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RESEARCH ARTICLE

Biodiversity of Belowground Invertebrates as an Indicator of Wet Meadow Restoration Success (Platte River, Nebraska)

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Abstract

Soil invertebrate communities are fundamental components of wet meadow ecosystems. We compared soil invertebrate biodiversity between restored and native wet meadows to assess the effectiveness of restoration practices. Biodiversity and biomass were measured in 2002 and 2003 from four native and three restored sites located along a 100-km stretch of the Platte River in south-central Nebraska. The sites ranged in age from 3 to 6 years since restoration. Samples were collected during May, July, and September each year. Soil temperature, soil moisture, percent litter cover, and root mass were measured at each site. Twelve 20 × 20 × 25–cm soil blocks were extracted at each site; soil was washed through a 1-mm sieve; and invertebrates were identified, counted, and weighed. Native sites had higher Shannon and Simpson diversity values and contained greater invertebrate biomass than restored sites. Five invertebrate taxa (isopods, scarab beetles, click beetles, earthworms, and ants) were collected with enough frequency to assess restoration effects on their occurrence. Of these, only ants occurred more frequently in restored sites. Restored sites generally had less litter cover, lower root mass, lower soil moisture, and higher soil temperature than native sites. Current restoration practices may not be completely effective at returning sites to native conditions. Physical reconstruction of wet meadow topography and high-diversity reseeding may not be adequate to fully restore soil invertebrate communities, even over extended periods of time.

Key words: **biodiversity, habitat restoration, Nebraska, Platte River, soil invertebrates, taxonomic sufficiency, wet meadow.**

Introduction

Soil invertebrates are important components of any habitat but have crucial importance to the structure and function of grassland ecosystems. Their role as nutrient recyclers, decomposers, herbivores, predators, and soil conditioners make their community assemblages sensitive to changes in ecosystem conditions (Giller 1996). Soil invertebrates also fill important niches in the environment because they influence nutrient flow, improve soil aeration and fertility, and alter plant community structure. Relatively short generation time allows invertebrates to respond rapidly to changes in environmental quality, whereas relatively poor ability to disperse generally prolongs the recolonization process (Mattoni et al. 2000). These characteristics predispose soil invertebrates for use as indicators of ecological disturbance.

Invertebrates have been used as indicators of environmental changes in aquatic systems for more than 30 years (Hellawell 1978; James & Evison 1979). Their role as indicators of terrestrial restoration success is also well established (Kremen et al. 1993; Finnamore 1996; Peters 1997; Longcore 2003; Nakamura et al. 2003).

To allocate maximum resources to spatial and temporal replications (Beattie & Oliver 1994), many have attempted to use a higher level taxonomic resolution in hopes that it is adequate to satisfy the objectives of a study, an approach which has been termed "taxonomic sufficiency" (Ellis 1985). Indeed, assessments of freshwater and marine benthic communities have indicated that genus, family, and phylum were sensitive to the same changes as species identification (Herman & Heip 1988; Warwick 1988*a*, 1988*b*; Ferraro & Cole 1990, 1992, 1995; Wright et al. 1995). Taxonomic sufficiency has also been tested and applied in studies using terrestrial invertebrates as ecosystem indicators (Williams & Gaston 1994; Andersen 1995; Balmford et al. 1996; Andersen 1997; Pik et al. 1999). Successful ecosystem restoration requires the reestablishment of fundamental processes underlying nutrient cycling in the soil, including litter decomposition and soil conditioning (Jordan et al. 1987). Several abundant groups of soil invertebrates including earthworms, ants, and isopods are major contributors in this process.

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In addition to their role in soil formation and function, belowground wet meadow invertebrates along the Platte River in south-central Nebraska provide a critical resource to migratory birds. More than 500,000 Sandhill Cranes (*Grus canadensis*) and the endangered Whooping Crane (*G. americana*) rely on wet meadow invertebrates as a source of key nutrients that are unavailable elsewhere along their migration route (U.S. Fish and Wildlife Service 1981; Currier et al. 1985; Reineke & Krapu 1986). Although migratory waterfowl obtain the majority of their energetic requirements from foraging in grain fields, wet meadow invertebrates provide certain amino acids and minerals, such as calcium, which cranes cannot obtain from grain fields and which directly impact reproductive success (U.S. Fish and Wildlife Service 1981; Currier et al. 1985; Reineke & Krapu 1986).

More than 75% of native wet meadows along the Platte River in south-central Nebraska have been lost to agriculture (Sidle et al. 1989; U.S. Fish and Wildlife Service 1997). Land managers in the Platte River Valley have responded by restoring croplands to wet meadows during the past 15–20 years. Although some of these restorations are relatively old, it is not clear if these restorations are functioning similar to native wet meadows. In fact, little is known about the biotic communities of these restorations.

Properly executed ecological restoration must reestablish ecosystem function and composition, therefore requiring a robust method to monitor success. Modern restoration ecology theory cannot rely on vegetation alone to assess restoration success but should be capable of detailing success at an ecosystem-wide level (National Research Council 1992).

Soil invertebrate populations in native Platte River Valley wet meadows and grasslands have been documented previously (Nagel & Harding 1987; Davis & Vohs 1993; Davis et al. 2006). However, despite their importance both to ecosystem function and to migratory bird nutrition, no data exist that compare soil invertebrate communities in native and restored wet meadows. Soil invertebrate communities must be described in restored and native wet meadows to avoid anecdotal evaluation of restoration practices.

Wet meadows seem to be affected by disturbances because of sensitivity to environmental factors such as soil moisture, organic content, and root mass (Blair et al. 2000; Davis et al. 2006). Thus, we hypothesized that estimates of soil invertebrate biodiversity would differ between native and restored wet meadows. We also hypothesized that environmental parameters would differ between native and restored wet meadows, likely influencing the presence and abundance of soil invertebrates. Our primary objective was to evaluate wet meadow restoration success by comparing belowground invertebrate biodiversity between restored and native wet meadows. A secondary objective was to quantify environmental factors that might have important implications for invertebrate communities associated with these site types.

Methods

Wet Meadow Habitat

Wet meadows are subirrigated portions of floodplain grasslands that are characterized by a ridge and swale topography. This topography represents dry remnants of the braided river channel of the Platte River and its temporary sandy islands that have not been covered with regular flowing water during the past 300 years (O'Brien & Currier 1987). Ridges are typically oriented parallel to the river channel, with the swales lying on the side closest to the river. Wet meadows in the Platte River floodplain typically have high water tables, poor drainage, and high organic content (Jelinski & Currier 1996). Elevation and moisture gradients between ridges and swales create a unique habitat with substantial changes in microclimate occurring over short distances.

Water availability in wet meadows is directly affected by river flow levels because of subterranean flow through underlying gravel deposits (Hurr 1983; Wesche et al. 1994). Changes in river flow affect groundwater levels in the adjacent floodplains, which in turn affects availability of water in wet meadows (Hurr 1983). Moreover, changes in groundwater availability have previously been linked with changes in both plant and soil invertebrate communities (Henszey et al. 2004; Davis et al. 2006).

Platte River wet meadow ridges are relatively xeric and dominated by short grass prairie species such as Little bluestem (*Andropogon scoparius* Michx.), Prairie sandreed (*Calamovilfa longifolia* (Hook) Scribn.), and Hairy grama (*Bouteloua hirsuta* Lag.). Intermediate elevations are dominated by Big bluestem (*A. gerardii* Vitman), Indiangrass (*Sorghastrum nutans* (L.) Nash), and Switchgrass (*Panicum virgatum* L.). Swales are considerably wetter and are dominated by Sedges (*Carex*), Spikerush (*Eleocharis obtusa* (Willde.) J. A. Schult.), American bulrush (*Scirpus americanus* Pers.), Prairie cordgrass (*Spartina pectinata* Link), and Smartweeds (*Polygonum*) (Henszey et al. 2004).

Study Sites

Four native sites were selected from land managed by the Platte River Whooping Crane Maintenance Trust. Native sites consisted of mixed-grass prairie fragments that have never been cultivated. Sites were located along the central Platte River from Grand Island, NE, to Elm Creek, NE, and ranged in size from 55 to 110 ha. These areas were managed with cattle grazing, haying, idling, and periodic prescribed burns.

Three restored sites (previously agricultural fields) ranging in age from 3 to 6 years since restoration were selected near native sites. Restorations were completed by recreating ridges and swales with the aid of earthmoving equipment and then planting with high-diversity seeding of native species. Restored sites ranged in size from 22 to 389 ha.

Data Collection

We collected data during three sampling periods (late May, early July, and late August) in 2002 and 2003. At each study site, we delineated three transects (high, middle, and low elevation) within a ridge–swale complex. We used transects to account for environmental differences created by the ridge–swale topography in wet meadows. Four 20 × 20 × 25–cm soil blocks were collected along each transect. Prior to each soil extraction, we measured soil moisture at 6 cm using a ThetaProbe moisture meter (Delta-T Devices, Cambridge, England) and soil temperature at 10 cm using a digital electronic soil thermometer. We also visually estimated percent litter cover within each randomly placed quadrat and then removed the litter and placed it into a labeled bag. Afterward, we extracted each soil block with a spade, using the metal quadrat and a 25-cm measuring stick as digging guides.

Each soil block was placed into a labeled plastic bag and transported to the laboratory where they were broken apart and washed through 1-mm^2 screen sieves. All invertebrates retained on the sieve were preserved in 70% ethanol, except earthworms, which were preserved following Fender (1985). During invertebrate collection, we also collected all roots from each block. The roots were later dried at ambient temperature on a glasshouse bench for at least 2 weeks and weighed to the nearest 0.001 g.

Insects and snails were identified to family using appropriate keys. Specimens were dried at 70°C in a drying oven for 24 hours and weighed to the nearest 0.0001 g in a covered analytical scale to determine dry biomass. Sexually mature earthworms were identified to genus. Sexually immature earthworms were excluded from analysis. All other invertebrates (spiders and millipedes) were identified to order. Shannon diversity index was calculated using the following formula: $-\sum[p_i \times \ln p_i]$, where p_i is the proportion of number of individuals of species i divided by the total number of specimens collected (Shannon & Weaver 1949). Simpson index was calculated using the following formula: $\sum[n_i(n_i - 1)/N(N - 1)]$, where n_i is the number of individuals from species i and N is the total number of individuals in a sample (Simpson 1949). Both indices take into account the number of species in a sample (richness) and the relative abundance of each species (evenness) but through different calculations. Shannon values represent the relative richness and evenness of a species within a sample. The Simpson index represents the probability that any two individuals drawn randomly from the population are of the same species.

Analysis

Years were analyzed separately because of differences in rainfall patterns. A standard least squares analysis of variance (ANOVA) was conducted in JMP 6.2© with period, transect, site type, and their interactions as fixed effects and location as a random effect. LSMEANS (Least Square Means) were calculated where significant interactions were found and a slice was used to determine the relationships between factors involved in each interaction (slice contrasts each level in an interaction against every other level). Nonnormal data (number of specimens, root mass, soil moisture, soil temperature, and litter cover) were log transformed (ln $[n + 1]$) prior to analysis. F and p statistics from ANOVA of these transformed variables were calculated based on the transformed data and are reported as such; however, all means and SE reported for nonnormal variables were calculated on raw data and are reported as such. Where appropriate, mean separation was conducted using Tukey HSD (Honestly Significant Difference) test. Significance was judged at $\alpha = 0.05$. A Student's t test was conducted in JMP 6.2 with site type as a fixed effect and number of specimens collected as the variable for each of the five most abundant taxa and significance was judged at $\alpha = 0.05$.

We used canonical correspondence analysis (CCA) to assess the relationship between invertebrate abundance in restored and native sites and environmental variables (ter Braak 1986, Lepš & Šmilauer 2003). All analyses were conducted using CANOCO 4.5 (ter Braak & Šmilauer 2002). CCA is a direct gradient analysis that uses a combination of ordination and regression to define axes that are linear combinations of the environmental variables that "best" explain the variation in the invertebrate data. Infrequent taxa (taxa contributing <0.5% of total numbers counted) were deleted and invertebrate abundances were square root transformed prior to performing CCA (ter Braak 1986). Partial CCA was used to eliminate effects of year, period, and treatment covariables and to relate variation in invertebrate abundance to environmental variables. We used an unrestricted selection of environmental variables and Monte Carlo tests, with 999 randomizations, to test the significance of the first CCA axis. We constructed ordination diagrams of the first and second axes.

Results

Biotic Measures

We collected and identified 8,163 invertebrates during 2002 (3,445) and 2003 (4,718). We collected 4,226 specimens from native sites and 3,937 specimens from restored sites. Mean number of specimens collected during 2002 was affected by period ($F_{[2,62]} = 9.03$, $p = 0.0005$) (all others: $F < 2.24$, $p \geq 0.1179$), with 67 and 72% more specimens occurring in period 1 (LSMEANS = 101.86, SE = 33.91) than in periods 2 (LSMEANS = 33.48, SE = 8.45) and 3 (LSMEANS = 28.71, SE = 8.26), respectively. During 2003, both period ($F_{[2,62]} = 10.84$, $p = 0.0001$) and transect ($F_{[2,62]} = 4.14$, $p = 0.0224$) affected the number of specimens collected. Period 1 (LSMEANS = 131.0, SE = 30.37) had 59 and 69% more specimens than periods 2 (LSMEANS = 53.24, SE = 21.17) and 3 (LSMEANS = 40.43, SE = 15.33), respectively. Significantly more specimens were collected from high transects (LSMEANS =

113.52, SE = 28.60) than low transects (LSMEANS = 27.33, SE = 7.64), but medium transects (LSMEANS = 83.81, SE = 27.89) were similar to high and low transects.

In 2002, Shannon index values exhibited significant interactions of period by site type ($F_{[1,45]} = 3.61$, $p = 0.035$) and transect by site type ($F_{[1,45]} = 3.65$, $p = 0.034$) (Table 1). Thus, we examined effects of site type on diversity within periods. Shannon diversity was similar in native and restored sites during period 1 (Table 2). In periods 2 and 3, Shannon diversity was higher in native than in restored sites ($p = 0.001$ and 0.024, respectively) (Table 2). Medium transects in native and restored sites had similar Shannon diversity ($p = 0.929$) (Table 2). However, Shannon diversity in low and high transects of native sites was significantly greater than those in low and high transects of restored sites (Table 2). Shannon diversity was not affected by period in 2003 ($F_{[2,62]} = 2.82$, $p = 0.07$) but was affected by transect ($F_{[2,62]} = 7.38$, $p = 0.002$). During 2003, Shannon diversity in low transects (LSMEANS = 1.17, SE = 0.1) was nearly twice as much as in high transects (LSMEANS = 0.61, SE = 0.1), but medium transects (LSMEANS = 0.92, SE = 0.98) were similar to both low and high transects. Restored sites had approximately 49% lower Shannon diversity values than did native sites ($F_{[1,62]} = 23.52$, $p < 0.001$) (Table 1).

In 2002, Simpson diversity was 32% higher in native sites than in restored sites ($F_{[1,62]} = 4.87$, $p = 0.032$) (Table 1), but no other significant effects were detected during that year ($F < 2.75$, $p > 0.075$). In 2003, Simpson index was 42% higher in native sites than in restored sites ($F_{[1,62]} = 13.6$, $p < 0.001$) (Table 1) and approximately 32 and 51% higher in low transects than in medium or high transects ($F_{[2,62]} = 8.33$, $p < 0.001$). No other significant effects or interactions were detected for Simpson diversity in 2003 ($F \leq 2.96$, $p \geq 0.0619$).

Soil invertebrate biomass in 2002 was approximately 88% greater in period 1 (LSMEANS = 1.18, SE = 0.17) than in either period 2 (LSMEANS = 0.14, SE = 0.01) or period 3 (LSMEANS = 0.14, SE = 0.01) ($F_{[2,62]} = 13.1$, $p < 0.001$) and 57% higher in native compared to restored sites ($F_{[1,62]} = 4.17$, $p = 0.047$) (Table 1). No other significant interactions or effects were detected ($F < 1.55$, $p > 0.22$). Similarly, invertebrate biomass in 2003 was significantly higher in period 1 (LSMEANS = 1.29, SE = 0.21) than in periods 2 (LSMEANS = 0.53, SE = 0.12) and 3 (LSMEANS = 0.12, SE = 0.03), respectively ($F_{[2,62]} = 8.24$, $p < 0.001$) and 62% greater in native versus restored sites (Table 1) ($F_{[1,62]} = 5.01$, $p = 0.019$). No other significant interactions or effects were detected ($F \leq 2.04$, $p > 0.14$).

During both years of the study, 42 different taxa were collected from native and restored sites, with 34 from native sites and 33 from restored sites. Mean number of taxa recorded in 2002 was 30% higher in native versus restored sites (Table 1) ($F_{[1,62]} = 9.2$, $p = 0.004$). Period 1 (LSMEANS = 6.13, SE = 0.39) yielded approximately twice as many taxa versus period 2 (LSMEANS = 2.9, SE = 0.39) or period 3 (LSMEANS = 2.92, SE = 0.39) during 2002. Low transects (LSMEANS = 5.06, SE = 0.39) had 42% more taxa on average than high transects (LSMEANS = 2.92, SE = 0.39). However, mean number of taxa found in both low and high transects were similar to medium transects (LSMEANS = 3.97, SE = 0.39) during 2002 ($F_{[2,62]} = 7.47$, $p = 0.977$). The number of taxa recorded in 2003 was 16% higher in native sites than in restored sites (Table 1) ($F_{[1,62]} = 8.61$, $p = 0.005$). In 2003, period 1 (LSMEANS = 6.76, SE = 0.46) had the highest mean number of taxa, which was 26 and 51% higher than the mean number of taxa recorded in periods 2 (LSMEANS = 4.99, SE = 0.46) and 3 (LSMEANS = 3.35, SE = 0.46), respectively ($F_{[2,62} = 14.01$, $p < 0.001$). Nine taxa were exclusively encountered in native sites compared to eight in restored sites (Table 3). Of these nine taxa, only millipedes (Diplopoda) and crane fly (Tipulidae) larvae were represented by more than two specimens.

The five most abundant taxa encountered in this study were woodlice (Isopoda), earthworms (*Aporrectodea*), scarab beetles (Scarabaeidae), ants (Formicidae), and click beetles (Elateridae) (Table 4). Ants were 39% more abundant in restored sites, but the difference was not statistically significant due to high variability (Table 4). Earthworms within the genus *Aporrectodea* were more than twice as abundant in native sites than in restored sites

Table 1. LSMEANS (± SE) of invertebrate community parameters for belowground terrestrial invertebrates collected in native and restored Platte River wet meadows of central Nebraska.

	2002		*2003*	
	Native	*Restored*	*Native*	*Restored*
Shannon	0.87 ± 0.07**	0.54 ± 0.08**	1.19 ± 0.08*	0.61 ± 0.09*
Simpson	0.51 ± 0.05*	0.34 ± 0.06*	0.61 ± 0.05*	0.35 ± 0.05*
Biomass (g)	0.68 ± 0.13*	0.29 ± 0.15*	0.94 ± 0.16*	0.36 ± 0.18*
Taxa	4.67 ± 0.3*	3.3 ± 0.34*	5.81 ± 0.35*	4.26 ± 0.4*
Specimens	61.97 ± 20.57	44.96 ± 10.30	55.42 ± 15.95	100.85 ± 24.54

* A significant difference ($\alpha = 0.05$) between LSMEANS of native and restored sites within a particular year.
** The main effect was not tested due to significant two- or three-way interactions.

Table 2. LSMEAN (± SE) of Shannon index values in site type by management interaction and site type by transect interaction of belowground invertebrates of Platte River wet meadows in central Nebraska.

Shannon Index											
2002						2003					
Native			Restored			Native*			Restored*		
Period			Period			Period			Period		
1	2	3	1	2	3	1	2	3	1	2	3
0.95 ± 0.12	0.85 ± 0.12**	0.80 ± 0.12**	0.99 ± 0.13	0.23 ± 0.13**	0.39 ± 0.13**	1.35 ± 0.12	1.25 ± 0.12	0.97 ± 0.12	0.59 ± 0.13	0.80 ± 0.13	0.43 ± 0.13
Native			Restored			Native			Restored		
Transect			Transect			Transect*			Transect*		
High	Medium	Low	High	Medium	Low	High	Medium	Low	High	Medium	Low
0.85 ± 0.12**	0.63 ± 0.12	1.13 ± 0.12**	0.19 ± 0.13**	0.64 ± 0.13	0.78 ± 0.13**	0.92 ± 0.12	1.35 ± 0.12	1.30 ± 0.12	0.30 ± 0.13	0.48 ± 0.13	1.05 ± 0.13

Significance was judged when $p \leq 0.05$, and significantly different treatment levels were denoted with asterisks. There were no significant interactions among treatment levels for Shannon index during 2003. Significant main effects were indicated with (*). Treatment levels involved in a significant interaction were indicated with (**).

Table 3. Soil invertebrate taxa found exclusively in restored or native wet meadow sites in the Big Bend Reach of the Platte River Valley in central Nebraska, 2002–2003.

Restored	*Native*
Lithobiidae	Aphidae
Cucujidae	Cicadelidae
Dermestidae	Cicadidae
Haplotrematidae	Coreidae
Hesperidae	Diplopoda
Membracidae	Gracilariidae
Myrmeliontidae	Lycidae
Orthoperidae	Nabidae
	Tipulidae

(Table 4). Elaterids, isopods, and scarab beetles were also more abundant in native sites than in restored sites (Table 4).

Environmental Measures

Native sites contained significantly higher percentages of surface litter cover than restored sites in 2002 (Table 5). There were no other significant main effects or interactions ($F < 1.65$, $p > 0.2$). Percent litter cover in 2003 was approximately 45% lower in restored versus native sites (Table 5), but there was a significant interaction ($F_{[1,45]} = 7.34$, $p = 0.0017$) between site type and period; therefore, the effects of site type within period were analyzed. Percent litter cover in 2003 was substantially higher in native than in restored sites during all three periods but was only significantly different in periods 2 and 3 (Table 6). Native sites in 2003 had 77% more litter cover during period 2 than restored sites (Table 6). Similarly, native sites had approximately 76% more litter cover than restored sites during period 3 (Table 6).

Soil moisture in 2002 was significantly affected by interactions of period by transect ($F_{[2,45]} = 4.54$, $p = 0.0036$) and period by site type ($F_{[2,45]} = 6.73$, $p = 0.0028$); therefore, the soil moisture was analyzed by transect. Low transects had higher average soil moisture levels during all periods (followed by medium and high transects, respectively) but were only significantly different during period 1 (Fig. 1) ($F_{[2,45]} = 4.16$, $p = 0.02$). Native sites had approximately double the soil moisture as restored sites

Table 4. Mean (SE) abundance and t test results for the five most abundant soil-dwelling taxa encountered in native and restored Platte River wet meadows in central Nebraska during 2002 and 2003.

Taxa	*Native*	*Restored*	*p Value*
Aporrectodea	3.22 ± 0.68	1.37 ± 2.32	0.0076
Formicidae	40.18 ± 12.67	65.63 ± 13.21	0.9165
Isopoda	6.59 ± 1.52	2.28 ± 0.94	0.0088
Scarabaeidae	3.32 ± 0.69	0.58 ± 0.14	<0.0001
Elateridae	0.64 ± 0.11	0.26 ± 0.076	0.0025

Significance was judged when $p \leq 0.05$.

Table 5. LSMEAN (± SE) of environmental parameters measured in soil block samples of native and restored sites across all periods and transects in Platte River wet meadows in central Nebraska during 2002 and 2003.

	2002		*2003*	
	Native	*Restored*	*Native*	*Restored*
Litter cover (%)	57.64 ± 5.52*	37.04 ± 7.49*	85.09 ± 4.62**	35.85 ± 8.60**
Soil moisture (%)	20.57 ± 3.04	19.52 ± 2.66	23.86 ± 2.34	21.36 ± 2.53
Temperature (°C)	19.87 ± 0.77	21.26 ± 1.17	20.0 ± 0.54**	21.11 ± 0.49**
Root mass (g)	165.43 ± 16.03*	54.89 ± 7.04*	119.97 ± 12.17*	56.53 ± 9.3*

* Significant differences between observed values of abiotic factors in native versus restored sites during respective years ($\alpha = 0.05$).
** The main effect was not tested due to significant two- or three-way interactions.

during periods 1 and 3, but restored sites exhibited slightly higher soil moisture levels, although not significant, during period 3 (Table 6). During 2003, average soil moisture was significantly higher in low transects than in medium or high transects (Fig. 1) ($F_{[2,62]} = 19.13$, $p < 0.0001$).

Mean soil temperature during 2002 was significantly lower during period 1 than periods 2 and 3 (Table 6). Soil temperatures in low transects were significantly cooler than in high transects, but medium transects were similar to both low and high transects. Soil temperatures during 2003 were significantly affected by an interaction of period by site type ($F_{[2,45]} = 4.22$, $p = 0.0209$); therefore, the effects of site type on soil temperatures were examined within periods. Soil temperatures were lower in native sites than in restored sites during all three sampling periods but were significantly cooler only during period 1 ($F_{[1,45]} = 14.93$, $p = 0.0003$) (Table 6).

During 2002, dry root mass in restored sites was only 33% of that found in native sites (Table 5) ($F_{[2,62]} = 60.9$, $p < 0.0001$). Low transects (LSMEANS = 156.72, SE = 28.42) had higher root biomass than medium transects (LSMEANS = 97.85, SE = 15.14) but were similar to high transects (LSMEANS = 99.59, SE = 12.39) ($F_{[2,62]} = 3.72$, $p = 0.320$). In 2003, root biomass of restored sites was 47% of that found in native sites (Table 5) ($F_{[2,62]} = 23.48$, $p < 0.0001$).

Relationship of Soil Invertebrate Community to Environmental Factors

The first four axes of the CCA explained 17.5% of the total variation in relative abundances of 21 soil invertebrate taxa (Table 7). The first two axes alone accounted for 14.6% of the total variation. Results of the Monte Carlo test showed that the first axis explained more variation in soil invertebrate abundance than expected by chance ($F = 5.18$, $p = 0.001$). The taxa by taxa environment correlation coefficient for the first axis was 0.763, suggesting a strong relation between soil invertebrate taxa and environmental variables for the first CCA axis. The first CCA axis was positively correlated with soil moisture, whereas the second CCA axis was negatively correlated with root mass (Table 7).

The first CCA axis seems to represent a gradient of increasing soil moisture and litter depth (Fig. 2). Tipulidae and *Aporrectodea* were associated with wetter sites containing high amounts of litter, whereas Scarabaeidae, Meloidae, and Elateridae were associated with drier sites containing low amounts of litter. For the second CCA axis, the gradient is predominantly characterized by decreasing root mass. Succineidae and Strobilopsidae had the highest positive scores associated with the second CCA axis, whereas Acrididae, Staphylinidae, Isopoda, Araneida, and Curculionidae had the highest negative scores associated with the second CCA axis (Fig. 2).

Discussion

Soil invertebrates comprise one of the best groups for monitoring restoration success because of their importance to basal ecosystem function and a relatively poor ability to disperse. Earthworms (Binet et al. 1998), ants (Hölldobler & Wilson 1990), and isopods (Zimmer & Topp 1999; Kautz & Topp 2000) have all been linked with fundamental soil processes, including nutrient cycling, water drainage, and vegetation succession (Aina 1984; De Deyn et al. 2003).

Soil-dwelling invertebrate communities in restored sites appear to remain different from those in native sites. Diversity estimates, biomass, and number of taxa were generally greater in native sites than in restored sites. Additionally, the taxonomic makeup of invertebrate communities appears to differ, as indicated by the presence of certain groups exclusively in one site type.

Despite these differences, the mean number of specimens collected did not significantly differ between native and restored sites, probably because more ants were collected in restored sites than in native sites. In fact, of the five most abundant taxa encountered in this study, only ants were more abundant in restored sites. Other studies have found similar evidence that overall ant abundance increases in disturbed habitats (see review in Folgarait 1998). Hölldobler and Wilson (1990) also report ants to be more abundant in disturbed areas. This is usually attributed to the increased dominance of aggressive or exotic ant species. Increased ant abundance has been documented in conjunction with both increases and decreases in ant species richness, but this study does not address changes in ant species richness because ants were only

Table 6. LSMEAN (± SE) percent litter cover, percent soil moisture, and temperature (°C) of soil during 2002 and 2003 in native and restored wet meadows along the Platte River in central Nebraska during three sampling periods each year.

	2002						*2003*					
	Native			*Restored*			*Native*			*Restored*		
	Period			*Period*			*Period*			*Period*		
	1	*2*	*3*	*1*	*2*	*3*	*1*	*2*	*3*	*1*	*2*	*3*
Litter cover	64.53 ± 11.14	54.58 ± 11.14	53.80 ± 11.14	44.03 ± 12.87	30.15 ± 12.87	36.94 ± 12.87	84.83 ± 10.33	83.97 ± 10.33*	86.46 ± 10.33*	66.73 ± 11.93	19.64 ± 11.93*	21.17 ± 11.93*
Soil moisture	37.17 ± 2.45*	16.93 ± 2.45*	7.61 ± 2.45	31.36 ± 2.83*	14.83 ± 2.83*	12.38 ± 2.83	29.47 ± 2.96	23.55 ± 2.96	18.55 ± 2.96	21.92 ± 3.42	20.3 ± 3.42	21.85 ± 3.42
Temperature	14.11 ± 0.73	23.66 ± 0.73	21.83 ± 0.73	13.93 ± 0.84	25.35 ± 0.84	24.5 ± 0.84	15.92 ± 0.50*	22.0 ± 0.50	22.08 ± 0.50	18.66 ± 0.57*	22.22 ± 0.57	22.44 ± 0.57

Significance was judged when $p \leq 0.05$.
* Significantly different treatment levels.

identified to family level. Further research should be conducted to characterize ant species richness in this system because of their critical role in ecosystem functions (Jones et al. 1997; Folgarait 1998). Soil blocks with large numbers of ants rarely contained other soil invertebrates, presumably due to predation or territorial defense (J. J. Riggins, Department of Entomology, University of Arkansas, Fayetteville, personal observation). It is conceivable that greater ant abundance is itself a major force causing biodiversity of other families to be lower in restored versus native sites.

Four of the most numerous groups in this study (Isopoda, *Aporrectodea*, Scarabaeidae, and Elateridae) were more common in native sites. The results for terrestrial isopods are surprising because this group is composed entirely of exotic species in Nebraska and are often characterized as favoring disturbance and therefore would be expected to favor restored sites (Jass & Klausmeier 1996; Rapp 2001). However, in this study, we collected far more isopods in native sites. Isopods are important members of the soil invertebrate community because of their function in nutrient recycling and decomposition (Warburg 1987; Paoletti & Hassall 1999). Isopods have been suggested as good candidates for bioindicators because of their ubiquitous nature, high densities, poor ability to disperse, and ease of identification (Paoletti & Hassall 1999; Nakamura et al. 2003). Most isopods favor moist environments and feed on detritus and roots, which were significantly more abundant in native sites, possibly explaining why isopods were more abundant there.

Earthworms are also major contributors to ecosystem function and are crucial components of temperate soil invertebrate communities because they aid in decomposition, mix and aerate the soil, contribute to local microbial activity, and aid nutrient cycling (Jones et al. 1994; Binet et al. 1998). Earthworms are also an important part of the diet of migratory cranes (Reineke & Krapu 1986; Davis & Vohs 1993). We collected two genera of earthworms, *Aporrectodea* and *Diplocardia*. *Aporrectodea* is an exotic genus, whereas *Diplocardia* is native. *Aporrectodea* accounted for more than 85% of the sexually mature earthworms and more than 95% of the total sexually mature earthworm biomass collected during this study and were more abundant in native sites than in restored sites. There were no differences between abundance and biomass of *Diplocardia* between native and restored sites. These results are surprising because the native earthworms seem to be equally rare in both restored and native sites, whereas the exotic genus is far more abundant in native wet meadow habitat. We suspect that the larger exotic earthworms may be outcompeting native *Diplocardia* species.

The most abundant soil macroarthropod group was Scarabaeidae, which was also found in previous studies of wet meadows along the Platte River (Davis & Vohs 1993; Davis et al. 2006). It is likely that scarab beetles are more numerous in native sites because the root biomass that they feed upon was much higher there.

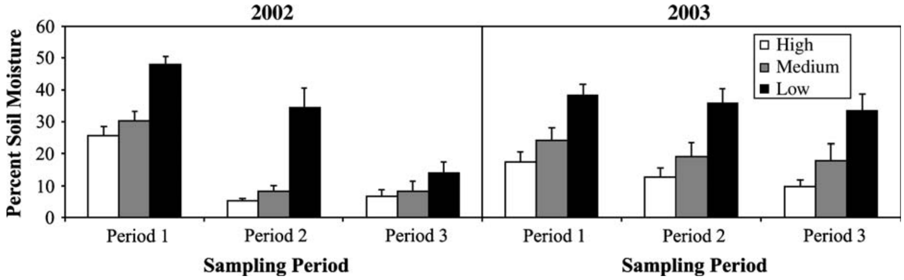

Figure 1. Mean percent soil moisture measured in top 6 cm of each soil block sample collected in central Nebraska Platte River wet meadows during 2002 and 2003.

These data indicate that overall invertebrate communities and some important families of invertebrates have not recovered to native conditions in restored sites, despite lengthy recovery times (all sites were restored between 3 and 6 years prior to the start of our study). Many of the biotic differences reported here may be explained by differences in environmental conditions in restored sites. Percent litter cover, root mass, and soil moisture were generally greater in native sites than in restored sites. It appeared that most soils of restored sites had lower organic content, thinner topsoil, and a prevalence of sandy substrate (J. J. Riggins, personal observation). Davis et al. (2006) linked water table fluctuations (linked to river flow levels) and the associated soil moisture levels to differences in soil invertebrate communities in wet meadows of the Platte River. Many of the environmental and biotic differences observed in the present study could also be because of these effects. Results from the CCA also suggest that soil moisture and primary productivity as indicated by root mass are important factors for determining differences in soil invertebrate communities between restored and native wet meadows. Higher soil moisture and its effects on primary production increase available detritus and in turn may drive soil invertebrate abundance. Greater soil moisture also has direct effects on invertebrates by preventing desiccation in sensitive taxa such as isopods, millipedes, and earthworms.

Differences of soil moisture, temperature, and litter cover encountered among site types may be a result of mechanical disturbance brought about by the restoration itself. Heavy machinery was used to recreate the ridge and swale topography and may have resulted in soil strata disturbance. Future Platte River wet meadow restorations should consider altering methods to specifically remove and replace topsoil during mechanical habitat reconstruction. Additional care is needed to ensure that future restorations recreate realistic ridge and swale topography, specifically taking into account water table depth based on the importance of hydrology to soil invertebrate communities in wet meadows (Davis et al. 2006).

One limitation of our study is the use of higher levels of taxonomy to test for effects of restoration on invertebrates versus the use of species or morphospecies identification. Longcore (2003) demonstrated that use of higher taxonomic classification can be misleading in determining ecosystem impacts. However, the use of higher level taxonomy provides a number of advantages including reductions in time and cost of analysis while providing an analysis of the overall community (Beattie & Oliver 1994; Hoback et al. 1999). Moreover, the fact that the majority of insect families are composed of members that perform the same trophic functions in the ecosystem makes family-level resolution sufficient to examine ecosystem-level effects. For example, most soil-dwelling elaterid larvae feed

Table 7. Results of CCA for soil invertebrates and environmental variable data for the first four axes of the CCA examining the relationship between the soil invertebrate community and the environmental variables for restored and native wet meadows along the Platte River in south-central Nebraska, 2002–2003.

	Axis 1	*Axis 2*	*Axis 3*	*Axis 4*
Eigenvalues	0.349	0.132	0.077	0.021
Species–environment correlations	0.763	0.540	0.503	0.314
Cumulative percentage variance of species data	10.6	14.6	16.9	17.5
Cumulative percentage variance of species–environment relation	58.3	80.3	93.2	96.7
Intraset correlation coefficients				
Litter cover	0.126	−0.010	−0.110	−0.227
Litter depth	0.320	−0.213	0.217	−0.186
Soil moisture	0.506	−0.250	−0.262	0.085
Soil temperature	−0.324	0.168	0.177	−0.099
Root mass	−0.374	−0.354	−0.100	−0.143

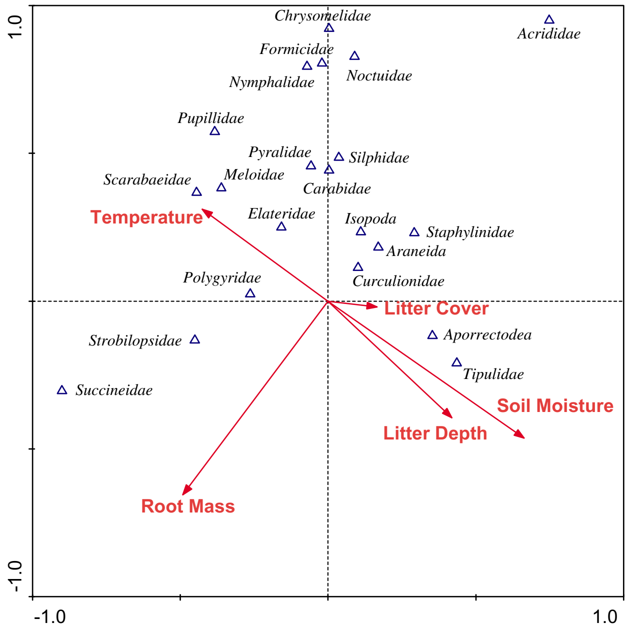

Figure 2. Biplot of the first and second CCA axes for soil invertebrate taxa inhabiting restored and native wet meadows along the Platte River in south-central Nebraska, 2002–2003.

on roots, and all scarab larvae are herbivores. Of course, as previously shown with ants (Hölldobler & Wilson 1990), this is not the case for all invertebrate families.

Other studies have used higher taxonomic levels to estimate terrestrial biodiversity, with varying degrees of success (Balmford et al. 1996; Williams et al. 1997; Hoback et al. 1999). Like these other studies, the present study indicates that higher level taxonomy of soil invertebrates can provide a measure of ecosystem change, but more in-depth appraisals would contribute more understanding in situations where subfamily differences are important, as in the case of ants (although others have suggested that a taxonomic sufficiency approach is adequate in some circumstances even for problem groups such as ants; Pik et al. 1999). Future Platte River wet meadow restoration assessments should use finer taxonomic resolution (genus- or species-level identification) or morphospecies to describe the communities of key taxa such as ants, earthworms, or isopods because of their importance and exhibited responsiveness to disturbance. If included, other sensitive taxa such as Collembola, Diplura, and Acari might further characterize differences between site types.

Overall, wet meadow restoration practices in the Platte River Valley have not completely restored soil invertebrate communities to a native condition. Number of taxa and Shannon and Simpson biodiversity indices were significantly lower in restored sites. The community assemblages also differed, as indicated by the presence of taxonomic groups exclusively in one of the site types, and significant differences exhibited between native and restored sites in several of the critical taxa. It is likely that differences also exist at lower taxonomic levels (i.e., genus, species) and may result in differences in energetic and nutrient cycling in the wet meadows. Because of the importance wet meadows and their invertebrate communities hold for migratory bird species and rare or endangered species, further consideration should be given to developing restoration methods that more completely restore invertebrate communities. It is possible that the observed differences in soil invertebrate communities affect the dietary and nutritive supply to species that feed in those communities. Such differences hold important implications for an extremely endangered habitat in North America and the numerous species of plants and animals that live in and depend upon wet meadows.

Implications for Practice

- The “If you build it, they will come” attitude toward restoration ecology may be inadequate for projects involving soil invertebrates.
- Soil moisture, and the underlying hydrology that controls it in wet meadows, may need special attention during future restorations because of the impact on invertebrate communities.
- Measures of family-level diversity of soil invertebrates appear to be sensitive enough to detect disturbances in wet meadows, but trade speed for potentially important information about the differences in assemblages of several “ecosystem engineer” groups.

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