Environmental Entomology, 50(5), 2021, 1075–1087
https://doi.org/10.1093/ee/nvab065
Advance Access Publication Date: 16 July 2021
Research

ENTOMOLOGICAL
SOCIETY OF AMERICA
SHARING INSECT SCIENCE GLOBALLY

OXFORD

Community Ecology

Disturbance-Induced Trophic Niche Shifts In Ground Beetles (Coleoptera: Carabidae) In Restored Grasslands

Azeem U. Rahman,[1] Holly P. Jones,[2,3] Sheryl C. Hosler,[2,4] Seth Geddes,[2] Melissa Nelson,[2] and Nicholas A. Barber[1,5]

[1]Department of Biology, San Diego State University, 5500 Campanile Dr., San Diego, CA 92182, USA, [2]Department of Biological Sciences, Northern Illinois University, 1425 W Lincoln Hwy, DeKalb, IL 60115, USA, [3]Institute for the Study of the Environment, Sustainability, and Energy, Northern Illinois University, 1425 W Lincoln Hwy, DeKalb, IL 60115, USA, [4]Department of Biological Sciences, University of Illinois Chicago, 845 W. Taylor St, Chicago, IL 60607, USA, and [5]Corresponding author, e-mail: nbarber@sdsu.edu

Subject Editor: Carmen Blubaugh

Received 16 February 2021; Editorial decision 6 June 2021

Abstract

Ecosystem restoration is a critical component of land management, countering the loss of native biodiversity. Restoration efforts are enhanced by reintroducing naturally occurring ecosystem processes, including disturbances that may impact species characteristics such as niche position or niche size. In grasslands, grazing and fire affect plant diversity and habitat complexity, which potentially influence insect dietary behaviors and thus their contributions to functions like seed and arthropod predation. Using carbon and nitrogen stable isotopes, we characterized variation in the dietary niche of six ground beetle species (Coleoptera: Carabidae) in response to grazing by reintroduced bison and prescribed fire disturbances in twenty tallgrass prairies. Management disturbances did not affect activity density for most beetle species and mean trophic position was mostly unaffected. However, five of six species exhibited increased trophic niche area and breadth with disturbances, indicating a switch to a more generalist diet that incorporated a wider range of food items. The combination of bison and fire impacts may increase vegetation patchiness and heterogeneity, driving these diet changes. Morphological traits and microhabitat preferences might mediate response to disturbances and the resulting heterogeneity. Combining prescribed fire and grazing, which increases plant diversity and vegetation structural diversity, may help beetle communities establish over time and support the ecological functions to which these insects contribute.

Key words: stable isotope analysis, ecosystem restoration, grazing, prescribed fire, tallgrass prairie

Natural grasslands have experienced extensive degradation and loss worldwide, primarily due to conversion to agricultural land for growing crops and grazing livestock (Knopf 1996, Hoekstra et al. 2005, Anderson 2006, Gibson 2009). Although North American grasslands historically covered 15% of the continent and consisted of many diverse vegetation assemblages, few remnant grasslands remain intact (Chapman et al. 1990, White et al. 2000), and remaining fragments face further degradation from invasive species, overgrazing, urbanization, and other disturbances (Knopf 1996). Widespread grassland restoration efforts attempt to recreate grassland ecosystems where they have been lost or degraded (Packard and Mutel 1997, Baer et al. 2019), and a necessary component of restoration is to re-establish functioning ecosystems (Holl 2020). Although insects make significant contributions to ecosystem functions (Weisser and Siemann 2008), their roles in restored habitats are often overlooked (Wodika and Baer 2015, Luong et al. 2019).

Two key processes that strongly influence grasslands are fire and grazing. These disturbances can maintain habitat characteristics, shape communities, and influence functions such as plant growth, nutrient cycling, predation, and seed dispersal (Howe 1995, Anderson 2006, McConkey et al. 2012, Koerner and Collins 2014, Nelson et al. 2021). Many of these impacts occur through a change in plant community composition. In North American tallgrass prairie, fire often increases the growth and seed production of C_4 grasses (Ehrenreich and Aikman 1957, Masters et al. 1993, McCarron and Knapp 2003), shifting plant communities and reducing the abundance of C_3 grasses and forbs, which make up the majority of prairie plant diversity (Hartnett 1991, Briggs and Knapp 1995, Copeland et al. 2003). Conversely, the presence of American bison (*Bison bison*) can also shift the plant communities through grazing that reduces C_4 grasses (Krueger 1986; Knapp et al. 1999) and enhances C_3 grass and forb cover. Bison effects also include wallowing, which increases spatial heterogeneity (Elson and Hartnett 2017) and supports a higher diversity of arthropods (Joern 2005, Moran 2014, Nickell et al. 2018). Bison and fire were historically widespread disturbances, including fires used by Indigenous communities to manage the landscape (Higgins 1986), a practice continued by communities today (Kimmerer and Lake 2001). Other land managers today also try to recreate these disturbances in restored and remnant prairies using prescribed fire and the introduction of bison or other grazing mammals (Knapp et al. 1999; Copeland et al. 2003; Blackburn et al. 2020).

Fire and grazing effects may also influence consumer trophic dynamics by changing food item availability and foraging behaviors. Prescribed fire and bison grazing in prairies should increase and decrease, respectively, the importance of C_4 grasses in food webs. C_4-dominated food webs in grasslands have been associated with lower overall arthropod diversity because of limited resources for herbivorous arthropods (Larsen and Work 2003, Joern 2005). Combined with changes in structural heterogeneity resulting from grazing and fire disturbances, this could shift, expand, or contract consumer diets by making new food items available or unavailable. Ground beetles (Coleoptera: Carabidae) are an abundant, diverse and important family of insects that consume a range of food items and have been used as biological indicators of plant communities (Lövei and Sunderland 1996, Ball and Bousquet 2001, Larsen and Work 2003, McCravy and Lundgren 2011). Although some species of ground beetles area primarily herbivorous, carnivorous, or omnivorous (Thiele 1977), many exhibit diet plasticity such that their trophic niche may change with environmental conditions (Vanbergen et al. 2010, McCravy and Lundgren 2011). Ground beetle foraging patterns have been used to study food web and predator-prey dynamics (Purtauf et al. 2004, Gaines and Gratton 2010, Mader et al. 2018). However, most ground beetle foraging studies are performed in the lab based on stomach content analyses (McNabb et al. 2001, Wise et al. 2006, Sasakawa et al. 2010). While informative, these studies may not reflect the true feeding habits of beetles in the field as they cannot show the dietary contributions of different food sources and only reflect an animal's most recent feeding (Ikeda et al. 2010, Sasakawa et al. 2010). Additionally, most field diet studies have focused on ground beetles in forested (Okuzaki et al. 2010, Zalewski et al. 2014) or agricultural (Birkhofer et al. 2011a) landscapes rather than grassland systems. As an alternative to in-lab observational diet studies, carbon and nitrogen stable isotope values can indicate basal resources in trophic chains in field settings (including C_3 vs. C_4 plants) and the trophic position and diet breadth of consumers (Fry 2006, Sasakawa et al. 2010, Crotty et al. 2012). A greater $\delta^{13}C$ value indicates the importance of C_4 plants in the diet of a beetle or its prey because C_4 plants are enriched in ^{13}C relative to C_3 plants, and a greater $\delta^{15}N$ value indicates greater reliance on prey items in higher trophic levels because ^{15}N is enriched in organisms at a higher trophic position (Post 2002).

We measured carbon and nitrogen stable isotopes in six ground beetle species collected from restored and remnant tallgrass prairies managed with prescribed fire and re-introduced bison to determine whether these management disturbances influence insect trophic position and diet breadth. We hypothesized that primarily herbivorous species will have reduced diet breadth (reduced variation in isotope ratios) and increased mean $\delta^{13}C$ values in the presence of fire and absence of bison, reflecting C_4 grass dominance in these environments (Fig. 1A). Conversely, carnivorous and omnivorous beetle species will have greater $\delta^{13}C$ and $\delta^{15}N$ variation with bison present because of increased plant and arthropod prey diversity (Fig. 1B). We also predicted that these carnivorous and omnivorous species will have decreased mean $\delta^{13}C$ and increased mean $\delta^{15}N$ values with bison present and without fire because these conditions reduce C_4 dominance and increase insect prey availability. Finally, we expected increased diet breadth would be associated with increased abundance because more diverse food items would support a positive population response. We also recorded the activity density of each species to estimate abundance and determine if density changes were related to trophic niche changes.

Methods

We sampled beetles from Nachusa Grasslands, a 1,500 ha reserve in Illinois, USA, owned and managed by The Nature Conservancy (TNC). Nachusa comprises restored and remnant prairies and other habitats including oak savanna and wetlands (Jones and Cushman 2004). TNC has restored former rowcrop land to tallgrass prairie since the early 1980s using manual and mechanical sowing of seeds from local remnants, prescribed fire, and exotic species removal (Hansen and Gibson 2014). Exotic weeds are controlled with herbicides annually, and prescribed fires generally take place on a 1–3 yr rotation (Barber et al. 2016). Remnant sites that were never converted to rowcrop agriculture also are managed with prescribed fire and herbicide application. In 2014, TNC introduced 30 American bison (*Bison bison*) to Nachusa, and the animals had access to a portion of the site. Today the herd has access to approximately half of Nachusa's total land (Barber et al. 2017) and is maintained at

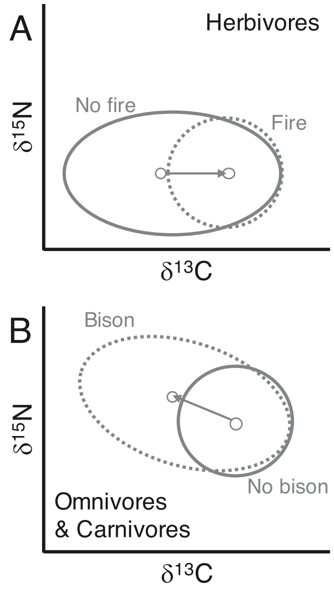

Fig. 1. Conceptual figure illustrating hypothesized changes in stable isotope ratios in response to disturbances. (A) Herbivorous ground beetles are expected to exhibit reduced diet breadth and increased mean $\delta^{13}C$ following prescribed fire. (B) Omnivorous and carnivorous beetles are expected to expand their diet breadth with reduced mean $\delta^{13}C$ and increased mean $\delta^{15}N$ in the presence of bison. In both panels, a solid ellipse represents the absence of the disturbance, and a dashed ellipse is the presence of the disturbance. Open circles represent mean $\delta^{13}C$ and $\delta^{15}N$ values. Relative changes in variation and mean values are exaggerated for illustrative purposes.

approximately 130 animals. Prairies contain a diverse assemblage of grasses and forbs. Dominant C_4 grasses at Nachusa include big bluestem (*Andropogon gerardii*), Indian grass (*Sorghastrum nutans*), switchgrass (*Panicum virgatum*), and little bluestem (*Schzachyrium scoparium*). The dominant C_3 grass species include wild rye (*Elymus canadensis*), bluegrass spp. (*Poa* spp.), and smooth brome (*Bromus inermis*), as well as sedge species (*Carex* spp.). Common C_3 forbs include Asteraceae such as stiff goldenrod (*Solidago rigida*), prairie coneflower (*Ratibida pinnata*), pale purple coneflower (*Echinacea pallida*), and Fabaceae including red clover (*Trifolium pretense*) and round-headed bush-clover (*Lespedeza capitata*) (Hansen and Gibson 2014, Barber et al. 2016, Blackburn et al. 2020).

We focused on six species of ground beetles commonly found in the Nachusa Grasslands: *Harpalus pensylvanicus* (Degeer, 1774), *Poecilus lucublandus* (Say, 1823), *Chlaenius platyderus* Chaudoir, 1856, *Cyclotrachelus seximpressus* (LeConte, 1846), *Amara rubrica* Haldeman, 1843/*musculis* (Say, 1823), and *Cicindela sexguttata* Fabricius, 1775. All species are nocturnally active, with *H. pensylvanicus* and *Ch. platyderus* reportedly omnivorous; *P. lucublandus*, *Cy. seximpressus*, and *Cic. sexguttata* primarily predators; and *A. rubrica/musculis* (hereafter referred to as *A. rubrica*) herbivorous (Larochelle and Larivière 2001, 2003). Beetles were collected from 20 sites at Nachusa, including 18 restorations and two remnants, in both 2017 and 2018 (Hosler et al. 2020, Nelson et al. 2021) (Table 1). These sites were selected for long-term monitoring to include a range of ages since planting, as well as variation in bison presence and fire schedule. Selected restorations were considered 'successful' by land managers because they were not heavily invaded by invasive weeds (Barber et al. 2017). In 2017 and 2018, pitfall trap arrays, each consisting of ten traps (12.1 cm deep, with 9.5 cm diameter openings) in two groups of five, were installed 75 m apart in each of the sites. Traps were opened in May–June (15 May–7 June 2017; 23 May–12 June 2018), July (24–31 July 2017; 9–16 July 2018), and September(8–15 September 2017; 14–21 September 2018) with contents collected every 3–7 d. See Hosler et al. (2020) and Nelson et al. (2021) for details of trapping methods. Beetles were identified using keys and a regional checklist (Ciegler 2000, Arnett et al. 2002, Messer 2009, Bousquet 2010).

In 2017, 2,599 individuals from the six species were captured, and in 2018, 1,908 were captured. The activity density of each species in each site was calculated as the number of individuals captured divided by the total number of trapdays at that site in each year to provide an estimate of abundance. We used a total of 578 specimens for isotopic analysis (*H. pensylvanicus* (n = 30), *P. lucublandus* (n = 111), *Ch. platyderus* (n = 154), *Cy. seximpressus* (n = 167), *A. rubrica/musculis* (n = 43), and *Ci. sexguttata* (n = 73), using specimens from both years of sampling across all sites for isotopic analysis, with a minimum of three individuals per species per site for each when possible. Sex was not recorded because there was no detectable difference in δ^{13}C and δ^{15}N between males and females in two previous studies of ground beetles (Goncharov et al. 2015, Ikeda et al. 2007). Beetles were stored in 70% ethanol before sample preparation, which does not significantly affect isotopic signals of samples when compared to samples that were preserved by freezing (Zalewski et al. 2014). Samples were washed with RO water, and abdomens were removed from specimens to avoid sampling gut contents. The remaining head and thorax of the individuals were dried at 60°C for at least 72 h (Ikeda et al. 2007), ground, and weighed into tin capsules. Samples were analyzed at the UC Davis Stable Isotope Facility (PDZ Europa 20-20 isotope ratio mass spectrometer) and the NIU Stable Isotope Laboratory (Thermo-Finnigan Delta plus Advantage EA mass spectrometer). Stable R_{standard} isotope values are expressed in standard delta (δ) notation in parts per thousand (‰),

$$\delta\,(\%) = \left(\frac{R_{sample}}{R_{standard}} - 1\right) \times 1000$$

and values were measured against laboratory standards: ^{13}C was calibrated against the Peedee Belemnite (PDB) limestone formation international standard and ^{15}N calibrated against atmospheric N_2 and USGS Nitrogen standards (Hood-Nowotny and Knols 2007).

We accounted for potential differences in isotopic values of basal resources (plants) among sites (Post 2002) because plant δ^{13}C and δ^{15}N could also hypothetically change with bison and fire disturbances (Kim et al. 2019). In a separate study (Farrell et al. 2018, Barber et al. 2019), plant communities at each site were surveyed in August 2017 and 2018, and leaves were collected

Table 1. Bison presence and prescribed burn schedule of all sites. Age is the number of growing seasons in 2017 since restoration planting (remnants were not planted and have no age)

Site	Bison	2017	2018	Age
CCE	No	Burn	No Burn	10
CCEE	No	Burn	No Burn	10
SF	No	Burn	No Burn	16
SB	No	No Burn	No Burn	8
SBEE	No	No Burn	No Burn	8
SBEW	No	No Burn	No Burn	8
CCW	No	No Burn	Burn	9
CCWE	No	No Burn	Burn	9
FC	No	No Burn	Burn	9
TC	No	No Burn	Burn	15
TCE	No	No Burn	Burn	15
TC Remnant	No	No Burn	Burn	–
MU	Yes	Burn	Burn	30
HF	Yes	Burn	Burn	4
HPN	Yes	Burn	No Burn	5
LOW	Yes	Burn	No Burn	6
HLP	Yes	No Burn	Burn	16
HPW	Yes	No Burn	Burn	9
Main Remnant	Yes	No Burn	Burn	–
WH	Yes	No Burn	Burn	25

from the ten most abundant species at each site in each year (average 62% of total cover at each site). Leaf tissues were analyzed at the NIU Stable Isotope Laboratory as described above. For each survey year, we calculated the mean $\delta^{13}C$ and $\delta^{15}N$ of each species using at least 3 individuals per species (mean n = 13.1 individuals, range 3–54). These mean isotope values were calculated by weighting each species' relative abundance in each community to calculate community-weighted mean $\delta^{13}C$ and $\delta^{15}N$ of that plant community.

Data Analysis

Effects of bison presence and prescribed fire management on activity density and trophic characteristics of each species were determined by analyzing count data and raw isotope values. Count data for the six species were used to calculate activity densities (individuals caught per trapping days) across the sites, which were log-transformed to meet assumptions of normality and homoscedasticity and analyzed using linear mixed models for each species in which bison presence/absence, fire presence/absence in the past year, sampling year (2017 vs. 2018), and the bison × fire interaction were fixed factors, and the site was a random factor to account for repeatedly sampling sites. Factors were evaluated with likelihood ratio tests using Type III tests with the function Anova in the car package (Fox et al. 2013). Mean $\delta^{13}C$ and $\delta^{15}N$ for each species in each site and year were analyzed using the same linear mixed model structure for activity density, and the same approach was used to examine mean plant isotope values.

Trophic niche space was estimated using the Stable Isotope Bayesian Ellipses package in R (SIBER v2.1.3, Jackson et al. 2011, Jackson and Parnell 2017). Standard ellipse areas based on the raw $\delta^{13}C$ and $\delta^{15}N$ values per ground beetle species were calculated to determine trophic niche space of species under each restoration management combination and subsequently corrected for small sample sizes (SEAc) (function plotSiberObject in SIBER). Bayesian multivariate normal distributions were fit to each site condition and individual species via the JAGS program (Plummer 2013) and differences in trophic niche sizes between species and site conditions were compared using the function siberMNV in SIBER. The calculated standard ellipse area is based on Bayesian estimates (SEAb) for each species and site conditions, and data were plotted using the function siberDensityPlot (Mader et al. 2018).

Results

Activity densities of only two species were significantly affected by site management (Tables 2 and 3). The prescribed fire increased the activity density of *Ch. platyderus*. There were a significant bison × fire interaction for *Cy. seximpressus,* with higher activity densities in sites with both bison presence and prescribed fire, and low densities where only one of these disturbances was present. *Cicindela sexguttata* was more abundant in 2018, but management activities did not significantly affect its density.

Five of the six species had $\delta^{15}N$ values in the range of 4–8‰ (Fig. 2). One species, *A. rubrica*, showed $\delta^{15}N$ values below 4‰, which is consistent with its herbivorous diet. There was less consistency for $\delta^{13}C$ values, with considerable differences among the generalist and carnivorous species, although herbivorous *A. rubrica* had the lowest $\delta^{13}C$ values. Bison presence was associated with significantly lower mean $\delta^{15}N$ values for *Ci. sexguttata* and significantly lower mean, but greater range, $\delta^{13}C$ for *H. pensylvanicus*. There also was a significant bison × fire interaction for *H. pensylvanicus* $\delta^{15}N$ values (highest where bison and fire were both absent) and *P. lucublandus* $\delta^{13}C$ values (highest with fire present and bison absent). Mean plant $\delta^{13}C$ and $\delta^{15}N$ did not vary with bison presence, prescribed fire, or their interaction (Table 4).

The combination of bison presence and prescribed fire was associated with larger standard isotopic niche areas (SEAc) than in sites without these disturbances for most of the species in this study (Table 5, Fig. 3 and 4), while prescribed fire without bison reduced niche breadth for four species (*Ci. sexguttata, Cy. seximpressus, H. pensylvanicus,* and *P. lucublandus*). There was a notable deviation from this pattern in *A. rubrica*, an herbivorous species, which had particularly small SEAc for sites where fire and bison were both absent. A small sample size for *H. pensylvanicus* prevented ellipse area calculation for sites with bison and no prescribed fire.

Discussion

We tested the impact of two grassland management treatments on the activity density, mean trophic position, and niche breadth of ground beetles in tallgrass prairies. The reintroduction of bison and prescribed fires had few and relatively weak effects on activity densities, but these management disturbances were associated with changes in trophic position and niche breadth for some of the

Table 2. Mean activity density (Number of beetles caught per 100 trap days)

Species	Fire	Bison	
		Absent	Present
A. rubrica	Burn	1.42	30.25
	No Burn	13.01	3.52
Ch. platyderus	Burn	94.28	257.91
	No Burn	63.29	85.24
Ci. sexguttata	Burn	22.96	17.78
	No Burn	26.48	10.21
Cy. seximpressus	Burn	69.50	253.12
	No Burn	170.06	81.46
H. pensylvanicus	Burn	1.18	16.38
	No Burn	3.57	2.712
P. lucublandus	Burn	17.77	18.67
	No Burn	25.77	9.246

Table 3. Results of linear mixed effect models of activity density against restoration site conditions, with the site as a random factor in each model

Species	Factor	χ^2	*df*	*P*
A. rubrica	Bison	0.263	1	0.608
	Fire	0.244	1	0.621
	Year	0.666	1	0.415
	Bison:Fire	0.006	1	0.936
Ch. platyderus	Bison	2.97	1	0.084
	Fire	**7.08**	**1**	**0.008**
	Year	0.709	1	0.400
	Bison:Fire	0.967	1	0.326
Ci. sexguttata	Bison	3.49	1	0.061
	Fire	3.03	1	0.082
	Year	**55.1**	**1**	**<.0001**
	Bison:Fire	2.53	1	0.112
Cy. seximpressus	Bison	0.168	1	0.682
	Fire	0.473	1	0.491
	Year	2.62	1	0.106
	Bison:Fire	**5.78**	**1**	**0.016**
H. pensylvanicus	Bison	1.83	1	0.177
	Fire	0.0514	1	0.821
	Year	3.72	1	0.054
	Bison:Fire	0.089	1	0.766
P. lucublandus	Bison	0.0531	1	0.818
	Fire	0.0038	1	0.951
	Year	2.39	1	0.122
	Bison:Fire	0.926	1	0.336

Bold indicates $P < 0.05$.

ground beetle species. There was a variety of responses exhibited by the different species to the treatments, but these were not driven by isotopic changes in baseline plant resources, for which mean isotope ratios did not systematically shift with bison or prescribed fire presence. Differences in ground beetle activity densities, as well as the trophic breadth and niche, may be attributed to patterns of vegetation patchiness and heterogeneity resulting from these two disturbances. The environmental preferences, as well as general dietary guild, of ground beetles, might explain species' responses to these disturbances.

Activity Density

Neither bison nor fire greatly impacted the activity densities (number of individuals caught per days of trapping) of most species in the study, and this may be attributed to their mobility. The four unaffected species (*A. rubrica, Ci. sexguttata, H. pensylvanicus,* and *P. lucublandus*) are macropterous or submacropterous (Larochelle and Larivière 2001, 2003), and so are capable of flight. Ground beetle dispersal abilities are highly variable in disturbed environments (Thiele 1977), with some species investing heavily in dispersal in more unstable environments rather than establishing stable populations (Den Boer 1970). The ability to fly allows for longer dispersal distances and may explain the similar densities across all site treatments for macropterous species: even if conditions (disturbances or lack thereof) temporarily reduced these species, dispersing individuals from nearby habitat could subsidize the reduced population, erasing potential differences in abundance. This dispersal process can be much slower for flightless species, allowing detection of impacts on activity density over a longer period of time (Den Boer 1970, Barber et al. 2017, Nelson et al. 2021).

Two species, *Ch. platyderus* and *Cy. seximpressus*, did respond to disturbance, and both are brachypterous (flightless) generalist predators (Larochelle and Larivière 2003) that represent a large proportion of the ground beetle communities at the study site (Barber et al. 2017, Nelson et al. 2021). Studies of arthropod communities under fire and grazing management have found a wide range of responses to these disturbances, with abundances shifting both positively and negatively under different regimes and for different taxa (Harper et al. 2000; Swengel 2001; Panzer 2002; Tscharntke et al. 2002; Stoner and Joern 2004; Bargmann et al. 2016). However, species with a higher trophic rank can have increased sensitivity to landscape changes (Purtauf 2005). The density responses by *Ch. platyderus* and *Cy. seximpressus* may thus be attributed to their higher trophic rank as generalist predators and physical limitations to dispersal due to being flightless, as well as species-specific environmental preferences. Grasslands may produce 20% more vegetation biomass than is decomposed in a single season, and the buildup of dead plant biomass can reduce the movement of ground-dwelling arthropods (Anderson 2006). Fire, which reduces thatch and standing dead plant biomass, when combined with the increased structural heterogeneity from bison activity (Larson 1940; Knapp et al. 1999), may have created ideal foraging conditions for *Cy. seximpressus* and *Ch. platyderus* that supported larger populations (Harvey et al. 2008, Michel and Adams 2009). This increase of ground beetle populations in response to disturbance is observed in other settings (da Silva et al. 2008; Birkhofer et al. 2014; Anjum-Zubair et al. 2015). However, Bargmann et al. (2016) found that beetle occurrences in post-burn habitats similar to the conditions of this study also were related to soil moisture preferences: species with higher soil moisture preference, which tended to be generalist predators, were less tolerant of fire. Both species that responded positively to fire, *Ch. platyderus* and *Cy. seximpressus*, prefer greater soil moisture than the other ground beetle species (Larochelle and Lariviere 2003), so their responses to fire are surprising. The absence of litter following burns increases the moisture evaporation from the soil surface, reducing soil moisture (Anderson 2006), and bison may further dry

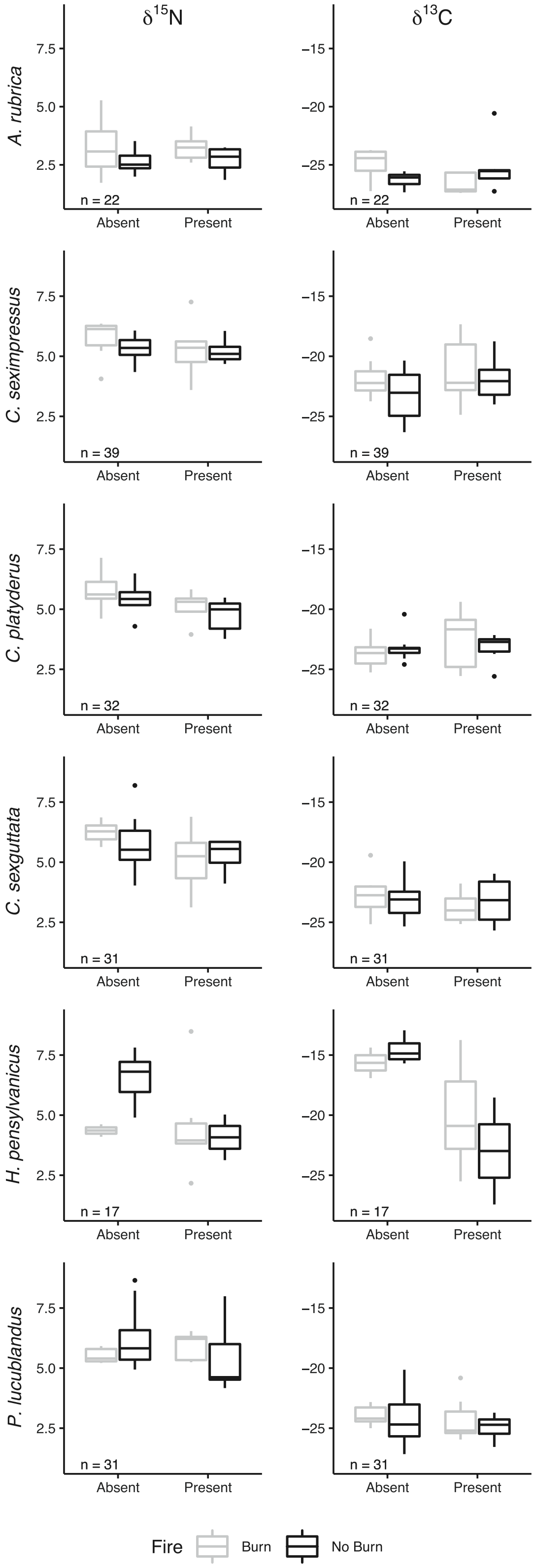

Fig. 2. $\delta^{15}N$ and $\delta^{13}C$ values for species at each site by disturbance treatment; gray represents burned sites, and black are unburned. Sample size, n, is the number of site-year combinations for which a mean δ value was calculated.

soils through grazing and wallowing (Pfeiffer and Hartnett 1995; Knapp 1999). Activity densities of *Cy. seximpressus* and *Ch. platyderus* suggest that their abundances may be less affected by soil moisture preferences than by preference for, or greater fitness in, habitats with increased spatial heterogeneity. For example, different life stages (belowground larvae vs. aboveground adults) or behaviors (breeding, foraging, avoiding predation) might require slightly different microhabitats that are all available where such fine-scale heterogeneity occurs. Preliminary analysis of pitfall trap bycatch suggests spiders may be less abundant following prescribed fires (Barber, unpubl. data), so reductions in these potential competitors could also explain the apparent benefits of fire for these two predatory ground beetles. Nonetheless, the activity density changes of *Cy. seximpressus* and *Ch. platyderus* were not associated with differences in trophic position or breadth as measured by stable isotopes.

Trophic Shifts

Five of the six species in this study had larger trophic niche sizes in sites with bison present, particularly when combined with prescribed fire, in agreement with the hypothesis that reintroducing bison to tallgrass prairies would increase beetle diet breadth. Averaged across fire conditions, bison presence increased trophic niche size in species that exhibit a variety of dietary preferences, including in the herbivorous *A. rubrica* by 75%, in generalist predator species including *Ch. platyderus* and *Cy. seximpressus* by 12–25%, as well as in the obligate predator *Ci. sexguttata* by 52%. Estimated niche size was larger in *H. pensylvanicus* as well, although limited sample size makes it difficult to quantify the magnitude of niche expansion. Bison may drive variety in beetles' diets through their roles as a keystone species that increase plant diversity in prairie communities as well as by increasing spatial heterogeneity (Knapp et al. 1999; Fuhlendorf and Engle 2001; Anderson 2006). Because of their preference for competitively dominant C_4 grasses, bison grazing can promote C_3 plant populations (Collins 1987; Hartnett and Fay 1998). We expected that this increase in plant species diversity, especially increased forb species, would increase the amount of basal resources in the food web with lower $\delta^{13}C$ values and support more herbivorous insect species (but see below). Herbivorous carabids may have distinct preferences for specific seeds, but these granivorous carabids possess morphological and physiological adaptations that allow them to expand their dietary breadth when in environments with a more diverse pool of resources (McCravy and Lundgren 2010). Additionally, light or intermediate grazing intensities often lead to overall greater insect species richness (Holmes et al. 1979; Joern 2005), and active and abandoned bison wallows also increase the abundance and diversity of plant communities (Rosas et al. 2008; McMillan et al. 2011) and some arthropod groups (Nickell et al. 2018). Together, these direct and indirect effects of bison likely increase the diversity of potential prey items for beetles and may drive the observed increase in trophic niche size.

Prescribed fire, when in combination with bison presence, further enlarged trophic niche areas for four species (*Ch. platyderus, Ci. sexguttata, Cy. seximpressus,* and *H. pensylvanicus*) by 3–42%, corresponding to a greater range of resource diversity. Although we predicted that fire would reduce the overall trophic niche area for carabids because of the associated reduction of C_3 plants at the expense of faster-growing C_4 plants (Collins and Gibson 1990; McCarron and Knapp 2003), plant mean $\delta^{13}C$ was not increased by fire but prescribed burns in combination with bison activity might have increased trophic niche areas by changing the spatial complexity of the prairie. Fire and bison impacts on plant communities can occur through changes in litter buildup, and reduced litter may allow predatory species to increase the range over which they forage for prey. Fires in tallgrass prairie can increase nitrogen use efficiency, increase above and below ground plant production, and enhance

Table 4. Results of linear mixed effect models of mean stable isotope values against restoration site conditions, with the site as a random factor in each model.

Species	Factor	χ^2	*df*	*P*	χ^2	*df*	*P*
		$\delta^{13}C$			$\delta^{15}N$		
A. rubrica	Bison	0.193	1	0.661	0.684	1	0.408
	Fire	1.30	1	0.254	0.577	1	0.447
	Year	16.4	1	**<0.001**	2.13	1	0.144
	Bison:Fire	1.53	1	0.216	0.142	1	0.706
Ch. platyderus	Bison	2.34	1	0.126	3.79	1	0.051
	Fire	0.275	1	0.600	1.12	1	0.289
	Year	0.957	1	0.328	0.177	1	0.674
	Bison:Fire	2.55	1	0.110	0.011	1	0.917
Ci. sexguttata	Bison	1.63	1	0.202	6.69	1	**0.010**
	Fire	0.171	1	0.679	2.71	1	0.099
	Year	0.005	1	0.945	2.90	1	0.089
	Bison:Fire	3.00	1	0.083	2.56	1	0.110
Cy. seximpressus	Bison	1.34	1	0.246	1.17	1	0.279
	Fire	0.623	1	0.430	1.04	1	0.307
	Year	10.3	1	**0.001**	0.213	1	0.645
	Bison:Fire	0.269	1	0.604	0.375	1	0.541
H. pensylvanicus	Bison	4.64	1	**0.031**	0.330	1	0.565
	Fire	0.107	1	0.743	41.8	1	**<0.001**
	Year	2.01	1	0.148	15.9	1	**<0.001**
	Bison:Fire	0.591	1	0.442	33.6	1	**<0.001**
P. lucublandus	Bison	0.974	1	0.324	0.388	1	0.533
	Fire	2.05	1	0.153	1.42	1	0.234
	Year	8.02	1	**0.005**	0.383	1	0.536
	Bison:Fire	7.83	1	**0.005**	1.68	1	0.195
Plant community	Bison	0.77	1	0.380	1.84	1	0.176
	Fire	1.09	1	0.297	2.85	1	0.091
	Year	0.68	1	0.410	42.82	1	**<0.001**
	Bison:Fire	2.88	1	0.090	0.05	1	0.817

Bold indicates $P < 0.05$.

Table 5. Total and standardized ellipse area sizes under each restoration condition

Species	Bison	Fire	TA	SEAc
A. rubrica	Absent	Burn	1.75	2.31
		No Burn	3.28	1.36
	Present	Burn	3.50	2.15
		No Burn	6.08	4.27
Ch. platyderus	Absent	Burn	26.4	6.90
		No Burn	30.4	6.42
	Present	Burn	40.2	8.75
		No Burn	16.7	6.17
Ci. sexguttata	Absent	Burn	8.14	3.35
		No Burn	23.5	6.72
	Present	Burn	12.4	7.54
		No Burn	14.6	7.77
Cy. seximpressus	Absent	Burn	18.5	5.39
		No Burn	38.4	8.07
	Present	Burn	30.4	9.21
		No Burn	23.6	7.51
H. pensylvanicus	Absent	Burn	3.34	6.52
		No Burn	22.3	10.2
	Present	Burn	47.8	29.1
		No Burn	10.3	2.77
P. lucublandus	Absent	Burn	1.75	2.31
		No Burn	44.7	9.20
	Present	Burn	17.6	5.85
		No Burn	11.0	7.57

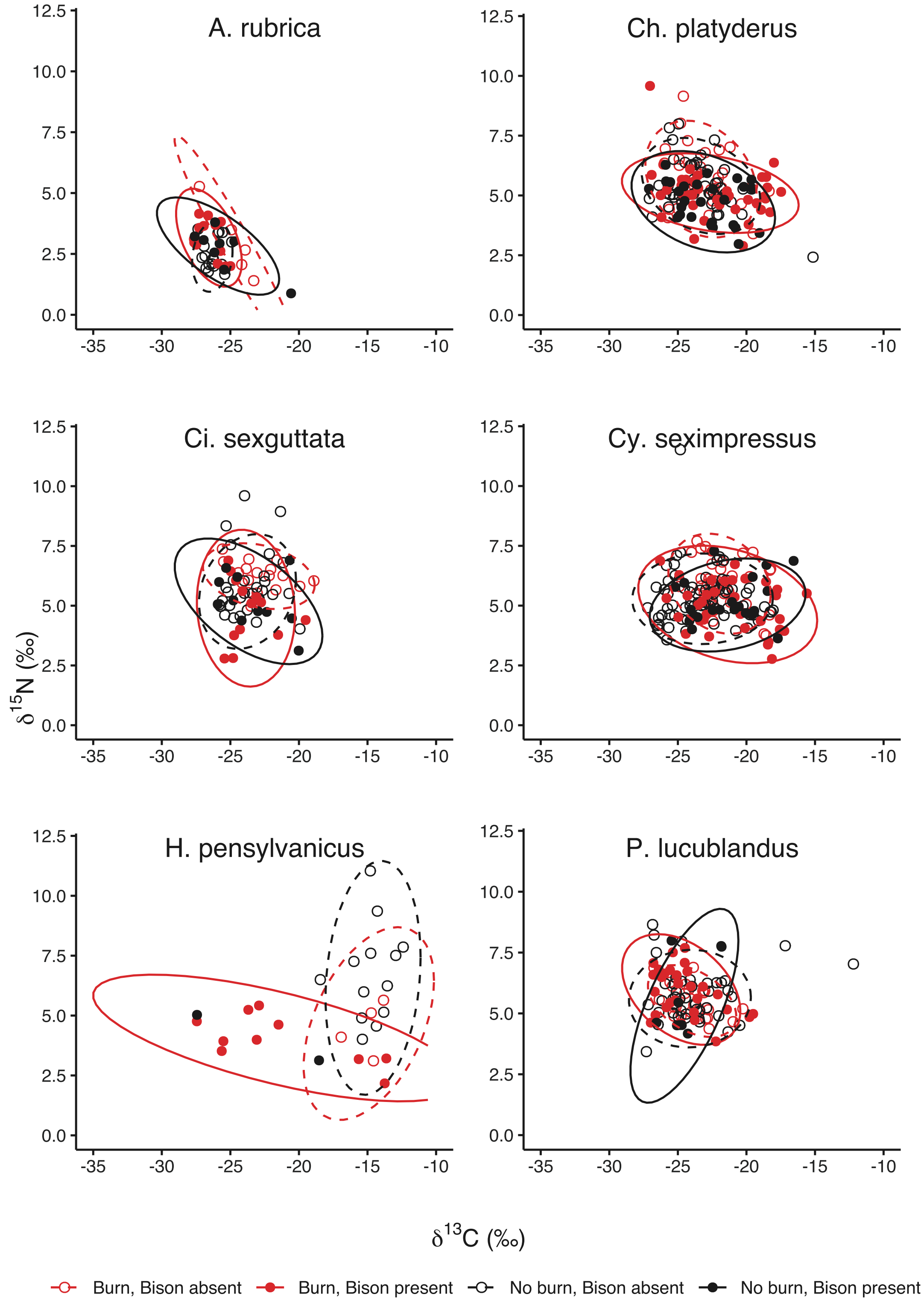

Fig. 3. Isotopic niche size of the six carabid species across site treatments. Ellipses encompass approximately 95% of the data. Lighter points and lines represent prescribed fire present, black represents fire absent; filled points and solid lines represent bison present, open points and dashed lines represent bison absent.

microbial activity (Ojima et al 1990, McCarron and Knapp 2003). These changes can lead to greater total productivity of prairies after fire by as much as 300% because of increased photosynthesis and biomass from C_4 plants (Hulbert 1969, Vogl 1974), potentially supporting increased diversity of prey items for ground beetles. Overall, ground beetles in restored tallgrass prairie used a wide range of food items, as demonstrated by the large variation in stable isotope values within and among species, but particularly when the disturbances of grazing and fire were combined. However, when the prescribed fire was applied in the absence of bison, the trophic niche areas of

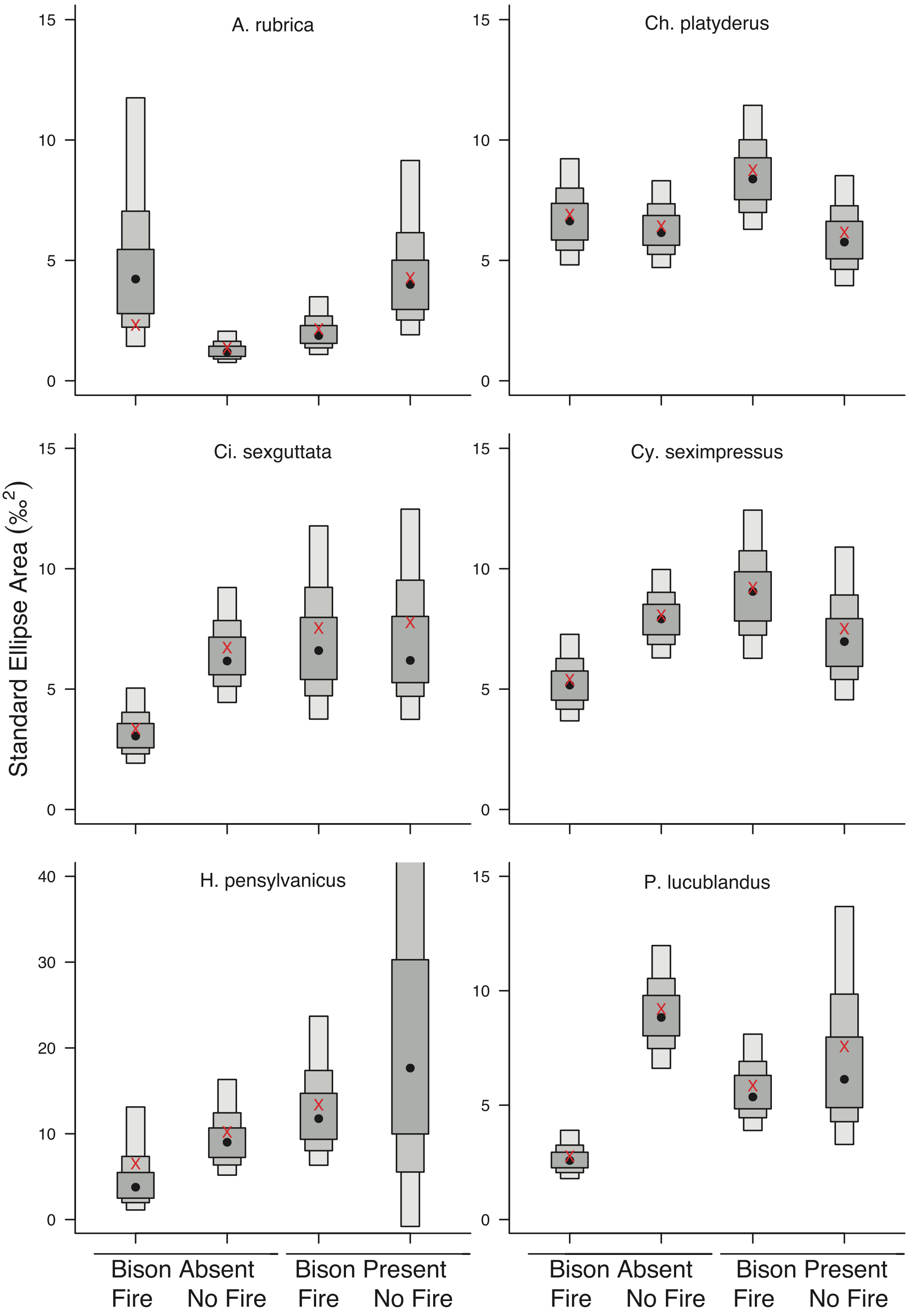

Fig. 4. Posterior estimates of the Bayesian standard ellipse areas (SEA_B) with 95%, 75%, and 50% credible intervals (light to dark grey), and with mode indicated by the black point for each species. Maximum-likelihood estimates for the corresponding SEA_C (Fig. 2) are indicated by x.

four species (*Ci. sexguttata, Cy. seximpressus, H. pensylvanicus,* and *P. lucublandus*) were reduced by 41–56%. Fire alone generally promotes a small number of prairie plant species and homogenizes vegetation structure (Collins and Gibson 1990; McCarron and Knapp 2003), and this homogeneity likely reduced prey diversity under these conditions so that these four species were feeding on the same limited subset of the arthropod community that could thrive in the post-fire environment.

Shifts in mean stable isotope values can help reveal the nature of trophic niche expansions. For example, increased trophic niche area of *Ci. sexguttata* in the presence of bison was associated with reduced mean δ^{15}N values. This is the most predatory species in this study (Larochelle and Larivière 2001), and together, these results suggest that *Ci. sexguttata* expanded its diet in bison sites to include more prey items from lower trophic levels (Okuzaki et al. 2010). A study of arthropods in bison wallows found that granivore abundance was higher outside of active bison wallows, while specialist carnivores were more abundant within them (Nickell et al. 2018), meaning wallows might be successful hunting locations for predators that move into the open spaces. The structural heterogeneity resulting from bison activities could also assist *Ci. sexguttata,* whose ambush-hunting is facilitated by the small-scale steep temperature and light gradients that occur with light gaps (Hadley and Schultz 1987). Although we lack detailed inventories for most invertebrate groups, preliminary analysis of bycatch from pitfall traps suggests that Orthoptera may be more abundant in sites with bison at Nachusa (Barber, unpubl. data). *Cicindela sexguttata* has not been observed eating Orthopterans (Larochelle and Larivière 2001), but if their abundance reflects the population of other herbivorous insects, herbivores might be more common diet items in bison sites, explaining the niche expansion and reduced trophic position of this predatory beetle. Prescribed fire seems to reduce spider abundances based on these same pitfall traps, but the reduction of these potential competitors apparently did not facilitate ground beetle diet expansion given that fire alone reduced trophic niche area for four species, nor did fire reduce trophic position through the loss of these high- δ^{15}N prey items.

We predicted that bison presence would increase the range of δ^{13}C value values and decrease average δ^{13}C signatures in ground beetle diets by promoting an increase of C_3 plant species as basal food resources. However, mean vegetation δ^{13}C values did not change in response to bison presence as we predicted. In the initial years after reintroduction, bison have not uniformly increased plant species diversity or forb cover (Blackburn et al. 2020), and recent diet analysis suggests bison diet shifts between C_3 and C_4 plants across a year (Blackburn et al. 2021). Nonetheless, our predictions were partially confirmed by *H. pensylvanicus,* which exhibited a lower mean and larger range of δ^{13}C values in sites with bison. However, we also found that mean δ^{15}N values were highest in sites where neither disturbance was applied. *H. pensylvanicus* is an omnivorous species, and some individuals appear to be acting primarily as a predator in these bison-free, unburned sites based on their δ^{15}N. Thus, in these conditions *H. pensylvanicus* probably incorporates herbivore and detritivore prey from the soil food web that are feeding on abundant plant litter (Symondson et al. 2000; Ikeda et al. 2010; Mader et al. 2018), whereas in sites with bison and/or prescribed fire, it is primarily granivorous, so isotopic signature changes for this beetle species are more likely attributed to differences in feeding behavior than isotopic shifts in baseline resources.

Conclusion

Although we found limited effects of management disturbances on ground beetle activity density, bison reintroduction and prescribed fire resulted in differences in trophic position and niche breadth for some beetle species. The changes in beetles' trophic position and niche breadth may be due to increased vegetation patchiness and heterogeneity that results from bison reintroduction and prescribed burns (Collins and Gibson 1990; Knapp et al. 1999; Joern 2005). Additionally, beetle morphology (especially flight ability) and environmental preferences may play a role in the magnitude of response to these disturbances. The expansion in isotopic, and thus trophic, niche in some ground beetle species might result from the increased abundance of diverse prey items, or it may signal an adaptation to changes in intraspecific competition caused by a decrease in preferred food sources following disturbance-induced vegetation changes. Because of this competition, niche expansion may occur when individuals use previously ignored or novel resources, lessening the intensity of the competition (Svanbäck and Perrson 2009; Agashe and Bolnick 2012). As habitat disturbances are among the most important variables that shape life-history traits and survival strategies of organisms in fluctuating environments (Lytle 2001), understanding their impacts on consumer ecological roles can help shape successful restoration management practices.

A significant limitation of this study is that stable isotope profiles cannot discriminate between different food resources with similar isotopic values, and ground beetles with similar isotopic profiles may not necessarily be using the same food resources (Birkhofer et al. 2017). Increased sampling of potential food items, especially the enormous diversity of grassland arthropods, would allow for the application of mixing model analysis to more precisely identify diet constituents. In particular, intraguild predation is known in some ground beetles, so carnivorous invertebrates should be included as possible diet items (Thiele 1977). Reconstructing dietary makeup with high precision ultimately will require multiple types of evidence, such as field observations and DNA barcoding of gut contents (Von Berg et al. 2008). Our methods also aggregated beetles across a year, which could mask changes in disturbance-driven food web effects that occur from spring to fall due to changes in habitat structure or prey item availability (Ikeda et al. 2010). More frequent focal sampling throughout the growing season would be necessary to understand if phenological shifts in trophic roles and if these are moderated by disturbances. Combined approaches like these will help reveal food web dynamics under habitat management, and the potential ecosystem consequences of these dynamics.

Restoration managers need to set clear goals for habitat projects (Hobbs and Harris 2001), and consideration of insect trophic roles should be incorporated into decision-making. To promote generalist predation in disturbance-dependent habitats, managers should carefully evaluate disturbance schedules, especially where multiple disturbances can interact. In tallgrass prairie, efforts to reintroduce bison to their historic range, in combination with prescribed fire, will not only increase plant diversity and structural heterogeneity but also may facilitate shifts in beetle diets that allow them to fill a wider range of predatory roles. This may be important in isolated reserves where dispersal limitations will slow the colonization of predatory species (Barber et al. 2017, Nelson et al. 2021). Expanded diet niches of species already present can ensure these roles are filled until other more specialized predators can colonize reserves and establish populations. Additionally, ground beetles can play an important role in post-dispersal seed predation, acting as a mechanism of weed control (Heggenstaller et al. 2006). Higher rates of granivory may be helpful in restorations where non-native weeds are a problem, but only if seed-eating beetles and other arthropods forage on these species (Linabury et al. 2019). Future studies of fire timing and frequency, in combination with bison effects, could elucidate how these disturbances mediate beetle effects on plant distribution through seed consumption (McCravy and Lundgren 2011).

Acknowledgments

We thank B. Patel, and C. Bennett for field and laboratory assistance. We thank R. Lewison and D. Stow for their assistance with revision and editing, and two anonymous reviewers for their helpful comments. We are indebted to the volunteers and staff at The Nature Conservancy's Nachusa Grasslands, especially B. Kleiman, C. Considine, and E. Bach. This project was supported by NSF-DEB #1647502 and the Friends of Nachusa Grasslands. A. U. R and N. A. B conceived and designed the project, N. A. B. and H. P. J. designed and led field sampling, A. U. R. analyzed data and led the writing of the manuscript with contributions from all of the authors. 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 funding agencies.

References Cited

Agashe, D., and D. I. Bolnick. 2012. Dietary niche and population dynamic feedbacks in a novel habitat. Oikos. 121: 347–356.

Anderson, R. C. 2006. Evolution and origin of the Central Grassland of North America: climate, fire, and mammalian grazers. J. Torrey Bot. Soc. 133: 626–648.

Anjum-Zubair, M., M. H. Entling, A. Bruckner, T. Drapela, and T. Frank. 2015. Differentiation of spring carabid beetle assemblages between semi-natural habitats and adjoining winter wheat. Agric. For. Entomol. 17: 355–365.

Arnett, R. H., M. C. Thomas, P. E. Skelley, and J. H. Frank. 2002. American Beetles, Volume II: Polyphaga: Scarabaeoi- dea through Curculionoidea, 1st ed. CRC Press, Boca Raton, FL.

Baer, S. G., D. J. Gibson, and L. C. Johnson. 2019. Restoring grassland in the context of climate change, pp. 310–322. *In* D. J. Gibson and J. A. Newman (eds.), Grasslands and Climate Change. Cambridge University Press.

Ball, G. E. and Y. Bousquet. 2001. American Beetles 1. Archostemata, Myxophaga, Adephaga, Polyphaga: Staphyliniformia. CRC Press, Boca Raton, FL.

Barber, N. A., H. P. Jones, M. R. Duvall, W. P. Wysocki, M. J. Hansen, and D. J. Gibson. 2016. Phylogenetic diversity is maintained despite richness losses over time in restored tallgrass prairie plant communities. J. Appl. Ecol. 54: 137–144.

Barber, N. A., K. A. Lamagdeleine-Dent., J. E. Willand, H. P. Jones. and K. W., McCravy. 2017. Species and functional trait re-assembly of ground beetle communities in restored grasslands. Biodivers. Conserv. 26: 3481–3498.

Barber, N. A., A. K. Farrell, R. C. Blackburn, J. T. Bauer, A. M. Groves, L. A. Brudvig, and H. P. Jones. 2019. Grassland restoration characteristics influence phylogenetic and taxonomic structure of plant communities and suggest assembly mechanisms. J. Ecol. 107: 2105–2120.

Bargmann, T., E. Heegaard, B. A. Hatteland, J. D. Chipperfield and J. A. Grytnes. 2016. Species trait selection along a prescribed fire chronosequence. Insect Conserv. Divers. 9: 446–455.

Birkhofer, K., A. Fließbach, D. H. Wise, and S. Scheu. 2011. Arthropod food webs in organic and conventional wheat farming systems of an agricultural long-term experiment: a stable isotope approach. Agric. For. Entomol. 13: 197–204.

Birkhofer, K., J. Ekroos, E. Corlett, and H. G. Smith. 2014. Winners and losers of organic cereal farming in animal communities across Central and Northern Europe. Biol. Conserv. 175: 25–33.

Birkhofer, K., H. Bylund, P. Dalin, O. Ferlian, V. Gagic, P. A. Hambäck, M. Klapwijk, L. Mestre, E. Roubinet, M. Schroeder, *et al.* 2017. Methods to identify the prey of invertebrate predators in terrestrial field studies. Ecol. Evol. 7: 1942–1953.

Blackburn, R. C., N. A. Barber, and H. P. Jones. 2020. Plant community shifts in response to fire and bison in a restored tallgrass prairie. Nat. Areas J. 40: 218–227.

Bousquet, Y. 2010. Illustrated identification guide to adults and larvae of Northeastern North America ground beetles. Pensoft Publishgint, Sofia, Bulgaria.

Briggs, J. M. and A. K. Knapp. 1995. Interannual variability in primary production in tallgrass prairie: climate, soil moisture, topographic position, and fire as determinants of aboveground biomass. Am. J. Bot. 82: 1024–1030.

Chapman, K., M. White, R. Johnson, and Z. M. Zong. 1990. An approach to evaluate long-term survival of the tallgrass prairie ecosystem. The Nature Conservancy, Midwest Regional Office, Minneapolis, MN, USA.

Ciegler, J. C. 2000. Ground beetles and wrinkled bark beetles of South Carolina: (Coleoptera: Geadephaga: Carabidae and Rhysodidae). Clemson University, Clemon, SC, USA.

Collins, S. L. 1987. Interaction of disturbances in tallgrass prairie: a field experiment. Ecology. 68: 1243–1250.

Collins, S. L. and D. J. Gibson. 1990. Effects of fire in community structure in tallgrass and mixed-grass prairie. *In* S. L. Colling and L. L. Wallace (eds.), Fire in North American tallgrass prairies. University of Oklahoma Press, Norman, OK.

Copeland, T. E., W. Sluis, and H. F. Howe. 2003. Fire season and dominance in an Illinois tallgrass prairie restoration. Restor. Ecol. 10: 315–323.

Crotty, F. V., S. M. Adl, R. P. Blackshaw, and P. J. Murray. 2012. Using stable isotopes to differentiate trophic feeding channels within soil food webs. J. Eukaryot. Microbiol. 59: 520–526.

da Silva, P. M., C. A. Aguiar, J. Niemelä, J. P. Sousa, and A. R. Serrano. 2008. Diversity patterns of ground-beetles (Coleoptera: Carabidae) along a gradient of land-use disturbance. Agric. Ecosyst. Environ. 124: 270–274.

Den Boer, P. J. 1970. On the significance of dispersal power for populations of carabid-beetles (Coleoptera, Carabidae). Oecologia. 4: 1–28.

Ehrenreich, J. H. and J. M. Aikman. 1957. Effect of burning on seedstalk production of native prairie grasses. Proc. Iowa Acad. Sci. 64: 205–212.

Elson, A. and, D. C. Hartnett. 2017. Bison increase the growth and reproduction of forbs in tallgrass prairie. Am. Midl. Nat. 178: 245–260.

Farrell, A. K. 2018. Effects of management on functional diversity in restored tallgrass prairie plant communities. MS thesis. Northern Illinois University, DeKalb, IL, USA.

Fox, J., M. Friendly, and S. Weisberg. 2013. Hypothesis tests for multivariate linear models using the car package. R. J. 5: 39–52.

Fry, B. 2006. Stable isotope ecology. Springer, New York, NY.

Fuhlendorf, S. D., and D. M. Engle. 2001. Restoring heterogeneity on rangelands: ecosystem management based on evolutionary grazing patterns. BioScience. 51: 625–632.

Gaines, H. R., and C. Gratton. 2010. Seed predation increases with ground beetle diversity in a Wisconsin (USA) potato agroecosystem. Agric. Ecosyst. Environ. 137: 329–336.

Gibson, D. J. 2009. Grasses and grassland ecology. Oxford University Press, Oxford, UK.

Goncharov, A. A., M. Zalewski, D. Dudek-Godeau, J.-F. Godeau, P. Sienkiewicz, W. Ulrich, and A. V. Tiunov. 2015. Sex-related variation in δ15N values of ground beetles (Coleoptera, Carabidae): A case study. Pedobiologia. 58: 147–151.

Hadley, N. F., and T. D. Schultz. 1987. Water loss in three species of tiger beetles (Cicindela): correlations with epicuticular hydrocarbons. J. Insect Physiol. 33: 677–682.

Hansen, M. J. and D. J. Gibson. 2014. Use of multiple criteria in an ecological assessment of a prairie restoration chronosequence. Appl. Veg. Sci. 17: 63–73.

Harper, M. G., C. H. Dietrich, R. L. Larimore, and P. A. Tessene. 2000. Effects of prescribed fire on prairie arthropods: an enclosure study. Nat. Areas J. 20: 325–335.

Hartnett, D. C., 1991. Effects of fire in tallgrass prairie on growth and reproduction of prairie coneflower (Ratibida columnifera: Asteraceae). Am. J. Bot. 78: 429–435.

Hartnett, D. C. and P. A. Fay. 1998. Plant populations; patterns and processes, pp. 81–100. *In* A. K. Knapp, J. M. Briggs, D. C. Hartnett, and S. L. Collins (eds.), Grassland dynamics: long-term ecological research in tallgrass prairie. Oxford University Press, New York, NY.

Harvey, J. A., W. H. van der Putten, H. Turin, R. Wagenaar, and T. M. Bezemer. 2008. Effects of changes in plant species richness and community traits on carabid assemblages and feeding guilds. Agric. Ecosyst. Environ. 127: 100–106.

Heggenstaller, A. H., F. D. Menalled, M. Liebman, and P. R. Westerman. 2006. Seasonal patterns in post-dispersal seed predation of Abutilon theophrasti and Setaria faberi in three cropping systems. J. Appl. Ecol. 43: 999–1010.

Higgins, K. F. 1986. Interpretation and compendium of historical fire accounts in the Northern Great Plains. Fish and Wildlife Service Resource Publication 161, United States Department of the Interior, Washington, DC.

Hobbs, R. J. and J. A. Harris. 2001. Restoration ecology: repairing the earth's ecosystems in the new millennium. Restor. Ecol. 9: 239–246.

Hoekstra, J. M., T. M. Boucher, T. H. Ricketts, and C. Roberts. 2005. Confronting a biome crisis: global disparities of habitat loss and protection. Ecol. Let. 8: 23–29.

Holl, K., 2020. Primer of ecological restoration. Island Press, Washington, DC.

Holmes, N., D. Smith, and A. Johnston. 1979. Effect of grazing by cattle on the abundance of grasshoppers on fescue grassland. Rangel. Ecol. Manag. 32: 310–311.

Hood-Nowotny, R. and B. G. Knols. 2007. Stable isotope methods in biological and ecological studies of arthropods. Entomol. Exp. App. 124: 3–16.

Hosler, S. C., H. P. Jones, M. Nelson, and N. A. Barber. 2020. Management actions shape dung beetle community structure and functional traits in restored tallgrass prairie. Ecol. Entomol.

Howe, H. F. 1995. Succession and fire season in experimental prairie plantings. Ecology 76: 1917–1925.

Hulbert, L. C. 1969. Fire and litter effects in undisturbed bluestem prairie in Kansas. Ecology. 50: 874–877.

Ikeda, H., K. Kubota, A. Kagawa, and T. Abe. 2007. Flight capabilities and feeding habits of silphine beetles: are flightless species really 'carrion beetles?'. Ecol. Res. 22: 237–241.

Ikeda, H., K. Kubota, A. Kagawa, and T. Sota. 2010. Diverse diet compositions among harpaline ground beetle species revealed by mixing model analyses of stable isotope ratios. Ecol. Entomol. 35: 307–316.

Jackson, A. L., R. Inger, A. C. Parnell, and S. Bearhop. 2011. Comparing isotopic niche widths among and within communities: SIBER–Stable Isotope Bayesian Ellipses in R. J. Anim. Ecol. 80: 595–602.

Jackson, A., A. Parnell, and M. A. Jackson. 2017. Package 'SIBER'. Stable Isotope Bayesian Ellipses in R.

Joern, A. 2005. Disturbance by fire frequency and bison grazing modulate grasshopper assemblages in tallgrass prairie. Ecology. 86: 861–873.

Jones, S. R. and R. C. Cushman. 2004. Field guide to the North American prairie. Houghton Mifflin, Boston, MA.

Kimmerer, R. W., F. K. Lake. 2001. The role of indigenous burning in land management. J. Forestry. 99: 36–41.

Knapp, A. K., J. Blair, J. Briggs, S. Collins, D. Hartnett, L. Johnson, and E. Towne. 1999. The keystone role of bison in North American tallgrass prairie. BioScience. 49: 39–50.

Knopf, F. L. 1996. Prairie legacies-birds, p. 135–148. *In* F. B. Sampson and F. L. Knopf (eds.), Prairie Conservation. Island Press, Washington, DC.

Koerner, S. E., and S. L. Collins. 2014. Interactive effects of grazing, drought, and fire on grassland plant communities in North America and South Africa. Ecology. 95: 98–109.

Krueger, K., 1986. Feeding relationships among bison, pronghorn, and prairie dogs: an experimental analysis. Ecology. 67: 760–770.

Larochelle, A., and M.-C. Larivière. 2001. Natural history of the tiger beetles of North America north of Mexico. Cicindela. 33: 41–162.

Larochelle, A., and M.-C. Larivière. 2003. Natural history of the ground-beetles (Coleoptera: Carabidae) of America north of Mexico. Pensoft, Sofia, Bulgaria.

Larsen, K. J. and T. J. Work. 2003. Differences in ground beetles (Coleoptera: Carabidae) of original and reconstructed tallgrass prairies in northeastern Iowa, USA, and impact of 3-year spring burn cycles. J. Insect Conserv. 7: 153–166.

Linabury, M. C., N. E. Turley, and L. A. Brudvig. 2019. Insects remove more seeds than mammals in first-year prairie restorations. Restor. Ecol. 27: 1300–1306.

Lövei, G. L. and K. D. Sunderland. 1996. Ecology and behavior of ground beetles (Coleoptera: Carabidae). Annu. Rev. Entomol. 41: 231–256.

Luong, J. C., P. L. Turner, C. N. Phillipson, and K. C. Seltmann. 2019. Local grassland restoration affects insect communities. Ecol. Entomol. 44: 471–479.

Lytle, D. A. 2001. Disturbance regimes and life-history evolution. Am. Nat. 157: 525–536.

Mader, V., E. Diehl, V. Wolters, and K. Birkhofer. 2018. Agri-environmental schemes affect the trophic niche size and diet of common carabid species in agricultural landscapes. Ecol. Entomol. 43: 823–835.

Masters, G. J., V. K. Brown, and A. C. Gange. 1993. Plant mediated interactions between above-and below-ground insect herbivores. Oikos. 66: 148–151.

McCarron, J. K. and A. K. Knapp. 2003. C3 shrub expansion in a C4 grassland: positive post-fire responses in resources and shoot growth. Am. J. Bot. 90: 1496–1501.

McConkey, K. R., S. Prasad, R. T. Corlett, A. Campos-Arceiz, J. F. Brodie, H. Rogers, and L. Santamaria. 2012. Seed dispersal in changing landscapes. Biol. Conserv. 146: 1–13.

McCravy K. W. and J. G. Lundgren. 2011. Carabid beetles (Coleoptera: Carabidae) of the Midwestern United States: a review and synthesis of recent research. Terr. Arthropod. Rev. 4: 63–94.

McMillan, B. R., K. A. Pfeiffer, and D. W. Kaufman. 2011. Vegetation responses to an animal-generated disturbance (bison wallows) in tallgrass prairie. Am. Midl. Nat. 165: 60–74.

McNabb, D. M., J. Halaj, and D. H. Wise. 2001. Inferring trophic positions of generalist predators and their linkage to the detrital food web in agroecosystems: a stable isotope analysis. Pedobiologia 45: 289–297.

Messer, P. W. 2009. An annotated checklist of Wisconsin ground beetles (Coleoptera: Carabidae). Great Lakes Entomol. 42: 30–61.

Michel, M. J., and M. M. Adams. 2009. Differential effects of structural complexity on predator foraging behavior. Behav. Ecol. 20: 313–317.

Moran, M. D. 2014. Bison grazing increases arthropod abundance and diversity in a tallgrass prairie. Environ. Entomol. 43: 1174–1184.

Nelson, M., S. C. Hosler, F. A. Boetzl, H. P. Jones, and N. A. Barber. 2021. Reintroduced grazers and prescribed fire effects on beetle assemblage structure and function in restored grasslands. Ecol. Appl. 31: e02217.

Nickell, Z., S. Varriano, E. Plemmons, and M. D. Moran. 2018. Ecosystem engineering by bison (Bison bison) wallowing increases arthropod community heterogeneity in space and time. Ecosphere. 9: e02436.

Ojima, D. S., W. J. Parton, D. S. Schimel, and C. E. Owensby. 1990. Simulated impacts of annual burning on prairie ecosystems, pp. 118–132. *In* L. Wallace and S. Collins (eds.), Fire in tallgrass prairie ecosystem. University of Oklahoma Press, Norman, OK.

Okuzaki, Y., I. Tayasu, N. Okuda, and T. Sota. 2010. Stable isotope analysis indicates trophic differences among forest floor carabids in Japan. Entom. Exp. Appl. 135: 263–270.

Packard, S. and C. F. Mutel.1997. The tallgrass restoration handbook: for prairies, savannas, and woodlands. In 12th North American Prairie Conference, University of Northern Iowa (USA), 1990. Island Press.

Panzer, R. 2002. Compatibility of prescribed burning with the conservation of insects in small, isolated prairie reserves. Conserv. Biol. 16: 1296–1307.

Pfeiffer, K. E., and D. C. Hartnett. 1995. Bison selectivity and grazing response of little bluestem in tallgrass prairie. Rangel. Ecol. Manag. 48: 26–31.

Plummer, M. 2013. JAGS Version 3.4. 0 user manual. http://www.stats.ox.ac.uk/~nicholls/MScMCMC14/jags_user_manual.pdf

Post, D. M. 2002. Using stable isotopes to estimate trophic position: models, methods, and assumptions. Ecology. 83: 703–718.

Purtauf, T., J. Dauber, and V. Wolters. 2004. Carabid communities in the spatio-temporal mosaic of a rural landscape. Landsc Urban Plan. 67: 185–193.

Purtauf, T., I. Roschewitz, J. Dauber, C. Thies, T. Tscharntke, and V. Wolters. 2005. Landscape context of organic and conventional farms: influences on carabid beetle diversity. Agric. Ecosyst. Environ. 108: 165–174.

Rosas, C. A., D. M. Engle, J. H. Shaw, and M. W. Palmer. 2008. Seed dispersal by Bison bison in a tallgrass prairie. J. Veg. Sci. 19: 769–778.

Sasakawa, K., H. Ikeda, and T. Kubota. 2010. Feeding ecology of granivorous carabid larvae: a stable isotope analysis. J. Appl. Entomol. 134: 116–122.

Stoner, K. J., and A. Joern. 2004. Landscape vs. local habitat scale influences to insect communities from tallgrass prairie remnants. Ecol. Appl. 14: 1306–1320.

Svanbäck, R., and L. Persson. 2009. Population density fluctuations change the selection gradient in Eurasian perch. Am. Nat. 173: 507–516.

Symondson, W. O., D. M. Glen, M. L. Erickson, J. E. Liddell, and C. J. Langdon. 2000. Do earthworms help to sustain the slug predator Pterostichus melanarius (Coleoptera: carabidae) within crops? Investigations using monoclonal antibodies. Mol. Ecol. 9: 1279–1292.

Thiele, H. U. 1977. Differences in measurement of day-length and photoperiodism in two stocks from subarctic and temperate climates in the Carabid beetle Pterostichus nigrita F. Oecologia. 30: 349–365.

Tscharntke, T., I. Steffan-Dewenter, A. Kruess, and C. Thies. 2002. Contribution of small habitat fragments to conservation of insect communities of grassland–cropland landscapes. Ecol. Appl. 12: 354–363.

Vanbergen, A. J., B. A. Woodcock, M. Koivula, J. Niemelä, D. J. Kotze, T. Bolger, V. Golden, F. Dubs, G. Boulanger, J. Serrano, *et al*. 2010. Trophic level modulates carabid beetle responses to habitat and landscape structure: a pan-European study. Ecol. Entomol. 35: 226–235.

Vogl, R. 1974. Effect of fire on grasslands, pp. 139–195. *In* T. T. Kozlowski and C. E. Ahlgren (eds.), Fire and ecosystems. Academic Press, New York, NY.

von Berg, K., M. Traugott, W. O. Symondson, and S. Scheu. 2008. The effects of temperature on detection of prey DNA in two species of carabid beetle. Bull. Entomol. Res. 98: 263–269.

Weisser, W. W., and E. Siemann, editor. **2008**. The various effects of insects on ecosystem functioning, pp. 3–24. Insects and ecosystem function. Springer, New York, USA.

White, R., S. Murray, and M. Rohweder. 2000. Pilot analysis of global ecosystems: Grassland ecosystems. World Resources Institute, 10 G Street NE, Washington, DC, 100 p.

Wise, D. H., D. M. Moldenhauer, and J. Halaj. 2006. Using stable isotopes to reveal shifts in prey consumption by generalist predators. Ecol. Appl. 16: 865–876.

Wodika, B. R., and S. G. Baer. 2015. If we build it, will they colonize? A test of the field of dreams paradigm with soil macroinvertebrate communities. Appl. Soil Ecol. 91: 80–89.

Zalewski, M., D. Dudek, A. V. Tiunov, J. F. Godeau, Y. Okuzaki, H. Ikeda, P. Sienkiewicz, and W. Ulrich. 2014. High niche overlap in the stable isotope space of ground beetles. Ann. Zool. Fenn. 51: 301–312.