

Ant species assembly in constructed grasslands is structured at patch and landscape levels

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Abstract. 1. Agri-environmental incentive programmes encourage conversion of marginal agricultural land to grasslands to reduce soil erosion and support biodiversity of native flora and fauna. Most grassland animals colonise these constructed habitats as propagules from the surrounding landscape. Ants are slow to colonise and rely on resources within the patch, making them valuable as indicators of disturbance and recovery.

2. We studied how ant species diversity and composition are structured by patch and landscape variation of grasslands in Ohio, USA. Ant communities were collected from 23 constructed grasslands differing in area, age, vegetation, soils, management and surrounding land cover. We analysed trap frequency for 14 species that varied in habitat specialisation to identify species responses to patch- and landscape-level predictors.

3. Grassland age and soil texture determined ant species richness and community composition. Trap frequency analysis showed contrasting species responses to patch and landscape characteristics: habitat specialists were more abundant in older, larger patches with more surrounding grassland, while disturbance-tolerant species were more frequent in younger patches surrounded by intensive agriculture. Habitat generalists and open habitat species included a variety of patch- and landscape-level factors in best models.

4. Ant community assembly in constructed grasslands is shaped by time and physical characteristics at the patch-level, but the surrounding landscape acts as a filter for the colonising community. Our findings support the use of ants as ecosystem recovery indicators following disturbance in agricultural landscapes, but show that shifts in species composition are better indicators of grassland habitat variation than ant richness.

Key words. Agro-ecosystems, community assembly, conservation reserve program, indicators, landscape ecology, prairie, restoration ecology.

Introduction

Trends toward greater agricultural intensification over the last century have rapidly converted much of the natural and semi-natural land into agriculture (Tscharntke *et al.*, 2005). Landscapes with large amounts of intensive agriculture tend to have high input crop systems, structural simplicity and very low habitat diversity, resulting in declines

in biodiversity of flora and fauna (McLaughlin & Mineau, 1995; Stoate *et al.*, 2001; Hendrickx *et al.*, 2007). Private landowners, conservation organisations and community parks construct or restore habitats as conservation set-asides through incentive programmes aimed to enhance ecosystem services, aesthetic qualities or biodiversity within agriculturally dominated landscapes. For example, European agri-environmental schemes, in which farmers receive compensation for modifying their farming practice to provide environmental benefits, have reported increases in biodiversity for both plant and animal taxa (Kleijn & Sutherland, 2003; Knop *et al.*, 2006).

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The tall grass prairie of North America once spanned much of the Midwest US, but has declined dramatically over the last century (estimates of 82–99%) due to agricultural conversion and urbanisation (Samson & Knopf, 1994). The conservation reserve program (CRP) was first introduced in 1985 by the United States Department of Agriculture (USDA) to reduce cropland erosion and has created over 12 million ha of forage and prairie grasslands by removing cultivated lands from production and replacing them with more natural habitats (Dunn *et al.*, 1993). Studies of these and other constructed grasslands in North America and similar incentive-based grasslands in Europe demonstrate the gradual recovery of organic matter and nutrients to the soil (Burke *et al.*, 1995; McLaughlan *et al.*, 2006) and increases in biodiversity (Söderström *et al.*, 2001; Tscharrntke *et al.*, 2002; Martin *et al.*, 2005; Panzer *et al.*, 2010).

Constructed grasslands harbour a diversity of taxa that have been used to evaluate success of agri-environmental schemes and CRP incentive programmes (Dunn *et al.*, 1993; Millenbah *et al.*, 1996; Kleijn & Sutherland, 2003). Colonisation and establishment of some invertebrates and other taxa are affected by landscape-level factors, such as the proximity of different habitats that may provide complementary resources for foraging, nesting or overwintering (Fahrig *et al.*, 2011). For highly vagile organisms, such as bees and butterflies, grasslands themselves are used for floral resources, and the surrounding landscape might be used for additional resources (Mandelik *et al.*, 2012; Crist & Peters, 2014). For less vagile organisms, such as ants, the surrounding landscape is the source of colonising propagules, and once established, they exhibit long-term dependence on the grassland with little to no use of resources outside of the grassland patch.

Ants are often used as environmental indicators of ecosystem disturbance and recovery because of their long-lived colonies, slow colonisation following disturbance, and known habitat affinities (Folgarait, 1998; New, 2000; Andersen & Majer, 2004; Underwood & Fisher, 2006; Mitrovich *et al.*, 2010). Ants are also widely recognised as important regulators of biodiversity and ecosystem functioning because they modify soils and plant communities and play key roles in species interactions (Folgarait, 1998; Crist, 2008). As widespread organisms, ants can be exposed to an equally wide range of disturbances including prescribed fire, agricultural intensification, grazing, urbanisation and habitat fragmentation (Folgarait, 1998; Underwood & Fisher, 2006). Their sensitivity to disturbance and ecosystem change, as well as their significance to ecosystem functioning, have increased their use in ecological studies of conservation and restoration ecology.

Few ant species establish colonies in intensive agricultural fields, such as corn and soybeans of the Midwest US, even under limited tillage regimes (House & Stinner, 1983; House, 1989; Stinner & House, 1990; Peck *et al.*, 1998). Therefore, ants slowly colonise constructed grasslands on formerly cultivated fields from the surrounding landscape over several years. Most ant species disperse

during mating flights as alates (winged sexual forms), and these foundress queens select appropriate habitats based on land use and abiotic conditions (Folgarait, 1998; Gómez *et al.*, 2003; Dauber *et al.*, 2005). Ant community assembly in constructed grasslands has been studied primarily through the use of chronosequences, or sites that vary in age. For example, a study of 12 CRP grasslands showed ant species richness and abundance to be positively associated with the age of the grasslands, peaking in 7–8-year-old fields (Phipps, 2006). Menke *et al.* (2015) also found increasing species richness and incidence as restorations age. Similarly, a study of grasslands in Germany found nest density and species richness increased with time, and ant community composition and functional group dominance shifted to favour subterranean foragers (Dauber & Wolters, 2005). In calcareous grasslands of England, total ant richness and abundance of an indicator species (*Myrmica sabuleti*) was higher in older sites (Fagan *et al.*, 2010).

Thus far, landscape-level studies of ant communities have focused less on the composition of the landscape and more on fragmentation and isolation of remnant patches including Brazilian forests (Schroeder *et al.*, 2004), Florida sandhills (Spiesman & Cumming, 2008) and arid woodlands of Australia (Debus *et al.*, 2007). The importance of land use type or composition has been investigated by only a couple of studies. Spiesman and Cumming (2008) demonstrated the effects of the pine industry and urbanisation on composition of sandhill ant communities, and Dauber *et al.* (2003, 2005) noted that adjacent land-use type was a good predictor of overall ant richness and abundance in European grasslands. For patches recovering from severe disturbance associated with intensive agriculture, the composition of the surrounding landscape may be very important as both a source of colonising propagules and in filtering the species composition of potential colonists.

Ant communities in grasslands are further structured by patch-level variation due to periodic disturbance (typically controlled burns or grazing), or heterogeneity in soil moisture, and soil texture (Dauber *et al.*, 2005; Debus *et al.*, 2007; Graham *et al.*, 2009; Gollan *et al.*, 2014). Periodic fire is the most common land management technique in most of the US for maintaining constructed grasslands, and can have positive, negative, or no apparent effects on invertebrate taxa (Swengel, 2001; Debinski *et al.*, 2011). Most ants are protected underground from direct mortality by fire but may experience indirect effects of fire through changes in other abiotic and biotic conditions, such as insolation, litter depth, prey availability, temperature, moisture and soil nutrients. The responses of ants to fire, range from no change, to positive or negative effects on abundance and richness and shifts in functional groups and community composition (Underwood & Fisher, 2006; Moranz *et al.*, 2013; Menke *et al.*, 2015). Similarly, ants show diverse responses to variation in soil characteristics (texture, moisture, bulk density). For example, soil texture affects species evenness (Graham *et al.*, 2009) and

community composition (Bestelmeyer & Wiens, 2001). Likewise, in short grass prairies, ant species richness, abundance and community composition were primarily determined by a variety of soil attributes and showed little to no relationship with plant community characteristics (Boulton *et al.*, 2005).

The goals of this study were to determine the effects of grassland patch characteristics and the surrounding land use and land cover (LULC) on ant communities in constructed grasslands. At the patch level, we hypothesised that: (i) colonisation of grasslands by ants is determined by dispersal limitations and tolerance to disturbance, such that disturbance-tolerant species (found primarily in urban environments) are more common in younger sites, while uncommon specialist species are primarily associated with older sites; (ii) soil texture acts as a filter of ant species composition, such that sites with coarse-textured soils would be suitable to a wider range of ant species compared to those with fine-textured soils; and (iii) ant communities are structured by disturbance in constructed grasslands, and respond primarily to abiotic environmental characteristics (e.g. age, management, edge effects) rather than biotic (vegetation) components. At the landscape level, we predicted that: (i) the surrounding landscape would act as the source of propagules for the ant community; and (ii) patches surrounded by grasslands and pasture/hay fields (extensive agriculture) would have higher frequencies of specialist ants and open habitat species, while intensive agriculture and urban LULC would have a higher frequencies of disturbance-tolerant ants.

Methods

Study sites

We studied a total of 23 warm-season constructed grasslands during the summers of 2011 and 2012 in Butler, Preble and Montgomery Counties of SW Ohio in the Midwestern USA (Fig. S1, Table S1). The grassland patches were planted and managed by private landowners (primarily through enrolment in the CRP), MetroParks of Butler County, Five Rivers MetroParks, a high school, and the Miller-Coors Corporation. Participation by landowners was voluntary and due to changes in property availability only 20 grasslands were used each year, with 17 grasslands sampled in both of the years. Sites ranged in size from 0.83–17.8 ha (mean = 7.3 ha), and time since planting (age = 1–31 years, mean = 10.7 years). Most of the sites were managed with burning every 3–5 years with periodic spot treatment of invasive plants with mowing or herbicides. Two grasslands were burned at the beginning of the 2011 season, and three were burned or partially burned at the beginning of 2012. Dominant vegetation consisted primarily of C4 prairie grasses including Indian grass (*Sorghastrum nutans*), big blue stem (*Andropogon gerardii*) and little blue stem (*Schizachyrium scoparium*), and a wide variety of prairie forb species (Table S1). Our sites

were surrounded (500 m radius) by a variety of LULC types, including forest (mean = 34.5%, range = 0–74.3%), intensive agriculture (mean 29.0%, range = 0–65.5% or urbanisation (mean = 15.7%, range = 0–69.9%), with small amounts of grassland (mean = 3.2%, range = 0–11.8%) and extensive agriculture (mean = 5.9%, range = 0–21.1%) (Table S2).

Ant community sampling

Ant communities were surveyed using pitfall traps, a common and effective method for collecting active ground running arthropods (Andersen, 1991; Schlick-Steiner *et al.*, 2006; Underwood & Fisher, 2006). To account for heterogeneity of the habitat and to avoid under-sampling of large sites relative to small ones, the number of traps per site was scaled to the \log_e of the patch area. We established a transect through each grassland consisting of 5–10 pitfall traps spaced 25 m apart (Fig. S2). Each pitfall trap consisted of a 237-ml specimen cup (7 cm diameter 10 cm deep) inserted flush with the ground and propylene glycol added as a preservative. A wooden board, elevated with nails approximately 2 cm, was positioned over the cup to shield it from rain. Pitfall traps remained active for 1 week each sampling period. A total of 155 and 154 traps were used in 2011 and 2012, respectively, for each of three sampling periods spaced 5 weeks apart. Sampling periods across the 2 years were nearly identical (within one or 2 days) occurring early-mid June, mid-late July and late August-early September. Only worker ants were included in the analysis, and voucher specimens of ants were deposited at The Ohio State University Triplehorn Insect Collection.

Vegetation sampling

To quantify the local plant species richness and cover, we conducted vegetation surveys at paired 10-m² circular quadrats, on each side of the pitfalls adjacent to the transect (Fig. S2). All plant species within the quadrat were identified and percent cover was recorded by species as categorical variables: 0, 1, 5, 10, 25, 50, 75, or 100%. Plant richness and cover were analysed as trap averages across the site, and were tested in models by functional group (forbs, C4 grasses, C3 grasses and woody plants) (Table S1). Woody plants and C3 grasses comprised a very small proportion of cover and richness in any given patch, so we focused our analysis on overall plant richness, and total forb and C4 grass cover.

Soil analysis

We obtained three soil cores (10 cm deep × 5 cm diameter) adjacent to every other pitfall trap in the middle of the transect (50 m between core samples). Samples were

rolled in aluminium foil and transported to the lab for bulk density, soil organic matter (SOM) and soil texture (percentages of sand, silt and clay) analyses (Table S1). Cores were weighed, slightly crumbled and exposed to the air for 1 week. Air-dried sample mass and volume of the cores were used for bulk density calculations. The dry soil samples were crumbled further with a mortar and pestle and pushed through a 2 mm sieve to remove coarse fragments. Samples were ground again to reduce the small clay aggregates and homogenised for subsamples. SOM was quantified by burning three 20-g oven-dried subsamples of soil in a muffle furnace (450 °C for 8 h). We calculated the percent SOM as the average mass loss after ignition.

Soil texture methods followed the hydrometer method described by Sheldrick and Wang (1993). We shook a 40-g subsample with dispersing agent (Sodium hexametaphosphate) for 12 h on a reciprocating shaker. After mixing, we recorded hydrometer readings at 40 s (% sand) and 12 h (% clay) and subtracted these values from 100 for % silt.

Additional patch-level variables

We measured within-patch disturbance in two ways: time since planting (age, in years) and time since last management action (primarily burning). Since all of the sites were planted on former agricultural land we used time since planting (hereafter 'age') as a measure of disturbance recovery. We tested time since management (hereafter 'time since burn') as a second measure of disturbance. Although we did not sample ant communities at the edge of the habitat, the amount of edge relative to area has been shown to be important in the colonisation of invasive ants (Holway, 2005) and decreasing rare species (Golden & Crist, 2000). We measured grassland area as a potential predictor of ant community structure in terms of the target area for ants following disturbance (Table S1).

Landscape analysis

We created a LULC map of landscapes surrounding the grassland patches using 2011 National Agricultural Imagery Program Mosaics aerial photographs (1 m resolution) and Geographic Information Systems, ArcGIS version 9.3.1 (ESRI, 2009). We used six classes of LULC: (i) constructed grassland (warm season grasslands), (ii) intensive agriculture (corn and soy), (iii) extensive agriculture (pasture, cool season grasses), (iv) forest, (v) residential/urban and (vi) water. Total area of each LULC type was measured within a 500 m radius from the central point of the grassland transect (Fig. S1). In the case of constructed grassland LULC, we removed the focal grassland itself from this value to test the effects of additional or neighbouring grasslands on the focal patch and maintain this

as a separate test from grassland area (a patch-level predictor). We used percentages of total buffer area for LULC statistical analyses.

Few studies have identified dispersal distances of ants, so it is not clear what an appropriate buffer radius is for measuring the influence of the surrounding LULC. A study using population genetics found plant-mutualist *Crematogaster* ants to be dispersing on average 468 m (Türke *et al.*, 2010). Studies of ant biodiversity in European grasslands have used radii from 50 to 250 m (Dauber *et al.*, 2003, 2005), and a study of ants in sand hills used 500 m and noted that this radius explained the greatest amount of variation (Spiesman & Cumming, 2008). We selected a 500 m radius because it was within the range of these studies, while also preventing overlap of buffers across all but two sites.

Statistical analysis

The three sampling periods per year were pooled for our analysis; however, we analysed ant species richness and composition separately for 2011 and 2012 data because three of the sites differed between years. Richness and composition analyses, therefore, included 20 sites per year. We used generalised linear models (glm function, of the R programming language; R Core Development Team, 2015) with Poisson error distributions to test models of ant species with predictor variables representing patch-level (vegetation, soil, age, time since burn, area, edge:area) and landscape-level (relative amounts of surrounding LULC types) features of grassland habitats. We used natural log-transformed predictor variables of age, time since burn and area to stabilise the variances associated with larger values of these predictor variables. The lowest Akaike's Information Criterion (AIC) was used to identify best and competing (differing by 2 AIC points or less) regression models. We calculated *P*-values and percent deviance explained for the best and closely competing models by conducting a likelihood ratio test against a null model containing only an intercept. To avoid reporting uninformative parameters that can arise in competing models, we calculated model AIC weights (*w*) for best and competing models using the *AICcmodavg* package in R (Mazerolle, 2016). We report competing models only if they are within 0.1 of the best model's weight.

To test individual species responses to patch and landscape variables, we conducted species-level analyses using ant-trap frequency (proportion of traps with a given ant species) rather than overall site abundance. Often traps can be overwhelmed with great numbers of an individual species, simply because a colony is located in proximity to the trap. Ant-trap frequency can be used to reduce potential overestimation of social insects inherent in worker abundance (Andersen, 1991; Gotelli *et al.*, 2011). Setting the traps 25 m apart reduces the chance that ants from one colony would be captured in multiple traps. Some large bodied *Formica* ants can travel up to 20 m from

their nests (Schlick-Steiner *et al.*, 2006), but typically, grassland ants travel no more than 2 m (Albrecht & Gotelli, 2001; Schlick-Steiner *et al.*, 2006). Our personal observations using baits in these grasslands are that most ants do not travel more than a couple of metres from their nests (unpublished data). We conducted species-level analyses on ant data pooled from both years and all 23 sites, using ant species that were found at more than five sites, multiple traps within the sites and with at least 50 total individuals per site. A total of 14 ant species met the minimum requirements for trap frequency analysis. We grouped these species into four categories of habitat specialisation based on established habitat records (Covert, 2005; Nemeč, 2014): (i) disturbance-tolerant species (*Tapinoma sessile* (Say), *Tetramorium caespitum* (L.) – species that are more common in urban environments than natural settings, (ii) uncommon specialists (*Stenamma brevicorne* (Mayr), *Temnothorax ambiguus* (Emery), *Pheidole tysoni* Forel) – species recorded from 20 or less counties in Ohio; (iii) cosmopolitan open (*Myrmica americana* Weber, *Lasius neoniger* Emery, *Solenopsis molesta* (Say), *Monomorium minimum* (Buckley), *Formica pallidefulva* Latrielle) – very common species found in open habitats (lawns, pasture, grasslands), but not in closed (wooded) habitats across the state (i.e. showing affinity for open habitat types); and (iv) habitat generalists (*Lasius alienus* (Foerster), *Ponera pennsylvanica* Buckley, *Aphaenogaster rudis* Enzmann, *Myrmica latifrons* Stårcke) – very common species found frequently in both open and closed habitats across the state (i.e. showing little habitat affinity). Two of the uncommon specialist species, are known associates of prairie remnants. *T. ambiguus* nests in hollow stems and has been cited multiple times in remnants (Gregg, 1944; Hill & Brown, 2010; Nemeč, 2014), and *P. tysoni*, a seed harvester, is common in southern tall grass prairie remnants (Hill & Brown, 2010). *S. brevicorne*, though uncommon in Ohio, can be found in both mesic open habitats and woodlands, and may show less association with prairies than the former two species. Since these four groups have different levels of habitat specialisation and range limitations, they may respond differently to patch and landscape-level controls. We used general linear models with a binomial error distribution to test the effects of patch and landscape predictors.

We analysed patch- and landscape-level predictors of overall species composition (separately for the 2 years) among patches using distance-based redundancy analysis (dbRDA) multivariate constrained ordinations with Bray–Curtis dissimilarity (McArdle & Anderson, 2001). We used AIC to select the best-fitting ordination model and obtained *P*-values using random permutations (999 permutations). The *vegdist* function in the *vegan* package of R (Oksanen *et al.*, 2013) was used to calculate Bray–Curtis dissimilarity, and a dbRDA was conducted with a user-written function in R (M. Anderson, pers. comm.).

We conducted a Moran's *I* test for spatial autocorrelation of the residuals of the best-fitting models among sites (*correlog*, *ncf* package, R) and calculated *P*-values for

significance of the Moran's *I* correlation coefficients at each of 6 distance classes by conducting 999 resampling permutations (*resamp*, *correlog* function). We used Mantel tests with distance classes (*mantel.correlog*, *vegan* package, R) to test for correlation between the Euclidean distance of our sites and ant community dissimilarity. We corrected for multiple comparisons at distance classes with Benjamini–Hochberg adjustment to *P*-values. There was no evidence of spatial autocorrelation of residuals or ant community composition among sites (all *P* > 0.10).

Results

In 2011, 7978 ant individuals, comprising 28 species (site mean = 9.60, range = 3–14) were collected. In 2012, 4957 individuals of 31 species (site mean = 8.90, range = 4–13) were collected (Table S3). The model with the lowest AIC for overall ant richness in 2011 was site age (Fig. 1a;

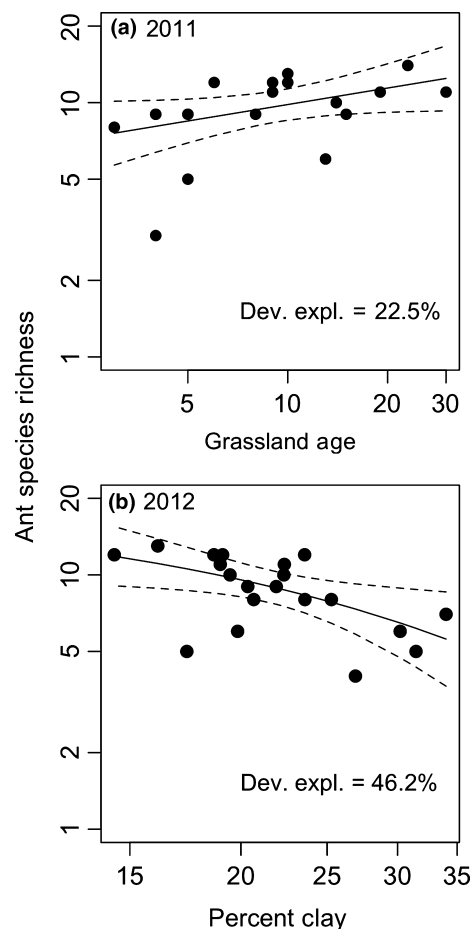


Fig. 1. Best models for ant species richness in (a) 2011 included time since planting (grassland age) and (b) 2012 included percentage of (–) clay and (+) sand fractions of the soil (X and Y axes log_e-scaled). Dotted lines represent 95% confidence intervals based on predicted values of the SE of regression coefficients.

Table 1. Best models for ant species richness in 2011 and 2012.

Ant richness	Best model	Δ AIC vs. null	% Dev. Expl.
2011	(+)Log _e (age)	-1.62	22.51%
2012	(+)% sand + (-)% clay	-3.88	46.22%

Table 1), and there was one competing model that also included clay ($w = 0.27$). The likelihood ratio test of the age model versus the null model was not significantly different ($P = 0.057$, d.f. = 1.18), and age explained 22.77% of the deviance ($w = 0.33$) (Table 1). Soil texture (% sand and % clay) was the best-fitting model for ant richness in 2012 ($P = 0.0194$, dev. expl. = 46.22%, d.f. = 2.17, $w = 0.34$) (Fig. 1b). Ant species richness was significantly greater in sandier sites than sites with higher clay content soils. Other patch-level predictors including plant richness, cover of plant functional groups, SOM, bulk density, time since burn, area, edge:area or landscape-level predictors (LULC) were not included among the best-fitting or competing models based on AIC for ant richness in 2011 or 2012.

Using ant-trap frequency data, we identified how 14 different ant species respond to patch and landscape-level predictors (Table 2). Disturbance-tolerant ants, *T. sessile* and *T. caespitum*, responded to both patch and landscape-level factors. The best model for *T. sessile* included site age (-), time since burn (+) and intensive agriculture (+) ($P < 0.001$, dev. expl. = 26.39%, d.f. = 3.19) (Fig. 2a). *T. caespitum*, was strongly predicted by % sand (+, $P < 0.0001$, dev. expl. = 89.13%, d.f. = 1.22).

The uncommon specialist ants included *T. ambiguus*, *S. brevicorne* and *P. tysoni*. Best or competing models for two of the species included anticipated responses to measures of disturbance (age, area and edge effects) and

responded positively to additional grassland land use in the surrounding landscape. The best model for *T. ambiguus* included age (+), area (+), and bulk density (-) and explained 40.47% of the deviance ($P < 0.0001$, d.f. = 3.19, $w = 0.51$); a competing model included grassland land use ($w = 0.49$). *S. brevicorne* frequency was best predicted by extensive agriculture (-) and edge:area (-) explaining 37.36% of the deviance (d.f. = 2.20). The best model for predicting *P. tysoni* frequency, was % sand alone (+, $P < 0.0001$, dev. expl. = 79.29%, d.f. = 1.22).

The other two groups of ant species with contrasting habitat specialisation (open habitat only vs. habitat generalists) responded differently to patch and landscape-level variables. Best models for open habitat cosmopolitan ants included patch-level (primarily soil texture and time since burn) and relevant open habitat landscape-level predictors (primarily negative responses to grasslands in the landscape). Best models for habitat generalist ant species all included landscape-level predictors and a variety of (primarily soil related) patch-level factors (Table 2). *S. molesta*, *M. minimum* and *L. alienus* had higher frequencies in sites that were recently burned, while *M. americana* had higher frequencies in less recently burned sites (Fig. 2c). C4 cover was in best-fitting models for *F. pallidefulva* (+), *A. rudis* (+) and *L. neoniger* (-). Multiple species responded to soil characteristics including *M. latifrons* (+ SOM), *M. minimum* and *S. molesta* (+ % Sand), *F. pallidefulva* (- % Silt) and *L. alienus* (+ % Silt). Most of the species (seven of the nine) included landscape-level predictors in their best models.

Ant species composition

Variation in ant community composition in both years was best explained by age and % sand. In 2011, age was

Table 2. Best models for trap frequency of 14 focal ant species.

Ant species	Habitat association	Best model	Δ AIC vs. null	% Dev. Expl.
<i>Tapinoma sessile</i>	D	(-)Log _e (age) + (+)Time since burn + (+)IntensiveLU	-17.34	26.39
<i>Tetramorium caespitum</i>	D	(+)% Sand	-96.35	89.13
<i>Temnothorax ambiguus</i>	U	(+)Log _e (area) + (+)Log _e (age) + (-)Bulk density	-39.78	40.47
<i>Pheidole tysoni</i>	U	(+)% Sand	-52.81	79.29
<i>Stenamma brevicorne</i>	U	(-)ExtensiveLU + (-) Edge:Area	-25.78	37.36
<i>Lasius neoniger</i>	O	(-)Log _e (age) + (-)C4 cover	-19.88	27.43
<i>Myrmica americana</i>	O	(+) Time since burn	-16.13	18.42
<i>Formica pallidefulva</i>	O	(-)% Silt+ (+)C4 cover + (-)GrasslandLU	-9.10	29.80
<i>Solenopsis molesta</i>	O	(-)Time since burn + (+)% Sand + (-)GrasslandLU	-28.65	26.78
<i>Monomorium minimum</i>	O	(-)Time since burn + (+)% Sand + (-)GrasslandLU	-73.64	50.50
<i>Aphaenogaster rudis</i>	G	(+)C4 cover + (-)IntensiveLU	-14.10	16.30
<i>Myrmica latifrons</i>	G	(+)Organic Matter + (+)ForestLU	-19.01	29.78
<i>Lasius alienus</i>	G	(+)% Silt + (+)GrasslandLU + (-)ExtensiveLU + (-)Time since burn	-33.75	46.69
<i>Ponera pennsylvanica</i>	G	(+)GrasslandLU + (-)ExtensiveLU + (+)Log _e (area)	-6.93	25.34

Habitat Association: disturbance-tolerant species (D), uncommon specialists (U), cosmopolitan open habitat species (O) or habitat generalists (G) (in open and closed habitats).

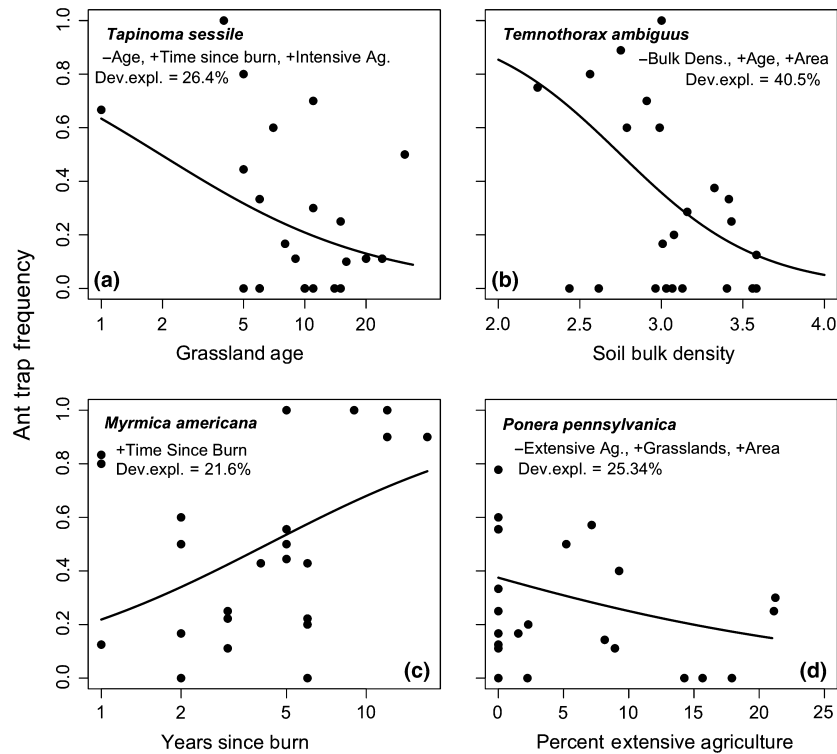


Fig. 2. Best-fitting models for (a) a disturbance-tolerant species (*Tapinoma sessile*), (b) an uncommon specialist species (*Temnothorax ambiguus*), (c) a cosmopolitan open habitat species (*Myrmica americana*), and (d) a habitat generalist species (*Ponera pennsylvanica*).

the more important predictor of composition (Pseudo- $F = 2.40$, $P = 0.001$, $R^2 = 22.0\%$; Fig. 3a) and a competing model included area ($\Delta\text{AIC} = +0.08$). In 2012, % sand explained more of the variation in composition (Pseudo- $F = 2.80$, $P = 0.001$, $R^2 = 24.8\%$; Fig. 3b). Two competing models for 2012 composition, included time since burn (+0.05) and urban land use (+0.05). While age, % sand and time since burn routinely came up in the species trap frequency models, urban land use was only present in two competing models suggesting that the less abundant 17 of the 31 ant species found at these sites may be driving this relationship with urban land use.

Discussion

Relative roles of patch and landscape-level predictors

Ant biodiversity in constructed grasslands depended on both patch- and landscape-level processes. Ant species richness and community composition was determined by two patch-level variables: age of the site and soil texture. The effect of age is consistent with other chronosequence studies of ant community development (Dauber & Wolters, 2005; Phipps, 2006). Soil texture is an important filter for ant communities (Bestelmeyer & Wiens, 2001; Boulton *et al.*, 2005; Graham *et al.*, 2009), and our findings add further support for the role of soil texture. In

particular, we find that grasslands with soils high in clay tend to harbour fewer ant species than those with sandier soils. Our trap-level species analysis, however, demonstrated that individual species often respond in contrasting ways to multiple patch- and landscape-level predictors, diluting the overall effect of these other predictors on total species richness. Our species analysis highlights the importance of identifying species-level or functional-group responses if ants are to be used as bioindicators of changes in soils, disturbance or other environmental conditions.

Disturbance-tolerant and uncommon specialist responses

One of the disturbance-tolerant ant species (*T. sessile*) responded positively, as predicted, to disturbance in surrounding land use (intensive agriculture). *T. sessile* was more frequent in young sites, disturbed by intensive agriculture, while *T. caespitum* frequency was determined by sandy soil reducing the signal of any urbanisation effects. Patches surrounded by urbanisation and intensive agriculture likely have higher propagule pressure of disturbance-tolerant species. While both of these species are common in human-dominated habitats, they have also been detected in remnant prairies. Contrary to our findings, Menke *et al.* (2015), found that both of these species were more frequent in remnant prairies than restorations. This

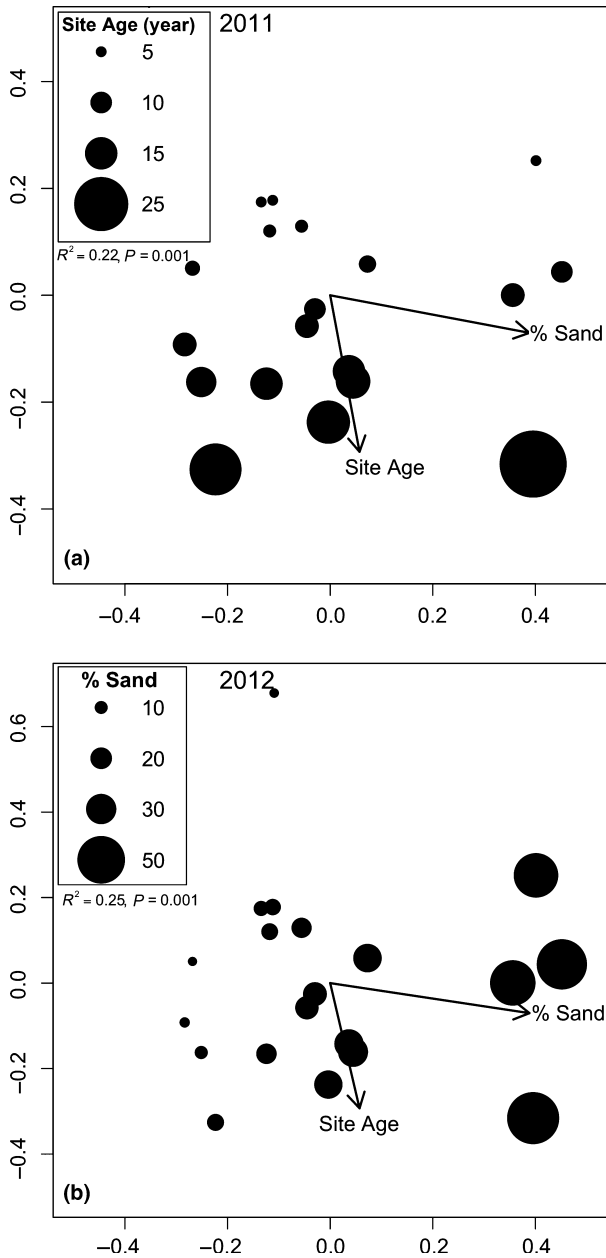


Fig. 3. Constrained multivariate ordination for ant community composition in (a) 2011 and (b) 2012. Symbols are site scores for individual grasslands scaled to the percentage value of the most important predictor variable (2011– Grassland age, 2012 – % Sand). Arrows are biplot correlations of significant predictor variables (Grassland age and % Sand).

disparity may be due to unmeasured soil or landscape level factors in the Menke *et al.* study.

We expected the three uncommon specialist species (*T. ambiguus*, *P. tysoni* and *S. brevicorne*) to respond negatively to disturbance in the surrounding landscape (intensive agriculture and urbanisation) and edge, while responding positively to site age, extensive agriculture and

grasslands in the landscape. *T. ambiguus* trap frequency was positively related to site age and area, and soil properties known to improve with time in CRP lands (decreased bulk density) (McLauchlan *et al.*, 2006). *T. ambiguus* and *S. brevicorne* both responded positively to additional grassland land use in the vicinity, however, these did not appear in best models. Additionally, *S. brevicorne* was negatively influenced by increased edge effects and contrary to our predictions, extensive agriculture. *T. ambiguus* is a known prairie associate (Gregg, 1944; Hill & Brown, 2010; Nemeč, 2014) and may be a potential indicator of grassland recovery from disturbance at the landscape and patch levels. Moranz *et al.* (2013), found that *T. ambiguus* was more abundant in remnant prairies, which is supported by our findings, but was sensitive to grazing and burning a factor that did not appear in our best models for this species. *S. brevicorne*, not known to be associated with remnant prairies and also found in woodlands (Coovert, 2005), might still have potential as an indicator of disturbance in terms of edge effects and extensive agriculture. *P. tysoni*, also documented from remnants (Hill & Brown, 2010), was primarily associated with sandy sites and may be uncommon in our region simply due to lack of proper soil type.

Landscape-level responses

Landscape variables did not appear in best models for ant species richness or composition, yet they appeared in best or closely competing models for trap frequency of 9 of the 14 ant species, which suggests that the ant assemblages in these small grassland patches are highly dependent on, and likely colonise from, the surrounding landscape. We were surprised to find species-level responses to extensive agriculture were negative in all three models in which it appeared, since we predicted these habitats to be potential sources of grassland ant propagules. Grazing can negatively affect ant richness (Bestelmeyer & Wiens, 2001; Boulton *et al.*, 2005; Moranz *et al.*, 2013), and since most of the extensive agricultural fields in our region are either harvested or used as pasture, they may have reduced propagule contribution to constructed grasslands.

We observed different influences of surrounding land use on the two cosmopolitan ant species groups (open habitat and habitat generalist species). Best models for habitat generalist ant species all included landscape variables. Open habitat ant species were primarily affected by patch-level variables and had negative responses to increased grassland land use. Our five open habitat ant species are also very abundant in mowed lawns, extensive and intensive agriculture fields, therefore, they may be colonising directly from the field margins or already present within the field at the time of planting. Over time they may be replaced by more competitive habitat specialists. Surprisingly, forest land use was not the most common of landscape predictors (except for

M. latifrons) for the habitat generalist ant species. Instead habitat generalist ants exhibited negative responses to intensive and extensive agriculture and positive responses to grassland land use, representing the overall positive influence of semi-natural habitat.

Management practices

The effect of grassland management, such as burning, on total ant richness or abundance typically has not shown consistent trends across ant studies; however, individual species or functional-group responses are often documented (Underwood & Fisher, 2006; Joern & Laws, 2013). In our study, time since burn was included in 5 of the 14 species models. *T. sessile* and *M. americana* responded positively to increased time since burn, while *S. molesta*, *M. minimum* and *L. alienus* responded negatively. *T. sessile* tended to make short term nests under layers of grass litter, while *M. americana* nested in large grass clumps building turret-like, thatch structures up the grass stems. We suspect that these two nest structures are highly susceptible to routine burning. *L. alienus*, *S. molesta* and *M. minimum* all nest in the soil and may simply be captured at higher rates, as shown in other studies (Melbourne, 1999), when the litter structure is less complex. The lack of generality among studies of grassland management may be largely driven by differences in species-level responses.

Soil characteristics

Soil texture and soil type have consistently shown strong associations with ant communities (Bestelmeyer & Wiens, 2001; Boulton *et al.*, 2005; Graham *et al.*, 2009), and our results support the importance of these predictors as environmental filters for the assembling ant community in constructed grasslands. Soil characteristics, especially soil texture, were included in best models for 8 of the 14 ant species in this study, across habitat association groups, total ant richness and community composition. Ant species responded differentially to components of soil texture likely due to species specific constraints related to the physical ability of ants to nest in the soil, for example soil moisture and ease of excavation. Soil variables associated with recovery from agriculture, lower bulk density and higher SOM (McLauchlan *et al.*, 2006) appeared in the best model for *T. ambiguus*, our most promising grassland indicator, and a habitat generalist, *M. latifrons*. The physical template of the soil is a significant patch-level control on ant community assembly, and ant communities may also act as sentinels of age-dependent recovery of soils.

Vegetation

Vegetation played a very limited role in the grassland ant community. The constructed grasslands in our study

showed no relationship between plant richness or cover of functional groups and grassland age, management, or soil characteristics (unpublished data). This is probably because constructed grasslands are highly dependent on the initial seed mix and weather conditions in the first few years of establishment, unlike remnant prairies (Dickson & Busby, 2009). Although ants are highly associated with dominant vegetation types (e.g. forests vs. grasslands), most studies have found little to no relationship with plant richness or cover within a given vegetation type (Hill *et al.*, 2008; Nemeček *et al.*, 2014; Peters *et al.*, 2016). Some studies have identified plant structure or vegetation height as a more important characteristic for predicting ants in grasslands (New, 2000; Debinski *et al.*, 2011). In our study, C4 grass cover appeared in three models for cosmopolitan ant species. *F. pallidefulva* and *A. rudis* were positively related to C4 cover, while *L. neoniger*, the most abundant and cosmopolitan ant species, was negatively influenced by C4 cover and age. Prescribed burns are typically conducted in the spring at our sites, a practice that tends to favour C4 grasses over time (Steuter, 1987; Howe, 2000). The inverse relationship between C4 cover and age may be paralleled by *L. neoniger*, an ant that can be found in crop fields and was more frequent in younger sites. Our results suggest that ant communities are primarily structured by the physical aspects of their environment (soil texture, plant structure and disturbance) rather than vegetation.

Comparison to remnant prairies

A potential limitation of our study is the lack of comparison to benchmark or remnant prairies. Most of the historical prairies were located in central and northern Ohio. In the Midwest US, most of the grasslands constructed through incentive programmes are less than 50 ha in size and are isolated from any native prairie remnants by 50 or more kilometres. For example, in our study region, the closest remnant prairie (Huffman Prairie, Dayton, OH) is outside the geographic range (>22 km away from) of our focal grasslands, on an air force base with limited access. Including this location in our study would, at best, lend only anecdotal evidence. We were limited in our statistical analysis to species that were relatively frequent within these sites, but true prairie specialists or remnant-dependent species may have been present in too low of numbers to be analysed. For example, several uncommon or rare species in our grasslands have previously been documented in remnants (Gregg, 1944; Hill & Brown, 2010), but were collected too infrequently for analysis: *Temnothorax pergandei*, *Pheidole pilifera*, *Crematogaster lineolata* and *Formica integra*. Hill and Brown (2010) noted that *P. pilifera* was found only in the most floristically intact and least disturbed of their remnant sites; however, like our uncommon specialist *P. tysoni*, *P. pilifera* was also associated with only the sandiest sites in our study. Although we did not

specifically test this, constructed grasslands in landscapes surrounded by greater proportions of grassland land cover or in closer proximity to remnants may accumulate more rare or prairie specialist species in addition to shifts in frequency of the more common species.

Conclusions

Ant communities showed turnover in species composition as constructed grasslands age, which may result in different functional roles and significance of ants at multiple points in the species assembly process. European studies have found increasing nest density during grassland development and a shift in the ant community from primarily aboveground foraging species to subterranean species in older sites (Dauber & Wolters, 2005). Several of the ant species in our study (especially *Lasius*) tend aphids above and belowground, and shifts in relative abundances of these species could affect grassland plant communities or have spillover effects on neighbouring cropland. Other species in our study are primarily predators and may alter grassland communities above and belowground through both inter- and intraguild predation. For example, ants in the genus *Strumigenys* prey on soil microarthropods and may cause shifts in the belowground food web, while *Formica* ants are wide ranging predators often observed foraging on insects and tending aphids on vegetation (Covert, 2005). Mutualisms among ants and the grassland community may also shift over time. Multiple *Formica* species are hosts to butterflies in the family Lycaenidae and *Microdon* flies (Syrphidae) that are pollinators, and *Pheidole* and *Aphaenogaster* species are significant seed dispersal agents (Covert, 2005). Understanding temporal shifts in ant communities can improve our understanding of species interactions in these constructed grassland communities. Likewise, a shift in ant species with larger belowground nests may result in greater effects on soil properties and nutrient dynamics.

Future work could elucidate if ant functional roles shift as the grassland develops and if the strength of species interactions varies in different environmental contexts. The sorting and assembly process in grasslands may lead to shifts from early colonisers that are primarily generalist predators with limited or generalist species interactions to later colonisers with more specialised interactions (mutualisms, seed dispersal and belowground food web interactions).

Ant community assembly in constructed grasslands is a time-dependent process, shaped by the suitability of the habitat patch, as well as the pool of ant species in the surrounding landscape that are available to colonise grassland habitats. Our findings demonstrate the importance of landscape-level perspectives when considering restoration and management of small preserves for biodiversity. Lastly, our research supports the use of ants as environmental indicators of time-dependent processes, disturbance and soil characteristics, but suggests that aggregate

measures of ant diversity (species richness) are less sensitive to variation in habitat quality and the surrounding landscape than targeted species responses or shifts in community structure.

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Supporting Information

Additional Supporting Information may be found in the online version of this article under the DOI reference: doi: 10.1111/icad.12215:

Fig. S1. Locations of 23 sites in Butler, Preble and Montgomery Counties, Ohio. Examples of surrounding landscapes for three sites are shown (numbered circles).

Fig. S2. Diagram of sampling methods. Pitfall traps and vegetation quadrats were spaced 25m apart along the transect.

Table S1. Descriptive table of patch-level variables. Divisions represent general site characteristics, disturbance, plant and soil variables.

Table S2. Descriptive table of landscape-level variables (LU=Land use).

Table S3. Ant species found across the 23 sites, abundance and number of sites.

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