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ORIGINAL PAPER

Species and functional trait re-assembly of ground beetle communities in restored grasslands

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Abstract Ecosystem restoration provides unique opportunities to study community dynamics under succession and can reveal how consumer communities re-assemble and respond to successional changes. Studying community dynamics from both taxonomic and functional trait perspectives also may provide more robust assessments of restoration progress or success and allow cross-system comparisons. We studied ground beetle (Coleoptera: Carabidae) communities for three years in a restored grassland chronosequence with sites from 0 to 28 years old. We measured traditional community metrics (abundance, richness, Shannon diversity) and functional trait metrics based on species' body length, wing morphology, activity time, phenology, and diet. Communities had high species richness and abundance in early successional stages, but these declined in later stages to low levels comparable to an adjacent grassland remnant. Species composition also shifted with time, converging with the remnant. Although functional richness, like species richness, declined as succession progressed, functional divergence quickly increased and was maintained over time, suggesting niche differentiation in established communities. Young sites were typified by small, macropterous, phytophagous species,

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while older sites contained larger species more likely to be flightless and carnivorous. Prescribed burns also affected traits, decreasing prevalence of larger species. This study demonstrates that functionally diverse consumer communities can self-assemble under restoration practices. In a relatively short amount of time both morphological and trophic level diversity are established. However, prescribed fire intended to control non-desirable plants may also shape beetle community functional composition, and restoration managers should consider if plant community benefits of fire outweigh potential declines in consumer function.

Introduction

The process of ecological succession in temperate grasslands has been long-studied and has played an important role in the development of ecological theory (Clements 1916; Gleason 1927). This knowledge has also been used to inform and guide ecosystem restoration (Palmer et al. 1997; Young et al. 2001), acknowledging that restoration management is an effort to steer successional processes toward a particular goal. Thus ecosystem restoration projects provide opportunities to examine community assembly processes (Young et al. 2001). This is particularly the case for consumer communities, as most terrestrial restoration is focused on active establishment and management of plant communities (Hobbs and Norton 1996; WallisDeVries et al. 2002; Van Andel and Aronson 2012; McAlpine et al. 2016) under the assumption that consumer communities re-assemble passively (Hilderbrand et al. 2005).

Studying community assembly from both taxonomic and functional trait perspectives may reveal more general mechanisms or patterns of community change in restored habitats because communities that differ in taxonomic composition can still be linked by common functional traits of those species (Díaz et al. 2001; Kahmen and Poschlod 2004). Functional traits are the measureable features of individuals that can affect fitness and performance (Violle et al. 2007), and they may also be useful in predicting which species will colonize and persist during succession, as abiotic and biotic filters operate on traits to determine colonization and establishment (McGill et al. 2006; Lebrija-Trejos et al. 2010; Woodcock et al. 2012). For example, when natural habitats or restoration projects undergoing succession are geographically isolated from other areas of similar habitat, dispersal ability and the morphological or physiological traits related to it may play important roles in shaping the composition of restored communities of both plants and consumers. Traditional species diversity measurements, like species richness, are important community metrics and can predict functions such as primary productivity, but functional trait composition may better describe the contribution to ecosystem function provided by a particular taxonomically- or ecologically-defined community (Díaz et al. 2006; McGill et al. 2006; Vandewalle et al. 2010; de Bello et al. 2010; Woodcock et al. 2014).

Given the important contributions of consumers to ecosystem function (Duffy 2002), evaluating the re-assembly of consumer communities in restored habitats from a functional trait perspective may help in our understanding of how ecosystem functions are established under both succession and restoration (Murdock et al. 2010). Yet consumer community assembly is relatively understudied when compared to the extensive research on the relationships between plant community structure, traits, and functions (Kahmen and

Poschlod 2004; de Bello et al. 2010; Moretti et al. 2013; Fountain-Jones et al. 2015). We focused on ground beetles (Coleoptera: Carabidae), a diverse family of insects that occupy a wide range of ecological niches in terrestrial ecosystems and that are often considered functionally important (Kromp 1999; McCravy and Lundgren 2011). Carnivorous species prey upon other arthropods and may contribute to pest control (Hance 1987; Lang et al. 1999; Lang 2003). Seed-eating species may control weeds in agriculture (Honek et al. 2007; Lundgren 2009; Gaines and Gratton 2010) and influence plant community composition. Past research on ground beetles has identified potentially informative functional traits that may vary with environmental changes ("response traits," sensu Violle et al. 2007), such as habitat disturbance due to flooding events (Gerisch et al. 2012) or the successional changes following ecosystem restoration.

Studying consumer community succession in ecosystem restorations can also inform practitioners and land managers, who often seek comprehensive assessments of restoration success but lack information about consumer communities because of the historical focus of ecosystem restoration on plants (Hobbs and Norton 1996; Van Andel and Aronson 2012; McAlpine et al. 2016). Knowledge of consumer community recovery in active habitat restorations is especially limited for invertebrates (Pöyry et al. 2004, 2009; WallisDeVries and Ens 2010; Woodcock et al. 2014; Wodika and Baer 2015). In the Midwest U.S., ecosystem restoration projects frequently attempt to re-create habitats resembling the historical tallgrass prairie, an enormous formerly contiguous ecosystem that has been largely converted to agriculture (Samson and Knopf 1994, 1996). Tallgrass prairie restoration projects typically start with agricultural fields or pastures, eliminate crops and other existing vegetation, and add a seed mix of native species (Packard et al. 1997). Managers use prescribed fire in fall or spring to mimic natural disturbances, reduce exotic weed populations, and drive plant community succession toward a compositional goal. Over time, most restorations see declines in plant species richness and diversity, with cover of grasses (especially warm-season C_4 grasses) increasing at the expense of forbs (Sluis 2002; Carter and Blair 2012; Grman et al. 2013; Hansen and Gibson 2014). For this reason most managers consider improvement of forb establishment and growth to be the primary goal of management activities like burning, mowing, and grazing (Rowe 2010). But it is not known if the consumer communities that inhabit these restorations follow a similar pattern of decline in richness or diversity.

Here we examine ground beetle community assembly in restored tallgrass prairie using a restoration succession chronosequence, describing beetles from both taxonomic- and trait-composition perspectives. The use of a chronosequence, or a space-for-time substitution (Pickett 1989), allows us to observe beetle communities typical of restored prairies at different times since restoration and document successional changes in beetle communities. We test three specific hypotheses: (1) The abundance and richness of ground beetles will increase during the first three decades after grassland restoration as more species arrive and establish (Pöyry et al. 2006; Dahms et al. 2010; Noordwijk et al. 2017). (2) Ground beetle community similarity among restorations will be spatially correlated because colonization relies on dispersal from nearby sites. (3) Functional trait diversity (broadly defined) of these communities will increase over this same period, as colonizing species incorporate a wider range of trait values into the community (Woodcock et al. 2012).

Materials and methods

Study site and chronosequence

The study was conducted at Nachusa Grasslands, a large-scale restoration project owned and managed by The Nature Conservancy (TNC). Most of the preserve contains restored tallgrass prairies with interspersed remnants that were never ploughed. Restoration of agricultural fields (generally corn/soy rotation) to diverse native grassland vegetation began in 1987. Restoration and management techniques have remained consistent across the preserve, including seeding with locally collected seeds and prescribed burns on a 1–3 years rotation. Annual exotic weed control focuses on a set of high-priority invasive species, including sweetclovers (*Melilotus* spp.) and Canada thistle (*Cirsium arvense*) that are sprayed with herbicides during annual monitoring (Barber et al. 2016). More details on site and management history are in Hansen and Gibson (2014), Wodika et al. (2014), and Barber et al. (2016).

In 2013, we selected twelve restored sites (>2 ha each) ranging from the first year of restoration (seeded the previous fall) to 26 years old, with the assistance of site managers who considered these as "successful" restorations, where success means the establishment of diverse native plant species with low exotic species presence (Table 1). The oldest site represents some of the earliest prairie restorations in the region. We also selected an adjacent corn field, representing pre-restoration conditions. In 2014 we added another restoration site (seeded the previous fall) as well as a remnant site that was never converted to rowcrop agriculture. We caution that this remnant has somewhat limited value as a reference site because, like other remnants at Nachusa Grasslands, it is on a rocky slope and was previously grazed by cattle. As in much of the former tallgrass prairie region, remnants are edaphically different with physiognomies that likely differ from the prairies that historically grew around them and are the sites of restoration today. Almost all (>99.9%) tallgrass prairie was converted to agriculture in the region, so true reference remnants do not exist. However, the remnants at Nachusa have received fire and weed

Table 1 Chronosequence sites listing year planted, burn status in each year in which ground beetles were sampled ('–' indicates no sampling in that year), and age range during the study

Site	Year planted	2013	2014	2015	Age range
AG	–	N	N	N	–
HF	2013	–	N	Y*	1–2
HN	2012	N	Y	Y*	1–3
L	2011	Y	Y	Y*	2–4
SB	2009	N	Y	N	4–6
CCW	2008	Y	N	Y	5–7
HW	2008	Y	Y	Y*	5–7
CCE	2007	Y	Y	N	6–8
FC	2006	N	N	N	7–9
TC	2002	N	N	N	11–13
SF	2001	Y	Y	Y	12–14
HLP	2001	Y	Y	N*	12–14
WH	1992	Y	N	Y	21–23
MU	1987	Y	Y	N	26–28
MR	–	–	Y	N	–

'*' indicates bison presence in 2015

control management practices consistent with the restored sites since prior to the earliest restoration plantings, and we include the largest and highest-quality remnant here for comparison. During the study, management practices on all sites continued, and there was no grazing until the third year of the study, when a small bison (*Bison bison*) herd was reintroduced to a portion of Nachusa Grasslands that included five of the twelve restoration sites (Table 1), although the bison spent most of their time in other areas of the preserve than our sites.

Beetle sampling

In each site, we established a pitfall trap array consisting of nine traps (475 mL, 8 cm opening) in a 3 × 3 grid with 5 m between traps. Arrays were re-established each spring in approximately the same location, except for the youngest planting in 2013, when a new array was established in late summer and fall trapping sessions because the original location was inaccessible. All arrays were at least 300 m apart. During each trapping session, all traps were opened on the same day and remained open for the same number of days, and the number of trapping sessions varied among years (see Supplementary Material). Sessions were usually 1–2 weeks in length, but some sessions were ended early if heavy rain was anticipated. Traps that flooded or were disturbed by vertebrates were excluded from trap day totals (total reported in Supplementary Material). All ground beetles were identified using keys (Ciegler 2000; Arnett et al. 2002; Bousquet 2010) and a checklist of an adjacent region (Messer 2009) to species or morphospecies (Oliver and Beattie 1996).

Functional traits

We identified five traits and obtained values for each species documented in the study from literature (Larochelle and Larivière 2003; Bousquet 2010): body length (midpoint of published range), wing morphology (macropterous, brachypterous, dimorphic), activity time (nocturnal, diurnal), breeding season (spring–early summer, late summer–autumn), and adult diet (phytophagous, carnivorous, omnivorous) (see Supplementary Materials). Following the framework of Fountain-Jones et al. (2015), these include all four trait types: morphological (body length, wing morphology), physiological (adult diet), phenological (breeding season), and ecological (activity time). We used these trait data to describe functional trait diversity using four complementary measures: FRic (functional richness), FEve (functional evenness), FDis (functional dispersion), and FDiv (functional divergence) (Mason et al. 2005; Villéger et al. 2008; Laliberté and Legendre 2010; Gerisch et al. 2012) using function dbFD in the FD package in R (Laliberté et al. 2014). Together, these metrics provide a comprehensive, multivariate description of trait diversity in a set of communities, which is important because traits often covary (Retana et al. 2015). FRic is a multidimensional measure of the trait space defined by the most extreme values for each trait in each community. FEve incorporates abundance and describes how evenly distributed individuals are within the multidimensional trait space of a community. FDis is the mean distance between species and the common centroid of the entire community in trait space. It incorporates abundance and is independent of species richness. Finally, FDiv also describes the distribution of the community in trait space, weighted by species abundance, so that FDiv is maximized when more abundant species have more extreme trait values. FDiv reflects niche differentiation, with high values suggesting reduced competition for resources (Mason et al. 2005).

Vegetation sampling

The focus of this project was not to describe the successional plant community changes in tallgrass prairie restorations, because these have been studied in detail by previous researchers both at Nachusa (Hansen and Gibson 2014; Barber et al. 2016) and elsewhere (Sluis 2002; Carter and Blair 2012; Grman et al. 2013). Rather, we wanted to verify that successional variation across our chronosequence mirrored changes previously documented in these other studies, particularly a decline in plant richness and diversity as grass cover increases. This may strengthen the generalizability of our results to other tallgrass prairie sites. In late August 2013, we recorded plant species and percent cover in two randomly-placed 0.5 m^2 quadrats in each site. All vegetation rooted within the frame was included in measurements. Site HF was not included in 2013 surveys because it was not planted until the following fall and SB was not included because it was inaccessible. In 2014 we recorded the same data in a single 1 m^2 quadrat placed at the center of every beetle trap array on 17 July. These surveys occurred at least five months after prescribed fires.

Analyses

We analysed how beetle abundance, rarefied richness, and Shannon diversity change following restoration using generalized linear mixed models (GLMMs), treating age as a continuous fixed predictor, and burn status (whether a site was burned in the previous year) and year as fixed factors. Site was included as a random variable to account for repeated samplings of sites across years, and log(trapdays) was included in abundance models as an offset term to correct for variation in sampling effort among sites and years, following (Kotze et al. 2012). Rarefied richness was calculated using ChaoRichness() in the iNEXT package (Chao et al. 2014). These models did not include values from the agricultural site or the remnant because the goal was to determine how communities change following restoration; agricultural sites are very different habitats and remnants have not undergone restoration. All analyses were carried out in R, using the nlme package (Pinheiro et al. 2014) for Shannon diversity assuming Gaussian error distribution, and the lme4 package (Bates et al. 2012) for abundance and richness (rounded to integers) assuming Poisson error distribution and including an observation-level random factor to account for overdispersion. Fixed factors were evaluated using likelihood ratio tests (Bolker et al. 2009), testing burn status, age, and survey year in that order.

We examined compositional differences among sites using NMDS based on Bray–Curtis dissimilarities to find two-dimensional solutions with the function metaMDS() in vegan (Oksanen et al. 2007), excluding species found only at a single site. We calculated dissimilarities and ordinations for all years combined, and each year individually. We used envfit() in vegan to assess the relationships between environmental variables (age and burn status) and each ordination using the full solution, not individual axis scores, and 10,000 permutations. Envfit() returns R^2 values of the relationships and compares each to a distribution of R^2 values generated by randomly shuffling the order of the environmental variables. We also included bison presence/absence to determine if they influenced beetle community composition in 2015. To examine spatial patterns in ground beetle communities, we used partial Mantel tests to compare Bray–Curtis dissimilarities of all sites within a year to pairwise spatial distances between trapping sites, controlling for age with age coded as 0 for the agricultural site and 50 for the remnant; age and burn patterns

reported below do not differ when the agricultural site and remnant are excluded from analysis (results not shown).

We took two approaches to determining how environmental variables (age and burn status) affected functional traits (response traits). First, we analysed the four functional trait diversity measures (FRic, FEve, FDis, and FDiv) using GLMMs, following the approach described above with Gaussian error distributions. Next we examined if individual traits explained how beetle species responded to environmental variables by calculating the proportion of individuals in each community in each year with a particular trait value for the four qualitative traits (wing morphology, activity time, breeding season, and diet) and the community-weighted mean (CWM) of body length from the function dbFD. We used GLMMs as above to analyse body length CWM. Trait proportion models used binomial error distribution and included an observation-level random factor to account for overdispersion. When a categorical trait had two values (e.g., nocturnal versus diurnal), we used a single model; for traits with three values (e.g., macropterous versus brachypterous versus dimorphic), each trait value was analysed individually.

We used the vegetation sampling data to calculate species richness, Shannon diversity, and percent of non-legume forbs, legumes, and grasses for each site (averaged among quadrats in 2013). These were analysed with GLMMs treating restoration age, burn status, and sampling year as fixed factors, and site as a random factor, and using Gaussian error distributions. This design allows us to account for potential differences in vegetation between years due to both environmental conditions such as weather and the different sampling methodologies employed in the two years. Factors were evaluated with likelihood ratio tests, as above.

Results

Beetle species diversity and composition

We captured 5844 ground beetles representing 56 species/morphospecies in the three years of sampling (see Supplementary Materials). Overall ground beetle abundance was highest in the first two years after restoration and declined significantly in later successional stages (Fig. 1a; Table 2). Burn status had no effect on abundance. Richness declined with age, similar to abundance, with no effect of burn status (Fig. 1b). Neither age nor burn status affected Shannon diversity (Fig. 1c). Both abundance and species richness in the oldest restoration were similar to those values in the remnant site (mean $\pm$ 1 s.e., 0.15 ± 0.02 beetles captured per trapday in oldest restoration versus 0.12 ± 0.05 in remnant; Chao richness: 6.9 ± 2.8 species versus 8.1 ± 2.2 species).

NMDS ordination for all years and individual years (all stresses <0.2) revealed significant relationships with age since restoration (all years, $R^2 = 0.44$, $P < 0.001$) (Fig. 2 and Supplementary Materials), but no effects of burn status (all years, $R^2 = 0.02$, $P = 0.463$) or bison in 2015 ($R^2 = 0.02$, $P = 0.498$). Results for individual years were qualitatively similar, except that burned and unburned sites clustered separately in 2013 ($R^2 = 0.28$, $P = 0.024$). The agricultural field community clustered separate from other sites in all three years. Young sites also tended to have similar communities that were different from older sites, with the exception of one site (site 'L') that ranged from two to four years old in the study years but had a community resembling five- to twelve-year-old sites. The two oldest restoration sites also had communities similar to the remnant (Fig. 2).

Fig. 1 Relationships between **a** abundance, **b** species richness, and **c** Shannon diversity of ground beetle communities and site age in study sites from 2013 to 2015. In all panels, *circles* represent restored sites, *diamonds* are an agricultural field, and *triangles* are a prairie remnant site. *Black lines* indicate overall significant relationship with age. Abundance is presented here as individuals captured per 10 trapdays to aid interpretation, with years color-coded to illustrate annual variation
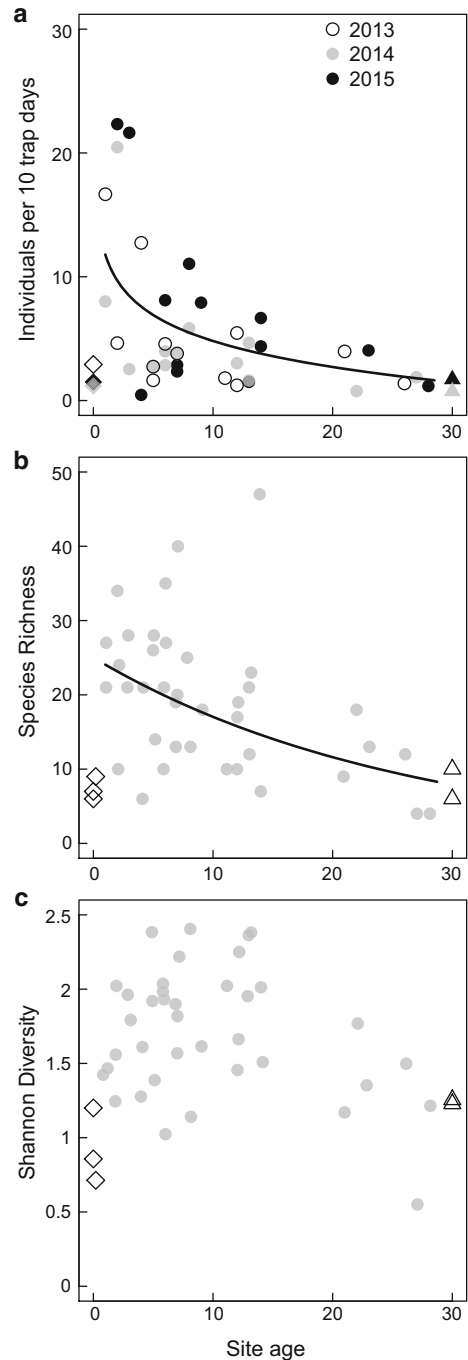
There was a strong spatial pattern in community similarity in 2013 and 2014 as indicated by the partial Mantel tests (Table 3), indicating that sites closer to each other had similar ground beetle communities, controlling for age differences (age and spatial distance

Table 2 Results of GLMMs testing effects of age, burn status, and year on ground beetle community metrics and vegetation measurements in restoration sites

	Site age		Burn status		Year	
	χ^2	P	χ^2	P	χ^2	P
Ground beetles						
Abundance	**6.15**	**0.013**	0.09	0.770	2.53	0.283
Species richness	**8.20**	**0.004**	1.35	0.246	0.81	0.669
Shannon diversity	1.37	0.241	0.00	0.980	0.84	0.657
Plants						
Species richness	3.27	0.071	0.17	0.680	1.41	0.235
Shannon diversity	**5.67**	**0.017**	0.43	0.513	**6.53**	**0.011**
% non-legume forbs	**6.23**	**0.013**	0.25	0.620	**16.95**	**<0.001**
% legumes	1.16	0.281	1.24	0.265	**5.67**	**0.017**
% grasses	**4.18**	**0.041**	0.01	0.994	**7.38**	**0.025**

Fixed factors were evaluated with likelihood ratio tests that approximate a χ^2 distribution

Bold text indicates $P < 0.05$

Fig. 2 Non-metric multidimensional scaling ordination of restored sites (*circles*, with ages), agricultural field (*diamonds*), and remnant site (*triangles*). Individual sites censuses in different years are connected by *gray arrows*, and *large arrow* illustrates significant age vector
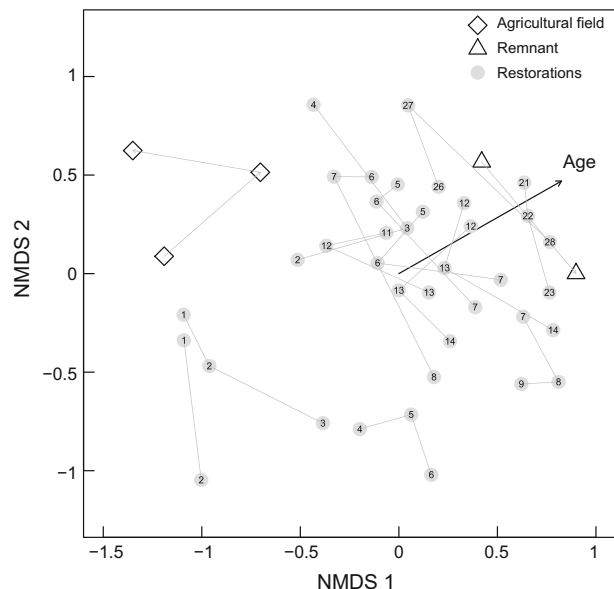
Table 3 Partial mantel results for correlations of spatial distances between sites and Bray–Curtis dissimilarities, controlling for age differences between sites

Study year	All sites		Youngest sites removed	
	Mantel statistic	P	Mantel statistic	P
2013	**0.26**	**0.034**	**0.34**	**0.027**
2014	**0.36**	**0.001**	**0.54**	**0.001**
2015	0.09	0.236	0.05	0.332

In the second analysis, the agricultural site and restorations in the first or second year of growth were removed, strengthening the correlation

Bold text indicates $P < 0.05$

not correlated, P > 0.3 in all years). These patterns were qualitatively the same even if the agricultural site, the remnant, or both were removed (data not shown). Given the compositional differences of young sites revealed by the NMDS analysis, we repeated the partial Mantel tests without the youngest sites (agricultural site and any one- and two-year-old sites in all years). The results were qualitatively similar, but correlations between Bray–Curtis dissimilarities and geographic distances were stronger (Table 3).

Beetle functional traits

Although burn status had no effects on trait diversity measures in restorations, restoration age affected both FRic and FDiv (Table 4; Fig. 3). FRic declined in older plantings, and FDiv increased with age due to low values in the youngest sites. Prescribed burns decreased the community-weighted mean of body length by about 5% in the following year (Table 4). Restoration age significantly affected the prevalence of brachypterous beetles, which were rare in early successional stages where macropterous beetles tended to be more common; body length CWM, which increased as sites aged; and phytophagous beetles,

Table 4 Results of GLMMs testing effects of age and burn status on functional trait diversity measures and on individual traits (proportion of individuals in each community with that trait, or body length community weighted mean)

	Burn status		Site age		Year	
	χ^2	P	χ^2	P	χ^2	P
Trait diversity measures						
FRic	0.30	0.584	**6.09**	**0.014**	**14.47**	**<0.001**
FEve	0.42	0.517	2.60	0.107	2.61	0.271
FDis	0.33	0.566	0.44	0.509	**7.83**	**0.020**
FDiv	0.88	0.348	**5.00**	**0.025**	1.49	0.475
Individual traits						
Wing morphology						
Macropterous	0.08	0.784	2.29	0.130	**20.86**	**<0.001**
Brachypterous	0.00	0.985	**5.69**	**0.017**	3.16	0.206
Dimorphic	0.25	0.614	0.53	0.465	**19.78**	**<0.001**
Body length						
Body length CWM	**4.69**	**0.030**	**5.09**	**0.024**	1.60	0.448
Activity time						
Nocturnal	2.13	0.145	2.05	0.152	**22.34**	**<0.001**
Breeding season						
Spring-early summer	0.20	0.658	0.06	0.804	**11.63**	**0.003**
Adult diet						
Carnivorous	2.66	0.103	0.61	0.434	4.18	0.124
Phytophagous	0.12	0.733	3.80	0.051	1.99	0.369
Omnivorous	2.15	0.142	0.02	0.901	3.94	0.139

Age and burn status were evaluated with likelihood ratio tests that approximate a χ^2 distribution

Bold text indicates $P < 0.05$
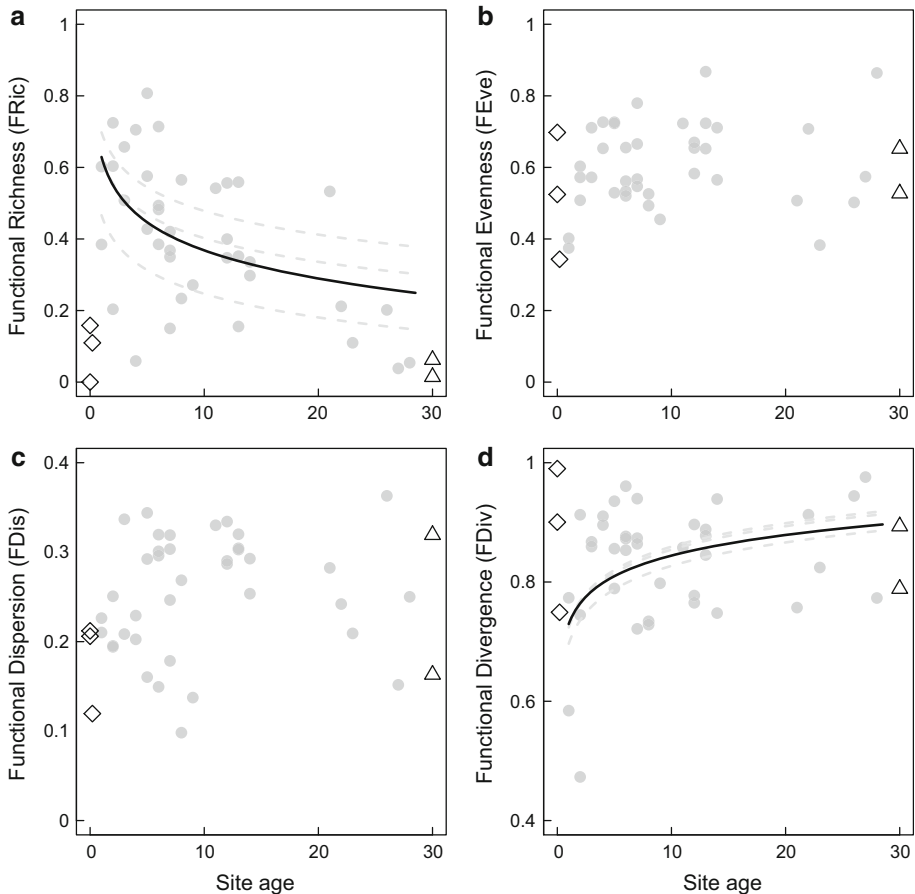
Fig. 3 Relationships between **a** functional richness (FRic), **b** functional evenness (FEve), **c** functional dispersion (FDis), and **d** functional divergence (FDiv) and site age in study sites from 2013 to 2015. In all panels, *gray circles* represent restored sites, *diamonds* are an agricultural field, and *triangles* are a prairie remnant site. *Black lines* indicate overall significant relationship with age, and *dashed gray lines* are the relationships in each of the 3 years of the study based on generalized linear mixed models. Age was log-transformed for analyses and back-transformed for figures

which tended to be more common in young sites and rare in the oldest restorations (Table 4 and Supplementary Material).

Vegetation

Consistent with other studies, plant communities changed with time across the chronosequence. There was a marginally significant trend of declining richness and a significant decline in Shannon diversity (Table 2). Over time, percent forb cover significantly decreased, and percent grass cover increased. Burn status did not affect any of these plant community measurements.

Discussion

Taxonomic and functional composition

We documented consistent patterns of change in both taxonomic and functional community patterns in ground beetle communities across a tallgrass prairie restoration chronosequence. Both abundance and species richness initially reach high values in the first two or three years after restoration planting. These then decline, with abundance and richness levels that approach the remnant site and are comparable to pre-restoration agricultural field condition. These successional changes have been documented in other restored grasslands, not just for ground beetles. Multiple arthropod groups, including several beetle and fly families, as well as Hymenoptera, had lower abundance in restored Dutch grasslands as time since fertilization management ceased (Hemerik and Brussaard 2002). In another set of Dutch grasslands, species richness of both ground beetles and weevils declined following restoration activities (Noordwijk et al. 2017).

However, in other grassland systems and taxa, abundance and diversity increase after restoration. In the second set of Dutch grasslands, millipede and true bug richness increased over time (Noordwijk et al. 2017). Species richness of open-habitat ants increased with time since restoration management began in Swedish grasslands (Dahms et al. 2010), and Lepidoptera richness increased with age in Finnish grasslands because age was associated with taller vegetation, which supported more species (Pöyry et al. 2006). In U.K. grasslands, phytophagous beetles increased after hay-spread treatments were applied, although the study did not monitor long-term changes (Woodcock et al. 2010). These differences may be due to the context of many European grassland restorations, where the starting point is abandoned pastures rather than intensive rowcrops as in the central U.S. The primary management technique, intensive short-term grazing to reduce woody plants, is very different from tallgrass prairie restoration that requires wholesale re-establishment of a native plant community, often followed by regular applications of prescribed fire (Török et al. 2011). For example, a study of phytophagous weevils in seminatural Swedish grasslands found that species composition in older restored sites was more similar to pastures that had been continuously grazed by livestock than to younger restored sites where management had begun more recently (Steiner et al. 2016).

The declines in abundance, richness, and diversity of ground beetles that we document are more similar to patterns that have been seen across disturbance gradients. Low disturbance frequency or intensity leads to reduced abundance and diversity of ground beetles for several disturbance types, including flooding (Gerisch et al. 2012), land-use disturbances (Cárdenas and Buddle 2008), and along an urbanization gradient (Magura et al. 2004). Initial restoration activities in tallgrass prairie often involve disturbance activities such as chemical or mechanical removal of existing vegetation (most often crops) prior to seeding (Packard et al. 1997). Because of this, consumer community patterns in new tallgrass prairie restorations that are in the early stages of succession may resemble those in other habitats that undergo frequent disturbances, where the average time since last disturbance is short.

In addition to taxonomic diversity changes, the ground beetle community also showed variation in functional trait composition that was associated with both successional age and, to a lesser extent, recent burn history. Two of the four multivariate measures of trait diversity, functional richness and functional divergence, changed significantly with site age, but in different ways. Functional richness declined in older sites in a way that mirrored

declining species (taxonomic) richness, which may be somewhat expected, as a limited number of species would be expected by chance to possess a more limited number of trait values. Because functional richness does not incorporate relative abundance, it can be inflated by rare species with more extreme trait values (Laliberté and Legendre 2010). The high initial functional richness following prairie restoration may be due to such rare species that fail to establish in the long-term, as in ground beetle communities in flood-prone habitats shortly after flooding occurred (Gerisch et al. 2012).

In contrast, functional divergence, which incorporates relative abundance and thus may better describe the overall diversity of functional traits in a community, increased with age due to very low values in the youngest sites and consistently high values once restorations were several years old. Functional divergence is maximized when a large proportion of the total community abundance is represented by species with more extreme trait values (Villéger et al. 2008; Mouchet et al. 2010). Two processes may be contributing to this rapid increase in functional divergence in prairie restorations. First, although species richness in the earliest years following restoration was high, these communities were numerically dominated by small, winged species that were somewhat more likely to be phytophagous or omnivorous and perhaps were subsidized by an abundance of weed seeds (see below). The similarities between these abundant species would cause functional divergence to be low, as is seen in communities of ground beetles (Gerisch et al. 2012) and tropical fish (Villéger et al. 2010) under environmental disturbances. Second, later-colonizing species may have been more likely to have trait values very different from these early-abundant species. Woodcock et al. (2012) showed that flightless beetle species and those relying on a more limited food breadth (i.e., dietary specialists) took longer to colonize grassland following restoration. For example, in our chronosequence *Chlaenius platyderus* and *Cyclotrachelus seximpressus* are two large-bodied, flightless species that were absent or rare in sites younger than five years old but fairly common in most older sites. These same shifts in ground beetle body size and flight ability occurred across a coastal heathland successional gradient (Schirmel et al. 2012), in which winged and phytophagous species predominated in the earliest successional stages. There may be a general pattern of ground beetle community succession, with early stages typified by small, phytophagous species with strong dispersal capability, and mature stages containing more large, flightless carnivores (Holliday 1991). This pattern might be strongest when successional or restored habitats are isolated, as is the case for our study site, with few other prairies in a region dominated by corn-soy agriculture.

These functional patterns in beetle communities likely reflect the functional diversity of the plant communities they inhabit and the changes in these plant communities that follow restoration activities. In a study examining a variety of habitat types in Scotland, ground beetle functional trait diversity was predicted by plant functional characteristics (Pakeman and Stockan 2014). We document a decline in plant richness and diversity with time since restoration in our sampled plantings, in agreement with previous work at the study site (Hansen and Gibson 2014). However, phylogenetic diversity of these restored plant communities remains stable over time, even when richness decreases (Barber et al. 2016). Phylogenetic diversity may be correlated with plant functional diversity (Cadotte et al. 2009), so that although individual plant species may be lost, there is phylogenetic (and possibly functional) redundancy that continues to support consistent high levels of beetle FDiv in later successional stages, once restored sites are established.

While we found patterns in taxonomic and functional composition that varied with time since restoration, there was still some variation among sites at the same age. Our finding that there is a spatial pattern in taxonomic similarity, with closer sites having more similar

communities, indicates that dispersal and colonization dynamics contribute to this variation (Young et al. 2001). Although this leads to similarity between adjacent sites, variation among distant sites is likely supporting greater ground beetle diversity (taxonomic, and perhaps functional as well) at a landscape scale.

Restoration implications

A goal of ecosystem restoration is to re-establish ecosystem functions, but compared to plants, arthropod community recovery following restoration is less-well studied. The contributions of arthropods to ecosystem function also are poorly known compared to those of plant communities. This limits ecologists' ability to predict how consumer community succession during restoration contributes to changes in ecosystem functions and services (de Bello et al. 2010; Moretti et al. 2013). We show that functionally diverse (as measured by functional divergence) ground beetle communities can self-assemble under restoration practices in a relatively short amount of time. This success is likely due to the active restoration and management practices that are necessary in tallgrass prairie restoration, where passive restoration (Suding 2011) is impractical because native plant propagules are usually absent on the landscape (Willand et al. 2013). Active restoration (hay spreading) resulted in phytophagous grassland beetle communities that were more similar to reference sites than passively restored grasslands that relied on natural plant colonization (Woodcock et al. 2012).

Unlike some other grassland systems, tallgrass prairies are managed with prescribed fire that is applied to control non-desirable plants such as encroaching woody species and invasive exotic species (Packard et al. 1997). Although prescribed fire did not affect any taxonomic or functional community metrics, it did result in communities with smaller species, thus temporarily shifting the successional trajectories of beetle communities. Grassland fires may reduce insect populations, and although these effects are generally temporary (Panzer 2002; Pryke and Samways 2012), large-bodied insects could to be particularly vulnerable to fires. In boreal forests, average ground beetle body size also increased with time following fire (Holliday 1991), and Pakeman and Stockan (2014) found that disturbances in grasslands favored small, winged ground beetles. If fires reduce abundances of large-bodied ground beetles, it underscores the importance of unburned refugia or a burn rotation strategy in managed grasslands that maintains microhabitat diversity to ensure rapid recolonization (Panzer 2002).

The taxonomically and functionally distinct ground beetle communities that we document in early-succession prairie plantings are probably due in part to the plant community in these young sites, which is characterized by rapid turnover. Agricultural weeds dominate plant communities in the first year after planting (Camill et al. 2004). In our region, these include *Conyza canadensis* (mare's tail), *Ambrosia* spp. (ragweed), and *Amaranthus palmeri* (amaranth), but over the following two years, abundances of these species drop significantly. These weeds also produce an enormous pulse of seeds in late summer and fall; for example, individual *C. canadensis* plants can produce over 200,000 seeds (Bhowmik and Bekech 1993; Weaver 2001). This pulse may subsidize populations of seed-eating ground beetles (Blubaugh et al. 2016), and indeed several phytophagous and omnivorous beetle species known to consume seeds reached high abundances in these early stages, such as *Harpalus pensylvanicus*, *H. herbivagus/somnulentus*, *Notiobia* sp., and several *Amara* sp. Even in the second and third year, when many of these weed plants have been displaced by planted species, the remaining seed bank may continue to support these beetle species.

Indeed, the high abundance of seed-eating ground beetles in early years may help to reduce the weed seed bank, reducing competition with desirable planted species during their early establishment and speeding succession toward a community dominated by perennial native prairie species. Ground beetles can play an important role in suppressing weed seed banks in agriculture (Gaines and Gratton 2010; Bohan et al. 2011), and this same function could be benefiting grassland restorations at other sites if the pulse of high beetle abundances observed here occurs elsewhere. This hypothesis could be tested with carefully designed experiments that exclude arthropod seed predators in the establishment phases of restoration.

Ultimately, determining the functional importance of ground beetle community re-establishment, or using these insects to assess restoration success, will require measurements of actual functions and interactions, such as measurements of seed and arthropod predation. Nonetheless, we demonstrate that even in a situation where species richness declines over time, ground beetle communities can maintain trait diversity. The impact of prescribed burns on trait prevalence demonstrates how disturbances can continue to shape community characteristics, and that careful monitoring of community responses will aid in a more thorough understanding of how management activities may be scheduled or modified to support both biodiversity and ecosystem function in restored habitats.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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