged, to account for the staggered breeding seasons among species. Additional details on the bird surveys are reported in Anderson and Rooney (2019).

Aquatic Macroinvertebrates

We applied a revised version (Gleason and Rooney 2017) of the quadrat-column-core method (Meyer et al. 2013) to survey aquatic macroinvertebrates. We sampled aquatic macroinvertebrates in both the open water (submersed and floating vegetation) and the emergent (cattail, bulrush, or other robust perennial sedges) zones, when both were present. In each zone, we collected three replicates of a: 1) vigorously washed and clipped 0.25 m² vegetation sample, from the emergent or submersed aquatic vegetation; and 2) two, 10-cm diameter water column samples. We composited the replicates of each sample type; this yielded one water column, sediment core, and vegetation sample in each wetland vegetation zone (open water and emergent). Following, for water column samples, we sorted aquatic macroinvertebrates to identify them to the lowest practical taxonomic level (typically Family), following Clifford (1991) Merrit et al. (2008). We used a Marchant box to sub-sample the vegetation sample, which was based on the protocol of the Canadian Aquatic Biomonitoring Network (Environment Canada 2014). Here, taxon abundances are area-weighted to estimate density per meter-squared.

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For both vegetation and water column samples, aquatic invertebrates were scaled to the meter squared. Next, we summed densities to represent each wetland zone, and subsequently averaged across zones for wetland-level invertebrate relative abundances. Additional information on the aquatic macroinvertebrates sampling are reported in Gleason and Rooney (2017), and a comprehensive taxonomic list is provided in Appendix S1B.

Plants

We conducted plant surveys during peak aboveground biomass (late July to August). During peak biomass, the presence of inflorescences allows for herbaceous plants to be confidently identified and cover values are at their maximum. We first delineated the wetland boundary based on the 50:50 rule for vegetation classification. After mapping the extent of each plant assemblage based on their vegetative structure (e.g., deciduous tree, forb, floating-leaved vegetation), we then mapped them by which species were co-dominant or dominant. We used a GPS/GNSS unit (SX Blue II receiver, by Geneq Inc., Montreal, Canada) to map these assemblages. For communities sized between 100-5000 m², we identified the percentage cover (modified Braun-Blanquette approach) of each vascular plant species within five, 1 m² quadrats. When communities were larger than 5000 m², we surveyed an additional quadrat per 1000 m² of plant community area. We also recorded the percentage cover of algae, bryophytes, bare ground, litter, rock, seedling/unidentified forb, standing dead litter, and open water (species list in Appendix S1C), but these cover classes were not included in subsequent analyses of vascular plant cover. For more details on plant survey methods, see Bolding et al. (2020).

Characterizing Prairie Pothole Permanence

Wetland permanence is a latent variable that cannot be directly measured but can be quantified nonetheless by a set of correlated indicators within a structural equation modelling

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framework (Grace et al. 2010). We used four proxies for wetland permanence, all related to the concept of hydroperiod. We used a matrix including the :1) approximate number of days a wetland contained ponded water based on ca. biweekly staff gauge measurements during the open water season (May-September), 2) the maximum water depth observed during the survey period 3) water amplitude (i.e., maximum – minimum observed water depths) standardized by maximum water depth observed during the survey period, and 4) an index of evaporative losses to the atmosphere relative to water inputs based on stable isotopes analysis. For details on the stable isotope analysis, see Meyers (2018).

Statistical Analysis

Calculating Functional Dispersion

We used functional dispersion as a proxy for community structure in studying community assembly process. Generally, when functional dispersion is high, some functional traits are more abundant than others indicating low evenness among functional traits; if abundances of different functional traits within a community are equal, we will see low functional dispersion (Finke and Snyder 2008, Comte et al. 2016). To measure the functional dispersion of each taxon, we used Rao's quadratic entropy with the dBF function in the FD package (Laliberte et al. 2014) in R (R Core Team 2019). This functional dispersion index uses the weighted mean distance of each species to the group centroid, where weights are based on species relative abundances. Thus, functional dispersion is the variance in a species' traits and where they are located in trait space (Schleuter et al. 2010), and it uses both species relative abundances and the pairwise functional differences to summarize functional diversity. Importantly, this index is not influenced by richness (Rao 1982).

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The traits we select for functional diversity indices can have profound effects on our understanding of a communities' ecology (Zhu et al. 2017); this suggests that our trait selection can affect our interpretation of the relative influence of permanence and cross-taxon interactions on functional dispersions. Because we aimed to capture as many assembly processes as possible, and not bias our analyses to traits related to abiotic filtering (Spasojevic and Suding 2012), we selected a wide range of traits and not simply those likely to be sensitive to wetland hydroperiod. For birds, we selected functional traits indicative of feeding behavior (e.g., ground gleaner, dabbler) nesting ecology (e.g., bank, reed), primary habitat (e.g., shoreline, grassland), wetland status (e.g., obligates versus facultative) and migratory status (e.g., neo-tropical migrant) (Appendix S2A). With macroinvertebrates, we used traits on feeding (e.g. filter feeder), behavior class (e.g., climbers) and desiccation strategy (e.g., disperser) (Appendix S2B). For plants, however, we used wetland indicator status (e.g., emergent), dispersal (e.g. wind), reproduction (e.g. vegetative), and nativity (e.g., native vs exotic) (Appendix S2C).

Partitioning the Influences of Community Composition into Environmental and Biological Components

We used structural equation models to evaluate the pathways that could explain the relative influence of abiotic and biotic filters on functional dispersion. We compared the fit of six candidate models. Our first model examined whether functional dispersion was explained by permanence alone, our second to forth models assessed whether there was a direct or indirect influence of permanence and our fifth to sixth models were assessments of the relative influence of permanence and biological interactions.

We implemented the structural equation models in the lavaan package (Rosseel 2012) of R (R Core Team 2019). Before implementing each model, we relativized each variable by their

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respective maximum values because they differed in range and scale. We were confident that our relativized data did not violate the assumption of multivariate normality, which is required for structural equation models, based on results of a Mardia's multivariate kurtosis of multiple variables test ($z = -0.325$, $p\text{-value} = 0.774$), implemented using the `mardiaKurtosis` function in the `semTools` package (Jorgensen et al. 2018) in R (R Core Team 2019). For each model, we set the endogenous covariances to zero, fixed the factor loading of the approximate number of days that a wetland contained ponded water to 1.0 and used an unbiased estimator (`wishart`) for maximum likelihood estimation. To rank the candidate models, we used AIC_c and model fit statistics. Finally, we standardized all parameter estimates, to ensure that we could compare the relative influence of hydroperiod and biological interactions on each taxonomic group's functional dispersion.

Results

Partitioning the Influences of Community Composition into Environmental and Biological Components

We compared the fit of six structural equation models (Fig. 1), each representing a different hypothesis about the relative influence of co-occurring taxonomic groups and ponded-water permanence on the functional dispersion of birds, aquatic macroinvertebrates and vascular plants in our study wetlands.

Our best model was model 1E, which hypothesized a direct influence of permanence on the functional dispersion of all three taxa and a further influence of plant functional dispersion on the functional dispersion of birds and aquatic macroinvertebrates (Table 1). Because no models were within two ΔAIC units of this top-performing model (Arnold 2010), we conclude that there is strong support for this model. More, the AIC weights indicate that a direct influence of

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permanence and plant functional dispersion on the functional dispersion of birds and aquatic macroinvertebrates was substantially more likely (AIC weight = 98), given the data, than the other five models (Table 1; Wagenmakers and Farrell 2004). Based on the p-value and chi-square statistic for this model (Table 1), we are confident there is strong support for this model, and it fit our data well. The standardized regression coefficients for this model are presented in Fig. 3.

While permanence alone did not explain functional dispersion of our three wetland taxa (research question one), there was a direct influence of permanence on the functional dispersion of each taxon (research question two). Interestingly, the relative influence of permanence and the functional dispersion of plants on the functional dispersion of birds and invertebrates differed, depending on the taxon considered (research question three). Plant functional dispersion was solely influenced by hydroperiod. Hydroperiod had a much stronger influence on aquatic macroinvertebrate functional dispersion (standardized regression coefficient = -0.52) than did plant functional dispersion (standardized regression coefficient = 0.30). In contrast, for birds, the influence of hydroperiod (standardized regression coefficient = 0.25) was slightly weaker than that of plant functional dispersion (standardized regression coefficient = 0.29), even when incorporating its indirect effect through plants (direct + indirect relative influence = 0.288). Generally, we conclude that the abiotic filter of hydroperiod is equal to or greater an influence on functional dispersion in each of our wetland taxa than the functional dispersion of co-occurring taxa, but the results are contingent on the taxon of interest.

Discussion

Using the functional dispersion of co-occurring taxonomic groups in PPR wetlands, we evaluated whether there was support for Poff's nested filter model in describing community

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assembly processes. We assumed that support for Poff's model would be evidenced by a stronger direct influence of hydroperiod on functional dispersion than cross-taxon interactions. We find limited support for Poff's nested filter model – abiotic filtering primarily influences functional dispersion and biotic filters are of lesser importance, at least for plants and aquatic macroinvertebrates. In birds, the functional dispersion of plants and the hydroperiod exerted similar influence. We asked three questions: 1) does the abiotic filter of ponded-water permanence alone structure prairie pothole wetland communities, 2) is the influence of this abiotic filter primarily direct or indirect and mediated through biological interactions, 3) what is the relative influence of this abiotic filter and the biological filtering of co-occurring communities?

To address our first question, we report that both the functional dispersion of co-occurring taxa and hydroperiod are important determinants of functional dispersion in these wetlands. This conclusion is supported by both observational studies and manipulative experiments, which report that biological interactions and environmental conditions structure resource availability for establishing taxa (e.g., Tiunov and Scheu 2005, Wardle 2006, Maynard et al. 2018). Environmental conditions can influence resource availability for primary producers by limiting whether nutrients necessary for growth are present (Fourqurean et al. 1992, Bowman et al. 1993, Guignard et al. 2017); and for consumers, environmental conditions determine whether energy gained (i.e., from feeding) (e.g., Schoo et al. 2012) is lower than the energetic costs to establish (e.g., from maintaining optimal body temperature, or time and effort placed into foraging) (Magnuson et al. 1979, Reid and Sprules 2018). Biological interactions, however, can influence resource availability through prey availability (for consumers) (Spivak et al. 2009, Groendahl and Fink 2017) or habitat provisioning (Thompson et al. 1996, Jackson et al. 2008).

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Thus, in predicting environmental change (Urban et al. 2016) or even species ranges (Dormann et al. 2018, Palacio and Girini 2018), we must also consider biological interactions.

To address our second question, whether the influence of hydroperiod was mainly direct or was mediated through the functional dispersion of co-occurring taxa, we find that the influence of hydroperiod was primarily direct. The functional dispersion of plants was driven exclusively by hydroperiod (standardized regression coefficient = 0.13). The functional dispersion of birds and aquatic macroinvertebrates included both a direct influence of hydroperiod (standardized regression coefficient = 0.25 and -0.52, respectively) and a much smaller indirect component. This mediated effect was through the influence of plant functional dispersion on birds (indirect standardized regression coefficient = 0.0377) and on aquatic macroinvertebrates (indirect standardized regression coefficient = 0.0390). Consequently, we conclude that taxon community structure in prairie pothole wetlands is mainly influenced by hydroperiod directly, even where indirect pathways of influence are supported by the data.

In terms of our third question, if there was support for Poff's nested filter model of community assembly, wherein abiotic filters take primacy over secondary biological filters, we find moderate support for Poff. Hydroperiod was the most influential factor in determining the functional dispersion of our wetland taxa, but the functional dispersion of plants served to exert a secondary influence. In the case of birds, however, the influence of plant functional dispersion was slightly larger than the direct effect of wetland permanence, and on par with its combined direct and indirect effect. Hydroperiod appears to first filter out species from the regional species pool that lack the necessary adaptations or tolerances to persist, and only subsequently do biological interactions constrain community assembly. We can conclude that biotic filters may be less influential than abiotic filters in community assembly processes.

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Though our model fit our data well, we could not account for some community assembly processes. Unknown is whether our hypothesized direct effects are not, in fact, mediated effects that we have categorized as direct effects. For instance, wetlands with longer hydroperiods may come to have higher bird functional dispersion because they are larger and some microhabitats are more abundant (Kantrud and Stewart 1984). If microhabitat availability is the direct pathway influence bird functional dispersion, the influence of hydroperiod would be best described as indirect, contrary to our findings. An additional missing link in our model is intra-taxon interactions. Widely debated before Poff's (1997) nested filter model was introduced is Diamond's (1975) assertion that the "checkered" distribution of species could be explained by competition-driven assembly. Though Diamond's (1975) hypothesis sparked debates lasting several decades (e.g., Connor and Simberloff 1979, Gotelli 2000), some authors have found support for this model (e.g., Gotelli and McCabe 2002, Gotelli and Rohde 2002, Maestre et al. 2008). Because our models focused on cross-taxon interactions, we were unable to incorporate the influence of intraspecific competition as a community assembly process, which should be included in future studies.

Our model also excludes other possible drivers of community assembly [(e.g., influence of proximity to other wetlands on the regional species pool (Lokemoen and Woodward 1992, Galatowitsch 2006); water chemistry as an abiotic filter on aquatic macroinvertebrates (Longcore et al. 2006, Maurer et al. 2014); and influence of physio-chemical conditions on plants (Roy et al. 2019, Kraft et al. 2019)]. Inclusion of such factors could improve the predictive power regarding functional dispersion, though based on prior research (e.g., Gleason and Rooney 2017, Kraft et al. 2019, Anderson and Rooney 2019) we predict that hydroperiod will remain the most important environmental filter in our study system. Future modeling should investigate the

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relative importance of these factors in parsimoniously describing community assembly in PPR wetlands.

Conclusion

Using structural equation modelling, we demonstrate that the functional dispersion of birds, aquatic macroinvertebrates and plants are explained by both hydroperiod and the functional dispersion of co-occurring taxa. Because environmental conditions generally had a stronger influence, even if indirect effects are considered, we find support for Poff's nested filter model in the community assembly of co-occurring birds, vegetation and aquatic macroinvertebrates in PPR wetlands.

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References

Ackerly, D. D., and W. K. Cornwell. 2007. A trait-based approach to community assembly: partitioning of species trait values into within- and among-community components. Ecology Letters 10:135–145.

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- Anderson, D. L., and R. C. Rooney. 2019. Differences exist in bird communities using restored and natural wetlands in the Parkland Region, Alberta, Canada. *Restoration Ecology* 27:1495–1507.
- Aronson, M. F. J., C. H. Nilon, C. A. Lepczyk, T. S. Parker, P. S. Warren, S. S. Cilliers, M. A. Goddard, A. K. Hahs, C. Herzog, M. Katti, F. A. La Sorte, N. S. G. Williams, and W. Zipperer. 2016. Hierarchical filters determine community assembly of urban species pools. *Ecology* 97:2952–2963.
- Austin, J. E., and D. A. Buhl. 2011. Nest survival of American Coots relative to grazing, burning, and water depths. *Avian Conservation and Ecology* 6: art1. <http://dx.doi.org/10.5751/ACE-00472-060201>
- Ayers, C. R., K. C. Hanson-Dorr, S. O'Dell, C. D. Lovell, M. L. Jones, J. R. Suckow, and B. S. Dorr. 2015. Impacts of colonial waterbirds on vegetation and potential restoration of island habitats. *Restoration Ecology* 23:252–260.
- Azeria, E. T., D. Fortin, J. Lemaître, P. Janssen, C. Hébert, M. Darveau, and S. G. Cumming. 2009. Fine-scale structure and cross-taxon congruence of bird and beetle assemblages in an old-growth boreal forest mosaic. *Global Ecology and Biogeography* 18:333–345.
- Bolding, M. T., A. J. Kraft, D. T. Robinson, and R. C. Rooney. 2020. Improvements in multi-metric index development using a whole-index approach. *Ecological Indicators* 113:106191.
- Bowman, W. D., T. A. Theodose, J. C. Schardt, and R. T. Conant. 1993. Constraints of nutrient availability on primary production in two alpine tundra communities. *Ecology* 74:2085–2097.

Daniel and Rooney. 2020. Functional dispersion of wetland birds, invertebrates and plants more strongly influenced by hydroperiod than each other. Pre-print. Contact rooney@uwaterloo.ca

Cabra-García, J., C. Bermúdez-Rivas, A. M. Osorio, and P. Chacón. 2012. Cross-taxon congruence of α and β diversity among five leaf litter arthropod groups in Colombia. *Biodiversity and Conservation* 21:1493–1508.

Campeau, S., H. R. Murkin, and R. D. Titman. 1994. Relative importance of algae and emergent plant litter to freshwater marsh invertebrates. *Canadian Journal of Fisheries and Aquatic Sciences* 51:681–692.

Casanova, M. T., and M. A. Brock. 2000. How do depth, duration and frequency of flooding influence the establishment of wetland plant communities? *Plant Ecology* 147:237–250.

Chase, J. M., and J. A. Myers. 2011. Disentangling the importance of ecological niches from stochastic processes across scales. *Philosophical Transactions of the Royal Society B: Biological Sciences* 366:2351–2363.

Clifford, H. F. 1991. *Aquatic Invertebrates of Alberta*. University of Alberta Press, Edmonton, Alberta.

Comte, L., J. Cucherousset, S. Boulétreau, and J. D. Olden. 2016. Resource partitioning and functional diversity of worldwide freshwater fish communities. *Ecosphere* 7: e01356.

Connor, E. F., and D. Simberloff. 1979. The assembly of species communities: chance or competition. *Ecology* 60:1132.

Daniel, J., J. E. Gleason, K. Cottenie, and R. C. Rooney. 2019. Stochastic and deterministic processes drive wetland community assembly across a gradient of environmental filtering. *Oikos* 128:1158–1169.

Davis, C. A., and J. R. Bidwell. 2008. Response of aquatic invertebrates to vegetation management and agriculture. *Wetlands* 28:793–805.

Daniel and Rooney. 2020. Functional dispersion of wetland birds, invertebrates and plants more strongly influenced by hydroperiod than each other. Pre-print. Contact rooney@uwaterloo.ca

Devercelli, M., P. Scarabotti, G. Mayora, B. Schneider, and F. Giri. 2016. Unravelling the role of determinism and stochasticity in structuring the phytoplanktonic metacommunity of the Paraná River floodplain. *Hydrobiologia* 764:139–156.

Diamond, A. W. 1975. Assembly of species communities. Page in M. L. Cody and J. M. Diamond, editors. *Ecology and Evolution of Communities*. Harvard University Press, Cambridge, Massachusetts.

Dormann, C. F., M. Bobrowski, D. M. Dehling, D. J. Harris, F. Hartig, H. Lischke, M. D. Moretti, J. Pagel, S. Pinkert, M. Schleuning, S. I. Schmidt, C. S. Sheppard, M. J. Steinbauer, D. Zeuss, and C. Kraan. 2018. Biotic interactions in species distribution modelling: 10 questions to guide interpretation and avoid false conclusions. *Global Ecology and Biogeography* 27:1004–1016.

Downing, D. J., and W. W. Pettapiece. 2006. *Natural Regions and Subregions of Alberta*. Government of Alberta, Edmonton, Alberta.

Duan, M., Y. Liu, Z. Yu, J. Baudry, L. Li, C. Wang, and J. C. Axmacher. 2016. Disentangling effects of abiotic factors and biotic interactions on cross-taxon congruence in species turnover patterns of plants, moths and beetles. *Scientific Reports* 6:23511.

Euliss, N. H., J. W. Labaugh, L. H. Fredrickson, D. M. Mushet, M. K. Laubhan, G. A. Swanson, T. C. Winter, D. O. Rosenberry, and R. D. Nelson. 2004. The wetland continuum: a conceptual framework for interpreting biological studies. *Wetlands* 24:448–458.

Environment Canada, 2014. *CABIN laboratory methods: processing, taxonomy, and quality control of benthic macroinvertebrate samples*.

http://publications.gc.ca/collections/collection_2015/ec/En84-86-2014-eng.pdf

Daniel and Rooney. 2020. Functional dispersion of wetland birds, invertebrates and plants more strongly influenced by hydroperiod than each other. Pre-print. Contact rooney@uwaterloo.ca

- 433 Finke, D. L., and W. E. Snyder. 2008. Niche partitioning increases resource exploitation by
434 diverse communities. *Science* 321:1488–1490.
- 435 Fourqurean, J. W., J. C. Zieman, and G. V. N. Powell. 1992. Phosphorus limitation of primary
436 production in Florida Bay: Evidence from C: N: P ratios of the dominant seagrass
437 *Thalassia testudinum*. *Limnology and Oceanography* 37:162–171.
- 438 Fox, A. D., L. Cao, Y. Zhang, M. Barter, M. J. Zhao, F. J. Meng, and S. L. Wang. 2011.
439 Declines in the tuber-feeding waterbird guild at Shengjin Lake National Nature Reserve,
440 China - a barometer of submerged macrophyte collapse. *Aquatic Conservation: Marine and*
441 *Freshwater Ecosystems* 21:82–91.
- 442 Galatowitsch, S. M. 2006. Restoring prairie pothole wetlands: does the species pool concept
443 offer decision-making guidance for re-vegetation? *Applied Vegetation Science* 9:261–270.
- 444 Gallardo, L. I., R. P. Carnevali, E. A. Porcel, and A. S. G. Poi. 2011. Does the effect of aquatic
445 plant types on invertebrate assemblages change across seasons in a subtropical wetland?
446 *Limnetica* 29:87–98.
- 447 García, D. 2016. Birds in ecological networks: insights from bird-plant mutualistic interactions.
448 *Ardeola* 63:151–180.
- 449 Gerhold, P., J. F. Cahill, M. Winter, I. V. Bartish, and A. Prinzing. 2015. Phylogenetic patterns
450 are not proxies of community assembly mechanisms (they are far better). *Functional*
451 *Ecology* 29:600–614.
- 452 Gleason, J. E., J. Y. Bortolotti, and R. C. Rooney. 2018. Wetland microhabitats support distinct
453 communities of aquatic macroinvertebrates. *Journal of Freshwater Ecology* 33:73–82.
- 454 Gleason, J. E., and R. C. Rooney. 2017. Aquatic macroinvertebrates are poor indicators of
455 agricultural activity in northern prairie pothole wetlands. *Ecological Indicators* 81:333–339.

Daniel and Rooney. 2020. Functional dispersion of wetland birds, invertebrates and plants more strongly influenced by hydroperiod than each other. Pre-print. Contact rooney@uwaterloo.ca

- Gleason, J. E., and R. C. Rooney. 2018. Pond permanence is a key determinant of aquatic macroinvertebrate community structure in wetlands. *Freshwater Biology* 63:264–277.
- Gotelli, N. J. 2000. Null model analysis of species co-occurrence patterns. *Ecology* 81:2606.
- Gotelli, N. J., and D. J. McCabe. 2002. Species co-occurrence: a meta-analysis of J. M. Diamond's assembly rules model. *Ecology* 83:2091–2096.
- Gotelli, N. J., and K. Rohde. 2002. Co-occurrence of ectoparasites of marine fishes: a null model analysis. *Ecology Letters* 5:86–94.
- Government of Alberta. 2014. Alberta Merged Wetland Inventory. Alberta Environment and Parks, Government of Alberta, Edmonton, Alberta.
- Grace, J. B., T. M. Anderson, H. Olff, and S. M. Scheiner. 2010. On the specification of structural equation models for ecological systems. *Ecological Monographs* 80:67–87.
- Groendahl, S., and P. Fink. 2017. Consumer species richness and nutrients interact in determining producer diversity. *Scientific Reports* 7:44869.
- Guarino, R., B. Ferrario, and L. Mossa. 2005. A stochastic model of seed dispersal pattern to assess seed predation by ants in annual dry grasslands. *Plant Ecology* 178:225–235.
- Guignard, M. S., A. R. Leitch, C. Acquisti, C. Eizaguirre, J. J. Elser, D. O. Hessen, P. D. Jeyasingh, M. Neiman, A. E. Richardson, P. S. Soltis, D. E. Soltis, C. J. Stevens, M. Trimmer, L. J. Weider, G. Woodward, and I. J. Leitch. 2017. Impacts of nitrogen and phosphorus: from genomes to natural ecosystems and agriculture. *Frontiers in Ecology and Evolution* 5:70.
- Gurney, K. E. B., R. G. Clark, S. M. Slattery, and L. C. M. Ross. 2017. Connecting the trophic dots: responses of an aquatic bird species to variable abundance of macroinvertebrates in northern boreal wetlands. *Hydrobiologia* 785:1–17.

Daniel and Rooney. 2020. Functional dispersion of wetland birds, invertebrates and plants more strongly influenced by hydroperiod than each other. Pre-print. Contact rooney@uwaterloo.ca

- Hall, D. L., M. R. Willig, D. L. Moorhead, R. W. Sites, E. B. Fish, and T. R. Mollhagen. 2004. Aquatic macroinvertebrate diversity of playa wetlands: The role of landscape and island biogeographic characteristics. *Wetlands* 24:77–91.
- Hayashi, M., G. van der Kamp, and D. O. Rosenberry. 2016. Hydrology of prairie wetlands: understanding the integrated surface-water and groundwater processes. *Wetlands* 36:237–254.
- Horváth, Z., M. Ferenczi, A. Móra, C. F. Vad, A. Ambrus, L. Forró, G. Szövényi, and S. Andrikovics. 2012. Invertebrate food sources for waterbirds provided by the reconstructed wetland of Nyirkai-Hany, northwestern Hungary. *Hydrobiologia* 697:59–72.
- Hurt, G.C. and S.W. Pacala. 1995. The consequences of recruitment limitation: reconciling chance, history and competitive differences between plants. *Journal of Theoretical Biology* 176:1-12.
- Jackson, A. C., M. G. Chapman, and A. J. Underwood. 2008. Ecological interactions in the provision of habitat by urban development: whelks and engineering by oysters on artificial seawalls. *Austral Ecology* 33:307–316.
- Jorgensen, T. D., S. Pornprasertmanit, A. M. Schoemann, and Y. Rosseel. 2018. semTools: useful tools for structural equation modeling. R package version 0.5-1.
- Kantrud, H. a, and R. E. Stewart. 1984. Ecological distribution and crude density of breeding birds on prairie wetlands. *The Journal of Wildlife Management* 48:426.
- Klaassen, M., and B. A. Nolet. 2007. The role of herbivorous water birds in aquatic systems through interactions with aquatic macrophytes, with special reference to the Bewick’s Swan – Fennel Pondweed system. *Hydrobiologia* 584:205–213.

Daniel and Rooney. 2020. Functional dispersion of wetland birds, invertebrates and plants more strongly influenced by hydroperiod than each other. Pre-print. Contact rooney@uwaterloo.ca

501 Kraft, A. J., D. T. Robinson, I. S. Evans, and R. C. Rooney. 2019. Concordance in wetland
502 physicochemical conditions, vegetation, and surrounding land cover is robust to data
503 extraction approach. PLOS ONE 14: e0216343.

504 Kraft, N. J. B., P. B. Adler, O. Godoy, E. C. James, S. Fuller, and J. M. Levine. 2015.
505 Community assembly, coexistence and the environmental filtering metaphor. Functional
506 Ecology 29:592–599.

507 LaBaugh, J. W., D. O. Rosenberry, D. M. Mushet, B. P. Neff, R. D. Nelson, and N. H. Euliss.
508 2018. Long-term changes in pond permanence, size, and salinity in Prairie Pothole Region
509 wetlands: The role of groundwater-pond interaction. Journal of Hydrology: Regional
510 Studies 17:1–23.

511 Laliberte, E., P. Legendre, and B. Shipley. 2014. FD: measuring functional diversity from
512 multiple traits, and other tools for functional ecology. R package version 1.3.

513 Lee Foote, A., and C. L. Rice Hornung. 2005. Odonates as biological indicators of grazing
514 effects on Canadian prairie wetlands. Ecological Entomology 30:273–283.

515 van Leeuwen, C. H. A., Á. Lovas-Kiss, M. Ovegård, and A. J. Green. 2017. Great cormorants
516 reveal overlooked secondary dispersal of plants and invertebrates by piscivorous
517 waterbirds. Biology Letters 13:20170406.

518 Leibowitz, S. G., and K. C. Vining. 2003. Temporal connectivity in a prairie pothole complex.
519 Wetlands 23:13–25.

520 Lokemoen, J. T., and R. O. Woodward. 1992. Nesting waterfowl and water birds on natural
521 islands in the Dakotas and Montana. Wildlife Society Bulletin 20:163–171.

522 Longcore, J. R., D. G. McAuley, G. W. Pendelton, C. R. Bennatti, T. M. Mingo, and K. L.
523 Stromborg. 2006. Macroinvertebrate abundance, water chemistry, and wetland

Daniel and Rooney. 2020. Functional dispersion of wetland birds, invertebrates and plants more strongly influenced by hydroperiod than each other. Pre-print. Contact rooney@uwaterloo.ca

characteristics affect use of wetlands by avian species in Maine. *Hydrobiologia* 567:143–167.

Maestre, F. T., C. Escolar, I. Martínez, and A. Escudero. 2008. Are soil lichen communities structured by biotic interactions? A null model analysis. *Journal of Vegetation Science* 19:261–266.

Magnuson, J. J., L. B. Crowder, and P. A. Medvick. 1979. Temperature as an ecological resource. *American Zoologist* 19:331–343.

Maurer, K. M., T. W. Stewart, and F. O. Lorenz. 2014. Direct and indirect effects of fish on invertebrates and tiger salamanders in prairie pothole wetlands. *Wetlands* 34:735–745.

Maynard, D. S., K. R. Covey, T. W. Crowther, N. W. Sokol, E. W. Morrison, S. D. Frey, L. T. A. van Diepen, and M. A. Bradford. 2018. Species associations overwhelm abiotic conditions to dictate the structure and function of wood-decay fungal communities. *Ecology* 99:801–811.

Merrit, R. W., K. W. Cummins, and M. B. Berg. 2008. An introduction to the aquatic insects of North America. Fourth edition. Kendall Hunt Publishing Company, Dubuque, Iowa.

Meyer, M. D., C. A. Davis, and J. R. Bidwell. 2013. Assessment of two methods for sampling invertebrates in shallow vegetated wetlands. *Wetlands* 33:1063–1073.

Meyer, M. D., C. A. Davis, and D. Dvoretz. 2015. Response of wetland invertebrate communities to local and landscape factors in North Central Oklahoma. *Wetlands* 35:533–546.

Meyers, N. 2018. Use of water isotope tracers to characterize the hydrology of prairie wetlands in Alberta. Thesis. University of Waterloo, Waterloo, Ontario, Canada.

Daniel and Rooney. 2020. Functional dispersion of wetland birds, invertebrates and plants more strongly influenced by hydroperiod than each other. Pre-print. Contact rooney@uwaterloo.ca

546 Morissette, J. L., K. J. Kardynal, E. M. Bayne, and K. A. Hobson. 2013. Comparing bird
547 community composition among boreal wetlands: is wetland classification a missing piece
548 of the habitat puzzle? *Wetlands* 33:653–665.

549 Mushet, D. M., O. P. McKenna, J. W. LaBaugh, N. H. Euliss, and D. O. Rosenberry. 2018.
550 Accommodating state shifts within the conceptual framework of the wetland continuum.
551 *Wetlands* 38:647–651.

552 Niemuth, N. D., M. E. Estey, R. E. Reynolds, C. R. Loesch, and W. A. Meeks. 2006. Use of
553 wetlands by spring-migrant shorebirds in agricultural landscapes of North Dakota's Drift
554 Prairie. *Wetlands* 26:30–39.

555 O'Neal, B. J., E. J. Heske, and J. D. Stafford. 2008. Waterbird response to wetlands restored
556 through the conservation reserve enhancement program. *Journal of Wildlife Management*
557 72:654–664.

558 Palacio, F. X., and J. M. Girini. 2018. Biotic interactions in species distribution models enhance
559 model performance and shed light on natural history of rare birds: a case study using the
560 straight-billed reedhaunter *Limnortyx rectirostris*. *Journal of Avian Biology* 49: e01743.

561 Poff, N. L. 1997. Landscape filters and species traits: towards mechanistic understanding and
562 prediction in stream ecology. *Journal of the North American Benthological Society*
563 16:391–409.

564 Qian, H., and W. D. Kissling. 2010. Spatial scale and cross-taxon congruence of terrestrial
565 vertebrate and vascular plant species richness in China. *Ecology* 91:1172–1183.

566 R Core Team. 2019. R: A language and environment for statistical computing. R Foundation for
567 Statistical Computing, Vienna, Austria.

Daniel and Rooney. 2020. Functional dispersion of wetland birds, invertebrates and plants more strongly influenced by hydroperiod than each other. Pre-print. Contact rooney@uwaterloo.ca

568 Rao, C. R. 1982. Diversity and dissimilarity coefficients: A unified approach. Theoretical
569 Population Biology 21:24–43.

570 Reid, A. H., and W. G. Sprules. 2018. A comprehensive evaluation of *Daphnia pulex* foraging
571 energetics and the influence of spatially heterogeneous food. Inland Waters 8:50–59.

572 Rosseel, Y. 2012. lavaan: an R package for structural equation modeling. Journal of Statistical
573 Software 48:2.

574 Roy, M.-C., E. T. Azeria, D. Locky, and J. J. Gibson. 2019. Plant functional traits as indicator
575 of the ecological condition of wetlands in the Grassland and Parkland of Alberta, Canada.
576 Ecological Indicators 98:483–491.

577 Ruhí, A., E. Chappuis, D. Escoriza, M. Jover, J. Sala, D. Boix, S. Gascón, and E. Gacia. 2014.
578 Environmental filtering determines community patterns in temporary wetlands: a multi-
579 taxon approach. Hydrobiologia 723:25–39.

580 Schleuter, D., M. Daufresne, F. Massol, and C. Argillier. 2010. A user's guide to functional
581 diversity indices. Ecological Monographs 80:469–484.

582 Schoo, K. L., N. Aberle, A. M. Malzahn, and M. Boersma. 2012. Food quality affects secondary
583 consumers even at low quantities: an experimental test with larval European Lobster. PLoS
584 ONE 7: e33550.

585 Soons, M. B., A.-L. Brochet, E. Kleyheeg, and A. J. Green. 2016. Seed dispersal by dabbling
586 ducks: an overlooked dispersal pathway for a broad spectrum of plant species. Journal of
587 Ecology 104:443–455.

588 Spasojevic, M. J., and K. N. Suding. 2012. Inferring community assembly mechanisms from
589 functional diversity patterns: the importance of multiple assembly processes. Journal of
590 Ecology 100:652–661.

Daniel and Rooney. 2020. Functional dispersion of wetland birds, invertebrates and plants more strongly influenced by hydroperiod than each other. Pre-print. Contact rooney@uwaterloo.ca

- Spivak, A. C., E. A. Canuel, J. E. Duffy, and J. P. Richardson. 2009. Nutrient enrichment and food web composition affect ecosystem metabolism in an experimental seagrass habitat. PLoS ONE 4: e7473.
- Stewart, R. E., and H. A. Kantrud. 1971. Classification of natural ponds and lakes in the glaciated prairie region. Page Bureau of Sport Fisheries and Wildlife Resource Publication 92. Washington, DC.
- Thompson, R. C., B. J. Wilson, M. L. Tobin, A. S. Hill, and S. J. Hawkins. 1996. Biologically generated habitat provision and diversity of rocky shore organisms at a hierarchy of spatial scales. Journal of Experimental Marine Biology and Ecology 202:73–84.
- Tiunov, A. V., and S. Scheu. 2005. Facilitative interactions rather than resource partitioning drive diversity-functioning relationships in laboratory fungal communities. Ecology Letters 8:618–625.
- Tsai, J.-S., L. S. Venne, S. T. McMurphy, and L. M. Smith. 2012. Local and landscape influences on plant communities in playa wetlands. Journal of Applied Ecology 49:174–181.
- Urban, M. C., G. Bocedi, A. P. Hendry, J.-B. Mihoub, G. Peer, A. Singer, J. R. Bridle, L. G. Crozier, L. De Meester, W. Godsoe, A. Gonzalez, J. J. Hellmann, R. D. Holt, A. Huth, K. Johst, C. B. Krug, P. W. Leadley, S. C. F. Palmer, J. H. Pantel, A. Schmitz, P. A. Zollner, and J. M. J. Travis. 2016. Improving the forecast for biodiversity under climate change. Science 353: aad8466–aad8466.
- van der Valk, A. G. 1981. Succession in wetlands: a Gleasonian approach. Ecology 62:688–696.
- Vanausdall, R. A., and S. J. Dinsmore. 2019. Habitat associations of migratory waterbirds using restored shallow lakes in Iowa. Waterbirds 42:135.

Daniel and Rooney. 2020. Functional dispersion of wetland birds, invertebrates and plants more strongly influenced by hydroperiod than each other. Pre-print. Contact rooney@uwaterloo.ca

- 614 Wagenmakers, E.-J., and S. Farrell. 2004. AIC model selection using Akaike weights.
615 Psychonomic Bulletin & Review 11:192–196.
- 616 Wardle, D. A. 2006. The influence of biotic interactions on soil biodiversity. Ecology Letters
617 9:870–886.
- 618 Williams, N. S. G., M. W. Schwartz, P. A. Vesk, M. A. McCarthy, A. K. Hahs, S. E. Clemants,
619 R. T. Corlett, R. P. Duncan, B. A. Norton, K. Thompson, and M. J. McDonnell. 2009. A
620 conceptual framework for predicting the effects of urban environments on floras. Journal of
621 Ecology 97:4–9.
- 622 Wright, H. E. J. 1972. Quaternary history of Minnesota. Pages 515–546 in P. K. Sims and G.
623 Morey, editors. Geology of Minnesota: a centennial volume. Minnesota Geological Survey,
624 University of Minnesota, Saint Paul, Minnesota.
- 625 Zhu, L., B. Fu, H. Zhu, C. Wang, L. Jiao, and J. Zhou. 2017. Trait choice profoundly affected
626 the ecological conclusions drawn from functional diversity measures. Scientific Reports
627 7:3643.

Daniel and Rooney. 2020. Functional dispersion of wetland birds, invertebrates and plants more strongly influenced by hydroperiod than each other. Pre-print. Contact rooney@uwaterloo.ca

Table 1 – Performance of six candidate structural equation models predicting the relative influence of biological interactions and hydroperiod on community congruence. Direct influence of permanence and plants was the best model with the ΔAIC of all other models being > 9 units.

Model	Chi-square	<i>p</i> -value	AIC	ΔAIC	AIC weight
A: Hydroperiod alone structures taxon	30.983	0.006	-231.165	14.291	0.077
B: Mediated influence of hydroperiod through plants	42.022	0.000	-219.990	25.465	0.000
C: Mediated influence of hydroperiod through inverts on birds	24.093	0.020	-234.134	11.321	0.341
D: Mediated influence of hydroperiod on birds through plants and inverts	24.745	0.025	-235.475	9.980	0.667
E: Direct influence of hydroperiod and plants	12.902	0.376	-245.455	0.000	98.034
F: Direct influence of hydroperiod, and birds are structured by plants and inverts	22.220	0.035	-236.030	9.426	0.880

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Figure 1. Six candidate structural equation model to evaluate the relative influence of biological interactions and hydroperiod on community congruence.

Figure 2. Map of our study sites and region, which are situated in the northern prairie pothole region (inset map). Our 96 wetland sites represented temporary (n = 28), seasonal (n = 35), semi-permanent (n = 17), and permanent (n = 14) ponded-water permanence classes, and they covered the Grassland and Parkland Natural Regions. The number of wetlands in each permanence class matched the frequency distribution of permanence classes in the central and southern wetland inventories (Government of Alberta 2014).

Figure 3. Measurement model for the best fitting of the six candidate structural models (there is a direct influence of permanence on the functional dispersion of birds, aquatic macroinvertebrates and plants, and plants directly structure birds and aquatic macroinvertebrates functional dispersion). Unidirectional lines are standardized regression slopes while bi-directional lines are standardized variances. The dashed, unidirectional line indicates which exogenous variable was fixed to a factor loading of one. Lines in black indicate that there was a positive relationship, while red lines indicate that the relationship was negative. Line thickness reflects the magnitude of the standardized regression slopes.

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Appendix S1A. Code, scientific name, and common name of bird taxa observed at the 96 wetland sites.

Name	Scientific Name	Common Name
ALFL	<i>Recurvirostra americana</i>	Alder Flycatcher
AMAV	<i>Recurvirostra americana</i>	American Avocet
AMBI	<i>Botaurus lentiginosus</i>	American Bittern
AMCO	<i>Fulica americana</i>	American Coot
AMCR	<i>Corvus brachyrhynchos</i>	American Crow
AMGO	<i>Spinus tristis</i>	American Goldfinch
AMRE	<i>Setophaga ruticilla</i>	American Redstart
AMRO	<i>Turdus migratorius</i>	American Robin
AMWI	<i>Anas americana</i>	American Wigeon
BAIS	<i>Ammodramus bairdii</i>	Baird's Sparrow
BAOR	<i>Icterus galbula</i>	Baltimore Oriole
BARS	<i>Hirundo rustica</i>	Barn Swallow
BBMA	<i>Pica hudsonia</i>	Black-billed Magpie
BCCH	<i>Poecile atricapillus</i>	Black-capped Chickadee
BHCO	<i>Molothrus ater</i>	Brown-headed Cowbird
BLJA	<i>Cyanocitta cristata</i>	Blue Jay
BLTE	<i>Chlidonias niger</i>	Black Tern
BNST	<i>Himantopus mexicanus</i>	Black-necked Stilt
BOGU	<i>Chroicocephalus philadelphia</i>	Bonaparte's Gull
BRBL	<i>Euphagus cyanocephalus</i>	Brewer's Blackbird
BRTH	<i>Toxostoma rufum</i>	Brown Thrasher
BUFF	<i>Bucephala albeola</i>	Bufflehead
BWTE	<i>Anas discors</i>	Blue-winged Teal
CANG	<i>Branta canadensis</i>	Canada Goose
CANV	<i>Aythya valisineria</i>	Canvasback
CCSP	<i>Spizella pallida</i>	Clay-colored Sparrow
CEDW	<i>Bombycilla cedrorum</i>	Cedar Waxwing
CHSP	<i>Spizella passerina</i>	Chipping Sparrow
CITE	<i>Anas cyanoptera</i>	Cinnamon Teal
COGR	<i>Quiscalus quiscula</i>	Common Grackle
COLO	<i>Gavia immer</i>	Common Loon
CORA	<i>Corvus corax</i>	Common Raven
COYE	<i>Geothlypis trichas</i>	Common Yellowthroat
DOWO	<i>Picoides pubescens</i>	Downy Woodpecker
EAGR	<i>Podiceps nigricollis</i>	Eared Grebe
EAKI	<i>Tyrannus tyrannus</i>	Eastern Kingbird

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Name	Scientific Name	Common Name
EAPH	<i>Sayornis phoebe</i>	Eastern Phoebe
EUST	<i>Sturnus vulgaris</i>	European Starling
FISP	<i>Spizella pusilla</i>	Field Sparrow
FRGU	<i>Leucophaeus pipixcan</i>	Franklin's Gull
GADW	<i>Anas strepera</i>	Gadwall
GBHE	<i>Ardea herodias</i>	Great Blue Heron
GRCA	<i>Dumetella carolinensis</i>	Gray Catbird
GRSP	<i>Ammodramus savannarum</i>	Grasshopper Sparrow
GWTE	<i>Anas crecca</i>	Green-winged Teal
HAWO	<i>Picoides villosus</i>	Hairy Woodpecker
HOGR	<i>Podiceps auritus</i>	Horned Grebe
HOLA	<i>Eremophila alpestris</i>	Horned Lark
HOSP	<i>Passer domesticus</i>	House Sparrow
HOWR	<i>Troglodytes aedon</i>	House Wren
KILL	<i>Charadrius vociferus</i>	Killdeer
LBCU	<i>Numenius americanus</i>	Long-billed Curlew
LCSP	<i>Ammodramus leconteii</i>	Le Conte's Sparrow
LEFL	<i>Empidonax minimus</i>	Least Flycatcher
LESA	<i>Calidris minutilla</i>	Least Sandpiper
LESC	<i>Aythya affinis</i>	Lesser Scaup
LEYE	<i>Tringa flavipes</i>	Lesser Yellowlegs
LISP	<i>Melospiza lincolnii</i>	Lincoln's Sparrow
MAGO	<i>Limosa fedoa</i>	Marbled Godwit
MALL	<i>Anas platyrhynchos</i>	Mallard
MERL	<i>Falco columbarius</i>	Merlin
MODO	<i>Zenaidura macroura</i>	Mourning Dove
NESP	<i>Ammodramus nelsoni</i>	Nelson's Sparrow
NOFL	<i>Colaptes auratus</i>	Northern Flicker
NOHA	<i>Circus cyaneus</i>	Northern Harrier
NOPI	<i>Anas acuta</i>	Northern Pintail
NRWS	<i>Stelgidopteryx serripennis</i>	Northern Rough-winged Swallow
NSHO	<i>Anas clypeata</i>	Northern Shoveler
OVEN	<i>Seiurus aurocapilla</i>	Ovenbird
PIWO	<i>Dryocopus pileatus</i>	Pileated Woodpecker
RBGR	<i>Pheucticus ludovicianus</i>	Rose-breasted Grosbeak
RBGU	<i>Larus delawarensis</i>	Ring-billed Gull
RBNU	<i>Sitta canadensis</i>	Red-breasted Nuthatch
RCKI	<i>Regulus calendula</i>	Ruby-crowned Kinglet

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Name	Scientific Name	Common Name
REDH	<i>Aythya americana</i>	Redhead
REVI	<i>Vireo olivaceus</i>	Red-eyed Vireo
RENP/RHNP	<i>Phalaropus lobatus</i>	Red-necked Phalarope
RNDU	<i>Aythya collaris</i>	Ring-necked Duck
RTHA	<i>Buteo jamaicensis</i>	Red-tailed Hawk
RUBL	<i>Euphagus carolinus</i>	Rusty Blackbird
RUDU	<i>Oxyura jamaicensis</i>	Ruddy Duck
RUGR	<i>Bonasa umbellus</i>	Ruffed Grouse
RWBL	<i>Agelaius phoeniceus</i>	Red-winged Blackbird
SACR	<i>Antigone canadensis</i>	Sandhill Crane
SAVS	<i>Passerculus sandwichensis</i>	Savannah Sparrow
SORA	<i>Porzana carolina</i>	Sora
SOSP	<i>Melospiza melodia</i>	Song Sparrow
SPPI	<i>Anthus spragueii</i>	Sprague's Pipit
SWHA	<i>Buteo swainsoni</i>	Swainson's Hawk
SWSP	<i>Melospiza georgiana</i>	Swamp Sparrow
SWTH	<i>Catharus ustulatus</i>	Swainson's Thrush
TEWA	<i>Oreothlypis peregrina</i>	Tennessee Warbler
TRES	<i>Tachycineta bicolor</i>	Tree Swallow
UNKN	Unknown	Unknown
UPSA	<i>Bartramia longicauda</i>	Upland Sandpiper
VESP	<i>Pooecetes gramineus</i>	Vesper Sparrow
WAVI	<i>Vireo gilvus</i>	Warbling Vireo
WEME	<i>Sturnella neglecta</i>	Western Meadowlark
WILL	<i>Tringa semipalmata</i>	Willet
WIPH	<i>Phalaropus tricolor</i>	Wilson's Phalarope
WISN	<i>Gallinago delicata</i>	Wilson's Snipe
WTSP	<i>Zonotrichia albicollis</i>	White-throated Sparrow
YEWA	<i>Setophaga petechia</i>	Yellow Warbler
YHBL	<i>Xanthocephalus xanthocephalus</i>	Yellow-headed Blackbird

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Appendix S1B. A list of all aquatic macroinvertebrate taxa identified with taxonomic resolution.

Class	Order	Family
Insecta	Coleoptera	Curculionidae Chrysomelidae Dytiscidae Elmidae Gyrinidae Halipidae Hydraenidae Hydrophilidae Phalacridae Ptiliidae Salpingidae Scirtidae Staphylinidae
	Diptera	Anthomyiidae Ceratopogonidae Chaoboridae Chironomidae Culicidae Dixidae Dolichopodidae Empididae Ephydriidae Psychodidae Sciomyzidae Stratiomyidae Syrphidae Tabanidae Tipulidae
	Ephemeroptera	Baetidae Caenidae Siphonuridae
	Hemiptera	Corixidae Gerridae Hebridae Mesoveliidae Notonectidae Saldidae Veliidae
	Lepidoptera	Noctuidae Pyralidae

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Class	Order	Family
	Odonata	Aeshnidae Coenagrionidae Lestidae Libellulidae
	Trichoptera	Brachycentridae
	Collembola [†]	Leptoceridae Limnephilidae
Entognatha		
Arachnida	Trombidiformes	Hydrachnidia [†]
Branchipoda	Anostraca [†]	
	Conchostraca [†]	
	Notostraca	Triopsidae
Malacostraca	Amphipoda	
Ostracoda [†]		
Bivalvia	Veneroida	Sphaeriidae
Gastropoda	Basommatophora	Lymnaeidae Planorbidae
Clitellata	Hirudinea [†]	
Oligochaeta [†]		
Hydrazoa [†]		
Nematoda [‡]		
Tardigrada		

[†]Not identified to Family level

[‡]Phylum level

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Appendix S1C. Code, scientific name, and common name of plant taxa observed at the 96 wetland sites.

Code	Scientific Name	Common Name
ACHALPIN	<i>Achillea alpina</i>	Siberian Yarrow
ACHMILLE	<i>Achillea millefolium</i>	Common Yarrow
ACOCALAM	<i>Acorus calamus</i>	Sweet-Flag
AGRCRIST	<i>Agropyron cristatum</i> ssp. <i>pectinatum</i>	Crested Wheatgrass
AGRGIGAN	<i>Agrostis gigantea</i>	Redtop
AGRSCABR	<i>Agrostis scabra</i>	Ticklegrass
AGRSTRIA	<i>Agrimonia striata</i>	Roadside Agrimony
ALITRIVI	<i>Alisma triviale</i>	Northern Water Plantain
ALOEAEQUA	<i>Alopecurus aequalis</i>	Short-Awn Meadow-Foxtail
ALOPRATE	<i>Alopecurus pratensis</i>	Field Meadow-Foxtail
AMARETRO	<i>Amaranthus retroflexus</i>	Redroot Pigweed
AMEALNIF	<i>Amelanchier alnifolia</i>	Saskatoon Berry
ANAMINIM	<i>Anagallis minima</i>	Chaffweed
ANECANAD	<i>Anemone canadensis</i>	Canada Anemone
ANTPARVI	<i>Antennaria parvifolia</i>	Small-Leaf Pussytoes
ARNCHAMI	<i>Arnica chamissonis</i>	Chamisso Arnica
ARTBIENN	<i>Artemisia biennis</i>	Biennial Sagewort
ARTCAMPE	<i>Artemisia campestris</i> ssp. <i>caudata</i>	Common Sagewort
ARTLONGI	<i>Artemisia longifolia</i>	Longleaf Sagebrush
ARTLUDOV	<i>Artemisia ludoviciana</i>	Gray Sagewort
ATRPROST	<i>Atriplex prostrata</i>	Triangle Orache
AVEFATUA	<i>Avena fatua</i>	Wild Oats
BECSYZIG	<i>Beckmannia syzigachne</i> ssp. <i>syzigachne</i>	American Sloughgrass
BIDCERNU	<i>Bidens cernua</i>	Nodding Beggarticks
BOLMARIT	<i>Bolboschoenus maritimus</i>	Cosmopolitan Bulrush
BRANAPUS	<i>Brassica napus</i>	Argentine Canola
BROINERM	<i>Bromus inermis</i>	Smooth Brome
CALCANAD	<i>Calamagrostis canadensis</i> var. <i>canadensis</i>	Bluejoint
CALIPALU	<i>Callitriche palustris</i>	Vernal Water-Starwort
CALLPALU	<i>Calla palustris</i>	Water Arum
CALSTRIC	<i>Calamagrostis stricta</i> ssp. <i>inexpansa</i>	Slimstem Reedgrass
CALTPALU	<i>Caltha palustris</i>	Yellow Marsh Marigold
CAPBURSA	<i>Capsella bursa-pastoris</i>	Shepherd's Purse
CARAQUAT	<i>Carex aquatilis</i>	Water Sedge

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Code	Scientific Name	Common Name
CARATHER	<i>Carex atherodes</i>	Awed Sedge
CARATHRO	<i>Carex athrostachya</i>	Slender-Beak Sedge
CARBEBBI	<i>Carex bebbii</i>	Bebb's Sedge
CARBREVI	<i>Carex brevior</i>	Shortbeak Sedge
CARCARVI	<i>Carum carvi</i>	Wild Caraway
CARDIAND	<i>Carex diandra</i>	Two-Stamened Sedge
CAREX_SP	<i>Carex sp.</i>	Sedge
CARLACUS	<i>Carex lacustris</i>	Lakebank Sedge
CARPELLI	<i>Carex pellita</i>	Woolly Sedge
CARPRAEG	<i>Carex praegracilis</i>	Clustered Field Sedge
CARPRATI	<i>Carex praticola</i>	Meadow Sedge
CARRETRO	<i>Carex retrorsa</i>	Knotsheath Sedge
CARSARTW	<i>Carex sartwellii</i>	Sartwell's Sedge
CARSYCHN	<i>Carex sychnocephala</i>	Many-Headed Sedge
CARUTRIC	<i>Carex utriculata</i>	Northwest Territory Sedge
CERARVEN	<i>Cerastium arvense</i>	Field Chickweed
CHAANGUS	<i>Chamerion angustifolium ssp. angustifolium</i>	Fireweed
CHEALBUM	<i>Chenopodium album</i>	Common Lambsquarters
CHECAPIT	<i>Chenopodium capitatum</i>	Strawberry Blite
CHERUBRU	<i>Chenopodium rubrum</i>	Red Goosefoot
CICMACUL	<i>Cicuta maculata var. angustifolia</i>	Spotted Water Hemlock
CIRARVEN	<i>Cirsium arvense</i>	Canada Thistle
CIRVULGA	<i>Cirsium vulgare</i>	Bull Thistle
COLLINEA	<i>Collomia linearis</i>	Narrow-Leaf Mountain Trumpet
COMPALUS	<i>Comarum palustre</i>	Purple Marshlocks
CORSERIC	<i>Cornus sericea ssp. sericea</i>	Red Osier Dogwood
CRETECTO	<i>Crepis tectorum</i>	Narrow-Leaf Hawk's Beard
DESCESPI	<i>Deschampsia cespitosa ssp. cespitosa</i>	Tufted Hairgrass
DESSOPHI	<i>Descurainia sophia</i>	Flaxweed Tansymustard
ECHCRUSG	<i>Echinochloa crus-galli</i>	Barnyard Grass
ELACOMMU	<i>Elaeagnus commutata</i>	Silverberry
ELEACICU	<i>Eleocharis acicularis</i>	Needle Spikerush
ELEPALUS	<i>Eleocharis palustris</i>	Creeping Spikerush
ELYREPEN	<i>Elymus repens</i>	Quackgrass
ELYTRACH	<i>Elymus trachycaulus</i>	Slender Wheatgrass
EPICAMPE	<i>Epilobium campestre</i>	Smooth Spike-Primrose
EPICILIA	<i>Epilobium ciliatum ssp.</i>	Fringed Willow-Herb

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Code	Scientific Name	Common Name
	<i>glandulosum</i>	
EPILEPTO	<i>Epilobium leptophyllum</i>	Bog Willow-Herb
EIPALUS	<i>Epilobium palustre</i>	Marsh Willow-Herb
EQUARVEN	<i>Equisetum arvense</i>	Common Horsetail
EQUFLUVI	<i>Equisetum fluviatile</i>	River Horsetail
EQUHYMAL	<i>Equisetum hyemale ssp. affine</i>	Scouring Horsetail
EQUPALUS	<i>Equisetum palustre</i>	Marsh Horsetail
EQUPRATE	<i>Equisetum pratense</i>	Meadow Horsetail
ERIGRACI	<i>Eriophorum gracile</i>	Slender Cotton-Grass
ERILONCH	<i>Erigeron lonchophyllus</i>	Low-Meadow Fleabane
ERIPHILA	<i>Erigeron philadelphicus</i>	Philadelphia Fleabane
ERUGALLI	<i>Erucastrum gallicum</i>	Common Dog-Mustard
ERYCHEIR	<i>Erysimum cheiranthoides</i>	Wallflower Mustard
EURCONSP	<i>Eurybia conspicua</i>	Western Showy Aster
FAGESCUL	<i>Fagopyrum esculentum</i>	Common Buckwheat
FALCONVO	<i>Fallopia convolvulus</i>	Black Bindweed
FALSCAND	<i>Fallopia scandens</i>	Climbing False Buckwheat
FESSAXIM	<i>Festuca saximontana</i>	Rocky Mountain Fescue
FRAVESCA	<i>Fragaria vesca</i>	Woodland Strawberry
FRAVIRGI	<i>Fragaria virginiana ssp. glauca</i>	Wild Strawberry
GALTETRA	<i>Galeopsis tetrahit</i>	Brittle-Stem Hedge-Nettle
GALTRIFI	<i>Galium trifidum</i>	Small Bedstraw
GALTRIFL	<i>Galium triflorum</i>	Sweet Bedstraw
GEUALEPP	<i>Geum aleppicum</i>	Yellow Avens
GEUMACRO	<i>Geum macrophyllum var. princisum</i>	Large-Leaf Avens
GEURIVAL	<i>Geum rivale</i>	Purple Avens
GLYBOREA	<i>Glyceria borealis</i>	Northern Manna Grass
GLYGRAND	<i>Glyceria grandis</i>	American Manna Grass
GLYSTRIA	<i>Glyceria striata</i>	Fowl Manna Grass
GRANEGLE	<i>Gratiola neglecta</i>	Clammy Hedge-Hyssop
GRISQUAR	<i>Grindelia squarrosa</i>	Curlytop Gumweed
HIEUMBAL	<i>Hieracium umbellatum</i>	Canadian Hawkweed
HIPVULGA	<i>Hippuris vulgaris</i>	Common Mare's Tail
HORJUBAT	<i>Hordeum jubatum</i>	Foxtail Barley
HORVULGA	<i>Hordeum vulgare</i>	Common Barley
JUNBALTI	<i>Juncus balticus ssp. ater</i>	Baltic Rush
JUNLONGI	<i>Juncus longistylus</i>	Long-Style Rush
JUNNODOS	<i>Juncus nodosus</i>	Jointed Rush
JUNVASEY	<i>Juncus vaseyi</i>	Vasey's Rush

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Code	Scientific Name	Common Name
KRALANAT	<i>Krascheninnikovia lanata</i>	Winterfat
LACSERRI	<i>Lactuca serriola</i>	Prickly Lettuce
LATOCHRO	<i>Lathyrus othroleucus</i>	Cream Peavine
LEMMINOR	<i>Lemna minor</i>	Common Duckweed
LEMTRISU	<i>Lemna trisulca</i>	Ivy-Leaf Duckweed
LINUSITA	<i>Linum usitatissimum</i>	Common Flax
LYCASPER	<i>Lycopus asper</i>	Rough Water Hore-Hound
LYSCILIA	<i>Lysimachia ciliata</i>	Fringed Yellow Loosestrife
LYSMARIT	<i>Lysimachia maritima</i>	Sea Milkwort
LYSTHYRS	<i>Lysimachia thyrsiflora</i>	Tufted Yellow Loosestrife
MAISTELL	<i>Maianthemum stellatum</i>	False Solomon's Seal
MALNEGLE	<i>Malva neglecta</i>	Roundleaf Mallow
MEDSATIV	<i>Medicago sativa</i>	Alfalfa
MELALBUS	<i>Melilotus albus</i>	White Sweet-Clover
MELIL_SP	<i>Melilotus sp.</i>	Sweet-Clover
MENARVEN	<i>Mentha arvensis</i>	Wild Mint
MONNUTTA	<i>Monolepis nuttalliana</i>	Nuttall's Poverty-Weed
MUHRICHA	<i>Muhlenbergia richardsonis</i>	Mat Muhly
MULOBLO	<i>Mulgedium oblongifolium</i>	Blue Lettuce
PENPROCE	<i>Penstemon procerus</i>	Pincushion Beardtongue
PERAMPHI	<i>Persicaria amphibia</i>	Water Knotweed
PERLAPAT	<i>Persicaria lapathifolia</i>	Curlytop Knotweed
PETFRIGI	<i>Petasites frigidus var. sagittatus</i>	Arctic Sweet Colt's-Foot
PHAARUND	<i>Phalaris arundinacea</i>	Reed Canary Grass
PHLPRATE	<i>Phleum pratense</i>	Common Timothy
PLAHYPER	<i>Platanthera hyperborea</i>	Northern Bog Orchid
PLAMAJOR	<i>Plantago major</i>	Broadleaf Plantain
PLASCOUL	<i>Plagiobothrys scouleri</i>	Scouler's Popcornflower
POAPALUS	<i>Poa palustris</i>	Fowl Bluegrass
POAPRATE	<i>Poa pratensis</i>	Kentucky Bluegrass
POLAVICU	<i>Polygonum aviculare ssp. depressum</i>	Prostrate Knotweed
POLRAMOS	<i>Polygonum ramosissimum</i>	Bushy Knotweed
POPBALSA	<i>Populus balsamifera</i>	Balsam Poplar
POPTREMU	<i>Populus tremuloides</i>	Trembling Aspen
POTANSER	<i>Potentilla anserina</i>	Silverweed Cinquefoil
POTGRAMI	<i>Potamogeton gramineus</i>	Variableleaf Pondweed
POTNORVE	<i>Potentilla norvegica</i>	Norwegian Cinquefoil
POTRICHA	<i>Potamogeton richardsonii</i>	Richardson's Pondweed

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Code	Scientific Name	Common Name
POTRIVAL	<i>Potentilla rivalis</i>	Brook Cinquefoil
PYRASARI	<i>Pyrola asarifolia</i>	Pink Wintergreen
RANAQUAT	<i>Ranunculus aquatilis</i> var. <i>diffusus</i>	Water Buttercup
RANCYMBA	<i>Ranunculus cymbalaria</i>	Alkali Buttercup
RANGMELI	<i>Ranunculus gmelinii</i>	Gmelin's Buttercup
RANMACOU	<i>Ranunculus macounii</i>	Macoun's Buttercup
RANSCELE	<i>Ranunculus sceleratus</i> var. <i>multifidus</i>	Celeryleaf Buttercup
RANUN_SP	<i>Ranunculus</i> sp.	Buttercup
RIBLACUS	<i>Ribes lacustre</i>	Prickly Currant
RIBOXYAC	<i>Ribes oxycanthoides</i>	Canadian Gooseberry
RORPALUS	<i>Rorippa palustris</i>	Marsh Yellowcress
ROSACICU	<i>Rosa acicularis</i> ssp. <i>sayi</i>	Prickly Rose
RUBPUBES	<i>Rubus pubescens</i>	Dwarf Red Raspberry
RUBSACHA	<i>Rubus sachalinensis</i> var. <i>sachalinensis</i>	Common Red Raspberry
RUMBRITA	<i>Rumex britannica</i>	Greater Water Dock
RUMCRISP	<i>Rumex crispus</i>	Curly Dock
RUMEX_SP	<i>Rumex</i> sp.	Dock
RUMFUEGI	<i>Rumex fueginus</i>	Golden Dock
RUMOCCID	<i>Rumex occidentalis</i>	Western Dock
RUMSALIC	<i>Rumex salicifolius</i>	Willow Dock
SAGCUNEA	<i>Sagittaria cuneata</i>	Arum-Leaf Arrowhead
SALBEBBI	<i>Salix bebbiana</i>	Bebb's Willow
SALDISCO	<i>Salix discolor</i>	Pussy Willow
SALEXIGU	<i>Salix exigua</i>	Sandbar Willow
SALIX_SP	<i>Salix</i> sp.	Willow
SALLASIA	<i>Salix lasiandra</i> var. <i>lasiandra</i>	Pacific Willow
SALLUCID	<i>Salix lucida</i>	Shining Willow
SALMACCA	<i>Salix maccalliana</i>	McCalla's Willow
SALPETIO	<i>Salix petiolaris</i>	Meadow Willow
SALPLANI	<i>Salix planifolia</i>	Plain-Leaf Willow
SALPSEUD	<i>Salix pseudomonticola</i>	False Mountain Willow
SALPYRIF	<i>Salix pyrifolia</i>	Balsam Willow
SALRUBRA	<i>Salicornia rubra</i>	Red Samphire
SALSERIS	<i>Salix serissima</i>	Autumn Willow
SCHACUTU	<i>Schoenoplectus acutus</i> var. <i>acutus</i>	Hard-Stem Bulrush
SCHOE_SP	<i>Schoenoplectus</i> sp.	Bulrush
SCHPUNGE	<i>Schoenoplectus pungens</i> var.	Common Three-Square Bulrush

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Code	Scientific Name	Common Name
	<i>pungens</i>	
SCHTABER	<i>Schoenoplectus tabernaemontani</i>	Soft-Stem Bulrush
SCIMICRO	<i>Scirpus microcarpus</i>	Panicked Bulrush
SCOFESTU	<i>Scolochloa festucacea</i>	Common Rivergrass
SCUGALER	<i>Scutellaria galericulata</i>	Marsh Skullcap
Sd_Forb	-	Unidentifiable seedling/forb
SENVULGA	<i>Senecio vulgaris</i>	Common Groundsel
SISMONTA	<i>Sisyrinchium montanum</i>	Mountain Blue-Eyed Grass
SIUSUAVE	<i>Sium suave</i>	Common Water Parsnip
SOLALTIS	<i>Solidago altissima ssp. gilvocanescens</i>	Canada Goldenrod
SONARVEN	<i>Sonchus arvensis</i>	Perennial Sow-Thistle
SONASPER	<i>Sonchus asper</i>	Prickly Sow-Thistle
SONOLERA	<i>Sonchus oleraceus</i>	Annual Sow-Thistle
SPAANGUS	<i>Sparganium angustifolium</i>	Narrow-Leaf Bur-Reed
SPAEURYC	<i>Sparganium eurycarpum</i>	Giant Bur-Reed
SPESALIN	<i>Spergularia salina</i>	Salt Sandspurry
SPHINTER	<i>Sphenopholis intermedia</i>	Slender Wedgegrass
SPOCRYPT	<i>Sporobolus cryptandrus</i>	Sand Dropseed
STAPILOS	<i>Stachys pilosa var. pilosa</i>	Hairy Hedgenettle
STELONGI	<i>Stellaria longifolia</i>	Long-Leag Starwort
STEMEDIA	<i>Stellaria media</i>	Common Chickweed
SUACALCE	<i>Suaeda calceoliformis</i>	Paiuteweed
SYMBOREA	<i>Symphyotrichum boreale</i>	Northern Bog Aster
SYMERICO	<i>Symphyotrichum ericoides var. pansum</i>	White Heath Aster
SYMLANCE	<i>Symphyotrichum lanceolatum var. hesperium</i>	White Panicle Aster
SYMOCCID	<i>Symphoricarpos occidentalis</i>	Western Snowberry
SYMPUNIC	<i>Symphyotrichum puniceum var. puniceum</i>	Purplestem Aster
TANVULGA	<i>Tanacetum vulgare</i>	Common Tansy
TAROFFIC	<i>Taraxacum officinale</i>	Common Dandelion
TEPPALUS	<i>Tephrosia palustris</i>	Marsh Fleabane
THLARVEN	<i>Thlaspi arvense</i>	Field Pennycress
TRADUBIU	<i>Tragopogon dubius</i>	Goat's Beard
TRIHYPRI	<i>Trifolium hybridum</i>	Alsike Clover
TRIMARIT	<i>Triglochin maritima</i>	Seaside Arrow-Grass
TYPLATIF	<i>Typha latifolia</i>	Common Cattail
UNKASTER	<i>Asteraceae</i>	Unidentifiable Asteraceae

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Code	Scientific Name	Common Name
UNKBRASS	<i>Brassicaceae</i>	Unidentifiable Brassicaceae
UNKCARYO	<i>Caryophyllaceae</i>	Unidentifiable Caryophyllaceae
UNKPOACE	<i>Poaceae</i>	Unidentifiable Poaceae
URTDIOCA	<i>Urtica dioica ssp. gracilis</i>	Stinging Nettle
UTRVULGA	<i>Utricularia vulgaris ssp. macrorhiza</i>	Common Bladderwort
VERPEREG	<i>Veronica peregrina</i>	Purslane Speedwell
VERSCUTE	<i>Veronica scutellata</i>	Marsh Speedwell
VICAMERI	<i>Vicia americana</i>	American Vetch
VIOADUNC	<i>Viola adunca</i>	Early Blue Violet
VIOCANAD	<i>Viola canadensis</i>	Canada White Violet
VIOSOROR	<i>Viola sororia var. affinis</i>	Common Blue Violet

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Appendix S2A. List of bird functional traits; traits values are reported in Anderson (2017)¹.

Group Class	Group Code	Meaning
Diet Classification	Carniv	Carnivore
Diet Classification	Herbiv	Herbivore
Diet Classification	Omniv	Omnivore
Migration Habitat	Res	Resident
Migration Habitat	TrpclMgr	Tropical Migrant
Primary Diet	AqInsect	Aquatic Insects
Primary Diet	AqPlnts	Aquatic Plants
Primary Diet	Carrion	Carrion
Primary Diet	Fish	Fish
Primary Diet	Fruit	Fruit
Primary Diet	Grains	Grains
Primary Diet	Insects	Insects
Primary Diet	Nuts	Nuts
Primary Diet	Plants	Plants
Primary Diet	Seeds	Seeds
Primary Diet	SmAnml	Small Animals
Primary Feeding Habit	ArlFrgr	Aerial Forager
Primary Feeding Habit	ArlPrst	Aerial Pursuit
Primary Feeding Habit	BrkGln	Bark Gleaner
Primary Feeding Habit	Dbblr	Dabbler
Primary Feeding Habit	FlgGln	Foliage Gleaner
Primary Feeding Habit	GrndFrg	Ground Forager
Primary Feeding Habit	GrndGln	Ground Gleaner
Primary Feeding Habit	HPatrol	Hawk and Patrol
Primary Feeding Habit	HvrGln	Hovers and Gleaners
Primary Feeding Habit	Insect	Insectivore
Primary Feeding Habit	Prbs	Probbing
Primary Feeding Habit	SrfcDvr	Surface Diver
Primary Feeding Habit	Stlknng	Stalking
Primary Habitat	Field	Field
Primary Habitat	Forest	Forest
Primary Habitat	Grsslnd	Grassland
Primary Habitat	LkPd	Lake or Pond
Primary Habitat	Marsh	Marsh
Primary Habitat	OpnWood	Open Woodland
Primary Habitat	RvrStrm	River or Stream
Primary Habitat	Scrub	Scrub
Primary Habitat	Shrln	Shoreline
Primary Nesting Location	Bank	Bank

¹ Anderson, D. 2017. Monitoring wetland integrity and restoration success with avifauna in the Prairie Pothole Region of Alberta, Canada. University of Waterloo

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Group Class	Group Code	Meaning
Primary Nesting Location	Cavity	Cavity
Primary Nesting Location	Fltng	Floating
Primary Nesting Location	Grnd	Ground
Primary Nesting Location	Reeds	Reeds
Primary Nesting Location	Shrb	Shrub
Primary Nesting Location	Strctr	Structure
Primary Nesting Location	Tree	Tree
Wetland Status	Facul	Facultative
Wetland Status	FaculDry	Facultative Dry
Wetland Status	FaculWet	Facultative Wet

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Appendix S2B. List of aquatic macroinvertebrates functional traits; traits values are reported in Gleason (2017)².

Group Class	Group Code	Meaning
Feeding Groups	ENGULF	Engulfing Predators
Feeding Groups	FCOLL	Filtering Collectors
Feeding Groups	GCOLL	Gathering Collectors
Feeding Groups	SCRAPE	Scrapers
Feeding Groups	SHRED	Shredders
Feeding Groups	PARA	Ecotoparasites
Feeding Groups	PIERCE	Piercing Predators
Behavioural Guilds	BUR	Burrowers
Behavioural Guilds	CLIMB	Climber
Behavioural Guilds	CLING	Clinger
Behavioural Guilds	DIVER	Diver
Behavioural Guilds	SKATE	Skater
Behavioural Guilds	SPRAWLER	Sprawler
Behavioural Guilds	SWIM	Swimmer
Desiccation Strategy Groups	TOLE	Tolerators
Desiccation Strategy Groups	WETL	Wet Layers
Desiccation Strategy Groups	DRYL	Dry Layers
Desiccation Strategy Groups	DISP	Dispersers

² Gleason, J. E. 2017. Aquatic macroinvertebrate communities and diversity patterns in the Northern Prairie Pothole Region. University of Waterloo.

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Appendix S2C. List of plant functional traits; traits values are reported in Bolding (2018)³.

Group Class	Group Code	Meaning
Wetland Plant Indicator Status	Forb	Forb
Wetland Plant Indicator Status	Graminoid	Graminoid
Wetland Plant Indicator Status	Vine	Vine
Wetland Plant Indicator Status	Hardwood	Hardwood
Wetland Plant Indicator Status	Tall_Shrub	Tall Shrub
Wetland Plant Indicator Status	Low_Shrub	Low Shrub
Wetland Plant Indicator Status	BroadLeaf_Emergent	BroadLeaf Emergent
Wetland Plant Indicator Status	Floating_Plant	Floating Plant
Wetland Plant Indicator Status	FreeFloating_Plant	FreeFloating Plant
Wetland Plant Indicator Status	NarrowLeaf_Emergent	NarrowLeaf Emergent
Wetland Plant Indicator Status	Robust_Emergent	Robust Emergent
Wetland Plant Indicator Status	Submersed_Plant	Submersed Plant
Vegetative Reproduction	Vegetative_Reproduction	Vegetative Reproduction
Nitrogen Fixing	Nitrogen_Fixer	Nitrogen Fixer
Litter Decomposal	Recalcitrant_Litter	Recalcitrant Litter
Native Status	Native_Graminoid	Native Graminoid
Native Status	Exotic_Graminoid	Exotic Graminoid
Native Status	Native_Perennials	Native Perennials
Native Status	Exotic_Perennials	Exotic Perennials
Native Status	Native_Annuals_Biennials	Native Annuals Biennials
Native Status	Exotic_Annuals_Biennials	Exotic Annuals and Biennials
Dispersal Mechanism	Anemochory	Anemochory
Dispersal Mechanism	Hydrochory	Hydrochory
Dispersal Mechanism	Zoochory	Zoochory
Dispersal Mechanism	Multiple_Dispersal	Multiple Dispersal

³ Bolding, M. 2018. Vegetation based assessment of wetland condition in the Prairie Pothole Region. University of Waterloo.