



## Effects of native megaherbivore *Bison bison* grazing and wallowing activities on lepidopteran species and community dynamics in a complex savanna-barrens grassland over a 6-year study

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**Abstract.** Evaluating land management practices to best return landuse health and resilience is a growing interest in the face of rapidly declining worldwide invertebrate populations. American bison (*Bison bison*), a native megaherbivore, is well understood to benefit the natural cycle of vegetation growth and soil on the landscape. Activities of these native grazers has also been found to benefit specifically lepidopteran populations, but additional evaluation is needed. To assess this, we conducted lepidopteran and groundcover surveys within an oak savanna landscape located at the Sandhill Wildlife Area from 2014–2019, during spring and summer seasons. Bison grazing pastureland was delineated into four cover types including open grassland areas (other), shrubs and trees (shrubs), areas of exposed mineral soil (disturbance), and wallows resulting from disturbance as generated directly by American bison wallowing activities (wallows). A total of 60 plots (15 per cover type) were assessed for percent groundcover categories, recent presence of bison (indicated through bison chip counts), and observations of all lepidopteran species. Bison wallowing activities increased over the course of the study, with more wallows visible during spring season. Bison chips were highly separated from wallows, suggesting that bison graze and wallow in different areas. Lepidopteran family groups (Lycaenidae, Nymphalidae, Pieridae, Hesperidae, Papilionidae, and Riodinidae, as well as grouped “moths” that were dominated by Geometridae) differed significantly across these areas of high and low disturbance. A total of 17 groups were observed, 13 of which were seen at least 3 times over the 10 surveys. Environmental predictors bison wallows, forbs, grass, nectar, and shrub cover were significantly associated with distribution of individual taxa. Bison wallows were significantly associated with lepidopteran family communities, while chips shaped trends in 6 groups identified to species, and vegetation types further significantly structured the community. Temporal trends captured significantly different community assemblages 2014–2019 and across seasons, with summer showing greater variation in families. Overall, this suggests that bison activities and resulting changes in groundcover impact habitat suitability and thus influence the abundance and distribution of lepidopteran family groups. A further assessment of bison influenced habitat features and breakdown of lepidopteran species units is needed to further understand how temporal bison activities may influence the habitat structure and subsequently the reliant lepidopterans within this ecotype and will be assessed in subsequent studies.

## INTRODUCTION

The effects of natural management versus anthropogenic practices on insect populations has become an area of interest in recent years (Rosenberger & Conforti, 2020; Schwerk et al., 2021; Thapa-Magar, 2022; Schieuer, 2023), particularly in the face of declining worldwide insect populations (Waite et al., 2022).

Worldwide decline of butterflies, and particularly grassland butterflies in developed and agro-areas, has been attributed to several factors including land management practices resulting in habitat loss and degradation (Geest, 2017; Waite et al., 2022), widespread pesticide use for landuse and agricultural purposes (Main et al., 2020), and added stresses of microclimate impacts in areas where habitat is greatly reduced (Patterson et al., 2020). These concerns have prompted land managers and researchers to assess the influence of land, and particularly, habitat management techniques on focal species groups considered indicative of overall ecosystem health, evaluating both species populations and species interactions within a community. These efforts attempt to balance predictable widespread landuse needs while determining the most effective and sustainable management techniques and landuse practices needed to successfully restore, establish, spread, and maintain habitat features on the landscape (Varriano et al., 2020; Schwerk et al., 2021; Tielkes & Altmann, 2021; Niederman et al., 2023). Overall, addressing this accumulation of issues will require evaluating land management practices that best achieve native ecotypes and/or landuse practices that maintain systems that are resilient to outside pressures (Rahman et al., 2021; Tielkes & Altman, 2021; Niederman et al., 2023).

Grassland habitat quality is deceptively difficult to maintain and easily influenced by general landuse practices. Appearing simplistic in nature, grasslands in fact contain a complex system of taxa diversity and structure, requiring continual, low to moderate intensity management to maintain the open complex habitat structure while providing the keystone species necessary for biological community interactions to function properly and generate self-maintenance (Anderson, 2006). Mechanical, prescribed fire, pesticide-induced, and both domestic and native megaherbivore grazing activities are demonstrated techniques that can restore and maintain these critical native ecotypes, including grassland and open-forest complex habitat types, upon which countless species depend (Yu, 2021; Niederman et al., 2023; Yu et al., 2023). However, these methods can be constrained due to expense, time, public perception (Yu et al., 2023), and the complexity of generating high-quality habitat suitable for both tenuous and resilient species. Subsequently, grassland species such as lepidopterans are susceptible to habitat loss due to the need for this regularly generated disturbance.

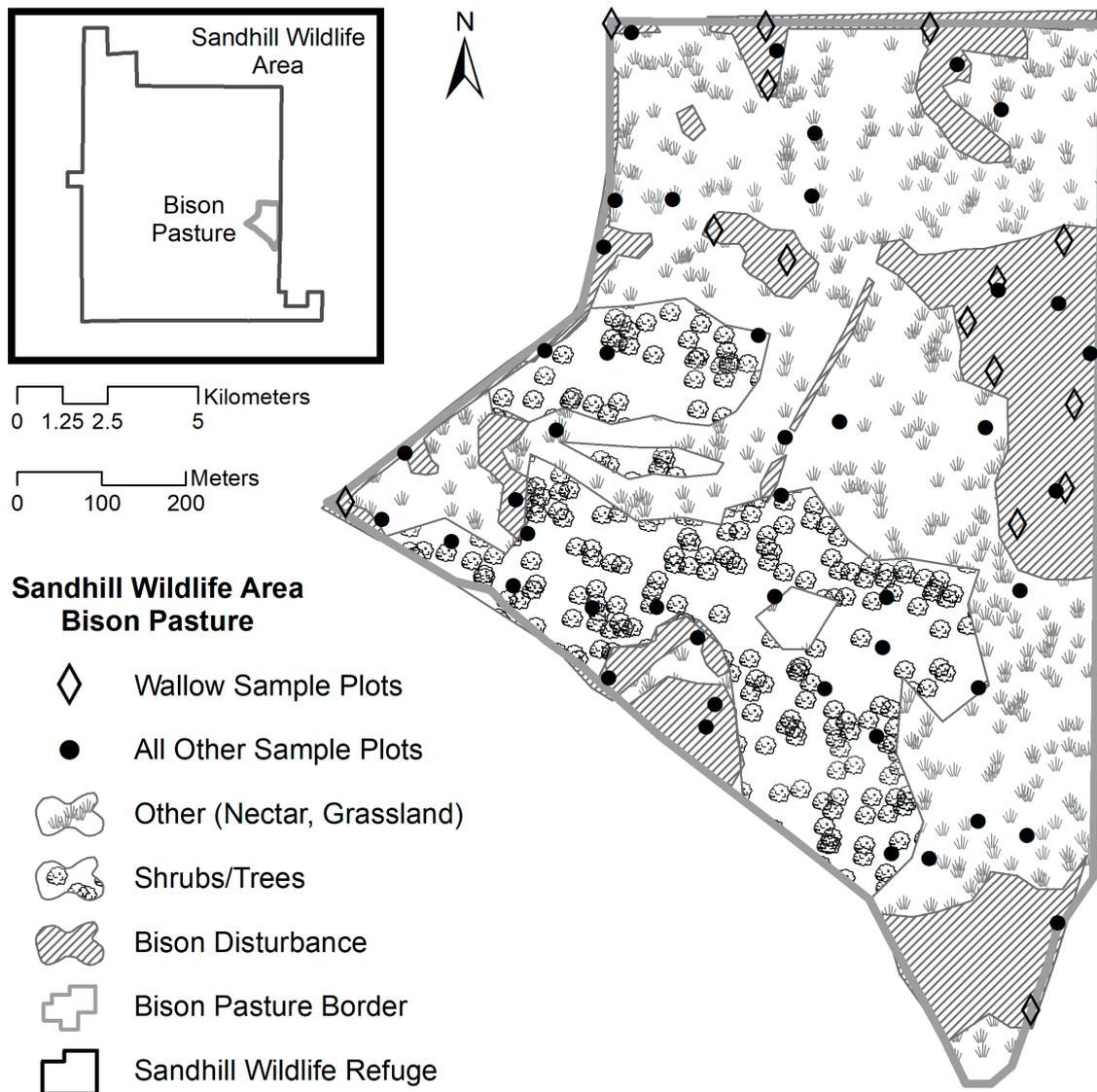
Although native megaherbivores are widely acknowledged as keystone species that kick-off the generation of suitable habitat and the cycles that maintain quality thereof, the direct, measurable influence of these groups, including American bison (*Bison bison*), are difficult to assess given

the relative absence of the fauna on the landscape (Kaplan et al., 2021; Mueller et al., 2021). These native species may also provide the single best solution to large-scale, continual, contiguous grassland habitat management, particularly for conservation purposes (Freese et al., 2007). American bison, referred to as “ecosystem engineers” by Kauffman et al. (2022) were once endemic and ubiquitous in vast numbers in North America, acting as foundational species that altered the landscape around them, generating habitat favorable for native plants and animals within grasslands (Kaplan et al., 2021; McMillan et al., 2021; Mueller et al., 2021; Tielkes & Altmann, 2021; Ling et al., 2023), forest (Tielkes & Altmann, 2021), and riparian areas (Yu, 2021; Kauffman et al., 2022; Yu et al., 2023). Although the importance of bison on the natural landscape is well-documented (Fuhlendorf et al., 2010; Kolipinski et al., 2014; Kaplan et al., 2021; Mueller et al., 2021; Yu, 2021; Tielkes & Altman, 2021; Yu et al., 2023), their influence on insect, and specifically lepidopteran, populations is less well-understood and requires further, and more long-term, assessments to fully comprehend, and eventually emulate, their engineering influence on the landscape (Hess et al., 2014; Rahman et al., 2021; Schwerk et al., 2021; Thapa-Magar et al., 2022).

Lepidopterans as a taxon provide a unique and measurable platform for assessing land management practices such as widespread grazing by a native species in grasslands due to their current decline and the dependence of lepidopterans on surrounding landscapes and conditions. The Sandhill Wildlife Area in Central Wisconsin provides the unique opportunity to assess prescribed native megaherbivore grazing as a management technique via the presence of an American bison herd. The American bison generate a natural, native oak savanna ecotype reminiscent of historical habitats that were once prominent on the Midwestern American landscape (Curtis, 1959; Anderson, 2006). Further, a previous study (Hess et al., 2014) found that bison activities at this location influenced changes in groundcover that appeared to impact habitat suitability and thus influence the abundance and distribution of lepidopteran family groups through generation of bare soil, increased growth of ruderal species and nectaring plants, and overall impacts on vegetation structure and distribution. Here we present a 6-year evaluation of American bison grazing and activity influence on general lepidopteran groups across a natural oak savanna landscape in the Upper Midwest to better assess the impacts of this native megaherbivore and ecological engineer on this critical and declining taxonomic group.

## MATERIAL AND METHODS

The Sandhill Wildlife Area consists of 3,703 ha of mixed deciduous forest, marshland, and open-grassland complexes within a largescale deposit of sand and loam-sand covering nearly 7 counties in Central Wisconsin. This unique site is entirely fenced to restrict the movement of large animals and used primarily as a research facility. The Wildlife Area hosts a small herd of American bison that range over 105 ha of additionally fenced area. Numbers for the bison herd range from 8–13 adults and calves per year, with one bull generally present and the remaining herd composed of cows and immature cows/bulls.



**Fig. 1.** Study site of Sandhill Wildlife Area including 60 randomized plots within 4 treatment areas.

To assess the influence of American Bison on the lepidopterans endemic to the area, we conducted lepidopteran and groundcover surveys within the Sandhill Wildlife Area bison pasture from 2014–2019, during spring and summer seasons, for a total of 10 surveys ranging from summer of 2014 to spring of 2019 (Fig. 1). For consistency of report, bison per year included: 2014 (10 adults, no calves), 2015 (10 adults, 1 adult culled, no calves), 2016 (8 adults, 1 calf born), 2017 (12 adults, 1 culled, 3 calves born), 2018 (13 adults, 1 culled, no calves), 2019 (13 adults, no calves). This results in a density of approximately 0.08–0.12 bison adults/ha/year, a low density compared to historical pre-settlement estimates of wild bison (0.44–0.88 bison/ha, Smits et al., 1994; Knapp et al., 1999).

#### Cover types and sampling

To assess the impacts of American bison grazing on the landscape, the pasture area was delineated into four cover types using aerial photograph interpretation from 2014 NAIP imagery, including: open grassland areas (other), shrubs and trees (shrubs), areas of exposed mineral soil (disturbance), and wallows resulting from disturbance as generated directly by American bison wallowing activities (wallows). A collection of 15 random sample plots were generated within each delineated cover type, resulting in 60 plots

overall. Cover type delineating and sample plot generation were conducted in ArcMap 10.2.2 and managed for interpretation purposes through ArcMap 10.8.2 and ArcGIS Pro (Environmental Systems Research Institute (ESRI), Inc. Redlands, CA). Random points were used as a centroid for sample plots. Sample plots were 5 m in diameter and located using a Garmin 64sx handheld GPS (2014) and Garmin Montana 680t handheld GPS (Garmin Ltd., Olathe, KS, USA) (2015–2019). Sample plot diameter was measured in the field using a centroid stick and 5 m line.

#### Field measurements

Groundcover measurements and lepidopteran surveys were conducted at each sample plot. Groundcover measurements included percent groundcover, the total number and dimensions of wallows that fell within the plot area, and the number of bison chips (considered indicative of the recent presence of bison). Chip abundances may have fluctuated yearly based on the number of bison present. The bison herd contained 8–13 adult bison each year, with some calves of mixed cow/bull gender. This results in a density of approximately 0.08–0.12 bison adults/ha/year.

Groundcover categories were estimated using an ocular estimate method via the Braun-Blanquet abundance scale (Braun-Blanquet, 1964, 1932). Groundcover categories included meas-

urements for: shrubs/trees, nectar plants [that were nectaring during the respective spring or summer seasons, including wild blue lupine (*Lupinus perennis*) important to Lycaenidae], general forbs, bareground (exposed mineral soil), grass/sedges, and “other” (i.e., ferns, moss, fallen woody materials, or other cover that may be present within the open-grassland complex). Bison wallows are circular areas of bare dirt generated through the rolling activities of individual or groups of bison on the ground. Individual wallows were considered part of the plot if a portion of the wallow overlapped with the 5 m circular plot area. If multiple wallows were located within a plot area, individual wallow measurements were taken, and a total size of bison wallows was combined to generate “total wallow area” or averaged to “average wallow area.”

Lepidopteran observations were recorded within the sample area if the lepidopteran specimen was within the circular plot resting, passing through/flying, mating, or foraging. Lepidopterans were counted and recorded per specimen and were not counted twice if they passed through/flew through the plot multiple times. Specimens were identified ocularly or with Nikon 8 × 25 close-range binoculars in the field and recorded to the family, genus and species level if the individual specimens were observed for long enough periods to identify species. Moths were not classified and were instead combined into one functional group, however it is worth noting that the majority of moths were identified in the family Geometridae (Beadle & Leckie, 2012). Groups not separated to species were skippers (Hesperiidae family); hairstreaks (Lycaenidae); checkerspot, fritillaries, wood nymphs and satyrs (Nymphalidae); and sulfurs (Pieridae).

Dragonflies as a group were also observed over the course of the study, to assist in determining influence of these potential predators on lepidopteran presence, abundance, and distribution. Dragonflies were recorded within the sample area if the specimens rested, passed through, mated, or foraged (while flying) in the sample site. These observations were recorded per specimen.

### Statistical analyses

We first analyzed differences in groundcover vegetation across the area’s four cover types: other/grass, shrubs, disturbed, and wallows. A type III ANOVA (Fox & Weisberg, 2019) tested overall differences among the four cover types, followed by Tukey’s post hoc contrasts (Lenth, 2024). Next, we used a multiple regression approach to discern which habitat variables best predicted abundance of Lepidoptera groups. We grouped lepidopterans by family or, for moths, functional group level to achieve higher numbers of observations and statistical power. We only analyzed Lepidoptera groups with > 20 individuals observed over the course of the study. Potential predictors included: bison activity captured as average wallow area (m<sup>2</sup>), chip abundance, and total wallow number; competition quantified as the abundance of individuals of other Lepidoptera groups, and vegetation cover (percent cover of bare ground, forbs, grass, nectar-producing plants, and shrubs). Total wallow area was omitted as a predictor due to high correlation with average wallow area. Focusing on bison, we then analyzed the ability of vegetation cover to predict average wallow area, chip abundance, and total wallow area. We do not present analyses of total wallow number as a response due to model convergence issues. All multiple regression analyses used generalized linear mixed models (Brooks et al., 2017; R Development Core Team, 2023). Random effects for plot were included to account for repeated measures. All models included covariates for season (spring, summer) and year (2014–2019) to quantify differences among collection times. One normally distributed vegetation cover variable, grass, was analyzed with a linear model. Models of zero-inflated vegetation cover vari-

ables and abundances used Poisson error distributions with log link-functions and zero-inflation terms. Continuous zero-inflated responses were analyzed with models specifying Tweedie family compound Poisson-gamma distributions with positive mass at zero. For analyses of Lepidoptera and bison responses, predictor variables were centered and scaled to allow for comparison of strength and direction of relationships. We subjected each full model to multi-model inference (Bartoń, 2023). We compared all possible combinations of predictors and covariates, identified the subset of models differing from the top ranked model by < 4 AICc, and for this subset took the full average of the model coefficients (with models not including a variable contributing zeroes to the average for that variable, thereby down-weighting coefficients for variables appearing less often in the subset of top models). Residuals of all constituent models were screened for fit and violation of assumptions (Hartig, 2022).

Next, we further explored the distributions of Lepidoptera groups. We chose non-metric multidimensional scaling (NMDS) ordination (Oksanen et al., 2022) as a relatively assumption-free method to visualize the community variation across two axes. We performed separate ordinations describing lepidopteran family groups and lepidopteran species. The species analysis was limited to observations that were identified to species level. Rare groups (< 3 observations across the ten site visits) were omitted. We selected the transformation options and dissimilarity indices that produced the best fits and used untransformed community matrices for both analyses. For analysis of lepidopteran families, we chose Cao dissimilarities (Cao et al., 1997), and for analysis of species we Chao dissimilarities (Chao et al., 2005). We specified 300 starting iterations wherein random configurations were compared via Procrustes analysis until reaching the lowest stress stable solutions. Purported predictors of community composition were plotted on the ordination solutions to explore potential patterns. For explicit tests of associations between habitat predictors and the community distance matrices, we used permutational multivariate analyses of variance (PERMANOVA), for which permutations were stratified by site visit (Oksanen et al., 2022). For categorical predictors, we tested  $\beta$  dispersion, as an assumption of PERMANOVA and as a comparison of community breadth across categories (Anderson et al., 2006). For categorical variables, we also assessed indicator associations (De Cáceres & Legendre, 2009).

## RESULTS

### Vegetation cover types

Measured groundcover corresponded to the four predetermined vegetation cover types. Grass made up a large proportion of all plots at the site, covering 36–49% of a plot on average, and was the dominant groundcover seen in disturbed, other/grass, and wallow type plots (Table 1). Plots assigned the shrub type were dominated by shrub cover (46%, Table 1). Shrub cover also was high in disturbed (24%) and other/grass (29%) plots but was lower in wallows (12%, Table 1). Wallow plots were also distinguished by a high amount of bare groundcover, averaging 16% of cover compared to 0–3% in other plot types (Table 1). Disturbed and other/grass type plots were similar in terms of vegetation composition. Regardless of type, plots showed similar, relatively low average proportions of forbs (11–13%) and nectar cover (6–16%, Table 1). Interpretation of the model covariates for year also showed that vegetation cover changed over the six years of the study, char-

**Table 1.** Mean  $\pm$  standard error of measured groundcover vegetation. Models compared vegetation across the pasture area's four cover treatment types, and statistics describe overall differences among types with asterisks denoting significance: \*\*\*  $p < 0.001$ . Superscript letters represent significant pairwise differences among treatment types, assessed via Tukey's post hoc contrasts, with groups sharing letters having no difference in cover and groups with different letters differing in cover.

	Other/grass	Shrub	Disturbed	Wallow	$\chi^2$	df	p value	Sig.
Bare cover	0.200 $\pm$ 0.085 <sup>ab</sup>	0.013 $\pm$ 0.009 <sup>a</sup>	3.033 $\pm$ 0.572 <sup>b</sup>	16.033 $\pm$ 1.530 <sup>c</sup>	54.618	3	<0.001	***
Forbs cover	10.607 $\pm$ 0.801 <sup>a</sup>	13.28 $\pm$ 0.992 <sup>a</sup>	12.533 $\pm$ 0.816 <sup>a</sup>	10.647 $\pm$ 0.860 <sup>a</sup>	3.624	3	0.305	
Grass cover	43.947 $\pm$ 1.552 <sup>a</sup>	35.913 $\pm$ 1.622 <sup>a</sup>	46.633 $\pm$ 1.605 <sup>a</sup>	49.227 $\pm$ 1.738 <sup>a</sup>	7.367	3	0.061	
Nectar cover	16.22 $\pm$ 1.222 <sup>a</sup>	5.593 $\pm$ 0.646 <sup>a</sup>	14.453 $\pm$ 1.317 <sup>a</sup>	12.833 $\pm$ 1.168 <sup>a</sup>	5.589	3	0.133	
Shrub cover	29.207 $\pm$ 1.795 <sup>bc</sup>	45.600 $\pm$ 1.832 <sup>c</sup>	23.613 $\pm$ 1.831 <sup>ab</sup>	11.900 $\pm$ 1.272 <sup>a</sup>	20.602	3	<0.001	***

acterized by increased bare ground ( $\chi^2 = 7.396$ ,  $df = 1$ ,  $p = 0.006$ ), forbs ( $\chi^2 = 4.634$ ,  $df = 1$ ,  $p = 0.031$ ), and shrubs ( $\chi^2 = 132.414$ ,  $df = 1$ ,  $p < 0.001$ ), alongside decreased grass ( $\chi^2 = 5.239$ ,  $df = 1$ ,  $p = 0.022$ ) and nectar plants ( $\chi^2 = 409.789$ ,  $df = 1$ ,  $p < 0.001$ ).

### Predictors of bison activity

Proxies of bison activity observed at the site showed some temporal variation. An increase in wallows was seen over the years of the study (Fig. 2A, C), and fewer chips happened to be encountered in later years (Fig. 2B). Seasonally, less wallow area was seen in summer than spring (Fig. 2A). Bison activity was also significantly associated with vegetation cover variables. Wallows and bare cover were necessarily associated, with wallowing disturbance producing areas of bare ground (Fig. 2A). The opposite trend was seen between bare ground and bison chips (Fig. 2B), either suggesting bison wallow and graze in separate areas, or that chips foster quick vegetation growth in their vicinity to the exclusion of bare spots. Data tend to support the former rather than the latter, given that chips were marginally negatively associated with other vegetation categories, nectar and shrub cover (Fig. 2B). Inability of bison to access shrubby areas might drive the relationship to shrub cover.

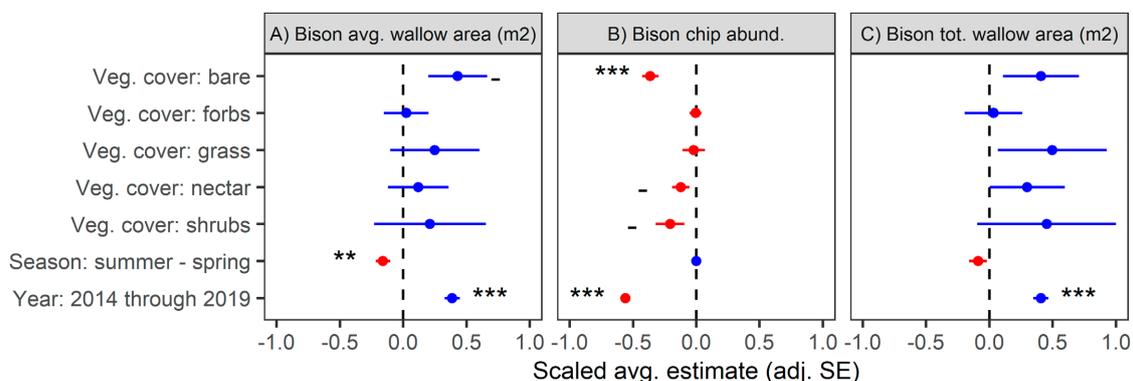
### Predictors of Lepidoptera abundance

We observed seven Lepidoptera groups over the entire course of the study: Lycaenidae ( $n = 779$  individual observations), Nymphalidae ( $n = 315$ ), moths ( $n = 270$ ), Pieridae ( $n = 36$ ), Hesperidae ( $n = 30$ ), Papilionidae ( $n = 5$ ), and Riodinidae ( $n = 2$ ). For the four most common groups, we analyzed predictors of abundance. Temporal variables

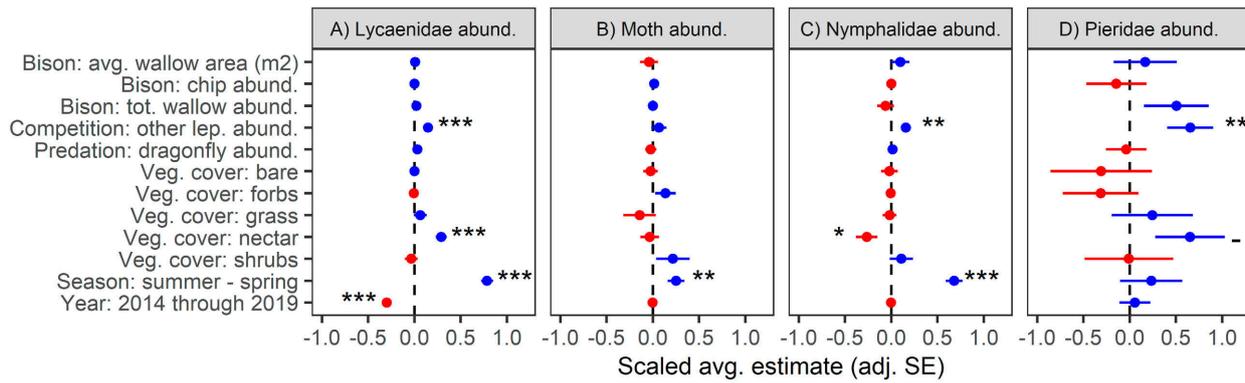
tended to predict Lepidoptera abundance, with more individuals observed in summer than spring for Lycaenidae, moths, and Nymphalidae (Fig. 3A–C). Abundance of Lycaenidae also significantly decreased over time for the years of the study, 2014–2019 (Fig. 3A). Cover of nectar plants was another significant predictor of Lepidoptera abundance. Positive associations with nectar plants were seen for Lycaenidae (Fig. 3A) and Pieridae (marginally significant, Fig. 3D), while Nymphalidae were negatively associated with nectar plants (Fig. 3C), suggesting differences in resource use among these groups. Finally, positive associations were seen between abundances of focal groups and other groups of lepidopterans (Fig. 3A, C, D). This finding suggested Lepidoptera coexist rather than compete with other groups of Lepidoptera observed at this site. Overall, dragonfly presence did not influence the presence, abundance, or distribution of lepidopteran families or individual species (Tables 2, 3) and we did not pursue further analyses.

### Lepidopteran community

We examined lepidopteran community assembly, analyzing the groups observed during the study  $> 2$  times. For families, we retained for analysis a total of 6/7 groups, omitting only Riodinidae. For analysis of species, we retained 6/17 observed groups, omitting rare species and also groups that were not separated to species level. Species analysis included: *Cupido comyntas* (Godart 1842), *Lycaeides melissa samuelis* (Nabokov 1944), *Lycaena phlaeas* (L. 1761), *Danaus plexippus* (L. 1758), *Limenitis archippus* (Cramer 1776), and *Papilio glaucus* (L. 1758). Two-axis ordination solutions were reached (Figs 4, 5) with stresses of 0.160 (family ordination) and 0.023 (spe-



**Fig. 2.** Centered and scaled parameter estimates expressed as full averages across top models ( $\Delta AICc < 4$ ) describing proxies of bison activity. Asterisks denote significance: \*\*\*  $p < 0.001$ , \*\*  $p < 0.01$ , \*  $p < 0.05$ . See Table S1 for full model summary statistics.



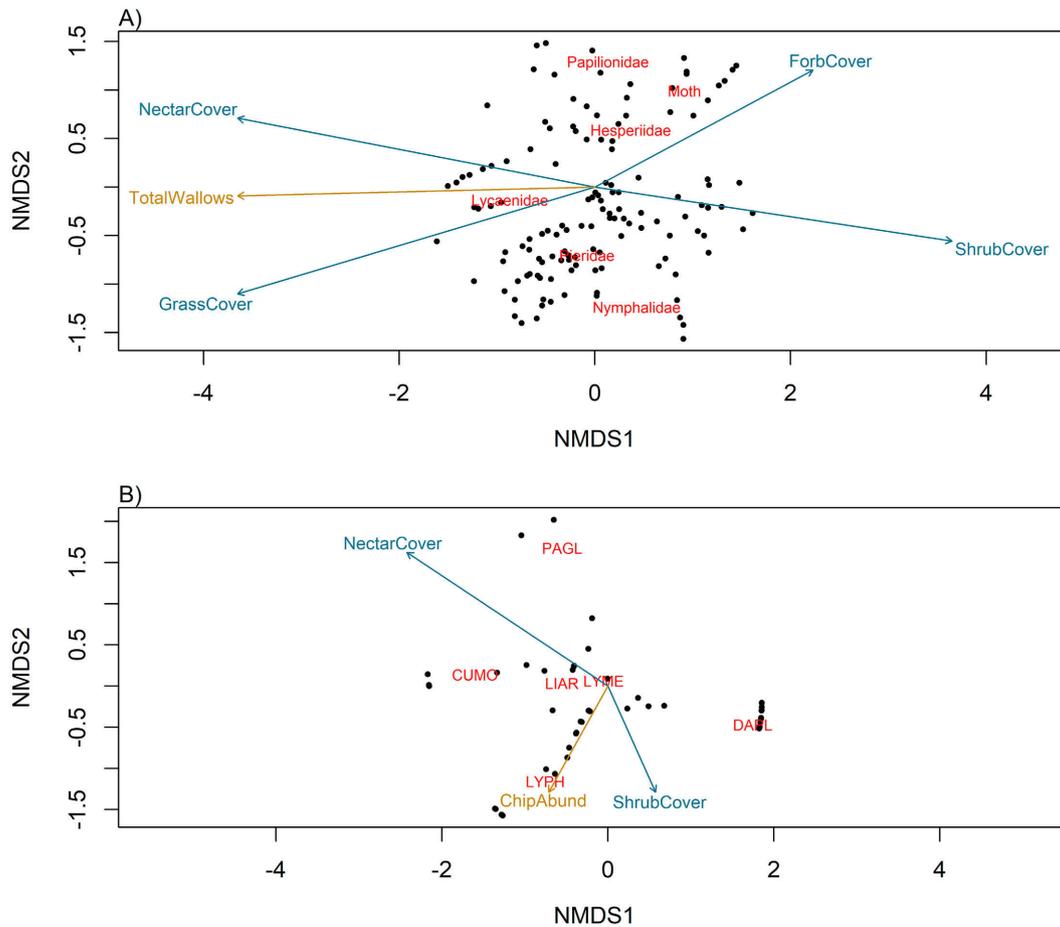
**Fig. 3.** Centered and scaled parameter estimates expressed as full averages across top models (delta AICc < 4) describing abundance of Lepidoptera groups: A – Lycaenidae, n = 779; B – Moths, n = 270; C – Nymphalidae, n = 315; D – Pieridae, n = 36. Asterisks denote significance: \*\*\* p < 0.001, \*\* p < 0.01, \* p < 0.05, – p < 0.10. See Table S1 for full model summary statistics.

cies ordination), stresses that indicated reasonable representations of the data in reduced dimensions (McCune et al., 2002). Several environmental predictors significantly plotted onto the ordination solutions as continuous vectors (Fig. 4), which allowed for intuitive summarization of the more complex nonlinear relationships (Figs S1, S2). Total bison wallows significantly predicted the family ordination solution ( $R^2 = 0.036$ ,  $p = 0.001$ , Fig. 4A), and wallows were also significantly associated with the raw community matrix (Table 2A). For species, bison chips drove community assembly ( $R^2 = 0.017$ ,  $p = 0.008$ , Fig. 4B, Table 3). Vegetation also structured the community. Vegetation type contributed to differentiation among families (Table 2A, Fig. 5A), with similar community breadth across vegetation types (Table 2A). The family ordination solution was also significantly predicted by cover of forbs ( $R^2 = 0.057$ ,  $p < 0.001$ ) and grass ( $R^2 = 0.037$ ,  $p < 0.001$ ). Both family and species solutions were shaped by nectar plants (families:  $R^2 = 0.080$ ,  $p < 0.001$ ; species:  $R^2 = 0.035$ ,  $p =$

0.010), and shrubs (families:  $R^2 = 0.063$ ,  $p < 0.001$ ; species:  $R^2 = 0.027$ ,  $p = 0.019$ ) (Fig. 4). Analysis of the raw community matrices (Tables 2A, 3) showed these same vegetation variables as significant predictors, except the relationship to shrubs was nonsignificant for the species matrix ( $R^2 = 0.006$ ,  $p = 0.171$ ). Finally, we observed temporal trends. The ten collection dates captured significantly different assemblages (Tables 2A, 3). Spring and summer collections likewise captured different communities, and the family communities differed in breadth with summer showing greater breadth in families (Tables 2A, 3, Fig. 5C, D). Some taxa showed seasonal fidelity, with *Papilio glaucus* (Papilionidae) more common in spring (Tables 2B, 4) and Hesperidae more common in summer (Table 2B). Assemblages and community breadths also diverged over the years of the study (Tables 2A, 3, Fig. 5E, F), with assemblages in the two latest years, 2018 and 2019, diverging most from the earlier years (Fig. 5E, F). Some lepidopteran groups were more abundant in certain years, with Lycaeni-

**Table 2.** Multivariate predictors of lepidopteran family abundance. Asterisks denote significance: \*\*\* p < 0.001, \*\* p < 0.01, \* p < 0.05, – p < 0.10. A – PERMANOVA is permutational multivariate analysis of variance, analyzing individual predictor effects. For categorical predictors,  $\beta$  dispersion tests for significant differences in multivariate breadth among categories. B – Indicator species analysis gives an index (0 to 1) and significance describing the strength of a species' association with a given category. Only significant indicators are shown.

		PERMANOVA		$\beta$ dispersion		
A) Hypothesis	Predictors	R <sup>2</sup>	p value	Sig.	p value	Sig.
Bison	Avg. wallow area (m <sup>2</sup> )	0.003	0.684			
	Chip abundance	0.006	0.168			
	Total wallow area (m <sup>2</sup> )	0.003	0.634			
	Total wallow number	0.015	<0.001	***		
Predation	Dragonfly abundance	0.001	0.922			
Veg. cover	Bare cover	0.002	0.559			
	Forbs cover	0.025	0.006	**		
	Grass cover	0.018	<0.001	***		
	Nectar cover	0.036	<0.001	***		
	Shrubs cover	0.031	<0.001	***		
Study design	Collection date (season + year)	0.168	<0.001	***	0.082	–
	Season (spring, summer)	0.042	<0.001	***	<0.001	***
	Year (2014–2019)	0.114	<0.001	***	0.028	*
	Vegetation type (disturbed, other/grass, shrub, wallow)	0.033	<0.001	***	0.143	
B) Indicators	Family	Indicator value	p value	Sig.		
Season: spring	Papilionidae	0.195	0.004	**		
Season: summer	Hesperidae	0.257	0.012	*		
Year: 2014, 2015, 2016 & 2017	Lycaenidae	0.871	<0.001	***		
Year: 2019	Papilionidae	0.211	0.016	*		



**Fig. 4.** Two-axis nonmetric multidimensional scaling (NMDS) ordination solutions describing lepidopteran family abundance (A – stress = 0.160) and species abundance (B – stress = 0.023). Plotted are site scores (black points) and taxon weighted averages (center of the red taxon name). Table 4 provides a key to lepidopteran species names and 4-letter abbreviations. Continuous predictors of community structure having significant ( $p < 0.05$ ) linear trends are plotted as vectors.

dae more common 2014–2017, *Lycaena phlaeas* in 2014, *Danaus plexippus* 2018–2019, and *Papilio glaucus* (Papilionidae) in 2019 (Tables 2B, 4).

**DISCUSSION**

Many studies have shown the overall use of prescribed and improved grazing practices can be highly beneficial to

specific ecotypes (Niederman et al., 2023). Although grazing by ungulates, including bison, can generate negative effects on the surrounding landscape, particularly when herds are confined to unnaturally small spaces, over-utilize grazing areas, or are projected on inappropriate ecotypes (Panza, 2020; Kaplan et al., 2021; Kauffman et al., 2022; Bussan & Schultz, 2023), landuse practices that incorpo-

**Table 3.** Multivariate predictors of lepidopteran species abundance. Asterisks denote significance: \*\*\*  $p < 0.001$ , \*  $p < 0.05$ . PERMANOVA is permutational multivariate analysis of variance, analyzing individual predictor effects. For categorical predictors,  $\beta$  dispersion tests for significant differences in multivariate breadth among categories.

Hypothesis	Predictors	PERMANOVA			$\beta$ dispersion	
		R <sup>2</sup>	p value	Sig.	p value	Sig.
Bison	Avg. wallow area (m <sup>2</sup> )	0.003	0.739			
	Chip abundance	0.017	0.045	*		
	Total wallow area (m <sup>2</sup> )	0.007	0.410			
	Total wallow number	0.002	0.645			
Predation	Dragonfly abundance	0.002	0.632			
	Bare cover	0.002	0.702			
Veg. cover	Forbs cover	0.010	0.283			
	Grass cover	0.002	0.778			
	Nectar cover	0.022	<0.001	***		
	Shrubs cover	0.006	0.171			
Study design	Collection date (season + year)	0.186	<0.001	***	<0.001	***
	Season (spring, summer)	0.029	<0.001	***	0.901	
	Year (2014–2019)	0.124	<0.001	***	<0.001	***
	Vegetation type (disturbed, other/grass, shrub, wallow)	0.008	0.622		0.875	

**Table 4.** Lepidopteran group names and abbreviations used in Figs 4, 5, and S2, total number observed over the course of the study, and results of significant indicator analyses performed on the species abundance matrix. Indicator value is an index (0 to 1), with significance describing the strength of a species' association with a given category. Asterisks denote significance: \*\*\*  $p < 0.001$ , \*\*  $p < 0.01$ , \*  $p < 0.05$ . Scientific names follow Integrated Taxonomic Information System, except when updated classification was available (Zhang et al., 2020).

Abbr.	Family	Species	Common name	n	Indicators	Indicator value	p value	Sig.
	Hesperiidae	Not classified	Skipper	30	–			
CUMO	Lycaenidae	<i>Cupido comyntas</i>	Eastern tailed-blue	12	Veg. type: disturbed & wallow	0.253	0.020	*
	Lycaenidae	<i>Glaucopsyche lygdamus</i>	Silvery blue	1				
LYME	Lycaenidae	<i>Lycaeides melissa samuelis</i>	Karner blue butterfly	714	–			
LYPH	Lycaenidae	<i>Lycaena phlaeas</i>	American copper	31	Year: 2014	0.472	0.010	*
	Lycaenidae	Not classified	Hairstreaks	21				
DAPL	Nymphalidae	<i>Danaus plexippus</i>	Monarch butterfly	26	Year: 2018 & 2019	0.564	0.001	**
	Nymphalidae	<i>Junonia coenia</i>	Common buckeye	1				
LIAR	Nymphalidae	<i>Limenitis archippus</i>	Viceroy	6	–			
	Nymphalidae	<i>Vanessa cardui</i>	Painted lady	1	–			
	Nymphalidae	Not classified	Fritillary	101	–			
	Nymphalidae	Not classified	Checkerspot	24	–			
	Nymphalidae	Not classified	Little wood-satyr, wood nymph, little eyed brown	156	–			
PAGL	Papilionidae	<i>Papilio glaucus</i>	Eastern tiger swallowtail	5	Season: spring	0.271	<0.001	***
					Year: 2019	0.487	0.003	**
	Pieridae	Not classified	Sulphur	36	–			
	Riodinidae	<i>Calephelis muticum</i>	Swamp metalmark	2	–			
	Not classified	Not classified	Moths	270	–			

rate grazing can be harnessed to benefit surrounding habitat types when native species are accounted for in management decisions (Schwerk et al., 2021; Kauffman et al., 2022; Niederman et al., 2023). Bison, a native megaherbivore endemic to varying stages of grasslands, have been shown to promote restoration work returning native species and land to sustainable, natural habitat states (Hess et al., 2014; Rosenberger & Conforti, 2020; Schieuer, 2023), particularly when managed to avoid overgrazing (Kauffman et al., 2022; Doan et al., 2024).

Our selected study site provides an incredibly unique opportunity to evaluate in real-time the effects of native megaherbivores on complex grassland habitat and the critical lepidopteran taxa that occupy this area. Overall, we explored habitat predictors of lepidopteran community composition.

### Bison influence

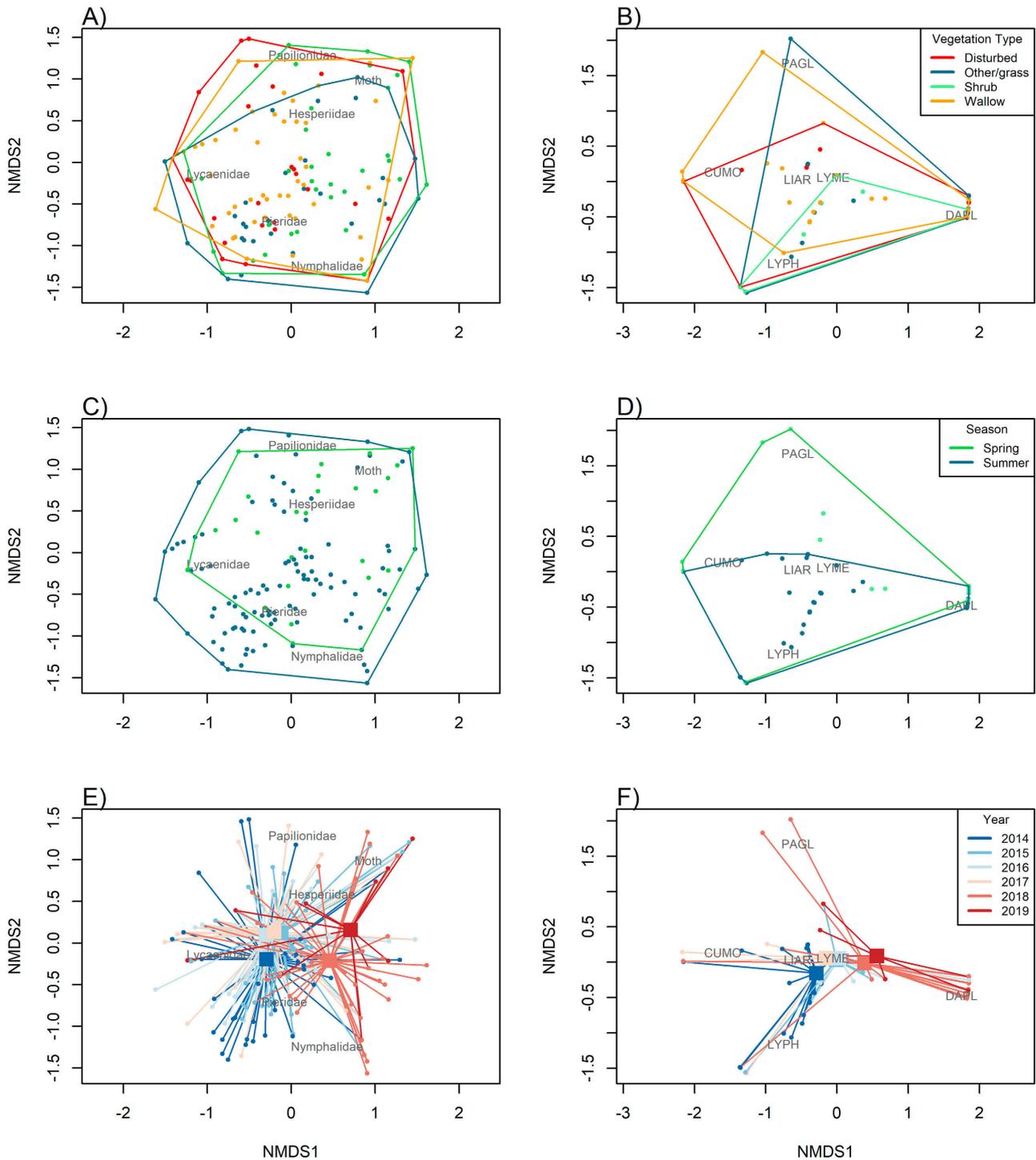
Bison are widely regarded as a keystone species that benefits habitat structure and diversity (Yu, 2021; Fagre et al., 2022; Yu et al., 2023). Though we are still learning how specific bison activities influence the landscape (Panza, 2020; McMillan et al., 2021), studies have found that bison grazing spreads over wider areas and with randomized patterns that improve overall habitat-vegetation quality (Ling et al., 2023). Findings of bison benefits on the landscape may be primarily driven by management that encourages grassland habitat development (Brockman et al., 2022) such as that at the Sandhill Wildlife Area. Bison activities throughout were expected to influence vegetation cover by encouraging ruderal species growth and reducing woody vegetation overall, due to the small proximity of the study area (105 ha) over which the bison graze, wallow, travel, mate, and conduct their general lifestage activities (i.e. Brockman et al., 2022).

Parallel to other studies, this evaluation strengthened the understanding that bison activities such as grazing and wallowing display key associations with groundcover variables, across geographic areas, generating heterogeneity in grasslands (e.g. Schoenecker et al., 2022; Ling et al., 2023) and added additional insight into temporal influences across years and seasons.

Disturbance areas, assumed to be areas where bison regularly grazed or traveled, were primarily occupied by grass cover over the course of the study, but additionally displayed the second highest amount of forb and nectar cover within the study site (Table 1). In contrast, wallows significantly displaced vegetation features through the generation of bare earth (Tables 1, S1, Fig. 2A, C), a high level of disturbance that subsequently assists in the generation of new growth in grassland systems. These findings are consistent with studies that have found bison wallowing and grazing encourage pioneer/ruderal species but generate a delay on secondary plant growth, with re-establishment of prairie species occurring in as few as 2 years and as great as 8–15 years after wallowing occurred (Polley & Collins, 1984; Polley & Wallace, 1986; Yu, 2021; Yu et al., 2023).

Bison chips, indicating the recent presence of individual bison, were significantly separated from bare ground areas (Table S1, Fig. 2B), and weakly associated with decreasing nectar and shrub cover, suggesting that bison wallowing and grazing/defecating occur in separate areas. These results suggest that bison may avoid grazing in shrub areas and navigate more towards grass cover (i.e. graminoids) likely due to their primary forage source and subsequently influencing regeneration of different types of vegetation cover over time through both grazing (Schoenecker et al., 2022; Chakravorty et al., 2024) and wallowing (Polley & Collins, 1984; Polley & Wallace, 1986).

Wallows themselves increased 2014–2019, with a decrease in bison chip counts, which suggests that American



**Fig. 5.** Two-axis nonmetric multidimensional scaling (NMDS) solutions describing lepidopteran family abundance (A, C, E; stress = 0.160) and species abundance (B, D, F; stress = 0.023). Plotted are site scores (points) and taxon weighted averages (center of the grey taxon name). Table 4 provides a key to lepidopteran species names and 4-letter abbreviations. Site observations are color-coded by categorical predictors, with polygons (A–D) or lines and centroids (E, F) added to visualize group membership.

bison individuals were ranging into and utilizing larger areas over different cover types across time (Fig. 2A, C). This may be due to several factors, including improved habitat conditions, seasonal or year-round grazing effects, or shifts in herd dynamics (McMillan et al., 2021; Yu, 2021; Yu et al., 2023). Smaller average wallowing areas were noted in study plots during the summer than in the spring, further suggesting that the bison ranged into a

wider area of habitat utilization as the summer progressed (Fig. 2A). These findings were consistent across surveys and displayed a cycle of wallow disturbance followed by vegetation recovery that is characteristic of bison grazing in grasslands (McMillan et al., 2021; Kauffman et al., 2022; Schoenecker et al., 2022), riparian zones (Yu et al., 2023), and forested areas (Gottlieb et al., 2024).

The density of bison/ha may also be an influential factor in the distribution and impact of bison on the landscape. Historically, bison density varied across the landscape as they roamed in search of resources, with very low and very high local density occurring based on climate (e.g. droughts) and local environmental context (Martin et al., 2022; Wendt et al., 2022). When historical populations were present, bison density is estimated to have been equivalent to other large ungulate populations across the world (Wendt et al., 2022), with an estimated 30–60 million bison present in the late 1800s across the entirety of the Great Plains covering approximately 68 million ha (0.44–0.88 bison/ha) (Smits et al., 1994; Knapp et al., 1999). Steenweg et al. (2016) utilized a Habitat Suitability Index to estimate the carrying capacity for re-establishing bison on the landscape and determined 0.48 bison/km<sup>2</sup> (0.504 bison/1.05 km<sup>2</sup> is comparative to 0.504 bison/ha) would optimize habitat and bison spatial distribution, a much higher density than the estimated approximately 0.08–0.12 bison adults/ha/year present in the Sandhill Wildlife Area bison pasture. Although not the purpose of this study, we can postulate that the Sandhill Wildlife Area bison herd is operating at a low density compared to historical or ecologically sustainable density of bison adults/ha.

### Lepidopteran community

Given the novelty of bison grazing on the landscape in modern times it is no surprise that the relationship between this endemic megaherbivore and insect communities largely remains a mystery, however important it may be to distribution and abundance of lepidopterans or insects in general. Bison grazing is known to influence vegetation communities, typically in a positive way (Fagre et al., 2022; Schoenecker et al., 2022; Alaniz et al., 2024), but negatively when undermanaged and overgrazing occurs (Kaufmann et al., 2022).

Lepidopteran populations were dominated by Lycaenidae, Nymphalidae, Pieridae, and moths within the study area, with additional low numbers of observations of Hesperidae, Papilionidae, and Riodinidae (Table 4). Overall, 17 groups were observed, with 10 groups identified to species, and six species with abundance appropriate for inclusion in multivariate community analyses (Table 4). We evaluated influences between lepidopterans, vegetation, bison-specific activities, and seasonal variation measures.

Total number of wallows significantly predicted the lepidopteran family community assemblage (Table 2, Fig. 4A), suggesting a relationship across the study site and habitat features that may be due to the influence of bison activities on vegetation cover through regular disturbance and regrowth cycles (Hess et al., 2014; Brockman et al., 2022). Bison chips also were significantly associated with assembly of the six species included in the species-only ordination (Table 3, Fig. 4B). Vegetation cover types overall additionally significantly structured the lepidopteran community (Tables 2A, 3, Figs 4, 5A, B), including forb, grass, nectar, and shrub cover. Linking the linear relationship of bison activities to cover types, specifically the recent presence of bison (chips) to decreasing nectar and shrub

cover to the subsequent influence of chips, wallows, nectar, shrubs, and other cover types on lepidopteran community (Tables 2A, 3, Fig. 4, 5A, B), suggests again that the bison activities within this area are influencing vegetation cover and subsequently lepidopteran community assemblage and distribution. This is consistent in view of studies that have shown the influence of bison grazing, specifically, on vegetation cover, often contributing to heterogeneity due to the selective grazing of bison on graminoids, and activities such as rubbing, horning, and wallowing that reduce overall shrub and tree cover, and generate patterns consistently though hetero-dispersed across the landscape (Hess et al., 2014; Polley & Collins, 1984; Polley & Wallace, 1986; Schoenecker et al., 2022; Ling et al., 2023). Specifically, cover of nectar plants was a significant predictor of some major lepidopteran groups, with a positive influence of nectar on Lycaenidae (Fig. 3A) and Pieridae (Fig. 3D). Nectar plants were negatively associated with Nymphalidae (Fig. 3C), suggesting a difference in resource utilization between this large lepidopteran group and Lycaenidae and Pieridae. Lycaenidae, Nymphalidae, and Pieridae were further influenced by the presence of other lepidopterans, suggesting acknowledgement of the presence of other family groups within resource areas (Table S1), a characteristic that has been observed among lepidopterans as they compete for foraging resources and mating territory (Bergman et al., 2021; Sokame et al., 2021) and react to outside pressures (Malaquias et al., 2022). Moth abundance as a group was overall more influenced by shrub and forb cover than other metrics, though not significantly, suggesting that moths were more evenly distributed across the landscape in search of resources (Table S1).

Specific cover type categories were not significant indicators of lepidopteran species apart from *C. comyntas*, which was positively influenced by disturbance areas and wallows (Table 4). This association might be explained by the reliance of *C. comyntas* on legumes. This species may be seeking on legumes and may be seeking out the presence of wild blue lupine, a plant found to be associated with bison wallowing (Hess et al., 2014). However, several species were highly associated with seasonal and yearly changes, including *D. plexippus*, *P. glaucus*, and *L. phlaeas*. This general disassociation with categorized cover types suggests that the individual species observed in this study are predominantly generalized species and utilize a widespread heterogeneous distribution of resources, except for *C. comyntas*, which preferred overall the light-disturbance areas and heavy-disturbance wallows (Table 4).

Seasonal separation of lepidopterans was observed, with greater abundances in summer (Fig. 3). Seasonal separations within the dataset most influenced Lycaenidae, likely due to the influence of *L. melissa samuelis* species, which are a bivoltine and display two short (1–3 week) population cycles per year, with the larger population occurring during the second or primary flight (Fig. 3A) (Hess & Hess, 2015) and upon occasion, a third flight (Brock & Kaufman, 2003) which occurs infrequently but may influence population

analyses or distributions across seasons and years. Lycaenidae population significantly decreased over time from summer 2014 to spring of 2019 (Fig. 3A). This decline may coincide with overall decline of *L. melissa samuelis* populations and is consistent with larger outside studies, suggesting that despite favorable habitat conditions and documented influence of *L. melissa samuelis* interacting with bison features within the study area, outside factors may be negatively influencing *L. melissa samuelis* populations (Patterson et al., 2020; Schuurman et al., 2023).

Other temporal trends included significantly different lepidopteran community assemblages over the ten site collections (spring vs. summer) 2014–2019 (Tables 2A, 3, Fig. 5E, F). Summer collections displayed greater breadth overall at the family level (Table 2A, Fig. 5C). Two families were strongly separated between seasons, Papilionidae (associated with spring) and Hesperidae (associated with summer) (Table 2B). These results are interesting regarding Papilionidae, specifically *P. glaucus* (Table 4), which flies from spring to fall, with 2–3 broods (Brock & Kaufman, 2003), suggesting that finer habitat variables may be influencing association with spring. Hesperidae, the skipper family, differs in both broods and emergence between species within this study area, ranging from 1–3 broods, with emergence from spring to early summer (Brock & Kaufman, 2003). The association of Hesperidae with summer (Table 2B) may have been driven by brood timing and populations of individual species; however, we can only speculate on species trends because we did not identify members of this family with confidence due to the nature of the study (observation only) and the similarities between species. Overall family assemblages diverged across years 2014–2019, with the greatest divergence occurring in 2018 and 2019 (Tables 2A, 3, Fig. 5E, F), and several lepidopteran groups showing higher relative abundances in some collection years (Tables 2B, 4).

These divergences over time in lepidopteran occurrences may be related to bison activities spreading out over wider areas as the seasons and years progressed, potentially influencing soil condition and herbaceous cover in more delineated ways (Panza, 2020; Schoenecker et al., 2022). Due to local management and breeding, bison numbers increased slightly from 2014–2019, from approximately 10 adults (2014), 10 adults with 1 adult cull (2015), 8 adults and 1 calf (2016), 12 adults with 1 adult cull and 3 calves (2017), 13 adults with 1 adult cull (2018), and 13 adults (2019). This increase in adults supports the observed increase in wallow areas (m<sup>2</sup>) 2014–2019 (Fig. 2A, C), but also resulted in a decrease in bison chip counts (Fig. 2B). Bison chips, as mentioned earlier, are considered indicative of the recent presence of bison. Chips were found to decrease with bare earth cover, suggesting that bison were not depositing scat around wallowing areas or on trails, but instead in grazing areas (i.e. graminoids) (Fig. 2B). Our results also showed that vegetation cover changed over the course of the study, and bare ground specifically increased. These observations may suggest a change in bison group dynamics over time, possibly with individuals utilizing

more widespread but more delineated areas, such as open grassland vs. edge movement, and subsequently differentially impacting the landscape across years, or may also be related to changes in prescribed fire and mechanical scarification techniques within the Sandhill Wildlife Area. The cause for a decrease in bison chips may be as simple as an increase in species that utilize and break down scat features on the landscape such as dung beetles (Cheng et al., 2022; Grzechnik & Cabrero-Sanudo, 2024; Maldaner et al., 2024; Tahoor et al., 2024), which are currently under researched within savanna areas (Reis et al., 2024). Bison have been found to spread out over wider areas and graze randomly when resources are abundant (Ling et al., 2023) which may have contributed to the large herd size utilizing more wallowing areas. Bison also are known to spread across grasslands (McMillan et al., 2021; Kauffman et al., 2022; Schoenecker et al., 2022), riparian areas (Yu et al., 2023) and forested areas (Gottlieb et al., 2024) seasonally (McMillan et al., 2021), as they select high quality resources at the beginning of the growing season and spread out more as habitat resources improve through the leaf-on season (Ling et al., 2023). Without question, these native megaherbivores are influencing cover types and subsequently the lepidopteran populations that utilize them within this open complex habitat matrix. Due to the uncertainty of bison activities related to additional land management practices, these observations on bison population dynamics, activities, and relationship to lepidopteran abundance and diversity merit more exploration.

## CONCLUSIONS

Concurrent with previous studies, our 6-year study found that areas of high bison disturbance, or wallowing activities, support robust levels of disturbance on mineral soil and promotes the growth of grass and nectaring plant vegetation. In comparison, disturbance areas outside of wallows did not differ greatly in vegetation composition, suggesting that light disturbance including grazing, horning, and rubbing does not displace the function of vegetation as substantially as wallowing activities. Despite this, lepidopteran family groups differed significantly across areas of low and high disturbance, suggesting that habitat differences and species preferences also play a major role in determining the abundance and distribution of lepidopteran species. Additional assessments of bison influenced habitat features and species evaluations are needed to further understand how temporal bison activities may influence the habitat structure and subsequently the reliant lepidopterans within this ecotype.

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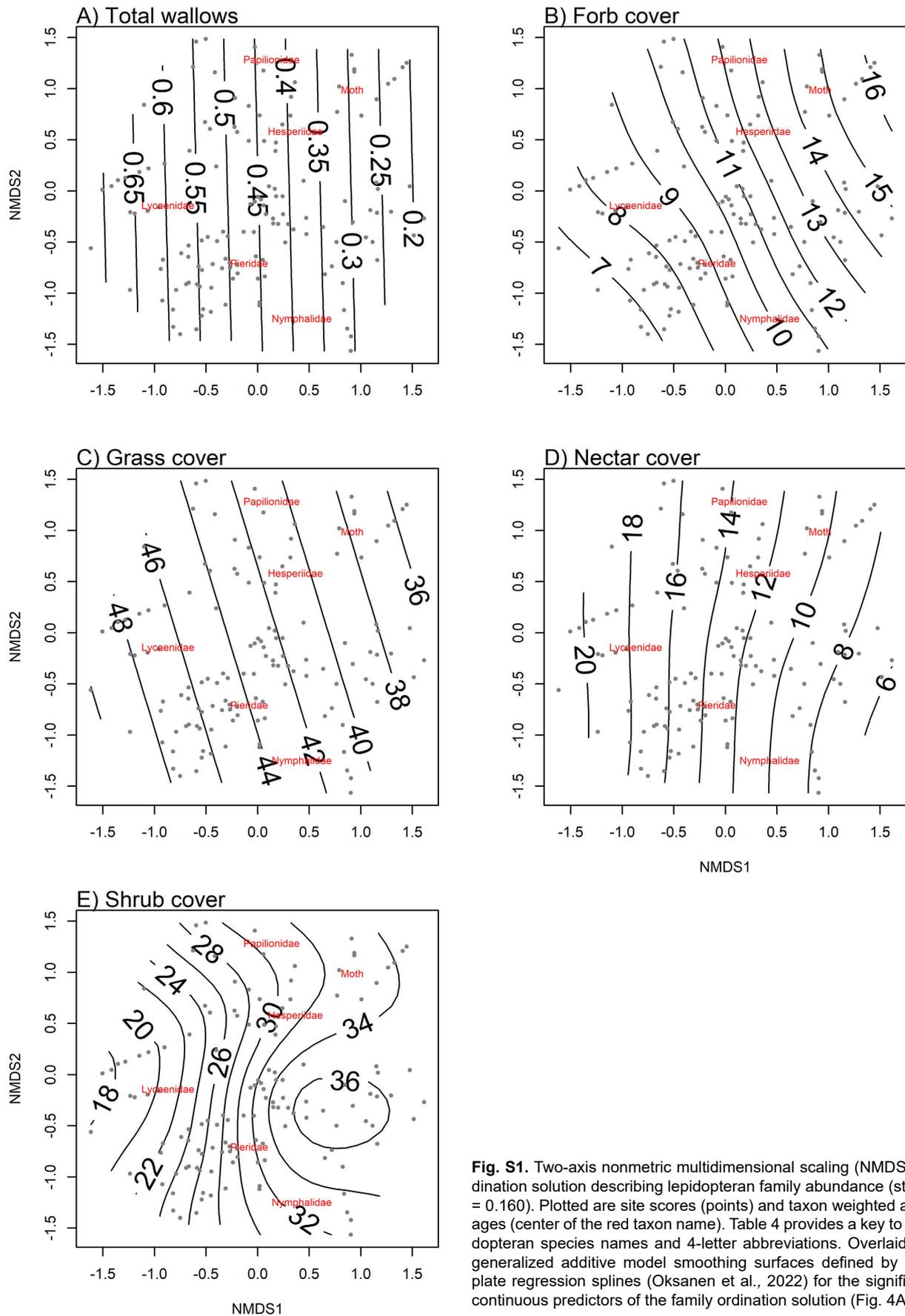
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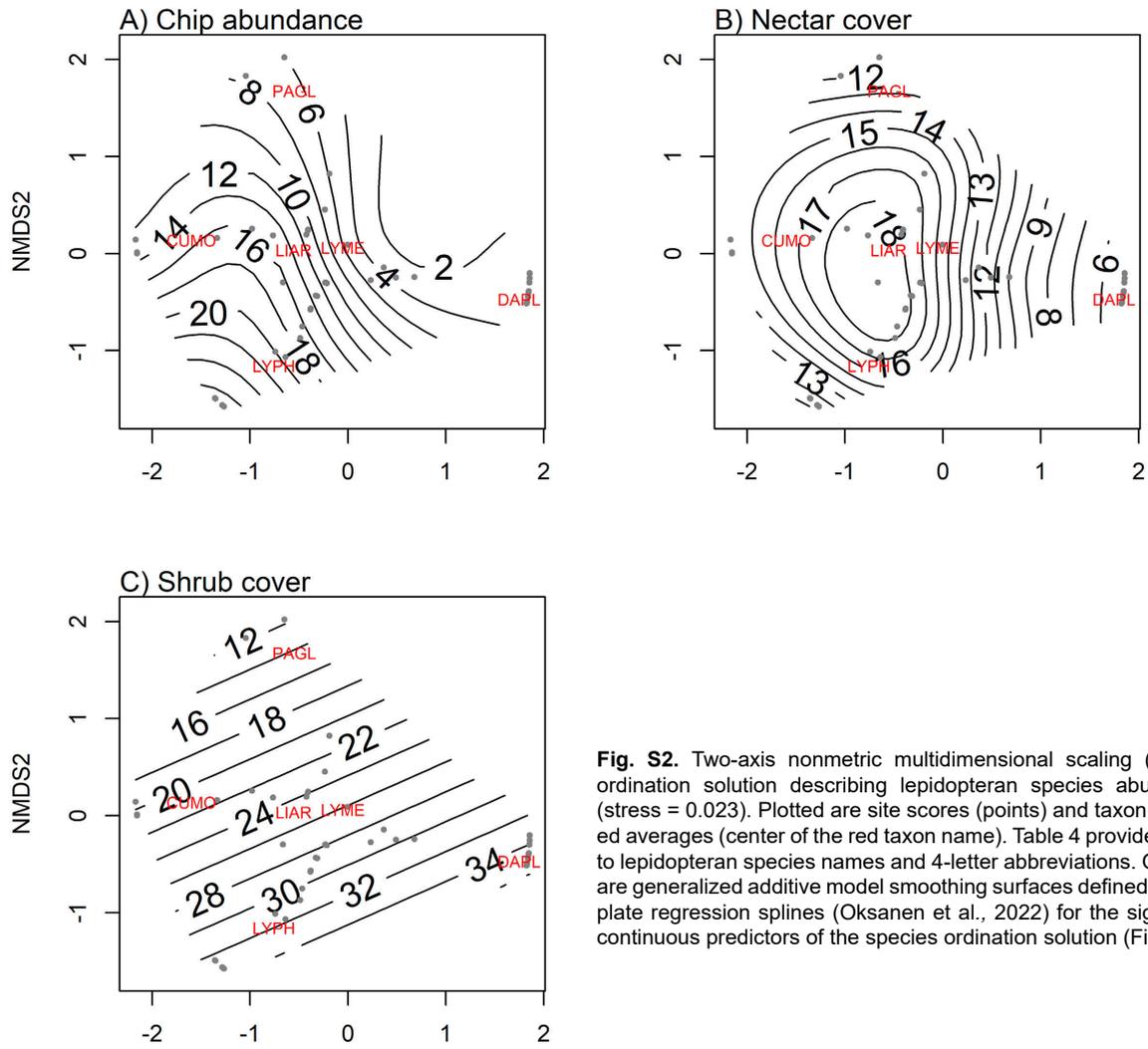
Supplementary Table S1 and Figs S1, S2 follow on next pages.

**Table S1.** Centered and scaled parameter estimates expressed as full averages across top models (delta AICc < 4) describing proxies of bison activity and abundance of Lepidoptera groups. Asterisks denote significance: \*\*\* p < 0.001, \*\* p < 0.01, \* p < 0.05, – p < 0.10.

	Parameter	Avg. estimate	Adjusted SE	z value	p value	Sig.
Bison avg. wallow area (m <sup>2</sup> )	Veg. cover: bare	0.431	0.233	1.849	0.065	–
	Veg. cover: forbs	0.025	0.177	0.141	0.888	
	Veg. cover: grass	0.250	0.352	0.709	0.478	
	Veg. cover: nectar	0.119	0.240	0.497	0.619	
	Veg. cover: shrubs	0.212	0.442	0.479	0.632	
	Season: summer – spring	–0.161	0.058	2.792	0.005	**
	Year: 2014 through 2019	0.387	0.060	6.444	<0.001	***
	Intercept term	–5.927	2.723	2.176	0.030	*
Bison chip abundance	Veg. cover: bare	–0.363	0.065	5.598	<0.001	***
	Veg. cover: forbs	–0.006	0.047	0.129	0.897	
	Veg. cover: grass	–0.020	0.088	0.225	0.822	
	Veg. cover: nectar	–0.122	0.068	1.789	0.074	–
	Veg. cover: shrubs	–0.206	0.113	1.820	0.069	–
	Season: summer – spring	0.001	0.011	0.065	0.948	
	Year: 2014 through 2019	–0.559	0.023	24.721	<0.001	***
	Zero-inflation term	–1.384	0.153	9.064	<0.001	***
Bison total wallow area (m <sup>2</sup> )	Intercept term	0.646	0.196	3.299	0.001	**
	Veg. cover: bare	0.408	0.300	1.363	0.173	
	Veg. cover: forbs	0.033	0.227	0.144	0.885	
	Veg. cover: grass	0.498	0.430	1.158	0.247	
	Veg. cover: nectar	0.300	0.296	1.013	0.311	
	Veg. cover: shrubs	0.453	0.549	0.826	0.409	
	Season: summer – spring	–0.089	0.070	1.280	0.200	
	Year: 2014 through 2019	0.407	0.060	6.805	<0.001	***
Lycaenidae abundance (n = 779)	Intercept term	–6.367	2.569	2.479	0.013	*
	Bison: avg. wallow area (m <sup>2</sup> )	0.009	0.038	0.236	0.814	
	Bison: chip abundance	0.001	0.012	0.069	0.945	
	Bison: total wallow number	0.021	0.039	0.533	0.594	
	Competition: other lep. abundance	0.149	0.039	3.863	<0.001	***
	Predation: dragonfly abundance	0.033	0.045	0.723	0.470	
	Veg. cover: bare	0.003	0.029	0.093	0.926	
	Veg. cover: forbs	–0.006	0.031	0.202	0.840	
	Veg. cover: grass	0.065	0.070	0.920	0.357	
	Veg. cover: nectar	0.291	0.061	4.788	<0.001	***
	Veg. cover: shrubs	–0.033	0.069	0.480	0.631	
	Season: summer – spring	0.787	0.063	12.406	<0.001	***
	Year: 2014 through 2019	–0.298	0.052	5.724	<0.001	***
	Zero-inflation term	–1.749	0.293	5.974	<0.001	***
Moth abundance (n = 270)	Intercept term	–0.220	0.095	2.313	0.021	*
	Bison: avg. wallow area (m <sup>2</sup> )	–0.040	0.098	0.410	0.682	
	Bison: chip abundance	0.015	0.033	0.451	0.652	
	Bison: total wallow number	0.002	0.032	0.075	0.940	
	Competition: other lep. abundance	0.066	0.082	0.800	0.424	
	Predation: dragonfly abundance	–0.022	0.062	0.360	0.719	
	Veg. cover: bare	–0.025	0.079	0.316	0.752	
	Veg. cover: forbs	0.137	0.113	1.215	0.224	
	Veg. cover: grass	–0.143	0.176	0.811	0.418	
	Veg. cover: nectar	–0.034	0.100	0.337	0.736	
	Veg. cover: shrubs	0.218	0.181	1.203	0.229	
	Season: summer – spring	0.253	0.091	2.794	0.005	**
	Year: 2014 through 2019	–0.002	0.026	0.080	0.936	
	Zero-inflation term	–0.233	0.208	1.120	0.263	
Nymphalidae abundance (n = 315)	Intercept term	–0.390	0.126	3.087	0.002	**
	Bison: avg. wallow area (m <sup>2</sup> )	0.098	0.099	0.985	0.325	
	Bison: chip abundance	–0.001	0.024	0.045	0.964	
	Bison: total wallow number	–0.062	0.090	0.690	0.490	
	Competition: other lep. abundance	0.159	0.055	2.904	0.004	**
	Predation: dragonfly abundance	0.015	0.051	0.301	0.763	
	Veg. cover: bare	–0.021	0.090	0.234	0.815	
	Veg. cover: forbs	–0.008	0.041	0.187	0.852	
	Veg. cover: grass	–0.017	0.075	0.226	0.821	
	Veg. cover: nectar	–0.266	0.117	2.264	0.024	*
	Veg. cover: shrubs	0.109	0.124	0.874	0.382	
	Season: summer – spring	0.680	0.090	7.567	<0.001	***
	Year: 2014 through 2019	–0.001	0.021	0.062	0.951	
	Zero-inflation term	–0.566	0.232	2.442	0.015	*
Pieridae abundance (n = 36)	Intercept term	–0.566	0.133	4.267	<0.001	***
	Bison: avg. wallow area (m <sup>2</sup> )	0.167	0.342	0.488	0.625	
	Bison: chip abundance	–0.144	0.327	0.441	0.659	
	Bison: total wallow number	0.504	0.350	1.440	0.150	
	Competition: other lep. abundance	0.654	0.248	2.641	0.008	**
	Predation: dragonfly abundance	–0.039	0.220	0.178	0.859	
	Veg. cover: bare	–0.308	0.550	0.561	0.575	
	Veg. cover: forbs	–0.315	0.410	0.767	0.443	
	Veg. cover: grass	0.243	0.439	0.555	0.579	
	Veg. cover: nectar	0.652	0.375	1.738	0.082	–
	Veg. cover: shrubs	–0.009	0.478	0.018	0.986	
	Season: summer – spring	0.234	0.336	0.695	0.487	
	Year: 2014 through 2019	0.056	0.168	0.333	0.739	
	Zero-inflation term	0.746	0.471	1.585	0.113	
Intercept term	–2.752	0.618	4.456	<0.001	***	



**Fig. S1.** Two-axis nonmetric multidimensional scaling (NMDS) ordination solution describing lepidopteran family abundance (stress = 0.160). Plotted are site scores (points) and taxon weighted averages (center of the red taxon name). Table 4 provides a key to lepidopteran species names and 4-letter abbreviations. Overlaid are generalized additive model smoothing surfaces defined by thin-plate regression splines (Oksanen et al., 2022) for the significant continuous predictors of the family ordination solution (Fig. 4A).



**Fig. S2.** Two-axis nonmetric multidimensional scaling (NMDS) ordination solution describing lepidopteran species abundance (stress = 0.023). Plotted are site scores (points) and taxon weighted averages (center of the red taxon name). Table 4 provides a key to lepidopteran species names and 4-letter abbreviations. Overlaid are generalized additive model smoothing surfaces defined by thin-plate regression splines (Oksanen et al., 2022) for the significant continuous predictors of the species ordination solution (Fig. 4B).