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ORIGINAL PAPER

Ground-dwelling invertebrate community responses to bison and prescribed fire management in tallgrass prairies

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Abstract Disturbances are drivers of ecosystem function and play important roles in shaping ecological communities. Prescribed fire and grazing disturbances are common management tools in restored and remnant grasslands. The effects of these management actions on plant communities and on vegetation-dwelling invertebrates are generally well studied. However, less is known about their effects on ground-dwelling invertebrates, which can contribute to important ecosystem processes like herbivory, predation, and decomposition. We examined bison grazing and prescribed fire effects on abundance, diversity, and community composition of ground-dwelling invertebrate groups in restored tallgrass prairies using pitfall trap samples. Surprisingly, invertebrate Shannon diversity decreased when bison were present and was unaffected by fire or the fire–bison interaction. Bison, and to a lesser extent fire, also shifted community composition, increasing abundance of ground, rove, and dung beetles, as well as orthopterans and spiders. Prescribed fire generally increased beetles but caused declines in several ecologically diverse invertebrate groups, including harvestmen and true bugs, although these reduced abundances did not lead to differences in overall diversity. Bison presence may amplify the abundances of dominant groups, such as ground and dung beetles and orthopterans, that outcompete other invertebrates and reduce diversity.

Implications for insect conservation Prescribed fire and grazing by bison change ground-dwelling invertebrate community composition, but bison presence did not reduce the abundance of most taxonomic groups. Fire may have short-term negative impacts on some invertebrate groups that promote desirable invertebrate-driven ecosystem processes, but these effects are likely short-lived, and the resulting environmental mosaic under bison and fire management could support biodiversity over the long-term.

Keywords Disturbance · Restoration · Pyric herbivory · Insects · Arthropods · Prairie

Introduction

Disturbance events, such as floods, drought, fire and grazing, are important drivers of ecosystem structure and function and play consequential roles in determining the diversity and abundance of species within an ecological community (Sousa 1984; Turner 2010). Disturbances vary in severity and intensity (Iwasaki and Noda 2018) and have historically shaped ecosystems. For example, prior to European settlement, North American tallgrass prairie was influenced by frequent fire, grazing by large ungulate herbivores such as bison, and the interaction of these factors (Axelrod 1985; Knapp et al. 1999). Tallgrass prairies historically extended across the North American central plains (Fay 2003) but today are some of the most drastically modified environments on Earth and have been largely eliminated by conversion for agricultural use (Samson and Knopf 1994, 1996). Prescribed fire and controlled grazing have become

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important methods for managing restored and remnant tallgrass prairies (Fuhlendorf et al. 2008).

The interaction between fire and grazing is described by the conceptual "pyric herbivory" model by Fuhlendorf et al. (2008): fire burns where grass biomass is abundant, further stimulating new grass growth. Grazers are then attracted to this new growth which decreases plant biomass in the area, therefore sparing other areas of vegetation. Plant growth and thatch in ungrazed areas become fuel for the next fire, and grazing locations then shift to the new plant tissues that grow following fire. Overall, the interactions between fire and grazing create a mosaic of different stages of grass growth reflecting variation in recent burning and grazing history, and this heterogeneity may support greater species diversity than a more homogenous environment with burning or grazing alone (Fuhlendorf and Engle 2001; Fuhlendorf et al. 2008).

Fire and grazing alter the structure of plant communities (Collins and Calabrese 2012; Elson and Hartnett 2017), which induces habitat changes that may affect invertebrate assemblages (Gómez et al. 2016; Minor et al. 2021). These effects on vegetation occur through several mechanisms. Bison preferentially feed on grasses, which can reduce competition on forbs to promote plant diversity (Knapp et al. 1999; Blackburn et al. 2021). Reduced vegetation density following grazing changes the physical environment experienced by invertebrates (Elson and Hartnett 2017). The waste produced by bison increases soil quality in grazed areas by recycling important nutrients such as nitrogen (Knapp et al. 1999). Similar to grazing, fire increases nutrients in the soil by accelerating decomposition of organic matter (Reinhart et al. 2016). Increased plant quality and diversity caused by fire and grazing consequently may increase the abundance, diversity, and richness of invertebrate herbivores (Callaham et al. 2003; Fay 2003).

Changes to invertebrate assemblages may be important because invertebrates are key contributors to ecosystem functions and services such as decomposition, dung removal, and seed predation (Losey and Vaughan 2006; Yang and Gratton 2014; Schowalter et al. 2018). Despite this importance, relatively few studies have examined grazing and fire effects on prairie invertebrates broadly compared to impacts on plants or specific insect groups. However, the few studies that have been conducted on invertebrates found that bison grazing can increase the abundance, diversity, and richness of herbivorous, carnivorous, and decomposer invertebrates (Moran 2014; Hosler et al. 2021; Nelson et al. 2021). Fire may decrease soil invertebrate density and biomass to varying extents based on degree of exposure to fire (Swengel 2001; Callaham et al. 2003), and total invertebrate biomass may be maximized 1–2 years after fire (Engle et al. 2008). Furthermore, high plant species diversity resulting from the combination of fire and grazing might promote high invertebrate richness and diversity (Fay 2003). Therefore, the use of fire and grazing as management methods in prairie restoration can have a positive effect on the invertebrate taxonomic and functional diversity, potentially supporting the functional goals of ecosystem restoration (Hobbs and Harris 2001).

However, the few studies broadly examining prairie invertebrate responses to fire and grazing (Fay 2003; Engle et al. 2008; Moran 2014) have focused primarily on vegetation-dwelling organisms by sampling with sweep netting or vacuuming. Here, we focus on ground-dwelling invertebrates and use a landscape-scale, replicated tallgrass prairie restoration project to study how grazing by re-introduced bison and prescribed fire affect invertebrate communities over two years. Bison are able to move among prairie restorations that differ in recent burn history, mimicking historical fire-grazing interactions. We hypothesize that abundance and diversity of invertebrate groups will be greater in sites with bison and further increased where fire recently occurred.

Methods

Study site and design

This study was part of the ReFuGE (Restoring FUnction in Grassland Ecosystems) project at Nachusa Grasslands, a 1500-hectare site in northern Illinois, owned by The Nature Conservancy. Nachusa is mostly composed of remnant and restored tallgrass prairies which vary in bison presence and fire schedule. Restored sites vary in age (3–31 years since reseeding) and largely consist of reseeded native forbs and grasses. Bison were reintroduced into the grasslands in October 2014, and by 2018 there were 132 bison. Bison are allowed to roam freely within a fenced 800 ha area that includes remnant and restored sites. All sites are managed with dormant season prescribed fire, with most burned approximately every 2 years in the spring or late fall (Rowland-Schaefer et al. 2022). Not all sites are burned at the same time, so in any given year the landscape is a mosaic of units that have or have not been burned in the previous year. Unburned sites typically have standing dead plant biomass and dense thatch present, but this litter is typically absent in burned sites where aboveground biomass almost entirely comprises the current year's growth. For more details on Nachusa management and plant communities, see Hansen and Gibson (2014), Barber et al. (2017, 2019), and Bach and Kleiman (2021).

We selected 20 total sites within 13 separate prairie restorations and two remnants ranging in size from 5.6 to

Table 1 Arthropod sampling sites with bison presence and application of prescribed fire in 2017 and 2018. Age is number of growing seasons since planting at the start of the study in 2017 (prairie remnants have no age)

Site	Age	Bison	Fire 2017	Fire 2018
CCE	10	N	Y	N
CCEE	10	N	Y	N
CCW	9	N	N	Y
CCWE	9	N	N	Y
FC	11	N	N	Y
HF	4	Y	Y	Y
HLP	16	Y	N	Y
HN	5	Y	Y	N
HPW	9	Y	N	Y
L	6	Y	Y	N
MR	–	Y	Y	Y
MU	30	Y	N	Y
SB	8	N	N	N
SBEE	8	N	N	N
SBEW	8	N	N	N
SF	16	N	Y	N
TC	15	N	N	Y
TCE	15	N	N	Y
TCR	–	N	N	Y
WH	25	Y	Y	N

20.6 ha and separated by 0.1 to 5.0 km (Table 1, Fig. S1). Seven of the restorations and one remnant were within the fenced bison area, and bison visited all these sites during the study. Sites varied in fire application, with prescribed burns occurring prior to both, one, or neither of the two years in which collections took place (Kleiman 2017, 2018). Thus, site management provided a quasi-experiment in which sites varied in bison and recent fire application. For further details on study design and sampling, see Hosler et al. (2021) and Nelson et al. (2021).

Invertebrate collection

Ground-dwelling invertebrates were collected using pitfall traps in 2017 and 2018. Two trap arrays were installed at each site, each consisting of five pitfall traps, spaced 5 m apart. The traps were 12.1 cm deep and 9.5 cm wide and were half-filled with a 1:1 mixture of propylene glycol and water. Traps were covered with a wire mesh (2.5 cm openings) to exclude vertebrates. Because dung beetles were focal taxa to understand bison impacts on ecosystems, one trap in each array was baited with fresh bison dung. The traps were opened in three sessions (May-June, July, and September) in both 2017 and 2018, with traps emptied every 3–7 days. May-June sessions were longer in both years (23 and 20 days, respectively) to more intensively sample the early season community when fire and post-fire grazing effects are expected to be strongest (Moran 2014). July and September sessions were all 7 days long. Samples were pooled from the 10 traps per site after each sampling session because the focal environmental drivers (fire and grazing) occur at the site-level, so all traps within a site experience the same conditions. Macroinvertebrate groups were identified to phylum, order, or family depending on the taxonomic group, excluding taxa for which pitfall traps are not an effective sampling technique (e.g., earthworms and flying insects like Diptera). Our goal was to broadly characterize the assemblage of invertebrates living and foraging on the soil surface. Given the wide taxonomic and ecological breadth that these organisms represent, and the large number of specimens, we identified to levels that we were confident could be identified correctly with finer resolution for some groups that were particularly dominant of ecological interest (e.g., dung beetles given the potential effects of reintroduced bison). Identified taxa are listed in Table 2.

Table 2 Identified taxonomic groups. Some groups (Arachnida, Orthoptera) were identified to finer resolution in 2017 than 2018. In 2018, rove beetle were included with "other beetles," and ants were not counted

Phylum	Class	Order	Family	Name
Arthropoda	Arachnida	–	–	arachnids
Arthropoda	Arachnida	Araneae	–	spiders (2017)
Arthropoda	Arachnida	Opiliones	–	harvestmen (2017)
Arthropoda	Diplopoda	–	–	millipedes
Arthropoda	Insecta	Coleoptera	Carabidae	ground beetles
Arthropoda	Insecta	Coleoptera	Scarabaeidae, Geotrupidae	dung beetles
Arthropoda	Insecta	Coleoptera	Staphylinidae	rove beetles (2017)
Arthropoda	Insecta	Coleoptera	–	other beetles
Arthropoda	Insecta	Hemiptera	–	true bugs
Arthropoda	Insecta	Hymenoptera	Formicidae	ants (2017)
Arthropoda	Insecta	Orthoptera	–	orthopterans
Arthropoda	Insecta	Orthoptera	–	crickets (2017)
Arthropoda	Insecta	Orthoptera	–	grasshoppers (2017)
Arthropoda	Malacostraca	Isopoda	–	isopods
Mollusca	Gastropoda	–	–	slugs and snails

Analysis

We expressed abundance of each identified group per 100 trapdays to standardize and account for variations in trapping effort because of traps that were disturbed. A trapday equals one trap open for one day, so all ten traps open for one week equals 70 trapdays. We divided abundances at each site by the total number of trapdays for that site and multiplied by 100. Thus, abundances are technically measures of activity density. We calculated Shannon diversity of invertebrate groups in each year using the diversity() function in the R package vegan (Oksanen et al. 2020). We analyzed Shannon diversity and the abundance of each group with linear mixed models, treating bison presence, prescribed fire, and their interaction as fixed factors. We also included year and site age as fixed covariates and site as a random factor to account for sampling each site in both years and for other potential year effects due to weather or other differences. Fixed factors were evaluated with type III tests using Anova() in the car package (Fox and Weisberg 2019). For groups only identified in a single year (rove beetles, ants, crickets, grasshoppers, spiders, harvestmen), we used general linear models with bison, fire, their interaction, and age as fixed factors. We used emmeans() in the emmeans package (Lenth 2022) to calculate effect sizes. Abundances (all groups except ants) were log transformed to meet model assumptions. To examine differences in ground-dwelling invertebrate communities between bison / non-bison and fire / non-fire sites, we performed PERMANOVA tests with the vegan package using the adonis2 function (Oksanen et al. 2020) with Bray-Curtis dissimilarities. We visualized community composition using these dissimilarities with principal coordinates analysis (PCoA) with the cmdscale function. All statistical tests were conducted in R version 4.3.2 (R Core Team 2023).

Results

We captured and identified 55,840 invertebrates, with the most abundant groups being dung beetles (22,676), other beetles (9,287), arachnids (7,712), isopods (5,089), and ground beetles (4,421). The particularly high abundance of dung beetles is due to the use of dung baited traps. Results of linear models examining abundance of each taxonomic group and Shannon diversity are in Table 3.

Bison had strong effects on the abundance of several invertebrate groups. They increased the average abundance of ground beetles by 108% (Fig. 1A), and other beetles by 67% compared to sites without bison. Orthopteran abundance was 245% greater in bison sites (Fig. 1B), driven in 2017 by both more crickets (158% greater) and more grasshoppers (274% greater). There were weaker bison effects on spiders (67% greater in 2017, Fig. 1C), slugs and snails (59% greater), and ants (37% fewer). For some groups, bison impacts depended on recent prescribed fire. Dung beetles were more abundant overall with bison, and this effect was amplified in the presence of fire: 59% greater without fire, but 202% greater with fire (Fig. 1D). These bison x fire interaction effects were weaker for rove

Table 3 Results of linear mixed models and general linear models testing effects of bison, fire, and their interaction on each arthropod group and Shannon diversity. Age and year were included in models as covariates, except for groups only quantified in one year (e.g., spiders and crickets) in which year was not a factor in the model

	Bison		*Fire*		*Bison x Fire*		*Age*		*Year*	
	X^2	*P*	X^2	*P*	X^2	*P*	X^2	*P*	X^2	*P*
arachnids	1.95	0.163	**9.96**	**0.002**	**4.69**	**0.030**	0.14	0.705	**7.17**	**0.007**
spiders	**4.70**	**0.049**	4.56	0.052	2.49	0.139	0.21	0.656	–	–
harvestmen	0.00	0.995	**32.87**	**< 0.001**	1.04	0.327	3.10	0.102	–	–
millipedes	0.02	0.894	0.36	0.550	2.48	0.115	0.53	0.467	0.06	0.813
ground beetles	**12.40**	**< 0.001**	**12.40**	**< 0.001**	0.60	0.439	**24.35**	**< 0.001**	0.00	0.955
dung beetles	**18.51**	**< 0.001**	0.01	0.910	**4.70**	**0.030**	0.91	0.341	**61.49**	**< 0.001**
rove beetles	0.57	0.463	0.00	0.927	**4.68**	**0.050**	2.54	0.135	–	–
other beetles	**6.26**	**0.012**	**8.12**	**0.004**	1.56	0.212	0.06	0.807	**6.30**	**0.012**
true bugs	2.40	0.121	**6.51**	**0.011**	0.51	0.477	0.17	0.676	0.04	0.851
ants	**5.10**	**0.042**	0.99	0.338	3.85	0.072	**6.59**	**0.023**	–	–
orthopterans	**28.20**	**< 0.001**	1.01	0.315	0.00	0.983	3.44	0.064	0.88	0.348
crickets	**5.31**	**0.038**	**6.35**	**0.026**	0.00	0.968	1.14	0.306	–	–
grasshoppers	**8.12**	**0.014**	0.03	0.863	0.16	0.693	1.90	0.191	–	–
isopods	1.96	0.162	0.78	0.379	1.28	0.258	0.06	0.808	0.46	0.496
slugs and snails	**3.91**	**0.048**	0.93	0.335	1.40	0.236	0.60	0.440	**38.30**	**< 0.001**
Shannon diversity	**10.24**	**0.001**	1.71	0.191	2.10	0.148	**6.07**	**0.014**	**101.31**	**< 0.001**

X^2 values are on 1 d.f. Note that for spiders, harvestmen, rove beetles, ants, crickets, and grasshoppers, test statistics are $F_{1,13}$ values from type III *F*-tests in (non-mixed) linear models

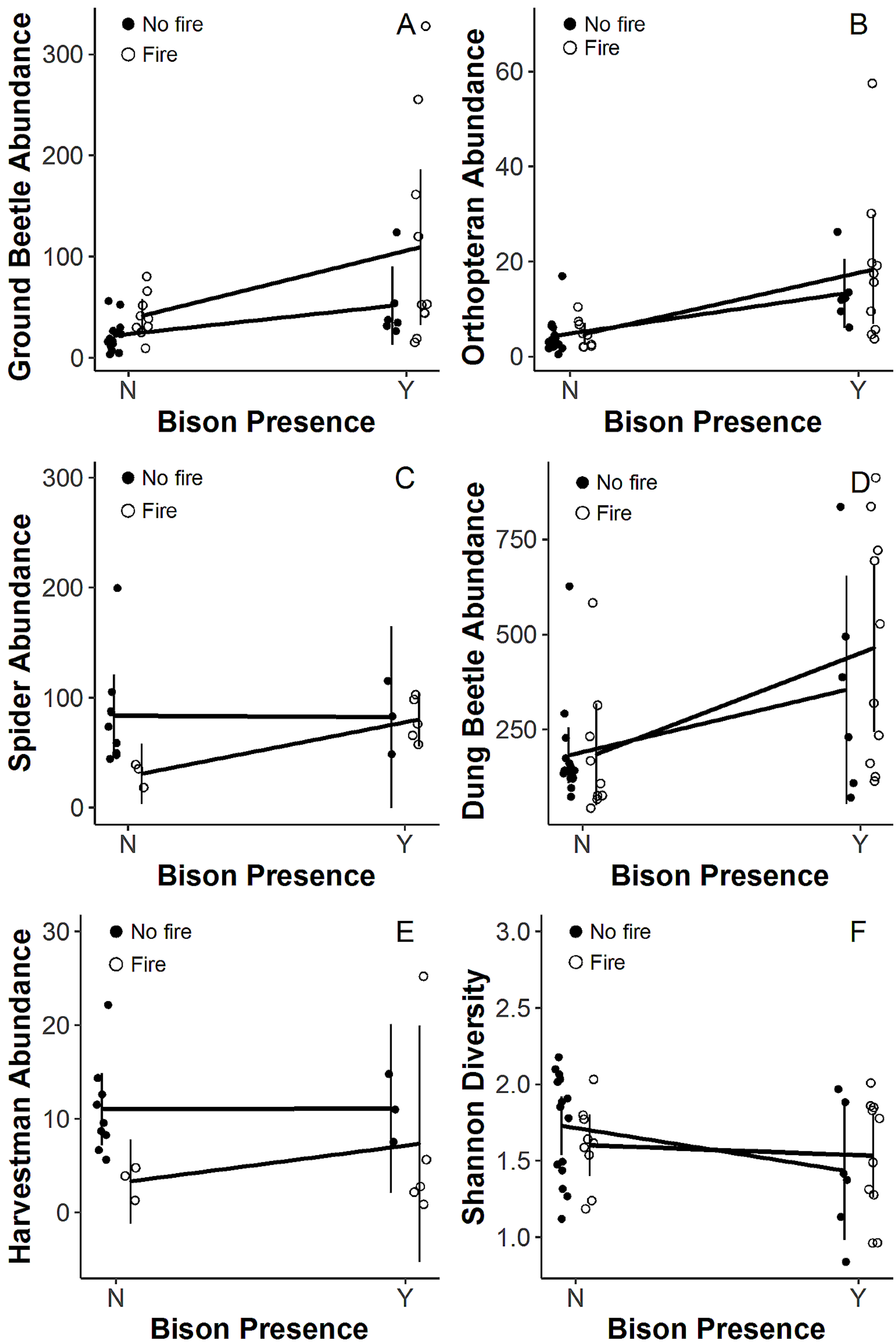

Fig. 1 Mean abundances of (**A**) ground beetles, (**B**) all orthopterans, (**C**) spiders, (**D**) dung beetles, (**E**) harvestmen, and (**F**) mean Shannon diversity with and without bison and fire presence in restored tallgrass prairies. Closed circles are sites that received fire in the previous dormant season, and open circles are sites that did not

beetles, which reached their highest abundance when both bison and fire were present, and for total arachnids, which were reduced by fire only in the absence of bison. However, arachnid results differed when spiders and harvestmen were examined separately.

Prescribed fire also had independent positive effects on ground beetles (106% greater, Fig. 1A), other beetles (62% greater), and crickets (183% greater). Fire decreased the abundance of harvestmen (78% fewer, Fig. 1E) and true bugs (38% fewer). Neither bison presence nor prescribed fire affected the abundances of millipedes or isopods.

Bison significantly reduced ground-dwelling invertebrate Shannon diversity (Fig. 1F). There was a significant difference in community composition between bison and non-bison sites in 2018 ($F_{1,15}$ = 9.46, P=0.001, R^2=0.35), and a trend toward different compositions in 2017 ($F_{1,15}$ = 1.70, P=0.092, R^2=0.09) (Fig. 2). Fire had a marginally significant effect on composition in 2018 ($F_{1,15}$ = 2.56, P=0.072, R^2=0.10), but no effect in 2017 ($F_{1,15}$ = 1.36, P=0.210, R^2=0.08). One site (with bison, without fire) was an outlier in 2017 due to high abundance of isopods.

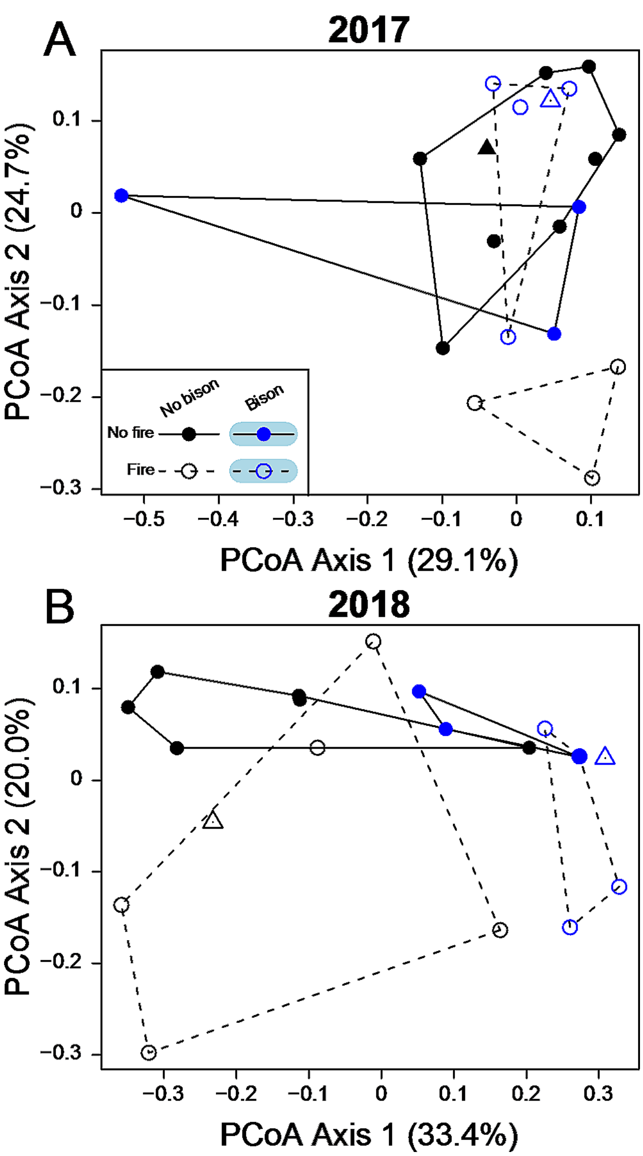

Fig. 2 PCoA plots showing invertebrate community composition differences in (**A**) 2017 and (**B**) 2018 between bison (blue shaded) and no bison (white unshaded) sites and sites with prescribed fire (dashed lines, open circles) and without (solid lines, closed circles). The two remnant sites are depicted with triangles

Discussion

We examined ground-dwelling invertebrate communities in restored and remnant tallgrass prairies managed with re-introduced grazing bison and prescribed fire. The responses to fire and grazing differed among the various taxonomic groups, but the most abundant arthropods (beetles) tended to benefit from disturbances, especially from bison, which increased their dominance, reduced overall invertebrate diversity, and led to changes in community composition. Prescribed fire generally increased beetles, as well as crickets, but caused short-term declines in other groups including harvestmen and true bugs. Nonetheless, reductions by fire were not sufficient to affect overall diversity, and fire had little effect on the overall invertebrate community composition. The responses of the different invertebrate groups, including no responses by such groups as isopods and millipedes, likely reflect the habitat homogeneity or heterogeneity promoted by these fire and bison disturbances, respectively, as well as the potential direct mortality by fire that affects some taxonomic groups but not others, depending on their life history and behaviors (Panzer 2002).

Bison presence increased most beetle groups, as well as orthopterans, spiders, slugs and snails, and ants. Ground beetles, dung beetles, rove beetles, and a combination of other beetle families, were all more abundant in sites in which bison had access. These families are ecologically and trophically diverse, so they may have responded to different impacts of bison, such as increased dung, new habitat created by wallowing (Nickell et al. 2018), and changes in plant species composition (Vinton et al. 1993) due to bison grazing such as increased forb cover (Blackburn et al. 2021). For example, although dung bait certainly increased capture rates of dung beetles compared to other groups, dung beetles were already common in all sites but the copious feces in bison sites likely amplified their dominance (Barber et al. 2019; Hosler et al. 2021). Prescribed fire also had a positive impact on beetle abundances, increasing ground beetles and other beetles, and strengthening the positive effect of bison on dung beetles. Beetles can be resilient to the effects of fire (Cook and Holt 2006) and may be dormant and sheltered in soil when burns occur (Nunes et al. 2019). When fire does cause direct mortality, flying species may quickly be able to re-establish or supplement populations. Dung beetles generally have great dispersal capabilities which allow them to quickly recolonize recently burned habitat (Silva and Hernández 2015). Even flightless beetles might benefit from fire-driven habitat changes: *Cyclotrachelus sodalis*, a common ground beetle at Nachusa (Barber et al. 2017; Nelson et al. 2021), displayed a short-term post-fire increase in another tallgrass prairie (Cook and Holt 2006). Whether bison-related disturbances, like grazing and wallowing, facilitate this post-fire recolonization remains an open question.

Orthopteran abundance responded positively to bison impacts, and this pattern was true when we examined grasshoppers and crickets separately. Crickets, but not grasshoppers, increased further with prescribed fire. This result is somewhat surprising given that grasshoppers have increased following fire in other systems (Rice 1932; Tester and Marshall 1961; Nagel 1973; Anderson et al. 1989; Kral et al. 2017). Bison effects on grasshopper abundance, which often are positively correlated with the availability of host plants (Anderson 1964; Evans 1984, 1988), may reflect preferential grazing on grasses by bison that reduces competitive pressure on forbs and allows crickets to increase in abundance (Joern 2005; Welti et al. 2019). Furthermore, habitat heterogeneity provided by the combined interaction of grazing and burning (Fuhlendorf et al. 2009) may support diverse host plants which maintain grasshopper populations. Although fire schedule varies among sites, all our sampling locations receive regular prescribed fire, so over the long-term, patterns we document in orthopterans might be better explained by the heterogeneity resulting from management resembling patch-burn grazing, in contrast with the homogeneity of fire-only management (Engle et al. 2008). Finally, orthopterans are often one of the most abundant insect groups in prairies (Rice 1932; Tester and Marshall 1961; Nagel 1973), yet the number of specimens trapped was quite low in our study, especially for grasshoppers. Pitfall traps are likely less suitable to survey grasshoppers than sweepnets or other methods to sample from vegetation, so these results should be interpreted with some caution.

Although fire increased cricket abundance, it reduced the abundance of some other taxonomic groups, and as with bison effects, these groups are not linked by a common trophic position. Carnivorous arachnids were less abundant following fire, driven by reductions in harvestmen, and so were true bugs, a group that encompasses a wide range of diets. Reduced arachnid abundance in burned sites has been documented before (Rice 1932; Nagel 1973; Engle et al. 2008; Kral et al. 2017) and potentially attributed to direct mortality from fire. Reduced vegetation structure can also reduce resources for spiders (Gomez et al. 2016), but this has been observed for web-building spiders rather than ground-foraging harvestmen. We mainly sampled ground-dwelling arachnids using pitfall traps, which might be expected to benefit from the more open environment created by thatch-reducing fires, unless fires reduce prey availability or increase mortality from arachnids' own predators. An examination of abundance correlations between arachnids and other groups shows that only true bugs and millipedes were positively correlated with spiders, indicating that some species in these groups could be important prey for spiders, but these positive correlations did not apply to harvestmen.

The open environment following thatch removal by fire also reduces ground-level moisture and increases temperature, which could negatively affect molluscs like slugs and snails that rely on moist conditions (Anderson et al. 1970), or influence predation given that some ground beetles are mollusc specialists. A common slug species (the introduced *Deroceras reticulatum*) is also an important prey item for small snakes at Nachusa (Virgin and King 2019), but snake responses to prescribed fire are unknown (King and Vanek 2020). Finally, a decline in true bugs is difficult to ascribe to a particular aspect of the post-fire environment because Hemiptera are so diverse. In a previous study, Membracidae were more frequent in unburned sites while other prairie bugs, such as Nabidae, were increased in burned sites (Nagel 1973). Previous studies have usually focused on individual bug species, with mixed responses (Gillon 1971; Prado et al. 2010; Wallner et al. 2012; Kral et al. 2017), so there is a lack of research on Hemiptera responses as a group. Eggs from species that oviposit on vegetation may be particularly vulnerable to fire, which could be one mechanism for reduction (Gillon 1971).

Bison and prescribed fire influenced the abundance of the taxonomic groups described above, but only bison effects translated to differences in Shannon diversity and community composition. Shannon diversity was reduced by bison presence, a result that contrasts with other studies of grazing by bison or cattle where grazing increased insect or invertebrate diversity (Fay 2003; Moran 2014). This is probably due in large part to our use of pitfall traps to characterize ground-dwelling invertebrates, rather than vegetation-dwelling invertebrates collected by sweepnet or vacuum sampling, which would be unlikely to sample particular groups like ground beetles or ground-hunting spiders. In contrast, species likely to be sampled from vegetation (such as leaf beetles (Chrysomelidae) or Lepidoptera larvae) might be more susceptible to fire mortality if they over-winter in leaves or stems (Uys et al. 2006), or affected differently by bison whose grazing and other activities alter aboveground vegetation structure. Indeed, the "reduced diversity" with bison is due in part to increased abundance of already common beetles. No taxonomic group showed a reduction in abundance due to bison, and bison presence tended to erase the potentially negative effects of fire for arachnids. Only ants were negatively affected by bison, and unaffected by fire, in contrast to another tallgrass prairie where ants showed a short-term increase after fire (Anderson et al. 1989). Combined, these results indicate that the reduced diversity in bison sites is unlikely to be a concern to prairie managers, for whom supporting biodiversity is often a primary goal. Instead, the high abundance of beetles and orthopterans might support desirable interactions and functions. For example, high abundances of dung beetles in response to bison reintroduction, amplified by the interaction with fire through pyric herbivory (Fuhlendorf et al. 2009), likely supports nutrient cycling (Hosler et al. 2021), and the resulting mosaic of environmental heterogeneity can benefit overall grassland biodiversity.

Finally, we focused on the invertebrate communities in tallgrass prairie restorations, but we also carried out similar sampling in two prairie remnants. There are differences between remnants and restorations beyond just disturbance history, including soil characteristics and topography (Hansen and Gibson 2014), which make comparisons challenging. Nonetheless, when we include the remnants in Fig. 2 for qualitative comparison, their invertebrate composition is similar to restoration sites with the same bison and fire status. Including the remnants in PERMANOVA tests also does not change the conclusion (results not shown). Again, this may provide prairie managers with peace of mind that remnants, despite edaphic differences, may not require specialized disturbance regimes to maintain desirable invertebrate taxonomic groups and composition. Unfortunately, the rarity of tallgrass prairie remnants is a significant barrier to well-replicated, landscape-scale studies that would allow robust comparisons to restorations.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s10841-024-00614-y.

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Author contributions All authors contributed to conceptualization and design of the study. S.C.H., H.P.J., and N.A.B. performed field work. M.N.A. and S.P. analyzed data, wrote the manuscript, and prepared figures with input from all co-authors. All authors reviewed the manuscript.

Declarations

Competing interests The authors declare no competing interests.

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