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Effects of grassland management practices on ant functional groups in central North America

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Abstract Tallgrass prairies of central North America have experienced disturbances including fire and grazing for millennia. Little is known about the effects of these disturbances on prairie ants, even though ants are thought to play major roles in ecosystem maintenance. We implemented three management treatments on remnant and restored grassland tracts in the central U.S., and compared the effects of treatment on abundance of ant functional groups. Management treatments were: (1) *patch-burn graze*—rotational burning of three spatially distinct patches within a fenced tract, and growing-season cattle grazing; (2) *graze-and-burn*—burning entire tract every 3 years, and growing-season cattle grazing, and (3) *burn-only*—burning entire tract every 3 years, but no cattle grazing. Ant species were classified into one of four functional groups. Opportunist ants and the dominant ant species, *Formica montana*, were more abundant in burn-only tracts than tracts managed with either of the grazing treatments. Generalists were more abundant in graze-and-burn tracts than in burn-only tracts. Abundance of *F. montana* was negatively associated with pre-treatment time since fire, whereas generalist ant abundance was positively associated. *F. montana* were more abundant in restored tracts than remnants, whereas the opposite was true for subdominants and opportunists. In summary, abundance of the dominant *F. montana* increased in response to intense disturbances that were followed by quick recovery of plant biomass. Generalist ant abundance decreased in response to those disturbances, which we attribute to the effects of competitive dominance of *F. montana* upon the generalists.

Keywords Functional group · Grazing · Prairie · Prescribed burning · Restoration · Terrestrial invertebrates

Introduction

Because fire is a naturally occurring phenomenon in most of the world's grasslands (Bond 2008), including prairies of central North America (Axelrod 1985; Anderson 2006), prescribed fire is an important tool for restoring conditions necessary for species that evolved with fire (Parr et al. 2004; Moretti et al. 2006; Churchwell et al. 2008). Grazing,

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like fire, is a disturbance that can affect the abundance and diversity of fauna (Andresen et al. 1990; Sutter and Ritchison 2005; Warui et al. 2005) and flora (Towne et al. 2005). Fire and grazing have also interacted for millennia (Fuhlendorf and Engle 2001; Archibald et al. 2005), a process labeled as pyric herbivory (Fuhlendorf et al. 2009) because fire alters distribution and foraging behavior of large ungulates in space and time. Patch-burn grazing is a management approach that has been implemented to restore pyric herbivory to grassland landscapes in North America (Fuhlendorf and Engle 2001; Brudvig et al. 2007; Fuhlendorf et al. 2009) and involves application of fire to discrete portions of the landscape; large ungulates typically respond by foraging heavily on recently burned patches while avoiding unburned areas. This practice is designed to increase habitat heterogeneity, thereby increasing biodiversity (Fuhlendorf and Engle 2001).

However, recent decades have seen an ongoing controversy concerning the effects of disturbance on grassland insects (Swengel 1996; Panzer and Schwartz 2000; Cook and Holt 2006), including ants (Hymenptera: Formicidae) (Underwood and Christian 2009). Ants play essential roles in nutrient cycling, soil aeration, and seed dispersal in grasslands (McClaran and Van Devender 1995). Disturbances such as fire and grazing tend to have little direct impact on ant abundance, instead acting indirectly by influencing habitat structure, food availability, and competitive interactions (Andersen 1995; Hoffmann and Andersen 2003). In contrast, grassland restoration via plowing of existing vegetation and seeding of native grasses and forbs can be so intense so as to directly reduce ant abundance, and some ant species might take years to recover. For example, in Europe, multiple ant species took more than 1 year to recolonize restored grasslands (Dauber and Wolters 2005), yet most did recolonize within 5–12 years (Dahms et al. 2010). The sensitivity of ants to disturbance makes them useful as indicators of anthropogenic ecosystem change, including change in fire regime (Andersen et al. 2006) and grazing (Bestelmeyer and Wiens 1996; Hoffmann 2010), and they have been used to indicate the success of grassland restoration (Andersen 1997).

Research on the response of New World ant communities to disturbance is limited, but has shown that fire and grazing alters ant abundance in California grasslands (Underwood and Christian 2009), and grazing intensity has differential effects on shrubland ant species (Bestelmeyer and Wiens 1996). In central North America, fire and grazing are widely used to manage prairie, and disruptive methods (e.g., herbicides, plowing) are often used to restore prairie; therefore it is important to understand how ant communities respond to these disturbances. Differences in ant foraging practices and social dominance permit the classification of ants into different functional groups (Andersen 1997). Compared to traditional measures such as species richness and total ant abundance, ant functional groups respond more consistently to disturbance (Stephens and Wagner 2006; Hoffmann and James 2011).

As reported in Debinski et al. (2011), we initiated an experiment in tallgrass prairies of Iowa and Missouri in 2006 to compare the effects of three different management regimes (patch-burn graze, graze-and-burn, and burn-only) on abundance, species richness, and diversity of key invertebrate taxa, namely ants, butterflies and chrysomelid beetles. We also examined these response variables in remnant grasslands and grassland restorations. Total ant abundance and ant species diversity were affected more by legacy of land use than by fire and grazing treatments that we applied (Debinski et al. 2011). For instance, total ant abundance and ant species diversity were greater in remnant grasslands than restorations. When we tested for responses on individual species, we detected a significant response of *Formica montana*, but not for any other ant species, which were much less abundant than *F. montana*.

However, ant functional group abundance can be a better metric for assessing effects of disturbance than total abundance, species richness, or individual species (Hoffmann and James 2011; Stephens and Wagner 2006). The functional group approach pools together data from species belonging to the same functional group. If the species within a functional group are similar in their response to disturbance, the greater abundance values obtained from pooling can increase the potential of detecting a response. Here, using data from the same experiment as the Debinski et al. (2011) study, we report on the response of ant functional groups to (1) three grassland management regimes, (2) remnant status [remnant versus restoration], (3) time since fire within patch-burn graze tracts, (4) pre-existing habitat characteristics, and (5) treatment-induced habitat characteristics. Given the anticipated effects of disturbance regimes on amount of bare ground, vegetation composition and vegetation structure, we hypothesized that grazing, burning and combinations thereof would alter ant functional group abundance, and that functional groups would differ in their responses. More specifically, we hypothesized that the responses of dominant ants and opportunist ants oppose one another, as had been shown elsewhere (Woinarski et al. 2002; Hoffmann and Andersen 2003).

Methods

Study tracts

We selected 12 grassland tracts in the Grand River Grasslands of southern Iowa and northern Missouri, USA.

A map showing the location of these tracts can be found in Moranz et al. (2012). Three tracts had been restored to grassland from row crops between 1980 and 2004; and nine tracts were tallgrass prairie remnants. At the start of the study in 2006, the tracts ranged in size from 15 to 34 ha and were within a grassland-dominated landscape, although the landscape was juxtaposed within a matrix of row crops, forest and woodland. All twelve were allocated to one of three treatments: (1) *patch-burn graze* (annual burning of spatially distinct patches and free access by cattle, $N = 4$), (2) *graze-and-burn*, (single burning of entire tract, with free access by cattle, $N = 4$), and (3) *burn-only* (single burning of entire tract, with no grazing, $N = 4$). From 2007 through 2009, the two grazing treatments were stocked with cattle at an average of 3.1 animal unit months per ha from about May 1 to October 1. Each tract was divided into three patches of approximately equal area. In patch-burn graze tracts, natural topographic features such as waterways, drainages, and ridgetops were used as patch boundaries to the extent possible, and starting in 2007, a different patch within each patch-burn graze tract was burned in early spring (mid-March) of each year (so that by the completion of the study, each patch had been burned once). Tracts in the burn-only and graze-and-burn treatments were burned in their entirety in spring 2009, except for one burn-only tract, which instead was burned in spring 2008.

Land-use history was classified in terms of remnant status as well as fire history. Remnants were defined as grassland tracts that had never been seeded with grassland vegetation; most of these had no or minimal history of plowing. Reconstructed grasslands were reconstructed from cropland with native plant seed planted in bare soil. Pre-treatment time since fire (ranged from 1 to 15 years) denoted the number of years since fire had been applied to each tract as of 2006, the year before treatments were first implemented. Land-use history of each tract was determined by interviewing landowners and agency land managers who owned/managed the tracts.

Sweep net sampling

Sweep net surveys of epigeic ants were conducted in each tract twice per year during the periods of major emergence (June to early July and mid-July to early August) from 2007 to 2009. Within each patch, a survey was conducted along a randomly placed 50 m transect, resulting in 6 samples per tract per year (1 transect per patch × 3 patches per tract × 2 sampling periods per year). Additional details of sampling are presented in Debinski et al. (2011). All ants were identified to species-level in the laboratory.

Vegetation sampling

We obtained pre-treatment values in 2006 of proportion native plant canopy cover, plant functional group composition, and vegetation height in each patch within a tract. Proportion native plant cover was derived from species-level plant cover data collected from ten 1 m^2 quadrats within a permanently-marked, modified Whittaker plot (Stohlgren et al. 1995) located 10 m west of each insect sampling transect, as described in McGranahan (2011). From Whittaker plot data, proportion native plant cover was calculated using the following equation: proportion native plant cover = total native plant cover/(total native plant cover + total exotic plant cover). Other vegetation characteristics were sampled in thirty 0.5 m^2 quadrats that were placed systematically within each patch as described in Pillsbury et al. (2011). Variables measured were vegetation height (referred to as visual obstruction in Robel et al. 1970), percent cover of bare ground, and percent canopy cover of non-leguminous forbs. Cover measurements used the following cover classes: 0–5, 6–25, 26–50, 51–75, 76–95, 96–100 % (Daubenmire 1959). Center points of each cover class were averaged within each patch (N = 30 quadrats/patch) and tract (N = 90 quadrats/tract). We repeated this sampling regime each July, with data from 2007 through 2009 referred to as during-treatment data.

Data analysis

Before data were analyzed, we classified each ant species (Table 1) into one of four functional groups, based on our knowledge of tallgrass prairie ant ecology and our familiarity with ant functional groups as described in Andersen (1995, 1997) and Phipps (2006). These functional groups were defined as follows: (1) *dominants* actively and mutually exclude each other and most generalists from their foraging territories, and tend to monopolize large prey and honeydew sources; (2) *subdominants* locally monopolize large prey and honeydew sources (except against dominants); (3) *generalists* recruit *en masse* to rich food sources by means of odor trails, but may be chased off by more dominant species (4) *opportunists* do not mass-recruit nest mates to rich food, but use a “grab and run” strategy, and are more specialized on small food sources such as very small insect prey and stray droplets of honeydew on the ground, litter, or low foliage. Each year, abundance of each species was calculated from each sample, averaged over the two sampling rounds, and then summed within functional group. Dominant ant abundance was log transformed, and abundance of the other three functional groups was square-root transformed to normalize the distribution

Table 1 Ant species sampled in the Grand River Grasslands, listed in descending order of abundance

Species	Functional group[a]	Number of individuals	% of total ant abundance
F. montana	Dominant	4,509	77.8
T. ambiguus	Opportunist	478	8.2
P. bicarinata	Opportunist	167	2.9
Formica exsectoides	Subdominant	117	2.0
Myrmica americana	Opportunist	116	2.0
Monomorium minimum	Generalist	110	1.9
Formica incerta	Opportunist	94	1.6
Tapinoma sessile	Generalist	59	1.0
Lasius neoniger	Generalist	54	0.9
Camponotus americanus	Generalist	26	0.4
Crematogaster cerasi	Generalist	20	0.3
Formica subsericea	Subdominant	17	0.3
Lasius alienus	Generalist	17	0.3
Solenopsis molesta	Generalist	10	0.2

[a] Species classified into one of four functional groups based on Trager (1998)

of residuals. Transformed abundance values were used in univariate statistical analyses.

We used analysis of covariance (ANCOVA) to test for treatment effects after accounting for the influence of pre-treatment habitat covariates. Before analyzing data, we reviewed the grassland ant literature to help guide our selection of covariates, and we tested the following models of the effects of treatment, year and pre-treatment covariates:

Model 1: abundance = Treatment + Year + Treatment × Year
Model 2: abundance = Treatment + Year + Treatment × Year + proportion native vegetation
Model 3: abundance = Treatment + Year + Treatment × Year + remnant status
Model 4: abundance = Treatment + Year + Treatment × Year + time since fire
Model 5: abundance = Treatment + Year + Treatment × Year + proportion native vegetation + remnant status + time since fire
Model 6: abundance = Treatment + Year + Treatment × Year + proportion native vegetation + remnant status + time since fire + forb cover + bareground cover

For each functional group, we performed repeated measures, mixed-effect ANCOVA to compare the fit of these six models. Second-order Akaike's Information Criterion (AIC_c) is the most commonly used information criterion for comparing candidate models when sample sizes are small ($n < 40$) (Burnham and Anderson 2002). AIC_c values represent the expected distance between a candidate model and the "true" model, therefore, in our study the model with the lowest value of the second-order AIC_c was selected as the best-fitting model. We then obtained that model's results with regards to testing effects of treatment, year and the treatment by year interaction on abundance, with $\alpha = 0.05$. When ANCOVA indicated a significant effect, we used differences of least squares means as our multiple comparison procedure. We performed mixed model analysis of variance (ANOVA) to test for the effect of remnant status on abundance of each functional group.

Using data from patch-burn grazing tracts only, we performed mixed model ANCOVA to compare four different levels (0 years, 1 year, 2 years, 3 or more years) of during-treatment time since fire on functional group abundance within patch-burn grazing tracts. For this, we used the same statistical procedures described earlier for testing treatment effects.

We performed two sets of mixed model multiple regressions. The first set tested for the effects of *pre-treatment* vegetation variables on functional group abundance data from 2007 through 2009, whereas the second set tested for the effects of *during-treatment* vegetation variables (using data from 2007 through 2009) on functional group abundance from the same years. Habitat variables included in these regressions were forb cover, proportion native plant cover, cover of bare ground, vegetation height, and time since fire. For both sets of tests, we used the Akaike information criterion (AIC_c) as our criterion for model selection. After finding the AIC_c best model, we examined the p value of each independent variable in the model, with $\alpha = 0.05$. All analyses were conducted using R statistical software (R Development Core Team 2010).

Results

General observations on ant fauna

Among the 5,794 ants captured and identified, there were 14 species, all of which are native to the central U.S. (Table 1). *F. montana* was the only dominant species, and it was the most abundant ant in our samples, making up nearly 81 % of all individuals. The opportunists, with four species comprising over 14.7 % of all individuals, composed the second most abundant functional group, with subdominants (two species) being the least abundant.

Response of ant functional groups to our three management regimes

The global model (which included all six covariates) was the best-fitting model (i.e., the model with the lowest $\mathrm{AIC_c}$ score) for assessing effects of treatment and year on abundance of the dominant ant species, *F. montana* (Table 2a). None of the other five models fit our data as well, having $\Delta\mathrm{AIC_c}$ values of 10.55 or greater. Performing analysis of covariance using the global model indicated that *F. montana* was more abundant in burn-only tracts than in patch-burn graze tracts ($P < 0.001$) and in graze-

Table 2 Models compared to assess effects of management treatment on ant abundance

Experimental factors in model	Pre-treatment covariates in model	K	$\mathrm{AIC_c}$	$\Delta\mathrm{AIC_c}$	lik	*Wi*
(a) Response variable: log-transformed abundance of *F. montana*						
[T + Y + T × Y]		4	194.34	12.90	0.002	0.002
[T + Y + T × Y]	Proportion native vegetation	5	196.22	14.78	0.001	0.001
[T + Y + T × Y]	Remnant status	5	191.99	10.55	0.005	0.005
[T + Y + T × Y]	Time since fire	5	195.64	14.20	0.001	0.001
[T + Y + T × Y]	Proportion native vegetation + remnant status + time since fire	7	194.46	13.02	0.001	0.001
[T + Y + T × Y]	Forb cover + bare ground cover + proportion native vegetation + time since fire + vegetation height + remnant status	9	181.44	0.00	1.000	0.984
(b) Response variable: sqrt-transformed abundance of subdominant ants						
[T + Y + T × Y]		4	217.99	2.32	0.314	0.151
[T + Y + T × Y]	Proportion native vegetation	5	219.27	3.60	0.165	0.079
[T + Y + T × Y]	Remnant status	5	215.67	0.00	1.000	0.482
[T + Y + T × Y]	Time since fire	5	219.98	4.32	0.115	0.056
[T + Y + T × Y]	Proportion native vegetation + remnant status + time since fire	7	217.88	2.21	0.331	0.159
[T + Y + T × Y]	Forb cover + bare ground cover + proportion native vegetation + time since fire + vegetation height + remnant status	9	219.46	3.80	0.150	0.072
(c) Response variable: sqrt-transformed abundance of generalist ants						
[T + Y + T × Y]		4	263.64	4.79	0.091	0.075
[T + Y + T × Y]	Proportion native vegetation	5	265.47	6.63	0.036	0.030
[T + Y + T × Y]	Remnant status	5	265.36	6.52	0.038	0.032
[T + Y + T × Y]	Time since fire	5	265.64	6.79	0.033	0.028
[T + Y + T × Y]	Proportion native vegetation + remnant status + time since fire	7	269.14	10.30	0.006	0.005
[T + Y + T × Y]	Forb cover + bare ground cover + proportion native vegetation + time since fire + vegetation height + remnant status	9	258.85	0.00	1.000	0.830
(d) Response variable: sqrt-transformed abundance of opportunist ants						
[T + Y + T × Y]		4	340.97	5.58	0.061	0.035
[T + Y + T × Y]	Proportion native vegetation	5	342.92	7.53	0.023	0.013
[T + Y + T × Y]	Remnant status	5	335.39	0.00	1.000	0.571
[T + Y + T × Y]	Time since fire	5	342.95	7.56	0.023	0.013
[T + Y + T × Y]	Proportion native vegetation + remnant status + time since fire	7	339.12	3.73	0.155	0.088
[T + Y + T × Y]	Forb cover + bare ground cover + proportion native vegetation + time since fire + vegetation height + remnant status	9	336.82	1.43	0.490	0.280

Every model includes a minimum of the independent variables Treatment, Year, and Treatment × Year, which is represented by the following character set: [T + Y + T × Y]. All covariates are pre-treatment values from 2006. Models are listed in ascending order by their number of parameters and-burn tracts ($P < 0.001$) (Fig. 1). *F. montana* was also more abundant in 2008 than in 2009 (year effect, $P = 0.013$).

The AIC$_c$-best model for assessing effects of treatment on subdominant ant abundance included remnant status as the only covariate (Table 2b). The other five models had ΔAIC$_c$ values of 2.21 or greater. Subdominant ant abundance did not differ with treatment or year (Fig. 1).

Model selection for generalist ants was similar to that for *F. montana*, as the global model was again AIC$_c$-best (Table 2c), with other models having $\Delta\text{AIC}_c \geq 4.79$ (Table 2c). Analysis of covariance indicated a significant effect of treatment on generalist ant abundance ($P = 0.02$), with generalist ants more abundant in graze-and-burn tracts than in burn-only tracts ($P = 0.005$) (Fig. 1). There were no effects of year on generalist ant abundance.

As with subdominant ants, the AIC$_c$-best model for predicting abundance of opportunist ants included remnant status as the only covariate (Table 2d). The global model fit the data almost as well, with $\Delta\text{AIC}_c = 1.43$, whereas the other models had $\Delta\text{AIC}_c \geq 3.73$. Performing analysis of covariance using remnant status as a covariate revealed that opportunist ant abundance was greater in burn-only tracts than in burn-and-graze tracts and patch-burn graze tracts ($P = 0.007$ and $P = 0.04$ respectively) (Fig. 1).

Effect of remnant status

Abundance of three ant functional groups was also affected by remnant status (Fig. 2). *F. montana* abundance was greater in restored tracts than remnant tracts ($P = 0.026$). In contrast, subdominant ants ($P = 0.04$) and opportunist ants ($P = 0.003$) were more abundant in remnant tracts than restored tracts. Remnant status did not significantly affect generalist ant abundance. Upon performing analysis of covariance on data from patch-burn graze tracts only, we found no significant effect of time since fire on abundance of any functional groups ($P > 0.05$).

Treatment effects on habitat characteristics

Treatments differed in their effects on vegetation variables (Fig. 3). Vegetation height was greater in burn-only tracts than in tracts managed with either of the grazing treatments; (Fig. 3a). Litter cover (Fig. 3b) was greater in the burn-only tracts than in either of the grazing tracts.

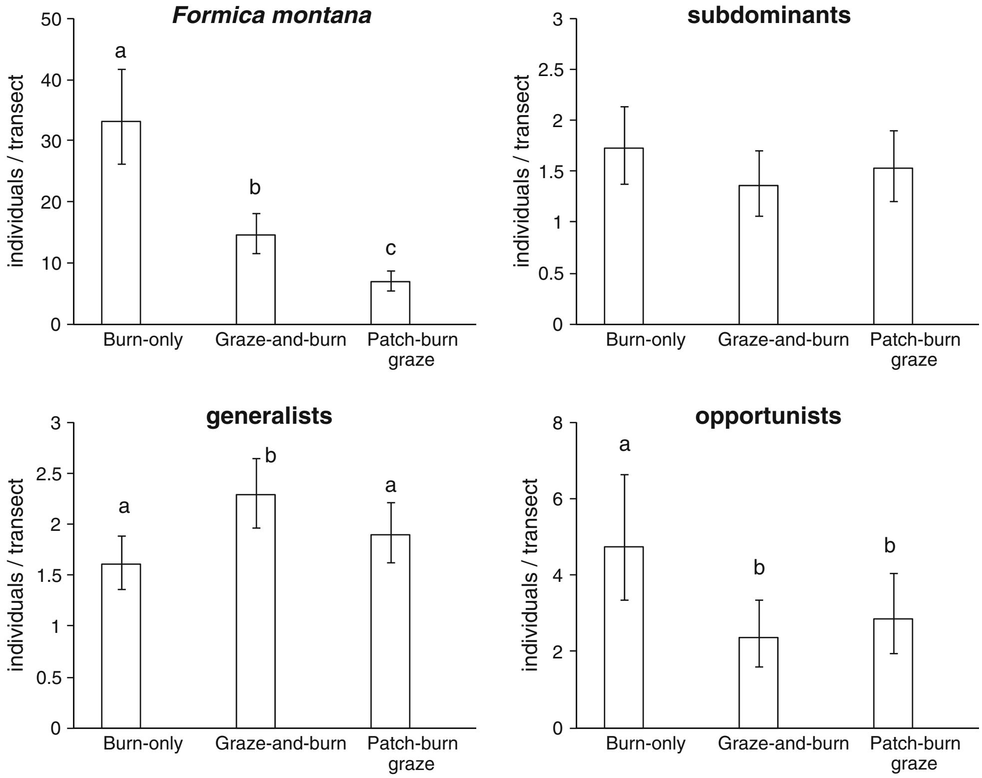
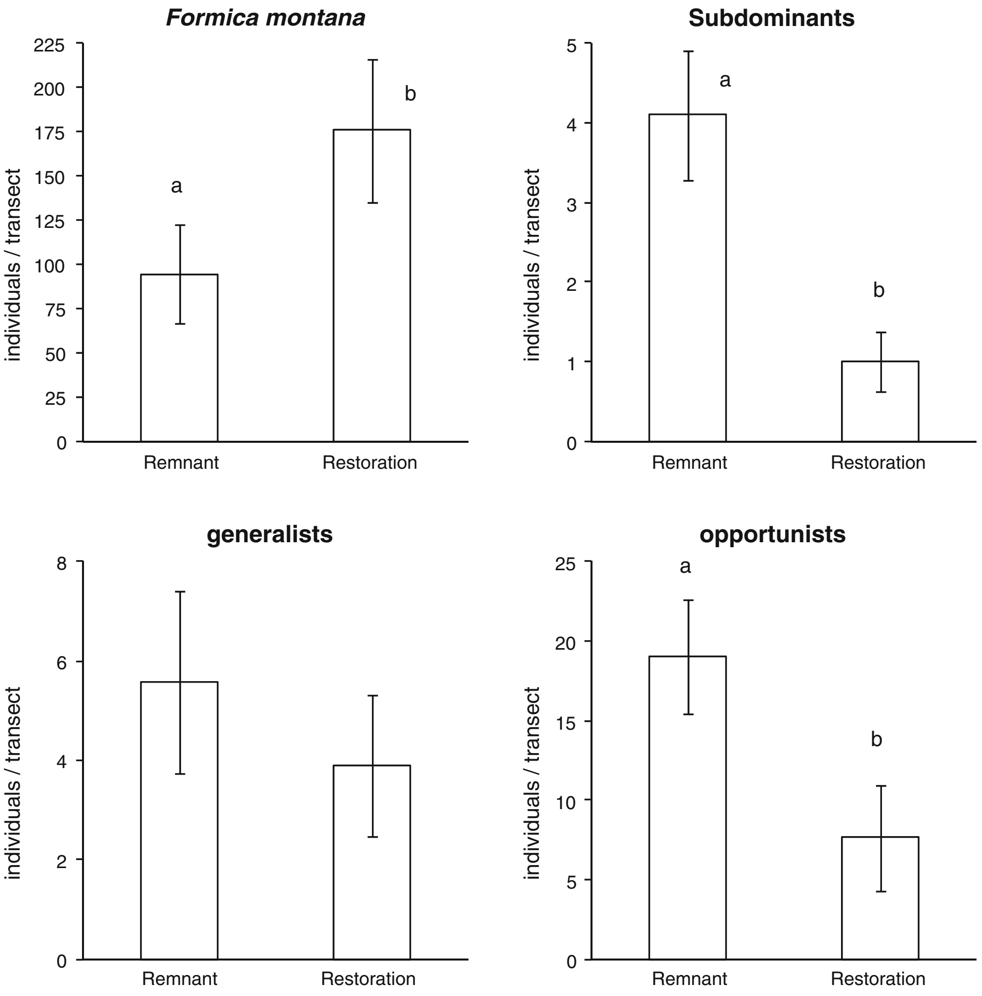


Fig. 1 Ant functional group abundance compared among treatments. *Columns* represent covariate-adjusted means of transect-level abundance values averaged across 3 years (2007–2009). *Error bars* indicate standard error around the mean. *Different letters* above *bars* indicate that treatments are significantly different at $\alpha < 0.05$

Fig. 2 Ant functional group abundance compared between remnant and restored grasslands. *Columns* represent transect-level abundance values averaged across 3 years (2007–2009). *Error bars* indicate standard error around the mean. *Different letters* above *bars* indicate that treatments are significantly different at $\alpha < 0.05$



Bare ground cover did not differ among the treatments (Fig. 3c).

Effects of pre-existing habitat characteristics

Comparing models of the effects of continuous pre-treatment variables on *F. montana* abundance revealed that the best fitting model included five pre-treatment variables (Table 3a), but only three of those (bare ground cover, vegetation height and time since fire) had significant effects on the response variable. A model with bare ground cover only and a model including bare ground cover and forb cover also had good fit ($\Delta AIC_c = 1.74$ and 1.98 respectively). We conclude that *F. montana* abundance was negatively associated with pre-treatment values of bare ground cover, vegetation height and time since fire, with bare ground cover having a particularly strong negative effect.

Six models for predicting the abundance of subdominant ants (Table 3b) had $\Delta AIC_c < 2.0$, thus were similar in their goodness of fit. Although the model including only bare ground cover was AIC_c-best, bare ground cover did not significantly affect abundance of subdominant ants, nor did any of the other pre-treatment variables. Generalist ant abundance was best explained by two models that included vegetation height and time since fire, both of which had positive effects on generalist ant abundance (Table 3c). Although these models also included proportion native plant cover, this variable was not a significant predictor. Lastly, opportunist ant abundance (Table 3d) was best explained by a model that indicated a positive relationship with pre-treatment vegetation height. The other eight models fit the data poorly ($\Delta AIC_c \geq 3.71$).

Associations between ant functional group abundance and during-treatment habitat characteristics

There were few significant associations between functional group abundance and habitat data obtained during treatment implementation (2007–2009). Three models of the effects

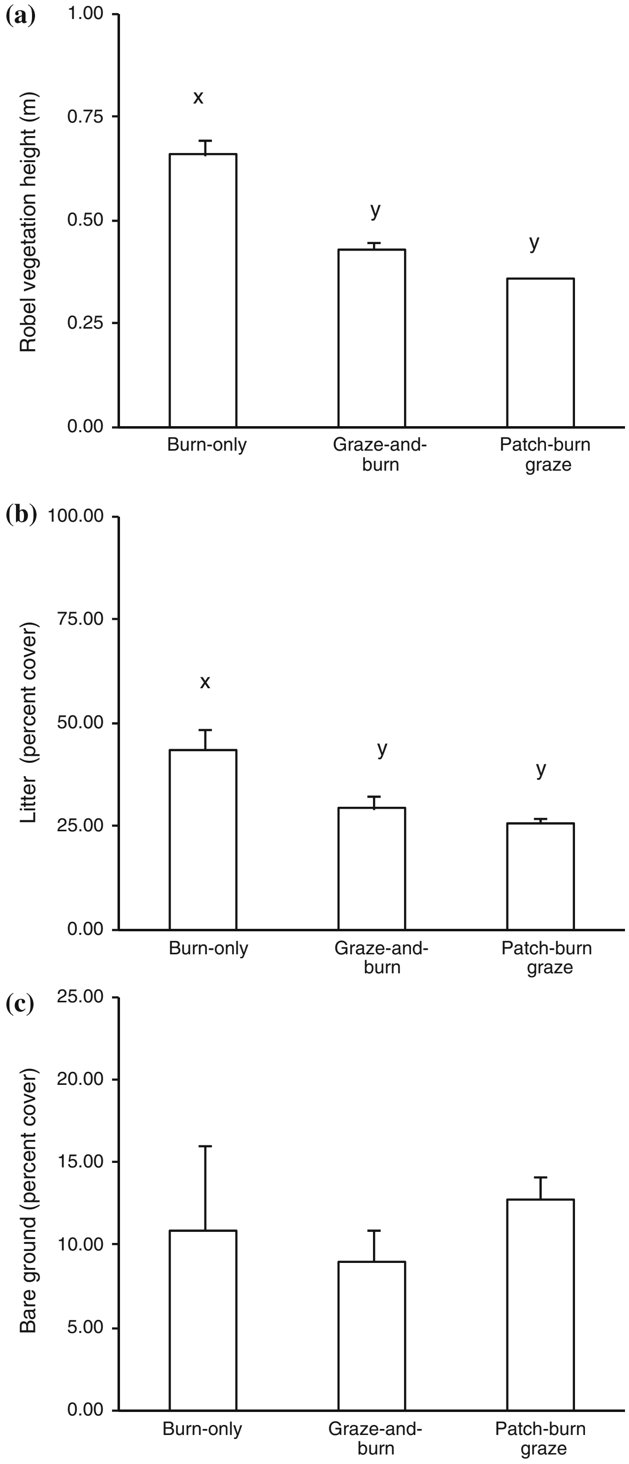


Fig. 3 Vegetation height (**a**), percent litter cover (**b**), and percent bare ground (**c**) compared among treatments. *Columns* represent tract-level values averaged across 3 years (2007–2009). *Error bars* indicate standard error around the mean. *Different letters* above *bars* indicate that treatments are significantly different at $\alpha < 0.05$

of during-treatment habitat variables on *F. montana* abundance had similarly good fit ($\Delta \mathrm{AIC_c} \leq 2.0$) (Table 4a). Whereas the global model had been the best-fitting model for pre-treatment habitat variables, this model fit poorly for during-treatment habitat variables. Instead, the best-fitting model showed a significant ($P = 0.046$) negative association between forb cover and *F. montana* abundance. Regarding subdominant ant abundance, regression of during-treatment variables revealed six models that had $\Delta \mathrm{AIC_c} < 2.0$ (Table 4b). The model including time since fire was $\mathrm{AIC_c}$-best, but neither this habitat variable nor any other was significantly associated with the abundance of subdominant ants. Generalist ant abundance (Table 4c) was best explained by a model that included only vegetation height, with a positive association between vegetation height and generalist ant abundance ($P = 0.04$). Four models exhibited good fit for predicting abundance of opportunist ants, with $\Delta \mathrm{AIC_c} < 2.0$ (Table 4d). The $\mathrm{AIC_c}$-best model included proportion native vegetation, vegetation height and time since fire. Though none of these variables reached statistical significance, time since fire (with a negative association) came closest ($P = 0.06$). The four best models included time since fire as a variable, providing additional evidence that this variable is negatively associated with opportunist ant abundance.

Discussion

Previous analyses of data from the same study sites showed no effects of fire and grazing treatments on total ant abundance or ant species richness (Debinski et al. 2011). Additionally, it showed treatment effects only for a single species, *F. montana*. However, results of this new analysis revealed multiple effects of treatment at the functional group level, supporting the concept that ant functional group abundance is a better metric for assessing effects of disturbance than total abundance or species richness (Hoffmann and James 2011; Stephens and Wagner 2006). All of the ant species we sampled have been characterized as "meat eaters with a sweet tooth" (Trager 1998). They consume invertebrate flesh, floral nectar (Henderson and Jeanne 1992), extrafloral nectar, and honeydew exuded from hemipterans such as aphids [superfamily Aphidoidea]). This similarity in diet might lead one to predict that abundance of different ant functional groups would fluctuate similarly in response to habitat disturbance. But instead, functional groups differed in their responses to fire, grazing, and restoration of croplands to grasslands. The main cause of this phenomenon might be varied resistance and resilience of each functional group to the disturbances and resultant habitat alteration. However, we suspect that an even more important cause is the alteration of competitive interactions.

As part of comparing the merits of these hypotheses, we will discuss responses of functional groups to each

Table 3 Pre-treatment habitat variables assessed for their influence on ant functional group abundance using multiple regression

Model	Variables in Model	K	AICc	ΔAIC_c	lik	*Wi*
(a) Response variable: log-transformed abundance of *F. montana*						
FIVE COVARIATES	Forb cover + bare ground cover + proportion native vegetation + time since fire + vegetation height	6	194.18	0.00	1.00	0.38
BAREGROUND06	Bare ground cover	2	195.93	1.74	0.42	0.16
FORB06 + BAREDAUB06	Forb cover + bare ground cover	3	196.16	1.98	0.37	0.14
TIMESINCEFIRE06	Time since fire	2	197.11	2.93	0.23	0.09
FORB06	Forb cover	2	197.87	3.69	0.16	0.06
PROPNAT06 + ROBEL06 + TSF06	Proportion native vegetation + time since fire + vegetation height	4	198.15	3.97	0.14	0.05
ROBELO6	Vegetation height	2	198.48	4.30	0.12	0.04
PROPNAT06	Proportion native vegetation	2	198.67	4.49	0.11	0.04
PROPNAT06 + TSF06	Proportion native vegetation + time since fire	3	198.88	4.69	0.10	0.04
(b) Response variable: square root-transformed abundance of subdominant ants						
BAREGROUND06	Bare ground cover	2	206.83	0.00	1.00	*0.26*
TIMESINCEFIRE06	Time since fire	2	207.83	1.00	0.61	*0.15*
FORB06	Forb cover	2	208.14	1.31	0.52	*0.13*
ROBELO6	Vegetation height	2	208.15	1.32	0.52	*0.13*
PROPNAT06	Proportion of native vegetation	2	208.15	1.32	0.52	*0.13*
FORB06 + BAREDAUB06	Forb cover + bare ground cover	3	208.82	1.99	0.37	*0.09*
PROPNAT06 + TSF06	Proportion native vegetation + time since fire	3	209.56	2.73	0.25	*0.07*
PROPNAT06 + ROBEL06 + TSF06	Proportion native vegetation + time since fire + vegetation height	4	211.46	4.63	0.10	*0.03*
FIVE COVARIATES	Forb cover + bare ground cover + proportion native vegetation + time since fire + vegetation height	6	213.32	6.49	0.04	*0.01*
(c) Response variable: square root-transformed abundance of generalist ants						
PROPNAT06 + ROBEL06 + TSF06	Proportion native vegetation + time since fire + vegetation height	4	252.19	0.00	1.00	0.44
FIVE COVARIATES	Forb cover + bare ground cover + proportion native vegetation + time since fire + vegetation height	6	252.76	0.58	0.75	0.33
ROBELO6	Vegetation height	2	254.33	2.14	0.34	0.15
FORB06	Forb cover	2	258.78	6.59	0.04	0.02
TIMESINCEFIRE06	Time since fire	2	258.82	6.63	0.04	0.02
BAREGROUND06	Bare ground cover	2	258.83	6.64	0.04	0.02
PROPNAT06	Proportion of native vegetation	2	259.05	6.86	0.03	0.01
FORB06 + BAREDAUB06	Forb cover + bare ground cover	3	260.45	8.26	0.02	0.01
PROPNAT06 + TSF06	Proportion native vegetation + time since fire	3	260.75	8.56	0.01	0.01
(d) Response variable: square root-transformed abundance of opportunist ants						
ROBEL06	Vegetation height	2	346.19	0.00	1.00	0.69
PROPNAT06 + ROBEL06 + TSF06	Proportion native vegetation + time since fire + vegetation height	4	349.89	3.71	0.16	0.11
PROPNAT06	Proportion of native vegetation	2	351.64	5.46	0.07	0.05
TIMESINCEFIRE06	Time since fire	2	351.78	5.59	0.06	0.04
BAREGROUND06	Bare ground cover	2	352.02	5.83	0.05	0.04
FORB06	Forb cover	2	352.70	6.51	0.04	0.03
PROPNAT06 + TSF06	Proportion native vegetation + time since fire	3	353.41	7.23	0.03	0.02
FIVE COVARIATES	Forb cover + bare ground cover + proportion native vegetation + time since fire + vegetation height	6	353.78	7.60	0.02	0.02
FORB06 + BAREDAUB06	Forb cover + bare ground cover	3	353.98	7.80	0.02	0.01

There is a separate table for each functional group, with models listed in ascending values of AIC_c

disturbance, beginning with grazing. The dominant ant, *F. montana*, which was by far the most abundant ant we sampled, was less abundant in grazed tracts than in burn-only tracts. Given that fire frequency was held constant among the three treatments, grazing appears to have been a decisive factor in reducing *F. montana* abundance. Grassland ants

Table 4 During-treatment habitat variables (from 2007, 2008, 2009) assessed for their influence on ant functional group abundance using mixed model multiple regression

Variables in model	K	AIC_c	ΔAIC_c	lik	*Wi*
(a) Response variable: log-transformed abundance of *F. montana*					
Forb cover	2	194.87	0.00	1.000	0.319
Time since fire	2	195.81	0.93	0.627	0.200
Forb cover + bareground cover	3	196.37	1.50	0.473	0.151
Proportion native vegetation + time since fire	3	197.44	2.57	0.277	0.088
Bareground cover	2	197.79	2.91	0.233	0.074
Vegetation height	2	198.75	3.88	0.144	0.046
Proportion native vegetation	2	198.79	3.92	0.141	0.045
Forb cover + bareground cover + proportion native vegetation + vegetation height + time since fire	6	198.89	4.01	0.135	0.043
Proportion native vegetation + vegetation height + time since fire	4	199.39	4.51	0.105	0.033
(b) Response variable: square root-transformed abundance of subdominant ants					
Time since fire	2	207.40	0.00	1.000	0.203
Vegetation height	2	207.85	0.44	0.801	0.163
Proportion native vegetation	2	208.05	0.64	0.725	0.147
Forb cover	2	208.06	0.65	0.722	0.147
Bareground cover	2	208.14	0.74	0.692	0.141
Proportion native vegetation + time since fire	3	208.89	1.48	0.476	0.097
Forb cover + bareground cover	3	210.03	2.62	0.269	0.055
Proportion native vegetation + vegetation height + time since fire	4	210.54	3.13	0.209	0.042
Forb cover + bareground cover + proportion native vegetation + vegetation height + time since fire	6	214.45	7.05	0.029	0.006
(c) Response variable: square root-transformed abundance of generalist ants					
Vegetation height	2	254.79	0.00	1.000	0.556
Bareground cover	2	258.61	3.82	0.148	0.082
Proportion native vegetation + vegetation height + time since fire	4	258.63	3.84	0.147	0.082
Time since fire	2	258.96	4.17	0.124	0.069
Forb cover	2	259.04	4.25	0.119	0.066
Proportion native vegetation	2	259.06	4.27	0.118	0.066
Forb cover + bareground cover	3	260.61	5.82	0.054	0.030
Proportion native vegetation + time since fire	3	260.93	6.14	0.046	0.026
Forb cover + bareground cover + proportion native vegetation + vegetation height + time since fire	6	261.13	6.34	0.042	0.023
(d) Response variable: square root-transformed abundance of opportunist ants					
Proportion native vegetation + vegetation height + time since fire	4	345.21	0.00	1.000	0.318
Proportion native vegetation + time since fire	3	346.85	1.64	0.441	0.140
Time since fire	2	346.87	1.65	0.437	0.139
Forb cover + bareground cover + proportion native vegetation + vegetation height + time since fire	6	346.89	1.68	0.432	0.137
Bareground cover	2	347.67	2.45	0.293	0.093
Proportion native vegetation	2	347.89	2.68	0.262	0.083
Vegetation height	2	349.09	3.87	0.144	0.046
Forb cover + bareground cover	3	349.67	4.45	0.108	0.034
Forb cover	2	352.48	7.27	0.026	0.008

There is a separate table for each functional group, with models listed in ascending values of AIC_c

prey upon various invertebrates, most of which are phytophagous and compete with ungulates for plant biomass (Watts et al. 1982). When ungulates are stocked heavily, they can consume enough plant biomass to reduce the amount of phytophagous invertebrate prey available to ants (Tscharntke and Greiler 1995; Sutter and Ritchison 2005). At our study tracts, grazing reduced vegetation height by almost 50 % in 2008 and 2009 (Moranz et al. 2012).

Although we did not directly measure aboveground biomass, vegetation height is strongly correlated with biomass (Robel et al. 1970). Ungulate removal of plant biomass can also reduce the abundance of honeydew-producing insects (Tscharntke and Greiler 1995) and nectar sources (Moranz 2010), thereby reducing the availability of sugar to ants. We suspect that reduced availability of these major food sources reduced abundance of *F. montana* in our grazed tracts. Alternative explanations for reduced abundance of *F. montana* include grazing-induced soil compaction (Bestelmeyer and Wiens 2001) and increased insolation due to reduction of aboveground biomass (Hoffmann and Andersen 2003).

If grazing reduces food availability to ants, we would expect the other three ant functional groups to be reduced by ungulate grazing, given that those functional groups also consume honeydew, nectar, and phytophagous arthropods. This indeed was the case with opportunist ants, which were less abundant in grazed tracts. Generalist ants, however, showed the opposite response. Why were generalist ants more abundant in grazed than ungrazed prairies? We cannot rule out the possibility that grazing increased biomass of particular food sources of generalist ants (even though it reduced total aboveground plant biomass). However, a stronger hypothesis for explaining this surprising result is that grazing, by reducing *F. montana* abundance, reduced the negative competitive interactions experienced by generalist ants, increasing their survival and fecundity. A corollary of this hypothesis is that moderate or intense grazing of tallgrass prairie by ungulates would increase ant species diversity by reducing the dominance of *F. montana*. Such a phenomenon has been conclusively demonstrated in Australia, where ungulates affected ant community composition (Hoffmann and Andersen 2003). It is important to note that meta-analysis of grazing effects on ants has shown that while grazing does alter community composition, it typically does not affect species richness substantially (Hoffmann and James 2011).

All of our ant functional groups appear to be at least somewhat adapted to fire, as none were eliminated by the prescribed burns we applied. This finding mirrors fire responses found for numerous ant species in California (Underwood and Christian 2009) and Australia (Hoffmann 2003). Except for *Temnothorax ambiguus*, which nests at the plant/soil interface, our ant species build nests underground, protecting immature stages and numerous adults from direct mortality during a fire (Henderson and Jeanne 1992). Our prescribed fires typically combusted at least 80 % of aboveground plant biomass, which might seem to be a greater disturbance than the cattle grazing we implemented. However, whereas cattle grazed our tracts from May to early October, during the active foraging season of temperate grassland ants, our prescribed burns were performed in early spring, when ants do little foraging due to the cold weather. Given that most native prairie plant species have evolved with fire (Anderson 2006), and resprout within a few months of early spring fires (Hartnett and Fay 1998), the plant resources upon which prairie ants depend for food would thus be available during most of the ants' foraging season.

Our study suggests that *F. montana* is particularly well-adapted to grassland fire; *F. montana* abundance was negatively correlated with pre-treatment time since fire (i.e., abundance was greatest the summer after a spring fire, and then declined in subsequent years until the tract was burned again). Fire alters many abiotic and biotic habitat characteristics (Whelan 1995), so there are numerous potential explanations for the post-fire increase of *F. montana* abundance. Standing herbaceous vegetation and litter shade the soil surface, keeping it cooler (Debano et al. 1998), so combustion of these layers provides more warmth to soil and soil-dwelling ants for months post-fire. Fire increases the biomass and floral production of some prairie plants (Hartnett and Fay 1998; Moranz 2010), possibly increasing the availability of honeydew and nectar sources. However, the effects of fire on the availability of honeydew-producing aphids and arthropod prey are not known for prairie systems.

Another issue that could weigh in on these interactions is mound-building behavior. *F. montana* builds mounds far larger than any of the other species we sampled, and places its nests within and beneath these mounds (Henderson et al. 1989). During the winter and early spring, *F. montana* workers remove vegetation growing near the mounds, exposing the bare soil. This increases the amount of solar insolation received in the winter and early spring, providing more warmth to *F. montana* colonies (Carpenter and DeWitt 1993). This behavior also diminishes the fuel bed near the mound, which might further reduce any direct mortality to these ants from fire. Building of such large mounds might be *F. montana*'s key trait for maintaining dominance, though we cannot separate the importance of the mound itself from the aggressiveness of this species or the population size required to build such large mounds.

As with grazing, the response of generalist ants to fire was opposite that of *F. montana*; abundance of generalist ants was positively associated with both pre-treatment and during-treatment time since fire. Like *F. montana*, generalist ants obtain protection from fire by nesting underground, so direct negative impact of fire seems unlikely. Indirect effects of fire on habitat conditions could be affecting generalist ant abundance. However, we propose that the population response of generalist ants to fire is mediated more by their interactions with *F. montana*.

When comparing ant functional group responses within restored sites, it is important to examine the results within an historical context. Although these grasslands had been tallgrass prairie before settlement by European Americans, all had experienced decades of corn and/or soybean cultivation. In the late 1990s and early 2000s, crops were plowed under, and diverse mixes of grassland plants were sown. We assume that few native ants had survived the decades of rowcrop cultivation, with its concomitant application of pesticides and herbicides. Therefore, finding large numbers of *F. montana* in restored tracts leads us to conclude that *F. montana* recolonized those tracts. Interestingly, *F. montana* abundance was greater in restored tracts than in remnant prairies. Tract productivity might be the explanation for this. We suspect that the restorations are more productive than the remnants, given that the restored tracts were regarded as acceptable farmland for decades, whereas the remnants were regarded as non-arable, and thus were not generally plowed. Greater productivity of restored tracts could mean greater availability of food resources for *F. montana*.

The other prairie ants in our study, particularly subdominants and opportunists, did not recolonize restorations as successfully as *F. montana*. We do not know the factors that enable *F. montana* to better recolonize restored prairie than other ants, although we suspect that the behavioral traits (high activity level, alertness, aggression) that lead to their competitive dominance may be important. In central Missouri, opportunist ants were among the first to recolonize grassland restorations (Phipps 2006), doing so more rapidly than in our restorations. We hypothesize that our results differ from those of Phipps (2006) because of the presence of a dominant ant species (*F. montana*) in our grasslands, whereas Phipps (2006) had found no dominant ant. In Australia, opportunists were slow to recolonize disturbed grasslands in which dominant ants had already become established, but quickly recolonized grasslands in which behavioral dominance by other ants was minimal (Andersen 1997). Those findings support our hypothesis that other ant functional groups recolonize restored prairies more quickly when *F. montana* is absent or sparse.

After reviewing functional group responses to the three disturbance types, we posit that the overwhelming numerical and behavioral dominance of *F. montana* appears to be a key factor in determining the population responses of other ant functional groups to each disturbance type. At tracts where *F. montana* was very abundant, generalist ants tended to be less abundant (though subdominant ants were not). Similarly, Hoffmann and Andersen (2003) found that abundance of some ant functional groups in Australia responded to disturbance in a manner opposite to that of dominant ants there, and suggested this was due to their competitive interactions with dominants.

Species categorized within a particular functional group were not always uniform in their responses. The opportunists among the smaller species of the subfamily Myrmicinae are the best example of this. *Pheidole bicarinata* appeared to thrive in heavily grazed tracts while *T. ambiguus* did not (Debinski et al. 2011). This difference in affinity for grazed tracts is likely based on known differences in the biology of these species. *Pheidole* is a hyperdiverse, tropical genus, with most of its North American species in more arid, southern ecoregions. *P. bicarinata* live in colonies with >200 individuals, and nest in burrows that penetrate deep into the ground, with little vulnerable architecture near the surface. They forage mostly on the ground, even during the heat of the day. *P. bicarinata* typically forages alone, but may occasionally lapse into the category of a generalist, mass recruiting to protein rich foods, especially during early summer, when their colonies are producing the large sexual castes. They are, however, easily displaced from large food sources by aggressive generalist ants with larger colonies.

In contrast, the genus *Temnothorax* has a strongly temperate zone distribution in North America. The smaller colonies (<100 individuals) of *T. ambiguus* typically nest among the roots or stem bases of living plants where they might easily be trampled by grazers, or could overheat if cover were removed. They forage low on plants, in the cooler hours of morning and late afternoon. The more vegetated and slightly cooler microhabitats, and more vulnerable nest architecture of *T. ambiguus* probably make them less suited than *P. bicarinata* for survival in moderately or intensely grazed sites, which have more bare ground than ungrazed sites (Holechek et al. 2001). As additional species-specific natural history information is uncovered, these fine scale differences in niche preferences may allow for a better understanding of even finer-scale habitat responses.

Implications to conservation

Our research shows that ant functional groups of North America's Grand River Grasslands differ in their responses to disturbance. Our study supports prior research (Andersen and Majer 2004; Stephens and Wagner 2006) in showing that assessing ant community responses via functional groups can be a valuable approach for grassland research and monitoring. Our results, like those of Hoffmann (2003) in Australia, emphasize the importance of dominant ant species in mediating the effects of disturbance on ant community structure. We need to be wary of assuming that the specific responses of our four functional groups apply to other grassland ecoregions of North America. As Hoffmann and Andersen (2003) have demonstrated, responses of ant functional groups to disturbance are context-specific. We posit that disturbance effects might change dramatically at other sites based on the presence or absence of dominant ant species, or based on the change in vegetative cover caused by disturbance (Hoffmann 2010). Additional research is necessary to validate these hypotheses for North American grasslands, but these results invoke substantial motivation for future work at the nexus of grassland ecology and ant natural history.

Given that our study sites are representative of the mesic tallgrass prairie ecoregion, we think it is reasonable to consider the implications of our findings to ant conservation within this ecoregion. Fire and grazing are two of the primary management activities in mesic tallgrass prairies (Fuhlendorf et al. 2009). Fire in particular has been shown to be essential for preventing invasion of woody plants into mesic prairie, thus is a necessary tool for conserving plant communities and grassland-obligate invertebrates. In our study, no ant functional groups (or species) were eliminated by fire. Given the importance of prescribed fire in tallgrass prairie management, this bodes well for the conservation outlook of tallgrass prairie ants. However, the increase in dominant ant abundance soon after prescribed burning, and the concomitant decrease in abundance of some other ant functional groups, suggests that frequent fire (fire return interval of 3 years or less) might maintain dominance of *F. montana* at a high level, which in turn might keep generalist ants at low abundance for many years. Millions of acres of tallgrass prairie are burned on a frequent basis (Wilgers and Horne 2006), therefore, recent prescribed fire practices might already have led to a dearth of generalist ants on a large scale. Furthermore, long-term use of frequent fire might lead to local extirpation of generalist ants. Grazing, in contrast, appears to reduce dominant ant abundance in mesic tallgrass prairie. Some conservationists have been reluctant to introduce cattle grazing to tallgrass prairie preserves in Iowa, Illinois, Missouri and other midwestern states. We speculate that introducing moderate-intensity cattle grazing to these preserves could make them better suited for generalist ants.

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Appendix

See Table 5.

Table 5 Characteristics of study tracts in the Grand River Grasslands of Iowa and Missouri

Treatment	Tract name	Remnant history	Previous pre-treatment fire	Tract area (ha)
Burn-only	*Kellerton Tauke*	Prairie restoration[a]	2003	32.4
Burn-only	*Pawnee*	Prairie remnant	2005	21.8
Burn-only	*Richardson*	Prairie remnant	1994 or earlier	15.6
Burn-only	*Ringgold North*	Prairie remnant	2004	15.4
Graze-and-burn	*Gilleland*	Prairie remnant	1994 or earlier	31.2
Graze-and-burn	*Lee Trail Road*	Prairie remnant	2004	34.0
Graze-and-burn	*Pyland West*	Prairie remnant	1994 or earlier	17.8
Graze-and-burn	*Sterner*	Prairie restoration[a]	1994 or earlier	32.4
Patch-burn graze	*Kellerton North*	Prairie remnant	2005	42.5
Patch-burn graze	*Pyland North*	Prairie restoration[a]	2004	32.4
Patch-burn graze	*Pyland South*	Prairie remnant	1994 or earlier	25.3
Patch-burn graze	*Ringgold South*	Prairie remnant	1994 or earlier	22.7

[a] Prairie restorations were restored from croplands between 1980 and 2004

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