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ARTICLE

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Functional consequences of animal community changes in managed grasslands: An application of the CAFE approach

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Abstract

In the midst of an ongoing biodiversity crisis, much research has focused on species losses and their impacts on ecosystem functioning. The functional consequences (ecosystem response) of shifts in communities are shaped not only by changes in species richness, but also by compositional shifts that result from species losses and gains. Species differ in their contribution to ecosystem functioning, so species identity underlies the consequences of species losses and gains on ecosystem functions. Such research is critical to better predict the impact of disturbances on communities and ecosystems. We used the "Community Assembly and the Functioning of Ecosystems" (CAFE) approach, a modification of the Price equation to understand the functional consequences and relative effects of richness and composition changes in small nonvolant mammal and dung beetle communities as a result of two common disturbances in North American prairie restorations, prescribed fire and the reintroduction of large grazing mammals. Previous research in this system has shown dung beetles are critically important decomposers, while small mammals modulate much energy in prairie food webs. We found that dung beetle communities were more responsive to bison reintroduction and prescribed fires than small nonvolant mammals. Dung beetle richness increased after bison reintroduction, with higher dung beetle community biomass resulting from changes in remaining species (context-dependent component) rather than species turnover (richness components); prescribed fire caused a minor increase in dung beetle biomass for the same reason. For small mammals, bison reintroduction reduced energy transfer through the loss of species, while prescribed fire had little impact on either small mammal richness or energy transfer. The CAFE approach demonstrates how bison reintroduction controls small nonvolant mammal communities by increasing prairie food web complexity, and increases dung beetle populations with possible benefits for soil health through dung mineralization and soil bioturbation. Prescribed fires, however, have little effect on small mammals and dung beetles, suggesting a resilience to fire. These findings illustrate the key role of re-establishing historical disturbance regimes when restoring endangered prairie ecosystems and their ecological function.

KEYWORDS
bison, community assembly, dung beetle, ecosystem function, prescribed fire, price equation, small mammal, species richness, tallgrass prairie restoration

INTRODUCTION

Understanding the relationship between biodiversity and ecosystem function has been a major goal in ecology for decades (Elton, 1958; Naeem et al., 2012; Tilman & Downing, 1994). Much of the motivation for this work has been to understand how biodiversity loss will influence ecosystem function to predict the consequences of ongoing contemporary extinctions (Ceballos et al., 2015; Hooper et al., 2012). However, at local and regional scales, communities rarely undergo simple declines in richness in response to environmental drivers: biodiversity change involves both the loss of species and the gain of species through colonization (Chase et al., 2019; Dornelas et al., 2019; Sax & Gaines, 2003). One outcome of this is that local species richness or alpha diversity is not declining in all places (Dornelas et al., 2014; Sax et al., 2002; Vellend et al., 2013), although losses can be acute under intense land use (Newbold et al., 2015). Instead, changes in species composition, rather than uniform loss of species richness, seem to be the strongest biodiversity response to stressors throughout the globe (Bannar-Martin et al., 2018; Blowes et al., 2019; Hillebrand et al., 2018; Sandau et al., 2017). Due to this complexity, it can be difficult to predict the success of conservation efforts, which limits their effectiveness amid human-driven environmental changes. Studies on change in ecosystem function (trophic and biogeochemical processes within ecosystems, Naeem et al., 1994) that separate the impacts of change in species richness versus community composition may therefore facilitate more effective conservation amid accelerating global change.

Community composition influences ecosystem functioning because species differ in their contributions to functions, so variation in function depends on which species are gained, lost, or remain during succession or following environmental perturbations (Larsen et al., 2005; Wardle et al., 2011). Overall function may decline when species that make large contributions are replaced by species with smaller contributions despite no net change in richness, such as a native pollinator that provides effective pollination services displaced by an ineffective exotic pollinator (Page & Williams, 2023) The opposite can also occur: for instance, when a nonnative trout replaced a native trout, its increased predation significantly reduced insect emergence from streams, with consequences for adjacent terrestrial communities (Benjamin et al., 2011). A species can also influence greater ecosystem function change because of large per-capita contributions or because of large population size, although the latter might be less likely to be locally extirpated. The species remaining in a community after compositional change can also shift ecosystem function contributions depending on interactions with lost or gained species (Ruesink & Srivastava, 2001), or environmental changes (Messina et al., 2021; Silva et al., 2021; Terry & Rowe, 2015). For example, removing individual species from a pollinator community reduced the floral fidelity of the remaining species, resulting in reduced seed production by a focal plant (Brosi & Briggs, 2013). Additionally, the gain of a strong competitor may suppress populations of a remaining species so that their effect on function is reduced, as in Fox and Kerr's (2012) analysis of grassland communities, where the gain of high biomass plants was associated with lower biomass of remaining species. Finally, in situations where remaining species are numerically dominant or have weak interactions with other species, overall richness, and compositional changes might have little impact on function. In these cases, differences in the remaining species' contributions may be context-dependent and a direct effect of environmental perturbations (such as logging, Messina et al., 2021) or variation along environmental gradients (like habitat edges, Silva et al., 2021).

The gradients and perturbations that alter community richness and composition also occur in applied ecological contexts. In restoration areas and managed habitats, disturbances are commonly imposed as part of strategies to achieve production or biodiversity goals (Holl, 2020). However, the changes in richness and composition that result from management activities and habitat succession over time, and the consequences these have on ecosystem function, may or may not align with management goals. Because it is often challenging to experimentally manipulate large-scale systems in applied settings, the extent to which species richness changes, compositional shifts, or changes in contribution drive ecosystem function variation is often unclear. A recent derivation of the Price equation (Price, 1970), which describes evolutionary or allele frequency change between generations (Lehtonen et al., 2020), has been applied to separate the effects of species richness, composition, and context-dependent changes (Bannar-Martin et al., 2018; Fox & Kerr, 2012). When applied to perturbations and disturbance such as habitat management, this recent method provides the opportunity to evaluate the alignment of management goals with biodiversity conservation goals.

Here, we studied the functional consequences of species gains and losses in North American tallgrass prairie restorations that are managed with prescribed fire and large native grazer (American bison, *Bison bison*) reintroduction. We used biomass data from dung beetle communities, and energy transfer data from small nonvolant (nonflying) mammal communities to ask how prescribed fire and grazing management impacts ecosystem functioning via changes in species richness and community composition. Dung beetles are important agents of ecosystem functioning in grassland ecosystems through their role in dung decomposition and nutrient cycling, as well as soil turbation and seed dispersal (Nichols et al., 2008). Per capita contributions to dung removal and soil turbation are positively correlated with beetle body size (Horgan, 2001; Larsen et al., 2005; Nichols et al., 2008; Rosenlew & Roslin, 2008; Slade et al., 2007), so beetle mass is a suitable proxy for potential contribution to function. Similarly, small nonvolant mammals (<350 g; Figure 1) are critical components of most terrestrial food webs by serving as prey for larger meso- and top predators and by consuming invertebrates, seeds, and plants. Their central location in food webs and seed predator roles means that they modulate much of the energy flow in food webs, especially in tallgrass prairies (Bricker et al., 2010; French et al., 1976; Schnurr et al., 2004). Importantly, energy assimilation efficiency also varies between small mammal species, so variation in community composition leads to differences in ecosystem energy flow (French et al., 1976). Previous studies of small nonvolant mammals and dung beetles in tallgrass prairies have additionally demonstrated that bison reintroduction and prescribed fire influence the abundance, richness, and composition of these communities (Barber et al., 2019; Burke et al., 2020; Hosler et al., 2021).

To address the question of how management-driven changes in community composition impact the ecosystem function of small nonvolant mammals and dung beetles ("study taxa"), we applied traditional statistical methods and the five-part Price equation (Bannar-Martin et al., 2018; Price, 1970) to test the hypotheses that (1) bison would increase the species richness and the

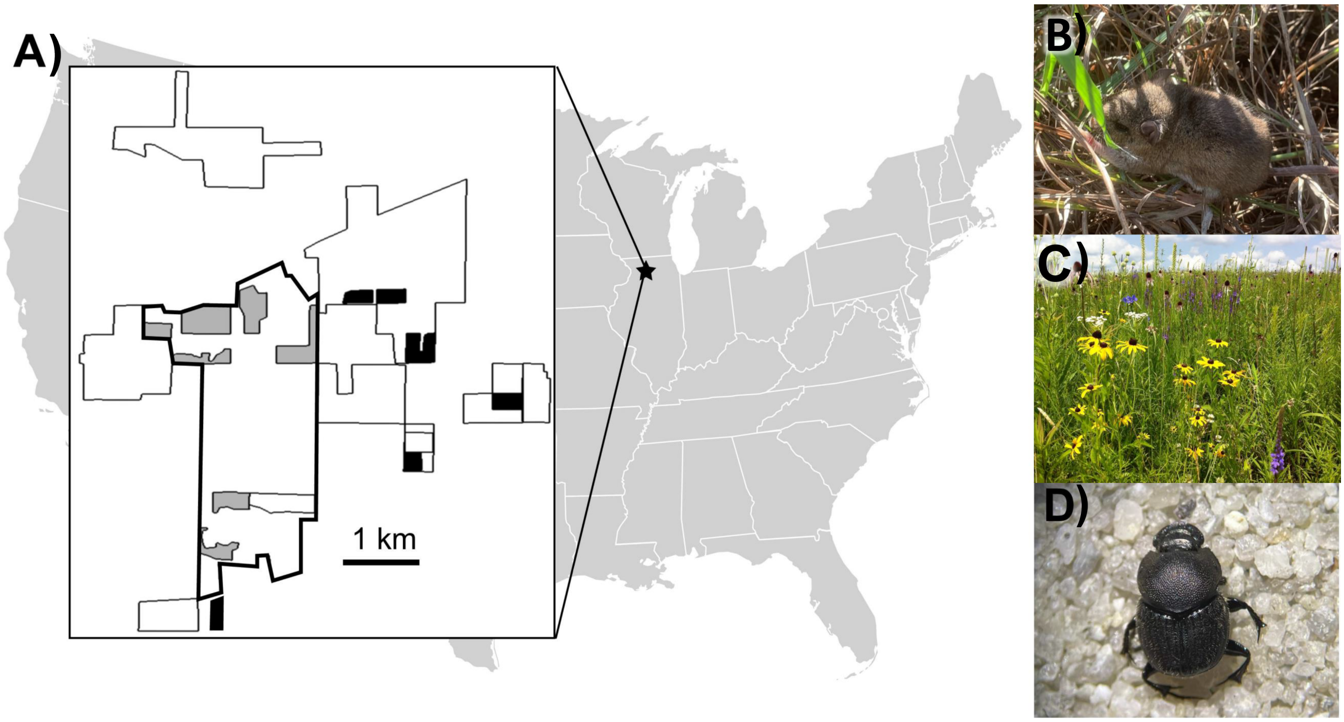

FIGURE 1 (A) Location of Nachusa Grasslands in Illinois, USA, and map of sampled restoration sites. Gray units within the heavy black line represent sites within the bison reintroduction unit. Black sites are bison-free. (B) Deer mouse (*Peromyscus maniculatus*) captured in one of the restorations. (C) Typical restored tallgrass prairie vegetation. (D) *Onthophagus hecate*, the most abundant dung beetle at Nachusa. Photographs taken by Holly P. Jones (B) and Nicholas A. Barber (C, D).

function of both study taxa by increasing habitat and vegetation heterogeneity, and (2) prescribed fire would decrease the species richness and the function of both study taxa by decreasing habitat and vegetation heterogeneity. We predicted that the spatial heterogeneity created by bison through creating wallows and varied vegetation heights (Knapp et al., 1999) would support additional species and increase the function of both study taxa through richness effects. For dung beetles, we also predicted that dung production by bison would boost populations of remaining species and thus their contributions to function comparatively more than small mammal remaining species and function. We predicted that the more homogeneous vegetation created by prescribed fire would reduce species richness and the function of both study taxa, and have little impact on the abundance and functional contributions of remaining species of both taxa.

MATERIALS AND METHODS

This study took place at Nachusa Grasslands (hereafter, Nachusa), *a* ~ 1500 ha natural area in Franklin Grove, Illinois, USA, dominated by restored and remnant (never plowed) tallgrass prairie, mixed with savanna and wetland habitats (Figure 1). Nachusa is owned and managed by The Nature Conservancy; managers there have been restoring new areas from decades of row crop agriculture (corn and soybeans) since the 1980s. Bison were reintroduced to Nachusa starting in 2014, with the current herd totaling around 125 animals. Bison have access to ~600 ha and are free-roaming within this portion of the reserve, which is enclosed by a fence. The only time their location is managed is during a yearly round-up for health checks and vaccination. Prescribed fire is regularly used as a restoration and management tool throughout the site; most burn units (which are 0.40–161 ha in size; median 38 ha) are burned every 1–3 years during the dormant season, based on manager discretion. This results in a patchwork of burned and unburned areas that varies from year to year, such that any given management site may have been burned in the previous dormant season or not.

For this research, we chose 13 prairie restorations to study, which varied in the time since restoration, whether they were burned or not the previous nongrowing season, and whether bison had access to them (Table 1), but otherwise were subject to similar restoration methods and ongoing management, such a chemical control of invasive weeds. Bison reintroduction occurred over 2 years as access was expanded to the full 600 ha, such that some sites switched bison presence status during our study. The sites are 5.6–20.6 ha in area, and were chosen because they had similar sizes and were high-quality restorations, as determined by the managers (i.e., they did not have serious invasive weed populations). The sites are separated from each other by 0.1–5.0 km. Each site contains a 60 m × 60 m research grid from which we obtained the small mammal and dung beetle data. Four of the nonbison sites included one or two additional 60 m × 60 m research grids within fenced mesopredator exclosures to manipulate predation on small mammals. Data from these grids (five total) were excluded from small mammal analyses, but included in dung beetle analyses because they do not influence beetle communities (Hosler et al., 2021).

TABLE 1 Prairie restoration sites (Site Code), with establishment year, bison presence (Y = Yes, N = No), and annual burn history (Y = Yes and N = No for every year from 2015 through 2019).

Site Code	Establishment year	Bison presence	Burned 2015–2019
HF	2013	Y	YYYYN
HPN	2012	Y	YYYNN
LOW	2011	Y	NYNYN
SB	2009	N	NYNNY
SBEE	2009	N	NYNNY
SBEW	2009	N	NYNNY
CCW	2008	N	NNNYY
CCWE	2008	N	NNNYY
HPW	2008	Y	YNNYN
FC	2006	N	NYNYN
CCE	2006	N	YYYNY
CCEE	2006	N	YYYNY
TC	2002	N	NYNYY
TCE	2002	N	NYNYY
HLP	2001	Y	NYNYN
SF	2001	N	YYYNY
WH	1992	Y	NYYNY
MU	1987	Y	NYNYN

Small mammal sampling methods

In each research grid, small mammal traps (Sherman size 7.6 × 8.9 × 22.9 cm and 12.7 × 12.7 × 38.1 cm) were spaced 15 m apart, yielding 25 small mammal trapping sites per grid. Small mammals were trapped every 6 weeks from April through October 2015–2019, yielding four trapping sessions per year. We baited traps with oats and peanut butter as close to dusk as possible and checked them as close to dawn as possible. Traps are closed throughout the day; thus, our target species were nocturnal or crepuscular. Our trap size and sensitivity excluded most shrews, so they are not considered focal species in this study. We instead focus on the granivorous/omnivorous small mammal community. Each caught individual was identified to species, and sex, age, weight, reproductive condition, right-hind foot, body length, and tail length were taken. Each focal individual was marked with a uniquely identifiable tag. We tagged mice and voles with 8 mm Biomark MiniChip Passive Integrated Tags (PIT tags hereafter; Model HPT8, Biomark, Boise, Idaho, USA). Other species were marked with four-digit ear tags. More details on small mammal trapping protocols and procedures can be found in Burke et al. (2020).

To estimate individual metabolic rates, we used basal metabolic rate (BMR) data from Elgar and Harvey (1987) for each study species (Appendix S1: Table S1), defining BMR as the rate at which an endothermic animal at rest expends energy (McNab, 1997). BMR values were transformed to field metabolic rate (FMR) by taking BMR × 2.75, providing an estimate of energy expenditure by free-living animals (Gessaman, 1973; Golley, 1960; Robbins, 2012). Small mammal abundance was the total number of unique captures per trapping session ($n = 20$), this accounted for recaptured individuals between trapping sessions, but not within, given that recaptured individuals are continually contributing to the community (White et al., 2004). Abundance and mass were averaged over a 1-year period for each species in each trapping site ($n = 13$). To calculate small mammal energy transfer, we first performed an allometric linear regression on $\log_{10}$ transformed mass and FMR values (Nagy et al., 1999); the data was then exponentiated to obtain the theoretically predicted ¾ slope and a b_0 of 2.910 ($r^2 = 0.32$). Energy transfer was calculated using the following equation: energy transfer $= 2.91(\text{individual mass})^{0.75}$, for each unique individual captured and then averaged for each site, year, and species.

Dung beetle sampling methods

At each research grid, we sampled dung beetles using 10 pitfall traps per grid in 2017 and 2018. We used two arrays at opposite corners of each research grid containing five traps per array. Traps were plastic cups (13 cm height, 9 cm diameter), which we filled halfway with diluted propylene glycol and topped with wire mesh to prevent capture of nontarget vertebrates. We put about 10 g of fresh bison dung, sourced from the research site, on a plastic fork suspended over the central cup in each array to bait the beetles. We used small platforms to shade baited traps and prevent dung desiccation during trap deployment and refreshed bait every time we collected trap contents. Sampling took place in three sessions in May–June, July, and September 2017 and 2018. The contents of all traps within a site were combined for each year. More details on dung beetle sampling can be found in Hosler et al. (2021).

All beetles were identified as species or morphospecies (24 total species/morphospecies) according to Harpootlian (2001). To measure community biomass, we determined the mean dry mass for each species in each site. In 2017, we dried at 60°C and weighed up to 30 individuals of each species in each site. When less than 30 individuals of a species were captured at a site, we measured all individuals. In 2018, we dried and weighed up to 10 individuals per species per site because we found this was sufficient to estimate mean body mass. Thus, our estimates of community body mass incorporate both inter- and intraspecific variation in mass.

Analysis

All analyses were conducted in the R statistical computing environment, version 4.2.2 or later (R Core Team, 2022). To assess the relationship of prescribed fire and bison grazing management with dung beetles and small mammals and complement the five-part Price analysis we fit linear mixed-effects models using the package lme4 (Bates et al., 2015) and calculated estimated marginal means using the package *emmeans* (Lenth, 2023). Bison and fire were included as fixed factors, and data were aggregated to annual averages per site. Site and year were included in the models as crossed random factors to account for the repeated-measures nature of the sampling design, in which sites were repeatedly sampled, and both the fire and bison status of a site could change from year to year. Fixed factors were tested first as main effects and then an interaction effect was added if the main effects were not significant at the $\alpha = 0.05$ level (Type II Wald's χ^2 test).

To complement traditional statistical approaches we used the "Community Assembly and the Functioning of Ecosystems" (CAFE) approach derived from the five-part Price equation (Fox & Kerr, 2012; Price, 1970). The CAFE approach allows consideration of how community change during community assembly influences changes in ecosystem function (Bannar-Martin et al., 2018). The CAFE approach partitions the functional consequences of species losses and gains to help disentangle species richness and composition change effects on ecosystem functioning. We use the five-part Price Equation Partition to determine whether management disturbances (prescribed fire and bison grazing) influence the ecosystem function of small mammals and beetles, and if function differences can be attributed to species richness or to assembly processes that cause compositional changes through species turnover or differences in abundance.

We used the *priceTools* R package (Kremer, 2018) to apply the five-part Price equation. This method partitions the effects of richness and composition changes on function between a baseline and comparison community. In our case, the baseline community was bison absent or had no prescribed fire in the past year, and comparison communities had bison present or received prescribed fire, respectively. Results describe the effects of species gains and losses in general, the effects of the particular gained or lost species, and the effects of the species occurring in both communities but changing in abundance or contribution to function. For details on the Price Equation Partition under the CAFE approach, see Box 1 for an explanation of the five components, and Figure 2 for a fictional visualization. All possible baseline–comparison community pairs were analyzed. Pairwise community comparisons were made only within years (to account for weather or other interannual differences) at the research grid scale by only comparing sites using sampling data from the same year.

RESULTS

Small mammals

Over the 5 years of mammal sampling, six species of nonvolant small mammals were recorded, with total richness ranging from three to six species per site (mean = 4.4 species/site, SD = 0.8). Energy transfer

BOX 1

The CAFE approach (Bannar-Martin et al., 2018) applies the ecological Price equation, an adaptation of the evolutionary Price equation by Fox and colleagues (Fox, 2006; Fox & Harpole, 2008; Fox & Kerr, 2012) to community–function analyses. For functions that are summative (i.e., total function is the sum of all species in the community), the CAFE approach partitions the differences in function level between two communities into five components based on which species are lost from the first community, gained by the second, or remain present in both communities:

1. Species **richness effect of losses** (Richness Loss), the effect of species losses on function assuming lost species are all "average" in their contribution to function in the initial community. This component represents functional change if species are lost randomly, regardless of their functional contributions.
2. Species **richness effect of gains** (Richness Gain), effects of species gains on function assuming gained species are "average" in their functional contributions in the comparison community. This component represents functional change if species are gained randomly, regardless of their functional contributions.
3. Species **identity effect of losses** (Identity Loss), effects on function of the actual species that are lost. This component will be less (more negative) if the species lost make large contributions to function relative to average species in the initial community, and greater (less negative/closer to zero) if the species make smaller contributions.
4. Species **identity effect of gains** (Identity Gain), effects on function of the actual gained species relative to "average" species in the comparison community. This component will be greater (more positive) if the species gained make large contributions to function relative to average species in the second community, and less (less positive/closer to zero) if the species make smaller contributions.
5. **Context-dependent effect** (Context), effects of changes in functional contribution by species shared between the two communities due to differences in their relative abundance, biomass, or per-capita contribution to function.

Thus the partitioning quantifies the contributions of changes in species richness (Richness Loss, Richness Gain) and changes in composition (Identity Loss, Identity Gain) to differences in levels of function between the two communities. The second pair of terms can identify whether the particular species establishing in or going extinct from a community due to assembly processes tend to be more or less important contributors to function. The Context term describes how changes in species that occur in both the initial and comparison communities influence the difference in function level between the two communities.

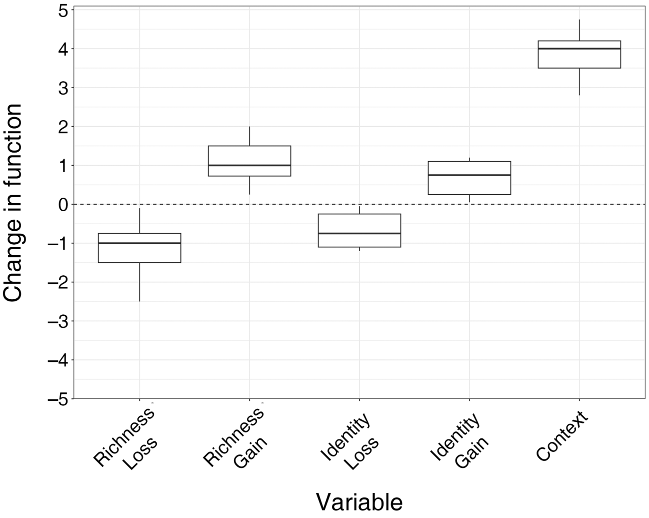

FIGURE 2 Fictional data to graphically represent the five components of the Price Equation Partition as box-and-whisker plots, to aid interpretation of the data presented in this study. The change in function of each community is on the *y*-axis, with each part of the Price Equation Partition on the *x*-axis. In this hypothetical case, Richness Loss and Richness Gain effects are stronger in magnitude than Identity Loss and Identity Gain effects. This means that changes in species, either through loss or gain, are causing a change in ecosystem functioning and species lost/gained are, on average, typical contributors to function for these communities. However, the similar absolute magnitude of Richness Loss and Richness Gain components means that gained species are functionally compensating for the lost species. The (positive) change in function here is driven by the remaining species shared in both fictional communities being compared, the Context effects. Specifically, the remaining species contribute more to functioning, either because they are more abundant, have more biomass, or their per-capita contribution to function is greater.

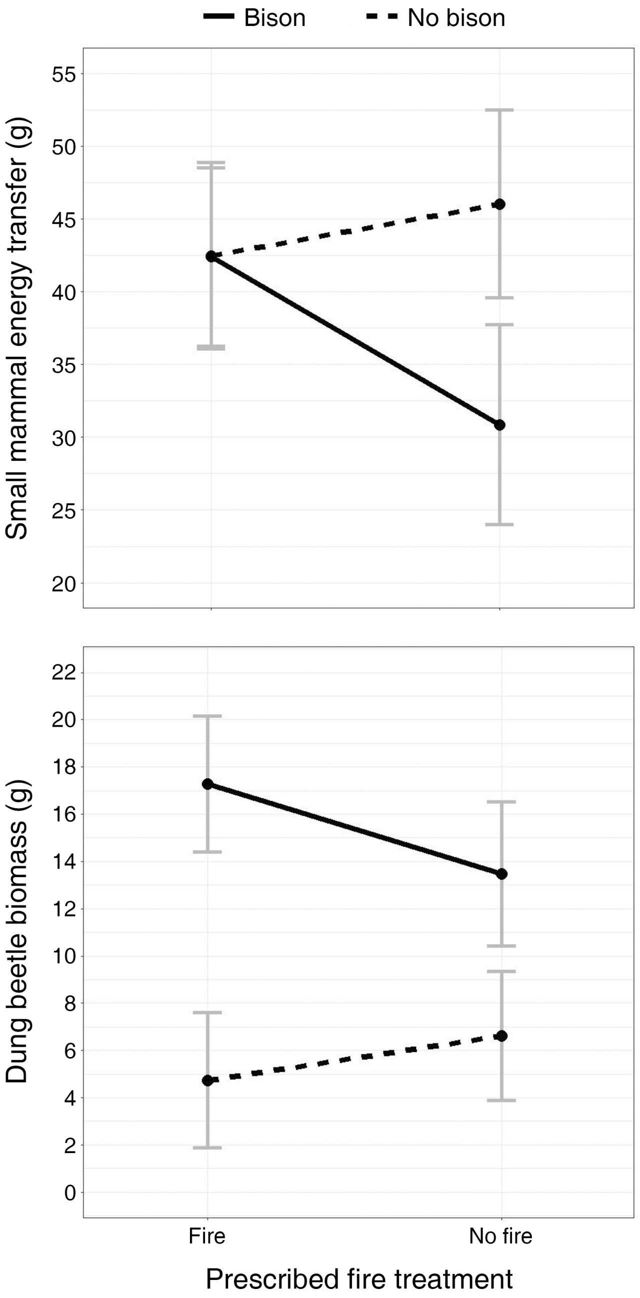

FIGURE 3 Interaction plots of small mammal (top) and dung beetle (bottom) community function under all combinations of bison and fire management. Points represent annual site mean function averaged to one group mean community function, with gray error bars representing group standard errors. Mean function and standard errors are estimated from separate linear mixed-effects models for small mammals and dung beetles and are presented together for interpretation purposes only. Models included site and year as crossed random factors and bison and fire as main and interaction effects. Only the estimated interaction means are visualized here.

ranged from 11.82 to 98.37 g per site overall years (mean = 40.22 g, SD = 20.74). Further details on site richness are available in Appendix S2: Table S1 and in Burke et al. (2020).

Bison reintroduction ($\chi^2 = 2.22$, df = 1, $p = 0.14$), prescribed fires ($\chi^2 = 0.89$, df = 1, $p = 0.34$), and their interaction ($\chi^2 = 3.32$, df = 1, $p = 0.07$) did not affect small nonvolant mammal energy transfer (Figure 3, top panel). The fixed effects in the model explained 7% of the variance in the data, however, the conditional variance (variance explained by random plus fixed effects) explained 31% of the variation in the data. This suggests that variation among sites or years (or both) is playing a stronger role in small mammal community energy transfer than bison or fire management.

Partitioning of the five-part Price equation indicated that the addition of bison had a small overall effect on small mammal communities (Figure 4A,B), with species turnover resulting in a slight average Richness Loss. Ecosystem function impacts were also minor, with a very slight function loss after bison reintroduction, decreasing from 41.6 to 38.4 g as Richness Gain or effects (+10.2 g gain) nearly compensated for Richness Loss or effects (−14.3 g loss). Both identity (Identity Loss and

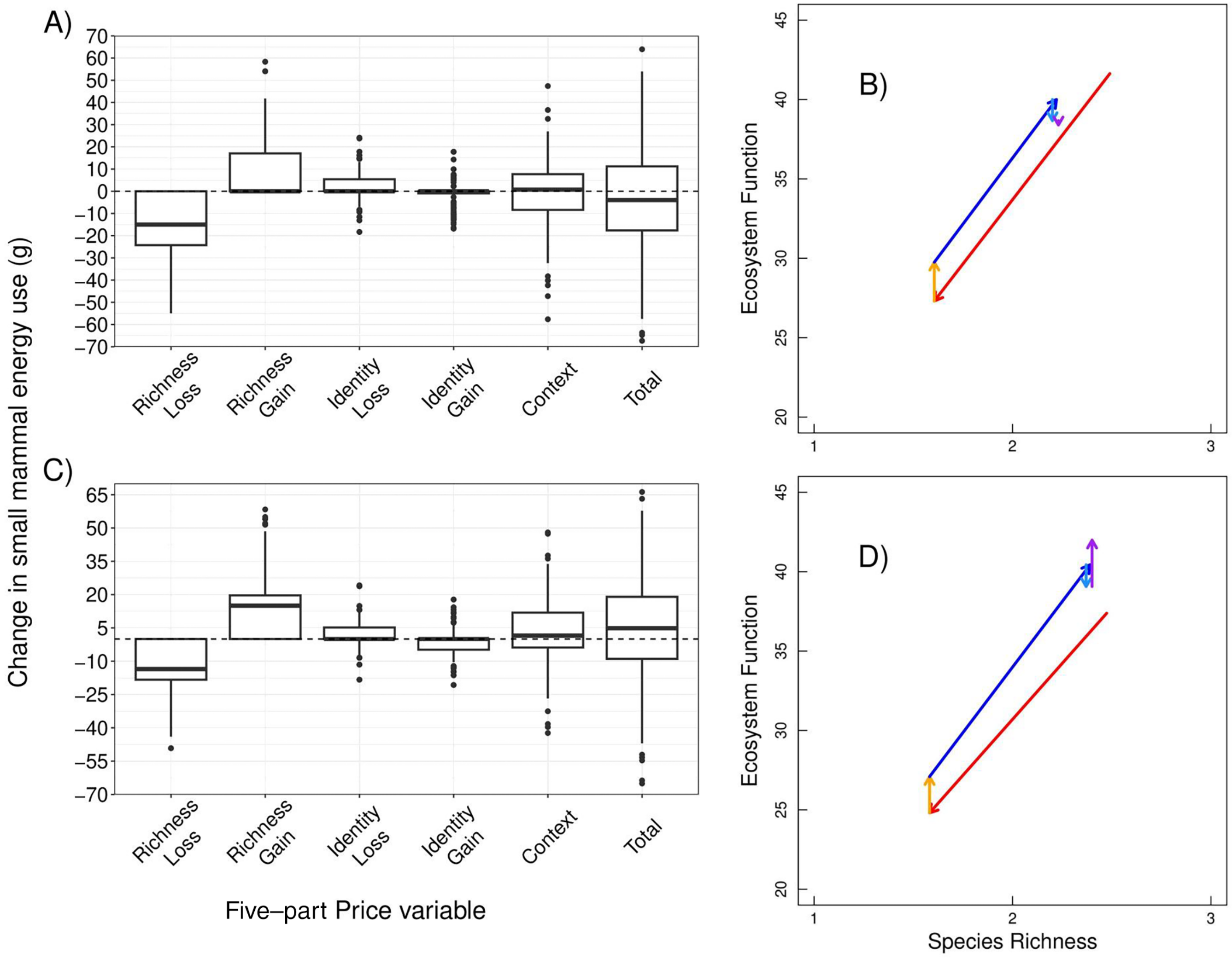

FIGURE 4 Functional response of small mammal communities to variation in restored tallgrass prairie management. Left side boxplot panels depict richness and function responses to bison reintroduction versus bison absent (A), and prescribed fire in the preceding dormant season versus no prescribed fire (C). For both boxplots, "Total" is the sum of the five Price partition vectors, and indicates the overall change in ecosystem function. Right side panels are vector plots of the five-part Price equation configuration, from CAFE analysis of small mammal community and ecosystem function responses to bison reintroduction (B) and prescribed fire (D). Vectors match the corresponding boxplot categories in the left hand panels, except for the "Total" category, and represent Richness Loss effects (red vector, SRE.L), Richness Gain effects (dark blue, SRE.G), Identity Loss (orange, SIE.L), Identity Gain (light blue, SIE.G), and context-dependent effect (purple, CDE). Arrows have been visually separated for interpretation. Ecosystem function is energy flow through the small mammal community For details on interpreting vector plots, see Bannar-Martin et al. (2018). For details on interpreting boxplot panels, see Box 1 and Figure 2.

Identity Gain) and context-dependent (Context) components were small (<2.5 g), so mammal species turnover did not consistently comprise large or small contributors to function, and the remaining species shared between pairs of bison and nonbison sites functioned similarly (Figure 4A, Context).

Prescribed fire had weak effects on small mammal richness based on the partition of the five-part Price equation (Figure 4C,D). The effect of species loss (12.6 g loss) was similar to the effects of species gains (13.3 g gain) in sites that were burned (Figure 4C, Richness effects), but fire impacts on small mammal ecosystem function were slightly positive, increasing from 37.4 to 42.0 g. As with bison introduction, the species turnover resulting from fire did not tend to be species that were particularly large or small contributors to function (Figure 4C; weak average Identity effects <3 g), and species shared between burned and unburned sites functioned similarly (Figure 4C, Context, <3 g increase).

Dung beetles

Over the 2 years of dung beetle sampling, 28 species were recorded, with total richness ranging from 8 to 16 species per site (mean = 11.4 species/site, SD = 2.4).

Biomass ranged from 1.83 to 31.13 g per site over both years (mean = 9.63 g, SD = 7.28). Further details on site richness and biomass are available in Appendix S2: Table S1 and Hosler et al. (2021). There was a significant interaction between bison and fire ($\chi^2 = 5.09$, $df = 1$, $p = 0.02$) on dung beetle biomass (Appendix S3: Table S1). Dung beetle biomass was consistently higher in bison sites ($\chi^2 = 32.53$, $df = 1$, $p < 0.001$), with the highest biomass in bison sites that were recently burned (17.3 ± 2.9 g, vs. 13.5 ± 3.1 g in unburned bison sites, Figure 3, bottom panel). Biomass was lowest in burned sites without bison (4.7 ± 2.9 g, vs. 6.6 ± 2.7 g in unburned bison-absent sites). Additionally, the fixed effects in the model explained 50% of the variation in the data, and the amount of variation explained increased to 76% when including the role of random effects. This suggests management is playing a more dominant role in driving dung beetle biomass than differences between site or years, or both.

Bison increased dung beetle richness with roughly two more species on average in bison sites than nonbison sites (Figure 5A,B), and they increased dung beetle biomass by almost 200% (Figure 5B) from 5.8 to 15.6 g. Bison effects on dung beetle species gains were stronger than the effects of dung beetle species lost (Figure 5A,

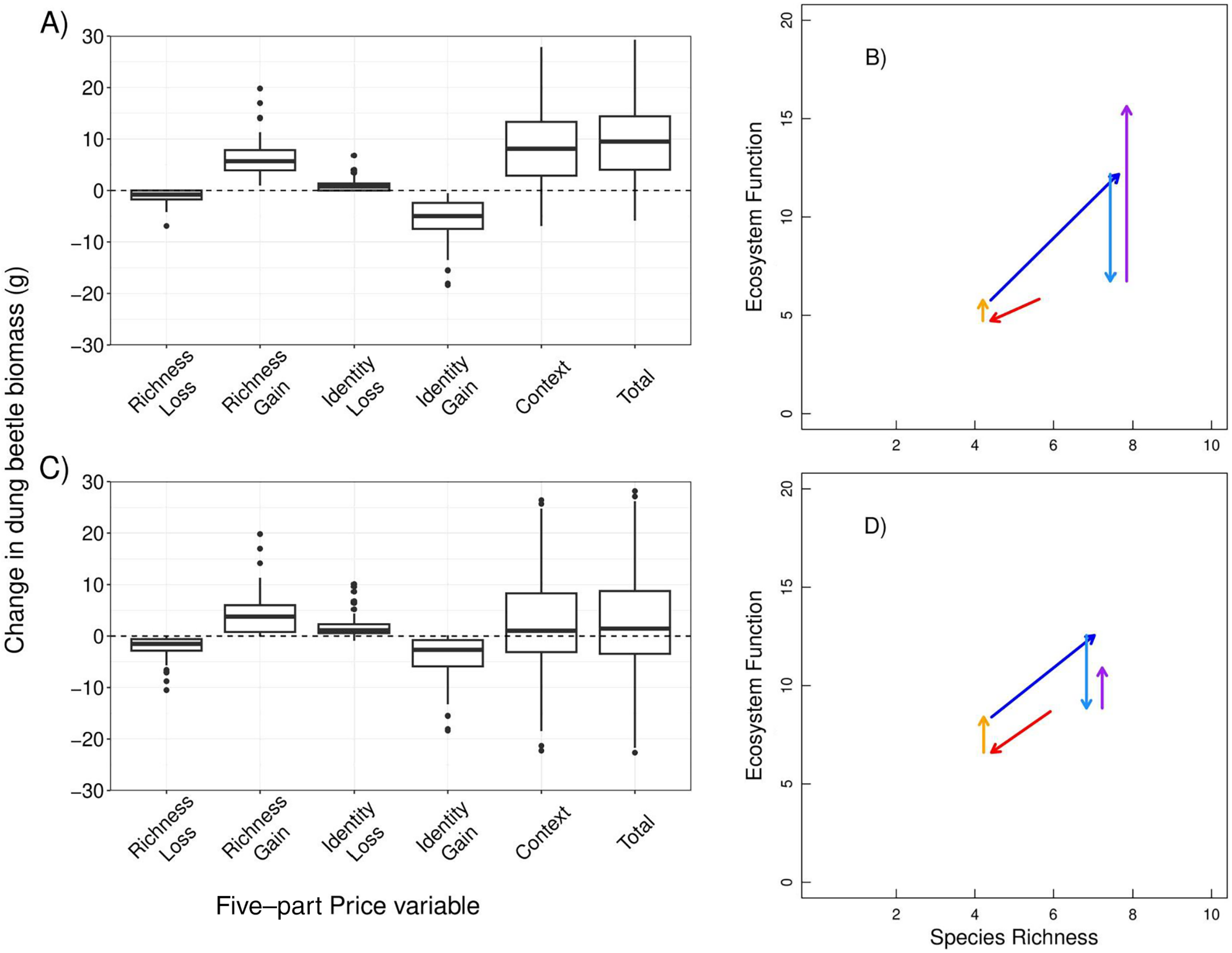

FIGURE 5 Functional response of dung beetle communities to variation in restored tallgrass prairie management. Left side boxplot panels depict richness and function responses to bison reintroduction versus bison absent (A), and prescribed fire in the preceding dormant season versus no prescribed fire (C). For both boxplots, "Total" is the sum of the five Price partition vectors, and indicates the overall change in ecosystem function. Right side panels are vector plots of the five-part Price equation configuration, from CAFE analysis of dung beetle community and ecosystem function responses to bison reintroduction (B) and prescribed fire (D). Vectors match the corresponding boxplot categories in the left hand panels, except for the "Total" category, and represent Richness Loss effects (red vector, SRE.L), Richness Gain effects (dark blue, SRE.G), Identity Loss (orange, SIE.L), Identity Gain (light blue, SIE.G), and context-dependent effect (purple, CDE). Arrows have been visually separated for interpretation. Ecosystem function is dung beetle biomass in grams. For details on interpreting vector plots, see Bannar-Martin et al. (2018). For details on interpreting boxplot panels, see Box 1 and Figure 2.

Richness effects). In other words, if the dung beetle species gained were average contributors to biomass, dung beetle biomass would increase in bison sites. However, both lost and gained dung beetle species tended to be weak contributors to biomass relative to the bison-absent communities from which they were lost, as shown by the Identity Loss and Gain components that are similar in magnitude but opposite in sign to Species Loss and Gain components (loss, −1.1 g vs. 1.0 g; gain, 6.4 g vs. −5.4 g). The main driver of biomass change was a shift in contribution from the remaining species (Figure 5A, Context); in prairie restorations, the remaining species' contributions are strongly positive (8.9 g) and account for essentially all biomass gains after bison introduction.

Prescribed fire had a smaller positive effect on dung beetle richness, resulting in a net increase of about one species (Figure 5C,D), and a roughly 20% increase in biomass (Figure 5D), from 8.7 g to 10.9 g. Species lost from unburned communities (Figure 5C, Identity Loss), and those gained into burned communities (Figure 5C, Identity Gain), were weak contributors to biomass, again illustrated by Identity Loss and Gain components that are similar in magnitude but opposite in sign to Species Loss and Gain components (loss, −2.1 g vs. 1.8 g; gain, 4.2 g vs. −3.7 g). The species shared between unburned and burned sites had a weakly positive effect (2.0 g) on biomass after burning (Figure 5C, Context), which accounts for most of the overall weak positive impact of prescribed fire on biomass.

DISCUSSION

We used the CAFE approach alongside traditional statistical approaches to understand the nuances of ecosystem functioning consequences of species losses and gains following prairie management. We predicted that bison would increase function (energy transfer and biomass) through an increase in species richness for both small mammals and dung beetles, but instead richness effects on function were weak for small mammal and dung beetle communities because richness effects (Richness Loss and Richness Gain components, see Box 1 and Figure 2) were largely offset by similar magnitude identity effects (Identity Loss and Identity Gain components). Dung beetle species shared between bison-reintroduced and bison-free sites yielded more biomass when bison was present, inferred by the positive context-dependent vector (CDE). Although we predicted lower richness and function (biomass and energy transfer) in burned sites, we found weak to moderate changes in richness and a slight increase in both small mammal and dung beetle-driven ecosystem functioning in burned prairies. As we predicted, there were weak or no changes in the abundance or contributions to the functioning of species shared between burned and unburned sites.

These two communities demonstrate the insight that can be gained from the CAFE approach when applied to questions of ecosystem functioning consequences due to community shifts. According to traditional statistical methods, prescribed fire and bison reintroduction had weak overall effects on small mammal function, and modest overall effects on dung beetle function. Incorporating the CAFE approach more specifically suggests the community losses, recolonizations, and context-dependent responses behind those effects, allowing us the opportunity for a more dynamic discussion of how two distinct taxa respond to disturbance-based management and conservation of endangered tallgrass prairies.

Mammal and beetle community responses

Small mammal communities play important roles in tallgrass prairies because the energy transfer for which they are responsible modulates the energy available to upper trophic levels and determines the strength of top-down pressure on seeds and invertebrates through consumption. In general, bison grazing and prescribed fire had small impacts on small mammal richness (on average less than one species lost or gained) and small mammal-driven energy transfer, indicating small mammal communities provide relatively constant levels of energy to support higher trophic levels. Species identity effects were particularly weak, indicating that turnover did not focus on high- or low-contributing species. In our study, granivorous mammal communities generally have low species richness and limited variation in richness, which is typical of other temperate grasslands (Brillhart et al., 1995; Kaufman et al., 2000; Rowe-Rowe & Lowry, 1982; Yarnell et al., 2007). Similar to small mammal communities at other tallgrass prairie sites (Kaufman et al., 2000), small mammal communities at Nachusa are dominated by two species, deer mice (*Peromyscus maniculatus*) and prairie voles (*Microtus ochrogaster*), which made up 79% of captures during this study. Studies have shown species-specific abundance responses of small mammal species present at Nachusa to fire (Brillhart et al., 1995; Burke et al., 2020) and grazing (Burke et al., 2020; Matlack et al., 2001). However, both dominant species are present in all sites, regardless of bison or fire management, yielding small energy transfer consequences for the other, much less common species that are lost and gained with different management strategies. That is, in addition to composition change not being biased according to species functional contribution, those species driving turnover usually made up small proportions of the community, further limiting their impacts on functional change. This is likely to be a common scenario, which we discuss below.

In the case of prescribed fire effects, a small average richness change was associated with a very small average increase in small mammal function (Figure 3, top), so at a whole-community level, fire is not important for function, although it can have significant species-specific effects. This underscores findings that animal diversity in fire-adapted ecosystems can be resilient to prescribed fire, including small mammal diversity in savanna habitats (Durigan et al., 2020), and other fire-dependent ecosystems such as pine forests (Conner et al., 2022). Fire does impact small mammal abundance (Burke et al., 2020; Glass & Eichholz, 2021; Hope et al., 2021), as it reduces thatch, which favors certain species over others, but diversity measures often show resilience to prescribed fire in fire-dependent ecosystems.

Dung beetles play an important role in decomposition, nutrient cycling, and other ecosystem-level processes in grasslands through dung feeding, redistribution, and tunneling behaviors (Nichols et al., 2008). Bison grazing and prescribed fire had stronger effects on dung beetle communities and function than on small mammals: bison reintroduction caused a moderate increase in species richness, from around six to eight species on average, and prescribed fire increased richness from around six to seven species. Both of these actions also increased dung beetle function, with bison reintroduction causing a large increase and fire a smaller effect. Dung beetle community responses to management depended on the environmental driver. Reintroduction of bison primarily affected function through compositional effects rather than richness effects with species richness effects essentially erasing species identity effects. In other words, species turnover comprised species with little overall importance to function, so dung beetles provided a similar level of functioning regardless of the species lost or gained. Instead, differences in function were due almost entirely to the species remaining in a community and changing their functional contributions (Context component). The prescribed fire had relatively weak but positive effects on the function that, again, were mainly due to community-dependent (i.e., context) effects. Although there were moderate richness effects of species joining communities after fire, species identity effects erased these, indicating that the species gained after fire had little impact on function.

The dung beetle species turnover following bison reintroduction comprised species that were generally weak contributors to function. That is, the species gained and lost were rare and/or were small-bodied species. Members of the subfamily Aphodiinae might have driven these patterns. Most Aphodiinae are dung-dwelling beetles that live within and consume dung pats rather than removing and burying portions of a pat-like rolling or tunneling species (Hanski & Cambefort, 2014). The species in this subfamily that occur at our sites tend to be fairly small compared to more abundant species. Although they represented more than 50% of the species recorded, they were only about 5% of the individual beetles sampled (Hosler et al., 2021). Size and abundance distributions differ among dung beetle communities in other habitats, such as tropical rainforests (Slade et al., 2007) and managed pastures (Roslin & Koivunen, 2001). Where Aphodiinae or other small-bodied beetles are a significant proportion of taxonomic diversity but contribute relatively little to total community biomass, these weak richness effects might be common. Turnover among larger-bodied species (such as *Geotrupes opacus* and *Phanaeus vindex*) apparently had little impact on function in relation to management, which is somewhat surprising. Large dung beetle species were more likely to go extinct in secondary and invaded forests (Gardner et al., 2008), and similarly, in a forest fragmentation study, large-bodied dung beetles were the first to go extinct from recently created island fragments (Larsen et al., 2005). It might be expected that the reconnection of fragmented prairie sites would reverse this pattern and encourage recolonization in larger sites, but this was not the case. It is possible that recolonization of some species is not even possible, if potential grassland-dependent species that historically inhabit prairies in the region no longer occur here given the long-term isolation of remnant prairies and the historic extirpation of bison (Tiberg & Floate, 2011).

The notable net increase in function with bison reintroduction was almost entirely due to context-dependent effects. Changes in the abundance of the dominant species (*Onthophagus hecate*, 83% of individuals) are likely behind this pattern. This species, which was collected in every site, was significantly more abundant in sites with reintroduced bison (Hosler et al., 2021) (91% greater abundance in 2017 and 153% in 2018). Although abundance changes are clearly driving context-dependent effects, increased body mass of individual beetles could also contribute, given the easy access to dung resources in bison sites. Mean individual *O. hecate* biomass was 13% greater in bison sites in 2018 (16.1 ± 0.4 mg vs. 14.2 ± 0.2 mg, mean ± 1 SE) but 7% smaller in 2017 (15.3 ± 0.3 mg vs. 14.3 ± 0.4 mg). Further, the increased abundance of *O. hecate* may represent a mechanism by which bison could improve soil health. This is a tunneling species that pulls dung into the ground through tunnels dug below a pat, directly moving organic matter into the soil. The bioturbation of tunneling beetles may also increase soil aeration and water infiltration, possibly counteracting the soil compaction effects of large herbivores (Brown et al., 2010; Manning et al., 2016), but whether these benefits occur specifically with bison is unknown.

The small mammal communities we analyzed had low average richness (mean = 2.4, range 0–5 species), and composition changes in response to bison and fire were due to losses and gains of less than one species on average. Together these may explain some of the limited effects of management on small mammal community function that we documented. Previous applications of the CAFE approach showed strong functional consequences of changes in community composition following the addition or removal of invasive species, or following a significant flooding event (Bannar-Martin et al., 2018). Both of these case studies had greater average richness and more variation in richness among the sampled plots or communities than our small mammal communities. Alternatively, in the current study and in many ecosystems, low small mammal richness and the presence of two strong interactors regardless of management contexts, CAFE analysis helped us show that regardless of how tallgrass prairies are managed, small mammals will provide a certain level of energy to support higher trophic levels. Fox (2006) suggested that species richness effects might only become larger than compositional impacts when 50% or more species are lost from a system. In scenarios with very low mean richness and low variation in richness, species number decreasing (or increasing) by half may be unlikely. The CAFE approach demonstrated compositional impacts on function for dung beetle communities (mean = 6.8, range = 3–13 species), so very high richness per se may not be necessary to result in functional change.

Previous studies applying the CAFE approach have largely studied community changes where dominant species are gained or lost, such as in the case of invasive species establishment or removal (Bannar-Martin et al., 2018; Fox, 2006; Fox & Harpole, 2008). Our study communities, on the other hand, are largely dominated by the same species regardless of the management context studied. For example, *O. hecate* was the most abundant dung beetle species in all sites regardless of site characteristics. If dominant species are particularly important contributors to ecosystem functioning, as predicted by the mass ratio hypothesis (Grime, 1998), then we might have expected to see relatively small richness and identity impacts on functioning and stronger context-dependent effects. This is because these dominant species should usually represent a large proportion of the remaining diversity following environmental change or perturbation, whereas much of the species turnover that drives richness losses and gains is due to relatively rare species (Diamond, 1971). We found evidence of this for dung beetles. An exception would occur if perturbation drives turnover of highly influential keystone species that impact function without being abundant, such as by having very high per-capita functional effects or strong interactions with dominant species. Context-dependent effects were weak or absent in analyses of fire effects. In systems where a single dominant species accounts for a large proportion of abundance or biomass, that species' response to a perturbation may be sufficient for predicting the ecosystem function consequences of the perturbation. In the case of fire, that species may be resistant or resilient to the perturbation imposed by prescribed burns.

Particular environmental contexts may also be an important determinant of ecosystem impacts as revealed by CAFE. In our case, we studied press (bison presence) and pulse (prescribed fire) disturbances. Our results suggest that bison presence may have a stronger impact on contributions to functioning, particularly by the remaining dung beetle community (context-dependent effects), than prescribed fire. Alternatively, prescribed fire had a weak impact on functional changes as a result of species net species gain and context-dependent effects. Importantly, the frequency of prescribed fire (on average every other year) means that the recovery time following this disturbance is rather short at this study site. Longer fire intervals might allow for further richness or compositional changes that amplify community differences between recently burned and unburned, and thus perhaps greater functional impacts of fire (Gordijn et al., 2018; Jonas & Joern, 2007). However, this would be inconsistent with invasive and woody plant management needs in this fire-dependent ecosystem. Applying CAFE to different taxa in other ecosystems to quantify the impacts of disturbances on communities could help determine if press versus pulse disturbances consistently affect function via richness or composition effects, or could be used to gauge the degree of recovery over time following a disturbance, as demonstrated by Bannar-Martin et al. (2018).

Conclusion

We used two animal communities to explore the relationships between species richness, composition, and ecosystem function using the CAFE approach. Habitat management had different impacts on these two ecologically different groups. The low-richness small mammal community with co-dominant species showed weak relationships between richness or composition and function in response to environmental variation, and little response to fire or bison management. But for dung beetles, CAFE helped reveal that some function changes following management, especially bison reintroduction, were due to the responses of a dominant species rather than compositional change. For species groups with sufficient richness variation, CAFE can be a valuable approach for understanding how environmental variation in restored prairies affects their ecological function, providing further nuance when complementing traditional statistical approaches. Paired with sufficient knowledge about focal species, CAFE could assist in the restoration of critically endangered ecosystems like tallgrass prairies by predicting biodiversity change due to necessary management activities or environmental perturbation. Studies utilizing approaches like CAFE and the Price equation partitions have the potential to enhance predictive restoration frameworks, and empower endangered ecosystem conservation amid global change.

AUTHOR CONTRIBUTIONS

Holly P. Jones and Nicholas A. Barber designed the study. All authors except Katharine F. E. Hogan collected the data. Holly P. Jones, Nicholas A. Barber, Katharine F. E. Hogan, and Kirstie Savage analyzed data and wrote the manuscript with input from all other authors.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Hogan, 2023) are available in Zenodo at https://doi.org/10.5281/zenodo.8363960.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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