

Aquatic macroinvertebrate community responses to wetland mitigation in the Greater Yellowstone Ecosystem

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Abstract

1. Wetlands are critical components of freshwater biodiversity and provide ecosystem services, but human activities have resulted in large-scale loss of these habitats across the globe. To offset this loss, mitigation wetlands are frequently constructed, but their ability to replicate the functions of natural wetlands remains uncertain. Further, monitoring of mitigation wetlands is limited and often focuses exclusively on vegetation and physical characteristics.
2. Wetland fauna are assumed to be present if suitable habitat restoration is achieved, but this assumption is rarely tested. We used the macroinvertebrate community as a proxy for wetland function to compare recently created mitigation wetlands, natural wetlands impacted but not destroyed by road construction activity, and unimpacted reference wetlands along a highway corridor in the Greater Yellowstone Ecosystem. Unlike most other studies of invertebrate communities in created wetlands which have occurred in warm climates, our study area has a cold temperate climate with short growing seasons.
3. We estimated macroinvertebrate taxonomic richness and used linear models to test for effects of wetland design features (wetland age, isolation, depth, vegetation, size, and pH) on invertebrate richness. We also used non-metric multidimensional scaling to visualise differences in community composition among wetland types and used indicator species analysis to determine which taxa were causing observed differences.
4. Taxonomic richness of macroinvertebrates was lower in created wetlands than impacted or reference wetlands, whereas richness was similar in impacted and reference wetlands. Wetland age was positively correlated with taxonomic richness. The amount of aquatic vegetation in wetlands had the greatest influence on taxonomic richness, so that recently created wetlands with little vegetation had the simplest invertebrate communities. Community composition of invertebrates in created wetlands also differed from community composition in reference and impacted wetlands. Most notably, created wetlands lacked some passive dispersers that were common in other wetland types, although we found no relationship between taxonomic richness and wetland isolation.

5. Overall, constructed wetlands had diminished and altered macroinvertebrate communities relative to reference and impacted wetlands, suggesting that periods in excess of 5 years may be required for wetland mitigation projects in cold temperate climates to attain full functionality.

KEYWORDS

Clean Water Act, community composition, restoration, species richness, wetland creation

1 | INTRODUCTION

Freshwater wetlands perform important functions, including water purification, flood protection, carbon storage, and they provide habitat for diverse flora and fauna (Contanza et al., 1997). Human activities such as urban development, agriculture, and road construction have caused a large-scale reduction in wetland area worldwide (Zedler & Kercher, 2005). Conservation education and legislation have slowed this trend in recent years (Dahl, 2011), and mitigation of wetland loss from large scale projects such as road construction and industrial development is now required under Section 404 of the Clean Water Act (Hough & Robertson, 2008). The Section 404 permitting process is largely guided by the 1989 executive policy of *no net loss* that states loss of wetland area and function must be mitigated by an equal or greater area of gain, achieved either through wetland restoration or construction (Turner, Redmond, & Zedler, 2001). Nevertheless, the capacity of mitigation wetlands to replace natural wetland functions remains uncertain.

Both wetland restoration and creation are used to fulfil Section 404 permitting requirements (Grenfell, Ellery, Garden, Dini, & van der Valk, 2007). Wetland restoration refers to restoring natural wetland structure and function to an area with previous wetland history that has been degraded. Wetland creation refers to the construction of new wetlands in upland areas. Because created wetlands do not have a history of inundation, successional processes start from zero and can be slow. Wetland restoration is generally more successful at replicating the biotic communities and ecosystem services of nearby reference wetlands (Sebastián-González & Green, 2016; Spadafora et al., 2016), but permit conditions often require onsite mitigation through wetland creation.

Evaluating the success of wetland creation projects is challenging. It is logistically and fiscally impossible to monitor all of the factors that contribute to wetland function, and most mitigation wetlands are not monitored at all (GAO, 2005). When monitoring does occur, it is typically short term (2–5 years) and focuses on the establishment of vegetation and hydric soils, which may be poor surrogates for wetland function (Cole & Shafer, 2002; Kihlslinger, 2008). Recovery of wetland fauna (e.g. invertebrates, amphibians, birds) is a central objective of most wetland mitigation projects, but these taxa are rarely included in monitoring protocols. Invertebrates are a taxonomically diverse and important component of wetland ecosystems that include all functional feeding guilds and contribute to nutrient cycling within wetlands and between the wetland and surrounding terrestrial environment.

Because of their centrality, they may be particularly good surrogates for comparing function of created and reference wetlands (Balcombe, Anderson, Fortney, & Kordek, 2005; Ruhí & Batzer, 2014).

Many factors influence colonisation and persistence of invertebrates in new habitats. First, species vary in their ability to colonise newly created wetlands (Bilton, Freeland, & Okamura, 2001). Active dispersers, such as species with flying adult stages, typically arrive first, followed by passive dispersers that rely on external vectors such as wind or other animals to disperse (Coccia, Vanschoenwinkel, Brendonck, Boyero, & Green, 2016). Distance from a source population and wetland size can also influence the likelihood of colonisation and persistence of both active and passive dispersers (Hall et al., 2004; Semlitsch & Bodie, 1998). Second, physical habitat characteristics such as hydroperiod and water chemistry influence which species can persist (Ebel & Lowe, 2013). Third, biotic interactions can further structure invertebrate communities, with predators such as fish, amphibians, and invertebrates exerting strong top-down influences (Hanson & Riggs, 1993; Shulse, Semlitsch, & Trauth, 2013). As a result of these multiple interacting factors, invertebrates can quickly colonise newly constructed wetlands and even reach similar levels of richness as nearby reference wetlands (Balcombe et al., 2005; Coccia et al., 2016), but community composition often remains distinct even many years after wetlands are constructed (Moreno-Mateos, Power, Comín, & Yockteng, 2012). Differences in community composition are especially likely to persist in cold climates, where activity is limited to a short ice-free period each year (Moreno-Mateos, Meli, Vara-Rodríguez, & Aronson, 2015; Moreno-Mateos et al., 2012; Ruhí, Herrmann, Gascón, Sala, & Boix, 2012).

Our objective was to evaluate the ability of recently created wetlands and wetlands impacted but not destroyed by road construction activity to support invertebrate communities relative to reference wetlands along a highway corridor in northwest Wyoming. Our study area is within the Greater Yellowstone Ecosystem (GYE), just outside Grand Teton National Park. Wetlands in the GYE comprise only 3% of the total land area, but an estimated 90% of wildlife species use wetlands or riparian areas on a daily or seasonal basis (Nicholoff, 2003). Despite their importance, wetlands have been understudied in the GYE and throughout the Intermountain West (Copeland et al., 2010; Newell & Hossack, 2009; Ray et al., 2015). We hypothesised that taxonomic richness would be lower in created wetlands than in impacted and reference wetlands, possibly because colonisation is limited by the short growing season in this region. We also expected that community

composition would differ among created, impacted, and reference wetlands, and that invertebrate communities in created wetlands would be dominated by active dispersers. We predicted that distance to nearest natural wetland and time since construction would be positively correlated with taxonomic richness in created wetlands. Across all wetland types, we predicted that aquatic vegetation, wetland size, and depth would be positively associated with richness, while elevation would be negatively associated with taxonomic richness.

2 | METHODS

2.1 | Study area

To mitigate wetland loss and impacts associated with the reconstruction of Highway 287/26 over Togwotee Pass between Moran

and Dubois Wyoming, the Wyoming Department of Transportation (WYDOT) constructed new wetlands along the highway corridor between 2008 and 2014. Wetlands were located in the Bridger-Teton National Forest, approximately 12 km east of Grand Teton National Park, USA (Figure 1). We sampled aquatic macroinvertebrates in created, impacted, and reference wetlands ($n = 10, 7, 13$, respectively) once per year from 2013 to 2015 to assess differences in invertebrate taxonomic richness and community composition among wetland types. Created wetlands were excavated with heavy equipment down to the water table and planted with a wetland seed mix and willow (*Salix* spp.) cuttings. Impacted wetlands were natural wetlands that were altered by road construction (e.g. modified banks, some filling, and erosion control). Most wetland impacts were limited to a small (i.e. <25%) portion of the wetland perimeter. Reference wetlands were natural wetlands that did not sustain impacts from road

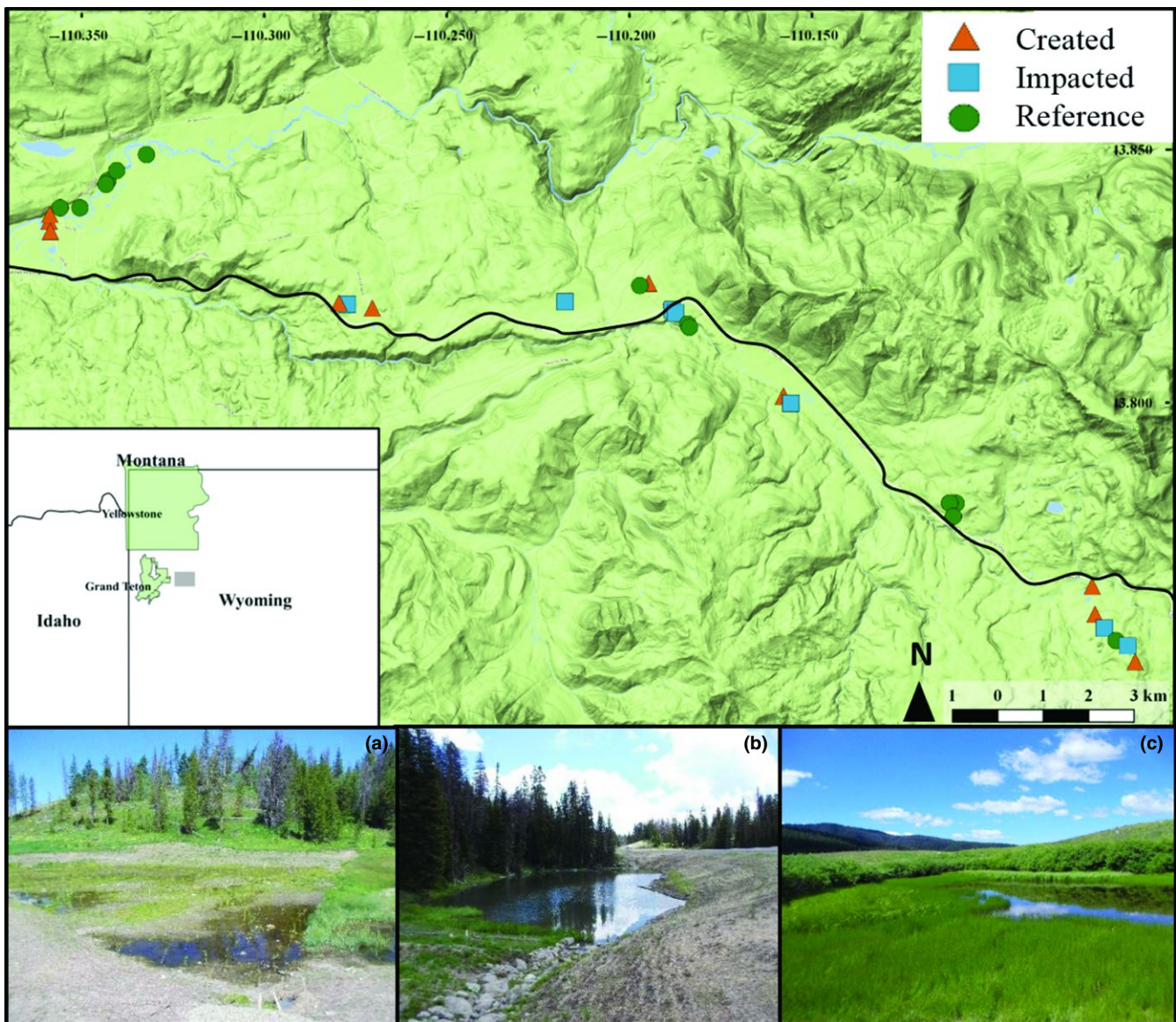


FIGURE 1 Locations of wetlands where we sampled invertebrates near Moran, Wyoming, U.S.A. (grey inset) from 2013 to 2015 to determine differences in taxonomic richness and community composition among created (a), impacted (b) and reference (c) wetlands. Representative photos illustrate each wetland type. The black line is U.S. Highway 26-287 [Colour figure can be viewed at wileyonlinelibrary.com]

TABLE 1 Created mitigation wetlands, impacted (natural wetlands impacted but not destroyed by road construction), and reference (natural, unimpacted) wetlands surveyed for invertebrates near Moran, WY from 2013 to 2015

Site	Wetland type	Year constructed	Fish detected	Years surveyed
12DC	Created	2012	No	2015
13AC	Created	2012	No	2013, 2014, 2015
16BC	Created	2010	No	2013, 2014, 2015
19AC	Created	2012	No	2015
24CC	Created	2012	No	2015
25AC	Created	2012	No	2015
26BC	Created	2012	No	2013, 2014, 2015
ML	Created	2014	No	2014, 2015
QU	Created	2008	No	2013, 2014, 2015
SP	Created	2005	No	2013, 2014, 2015
12CI	Impacted	-	No	2015
15AI	Impacted	-	No	2013, 2014, 2015
17AI	Impacted	-	No	2015
17BI	Impacted	-	No	2013, 2014, 2015
19BI	Impacted	-	No	2015
25BI	Impacted	-	Yes	2013, 2014, 2015
26AI	Impacted	-	Yes	2015
16CR	Reference	-	No	2013, 2014, 2015
17DR	Reference	-	No	2015
17ER	Reference	-	No	2013, 2014, 2015
21AR	Reference	-	No	2015
21BR	Reference	-	No	2015
21CR	Reference	-	No	2015
25CR	Reference	-	No	2013, 2014, 2015
HE	Reference	-	Yes	2013, 2014, 2015
MW	Reference	-	Yes	2013, 2014
ND	Reference	-	Yes	2013, 2014
OX	Reference	-	Yes	2013, 2014
RW	Reference	-	No	2013, 2014, 2015
SD	Reference	-	No	2015

construction and thus should provide a baseline against which to compare constructed and impacted sites. Fish (*Salmonidae* spp.) were detected in four reference and two impacted wetlands (Table 1), all of which were permanent and had a stream or river connection. In 2013 and 2014, we sampled a slightly different and reduced subset of the wetlands that were sampled in 2015, but we sampled each type of wetland each year (Table 1). In 2015, we sampled all created wetlands that held water through July as well as the closest reference and impacted wetlands. Sampled wetlands ranged in elevation from 2,100 to 3,050 m.

Vegetation surrounding wetlands was dominated by mixed conifer forest at higher elevations and mixed sagebrush-grassland vegetation at lower elevations. This area is characterised by long, cold winters with heavy snowfall and short, cool summers. Precipitation at the top of Togwotee Pass, where our highest elevation sites were located, averages 118.98 cm annually, falling primarily as snow between November and April (<https://wcc.sc.egov>.

[usda.gov/nwcc/site?sitenum=822](https://www.usda.gov/nwcc/site?sitenum=822)). Temperatures vary considerably throughout the year, with a monthly mean temperature of -7.6°C in January and monthly mean temperature of 15.6°C in July (<https://www.ncdc.noaa.gov/cdo-web/datasets/GHCND/stations/GHCND:USR0000WBUH/detail>). Wetlands thaw and fill with snow-melt between early May (lower elevations) and early June (higher elevations).

2.2 | Sampling

To collect a representative sample of invertebrates from wetlands, we conducted nine 1.5 m sweeps using a D-framed net (500- μm mesh) in each site. We conducted four sweeps along each axis of the wetland (north-south and east-west) at two shallow points, two mid-depth points, and one in the deepest part of the wetland. We sampled all wetlands in mid-late July when invertebrate diversity was expected to be highest and immature invertebrates developed enough

for identification (Duffy, 1999). Invertebrates from the nine sweeps were pooled into a single container and preserved in 70% ethanol for later identification to the lowest taxonomic level practical (Larsen, Alarie, & Roughley, 2000; Merritt & Cummins, 1996; Wiggins, 1996).

Because wetland invertebrates have received relatively little research attention, particularly in the Intermountain West, keys for larval stages of many species do not exist. Amphipoda, Mollusca, Ephemeroptera, and Coleoptera were identified to genus level, while Diptera, Hemiptera, Odonata, and Hirundinea were identified to family level. Collembola, Oligochaeta, and Hydracarina were not identified to lower taxonomic levels. When some members of a group were identified to a lower taxonomic level than others, we aggregated to the higher taxonomic level so that resolution was consistent across all sites (Appendix). For example, snails of the genus *Lymnaea* were sometimes identified to species (*Lymnaea elodes* and *Lymnaea stagnalis*) but identification was limited to genus in some samples. For consistency in cases like these, we classified all *Lymnaea* spp. in all samples to genus.

Beyond wetland type, we measured environmental and design characteristics that we hypothesised would influence richness and composition of wetland invertebrate communities. We measured total wetland area and wetted wetland area using the area estimation tool in a Garmin e-trex Global Position System. We defined total wetland area as the high-water line or boundary of wetland creation disturbance (i.e. willow plantings in created wetlands) and wetted wetland area as the portion of the wetland that held water in early June when wetlands achieved their maximum size. We recorded maximum depth at the same time as wetted wetland area in June. We extracted elevation and identified the nearest natural (reference or impacted) wetland using Google Earth (version 7.1.7.2606). We measured distance to nearest natural wetland using the `distHaversine` function in the R package *geosphere* (Hijmans, 2017). We estimated cover by aquatic vegetation in the same week that we collected invertebrate samples in late July, using a 1-m² quadrat every 80 m along the wetland shore, both at 1 and 5 m from the shore. Within each quadrat, we estimated percent cover of aquatic vegetation and calculated the mean for the entire wetland. We measured pH every 2 weeks throughout the summer using a YSI Multimeter (Model 63) and used the mean value for analyses. We also recorded presence of fish when they were detected visually or in minnow traps set out for amphibian larvae (Swartz, 2017).

2.3 | Data analysis

2.3.1 | Taxonomic richness

We estimated asymptotic taxonomic richness of invertebrates for each wetland using a first-order jackknife estimator implemented in program SPECRICH (Hines, 1996). Jackknife estimators use the frequency that different taxa occur in a sample to estimate the number of undetected taxa (Burnham & Overton, 1979). We tested for differences in log-transformed taxonomic richness among wetland types using a linear mixed effects model in the R package *nlme* (Pinheiro, Bates, DebRoy, & Sarkar, 2018) with wetland type

and standardised elevation as explanatory variables. We included site as a random effect to account for repeated sampling of some wetlands over multiple years. Because fish can have strong effects on invertebrate communities, we included fish as a covariate (Hanson & Riggs, 1993). We also included elevation in all models as a nuisance covariate because it is not strictly a design feature, but could have strong effects on richness due to differences in growing season length and temperature across elevation gradients (Rahbek, 1995).

To assess the influence of habitat features on invertebrate taxonomic richness, we used only data from 2015 because we did not measure the full complement of environmental variables in previous years. We fit multiple generalised linear models to determine which variables best explained variation in richness. All pairwise correlations between explanatory variables ($r \leq |0.62|$) were below the threshold typically used to identify redundant variables in regression analyses (Dormann et al., 2013). In our initial data visualisation, maximum depth appeared to have a quadratic relationship with taxa richness, so we added a squared term to the model. Starting with a global model that included elevation, wetted wetland area, maximum depth, maximum depth squared, pH, and percent cover of aquatic vegetation, we used backwards selection until only significant variables remained ($p < 0.1$).

To test for effects of wetland age and distance to the nearest natural wetland (reference or impacted) on taxonomic richness in created wetlands, we used linear mixed effects models. We used data from all years, so site was included as a random effect. Again, we included standardised elevation as a nuisance covariate. We also included a quadratic term for wetland age to determine if richness plateaued after an initial increase (Moreno-Mateos et al., 2012).

2.3.2 | Community composition

To determine if species assemblages differed among created, impacted and reference wetlands, we constructed Bray-Curtis community dissimilarity matrices based on rank orders of species abundance data from each wetland. We used non-metric multidimensional scaling (NMDS) implemented in the R package *vegan* (Oksanen et al., 2017) to visualise differences. Because we could not account for repeated sampling of some wetlands over multiple years in NMDS, we used only the data from 2015, when we sampled the full suite of wetlands. To test for differences in invertebrate community composition among wetland types, we conducted a permutational multivariate analysis of variance (PERMANOVA) using the `adonis` function in *vegan* (Oksanen et al., 2017). Next, we used indicator species analysis to investigate which taxonomic groups had the greatest influence on observed differences in community composition among created, impacted, and reference wetlands (Dufrene & Legendre, 1997). This method calculates indicator values as a product of the relative frequency and relative average abundance (in this case, rank order) for each taxonomic group in each wetland type. Indicator values range from 0 (no association with a particular wetland type) to 1 (perfect association). Indicator values were tested for statistical significance using a Monte-Carlo permutation test with

1,000 iterations. All statistical analyses were completed in Program R version 3.3.2 (R Core Team, 2016).

3 | RESULTS

3.1 | Taxonomic richness

We identified 75 invertebrate taxa from 13 orders in our wetland samples (Appendix). Observed richness ranged from 5 to 25 taxa per wetland and estimated richness ranged from 6 to 51.63 invertebrate taxa per wetland. Fish presence did not have a significant effect on species richness (coeff [SE] = $-0.01[0.07]$, $t_{25} = -0.186$, $p = 0.854$) so we removed it from the model. After accounting for elevation, reference (mean [95% confidence interval] = 21.40 [17.98, 25.47]) and impacted (18.46 [14.32, 23.80]) wetlands had higher taxonomic richness than created wetlands (15.76 [12.99, 19.13]; Figure 2). Invertebrate richness declined with elevation (coeff [SE] = $-0.09[0.03]$, $t_{26} = -3.165$, $p = 0.004$), with an estimated 11 more taxonomic groups of invertebrates in the lowest elevation wetlands (2,100 m) than the highest elevation wetlands (3,050 m).

On average, created wetlands were shallower than reference or impacted wetlands (Table 2). Eight out of 10 created wetlands dried partially (i.e. at least one isolated waterbody dried completely) by the end of July 2015, whereas no reference or impacted wetlands dried over the same time period. Created wetlands also had smaller surface areas, lower mean percent cover of aquatic vegetation, and slightly higher pH than reference wetlands. There were no major differences in habitat variables between reference and impacted wetlands (Table 2). After accounting for elevation, the top model describing the influence of habitat features on taxonomic richness only included a moderate positive effect of aquatic vegetation (0.002 [0.001]; $t_{26} = 1.85$, $p = 0.08$; Figure 3).

Within created wetlands, we found no evidence that taxonomic richness increased with wetland age (0.006 [0.025]; $t_{10} = 0.26$, $p = 0.80$). However, this apparent lack of a relationship was driven by one wetland with abnormally low species richness. This wetland (Swan Pond) was the only one in our data set that filled from an irrigation ditch that must be manually opened and closed, resulting in unpredictable hydrology and unusual variation in depth among and within years. After removing Swan Pond data from the analysis, taxonomic richness increased with wetland age by an estimated 15.79% each year (0.064[0.024]; $t_{10} = 2.63$, $p = 0.03$; Figure 4). A quadratic effect of wetland age was not supported. Created wetlands were constructed on

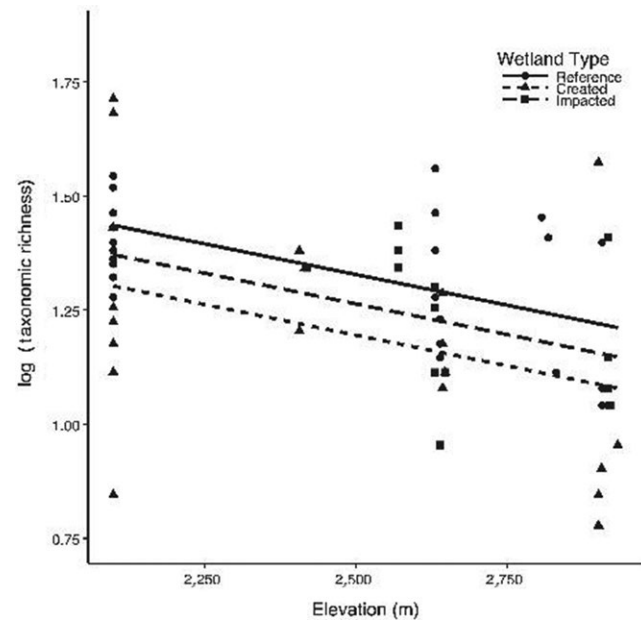


FIGURE 2 Estimated invertebrate taxonomic richness in created, impacted, and reference wetlands across elevation. Points represent richness in individual wetlands. Richness was estimated using SPECRICh software to account for uneven detection probabilities among taxa

average 274.4 m ($SD = 156.77$ m) from the nearest natural wetland, but taxonomic richness was not associated with distance to the nearest natural wetland ($-0.0003 [0.0004]$; $t_7 = -1.06$, $p = 0.32$).

3.2 | Community composition

The stress value in our NMDS (0.21) on two axes of ordination was at the upper end of the acceptable range (0.0–0.2; Clarke & Warwick, 2001), indicating moderate lack of fit. Increasing the number of dimensions to three reduced stress to 0.14, but because this did not change the results, we present the two-dimensional solution for easier visual interpretation. Species-poor communities in created wetlands clustered separately from communities in reference and impacted wetlands, indicating that community compositions differed (Figure 5). Points representing community composition in created and impacted wetlands were widely scattered in our NMDS plot, indicating inter-wetland variability in community composition, while communities in reference wetlands were more similar to each other (Figure 5; PERMANOVA $F' = 2.34$, $p = 0.002$).

TABLE 2 Habitat characteristics hypothesised to influence taxonomic richness of invertebrates (mean [SD]) by wetland type: created, impacted, reference)

Variable	Created (n = 10)	Impacted (n = 7)	Reference (n = 10)
Elevation (m)	2,515.50 (342.21)	2,678.14 (182.54)	2,556.80 (329.63)
Wetted wetland area (m ²)	2,644.70 (3,768.83)	5,377.71 (3,637.66)	3,678.00 (3,773.19)
Max depth (cm)	38.35 (25.62)	124.08 (45.59)	111.70 (35.81)
pH	8.46 (0.69)	7.68 (1.08)	7.92 (0.54)
Aquatic vegetation (% cover)	24.07(29.48)	46.43 (33.39)	49.39(33.06)

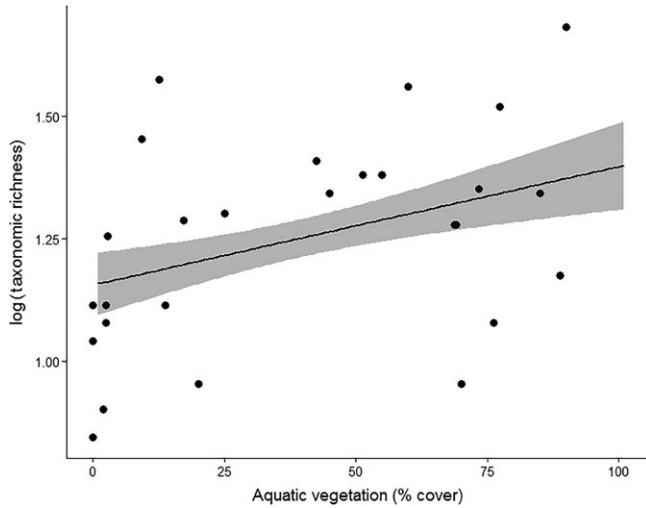


FIGURE 3 Relationship between taxonomic richness of invertebrates and aquatic vegetation in all wetland types. Shaded confidence band represents the standard error

Indicator species analysis also highlighted differences in community composition among wetland types (Table 3). Because community composition in reference and impacted wetlands were so similar in the NMDS ordination, we grouped these wetland types together for the indicator analysis. Three taxa with flying adult stages, Notonectidae (backswimmers, order Hemiptera), *Berosus* (water scavenger beetles, order Coleoptera), and *Helophorus* (order Coleoptera), were identified as indicators of created wetlands. *Berosus* and *Helophorus* were each only found in three created wetlands, while Notonectidae was found in eight wetlands (five created, one impacted, and two reference). In contrast, five taxa were identified as indicators of reference/impacted wetlands: *Pisidium* (pea clams, order Veneroida), Chaoboridae (phantom midges, order Diptera), Oligochaeta (aquatic worms), *Procladius* (mayfly, order Ephemeroptera), and Hydracarina (water mites). Of these, *Pisidium* was the strongest indicator—of the 17 wetlands where it was found, only one was a created wetland (Quarry).

4 | DISCUSSION

Understanding the capacity of created mitigation wetlands to support native species is critical, especially as natural wetlands continue to be modified and destroyed. We used the macroinvertebrate community as a proxy for wetland function to compare created mitigation wetlands, natural wetlands impacted by development activity, and unimpacted reference wetlands along a highway corridor in the GYE. We found that created wetlands had lower taxonomic richness and distinct community composition relative to reference wetlands, whereas invertebrate communities in impacted wetlands had greater overlap with reference wetlands in both composition and richness.

With the exception of one outlier that we suspect reflects management practices (see below), invertebrate richness in created wetlands increased with wetland age in the first few years following wetland construction. This pattern is probably due to the time required for vegetation establishment in newly-created wetlands and a time lag for some taxa to colonise new ponds (Coccia et al., 2016; Ruhí, Boix, Gascón, Sala, & Quintana, 2013). Indeed, after accounting for elevation, the model that best explained differences in richness across wetland types included just aquatic vegetation cover as an explanatory variable. For every 1% increase in aquatic vegetation, taxonomic richness was predicted to increase by 0.55%. Vegetation cover is often important for structuring invertebrate communities in constructed wetlands, with higher amounts of vegetation and organic matter generally correlated with greater diversity due to increased structural habitat, food resources, and predator refuge (Stewart & Downing, 2008; Ruhí, Winfield-Fairchild, Spieles, Becerra-Jurado, & Moreno-Mateos, 2016; Batzer, Rader, & Wissinger, 1999).

Interestingly, the outlier (Swan Pond) that we removed from the wetland age model because it had abnormally low taxonomic richness, is the oldest created wetland in the study area (constructed in 2005) and is at low elevation, factors associated with increased richness for most wetlands. However, because it is manually controlled by opening and closing a head gate on an irrigation ditch, Swan Pond

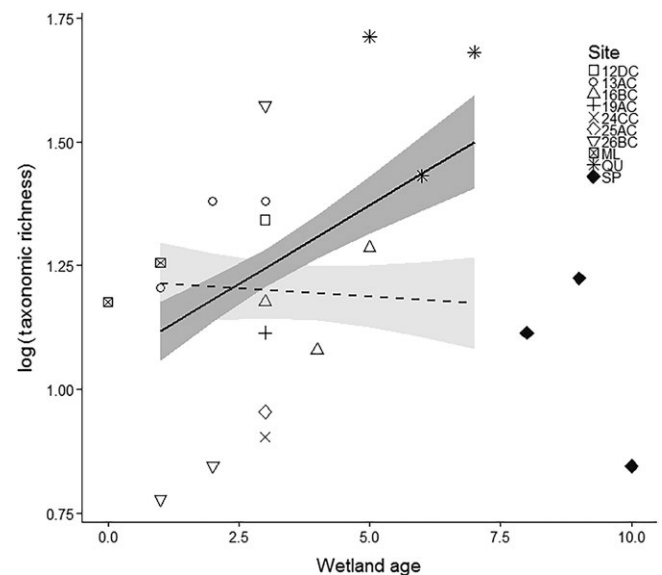


FIGURE 4 Relationship between taxonomic richness of invertebrates in created wetlands and wetland age with Swan Pond (SP) included (dashed line) and with SP removed (solid line). Swan Pond was removed because it is the only wetland in our data set that is controlled by an irrigation ditch that must be manually opened and closed. Because of this, depth of SP has unpredictable hydrology and unusual variation in depth among and within years. All other created wetlands in the study fill naturally from groundwater and precipitation. Shaded confidence band represents the standard error. Shapes represent individual wetlands over multiple years. SP is represented as a filled diamond. A quadratic effect of wetland age was evaluated but was not significant

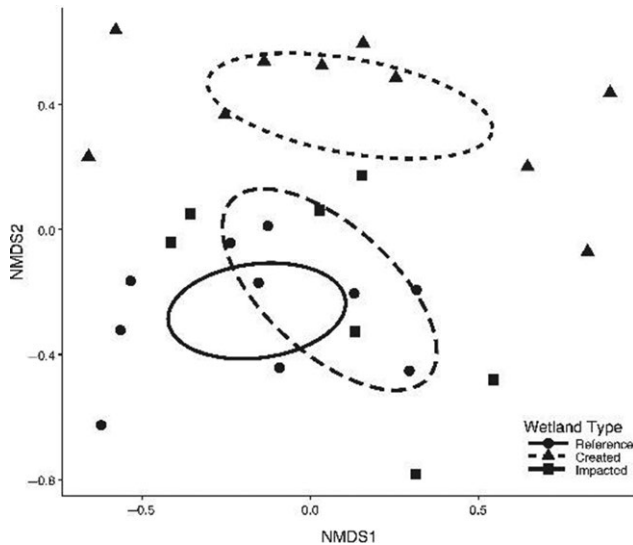


FIGURE 5 Non-metric multidimensional (NMDS) ordination of invertebrate community composition in created, impacted, and reference wetlands (2015 only; stress = 0.21). Each point represents the community composition of invertebrates in a single wetland, points that are closer in ordination space have more similar community composition than points that are more distant. Ellipses represent 95% confidence intervals around the mean axis score for each group

has extremely variable hydroperiods both within and between years, very little aquatic vegetation, and much colder water than other sites. Swan Pond is <300 m from Quarry, a created wetland that had the highest taxonomic richness of any site we sampled. Constructed in 2008, Quarry is the second oldest created wetland in our study area. Differences between these two sites are obvious: Quarry has abundant emergent and submersed aquatic vegetation, typically holds water through the summer, and supports a rich and abundant amphibian community (Swartz, 2017). This dichotomy clearly illustrates the importance of design and management features in shaping biological communities in created wetlands.

Beyond vegetation, wetland hydroperiod is one of the most important drivers of community composition in wetlands (Ray et al.,

2016; Wellborn, Skelly, & Werner, 1996). In our study area, most created wetlands were designed to have temporary-to-intermediate hydroperiods and were generally shallower than reference and impacted wetlands (Table 3). In 2015, eight of 10 created wetlands dried partially (i.e. at least one isolated waterbody dried completely) and one created wetland dried completely by late July, while no reference or impacted wetlands dried in this same time frame. Therefore, we were surprised to find little support for the effects of depth on invertebrate richness across wetland types, although our inference is limited by the correlation between depth and wetland type (i.e. created wetlands were constructed to be shallower than reference and impacted wetlands). Despite this result, shallow wetlands are expected to be more vulnerable to drying under future climate change in the Intermountain West, reinforcing the importance of designing mitigation wetlands that are structurally complex yet deep enough to be resilient to climatic fluctuations, allowing them to function as refuges for aquatic biota (Brooks, 2009; Corn et al., 2003; Hossack et al., 2013; Sepulveda et al., 2015).

Most studies examining invertebrate response to wetland mitigation have been conducted in areas with warm climates (Balcombe et al., 2005; Batzer, Taylor, DeBiase, Brantley, & Schultheis, 2015; Ruhí, Boix, Sala, Gascón, & Quintana, 2009). In contrast, the GYE is characterised by long winters and wetlands are only ice-free for a few months of the year, which might slow colonisation of invertebrates in newly created wetlands (Ruhí et al., 2012). Vegetation also takes longer to establish in cold climates (Moreno-Mateos et al., 2012). In our study, the lack of support for a quadratic effect of wetland age indicates that taxonomic richness had not equilibrated in the time period in which monitoring is typically required under section 404 permit conditions (5 years or less; National Research Council 2001). Also, increasing elevation was associated with reduced taxonomic richness across all wetland types, probably due to the even shorter growing seasons and harsher conditions at higher elevations (de Mendoza & Catalan, 2010). This pattern suggests that mitigation wetlands constructed in cold climates may require longer monitoring periods to capture slow changes in vegetation and biotic communities. Future studies should examine a greater range of wetland ages to more explicitly test this hypothesis.

TABLE 3 Indicator species analysis results for created and reference/impacted wetlands

Taxa	Flying adult stage	Wetland type	Indicator value	p-value	Frequency
Notonectidae	Yes	Created	0.426	0.032	8
<i>Berosus</i> spp.	Yes	Created	0.300	0.047	3
<i>Helophorus</i> spp.	Yes	Created	0.300	0.035	3
<i>Pisidium</i> spp.	No	Reference/impacted	0.921	0.001	17
Chaoboridae	Yes	Reference/impacted	0.459	0.068	11
Oligochaeta	No	Reference/impacted	0.458	0.071	12
<i>Proclleon</i> spp.	Yes	Reference/impacted	0.353	0.065	6
Hydracarina	No	Reference/impacted	0.353	0.064	6

Note. Only taxa with a p-value ≤ 0.1 are shown. Frequency is the number of wetlands in which a given taxon was found, where the total number of wetland surveyed was 27. Indicator values range from 0 (no association with a particular wetland type) to 1 (perfect association) and were tested for statistical significance using a Monte-Carlo permutation test with 1,000 iterations.

Consistent with lower taxonomic richness in created wetlands, NMDS ordination showed that community composition differed between created wetlands and reference wetlands, but impacted wetlands had similar communities to reference wetlands. Notably, the indicator taxa for reference and impacted wetlands included three groups without flying adult stages (*Pisidium*, Oligochaeta, and Hydracarina). While some species of Hydracarina (water mites) parasitise adult winged insects (Smith & Cook, 1991), their weak dispersal ability may limit their potential to colonise new wetlands. Oligochaeta (aquatic worms) and *Pisidium* (pea clams) require hydrologic connectivity or an external vector to colonise wetlands. Indeed, the only created wetland where we found *Pisidium* is the second oldest in the study area (Quarry) and is also frequented by waterfowl, which often transport aquatic invertebrates (van Leeuwen, van der Velde, van Lith, & Klaassen, 2012).

We included impacted wetlands in this study because development does not always cause complete destruction of a wetland, but often damages or impairs just a portion of a wetland. An important finding from our research was that impacted wetlands did not differ significantly from natural wetlands in physical habitat characteristics, invertebrate richness, or invertebrate community composition. This result suggests that natural wetlands can be resilient to some disturbances and retain their functionality if the impact is small (i.e. <25% of perimeter). This result also supports current policies that encourage developers to avoid and minimise impacts to existing wetlands, rather than relying on wetland construction to mitigate destruction of natural wetlands.

Overall, wetland creation has the potential to offset negative effects of wetland loss on freshwater biodiversity, but our study and others show that it remains unclear whether constructed wetlands can replicate the structure and function of lost reference wetlands (Kolozsvary & Holgerson, 2016; Moreno-Mateos et al., 2012; Spadafora et al., 2016). Our results provide further evidence that some wetland invertebrates are capable of rapidly colonising newly created wetlands, but we also show that diversity and community composition in constructed wetlands may take longer than the short time periods specified in permit requirements to resemble nearby reference wetlands, particularly in areas limited by harsh climatic conditions and short growing seasons. Transplanting or reseeding aquatic vegetation and passive dispersers may speed the recovery of the invertebrate community, especially in cold climates where recovery is slow.

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APPENDIX

Macroinvertebrate taxa identified in wetland samples

Taxonomic rankings retrieved [December, 16, 2017] from the Integrated Taxonomic Information System (ITIS) (<http://www.itis.gov>)

Kingdom Animalia, Phylum Arthropoda, Subphylum Crustacea

Order Amphipoda

Family Gammaridae

Gammarus

Family Hyalellidae

Hyalella

Kingdom Animalia, Phylum Mollusca

Class Bivalvia

Family Pisidiidae

Pisidium

Class Gastropoda

Family Lymnaeidae

Lymnaea

Family Physidae

Aplexa

Physa

Family Planorbidae

Armiger

Gyraulus

Helisoma

Promenetus

Family Valvatidae

Valvata

Kingdom Animalia, Phylum Arthropoda, Class Insecta

Order Coleoptera

Family Dytiscidae

Acilius

Agabus

Colymbetes

Dytiscus

Graphoderus

Hydaticus

Hydrotus

Ilybius

Laccophilus

Laccornis

Liodessus

Oreodytes

Rhantus

Family Emidae

Heterlimnius

Family Gyridae

Gyrinus

Family Halipidae

Brychius

Halipus

Family Helophoridae

Helophorus

Family Hydrophilidae

Berosus

Enochrus

Hydrophilus

Laccobius

Tropisternus

Order Diptera

Family Ceratopogonidae

Family Chaoboridae

Family Chironomidae

Family Culicidae

Family Dixidae

Family Dolichopodidae

Family Ephydriidae

Family Psychodidae

Family Stratiomyidae

Family Tabanidae

Family Tipulidae

Order Ephemeroptera

Family Baetidae*Baetis**Callibaetis**Proclleon***Family Caenidae***Caenis***Family Ameletidae***Ameletus***Family Siphonuridae***Siphonurus***Order Hemiptera****Family Belostomatidae****Family Corixidae****Family Gerridae****Family Notonectidae****Order Odonata****Suborder Anisoptera****Family Aeshnidae****Family Libellulidae****Suborder Zygoptera****Family Coenagrionidae****Family Lestidae****Order Trichoptera****Family Hydroptilidae***Agraylea***Family Leptoceridae***Mystacides**Ylodes***Family Limnephilidae***Ecclisomyia**Hesperophylax**Limnephilus**Onocosmoecus**Psychoglypha*

Kingdom Animalia, Phylum Arthropoda, Class Collembola

Kingdom Animalia, Phylum Annelida, Class Clitellata

Order Hirudinida**Family Erpobdellidae****Family Glossiphoniidae****Family Hirudinidae****Subclass Oligochaeta**

Kingdom Animalia, Phylum Arthropoda, Class Arachnida

Hydracarina

Kingdom Animalia, Phylum Cnidaria, Class Hydrozoa, Order Anthoathecatae

Family Hydridae*Hydra*

Kingdom Animalia, Phylum Platyhelminthes, Class Rhabditophora

Order Tricladida