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## **Wetlands**

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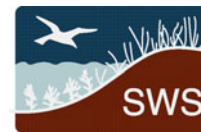
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# Weak Relationships Between Environmental Factors and Invertebrate Communities in Constructed Wetlands

Lauren E. Culler · Robert F. Smith · William O. Lamp

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**Abstract** Growing awareness of essential wetland functions is providing support for wetland construction projects. Bio-monitoring using invertebrates is a common way to evaluate project success, but relationships between wetland invertebrates and environmental factors are often weak. In recently constructed wetlands on Maryland's Eastern Shore, we tested the hypothesis that focusing on predator and primary consumer invertebrate assemblages versus the entire community would elucidate stronger relationships with environmental factors. Despite variation in factors that are hypothesized to control wetland invertebrates (e.g., vegetation and tendency to dry), our results indicated weak relationships between environmental factors and the structure and composition of the entire community as well as predator and primary consumer assemblages separately. Examining the entire community and individual assemblages, however, showed that invertebrates were influenced by temporal factors. We propose that a complex interaction between wetland shape/size, local weather, and seasonal changes may have driven invertebrate

community patterns among wetlands. Such interactions would complicate bioassessments of wetlands that differ in size, hydrology, and local weather conditions. Further study of specific factors controlling wetland invertebrates and developing new metrics that incorporate seasonal environmental change could improve biomonitoring results and thus management strategies aimed at enhancing wetland function.

**Keywords** Invertebrates · Constructed wetlands · Biomonitoring · Predators · Primary consumers

## Introduction

Growing public awareness of the essential role of wetlands for improving water quality, controlling floods, and supporting diverse aquatic communities is providing support for wetland construction projects worldwide (Brinson and Malvarez 2002; Zedler 2006; Moreno-Mateos et al. 2012; Mitsch and Hernandez 2013). The economic value of wetlands for ecosystem goods and services exceeds that of the most valuable terrestrial ecosystems (Costanza et al. 1997; Moreno-Mateos et al. 2012; Junk et al. 2013) and freshwaters harbor a large part of the earth's biodiversity, including many endemic plant and animal species (Junk et al. 2013). Many of these taxa are crucial for supporting wetland food webs, controlling nuisance species, and decomposing plant and animal material (Batzer and Wissinger 1996).

Success of wetland construction projects is typically evaluated through post-construction biomonitoring of ecological conditions including plants, soils, water chemistry, and the abundance and taxonomic composition of animals that colonize wetlands (Rader et al. 2001; Batzer et al. 2005). Knowledge of taxa present and the characteristics of the biotic community (e.g., richness, density) can serve as indicators of ecosystem health (Sharitz and Batzer 1999) and help identify

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L. E. Culler · R. F. Smith · W. O. Lamp  
Department of Entomology, University of Maryland, 4112 Plant  
Sciences Bldg., College Park, MD 20742-4454, USA

*Present Address:*

L. E. Culler (✉)  
Department of Biological Sciences, Dartmouth College, 78 College  
Street, Hanover, NH 03755-3563, USA  
e-mail: leculler@gmail.com

*Present Address:*

R. F. Smith  
Massachusetts Cooperative Fish and Wildlife Research Unit,  
Department of Environmental Conservation, University of  
Massachusetts, Room 225, 160 Holdsworth Way, Amherst,  
MA 01003-9285, USA

effective restoration strategies. The ubiquitous occurrence, high species richness, ability to integrate short and long term environmental changes, and compatibility with inexpensive sampling equipment make aquatic invertebrates useful bioindicators of stream ecosystem health (Bonada et al. 2006), but their utility for wetland bioassessment remains questionable (Batzer 2013).

Studies examining how wetland invertebrates respond to constructed wetland habitats are common (e.g., Spieles and Mitsch 2000; Balcombe et al. 2005; Villagrán-Mella et al. 2006; Stewart and Downing 2008; Moreno-Mateos et al. 2012). Results from individual studies detect relationships between abiotic habitat characteristics and the distribution and abundance of wetland invertebrates (e.g., Spieles and Mitsch 2000; Stewart and Downing 2008; Mereta et al. 2012) but consistent, unequivocal relationships have yet to emerge (e.g., Tangen et al. 2003; Batzer et al. 2004; Kratzer and Batzer 2007; Batzer 2013). Wetland habitats cycle through seasonal conditions (e.g., wet to dry) in a semi-predictable manner, and wetland invertebrates are well adapted to these variable conditions (Wiggins et al. 1980; Batzer 2013). Temporal changes in wetland environmental characteristics can therefore drive patterns in community structure and composition at a particular point in time for that wetland (Batzer 2013) and can obscure inter-site comparisons of the relationships between wetland invertebrate communities and abiotic conditions.

Wetland invertebrate communities consist of primary consumer taxa that feed on live vascular plants, algae, bacteria, fungi, and detritus formed from these and other dead organisms (Batzer and Wissinger 1996) and predator taxa that feed on primary consumers. Our primary goal was to determine if predators and primary consumer assemblages would show clearer relationships with abiotic factors than the entire community. We predicted that structure and composition of the primary consumer assemblage would be related to abiotic factors, such as nutrient levels, pH, and conductivity (Mizuno et al. 1982; Campeau et al. 1994; Gabor et al. 1994; Batty and Younger 2007), that affect their basal resources. We further predicted that predator assemblages would be less related to abiotic factors and mostly influenced by biotic factors, such as primary consumer density or composition. We also examined how time and its potential interaction with abiotic factors affected patterns in the primary consumer and predator assemblages.

We analyzed a 3-year dataset of monthly (March–August) invertebrate samples from nine recently constructed wetlands on the Eastern Shore of Maryland. We tested if invertebrate predator and primary consumer richness and density varied 1) among wetlands with different abiotic characteristics and 2) among months. We performed a post-hoc analysis of the community data to investigate the potentially complicated interactions between invertebrate community composition and the environmental conditions in each wetland while

accounting for the effect of time and seasonality. Based on our results, we suggest a framework for examining the relationships between invertebrate communities and environmental conditions in wetlands that incorporates the complex seasonal interactions between wetland shape/size and weather.

## Methods

### Study Area

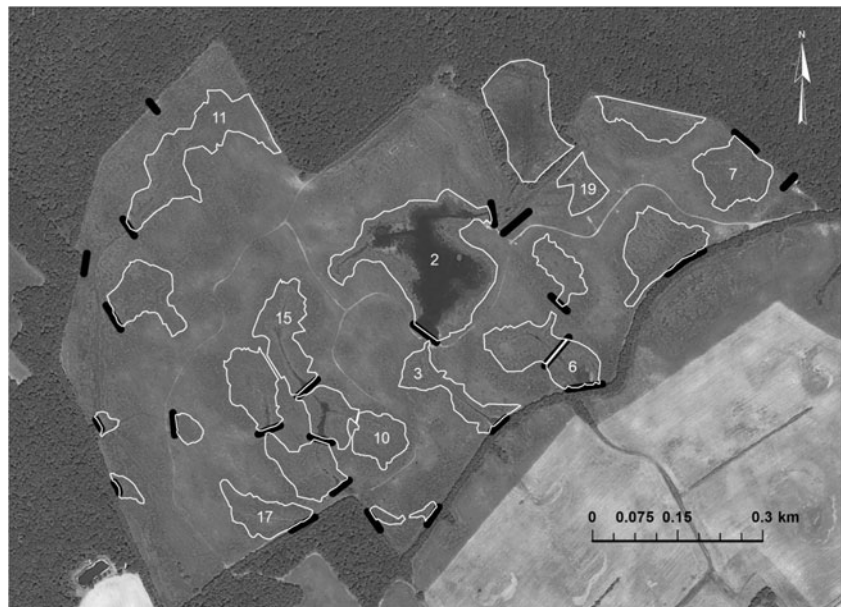
The Jackson Lane Restoration Site is located in the Choptank River watershed in Caroline County, Maryland (39°03'11.9"N, 75°44'50.2"W). Aerial photography revealed that the site consisted of several seasonal depressional wetlands prior to agricultural conversion in the 1970's. In 2003, The Nature Conservancy, U.S. Fish & Wildlife Service, Maryland Department of the Environment, and the Natural Resource Conservation Service reconstructed approximately 30 wetland "cells" at this site. Restoration activities began in August 2003 and included plugging drainage ditches with 23 earthen ditch plugs (Fig. 1). Coarse woody debris was placed in the wetlands to provide microhabitat and straw was added to deter establishment of cattails (*Typha* spp.). The project goal was to recreate natural geomorphology and hydrology to provide suitable habitat for wetland plants, animals, and microorganisms.

### Sampling Methods

In 2005, 2006, and 2007 we measured environmental characteristics and sampled invertebrate communities in nine of the 23 constructed wetlands (Fig. 1) in March, April, May, June, July, and August, as long as they were not dry (Online Resource Table 1). pH and specific conductivity ( $\mu\text{S}/\text{cm}$ ) were measured using a handheld YSI Model 63 Probe (YSI Inc., Yellow Springs, Ohio) during each monthly sampling event for each year of the project. At the same time, water samples were collected in acid washed bottles and returned on ice to the Wye Research and Education Center for analysis. Each sample was put through a 0.45  $\mu\text{m}$  filter and analyzed for ppm of total nitrogen (TN), total phosphorus (TP), chlorine ( $\text{Cl}^-$ ), and sulfate ( $\text{SO}_4^{2-}$ ) using standard methods (USEPA 1979; Parsons et al. 1984).

Habitat was visually assessed in each wetland during each monthly sampling event (Stranko et al. 2007). Percent of wetted area of each wetland that was covered with metaphyton algae, coarse woody debris, and vegetation (emergent and submerged) were each estimated to the nearest 5 %. Water depth (cm) was measured at the same location in the center of each wetland once or twice a month from January 2005 to December 2007 (D. Samson, unpublished data). Single measures or the average of two measures for each month were used as the monthly measure of depth. The location where

**Fig. 1** Map of the Jackson Lane restoration site in Caroline County, Maryland (39°03'11.9" N, 75°44'50.2"W). Constructed wetland locations are indicated by white outlines and the nine wetlands sampled are labeled by number. Black lines represent the approximate locations of ditch plugs. Map was created from GIS data collected by Towson University in 2004 (see [Methods](#)) and modified to represent the full wetland perimeters observed during the study period (2005–2007) based on visual observations



depth was monitored was not necessarily the deepest location in each wetland, and thus, measurements of 0 cm depth were sometimes recorded when invertebrate and chemistry samples were taken. A hydrological metric that described the tendency for each wetland to dry was determined by estimating the percent of sample dates when wetland water levels were at or above 50 % of the maximum level for all depth measurements (20 to 26 measures per year in each wetland) between January and December in each year separately (D. Samson, unpublished data). Approximate wetland area (ha) was calculated in ArcGIS 10.1 using GPS boundary data from Towson University, and modified by Dr. Doug Samson (The Nature Conservancy) in the spring of 2004 after a particularly wet winter. Thus, estimated wetland areas represent a single measure of the area when each wetland was at its designed capacity.

We sampled invertebrates monthly in each wetland using 20 sweeps of a 500  $\mu\text{m}$  D-net. We allocated the 20 sweeps by habitat type (metaphyton algae, coarse woody debris, vegetation, or open water, described above) to obtain a representative sample of invertebrates in the entire wetland. A sweep consisted of using the D-net (0.3 m width) to disturb the bottom for approximately 1 m and then passing back through the disturbed area with the net to capture dislodged invertebrates. This resulted in an area of approximately 0.3  $\text{m}^2$  sampled with each sweep. All 20 sweeps were combined in a 3.8 L sample jar and preserved with 80 % ethyl alcohol.

Prior to sorting and subsampling, all large debris and vegetation were rinsed off and removed from the sample to facilitate subsampling procedures. King and Richardson (2002) found that a  $\geq 200$  individual fixed count subsample from a composite sample most effectively provided quality macroinvertebrate data for wetland bioassessment. The entire sample was spread evenly across a  $7 \times 7$  square gridded tray (one square = 16  $\text{cm}^2$ ). The

sample debris from randomly selected individual squares was placed in a tray and sorted under magnification using a dissecting scope.

We removed and counted all macroinvertebrates from the first randomly selected square. A second randomly selected square was sorted if a total of 300 macroinvertebrates was not found after sorting the first square and this process continued until  $\geq 300$  macroinvertebrates were removed. All macroinvertebrates were identified to the lowest practical taxonomic level (usually genus) using local and regional keys and each taxon was classified as a predator, primary consumer, or neither, according to Merritt et al. (2008). Aquatic beetles from the family Hydrophilidae change from predators to consumers as they grow from larvae to adults, and thus were classified as a consumer if an adult was found and a predator if a larva was found.

Microcrustaceans (Subclass Copepoda, Order Cladocera, and Class Ostracoda) retained in the 500  $\mu\text{m}$  D-net were counted and removed from only the first square and were not included in the subsample count of macroinvertebrates. The high abundance of microcrustaceans would have led to under-sampling of the macroinvertebrates if they were included in the 300 specimen subsamples. Microcrustaceans make up a large part of the primary consumer invertebrate assemblage, and abundances of these taxa were enumerated and included in the community analyses (see below). These taxa were not identified past subclass and were classified as primary consumers.

#### Data Analysis

##### *Assumption About Abiotic Habitat Characteristics*

Multivariate analysis of abiotic habitat characteristics of the Jackson Lane wetlands was done to test our assumption that

**Table 1** Chemical, physical, and habitat characteristics of wetlands sampled at the Jackson Lane Preserve, 2005–2007

Wetland	pH	Sp. Cond (µS/cm)		Chloride (ppm)		Sulfate (ppm)		Total N (ppm)		Total P (ppm)		% days ≥ half-full			Depth (cm)		% metaphyton		% CWD		% vegetation			
		Avg	Range	Avg	Range	Avg	Range	Avg	Range	Avg	Range	Avg	Range	'05	'06	'07	Avg	Range	Avg	Range	Avg	Range		
2	6.5–7.4	71.1	34.3–147.2	5.5	1.3–20.1	1.6	0.2–4.9	4.4	1.0–26.3	0.32	0.05–1.81	3.68	91	96	48	48.2	0.0–68.5	0.0	0.0–0.0	5.0	0.0–10.0	30.0	10.0–80.0	
3	7.0	6.3–7.3	68.8	27.7–115.0	4.1	1.1–9.3	1.8	0.4–4.2	4.8	0.9–21.5	0.48	0.06–2.79	0.85	70	65	40	50.4	7.3–79.0	2.3	0.0–20.0	13.3	0.0–30.0	33.7	20.0–55.0
6	7.0	6.7–7.3	67.7	38.1–146.7	4.7	2.0–19.5	1.4	0.4–2.8	3.6	1.0–25.9	0.28	0.04–2.10	0.57	50	65	44	53.7	0.0–85.0	1.4	0.0–25.0	1.7	0.0–20.0	33.6	0.0–60.0
7	6.9	6.1–7.5	63.9	28.5–95.3	2.3	0.2–6.6	0.7	0.1–2.3	3.6	1.1–18.1	0.33	0.06–1.34	1.09	62	69	44	39.1	17.8–58.5	1.7	0.0–25.0	0.0	0.0–0.0	87.3	40.0–100.0
10	6.9	6.1–7.4	63.9	11.5–100.2	3.2	0.3–6.3	1.4	0.4–3.8	3.4	0.9–10.2	0.39	0.06–1.09	0.57	48	62	40	21.4	13.0–32.0	22.5	0.0–70.0	6.3	0.0–30.0	80.0	20.0–100.0
11	4.9	4.4–6.2	39.4	18.9–60.0	3.2	1.7–6.0	1.1	0.1–4.3	1.8	0.8–2.8	0.21	0.02–0.69	1.90	59	62	40	35.0	0.0–51.5	1.9	0.0–25.0	0.0	0.0–0.0	56.2	40.0–90.0
15	6.9	6.4–7.6	60.8	34.0–104.7	3.6	0.3–9.9	1.4	0.3–3.6	2.3	0.9–4.8	0.25	0.04–0.58	1.17	82	77	44	53.5	24.8–71.5	3.9	0.0–30.0	0.4	0.0–5.0	79.6	35.0–100.0
17	7.1	6.6–8.5	71.5	31.9–104.4	3.9	0.7–9.9	1.3	0.3–3.5	4.3	0.9–25.2	0.59	0.05–3.26	0.77	77	69	40	30.6	0.0–49.5	14.7	0.0–60.0	0.9	0.0–10.0	58.2	25.0–95.0
19	6.9	6.0–7.7	58.9	19.5–128.6	3.2	0.2–7.4	1.3	0.1–5.0	2.5	0.8–4.7	0.19	0.04–0.49	0.32	60	65	40	36.6	12.0–58.5	2.1	0.0–25.0	2.5	0.0–30.0	67.9	20.0–95.0

Average (Avg) and Range (minimum and maximum) are reported except for Area (ha) and % days at or above half-full  
CWD is coarse woody debris

environmental conditions differed between wetlands. Monthly measures of pH, specific conductivity, chloride, sulfate, total nitrogen, total phosphorus, depth, percent metaphyton algae, percent coarse woody debris, and percent vegetation, yearly measures of percent of days at or above half-full, and the single measure of wetland area were used in a partial redundancy analysis (RDA) to determine if these abiotic habitat characteristics differed between wetlands (CANOCO version 5.0, Biometris – Plant Research International, The Netherlands and Petr Šmilauer, Czech Republic). The environmental measurements were used as the response variables and the identity of the wetland from which the samples were taken (a categorical variable) was used as the predictor variable. Month and year were used as covariates, and the response variables were centered and standardized. A Detrended Correspondence Analysis (DCA) indicated that a linear (RDA) model was more suited than a unimodal (Canonical Correspondence Analysis, CCA) model for this direct gradient analysis (gradient lengths less than 3, Lepš and Šmilauer 2003). A Monte Carlo test with 9,999 unconstrained permutations was used to determine if wetland identity explained a significant portion of the variance in environmental measurements between samples.

*Variation in Invertebrate Richness and Density*

Richness and density were calculated for each monthly sample from each wetland for the entire invertebrate community and for the predator and primary consumer assemblages individually. Invertebrate total richness was calculated as the total number of macroinvertebrate and microcrustacean taxa from the 300 individual and single square subsamples, respectively. Richness of the predator and primary consumer assemblages were the number of macroinvertebrate and microcrustacean taxa from each of those groups. Microcrustaceans were only identified to one of three taxa, thus any bias in calculating overall richness resulting from the use of a single square subsample for the microcrustaceans was likely minimal (over 80 % of all samples had ≥2 microcrustacean taxa).

Density of invertebrates (No. individuals/m<sup>2</sup>) was calculated as:

$$\frac{Count \times \frac{49}{No.squares}}{6m^2}$$

where *Count* = number of individuals counted in the subsample, *No. squares* = the number of squares sorted to reach ≥300 individuals for the subsample, 49 = the total number of squares in the sample, and 6 m<sup>2</sup> = total area sampled in the original sweep sample. Density of microcrustaceans was calculated the same way, but *No. squares* = 1 since only the first square of

the subsample was sorted for this group. Total invertebrate density was the sum of macroinvertebrate and microcrustacean densities, and the densities for the predator and primary consumer assemblages were the sums of the densities of taxa belonging to each group.

Prior to testing how total, predator, and consumer richness and density varied among wetlands and months, we calculated a Pearson correlation coefficient between each of the richness response variables (total, predator, and consumer richness) and each of the density response variables (total, predator, and consumer density) to determine how response variables were related to each other within each analysis (PROC CORR, SAS v.9.3). Based on the results, we conducted two two-way analyses of variance (ANOVA) and Tukey's post-hoc multiple comparisons to test for effects of month and wetland on total invertebrate 1) richness and 2) density (PROC MIXED, SAS v.9.3). We used multivariate analyses of variance (MANOVA) to test for effects of month and wetland on 1) predator and primary consumer richness simultaneously and 2) predator and primary consumer density simultaneously (PROC GLM, SAS v.9.3). When a significant treatment effect was found in a MANOVA, results from simultaneously conducted two-way ANOVAs on the response variables independently were examined. If appropriate, we used results from univariate Tukey's post-hoc multiple comparisons to determine differences between treatment levels (months and wetlands) for each response variable (predator richness, consumer richness, predator density, and consumer density) individually (PROC GLM, SAS v.9.3). Density data were square root transformed to meet assumptions of normality and homogeneity of variances. Pearson correlation coefficients were examined between the response variables in the MANOVAs to ensure that variables (e.g., predator richness and consumer richness) were not highly correlated. Year was included as a random factor in all analyses to control for the variance in annual responses. Wetland 10 was dry in August in 2005, 2006, and 2007, resulting in an incomplete factorial design. Thus, wetland 10 was excluded from these analyses. Samples without sorting information (Online Resource Table 1) were excluded from the density measures but were included in analyses of richness.

#### *Community Composition and Environmental Conditions*

Post-hoc multivariate analyses of the relationships between community composition and 1) environmental measures and 2) wetland identity as predictor variables were conducted to determine if abiotic factors or the individual wetland explained patterns in invertebrate community composition. Each monthly sample of invertebrates (March to August) for 3 years (2005–2007) were analyzed with a partial CCA (CANOCO version 5.0, Biometris – Plant Research International, The Netherlands and Petr Šmilauer, Czech Republic). Taxon

density of invertebrates was used as the dependent variable. Samples without sorting information (Online Resource Table 1) were excluded from the analysis, which resulted in the exclusion of two rare taxa (1 individual of each taxon) that were found in only one of the excluded samples. Also, four samples contained no predators and were excluded from the CCA done on the predator assemblage. The same environmental measurements used in the RDA (see above) or wetland identity were used as the independent variables in the analyses examining compositional differences among wetlands. The month and year that each sample was collected were used as categorical covariates in both sets of analyses. Separate analyses were performed for 1) the entire invertebrate community, 2) the consumer assemblage, and 3) the predator assemblage. Adult and larval beetles for all taxa were included as separate taxonomic units in each partial CCA even if their trophic status did not change between life stages. We did this expecting that changes in the abundance of larval and adult coleopteran taxa within a year would result in temporal shifts in community composition accounted for by the covariables. A DCA indicated that a unimodal model was appropriate (gradient lengths greater than 3, Lepš and Šmilauer 2003). For each analysis, the taxon densities were square root transformed due to differences in densities between microcrustacean and invertebrate taxa (McCune and Grace 2002). A Monte Carlo permutation test with 9,999 unconstrained permutations was used to determine if the independent variables explained a significant portion of the variance in the community or assemblage datasets.

## **Results**

### **Invertebrate Communities**

From all of our samples we identified a total of 122 taxonomic units (Online Resource Table 1). Representatives of 7 insect orders and 39 insect families were found in the nine wetlands sampled in addition to 5 families of freshwater snails (Gastropoda) and one family of Amphipoda. Copepoda, Cladocera, and Ostracoda (microcrustaceans) accounted for 98.2 % of the overall estimated density of invertebrates sampled. Of the 122 taxonomic units identified, 76 were classified as predators and 45 were classified as primary consumers (Annelida and Nematoda were not classified).

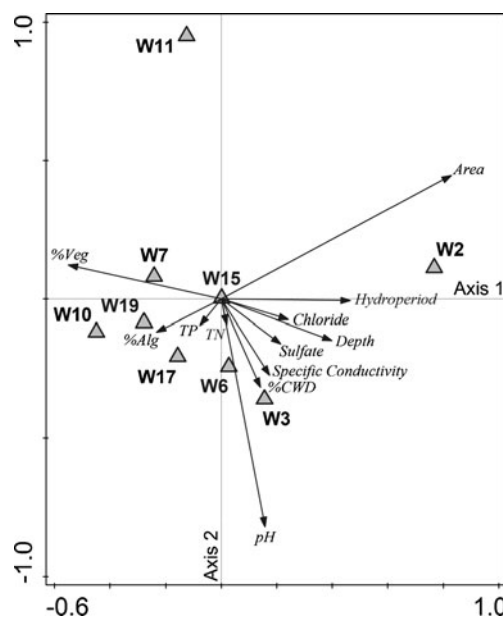
### **Abiotic Habitat Characteristics**

The measured abiotic characteristics varied among wetlands (Table 1). Average pH of most wetlands was generally close to neutral except in wetland 11, which was more acidic than the other wetlands (Table 1). Average specific conductivity was also generally similar among all wetlands except wetland 11

(Table 1). Minimum values ranged from 11.5 to 38.1  $\mu\text{S}/\text{cm}$ , and maximum values ranged from 60.0 to 146.7  $\mu\text{S}/\text{cm}$ . Chloride concentration was highest in wetland 2 and lowest in wetland 7 (Table 1) and ranged from 0.2 ppm in wetland 7 and 19 to 20.1 ppm in wetland 2 (August of 2007). Average sulfate concentrations ranged from 0.7 ppm in wetland 7 to 1.8 ppm in wetland 3 (Table 1). Minimum and maximum values were generally consistent among wetlands. Average total nitrogen ranged from 1.8 ppm in wetland 11 to 4.8 ppm in wetland 3 (Table 1). Minimum values were similar among wetlands, but maximum values ranged from 2.8 ppm in wetland 11 to 26.3 ppm in wetland 2. Average total phosphorus ranged from 0.19 ppm in wetland 19 to 0.59 ppm in wetland 17 (Table 1). Minimum concentrations were generally similar among all wetlands but maximum concentrations ranged from 0.49 ppm at wetland 19 to 3.26 ppm in wetland 17. The measured areas of the wetlands ranged from 0.32 ha (wetland 19) to 3.68 ha (wetland 2, Table 1, Fig. 1). Percent of days with water levels at or above half full ranged from 40 % (several wetlands in 2007) to 96 % (wetland 2 in 2006, Table 1). Wetland 10 was always dry in August. In 2007, 7 out of 9 wetlands had dried by August (Online Resource Table 1). Average measured depths during the study ranged from 21.4 to 53.7 cm (Table 1). Several wetlands had measures of 0 cm for minimums, but as stated above, this did not mean that the wetland was completely dry. Maximum depths ranged from 32.0 to 85.0 cm.

Habitat types also varied among wetlands (Table 1). Average percent of the wetland with metaphyton algae ranged from 0 to 22.5 %. All wetlands contained no metaphyton algae at some point during the sampling regime, and the maximum algal amounts ranged from 0 to 70 %. Coarse woody debris was less prevalent than metaphyton algae and its average coverage ranged from 0 to 13.3 %. Maximum percent coarse woody debris was 30.0 % (wetlands 3, 10, and 19). Vegetation (*Scirpus*, *Ludwigia*, *Juncus*, *Eleocharis*) was the most dominant habitat feature and its average coverage ranged from 30 to 87.3 %. Six of the 9 wetlands sampled had maximum vegetation coverage estimates greater than or equal to 90.0 %.

The wetland sampled explained 43.6 % of the total variance in environmental measurements among samples (Fig. 2). The time covariates explained 22.7 % of the total variance in environmental measurements, but the 2005-year and April-month covariates were linearly dependent and ignored in the analysis. The wetland sampled explained a significant portion of variance in the environmental measurements among samples (pseudo- $F=11.4$ ,  $p=0.0001$ ). Wetlands were generally separated along the first axis by percent of days at or above half-full, wetland area, and percent vegetation (Fig. 2). The second axis separated the wetlands by pH; most likely because of the acidic conditions found in wetland 11.



**Fig. 2** Ordination biplot from the partial RDA of environmental measurements using wetland as the independent variable. Wetlands are represented by centroids (gray triangles) and labeled with a W and the number identifying the wetland. TP is total phosphorus, TN is total nitrogen, %Alg is percent metaphyton algae, %CWD is percent coarse woody debris, and %Veg is percent vegetation. The biplot represents 68.0 % of total variance explained by wetland (39.7 % and 28.3 % by the first and second axes, respectively)

#### Variation in Invertebrate Richness and Density

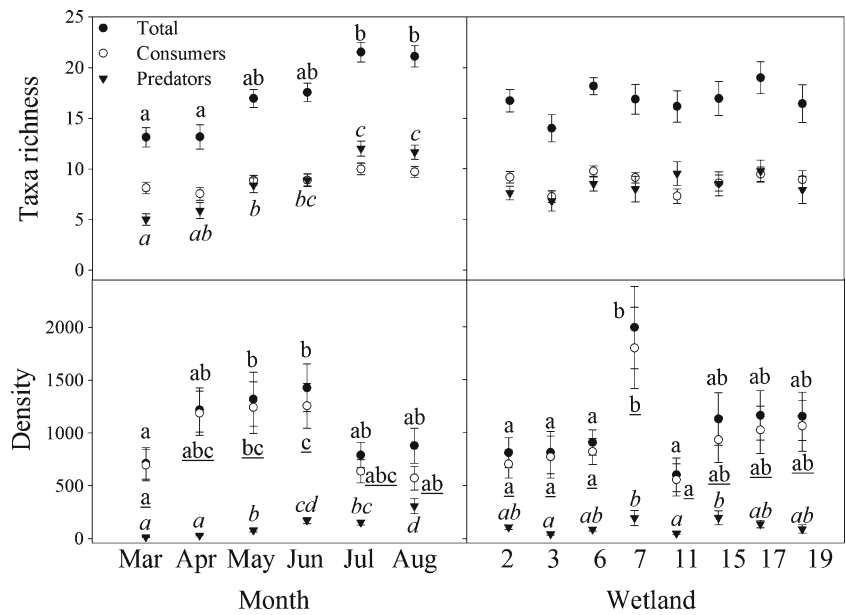
The Pearson correlation analyses showed that several of the response variables were highly correlated. All richness values were significantly correlated ( $p<0.05$ ). The Pearson correlation coefficient was 0.91 for total taxa richness with predator richness and 0.79 for total taxa richness with consumer richness. The correlation coefficient for predator and consumer richness was 0.46. The correlations between total density and consumer density ( $r=0.99$ ) and total density and predator density ( $r=0.32$ ) were significant ( $p<0.05$ ), but the correlation between predator and consumer density ( $r=0.15$ ) was not significant ( $p=0.09$ ).

Analyses indicated a significant effect of month on total invertebrate community richness ( $F_{5, 76}=10.23$ ,  $p<0.001$ , Fig. 3), but no main effect of wetland ( $F_{7, 76}=1.23$ ,  $p=0.30$ ), and no interaction between month and wetland ( $F_{35, 76}=0.53$ ,  $p=0.98$ ). Multiple mean comparisons showed that total richness per sample, averaged among all wetlands ( $\pm 1\text{SEM}$ ), increased from March ( $13.13\pm 0.97$ ) through August ( $21.12\pm 1.04$ , Fig. 3).

The MANOVA examining predator and consumer richness as response variables indicated a significant effect of month ( $F_{10, 150}=6.81$ , Wilks'  $\lambda=0.47$ ,  $p<0.0001$ ) but no significant effect of wetland ( $F_{14, 150}=1.65$ , Wilks'  $\lambda=0.75$ ,  $p=0.07$ ) or interactive effects of wetland and month ( $F_{70, 150}=0.57$ , Wilks'  $\lambda=0.62$ ,  $p=1.0$ ). Simultaneously conducted univariate



**Fig. 3** Total, consumer, and predator taxa richness (*top panel*) and density (*bottom panel*) by month (*left panel*) and wetland (*right panel*). Each point represents mean taxa richness per sample or density by month or wetland from 2005 to 2007. Bars represent  $\pm 1$  standard error of the mean. Letters indicate significant differences ( $p < 0.05$ ) calculated using a Tukey's correction for post-hoc multiple comparisons for total (*bold*), predator (*italics*), and consumer (*underline*) richness and density



analyses indicated no effect of month on consumer richness ( $F_{5, 76} = 1.96, p = 0.10$ ), but did find a significant effect of month on predator richness ( $F_{7, 76} = 15.99, p < 0.0001$ ). Predator richness per sample, averaged among all wetlands ( $\pm 1$ SEM), increased from March ( $5.00 \pm 0.56$ ) through August ( $11.65 \pm 0.69$ , Fig. 3). Consumer richness averaged among all wetlands, remained relatively constant at a mean of 8.76 taxa per sample (range: 7.54–10.00) among all months.

Analyses indicated significant effects of month ( $F_{5, 72} = 4.30, p = 0.0018$ ) and wetland ( $F_{7, 72} = 4.17, p = 0.0007$ , Fig. 3) on density of the entire invertebrate community, but no significant interaction ( $F_{35, 72} = 0.94, p = 0.57$ ). Multiple mean comparisons showed that mean density of all taxa (per  $m^2$ ) averaged among all wetlands ( $\pm 1$ SEM), generally increased from March ( $711.59 \pm 154.07$ ) until June ( $1429.36 \pm 227.80$ ) and then decreased in July ( $790.83 \pm 119.12$ ) and August ( $881.16 \pm 167.19$ , Fig. 3). Additionally, mean density (per  $m^2$ ), averaged among all months ( $\pm 1$ SEM), was highest in wetland 7 ( $1992.08 \pm 388.56$ ), and lowest in wetlands 2 ( $809.61 \pm 140.19$ ), 3 ( $812.15 \pm 199.36$ ), 6 ( $907.30 \pm 10.16$ ), and 11 ( $601.78 \pm 158.44$ , Fig. 3).

The MANOVA indicated main effects of month ( $F_{10, 142} = 16.44$ , Wilks'  $\lambda = 0.21, p < 0.0001$ ) and wetland ( $F_{14, 142} = 3.48$ , Wilks'  $\lambda = 0.55, p < 0.0001$ ) and a significant interaction between month and wetland ( $F_{70, 142} = 1.38$ , Wilks'  $\lambda = 0.35, p = 0.05$ ) on predator and consumer density. Simultaneous ANOVAs indicated that the interaction was driven by interactive effects of month and wetland on predator density ( $F_{35, 72} = 1.90, p = 0.011$ ) but not consumer density ( $F_{35, 72} = 0.90, p = 0.63$ ). Univariate analyses indicated a significant effect of month ( $F_{5, 72} = 4.42, p = 0.0014$ ) and wetland ( $F_{7, 72} = 3.54, p = 0.0025$ ) on consumer density (Fig. 3). Mean consumer density (per  $m^2$ ), averaged among all wetlands ( $\pm 1$ SEM), followed similar patterns as total density, and increased from

March ( $697.29 \pm 153.54$ ) until June ( $1257.39 \pm 212.28$ ) and decreased by August ( $572.56 \pm 110.68$ , Fig. 3). Additionally, mean consumer density (per  $m^2$ ), averaged among months, was highest in wetland 7 ( $1797.38 \pm 384.20$ ) and lowest in wetlands 2 ( $702.49 \pm 132.18$ ), 3 ( $769.97 \pm 198.13$ ), 6 ( $820.29 \pm 121.61$ ), and 11 ( $554.41 \pm 151.90$ ). We also examined main effects on predator density and found a significant effect of month ( $F_{5, 72} = 34.24, p < 0.0001$ ) and wetland ( $F_{7, 72} = 4.66, p = 0.0002$ , Fig. 3). Mean predator density (per  $m^2$ ), averaged among wetlands ( $\pm 1$ SEM), generally increased from March ( $14.29 \pm 3.79$ ) and April ( $30.89 \pm 6.81$ ) through August ( $308.61 \pm 70.97$ , Fig. 3). Additionally, mean predator density (per  $m^2$ ), averaged among months, was highest in wetlands 7 ( $194.70 \pm 71.90$ ) and 15 ( $196.02 \pm 65.28$ ) and lowest in wetlands 3 ( $42.19 \pm 10.99$ ) and 11 ( $47.37 \pm 12.70$ ). We suggest cautious interpretation of main effects for mean predator density because month effects are dependent on wetland and vice versa.

#### Community Composition and Environmental Conditions

Six separate CCAs were conducted using predator taxa, primary consumer taxa, and the entire invertebrate community in two sets of analyses examining environmental measures and wetland identity as predictor variables. The permutation test was significant for five analyses, but the environmental variables explained only a small portion of the total variance in the community or assemblage data in all analyses. The August (month) and 2007 (year) covariates were linearly dependent and ignored in each of the analyses. The low amount of variability explained for the entire invertebrate community and each assemblage prevents meaningful interpretations from an ordination of the data, so bi-plots were not generated for analysis.

Environmental measurements explained 14.5 % of the total variance in the invertebrate community data. The Monte Carlo permutation test showed that the environmental measurements explained a significant, although small, portion of the variance of the invertebrate community data among samples (pseudo-F=1.6,  $p=0.0001$ ). The environmental variables also explained a significant, although small, portion of total variance in the predator (variance explained=17.9 %, pseudo-F=2.0,  $p=0.0001$ ) and primary consumer (variance explained=13.9 %, pseudo-F=1.5,  $p=0.0026$ ) assemblage data as well. Wetland identity explained 7.9 % of the total variance in the invertebrate community data. The Monte Carlo permutation test showed that wetland identity explained a significant, although small, portion of the variance of the invertebrate community data among samples (pseudo-F=1.3,  $p=0.0085$ ). Wetland identity explained a significant, although small, portion of total variance in the predator assemblage (variance explained=20.1 %, pseudo-F=1.7,  $p=0.0001$ ) but not the primary consumer assemblage (variance explained=7.1 %, pseudo-F=1.1,  $p=0.171$ ). The time covariates (month and year) explained 15.5 %, 20.1 % and 14.9 % of the total variation in the entire invertebrate community, predator, and consumer assemblages respectively for both sets of analyses.

## Discussion

Invertebrates colonized all of the wetlands at Jackson Lane shortly after restoration, a pattern that is typical for wetland habitats (Batzer et al. 2005; Stewart and Downing 2008). The measured environmental characteristics of the wetlands, specifically percent of days at or above half full, size (area), percent vegetation, and pH, differed among the wetlands, although pH was similar in all wetlands except for wetland 11. Thus, we believe our study design would have allowed us to detect relationships between the environmental conditions of the wetlands and the invertebrate community if such relationships were present.

The only differences in invertebrate community structure and composition among wetlands were the mean densities of the entire invertebrate community and the mean densities of the primary consumer assemblage, despite the differences in wetland environmental characteristics. No significant differences in richness of any group were found among wetlands and post-hoc multivariate analyses of the composition of predator and consumer assemblages did not show a clearer relationship with the measured environmental variables than the entire community. The partial CCAs for each assemblage and the entire community showed that the environmental measures explained a significant portion of the variance in the macroinvertebrate community data, but the portion of the variance explained for each was likely too small to be biologically relevant. This suggested that invertebrate community

composition was weakly related to the environmental measures included in this study.

A recent and comprehensive synthesis by Batzer (2013) highlighted the lack of predictable patterns of wetland invertebrates with environmental factors in several well-studied wetland systems. Focusing on smaller trophic groups did not elucidate stronger relationships between environmental characteristics and the invertebrate assemblage, despite our extensive dataset. The close proximity of wetlands may have caused the weak relationships between abiotic habitat characteristics and invertebrate richness and composition. The two furthest wetlands (7 and 17, Fig. 1) are an estimated 887 m apart (measured with ArcGIS 10.1, between the boundaries shown in Fig. 1). Flight capable taxa are generally capable of moving these distances. Wetland proximity and occasional connectedness during high water events suggest that movement among wetlands may have occurred at a high rate, potentially leading to assemblage homogenization among wetlands and obscuring more subtle relationships between the invertebrate community and wetland environmental characteristics (Van de Meutter et al. 2007). Stochastic colonization events for passive dispersers can lead to divergent communities among wetlands (Ruhí et al. 2013), but the connectedness through overland flow likely allowed the most abundant passive dispersers in this study, i.e., microcrustaceans, to readily colonize all the studied wetlands.

Hydrology is often mentioned as a potential control on wetland invertebrates (Batzer 2013) but we found no differences in richness and composition for all taxonomic groups among wetlands despite variation in the percent of days that each wetland remained at or above half-full. Hydrology is hypothesized to control invertebrate communities because certain taxa are intolerant to drying conditions, and typically, wetlands that stay wet for longer periods of time tend to have higher richness (Williams 1996; Brooks 2000; Stendera et al. 2012). Wetland 10 was dry in August of every year, but its mean richness in the other months (averaged among the 3 years) was not different from other wetlands that did not dry (Online Resource Figure 1). Although it is intuitive for a hydrologic gradient to explain patterns in invertebrate communities (Batzer 2013), invertebrates may be less sensitive to the intermediate hydrological conditions measured in our study.

Vegetation is also cited as an important factor controlling wetland invertebrate community structure and composition (Batzer 2013). Percent of submergent and emergent vegetation differed among the wetlands and could explain the differences in densities of total invertebrates and primary consumers among wetlands. Individual mean comparisons showed the highest densities of total invertebrates and primary consumers in the wetland with the highest percent vegetation cover (wetland 7), and the lowest densities in wetlands with lower percent vegetation cover (wetlands 2, 3, 6, and 11). We

found no compositional or richness differences among wetlands however, so these density differences may be the result of taxon independent responses to local habitat conditions in each wetland, including plant-mediated factors such as resource availability and structural habitat (Sharitz and Batzer 1999). Wetland invertebrates tend to be generalists that feed on whatever source of carbon is most prevalent (Batzer 2013). Wetlands with higher plant cover may generate more detritus and microorganisms that are important sources of food for wetland primary consumer invertebrates (Sharitz and Batzer 1999). Alternatively, these density differences could be related to crowding as a result of dry down, but we were unable to disentangle this from other factors in our study.

One emerging pattern was how the structure and composition of the entire community and the individual assemblages responded to temporal factors. We measured differences in macroinvertebrate richness and density among months, but community composition was only slightly better explained by the time covariates (month and year) than the environmental variables. The strong correlation between total and predator richness and the lack of an effect of month on consumer richness suggested that increases in predator richness over the season, a pattern that is common in wetland systems (Williams 1996; Brooks 2000), drove the increases in total invertebrate richness. Predator density also increased from March through August, whereas consumer density increased through June and then rapidly decreased in July and August. Food availability may have limited predator density early in the spring, but the increase in consumer density through June may have provided enough food resources to allow an increase in predator richness and density. Similarly, the decreased density of consumers in late summer may have resulted from increased predation as predator density increased and more predator taxa colonized the wetlands. Primary consumer density may have increased early in the year before a diverse and dense assemblage of predators colonized the wetlands (Culler and Lamp 2009).

While we present no definitive causal relationships between temporal changes in the predator and primary consumer assemblages, focusing on the entire invertebrate community may ignore patterns that are important for assessing and monitoring wetland ecosystems. Our results suggested that temporal changes in the richness and density of the entire community are related to the seasonality of individual assemblages and predator-prey dynamics at the assemblage level (Batzer 1998). Future research directed at manipulating wetland predator and primary consumer richness and density may provide empirical evidence to elucidate causal relationships between these groups.

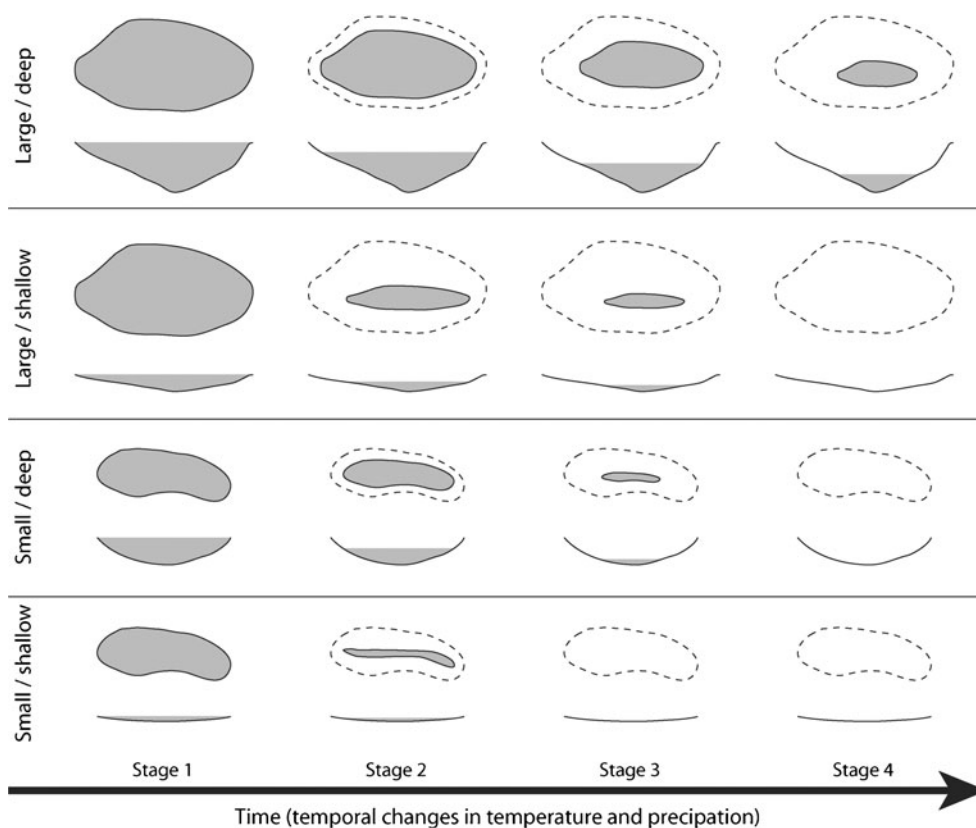
Month and year did not explain a large portion of the variance in community composition among the wetlands in our study, but temporal factors related to environmental conditions may have great potential for explaining patterns of invertebrate communities within wetlands. Wetlands change temporally in a predictable pattern and the processes of filling and

drying are major drivers of invertebrate community composition in wetland ecosystems (Batzer 2013). From late-winter through summer, the water level drops, temperature increases, dissolved oxygen decreases, volume (i.e., habitable space) decreases, and biological processes change within wetlands. Changes in wetland fauna along this trajectory are well studied (Wiggins et al. 1980; Miller et al. 2008). Wetland shape and size partly set initial conditions since these characteristics determine volume, depth, and other physical aspects of the wetland. Wetland dry-down is determined by local weather conditions (i.e., temperature, precipitation, etc.) as well as local environmental conditions (e.g., soils, land-use). Thus, the dynamic interaction between temporal fluctuations (daily and yearly) in precipitation and temperature and wetland size and shape likely cause environmental conditions (i.e., cues species use for colonization, growth, and emigration) to differ among wetlands in a way that obscures direct comparisons among wetlands.

Given that initial conditions may differ based on wetland size/shape and that geographically distant wetlands may experience different weather patterns, point measures of environmental conditions and community structure among wetlands may be insufficient for comparing wetlands for ecological studies or bioassessments. For example, a small wetland will likely dry down faster and get smaller earlier in the year than a large/deep wetland (Fig. 4). Thus, the stage 2 large/deep wetland (Fig. 4) may have different structural and functional properties than a stage 2 small wetland at the same calendar date (Brooks 2000; Hansson et al. 2005). Similarly, point measures during winter or spring, when wetlands are generally full, will likely miss patterns of colonization that occur as the wetland dries down. We found that the predator community was richer later than earlier in the year; early season samples may not capture differences in community structure among wetlands. Seasonal changes in environmental conditions also limit meaningful comparisons between point measurements at different times of the year. For example, in Fig. 4, the large/deep wetland in stage 4 may be most similar in size to the small/deep wetland in stage 2, but seasonal difference in weather conditions likely cause water temperatures and other environmental properties of the wetlands to differ. Thus, the environmental conditions in large and small wetlands may never be the same within a particular year. We posit that the focus on point measures may help explain the inconsistent response by wetland invertebrate communities to environmental conditions (Batzer 2013).

We hypothesize that summary measures of the trajectory of conditions from winter to summer may improve wetland comparisons. By using the calendar month that samples were taken, we did not adequately represent the interaction of all the environmental factors that change with time and the physical structure of the wetland (depth, shape, and volume) that likely shaped the invertebrate communities in our study system. Detailed measures of temporal changes in weather (air

**Fig. 4** Representation of the dry down process of wetlands with different sizes and shapes. *Small and large* refer to the area of the wetland when full. Each stage represents a fixed point in time consistent among each type of wetland. *Dashed lines* represent the perimeter of the wetland when it is full. *Gray areas* show the water level within the wetland. An aerial (*top half*) and cross section (*bottom half*) is provided for each wetland at each stage. Only four scenarios are shown even though wetland size and shape vary along a gradient



temperature and precipitation patterns), wetland volume and depth, and environmental conditions may have allowed us to assess the conditions along a trajectory of change and make comparisons among wetlands by examining 1) points in time along the trajectory when conditions were most similar or 2) the trajectories themselves.

The dynamic relationship between weather and wetland shape/size through time is even more complex when considering inter-year variation in weather. The environmental conditions in our wetlands on a particular calendar date (i.e., month) were not the same among years in our study. Wetlands dried faster in 2007 because of drought, and thus, conditions in the same month between that year and in 2005 and 2006 differed substantially. Thus, any metrics describing temporal trends must be able to account for inter-year variation.

The lack of clear reproducible relationships between environmental factors and invertebrate communities for wetland bioassessments is well documented (Batzer 2013). Given our hypothesis that the dynamic interaction between wetland shape/size and weather contributes to the lack of understanding, we believe that future work developing bioassessment methods for wetland invertebrate communities must incorporate the types of temporal interactions we describe above. At a minimum, detailed measures of within and between year variations in local weather and wetland size/shape should be included as covariates, but a metric that characterizes the trajectory of environmental and invertebrate community seasonal

changes would be ideal. Doing so will likely require region specific analytical methods and reference conditions, similar to what is done for bioassessments of stream ecosystems (Barbour and Gerritsen 2006). Furthermore, wetland size and shape can be influenced by human activities such as water withdrawals or agriculture (Jackson 2006) and restoration protocols. Thus, the dynamic interactions between weather and wetland size/shape may be confounded with anthropogenic impacts when examining invertebrate community change in constructed or restored wetlands along a gradient of human impacts.

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