Ecological Entomology

Ecological Entomology (2020), DOI: 10.1111/een.12950

Management actions shape dung beetle community structure and functional traits in restored tallgrass prairie

SHERYL C. HOSLER,[1,2] HOLLY P. JONES,[2,3] MELISSA NELSON[2] and NICHOLAS A. BARBER[4] [1]Department of Biological Sciences, University of Illinois, Chicago, Illinois, U.S.A., [2]Department of Biological Sciences, Northern Illinois University, DeKalb, Illinois, U.S.A., [3]Institute for the Study of the Environment, Sustainability, and Energy, Northern Illinois University, DeKalb, Illinois, U.S.A. and [4]Department of Biology, San Diego State University, San Diego, California, U.S.A.

Abstract. 1. Ecosystem restoration often focuses on re-establishing species richness and diversity of native organisms. However, effective restoration requires re-establishment of ecosystem functions and processes by all trophic levels. Functional trait descriptions of communities, including decomposer communities, may provide more comprehensive evaluations of restoration activities and management than taxonomic community metrics alone.

2. We examined species and functional trait composition of dung beetle (Coleoptera: Scarabaeidae, Geotrupidae) communities across a 3–31 yearchronosequence of restored prairies, in which sites varied in the presence of re-introduced bison and prescribed fire. We calculated functional diversity metrics and community-weighted mean trait values using behavioural and morphological measurements. We also performed a dung decomposition experiment to measure an ecosystem function driven by these insects.

3. Bison presence doubled beetle abundance and increased richness by 50%. Shannon diversity increased with restoration age, nearly doubling from the youngest to oldest restorations. Functional diversity was unchanged by site characteristics, except functional richness, which was reduced by bison and fire presence. Beetles were, on average, smaller in older restorations, although this pattern was weaker when bison were present.

4. Dung decomposition was unaffected by site characteristics but increased with community weighted mean beetle mass. Dung decomposition was better predicted by mean trait values, suggesting that supporting large-bodied species may be more important than species diversity in settings where maximizing decomposition function is a goal.

5. Restoration managers should consider dung beetle communities and their functional characteristics when making management decisions, particularly where large grazers are a component of management strategies.

Key words. bison, ecosystem function, ecosystem service, grassland, prescribed fire, restoration ecology.

Introduction

Ecosystem restoration and management can remediate degraded landscapes and support their ability to function as intact ecosystems (Dobson *et al.*, 1997, Shackelford *et al.*, 2013). Ecosystem functions (Mouillot *et al.*, 2011) are facilitated by organisms, so functions vary with community composition and the traits of species in a community (Violle *et al.*, 2007; Barragán *et al.*, 2011; Cadotte *et al.*, 2011; Mouillot *et al.*, 2013). Functional traits reflect an organism's niche space and contributions to ecosystem functioning (McGill *et al.*, 2006; Mason

Correspondence: Department of Biological Sciences, University of Illinois at Chicago, 845 W. Taylor Street, Chicago, IL 60607, U.S.A. E-mail: sherylhosler@gmail.com

et al., 2013). Thus, environmental drivers that change the species richness, diversity, or composition of a community may also change ecosystem functions through shifts in community functional trait structure (Slade *et al.*, 2007). However, knowledge of how environmental variation alters ecosystem function via community trait changes in restored habitats is limited, especially for decomposers (Barnes *et al.*, 2014). It is assumed that species recolonizations will re-establish normal ecosystem functions in restorations, but this is rarely tested (Dobson *et al.*, 1997; Young, 2000; Slade *et al.*, 2007).

Community functional trait structure can be described by both the typical trait values in the community and the variation in those traits. If a particular trait value drives an ecosystem function, communities where this value is prevalent will have higher function ('functional identity hypothesis', *sensu* [Gagic *et al.*, 2015]). However, if function is maximised by complementarity of multiple trait values in the community, it will positively correlate with some metric of functional trait diversity ('functional complementarity hypothesis', *sensu* [Gagic *et al.*, 2015; Mason *et al.*, 2005, 2013]). Finally, if species contributions to function are not determined by trait identity or diversity, function may simply correlate with traditional taxonomy-based measures of the community. Ecosystem restorations provide a unique opportunity to test these ideas in a predictive context that can shape future management strategies (Brudvig, 2017). If the environmental variation caused by management actions drives trait variation in communities with subsequent impacts on function, this can be used to identify and prioritise strategies that maximise functional objectives.

In restored North American grasslands, ruminant grazing and prescribed fire are often used as management tools that mimic historical disturbances to maintain diverse native plant communities (Steinauer & Collins, 1996). In addition to plant effects, reintroduction of large grazers to restored landscapes can influence nutrient cycling through dung deposition. This effect is mediated in part by the dung removal and burying functions of dung beetles (Coleoptera: Scarabaeidae and Geotrupidae) (Nichols *et al.*, 2008), which are reliable bioindicators of ecosystem health because they are sensitive to biotic and abiotic changes in ecosystems (Hanski & Cambefort, 1991; Davis *et al.*, 2004; Nichols *et al.*, 2008; Derhé *et al.*, 2016; Moretti *et al.*, 2016). Large herbivores tend to prefer grazing in areas that have been more recently burned (Joern & Laws, 2013), which causes an interactive effect between introduced grazers and prescribed fire in grasslands (Fuhlendorf & Engle, 2001). Shifts in habitat characteristics resulting from this interaction may alter the taxonomic and functional trait composition of dung beetle communities, with consequences for dung decomposition functioning (Rosenlew & Roslin, 2008; Barnes *et al.*, 2014; Correa *et al.*, 2020). Despite the functional importance of these insects, they are poorly studied in North America compared to European grasslands (Negro *et al.*, 2011; Kaartinen *et al.*, 2013) and tropical or subtropical environments (Davis *et al.*, 2004; Barragán *et al.*, 2011). Nichols *et al.* (2008) specifically identified research on dung beetle communities in complex nonagricultural plant communities as an imperative next step in understanding dung beetle ecosystem services.

Here we investigate how two restoration management tools, prescribed fire and American bison (*Bison bison*) reintroduction, affect the dung beetle community structure and function in North American tallgrass prairies. We surveyed dung beetles in sites where bison and fire were present or absent alone and in combination. We quantified the functional trait structure of these communities and measured *in situ* dung decomposition to better understand how restoration management strategies shape communities and ecosystem function and address three research questions: (i) How do restoration management activities shift the taxonomic and functional structure of dung beetle communities? (ii) Do these management activities lead to changes in dung decomposition rates? and (iii) Are these relationships best explained by dung beetle functional trait values, functional trait diversity, or traditional taxonomy-based community metrics? We predicted that prescribed fire and bison would increase abundance and functional diversity by supplementing resources and increasing habitat heterogeneity that allows more species to persist and increases mobility within vegetation (Jameson, 1989; Nunes *et al.*, 2018). We also predicted that these factors would increase dung decomposition, both via increased dung beetle abundance and increased trait diversity, so decomposition would be most strongly correlated with measures of functional trait diversity (Slade *et al.*, 2007).

Materials and methods

The study was conducted at The Nachusa Grasslands (41°53′28″N, 89°20′37″W), a 1500-hectare site that spans Lee and Ogle counties in northwestern Illinois, U.S.A., and is owned and managed by The Nature Conservancy (Figure S1). This site is predominantly remnant and restored tallgrass prairie, with additional areas of oak woodland, oak savannas, and wetlands. The original land holdings for this site were purchased in 1986, and at the time were considered to be heavily degraded tallgrass prairie remnants. In the ensuing decades, TNC staff and volunteers have instituted an active management regimen including reseeding former agricultural land with native plant species, invasive plant removal, prescribed fire rotations, and the reintroduction of large native grazing herbivores.

This research was part of the ReFuGE (Restoring Function in Grassland Ecosystems) project (Barber *et al.*, 2019a,b), in which 15 tallgrass prairie restorations and two remnants were identified for detailed monitoring of organismal groups from multiple trophic levels. Restored sites vary in age (3–31 years since reseeding) and presence of reintroduced bison (*Bison bison*) (Table 1). Bison roam freely within a fenced 800 ha area that includes multiple restored and remnant prairies. In our study, 7 restorations and 1 remnant are within this fenced bison unit. We selected sites to include a range of restoration ages and areas with and without bison. All sites are managed with prescribed fire and burned approximately every 2 years, but not all sites are burned at the same time, creating variation in time since most recent burn. Sites range in size between 5.6 and 20.6 ha in area and separated from each other by 0.1–5.0 km. Nachusa exists within an agricultural matrix, and most sites are adjacent to both row-crops (corn or soybean) and other restored or remnant

Table 1. Sites used for dung beetle sampling and dung decomposition measurements. Age is number of growing seasons since a site was restored at the start of this study (2017), bison indicates the presence or absence of reintroduced bison, and fire indicates if the site received prescribed fire since the previous growing season (i.e. in the spring prior to each study season).

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

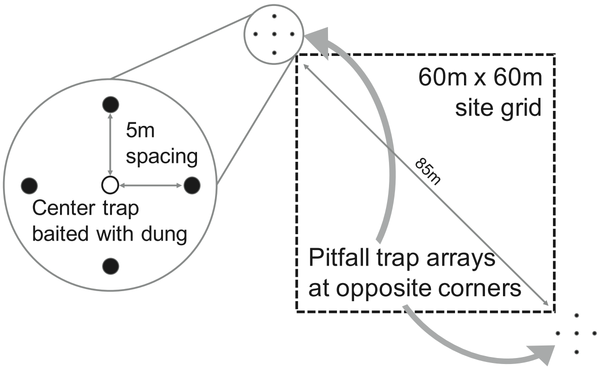

Fig. 1. Pitfall trap array arrangement. Each site had two arrays of five traps each, arranged at opposite corners (85 m apart) of a 60 m × 60 m research grid. Traps in each array were 5 m apart. The center trap in each array was baited with fresh bison dung.

prairie. We also established five mesopredator exclosure fences in four bison-absent sites to study effects of mesopredators on small mammals and their trophic interactions, although these had no effect on dung beetle abundances (data not shown). Each site, including the mesopredator exclosures, contains a 60 m × 60 m research grid, for a total of 20 research sites (18 grids in restorations and 2 in remnants). No cattle or other livestock are present in the study sites.

Dung beetle community and traits

We sampled the dung beetle community at each site using arrays of pitfall traps. Five traps were placed 5 m apart in a cross pattern at each of two opposite corners of each research grid for a total of 10 traps per grid (Fig. 1). The central trap of each cross array was baited with approximately 10 g of fresh bison dung. This baiting arrangement was employed because the pitfall traps were simultaneously in use to sample ground beetles (Carabidae) and other ground-dwelling arthropods. Previous work at the site (Barber *et al.*, 2019a,b) had shown that a single baited pitfall trap attracted large numbers of dung beetles, and this technique captured hundreds to thousands of beetles at each site across each sampling season. Traps were plastic cups (13 cm height, 9 cm diameter) half-filled with dilutedpropylene glycol, capped by wire mesh to prevent capture of nontarget vertebrates, and the bait held on a plastic fork suspended over the cup. Baited traps were shaded by small platforms to reduce desiccation of bait between collection dates, and baits were refreshed every time traps were collected, so every 3–7 days as the weather permitted. Trapping took place in three sessions (May–June, July, and September) in 2017 and 2018 (Table S1). We collected across the vegetation growing season to account for seasonal variation in community composition due to species' emergence and activity phenologies. Dung beetles (Coleoptera: Scarabaeidae (subfamilies Scarabaeinae, Aphodiinae, Bolboceratinae) and Geotrupidae) were identified to genus and/or species using Harpootlian (2001).

We standardised abundance and total community biomass by dividing total number of captured beetles and total community biomass by trapdays (number of pitfall traps open x number of days in session). Total community biomass was determined using each species' abundance and site-specific mean biomass (see below). We calculated rarefied richness and Shannon diversity using ChaoRichness() and ChaoShannon() functions, respectively, in the iNEXT package (Hsieh *et al.*, 2020) of R (R Development Core Team 2016).

Individuals of each species from each research grid were dried at 60 °C for 2 weeks, massed, and measured using a microscope reticle to determine morphological measurements for use in calculating functional traits. We chose a set of traits related to dung beetle activity and mobility that influence their ability to decompose dung (Slade *et al.*, 2007; Barragán *et al.*, 2011; Audino *et al.*, 2014; Barnes *et al.*, 2014; Nervo *et al.*, 2014). We measured dry mass, body shape index (BSI, the ratio of dry mass to pronotum width) from Barnes *et al.* (2014), profemur length and metafemur length (Griffiths *et al.*, 2015, 2016), and behavioural guild (tunneler, roller, or dweller). Femur measurements are functionally relevant traits because they influence mobility and the amount of dung and soil a beetle can move (Griffiths *et al.*, 2015, 2016). The three behavioural guilds differ in how they process dung, with tunnelers digging their nests immediately under a dung pat, rollers provisioning their nests with dung balls rolled a distance away from a dung pat, and dwellers laying their eggs directly in a dung pat (Hanski & Cambefort, 1991; Rosenlew & Roslin, 2008). In 2017, we measured 30 individuals per species per site, and in 2018, we measured 10 individuals per species per site. When less than 30 or 10 individuals were captured in 2017 or 2018, respectively, we measured all individuals for that species/site combination.

Any missing trait values for a species at a particular site were replaced with the average trait value for that species across the sampling sites (<1% of trait values).

Using these site-specific mean trait values, we calculated community-weighted means (CWMs) and four metrics of functional diversity that describe different aspects of trait value variation in a community: functional richness (FRic), functional evenness (FEve), functional divergence (FDiv), and functional dispersion (FDis) (Mason *et al.*, 2005; Laliberte & Legendre, 2010; Mouillot *et al.*, 2013). These calculations used dbFD() in the R package FD (Laliberte *et al.* 2014).

Dung decomposition

To measure ecosystem function, we carried out a dung decomposition assay concurrent with the May/June trapping session in 2018. Fresh bison dung (less than 6 hours old) was collected and frozen to kill arthropods that may have already colonised it. Bison at the study site were given Safe-Guard (fenbendazole) bison cube (Merck Animal Health, Madison, New Jersey) in 2017 to treat roundworms (E. Bach, personal communication), and some bison in the herd have been treated with ivermectin, which has negative effects on dung beetle performance (Verdú *et al.*, 2015). However, the ivermectin treatment is only administered once a year to bison that appear underweight or otherwise unhealthy (fewer than 10 animals per year) (E. Bach, pers. comm.), so we do not anticipate that the presence of ivermectin in the herd would have had strong impacts on the dung beetle population. After thawing, the dung was stirred to homogenise it. Dung was partitioned using large plastic syringes into 200 ml pats on square platforms of 2.54cmhardware cloth (openings large enough to permit beetle access) and massed. Control dung pats were contained within screen cages to prevent access by dung beetles and other dung-associated arthropods (Barber *et al.*, 2019a,b), representing decomposition effects of microbial activity and weathering (Halffter & Matthews, 1966; Slade *et al.*, 2007; Kaartinen *et al.*, 2013; Slade & Roslin, 2016). Five control (caged) and five experimental (uncaged) pats were placed in a 60 m transect (6 m apart) along one edge of each research grid for a total of 10 pats per site. Pats were left in the field for 3 weeks, then retrieved and dried at 60 °C for 1 week to achieve a constant dry weight before massing (Barnes *et al.*, 2014; Nervo *et al.*, 2014; Derhé *et al.*, 2016).

Ten additional pats were made from the same batch of homogenised dung and immediately dried at 60 °C for 1 week to achieve a constant dry weight, then massed. From these, the linear relationship between starting wet and dry mass was calculated ($R^2 = 0.938$). This relationship was then used to calculate the approximate starting dry mass of dung for each of the pats put in the field, after which we calculated the percentage of dry dung mass lost to removal and decomposition (Barnes *et al.*, 2014). One pat was excluded because of an error in recording the initial mass. There was variation in mass changes, including some pats that gained mass during the experiment, possibly due to variation in liquid content of the dung pats or to soil added to the pats by tunnelling dung beetles.

Analysis

We calculated functional diversity metrics (FRic, FEve, FDiv, FDis, and CWMs of continuous variables) using the FD package in R (Laliberte & Legendre, 2010). To determine ifrestoration management activities affect dung beetle communities (question 1), we examined measures of taxonomic community structure (abundance, rarefied richness, Shannon diversity) and functional community structure (FRic, FEve, FDiv, FDis, and CWMs of continuous variables) using linear mixed models. Fixed factors were bison (present or absent), fire (burned in previous dormant season or not), age (number of years since planting), and all two-way interactions between these factors, as well as year (2017 or 2018), and Site was a random factor. Remnants were excluded from community analyses because they do not have an age, but they are presented in figures for reference. Fixed factors were evaluated using likelihood ratio tests, retaining significant interactions and main effects. We conducted sample coverage analyses using the iNEXT package in R (Hsieh *et al.*, 2020) to ensure that our sampling methods adequately represented the dung beetle communities.

To answer if management activities lead to changes in dung decomposition rates (question 1), we first used a *t*-test to determine if there was a difference in mean dry mass lost between pats with and without arthropod access (caged vs. open). Next, we evaluated the effects of bison, fire, age, and two-way interactions on mean dung decomposition of experimental (uncaged) pats in each site using a general linear model, following the same approach as for community analysis above. Finally, to determine if dung decomposition rates are best explained by beetle functional trait values, functional trait diversity, or taxonomy-based metrics (question 3), we compared each community variable to mean dung decomposition. We treated decomposition as the dependent variable and each community variable as an independent variable in a unique general linear model and determined R^2 of the model. We do not evaluate statistical significance of these models to avoid inflated type I error and because our goal is to compare explanatory power of the variables. Community variables were CWMs of each continuous functional trait (dry mass, BSI, profemur length, metafemur length; functional trait values); FRic, FEve, FDiv, and FDis (functional trait diversity); and standardised abundance, rarefied richness, and Shannon diversity (taxonomic metrics).

Results

Dung beetle community

We captured 27 028 individual dung beetles from 24 species across the study sites during the six cumulative trapping sessions of the 2017 and 2018 seasons (Table S2). Sample coverage analyses indicate that our sampling techniques were an adequate representation of the dung beetle community present in our sites (all sites coverage >0.98, Table S3). The number of dung beetles captured per trap day in sites with bison was more than double that of nonbison sites (Table 2, Fig. 2a), and there was a weak interaction with fire such that the bison effect was slightly stronger in burned sites. The presence of bison increased species

Table 2. Effects of restoration site characteristics on dung beetle abundance, richness, and Shannon diversity. Main effects were not tested if included in a significant interaction.

	Total Abundance		Species Richness		Shannon Diversity	
Factor	χ^2	*P*	χ^2	*P*	χ^2	*P*
Year	**24.804**	**<0.001**	1.102	0.294	**10.993**	**<0.001**
Bison	–	–	3.717	0.054	0.072	0.789
Fire	–	–	0.007	0.936	1.006	0.316
Age	1.240	0.265	1.192	0.275	0.921	0.337
Bison × fire	**5.895**	**0.015**	2.047	0.153	2.262	0.133
Bison × age	0.424	0.515	0.168	0.682	0.243	0.622
Fire × age	0.872	0.350	0.364	0.547	1.502	0.220

Boldface is used in these tables to indicate results with p-values of less than 0.05.

richness by almost 50% (Table 2, Fig. 2b). Shannon diversity increased with restoration age, nearly doubling on average from sites <10 years old to sites >25 years old (Table 2, Fig. 2d) and was also influenced by an interaction between bison and fire in which fire increased diversity but only in non-bison sites.

Both bison and prescribed fire reduced dung beetle functional richness, but none of the other functional diversity metrics were related to restoration characteristics (Table 3, Fig. 2c). CWM dry mass and BSI declined in older sites, but this pattern was partly offset by bison presence, which increased both of these morphological traits (Table 4, Fig. 3). Profemur and metafemur mean lengths also declined with restoration age, and there was a weak trend for the decline in profemur length to be stronger in non-bison sites. Behavioural guild was not analysed because tunnelers constituted ~95% of all beetles captured, so there was insufficient variation in this categorical trait.

Dung decomposition

There was no difference in the decomposition of caged (control) and uncaged (experimental) dung pats ($t = 0.101$; $P = 0.921$). Prescribed fire resulted in a marginally significant 25% decrease in uncaged dung decomposition ($\chi^2 = 1251.4$, $P = 0.061$) (Fig. 4a), but other site characteristics (bison presence, site age, and interactions), did not affect decomposition. Decomposition of the experimental (uncaged) dung pats was best explained by CWM dry mass, with greater decomposition in sites with larger CWM dry mass. In general, community functional trait metrics explained decomposition better than taxonomic or functional trait diversity metrics (Table 5, Fig. 4b).

Discussion

Restoration management includes implementing disturbances that can shape community structure and ecosystem functioning, but the importance of insects in these processes is not well understood (Watts & Mason, 2015).Bison have been reintroduced to Nachusa Grasslands and other prairie preserves in an effort to incorporate a historical disturbance back into the prairie system, particularly with the goal of enhancing plant community diversity (Steinauer & Collins, 1996). The reintroduction of this large native grazer and ecosystem engineer increased dung beetle abundance, species richness, and Shannon diversity. However, restoration management had less clear effects on community functional trait structure and the ecosystem function of dung decomposition. CWM trait values of the dung beetle community responded to site characteristics more than trait diversity and better predicted dung decomposition rates.

Dung beetle community

As expected, restored and remnant sites where the bison herd had access had significantly more dung beetles per trap day than non-bison sites. This might be credited both to the availability of fecal resources (Lumaret *et al.*, 1992; Holter, 2016) and to habitat heterogeneity resulting from bison activities in the prairie (Verdú *et al.*, 2007; Tocco *et al.*, 2013). Reintroduced bison provide an ample supply of dung, a historical resource for these insects, and increase environmental heterogeneity through foraging, wallowing, and other behaviours. Correa *et al.* (2020) found that removal of cattle grazing from tropical grasslands had an immediate adverse effect on dung beetle populations, although abundance and species richness did partially recover in the long term. Dung beetles are sensitive to changes in vegetation structure (Andresen, 2005; Verdú *et al.*, 2007; Barragán *et al.*, 2011), and grazing provides heterogeneity in vegetation that can lead to increased biodiversity (Fuhlendorf & Engle, 2001). Whether the increases in dung beetle species richness and Shannon diversity that we document in the presence of bison are due to dung inputs, habitat heterogeneity, or a combination of these causes is not clear. This question could be investigated with carefully designed manipulations of grazing and dung addition or removal.

Prescribed fire, another historical disturbance in tallgrass prairie (Steinauer & Collins, 1996; Fuhlendorf & Engle, 2001; Alstad *et al.*, 2016), interacted with bison presence to influence dung beetle abundance and Shannon diversity. As with grazing alone, burning patches of prairie creates a heterogeneous landscape (Alstad *et al.*, 2016) that may appeal to a broader diversity of dung beetles. Previous studies indicate that dung beetles and other highly mobile arthropods may prefer open areas like those created after fire (Hartley *et al.*, 2007; Louzada *et al.*, 2010). In this study, a community-wide preference for these disturbed areas may have recruited more individuals through greater colonization or higher survival. Additionally,

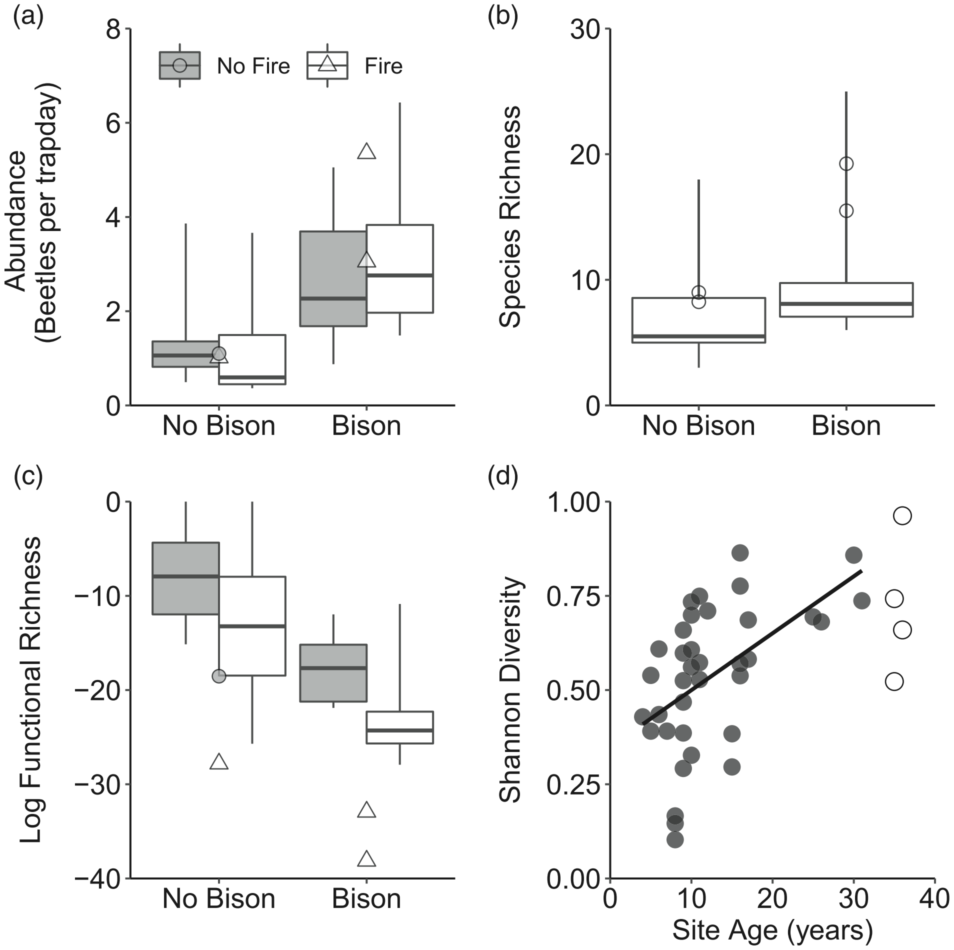

Fig. 2. Effects of bison presence, prescribed fire, and restoration age on dung beetle community (a) abundance (number of beetles captured per trap day), (b) rarefied species richness, (c) functional richness (log-transformed), and (d) Shannon diversity. In (d), open circles indicate remnant prairie sites.

Table 3. Effects of restoration site characteristics on dung beetle community functional diversity metrics.

	Functional Richness		Functional Evenness		Functional Divergence		Functional Dispersion	
Factor	χ^2	*P*	χ^2	*P*	χ^2	*P*	χ^2	*P*
Year	**9.480**	**0.002**	0.002	0.965	**9.387**	**0.002**	**11.206**	**<0.001**
Bison	**16.327**	**<0.001**	0.325	0.568	3.229	0.072	2.451	0.117
Fire	**6.476**	**0.011**	<0.001	0.985	0.158	0.691	1.201	0.273
Age	0.116	0.734	0.282	0.596	0.048	0.827	0.916	0.339
Bison × fire	0.073	0.787	0.482	0.487	0.198	0.657	0.827	0.363
Bison × age	<0.001	0.994	0.272	0.602	0.278	0.598	1.397	0.237
Fire × age	1.724	0.189	2.155	0.142	0.110	0.74	0.824	0.364

Boldface is used in these tables to indicate results with p-values of less than 0.05.

bison demonstrate pyric herbivory (Fuhlendorf *et al.*, 2009), in which bison preferentially graze in recently burned areas, leading to an increase in dung resources deposited in those areas. Both of these scenarios may have contributed to the high beetle abundances we documented in sites with both bison and fire. Although recent fire severely reduces saprophagic arthropod abundances in the short-term and slows long-term population recovery (Moretti *et al.*, 2006), species that take refuge underground or in materials protected from fire may escape the negative effects of burning (Swengel, 2001; Nunes *et al.*, 2018). In situations where unburned prairie occurs adjacent to a burned area, beetles also might disperse into the burned area, supplementing populations. Sites lacking bison and fire tended to have lower Shannon diversity, supporting the idea that the absence

Table 4. Effects of restoration site characteristics on dung beetle community weighted mean functional traits.

	CWM Dry mass		CWM BSI		CWM Profemur Length		CWM Metafemur Length	
	χ^2	*P*	χ^2	*P*	χ^2	*P*	χ^2	*P*
Year	**12.616**	**<0.001**	**6.692**	**0.010**	**27.578**	**<0.001**	**19.673**	**<0.001**
Bison	**9.490**	**0.002**	3.289	0.070	0.954	0.329	0.701	0.403
Fire	0.279	0.597	0.008	0.929	0.065	0.798	0.429	0.512
Age	**5.456**	**0.020**	3.768	0.052	**14.317**	**<0.001**	**9.045**	**0.003**
Bison × fire	0.315	0.575	0.56	0.454	1.329	0.249	2.748	0.097
Bison × age	0.516	0.473	0.121	0.728	2.823	0.093	2.579	0.108
Fire × age	0.335	0.563	0.679	0.410	0.278	0.598	0.360	0.549

Boldface is used in these tables to indicate results with p-values of less than 0.05.

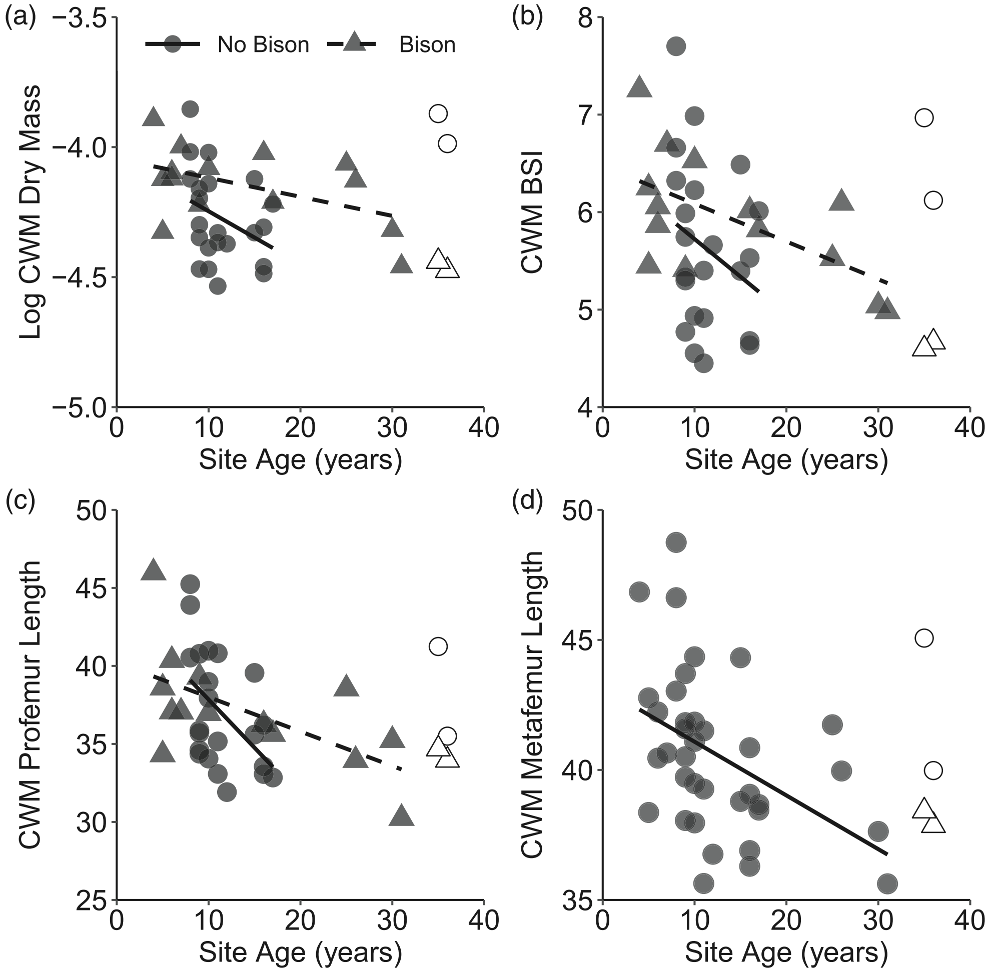

Fig. 3. Community weighted mean (CWM) values of dung beetle traits. (a) mean dry mass, log-transformed, (b) mean body shape index, (c) mean profemur length, (d) mean metafemur length. Open symbols indicate remnant prairie sites.

of disturbances leads to a homogeneous habitat with lower biodiversity.

Remnant sites are often held up as the goal posts for restoration (Jones *et al.*, 2018). Therefore, we expected to see an effect of site age on the abundance and diversity of the dung beetle community, with older restored sites more closely resembling the remnants than younger sites (Davis *et al.*, 2002; Audino *et al.*, 2014). This was somewhat true for Shannon diversity, with older restored sites nearing the high taxonomic diversity values of the remnant sites, although there was considerable variation in diversity among younger restored sites. This could be due in part to year effects on the trajectories of restorations (Groves & Brudvig, 2019), in which the initial conditions under which restorations are established shape later restoration outcomes.

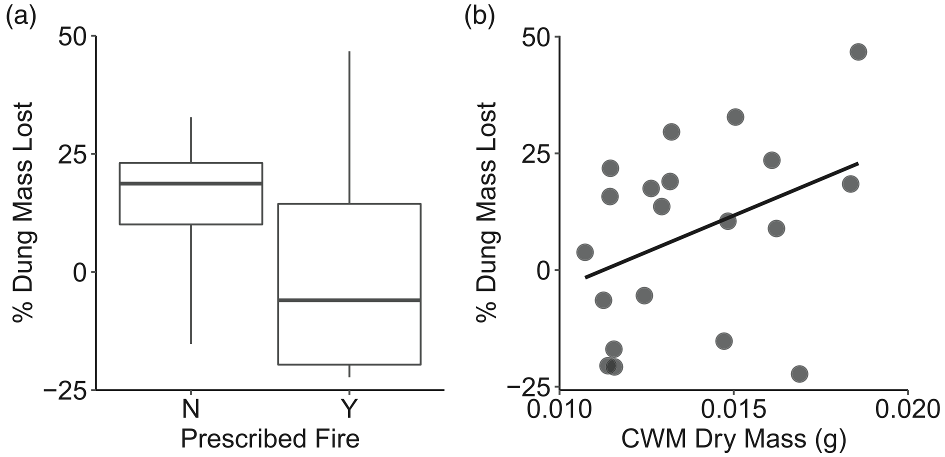

Fig. 4. Dung decomposition, measured as percent mass lost, tended to be reduced in sites with prescribed fire compared to unburned sites. Decomposition also tended to increase with dung beetle CWM dry mass.

Table 5. Relationships between dung beetle community taxonomic, functional trait value, and functional trait diversity metrics on experimental dung decomposition. Each line is an individual general linear model, ranked by R^2.

Community metric	Metric type	R^2
CWM Dry Mass	Functional trait value	0.150
CWM Metafemur Length	Functional trait value	0.100
Shannon Diversity	Taxonomic	0.096
CWM BSI	Functional trait value	0.082
CWM Profemur Length	Functional trait value	0.069
FRic	Functional trait diversity	0.059
Species Richness	Taxonomic	0.030
Abundance	Taxonomic	0.026
FEve	Functional trait diversity	0.025
FDiv	Functional trait diversity	0.024
FDis	Functional trait diversity	0.015

Restoration projects often treat remnants as references, with the goal of recreating remnants' biotic and abiotic conditions in restored sites (Jones *et al.*, 2018). However, tallgrass praire remnants' management history and site characteristics may make them unsuitable for this role (Barber *et al.*, 2017a,b): many tallgrass prairie remnants, including those at our study site, exist because they are situated on hillsides with rocky soils and thus were never plowed for row-crop agriculture. Conversely, most of the restored sites in this study were reconstructed on relatively flat, former row-crop fields. Therefore, the slope aspect and soil composition of the remnants may result in plant and consumer communities that differ from nearby restorations. Nonetheless, although diversity was influenced by bison and fire, the oldest restorations supported higher taxonomic diversity, a promising sign for restoration projects with a goal of supporting multitrophic biodiversity (Fraser *et al.*, 2015). Older sites with more established plant communities and soil structure may facilitate increases in dung beetle diversity by facilitating mobility through the habitat and providing better breeding conditions for a broader range of species (Correa *et al.*, 2020).

Functional traits

We quantified dung beetle functional traits in two ways, as metrics of functional diversity that describe the variation in traits at each site and as CWMs that describe average values for each trait at each site. Mean trait values showed distinct relationships with restoration age and bison presence. All four morphological measures declined in older restorations so that, on average, dung beetles were smaller, narrower, and shorter-legged than in young restorations. However, reintroduced bison partly offset these trends, increasing mean dry mass and BSI in sites with grazing and other bison disturbances. We used site-specific measurements to incorporate intraspecific variation into calculations of trait metrics, so these declines in average beetle size are likely due not just to the inclusion of smaller species that increased taxonomic richness in bison sites and Shannon diversity in older sites, but also to smaller size of the dominant species (*Onthophagus hecate* and *Onthophagus knausi*) due to plasticity or selection favouring smaller-bodied individuals.

In contrast to trait means, restoration management and characteristics had no effect on most measures of functional diversity. Only FRic was affected by management, with significant reductions due to both bison reintroduction and prescribed fire. FRic indicates the range of trait values represented in a community and is often correlated with species richness (Mason *et al.*, 2005; Mason *et al.*, 2013). Unlike the other measures of functional diversity we investigated (functional evenness, divergence, and dispersion), it does not incorporate relative abundance of beetles with those trait values. Thus even though FRic varied with bison and fire, the other functional diversity measures did not, perhaps because the communities were numerically dominated by one or two common species, *O. hecate* Panzer (1794) and *O. knausi* Brown (1927), or perhaps because these species provided functional redundancy for other species within the community. The addition or subtraction of other species could shift species and functional richness, but their rarity means they have little impact on functional evenness, divergence, or dispersion. Furthermore, the impact of bison on FRic was opposite to the effect on species richness: bison presence increased species richness but, along with fire, decreased FRic. These patterns could arise if the rare species colonizing or persisting in grazed or burned sites have similar trait values to dominant species, or if those in ungrazed and unburned restorations had more extreme trait values, expanding the volume of the community in multivariate trait space and increasing FRic. For example, we only found *Onthophagus orpheus* Panzer (1794) and *Onthophagus taurus* Schreber (1759) in site with fire and/or bison present, and these species are similar to the two *Onthophagus* species that dominated abundances. Disturbances like grazing and fire might impose environmental filtering, limiting the trait values that can persist in these communities and reducing FRic.

Several studies have indicated that FRic increases with site age (Audino *et al.*, 2014; Derhé *et al.*, 2016), but we found no effect of restoration age on functional diversity. Taxonomic diversity increased with age, but functional trait variation was similar in young and old sites. Thus, from a trait variation perspective, dung beetle communities may assemble quickly, with later variation mostly driven by disturbances.

Dung decomposition

We measured dung decomposition rates in restored and remnant prairie to determine if decomposition varied with site characteristics and if it was related to dung beetle community structure. Site characteristics did not influence dung decomposition rates, although there was a marginally significant trend for reduced decomposition in sites that received prescribed fire in the previous dormant season. When we compared decomposition to the beetle community, decomposition was best predicted by CWM size measurements, with greater decomposition rates in sites with larger average beetle body size. Mesocosm experiments that manipulate dung beetle composition have also shown that larger body size maximises dung removal rates (Kaartinen *et al.*, 2013; Nervo *et al.*, 2014; Slade & Roslin, 2016). These results support the ‘functional identity hypothesis’ that function levels are determined by dominant trait values in the community of organisms driving that function, rather than by trait diversity of that community (Gagic *et al.*, 2015). Surprisingly, even though total dung beetle abundance varied among sites, this was not a strong predictor of function. These results partially agree with a study of dung beetles in Australian tropical forests, in which functional diversity was a better predictor of dung removal than abundance or taxonomic richness (Derhé *et al.*, 2016), although that study did not examine the relationship between dung removal and trait CWMs. Nonetheless, the site characteristics that influenced body size in our prairie restorations (age and bison presence) were not strong enough to drive detectable direct effects on variation in dung decomposition. This suggests that the links between restoration management, dung beetle community structure, and dung decomposition rates are generally weak in this ecosystem.

Decomposition rates were quite variable, both among and within sites, underscoring several challenges in measuring this ecosystem function. We assumed that the majority of the dung decomposition and removal would be performed by the dung beetles in the prairie community (Kaartinen *et al.*, 2013; Nervo *et al.*, 2014; Manning *et al.*, 2016). However, dung pats exposed to arthropod activity in our study demonstrated such a broad variation in mass loss that we did not detect a significant difference between the caged and uncaged pats. This variation may be due to characteristics of the dung used in the study, as well as to the composition of the dung beetle community in these sites. Fresh bison dung collected in the spring and summer has a high liquid content, and evaporation during experimental dung processing may have added variation to measurements of pre-decomposition dung and to control pats used to estimate starting dry mass. Furthermore, the dung beetle community in our system is composed primarily of small-bodied dweller species and small-, medium-, and large-bodied tunneler species (only one roller species was recorded).Some tunneler beetles may mix soil into dung while feeding or gathering dung (Arellano, 2016).This addition of soil may have contributed to those experimental dung pats that were calculated to have gained mass at the end of the assay. Other invertebrates also contribute to dung decomposition, including earthworms (Annelida), flies (Diptera), and carrion beetles (Coleoptera: Silphidae), and variation in their abundance or guild composition might be important determinants of decomposition rates (Finn & Gittings, 2003).

Conclusions

Combining traditional taxonomic community descriptors with functional trait measurements provided a more comprehensive picture of dung beetle communities under active land management strategies in restored tallgrass prairie. Beetle communities change over time as restorations age, but they are further shaped by prescribed fire and the reintroduction of bison. These management activities impose regular disturbances and, together, likely increase heterogeneity that supports insect biodiversity. Supporting ecosystem function is also a goal of restoration, but here the relationships between management, dung beetle community structure, and dung decomposition function were unclear. In cases where a single functional guild like dung beetles is numerically dominated by only a few species, or when an ecosystem function is facilitated by a broad array of organismal groups, the relationship between functional diversity of one guild and ecosystem function might be expected to be weak. Additional studies that combine functional trait measurements with assessments of function levels, encompassing a broader range of taxonomic groups, will help clarify the direct and indirect effects of habitat restoration and management on ecosystem processes in tallgrass prairie.

Acknowledgements

We would like to acknowledge The Nature Conservancy and the staff, especially B. Kleimann, E. Bach, and C. Considine, and volunteers at Nachusa Grasslands. Their tireless work and dedication to doing quality ecosystem restoration has been inspiring, and their enthusiasm for our research has meant so much. We are also grateful to all of the undergraduate research assistants who worked on portions of this project. This work was funded by NSF-DEB 1647502, Friends of Nachusa Grasslands, Prairie Biotic, Inc., and Northern Illinois University. Any opinions, findings, and conclusions or recommendations expressed in this material are those of the authors and do not necessarily reflect the views of the National Science Foundation. The authors declare no conflicts of interest.

Author contribution

All authors designed the project. SCH and MN collected the data. SCH and NAB performed analysis and wrote the manuscript. All authors contributed to editing the manuscript.

Data availability statement

The data that support the findings of this study are openly available in Dryad at https://doi.org/10.5061/dryad.0p2ngf1z6.

Supporting Information

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

Table S1. Trapping dates in the three trapping sessions during 2017 and 2018 with total number of trap days in parentheses.

Table S2. Dung beetle species identified in this study.

Table S3. Observed Sample Coverage results for each site in both years.

Figure S1. A map of the Nachusa Grasslands property with areas of interest highlighted in color blocks. Study sites are indicated by the small squares.

References

Alstad, A.O., Damschen, E.I., Givnish, T.J., Harrington, J.A., Leach, M.K., Rogers, D.A. *et al.* (2016) The pace of plant community change is accelerating in remnant prairies. *Science Advances*, **2**, 1–6.

Andresen, E. (2005) Effects of season and vegetation type on community organization of dung beetles in a tropical dry forest 1. *Biotropica*, **37**, 291–300.

Arellano, L. (2016) A novel method for measuring dung removal by tunneler dung beetles (Coleoptera: *Scarabaeidae*: *Scarabaeinae*) in pastures. *The Coleopterists Bulletin*, **70**, 185–188.

Audino, L.D., Louzada, J. & Comita, L. (2014) Dung beetles as indicators of tropical forest restoration success: is it possible to recover species and functional diversity? *Biological Conservation*, **169**, 248–257.

Barber, N.A., Jones, H.P., Duvall, M.R., Wysocki, W.P., Hansen, M.J. & Gibson, D.J. (2017a) Phylogenetic diversity is maintained despite richness losses over time in restored tallgrass prairie plant communities. *Journal of Applied Ecology*, **54**, 137–144.

Barber, N.A., Lamagdeleine-Dent, K.A., Willand, J.E., Jones, H.P. & McCravy, K.W. (2017b) Species and functional trait re-assembly of ground beetle communities in restored grasslands. *Biodiversity and Conservation*, **26**, 3481–3498.

Barber, N.A., Hosler, S.C., Whiston, P. & Jones, H.P. (2019a) Initial responses of dung beetle communities to bison reintroduction in restored and remnant Tallgrass prairie. *Natural Areas Journal*, **39**, 420–428.

Barber, N.A., Farrell, A.K., Blackburn, R.C., Bauer, J.T., Groves, A.M., Brudvig, L.A. *et al.* (2019b) Grassland restoration characteristics influence phylogenetic and taxonomic structure of plant communities and suggest assembly mechanisms. *Journal of Ecology*, **107**, 2105–2120.

Barnes, A.D., Emberson, R.M., Krell, F.T. & Didham, R.K. (2014) The role of species traits in mediating functional recovery during matrix restoration. *PLoS One*, **9**, 1–19.

Barragán, F., Moreno, C., Escobar, F., Halffter, G. & Navarrete, D. (2011) Negative impacts of human land use on dung beetle functional diversity. *PLoS One*, **6**, 1–8.

Brudvig, L.A. (2017) Toward prediction in the restoration of biodiversity. *Journal of Applied Ecology*, **54**, 1013–1017.

Cadotte, M.W., Carscadden, K. & Mirotchnick, N. (2011) Beyond species: functional diversity and the maintenance of ecological processes and services. *Journal of Applied Ecology*, **48**, 1079–1087.

Correa, C.M.A., Audino, L.D., Holdbrook, R., Braga, R.F., Menéndez, R. & Louzada, J. (2020) Successional trajectory of dung beetle communities in a tropical grassy ecosystem after livestock grazing removal. *Biodiversity and Conservation*, **29**, 2311–2328.

Davis, A.L.V., Van Aarde, R.J., Scholtz, C.H. & Delport, J.H. (2002) Increasing representation of localized dung beetles across a chronosequence of regenerating vegetation and natural dune forest in South Africa. *Global Ecology and Biogeography*, **11**, 191–209.

Davis, A.L.V., Scholtz, C.H., Dooley, P.W., Bham, N. & Kryger, U. (2004) *Scarabaeine* dung beetles as indicators of biodiversity, habitat transformation and pest control chemicals in agro-ecosystems. *South African Journal of Science*, **100**, 415–424.

Derhé, M.A., Murphy, H., Monteith, G. & Menéndez, R. (2016) Measuring the success of reforestation for restoring biodiversity and ecosystem functioning. *Journal of Applied Ecology*, **53**, 1714–1724.

Dobson, A.P., Bradshaw, A.D. & Baker, A.J.M. (1997) Hopes for the future: restoration ecology and conservation biology. *Science*, **277**, 515–522.

Finn, J.A. & Gittings, T. (2003) A review of competition in north temperate dung beetle communities. *Ecological Entomology*, **28**, 1–13.

Fraser, L.H., Harrower, W.L., Garris, H.W., Davidson, S., Hebert, P.D.N., Howie, R. *et al.* (2015) A call for applying trophic structure in ecological restoration. *Restoration Ecology*, **23**, 503–507.

Fuhlendorf, S.L. & Engle, D.M. (2001) Restoring heterogeneity on rangelands: ecosystem management based on evolutionary grazing patterns. *Bioscience*, **51**, 625–632.

Fuhlendorf, S.D., Engle, D.M., Kerby, J. & Hamilton, R. (2009) Pyric herbivory: rewilding landscapes through the recoupling of fire and grazing. *Conservation Biology*, **23**, 588–598.

Gagic, V., Bartomeus, I., Jonsson, T., Taylor, A., Winqvist, C., Fischer, C. *et al.* (2015) Functional identity and diversity of animals predict ecosystem functioning better than species-based indices. *Proceedings of the Royal Society B: Biological Sciences*, **282**, 1–8.

Griffiths, H.M., Louzada, J., Bardgett, R.D., Beiroz, W., França, F., Tregidgo, D. *et al.* (2015) Biodiversity and environmental context predict dung beetle-mediated seed dispersal in a tropical forest field experiment. *Ecology*, **96**, 1607–1619.

Griffiths, H.M., Louzada, J., Bardgett, R.D. & Barlow, J. (2016) Assessing the importance of intraspecific variability in dung beetle functional traits. *PLoS One*, **11**, 1–14.

Groves, A.M. & Brudvig, L.A. (2019) Inter-annual variation in precipitation and other planting conditions impacts seedling establishment in sown plant communities. *Restoration Ecology*, **27**, 128–137.

Halffter, G. & Matthews, E.G. (1966) The natural history of dung beetles of the subfamily *Scarabaeinae* (Coleoptera, *Scarabaeidae*). *Folia Entomologia Mexicana*, **12**, 1–312.

Hanski, I. & Cambefort, Y. (1991) *Dung Beetle Ecology*. Princeton University Press, Princeton, New Jersey.

Harpootlian, P.J. (2001) Scarab beetles (Coleoptera: *Scarabaeidae*) of South Carolina. (ed. by A. G. Wheeler). Clemson University Public Service Publishing, Clemson, South Carolina.

Hartley, M.K., Rogers, W.E. & Siemann, E. (2007) Responses of prairie arthropod communities to fire and fertiliser: balancing plant and arthropod conservation. *The American Midland Naturalist*, **157**, 92–105.

Holter, P. (2016) Herbivore dung as food for dung beetles: elementary coprology for entomologists. *Ecological Entomology*, **41**, 367–377.

Hsieh, T.C., Ma, K.H., Chao, A. (2020). *iNEXT: Interpolation and Extrapolation for Species Diversity*. R package version 2.0.20. URL http://chao.stat.nthu.edu.tw/wordpress/software_download/

Jameson, M.L. (1989) Diversity of Coprophagous Scarabaeidae (Coleoptera) in grazed versus Ungrazed Sandhills Prairie in Western Nebraska. *Transactions of the Nebraska Academy of Sciences*, **17**, 29–35.

Joern, A. & Laws, A.N. (2013) Ecological mechanisms underlying arthropod species diversity in grasslands. *Annual Review of Entomology*, **58**, 19–36.

Jones, H.P., Jones, P.C., Barbier, E.B., Blackburn, R.C., Rey Benayas, J.M., Holl, K.D. *et al.* (2018) Restoration and repair of Earth's damaged ecosystems. *Proceedings of the Royal Society B: Biological Sciences*, **285**, 1–8.

Kaartinen, R., Hardwick, B. & Roslin, T. (2013) Using citizen scientists to measure an ecosystem service nationwide. *Ecology*, **94**, 2645–2652.

Laliberte, E. & Legendre, P. (2010) A distance-based framework for measuring functional diversity from multiple traits. *Ecology*, **91**, 299–305.

Laliberté, E., Legendre, P. & Shipley, B. (2014). FD: measuring functional diversity from multiple traits, and other tools for functional ecology. R package version 1.0-12.

Louzada, J., Lima, A.P., Matavelli, R., Zambaldi, L. & Barlow, J. (2010) Community structure of dung beetles in Amazonian savannas: role of fire disturbance, vegetation and landscape structure. *Landscape Ecology*, **25**, 631–641.

Lumaret, J.P., Kadiri, N. & Bertrand, M. (1992) Changes in resources: consequences for the dynamics of dung beetle communities. *Journal of Applied Ecology*, **29**, 349–356.

Manning, P., Slade, E.M., Beynon, S.A. & Lewis, O.T. (2016) Functionally rich dung beetle assemblages are required to provide multiple ecosystem services. *Agriculture, Ecosystems and Environment*, **218**, 87–94.

Mason, N.W.H., Mouillot, D., Lee, W.G. & Wilson, J.B. (2005) Functional richness, functional evenness and functional divergence: the primary components of functional diversity. *Oikos*, **111**, 112–118.

Mason, N.W.H., De Bello, F., Mouillot, D., Pavoine, S. & Dray, S. (2013) A guide for using functional diversity indices to reveal changes in assembly processes along ecological gradients. *Journal of Vegetation Science*, **24**, 794–806.

McGill, B.J., Enquist, B.J., Weiher, E. & Westoby, M. (2006) Rebuilding community ecology from functional traits. *Trends in Ecology & Evolution*, **21**, 178–185.

Moretti, M., Duelli, P. & Obrist, M.K. (2006) Biodiversity and resilience of arthropod communities after fire disturbance in temperate forests. *Oecologia*, **149**, 312–327.

Moretti, M., Dias, A.T. C., de Bello, F., Altermatt, F., Chown, S.L., Azcárate, F.M., Bell, J.R., Fournier, B., Hedde, M., Hortal, J., Ibanez, S., Öckinger, E., Sousa, J.P., Ellers, J., and Berg, M.P. (2016) Handbook of protocols for standardized measurement of terrestrial invertebrate functional traits. *Functional Ecology*, **31**, 5 58–567.

Mouillot, D., Villéger, S., Scherer-Lorenzen, M. & Mason, N.W.H. (2011) Functional structure of biological communities predicts ecosystem multifunctionality. *PLoS One*, **6**, 1–9.

Mouillot, D., Graham, N.A.J., Villéger, S., Mason, N.W.H. & Bellwood, D.R. (2013) A functional approach reveals community responses to disturbances. *Trends in Ecology & Evolution*, **28**, 167–177.

Negro, M., Rolando, A. & Palestrini, C. (2011) The impact of overgrazing on dung beetle diversity in Italian maritime Alps. *Environmental Entomology*, **40**, 1081–1092.

Nervo, B., Tocco, C., Caprio, E., Palestrini, C. & Rolando, A. (2014) The effects of body mass on dung removal efficiency in dun beetles. *PLoS One*, **9**, 1–9.

Nichols, E., Spector, S., Louzada, J., Larsen, T., Amezquita, S., Favila, M.E. *et al.* (2008) Ecological functions and ecosystem services provided by *Scarabaeinae* dung beetles. *Biological Conservation*, **141**, 1461–1474.

Nunes, C.A., Beiroz, W., da Silva, P.G., Braga, R.F., Fernandes, G.W. & Neves, F.d.S. (2018) Fire? They don't give a dung! The resilience of dung beetles to fire in a tropical savanna. *Ecological Entomology*, **44**, 315–323.

R Core Team. (2016) R: A Language and Environment for Statistical Computing, Vienna, Austria. Available at: https://www.R-project.org/.

Rosenlew, H. & Roslin, T. (2008) Habitat fragmentation and the functional efficiency of temperate dung beetles. *Oikos*, **117**, 1659–1666.

Shackelford, N., Hobbs, R.J., Burgar, J.M., Erickson, T.E., Fontaine, J.B., Laliberté, E. *et al.* (2013) Primed for change: developing ecological restoration for the 21st century. *Restoration Ecology*, **21**, 297–304.

Slade, E.M. & Roslin, T. (2016) Dung beetle species interactions and multifunctionality are affected by an experimentally warmed climate. *Oikos*, **125**, 1607–1616.

Slade, E.M., Mann, D.J., Villanueva, J.F. & Lewis, O.T. (2007) Experimental evidence for the effects of dung beetle functional group richness and composition on ecosystem function in a tropical forest. *Journal of Animal Ecology*, **76**, 1094–1104.

Steinauer, E.M. & Collins, S.L. (1996) Prairie ecology – the Tallgrass Prairie. *Prairie Conservation*, F.L. Knopf edn (ed. by F. B. Samson), pp. 39–52. Washington, District of Columbia: Island Press.

Swengel, A.B. (2001) A literature review of insect responses to fire, compared to other conservation managements of open habitat. *Biodiversity and Conservation*, **10**, 1141–1169.

Tocco, C., Probo, M., Lonati, M., Lombardi, G., Negro, M., Nervo, B. *et al.* (2013) Pastoral practices to reverse shrub encroachment of sub-alpine grasslands: dung beetles (Coleoptera:*Scarabaeoidea*) respond more quickly than vegetation. *PLoS One*, **8**, 1–11.

Verdú, J.R., Moreno, C.E., Sánchez-Rojas, G., Numa, C., Galante, E. & Halffter, G. (2007) Grazing promotes dung beetle diversity in the xeric landscape of a Mexican Biosphere Reserve. *Biological Conservation*, **140**, 308–317.

Verdú, J.R., Cortez, V., Ortiz, A.J., González-Rodríguez, E., Martinez-Pinna, J., Lumaret, J. *et al.* (2015) Low doses of ivermectin cause sensory and locomotor disorders in dung beetles. *Scientific Reports*, **5**, 1–10.

Violle, C., Navas, M.L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I. *et al.* (2007) Let the concept of trait be functional! *Oikos*, **116**, 882–892.

Watts, C.H. & Mason, N.W.H. (2015) If we build - they mostly come: partial functional recovery but persistent compositional differences in wetland beetle community restoration. *Restoration Ecology*, **23**, 555–565.

Young, T.P. (2000) Restoration ecology and conservation biology. *Biological Conservation*, **92**, 73–83.

Accepted 16 August 2020
Associate Editor: Joshua King