

Ecosystem engineering by bison (*Bison bison*) wallowing increases arthropod community heterogeneity in space and time

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Abstract. Ecosystem engineers have important effects on abundance and diversity of organisms and are vital for conservation efforts. Some large mammalian grazers are engineers because their grazing activity radically changes plant community structure, an effect which then cascades to other consumers. Many large grazers also behaviorally modify the physical environment. American bison (*Bison bison*) are known for their wallowing, a behavior that creates distinct areas of high disturbance with modified biological and physical characteristics, but how this behavior affects other consumers is poorly understood. In this study, we investigated arthropod abundance and diversity patterns in active and abandoned wallows compared to those in surrounding tallgrass prairie. We found that active wallows contained lower arthropod abundance and diversity compared to surrounding prairie. Herbivorous arthropods were particularly affected and only about 50% as abundant in wallows, while carnivores and detritivores were affected similarly, but to a lesser degree. In contrast, abandoned wallows had higher arthropod abundance seasonally and higher species richness in several feeding groups. Because of arthropod differences in active and abandoned wallows compared to adjacent prairie, it appears that the impact of wallowing is dependent on time since occurrence, with long-term effects creating patches of higher arthropod abundance and richness. These patches are likely important, at least seasonally, for other consumers higher on the food web. Together with publications documenting positive effects of bison grazing on arthropod abundance and diversity, our results indicate that wallowing effects are potentially additive. These results suggest that physical changes caused by bison behavior are important for maintaining arthropod biodiversity of tallgrass prairies, and bison may therefore be valuable conservation tools. Bison have been proposed as important candidates for rewilding portions of North America, and our results suggest that they could indeed be valuable toward this end.

Key words: arthropod community; bison; *Bison bison*; disturbance; ecosystem engineer; rewilding; tallgrass prairie; wallowing.

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INTRODUCTION

Ecosystem engineers are those organisms that, through their behaviors, physically alter their environment and in the process affect other organisms and ecosystem function (Jones et al. 1994, 1997). Many taxa have representatives that perform ecosystem engineering functions,

including reptiles (Gibbs et al. 2010, Froyd et al. 2014), mammals (Naiman 1988, Naiman et al. 1988, Reichman and Seabloom 2002), arthropods (Meyer et al. 2011), cnidarians (Lenihan 1999), plants (Tanner 2001, Gilad et al. 2007), and algae (Coleman and Williams 2002). As many studies have shown, ecosystem engineering activities affect the abundance, distribution, and behavior

of individual species, as well as produce community-wide effects on species richness and food web dynamics (Jones et al. 1997, Cuddington et al. 2011). One prominent example is the beaver (*Castor* spp.), which drastically affects distribution of organisms and spatial habitat heterogeneity (Klotz 1998, Wright et al. 2002).

In grasslands, the two most important factors affecting ecosystem function are grazing and fire (Fuhlendorf and Engle 2004). In North America, the most important grazer was the American bison (*Bison bison*), while domestic cattle (*Bos taurus*) are today the most common large mammal grazers (Knapp et al. 1999, Allred et al. 2011). Fire affects the grassland communities directly, but also by modulating grazing intensity. These two factors interact in complex ways to determine plant community structure and have large effects on consumer distribution and abundance (Vinton et al. 1993, Collins and Smith 2006, Fuhlendorf et al. 2009).

Bison are strong allogenic ecosystem engineers (i.e., they behaviorally modify their environment) in the tallgrass prairies of North America. Engineering activities of bison include grazing, soil disturbance when moving, and wallowing. Many studies have addressed how bison grazing affects plant communities (Fahnestock and Knapp 1994, Collins and Smith 2006, Elson and Hartnett 2017, O'Keefe and Nippert 2017). Bison are graminoid specialists, and their preferential consumption of these competitively dominant plants increases plant diversity (Collins et al. 1998) and heterogeneity (Knapp et al. 1999), which in turn leads to cascading effects on other organisms (Joern 2005, Powell 2006, Moran 2014).

As in most terrestrial systems, arthropods are typically the most abundant and diverse macroscopic organisms in grasslands. They include important pollinators, consumers of vegetation, sources of food for other animals, detritivores, and predators that initiate strong trophic interactions (Moran et al. 1996, Moran and Hurd 1997, Pace et al. 1999, Borer et al. 2005, Meadows et al. 2017). Therefore, arthropods tend to occupy a variety of niches and have influences throughout the food web. Ungulate grazing can indirectly affect herbivorous, carnivorous, and detritivorous arthropods by altering plant quality and abundance as well as changing structural features of grasslands (Joern 2005, Moran 2014).

Grazing may reduce cover for carnivores (Blaum et al. 2009), and by consuming vegetation before it dies, reduce resource availability to detritivores (Zhu et al. 2012). Furthermore, grazing may change the nutritional quality of plant resources, which can then initiate complex cascades throughout the food web (De Mazancourt et al. 1998), including enhancement of herbivorous arthropod abundance (Moran 2014).

Herbivorous arthropods are extremely abundant in grasslands and can consume a considerable amount of primary productivity (Detling 1988). This feature of grassland arthropod communities in conjunction with the large impacts ungulate grazers cause, indicate a potentially important interaction (Pringle et al. 2007). However, interactions of large and small herbivores have been poorly studied in grasslands. Surprisingly, mammal–arthropod interaction studies have been rarely performed (for an exception, see Gómez and González-Megías 2002). Most authors have concluded that mammal–arthropod competitive effects are asymmetric (Gómez and González-Megías 2002, Gómez and González-Megías 2007) and that these effects demonstrate a size-dependent difference in ecosystem function (Bakker et al. 2006). Indeed, in our study system, the major grazer is drastically larger, on the order of two million times more massive than a typical grasshopper (e.g., *Melanoplus* sp.).

Wallowing is a behavior of bison that is important for grooming, insect repulsion, sun protection, and social interactions (McHugh 1958, Reinhardt 1985, McMillan et al. 2000). This behavior involves an animal repeatedly rolling on the ground, after which additional animals wallow in the same area. The result is a depression of compacted soil with high disturbance (Fig. 1) which contains a different plant community (Polley and Collins 1984, McMillan et al. 2011) and soil characteristics (Polley and Wallace 1986). Wallowing behavior can also change seed distribution (Rosas et al. 2008). As bison continue to use a wallow, the soil compaction leads to greater water retention, which then reduces the efficacy of the wallow for this bison behavior (i.e., increased moisture reduces dust levels). The wallow is then typically abandoned, and bison move to other areas to wallow. This abandoned wallow will then be colonized by a distinctive plant community, adding additional heterogeneity to the



Fig. 1. Photographs showing an (A) active bison wallow and (B) abandoned bison wallow.

ecosystem (Polley and Collins 1984, McMillan et al. 2011). These abandoned wallows are also important habitat for many animals. For example, abandoned wallows can occasionally retain a considerable amount of water, which allows them to be utilized as amphibian breeding sites (Busby and Brecheisen 1997), although the frequency and abundance of water-filled wallows varies greatly with short-term weather fluctuations (Gerlanc and Kaufman 2003).

Wallows can be long-lasting structures, having effects on prairie plant communities for many decades (Knapp et al. 1999). With the drastic reduction of the bison population on the Great Plains since 1850 and subsequent replacement with cattle (Allred et al. 2011), which do not wallow, this important ecosystem modification process was lost. While vegetation consequences of wallowing have been studied in tallgrass prairie (Polley and Wallace 1986), how these vegetational changes affect animal community structure is poorly understood.

It has been argued that bison are important management tools to the conservation of North

American prairies and that they should be widely reintroduced across the landscape through rewilding programs (Manning 2011). There are ongoing efforts to return bison to the Great Plains, and these current projects provide an opportunity to study bison ecosystem engineering effects, including their wallowing behavior, on prairie food webs. These studies will be particularly important if reintroductions expand across a larger portion of the landscape.

In this study, we investigated the role of bison wallowing on the arthropod community structure in a tallgrass prairie. We had two major questions to address: (1) How does the arthropod community structure in active wallows differ from surrounding prairie? and (2) How does the arthropod community in abandoned wallows differ from surrounding prairie?

MATERIALS AND METHODS

Field site

Our study was performed at the Tallgrass Prairie Preserve (TPP) located in Osage County, Oklahoma, USA (36.8461 N, 96.4229 W). The TPP is a 16,000-ha protected area owned by the Nature Conservancy and managed to preserve prairie habitat in the Flint Hills. The Flint Hills is a geographic formation that runs from eastern Kansas to extreme northeastern Oklahoma and is noteworthy in that it contains the largest area of intact North American tallgrass prairie. Tallgrass prairies in this region are dominated by four species of grasses: big bluestem (*Andropogon gerardi*), little bluestem (*Schizachyrium scoparium*), switchgrass (*Panicum virgatum*), and Indiangrass (*Sorghastrum nutans*), plus over 300 species of forbs (Knapp et al. 1999, see Palmer 2007 for TPP checklist). The TPP has an annual average temperature of 15.3°C with 1191 mm of precipitation (precipitation has high annual variation). It is managed using prescribed burning and grazing to simulate the pre-settlement disturbance regime. In 1993, 300 bison were reintroduced to the preserve, and the herd has grown to a managed number of about 2500, which is maintained by annual culling. The preserve contains most pre-European settlement fauna, with the exception of elk (*Cervus canadensis*), wolves (*Canis lupus*), and grizzly bears (*Ursus arctos*). The TPP is divided into numerous management units that

are periodically subjected to prescribe fire. Typically, a unit is burned on a three-year cycle.

Wallows were classified as active, if they were being utilized by bison during the study period. Active wallows have little vegetation (Fig. 1A) and experience frequent disturbance by bison activity. Wallows were classified as abandoned if bison had discontinued use of them and they had become revegetated (Fig. 1B). At similar study sites, abandoned wallows have been shown to have a different plant community (Polley and Collins 1984, McMillan et al. 2011). Active wallows have very little vegetation in the center, but tend to have a mixture of typical tallgrass prairie plants and early successional species along the wallow margins (Collins and Uno 1983, McMillan et al. 2000, Trager et al. 2004). Dominant plants in abandoned wallows include ragweed (*Ambrosia psilostachya*), sedges (*Carex* spp.), Canada bluegrass (*Poa compressa*), ridgeseed spurge (*Chamaesyce glyptosperma*), and hoary verbena (*Verbena stricta*). Noteworthy is that the most common plant species found in adjacent prairies (i.e., the four dominant grasses described above) are generally absent or greatly reduced in wallows (Trager et al. 2004, McMillan et al. 2011).

Experimental design

Experiment 1: active wallows.—This first experiment was designed to study the localized effects of active wallowing on arthropod communities. In May of 2015, we identified 15 active wallow sites and 15 control sites on a burn unit of the TPP that had a prescribed fire in the previous March. We sampled arthropods on a transect 4 m in length across each wallow, a distance that covered the central lightly vegetated portion as well as the raised area around the wallow which tends to be more highly vegetated. The entire area of the wallow transect typically undergoes high disturbance rates with numerous bison wallowing, often on a daily basis. For control sites, we sampled a 4-m transect that was located 8 m away from each sample wallow. This area we considered typical prairie that is grazed and undergoing moderate levels of disturbance from bison activities. Arthropods were collected by D-vac (Rincon-Vitova Insectaries) with a 0.20-m cone opening, which together with a 4-m transect resulted in 0.80 m² sampled. All collected

arthropods were killed by freezing and then sorted to order, trophic position, feeding type, and morphospecies. We sampled each site four times during the growing season: 5.5.15, 6.20.15, 8.6.15, and 9.22.15.

Experiment 2: abandoned wallows.—In 2016, we performed a field experiment to investigate the residual effects of bison wallowing behavior on arthropod communities by examining abandoned wallows. These wallows are typically 2–3 yr old and have been fully recolonized by plants, although plant community structure is much different than the surrounding prairie (Polley and Collins 1984). In a single management unit that was burned in March 2016, we located 12 abandoned wallows and 12 adjacent control areas of typical prairie. These were sampled three times during the growing season on 5.11.16, 7.6.16, and 8.5.16 with the same methods as in experiment 1.

Statistical analyses

To determine abundance of arthropods in different feeding categories, we first classified arthropods to order, and then to a taxonomic group small enough to determine general feeding behavior. We classified each arthropod into three broad trophic levels: herbivore, carnivore, and detritivore. We then further classified the herbivores as either sap-feeding (e.g., Hemiptera) or chewing (e.g., Orthoptera) herbivores and the carnivores as either generalist (e.g., Araneae) or specialist (e.g., parasitic Hymenoptera) carnivores. Sap-feeding herbivores were those that have a beak mouthpart and feed on plant fluid, typically phloem material, while chewing herbivores were those that have typical mandibulate mouthparts. Generalist carnivores were those that feed on a variety of prey, primarily based on size, not taxonomic affiliation, while specialist carnivores were those that utilize a narrow range of prey species. Ants, because of their varied feeding strategies and difficulty in the classification of worker caste (which is all we typically capture in the D-vac), were excluded from all analyses.

To study species richness patterns, we first determined the number of morphospecies in each of the feeding categories. Although not a perfect method of determining number of species, counting morphospecies is effective and

practical for measuring richness, as opposed to classifying each arthropod to its actual scientific name (Oliver and Beattie 1996). To estimate species richness, we used the repeated measures in each experiment to calculate rarefaction curves for each individual replicate (EstimateS 9.1.0, Colwell 2006). From these data, we therefore estimated total seasonal diversity for each replicate.

If any data sets had significant heteroscedasticity, we \log_{10} -transformed the data prior to statistical analysis. For abundance of arthropods in the various trophic levels, we analyzed these data by repeated measures MANOVA and examined the time, treatment (between-subjects), and treatment \times time interaction effects. Since we calculated a single total species richness estimate, the species richness results were analyzed by one-way ANOVA. All figures are presented with means (± 1 SE) of untransformed data. Although we had multiple statistical analyses for each experiment, many of our categories are not independent, so we presented all P -values without Bonferroni correction and interpreted results based on patterns of significance (Moran 2003). All ANOVA design analysis was performed on SPSS (IBM SPSS, Armonk, New York, USA).

To visualize the overall community structure between wallows and control plots, we used the abundance data for each morphospecies (combined community data for the all repeated samples in each replicate) and performed a nonmetric multidimensional scaling (NMDS) analysis (Bray-Curtis dissimilarity method). To test the null hypothesis that the community structure is the same between wallows and adjacent prairie, we performed a permutational multivariate analysis (PERMANOVA) and calculated a similarity percentage (SIMPER). All multivariate analyses were performed using PAST statistical program (Hammer et al. 2001).

RESULTS

Experiment 1: active wallows

Arthropod abundance increased over time for most groups (significant time effect; Table 1). Herbivore abundance was significantly higher outside of active bison wallows during the entire course of the experiment (significant between-subjects effect; Table 1, Fig. 2A). Early in the season, wallows and control areas had similar

Table 1. Results of repeated measures MANOVA for abundance in active wallows versus control plots for experiment 1.

Arthropod group	Time effect (P)	Treatment \times time effect (P)	Between-subjects effects (P)
Herbivores	<0.001*	0.540	<0.001*
Fluid-feeding	<0.001*	0.300	0.001*
Chewing	<0.011*	0.135	0.293
Carnivores	<0.001*	0.005*	0.077
Generalists	0.063	0.069	0.262
Specialists	<0.001*	0.045*	0.035*
Detritivores	0.003*	0.054	0.005*

* $P < 0.05$.

carnivore abundance, while later in the season control plots had about double the abundance of wallows (significant treatment \times time interaction; Table 1, Fig. 2B). Detritivore abundance was significantly higher in control plots compared to wallows (significant between-subjects effect; Table 1, Fig. 2C).

Within the herbivore trophic level, sap-feeding arthropods, which were the numerically dominant group, were more abundant in control plots (Table 1; Appendix S1: Fig. S1A). Chewing herbivores, which had much lower abundance overall, showed no change over time and no significant difference between wallows and control plots (Table 1).

Within the carnivore trophic level, generalist predators did not change over time, nor were they significantly different between wallows and controls plots (Table 1). Specialist carnivores increased over time, and although they showed similar abundance between treatment groups at the beginning of the experiment, by the end of the study, control plots had about double the abundance (significant treatment \times time interaction; Table 1; Appendix S1: Fig. S1B).

The species richness of herbivores, estimated by the rarefaction curves, was about double in control plots than in active wallows (\log_{10} -transformed data, $F_{1,28} = 10.56$, $P = 0.003$, Fig. 3A). A similar pattern was seen in carnivores, which also had about double the richness in control plots compared to wallows (\log_{10} -transformed data, $F_{1,28} = 4.62$, $P = 0.04$, Fig. 3A). Detritivores showed no significant difference between groups ($F_{1,28} = 0.06$, $P = 0.79$). When divided into broad feeding categories, we found significantly higher richness in

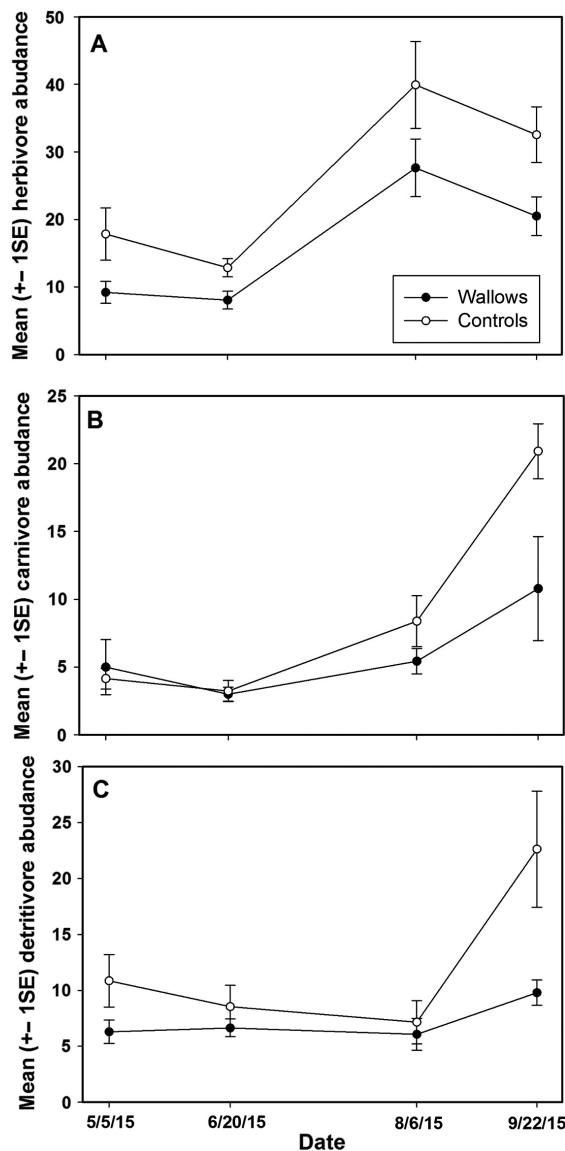


Fig. 2. Trends in arthropod abundance over the course of the growing season in active bison wallows and control plots in experiment 1 for (A) herbivores, (B) carnivores, and (C) detritivores.

control plots for both sap-feeding herbivores (log₁₀-transformed data, $F_{1,28} = 8.97$, $P = 0.006$) and chewing herbivores ($F_{1,28} = 9.89$, $P = 0.004$, Fig. 3B). For the carnivores, specialist species were more diverse in control plots ($F_{1,28} = 4.53$, $P = 0.04$), while generalist carnivores showed no significant difference ($F_{1,28} = 0.90$, $P = 0.35$, Fig. 3C).

The results of the PERMANOVA found that active wallows and control areas were significantly

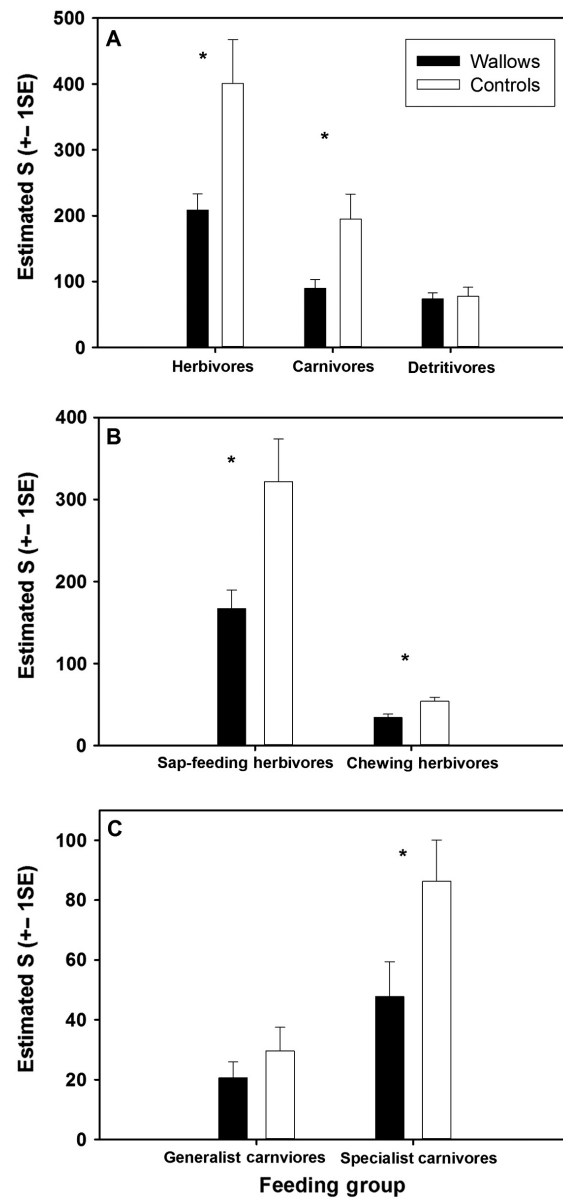


Fig. 3. Comparison of estimated species richness values from rarefaction curves for active wallows and control plots in experiment 1 for (A) major feeding groups, (B) herbivore feeding groups, and (C) carnivore feeding groups. * $P < 0.05$.

different in community structure ($F = 1.51$, $P = 0.013$), while the dissimilarity index was 80.49. The NMDS results showed a small amount of overlap in communities, with most wallow and control plots clustering reasonably well (stress = 0.35, type = Bray-Curtis, Fig. 4A).

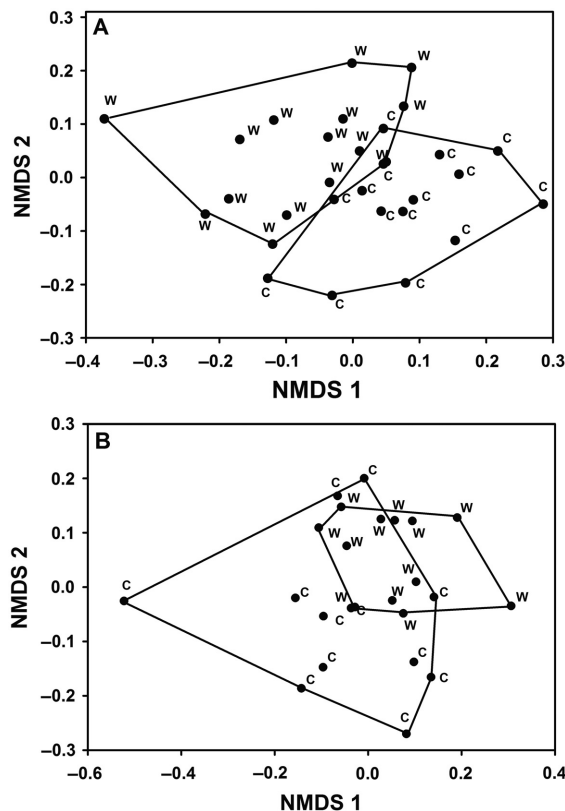


Fig. 4. NMDS results for wallows and control plots in (A) experiment 1 and (B) experiment 2. Community structure is based on presence and abundance measurements for each morphospecies captured in each plot during the entire course of the experiment.

Table 2. Results of repeated measures MANOVA for abundance in abandoned wallows versus control plots for experiment 2.

Arthropod group	Time effect (<i>P</i>)	Treatment × time effect (<i>P</i>)	Between-subjects effects (<i>P</i>)
Herbivores	<0.144	<0.001*	0.315
Fluid-feeding	0.272	0.023*	0.573
Chewing	<0.001*	0.016*	0.186
Carnivores	<0.001*	0.721	0.674
Generalists	<0.001*	0.018*	0.317
Specialists	<0.001*	0.135	0.917
Detritivores	0.001*	0.002*	0.587

* *P* < 0.05.

Experiment 2: abandoned wallows

Arthropod abundance increased over time for most groups (significant time effect; Table 2). There was a significant treatment × time

interaction for herbivore abundance (\log_{10} -transformed data; Table 2, Fig. 5A). This trend was evident in that during the May sample, herbivore abundance was about 50% higher in the wallows compared to control plots, while herbivore abundance was generally lower in wallows later in the experiment. Carnivore abundance indicated no treatment × time and between-subjects effects since abundance values were virtually identical between groups during the entire course of the experiment (Table 2, Fig. 5B). Detritivores showed a significant treatment × time interaction (Table 2, Fig. 5C). In the May sample, detritivore abundance was more than double in wallows, but was similar throughout the rest of the experiment (significant treatment × time interaction).

The sap-feeding herbivores tended to be more abundant in wallows during the May sample, after which they generally had lower abundance (significant treatment × time interaction; Table 2; Appendix S1: Fig. S2A). The chewing herbivores were much more abundant in the wallows in May, declined dramatically in the June sample, and then were virtually identical by the final sample (significant treatment × time interaction; Table 2; Appendix S1: Fig. S2B).

There were no significant treatment × time nor between-subjects effects on specialist carnivores (Table 2). However, there was a significant treatment × time interaction in generalist carnivore abundance (Table 2; Appendix S1: Fig. S2C). The abundance of generalist carnivores in wallows was 80% higher in the second sample but was virtually the same in the other two samples.

The estimated species richness of herbivores was not significantly different between wallows and control plots ($F_{1,22} = 0.292$, $P = 0.594$, Fig. 6A), while carnivores were about twice as diverse in wallows compared to control plots (\log_{10} – transformed data, $F_{1,22} = 4.62$, $P = 0.04$, Fig. 6A). Detritivores were also about twice as diverse in wallows compared to control plots ($F_{1,22} = 4.68$, $P = 0.04$, Fig. 6A). When divided into broad feeding categories, we found no significant richness differences between wallows and control plots for both sap-feeding herbivores ($F_{1,22} = 0.123$, $P = 0.729$) and chewing herbivores ($F_{1,22} = 0.226$, $P = 0.639$, Fig. 6B). Among carnivores, the estimated diversity of specialists was

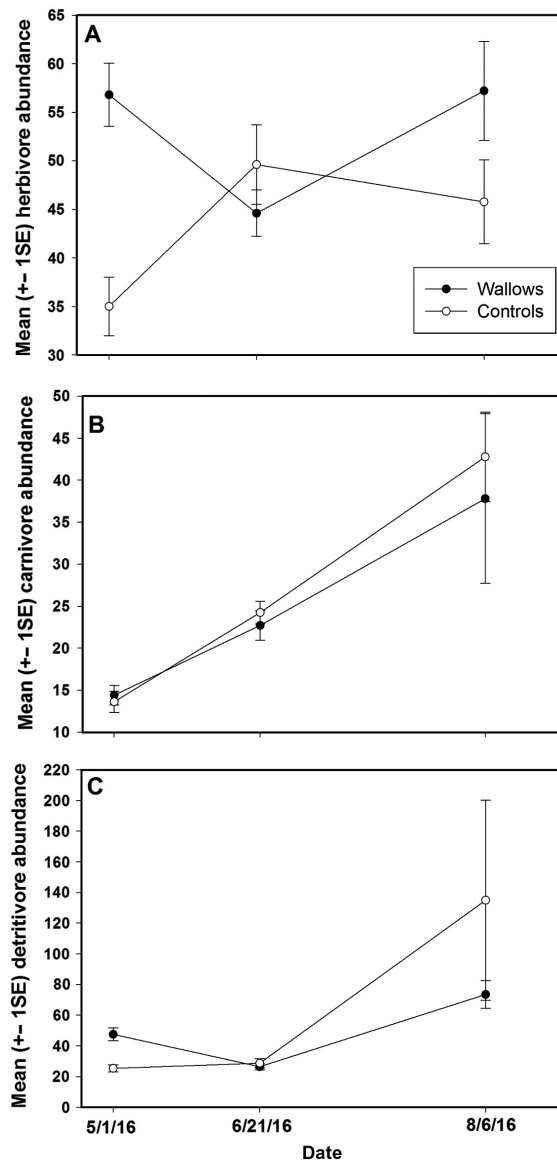


Fig. 5. Trends in arthropod abundance over the course of the growing season in abandoned bison wallows and control plots in experiment 2 for (A) herbivores, (B) carnivores, and (C) detritivores.

significantly higher—about double—in wallows compared to control plots ($F_{1,22} = 7.46$, $P = 0.01$), while generalist carnivores showed no significant difference ($F_{1,22} = 0.02$, $P = 0.90$, Fig. 6C).

The results of the PERMANOVA found that abandoned wallows and control areas were not significantly different in community structure ($F = 1.06$, $P = 0.401$), while the dissimilarity

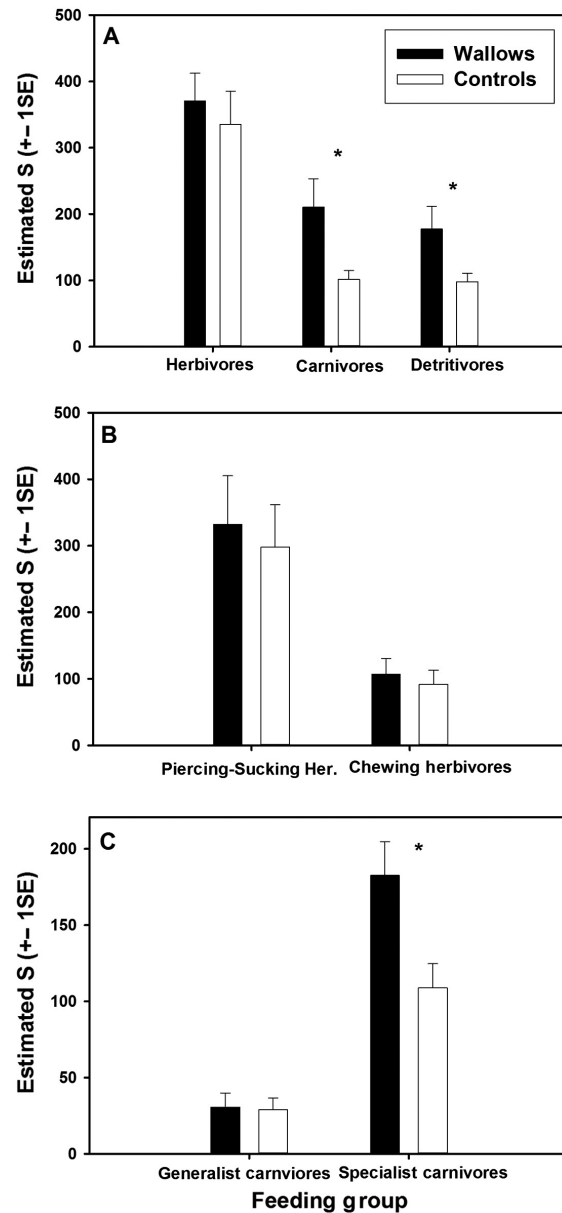


Fig. 6. Comparison of estimated species richness values from rarefaction curves for abandoned wallows and control plots in experiment 2 for (A) major feeding groups, (B) herbivore feeding groups, and (C) carnivore feeding groups. * $P < 0.05$.

index was 79.25. The NMDS results showed a large amount of overlap in communities, with the control plots showing a larger amount of variation compared to wallows (stress = 0.31, type = Bray-Curtis, Fig. 4B).

DISCUSSION

From our results, it appears that active wallows and abandoned wallows have different arthropod abundance and richness compared to surrounding prairie. General patterns show that active wallows have lower abundance and diversity of arthropods from a variety of feeding groups, with the exception of detritivores. The abandoned wallows show a more seasonally variable pattern in abundance, notably higher in wallows in the spring. We suspect that the generally lower arthropod numbers in active wallows are a direct result of the high disturbance regime and reduction in food availability (Petraitis et al. 1989). Bison wallowing causes much reduced plant biomass, reduced plant growth rates, and probably direct mortality to many arthropods from the extreme force of a 1000 kg animal. However, when a wallow is abandoned, the altered structure caused by past bison activity creates a microhabitat with modified physical resources and a subsequent distinctive biological community (Polley and Wallace 1986, Hartnett et al. 1997). Abandoned bison wallows retain different physical characteristics (e.g., higher water retention) compared to unmodified prairie, which allows them to support very different plant communities (Barkley and Smith 1934, Uno 1989). We showed in this experiment that these changes in physical and biological characteristics produce microhabitats that affect arthropod biodiversity, including patches of higher arthropod richness. The results therefore show that the area of the prairie the wallows occupy can support higher diversity of at least some arthropod groups. The pattern we found shows the importance of the disturbance time frame (Huston 1979). Although the short-term effects of bison wallowing were generally negative on arthropod abundance and diversity, the longer-term effects were much more complex (Gibson 1989).

In the abandoned wallows, there was a strong seasonal component in that arthropod abundance, especially in herbivorous species, was much higher in the early part of the season. Later into the season arthropod abundance was, depending on feeding group, lower or similar. Therefore, past bison wallowing appears to create a more seasonally variable arthropod community. Our results are potentially linked to

the seasonal plant community shifts seen in wallows (Polley and Collins 1984, Trager et al. 2004). Early season wallow plants are dominated by C_3 species, but later in the season C_4 species, including several grass species that bison prefer (Knapp et al. 1999), become common.

Our results support the notion that bison, through their wallowing behavior, produce ecosystem engineering effects (Collins and Uno 1983, Knapp et al. 1999). The heterogeneity created by the combination of active and abandoned wallows (Collins and Barber 1985) has effects that extend to plants (Gibson 1989, Trager et al. 2004), amphibians (Gerlanc and Kaufman 2003, Baruzzi and Krofel 2017), and arthropods (this study). Bison wallows can often cover a substantial proportion of North American prairie habitat (England and Devos 1969, Umbanhowar 1992) and can persist for many years (Knapp et al. 1999). Therefore, bison wallowing behavior creates both a constant modification and a persistent effect on the environment, and one that is likely to have pervasive impacts on ecosystem function (Hartnett et al. 1997). Previous research has shown that bison grazing increases arthropod abundance and diversity (Joern 2005, Moran 2014), while this study shows that bison physical disturbance behavior may lead to even higher abundance and diversity in select locations at certain time of the year. Therefore, when studying effects of potential ecosystem engineers, we argue it is important to investigate their myriad behaviors. In this case, the grazing and physical disturbances appear to have an additive effect, and these two factors together tend to increase consumer heterogeneity in both space and time (Collins and Barber 1985).

The higher early season arthropod numbers seen in this experiment could be particularly important for supporting higher trophic level consumers. For instance, insectivorous birds need substantially more resources in the early season when they are nesting and raising offspring (Martin 1987). The wallows may therefore represent areas of higher foraging success and, in turn, could increase reproductive success. It is known that bison presence has significant effects on many bird species, although most impacts are explained due to their grazing effects (Powell 2006, Coppedge et al. 2008). For example, the grasshopper sparrow (*Ammodramus savannarum*),

a species dependent upon arthropod resources, is more abundant in bison occupied areas (Powell 2006). Since bison are known to enhance arthropod abundance (Moran 2014) due to grazing and, according to this study, further enhance it (at least at times) because of their physical disturbance, we argue that their indirect effects on consumers should be more carefully considered. For example, insectivorous birds could benefit by foraging in these high resource areas (Askins 2002). Considering the drastic decline in many species of grassland specialists, the effects of the physical activities of bison should be investigated further.

Large ungulate grazers have profound effects on grassland communities (van Klink et al. 2015), and they are being used for conservation efforts in many regions. Our study supports the notion that bison are valuable conservation tools for North American tallgrass prairies. While some researchers have suggested bison and cattle (*Bos taurus*), because of their similar grazing behaviors, are ecological equivalents (Plumb and Dodd 1993, Towne et al. 2005), we argue that the bison-specific behaviors (in this case, wallowing) not seen in cattle could enhance their promotion of biodiversity. Therefore, all large mammalian grazers are not necessarily equal (Plumb and Dodd 1993) and their non-feeding behaviors must be considered as well (Hartnett et al. 1997).

Many researchers have suggested that a rewilding of the North American prairies could be beneficial to the biodiversity of the region (Matthews 1992, Donlan et al. 2005, Svenning et al. 2016) and, given the relatively large areas of natural habitat that remain, could help transform the Great Plains back into a well-functioning biome (Fuhlendorf et al. 2009). However, potential rewilding effects on ecosystem function remain poorly understood, underscoring the need for investigative studies. Such knowledge could make the rewilding process one that is performed with the full range of ecological expectations and consequences known.

This study supports that notion, and we urge the return of bison to larger areas of the North American Great Plains, including the encouragement of private ranches to raise bison instead of cattle, which may improve biodiversity protection. Based on our results, we argue that restoration ecology using bison, such as what is

occurring at the field site for this study (TPP) or other larger projects (e.g., American Prairie Preserve in Montana, Freese et al. 2007), is having meaningful impacts on biodiversity and ecosystem function of the Great Plains.

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