

Disturbance differentially affects alpha and beta diversity of ants in tallgrass prairies

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Abstract. Biodiversity conservation requires understanding how disturbance influences biodiversity patterns at multiple spatial scales. Because the total diversity of species within a given region (γ diversity) is influenced by both local diversity (α diversity) and dissimilarity in community composition (β diversity), understanding disturbance effects on both components of diversity is essential, especially if disturbance impacts α and β diversities differently. In this three-year study, we examined how a disturbance (annual harvesting of grasslands) and environmental gradients in the proportion of sand locally, habitat size, and landscape diversity influenced the abundance and α and β diversities of ants within tallgrass prairie habitat in Wisconsin. We used a null-model approach to examine how harvest and environmental factors influence β diversity. Following three years of treatments, we found that ant abundance was greater in harvested sites compared to control sites and ant abundance was positively correlated with soil sandiness. We also found that α diversity was lower in harvested sites compared to control sites and none of the measured environmental gradients influenced α diversity. The effects of harvest on α -diversity patterns may have been mediated through the competitive interactions of the two dominant ant species (*Formica montana* and *Lasius neoniger*). In contrast, β diversity (after adjusting for random effects and changes to α diversity) was higher in harvest sites compared to control sites, and variability in community composition was largely driven by the occurrence of rare species. The proportion of sand in the local habitat and habitat size positively influenced β diversity suggesting that community dissimilarity was due in part to environmental filtering and the size of species pools. Because biomass harvest had contrasting effects on ant α and β diversities, trade-offs in maintaining α vs. β diversity might need to be considered in land management and conservation efforts.

Key words: disturbance; environmental heterogeneity; haying; insect arthropods; null model; tallgrass prairies.

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INTRODUCTION

Biodiversity conservation requires an understanding of how disturbance influences biodiversity at multiple spatial scales. Previous studies have largely focused on disturbance effects on local diversity (α diversity), ignoring how variation in

community composition among sites (β diversity) might change following a disturbance. Evaluating compositional variation or dissimilarity between sites can shed light on community assembly processes, and this information can be used to inform conservation planning efforts such as strategic placement of protected areas and landscape design

(Socolar et al. 2016). Because the total diversity of species within a given region (γ diversity) is composed of both α and β diversities (e.g., $\beta = \alpha/\gamma$ [Whittaker et al. 2001] or $\beta = \gamma - \alpha$ [Veech et al. 2002]), understanding disturbance effects on both components of diversity is essential and ignoring disturbance impacts on broad-scale patterns of biodiversity can mislead conservation efforts (McKnight et al. 2007, Socolar et al. 2016), especially if α and β diversities respond differently to disturbance (Tylianakis et al. 2005, Clough et al. 2007, Myers et al. 2015). Therefore, evaluating disturbance effects on both components of diversity can provide complementary information about community assembly processes and better inform conservation strategies (Karp et al. 2012, Arnan et al. 2015).

Both α and β diversities are affected by processes that play out across different spatial scales. For example, local processes, such as competition and predation, and environmental filtering can structure ecological communities but processes occurring across larger spatial scales such as dispersal from a regional species pool can influence diversity as well. Disturbance can influence these processes to ultimately affect α and β diversities by affecting environmental heterogeneity both within and among sites (Clough et al. 2007). For example, disturbances such as fire and grazing can create patchiness in environmental conditions *within* sites which can have positive effects on α diversity by creating refuges and suppressing the dominant species (Sousa 1984, van Klink et al. 2015, Young et al. 2015). The positive effect of environmental heterogeneity on α diversity has been observed in many different systems for taxonomic groups including plants (Adler et al. 2001, Anderson et al. 2004), insects (Hendrickx et al. 2007), fish (Lepori et al. 2005), and birds (Fuhlendorf et al. 2006, Hovick et al. 2015). Disturbances can also influence β diversity (or community dissimilarity) by affecting environmental heterogeneity *across* sites. For example, if disturbances such as logging, urbanization, and agricultural intensification are consistent in intensity among sites, then disturbance can have a homogenizing effect on animal and plant communities by selecting disturbance-tolerant species or species with strong dispersal capabilities that can quickly recolonize following the disturbance (Gabriel et al. 2006, Holway and Suarez 2006,

McKnight et al. 2007). These disturbances can give rise to communities that are similar in species composition (low β diversity) and has been observed for ants (Holway and Suarez 2006), plants (Gabriel et al. 2006), and birds (Ferenc et al. 2014). In contrast, if disturbance intensity varies across sites, then β diversity might increase due to among-site differences in local extinction, competition, and colonization rates. Because disturbances can affect environmental heterogeneity both within and among sites differently, disturbances have the potential to have contrasting effects on α and β diversities. In this scenario, trade-offs between maintaining α and β diversities might need to be considered in conservation and management efforts.

Ants are useful organisms to use to test hypotheses regarding α and β diversities because ant communities are known to be structured by physical disturbances such as grazing and burning (Debinski et al. 2011, Moranz et al. 2013, Vasconcelos et al. 2017, Gray et al. 2018), local processes such as competition and environmental filtering (Sanders et al. 2007, Wiescher et al. 2012), dispersal (Bruna et al. 2011, King and Tschinkel 2016), and sizes of regional species pools (Dauber et al. 2006, Spiesman and Cumming 2008). Furthermore, ants carry out important ecological functions such as seed dispersal, predation, decomposition, and soil aeration (Carroll and Janzen 1973, Folgarait 1998, Del Toro et al. 2012); therefore, efforts to maintain ant diversity have ecosystem-level implications.

In this study, we examined how repeated disturbances (annual plant biomass harvest) affected ant abundance and diversity in tallgrass prairies. Specifically, we asked: (1) Do ant abundances vary with annual biomass harvest? (2) Do α and β diversities of ants vary with annual biomass harvest? (3) Which ant groups based on dominance, habitat preference, and nest sizes contribute to changes in α and β diversities? and (4) How do environmental gradients in factors uncorrelated with harvest influence α and β diversities? We expected harvesting to mimic the effects of grazing and low-intensity fire in grasslands and therefore expected α -diversity of ants to be higher in harvested sites because, like fire and grazing, harvesting plant biomass could increase local environmental heterogeneity thus reducing competition for space and allow less common ant

species to colonize locally and persist (Floren et al. 2008, Gray et al. 2018). In contrast, we expected β diversity to be lower in harvested sites because similarity in management practices can reduce environmental heterogeneity among sites compared to undisturbed controls (Tylianakis et al. 2005, Clough et al. 2007) and repeated harvest may select for disturbance-prone species or those with high dispersal abilities. Because harvest-mediated changes in ant abundances can affect α and β diversities and because α and β diversities are inter-related (e.g., $\beta = \alpha/\gamma$, Whittaker et al. 2001, or $\beta = \gamma - \alpha$, Jost 2007), any changes to abundances can affect both components of diversity by chance alone. Therefore, we use rarefied species richness (adjusted by the local ant abundance) as our measure of α diversity and a null modeling approach to quantify β diversity. Furthermore, the null modeling approach allows us to separate harvest effects on β diversity from stochastic variation that might be associated with changes to ant abundance and α diversity (Crist et al. 2003, Chase et al. 2011) thus providing an unbiased measure of β diversity. Overall, these approaches allow us to address how harvesting might independently affect α and β diversities of ants in grassland ecosystems.

METHODS

Study system

This study took place in tallgrass prairies in Wisconsin in 2013–2015 in 20 sites. Data from this study were a part of a larger study examining the effects of biomass harvest on arthropod communities and arthropod-derived ecosystem services (see Kim et al. 2017, Spiesman et al. 2017). Sites were managed by the US Fish and Wildlife Service ($N = 13$) and Wisconsin Department of Natural Resources ($N = 7$) and were at least 2 km away from one another. Sites were characterized as having a mixture of perennial grasses (such as *Schizachyrium scoparium*, *Panicum virgatum*, and *Elymus canadensis*) and perennial forbs and legumes such as *Rudbeckia hirta*, *Solidago altissima*, and *Trifolium pratense*. Soils at our sites had a loamy texture and are characterized as mollisols (Hartemink et al. 2012). Sites varied in size from 0.21 to 1.2 km², but we confined our ant sampling to a 50 m \times 50 m area at each site (at least 50 m from any edge to minimize edge effects). At the

end of the growing season in each year (September/October), biomass at half the sites was removed at the entire site level with standard commercial haying equipment leaving approximately 30 cm of standing plant residue with all harvestable biomass removed from the site (hereafter “harvest” sites). Sites were not tilled after haying. The other sites were unharvested “controls”. The first harvest event occurred in fall 2012. Prior to the experiment, sites were managed via burning and mechanical removal of woody vegetation. No management was conducted at the sites for at least three years prior to the start of the experiment, and treatments (harvest/control) were assigned randomly to each site. See Kim et al. (2017) for further details about site management history and site selection processes.

Ant sampling

Ants were sampled every year for once a month from June to August. The majority of sites were sampled for three years (2013–2015); however, there were three sites that were only sampled in two years (either 2013–2014 or 2014–2015) due to unforeseen circumstances that prevented us from sampling a third year (e.g., fire and federal government shutdown). At each site, three sampling stations were established with one pitfall trap at each station. Stations were placed at least 50 m from each other making it unlikely that workers from the same nest would be found in different traps. Stations were at fixed locations within years but varied in location across years. Pitfall traps consisted of 1-L plastic containers (10 cm diameter opening, Dart Conex, Mason, Michigan, USA) filled three-quarters full with 50:50 propylene glycol:water solution, placed flush with the ground, and covered with a 6-mm wire mesh to prevent small mammals and herpetofauna from entering into the traps. While mesh of any size could affect the capture of larger ant species, the use of mesh was necessary to reduce the capture of small vertebrates which could have biased capture efficiency of ants. Plastic covers (30 cm diameter) were staked 10 cm above the traps to prevent rainwater from flooding the cups. Pitfalls were placed out for two weeks continuously during each sampling session. While it is possible that pitfall sampling could bias community composition in the harvest and control sites by altering the likelihood of

certain species being captured (see citations in Lassau and Hochuli 2004), pitfalls were placed out in fields at multiple times per year for three years and continuously for 14 d per sampling session. Therefore, we feel confident that this was ample time to capture less active ant species. We selected pitfall sampling rather than other methods of ant sampling such as baiting or hand collection because we wanted an unbiased, passive, and efficient method of ant sampling (Romero and Jaffe 1989, Lassau and Hochuli 2004). While we recognize that we may have missed some ant species using only one ant sampling method, the same sampling method was used in both the control and harvest sites allowing for comparisons of relative abundance and diversity. Upon return to the laboratory, ants were identified to species. Voucher specimens were pinned and verified with specimens at the Wisconsin Research Insect Collection and the Chicago Field Museum, and with myrmecologist, Sean Menke (Lake Forest College). Our experimental design resulted in a total of 27 pitfalls to characterize ant communities within each site (18 pitfalls for three sites that were only sampled for two years), and we constructed species accumulation curves based on number of samples to confirm that sites were sampled adequately (see Appendix S1).

Environmental variables

Three environmental variables known to affect ant assemblages and species richness were measured for each site: soil texture, patch size, and landscape diversity (Yanoviak and Kaspari 2000, Wang et al. 2001, Wiescher et al. 2012). These variables were uncorrelated with harvest treatment (Kim et al. 2017) and did not correlate with one another ($VIF < 3$; Zuur et al. 2010). Soil sampling was done in 2014 and 2015. At each site, one transect (100 m long) was established through the center of the field, and at every 10 m, soil core samples were collected (10 samples per site). Soil cores were 5 cm in diameter and 25 cm in depth, and samples were dried in a 60°C oven for seven days. Soil texture (i.e., the proportion of sand, silt, and clay) was determined using a modified version of the hydrometer method (Bouyoucos 1962, Robertson et al. 1999). Dry soil was pulverized using a mortar and pestle, and then dry samples were suspended in a 250 mL solution of water

and 1.5 mL dispersing agent (5% sodium hexametaphosphate). After mixing the samples for 2 min, solutions settled for 48 h. The depth of each of the sand, silt, and clay layers and the total soil depth were measured, and the proportion of each texture type was quantified. The proportion of sand and silt were negatively correlated ($R^2 = 0.96$), but there were no correlations with clay. For ease of interpretation, we only used the proportion of sand in our analyses.

Patch size and landscape diversity were quantified using ArcGIS. We used the US Department of Agriculture (USDA) National Agriculture Statistics Service Cropland Data Layer (USDA 2013) to extract land cover information surrounding each site. Within each field, we centered circles of fixed radii (500, 1000, 1500, and 2000 m) and measured landscape variables (landscape diversity and patch size). Landscape diversity was the diversity of different habitat/crop types defined by USDA land cover classification (Simpson's index of diversity, 1-D) within each landscape. The number of different habitat/crop types ranged from 11 to 27, and the most common types included annual crops (e.g., corn and soybean) and perennial systems (e.g., grass pastures and herbaceous grasslands). Patch size was the area of the field in which each site was established. We selected this range of radii because they are beyond daily foraging ranges of ants (Carroll and Janzen 1973, Traniello 1989) and small enough to allow landscapes to be statistically independent from one another (i.e., sites and surrounding landscape did not overlap). Furthermore, the long-range dispersal of queens is generally limited to within 500 m of the natal nests (Mabelis 1994, Liautard and Keller 2001, Vitikainen et al. 2015). Preliminary analyses showed that the amount of variation explaining total ant abundance was greatest at 1000 m around the field center ($R^2 = 0.67$). Therefore, we used this spatial scale for our analyses below.

Statistical analyses

We were interested in understanding how disturbance affected ant abundances and α and β diversities. Site was treated as an independent replicate; therefore, ant data from all experimental years were combined to form a single site \times species matrix. Because the number of individuals captured could be influenced by the proximity of

pitfall traps to nests, we used trap incidence rather than the number of captured individuals to construct the site \times species matrix (Ellison et al. 2007, Menke et al. 2015). Furthermore, because not all sites were sampled for three years, we used proportional trap incidence as entries in the site \times species matrix (number of traps that captured individuals out of the total number of traps placed at each site [18 traps for sites sampled only for two years, or 27 traps for sites sampled for the full three years]). For each species, its proportional trap-incidence value was bounded between 0 and 1. We were also interested in understanding how gradients in environmental factors uncorrelated with harvest affected ant diversity, so we averaged the proportion of sand and landscape diversity across all experimental years for each site; habitat size remained constant across experimental years. We combined environmental variables from all experimental years for two reasons: (1) Environmental variables were highly correlated across the experimental years, and (2) we are not interested in the across-year variability on ant diversity and assembly processes. Analyses were performed using R v3.03 (R Development Core Team 2014).

To determine how ant abundance per site was affected by harvest, proportional trap incidence of all species was averaged and used as our metric of ant abundance at the site level. We used a linear model (LM) with harvest treatment (control/harvest), the proportion of sand, patch size, and landscape diversity as predictor variables. We arcsine square-root transformed the proportional trap-incidence values and tested whether data met LM assumptions (e.g., residuals normally distributed and homogeneity of variance). To determine how α diversity was affected by disturbance, we estimated species richness rarefied by the minimum incidence of ants at each site (Fisher et al. 1943, Heck et al. 1975). The incidence-based rarefaction estimates were highly correlated with the observed species richness ($R^2 = 0.88$); therefore, we are confident that we have the best α diversity approximation. We used the same LM structure as above with the incidence-based rarefied species richness as our response variable.

We also evaluated how harvesting affected different ant groups based on numerical dominance, habitat preference, colony nest size, and

subfamily. Group classifications were determined from literature sources (Covert 2005, Fisher and Cover 2007, Ellison et al. 2012) and expert opinion (Appendix S1). Rank trap-incidence curves (Fig. 1) were used to assign species into numerical dominance categories (rare, common, or intermediate). Rare species were defined as species occurring in $<10\%$ of traps (Gaston 1997), common species were defined as species with $>75\%$ trap incidence, whereas intermediate-ranked species were species ranked in between common and rare species. Habitat preference was based on whether species were typically found in closed-canopy habitat such as forest ("closed-habitat specialists") or open habitat such as grasslands, agriculture, disturbed areas ("open-habitat specialists") or both ("habitat generalist"). Ant colony nest size (small or large) was based on the number of individual workers ("small" nest size < 500 workers or "large" nest size > 1000 workers). We compared the average trap incidence of each ant group in the control and harvest sites using the same LM structure as above. To control for family-wise error rates typically associated with multiple tests, P values were adjusted using the Benjamini-Hochberg procedure (Benjamini and Hochberg 1995). Benjamini-Hochberg critical values were calculated as $(i/m)Q$, where i is the rank, m is the total number of tests, and Q is the false discovery rate set at 0.05.

To determine whether β diversity (compositional dissimilarity between communities) was affected by harvest, we used a null-model approach as described in Chase et al. (2011) and Kraft et al. (2011). Because α and β diversity measures are linked where harvest-mediated changes to local abundance and α diversity will affect community dissimilarity (β diversity), the null approach allows us to estimate β diversity while controlling for changes in abundance and random sampling effects (Chase et al. 2011). In short, the observed β diversity values (β_{obs}) were compared to β diversity values generated from null models (β_{null}) and standardized differences between β_{obs} and β_{null} were used as independent estimates of β diversity (β_{dev}). To accomplish this, we used a three-step process. First, we created an abundance-based (Bray-Curtis) dissimilarity matrix between all possible paired sites. Abundances (i.e., proportional trap incidence)

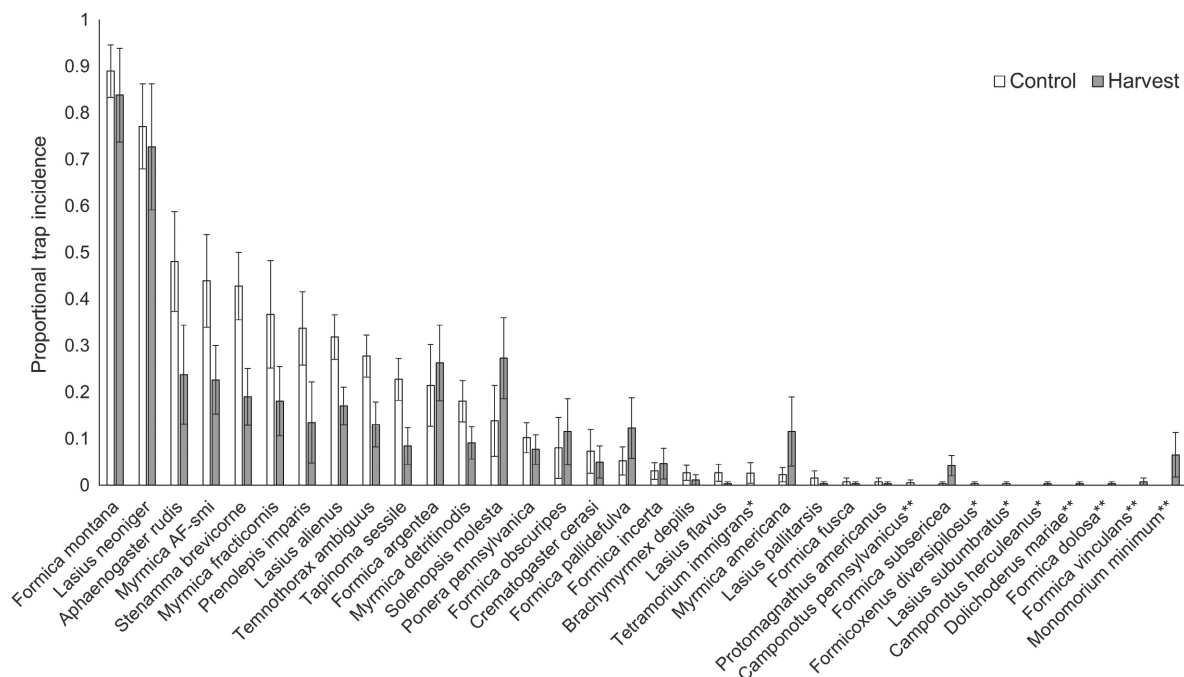


Fig. 1. Rank-incidence curves for ant species in the control (white bars) and harvest (gray bars) sites in 2013–2015. Rank incidence depicted as the proportion of traps that captured ant species per site averaged across sites. Error bars represent ± 1 SE. Rank-incidence values are arranged in descending order by the control (unmanipulated) treatment. Single asterisks denote species only present in harvest sites; double asterisks are species present in only control sites.

were used rather than the presence/absence because they are more robust to sampling effects (Tucker et al. 2016). These dissimilarity values represent observed β diversity (β_{obs}). Next, we created a null dissimilarity matrix (β_{null}) by developing a null model that randomly re-assigned abundance values among species and sites while maintaining the same relative abundances of each species within the region (column totals in the original site–species matrix) and the number of individuals at each site (row totals in the original site–species matrix). This null-model randomization was repeated 2000 times, and we estimated the mean β_{null} and standard deviation of β_{null} (see Appendix S2). With these null-model parameters, we created a third matrix, β_{dev} composed of z scores which represent the standardized difference from the observed β -diversity, β_{obs} , and the null model ($\beta_{\text{dev}} = (\beta_{\text{obs}} - \text{mean } \beta_{\text{null}}) / \text{SD } \beta_{\text{null}}$). These z scores or β_{dev} values represent standardized estimates of β diversity between pairs of sites that control for random sampling effects that might affect α diversity. The

β_{dev} values close to zero would suggest randomly structured ant communities, whereas β_{dev} values away from zero would suggest nonrandom ant communities where ecologically differentiation between species exists (Chase et al. 2011, Tucker et al. 2016). To determine whether β_{obs} diversity and β_{dev} -diversity differed between the harvest and control treatments, we performed non-parametric analysis of variance based on distance to centroid values (i.e., homogeneity of multivariate dispersion tests) with the betadisper function in R (Anderson et al. 2011, Myers et al. 2015). Like α diversity, we also evaluated how ant groups based on numerical dominance, habitat preference, and nest size, correlated with β_{dev} -diversity using Mantel tests. To control for family-wise error rates typically associated with multiple tests, P values were adjusted using the Benjamini-Hochberg procedure (Benjamini and Hochberg 1995).

To determine whether β_{dev} -diversity (our independent estimate of β diversity) was affected by environmental gradients or dispersal limitation,

we used distance-based redundancy analyses (dbRDA) with the proportion of sand, patch size, and landscape diversity as the environmental variables and UTM coordinates (easting and northing) as the spatial variables. Dissimilarity matrices, dbRDA, multivariate dispersion tests, and Mantel tests were performed using the vegan package in R (Oksanen et al. 2015).

RESULTS

A total of 33,031 individual ants belonging to 34 species were collected (Fig. 1, Appendix S3: Table S1). All sites reached asymptotes in species richness at the end of the experiment. Ant communities were mostly comprised of two species that made up 84.7% of the captured individuals (trap incidence for *Lasius neoniger* = 0.75; trap incidence for *Formica montana* 0.85). Most species were rare (i.e., <0.10 trap incidence) with 26 species making up less than 5% of all captured individuals. Total richness between the harvest and control sites was similar; harvest sites had a total of 30 species, including four unique species to the treatment, and control sites had 29 species in total, including five unique species (Fig. 1). The average proportional trap incidence of ants was greater in the control sites compared to the harvest sites (\bar{x} = 0.20 trap incidence in control sites, \bar{x} = 0.11 trap incidence in harvest sites, Table 1A, Fig. 2A, $F_{1,15} = 15.12$, $P = 0.001$).

Table 1. The effects of harvest on (A) ant trap incidence and (B) α diversity (rarefied species richness) in Wisconsin grasslands (2013–2015).

Variable	Estimate	SE	F	P
(A)				
Harvest treatment	−0.06	0.01	15.12	<0.01
Proportion of sand	0.07	0.05	1.66	0.21
Patch size	−0.02	0.13	0.03	0.86
Landscape diversity	−0.25	0.38	0.14	0.70
(B)				
Harvest treatment	−3.59	1.94	4.54	0.05
Proportion of sand	−1.57	5.91	0.07	0.79
Patch size	0.22	6.90	0.09	0.76
Landscape diversity	32.75	29.29	1.39	0.25

Notes: Environmental gradients in the proportion of sand, habitat size, and landscape diversity within landscapes (1 km radii from field centers) were included as covariates in the model. Boldface denotes significant effects ($P \leq 0.05$).

Harvest effects on α diversity

Control sites had greater α diversity compared to harvest sites ($F_{1,15} = 4.54$, $P = 0.05$; Table 1B, Fig. 2B) where control sites had on average 11.04 ant species per site compared to 7.06 species per site in the harvest sites. These values are comparable to previous studies in temperate grasslands where ant species richness is limited to <5–20 species per field (Menke et al. 2015, Trager et al. 2017) with rarely more than 40 species common to grasslands within a given region (Wheeler et al. 1994, Trager et al. 2017). None of the measured covariates (proportion of sand, patch size, and landscape diversity) affected α diversity.

In our study, we found that the occurrences of the two most common species (*L. neoniger* and *F. montana*) and rare species were not affected by harvest (common: $F_{1,15} = 0.30$, $P = 0.58$; rare: $F_{1,15} = 0.11$, $P = 0.76$, Fig. 3A). Instead, for species with intermediate trap occurrences, harvest sites harbored fewer of these species than control sites (\bar{x} = 0.18 trap incidence in harvest sites; \bar{x} = 0.33 trap incidence in control sites, $F_{1,15} = 8.76$, $P < 0.01$).

Harvest differentially affected habitat specialists and generalists (Fig. 3B). Specifically, harvest sites had fewer closed-habitat specialists compared to control sites (\bar{x} = 0.06 trap incidence in harvest sites; \bar{x} = 0.14 trap incidence in control sites, $F_{1,15} = 8.43$, $P = 0.01$), but there was no effect of harvest on generalists or open-habitat specialists (generalist: $F_{1,15} = 3.86$, $P = 0.06$; open-habitat specialist: $F_{1,15} < 0.01$, $P = 0.99$). Colony size also varied with harvest; there were fewer small-sized nesters in harvest sites ($F_{1,15} = 7.55$, $P = 0.01$, Fig. 3C) but no effect of harvest on large nesters ($F_{1,15} = 1.35$, $P = 0.26$). Finally, harvest differentially affected ants of different subfamilies (Fig. 3D). At harvest sites, the occurrence of ants from the subfamily Myrmicinae was generally lower compared to controls ($F_{1,15} = 0.11$, $P = 0.76$) while the occurrences of individuals in the Formicinae, Dolichoderinae, and Ponerinae subfamilies were not statistically significant (Formicinae: $F_{1,15} = 0.01$, $P = 0.89$; Dolichoderinae: $F_{1,15} = 4.87$, $P = 0.04$; Ponerinae: $F_{1,15} = 0.41$, $P = 0.53$).

Disturbance effects on β diversity

Harvest had no significant effect on β_{obs} diversity ($F_{1,18} = 0.01$, $P = 0.89$), but because harvest-

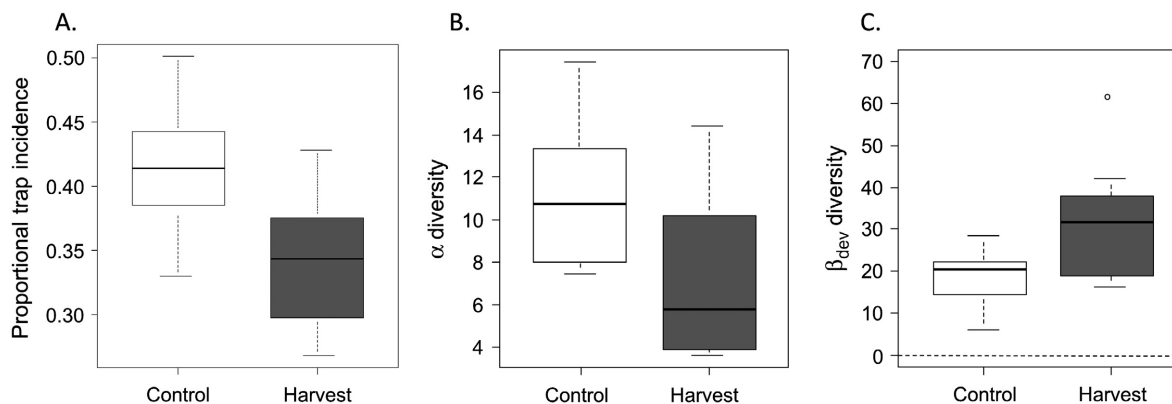


Fig. 2. Harvest effects on α and β diversities of ant communities in 2013–2015. (A) Average proportional trap incidence per site (arcsine square-root transformed), (B) α diversity estimated as rarefied species richness, and (C) β_{dev} -diversity is a standardized estimate of β diversity and estimated as the deviations of the observed dissimilarities from Bray-Curtis dissimilarities generated from null models ($\beta_{dev} = [(\beta_{obs} - \text{mean } \beta_{null})/\text{SD of the } \beta_{null}]$). Dotted line represents when $\beta_{dev} = \beta_{null}$ diversity. Estimates were generated from trap-incidence data across the experimental years (2013–2015) averaged across species. Boxes represent interquartile ranges, whiskers represent 1.5 times the interquartile range, and solid black lines present median values.

mediated changes in ant abundance and α diversity and stochastic processes can influence β_{obs} diversity, we compared β_{dev} -diversity between two treatments instead (Chase et al. 2011, Kraft et al. 2011). We found that β_{dev} -diversity was higher in harvest compared to control sites ($F_{1,15} = 5.67$, $P = 0.03$; Fig. 2C) indicating that communities in harvest sites were more dissimilar in community composition than communities in control sites (Fig. 4). β_{dev} -diversity in both the control and harvest sites was significantly greater than zero, implying that communities were 7more dissimilar in composition than by chance alone.

We found that differences in β_{dev} -diversity were largely due to the presence of rare (Pearson $r = 0.38$, $P < 0.01$) and small-sized nesters (Pearson $r = 0.32$, $P < 0.01$). To determine whether dissimilarity in community composition was due to dispersal limitation or environmental factors, we performed dbRDA with three environmental factors (proportion of sand, patch size, and landscape diversity) and spatial coordinates (northing and easting). There was no spatial autocorrelation between pairwise site distances and β_{obs} diversity ($F_{1,15} = 1.13$, $P = 0.10$) indicating that spatial structure did not affect community dissimilarity. Instead, we found that β_{dev} -diversity was affected by habitat size ($F_{1,15} = 1.30$, $P = 0.05$; Table 2) and

the proportion of sand within each site ($F_{1,15} = 1.42$, $P < 0.01$; Table 2).

DISCUSSION

We used a null-model approach to examine how annual harvesting of tallgrass prairies independently affected α and β -diversity of ants. We found that harvesting differentially affected ant α and β diversities; harvesting decreased α diversity but increased β diversity (adjusted for random sampling effects). Furthermore, we found that gradients in environmental factors not associated with the harvest treatment (e.g., proportion of sand and habitat size) affected β diversity but not α diversity. Because both α and β diversities are both important for determining diversity at regional scales, focusing on only one aspect of diversity may lead to an incomplete understanding of how disturbance affects community assembly processes.

Harvest decreased α diversity of ants in grasslands

Lower α diversity of ants in harvested sites may have been a direct and indirect consequence of biomass removal. The removal of plant biomass changed environmental conditions (e.g., increased bare ground cover, increased soil temperature, and lowered litter cover; Kim et al. 2017) which

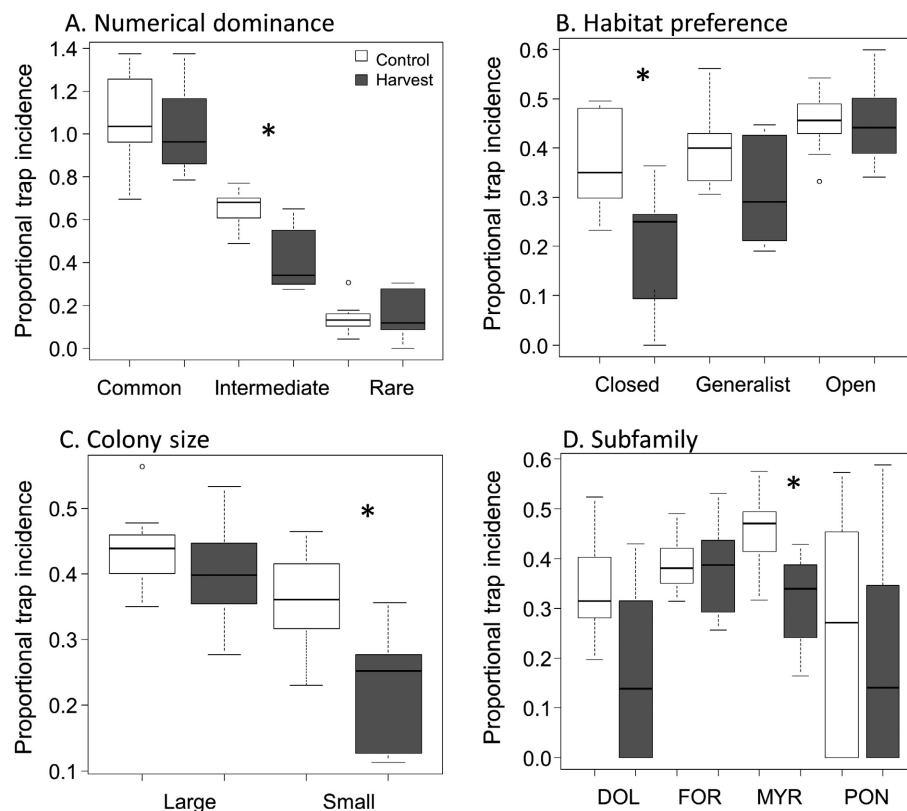


Fig. 3. Ant group responses to annual harvest. Groups were based on (A) numerical dominance (“common” group includes species with trap capture rates > 75%; “rare” group includes species with trap capture rates < 10%; “intermediate” group includes species with capture rates > rare but < common), (B) habitat preference (“closed”-habitat specialists, habitat “generalists”, and “open”-habitat specialists), (C) typical nest sizes (“large,” >1000 workers, “small,” 0–500 workers), and (D) subfamily (“DOL,” Dolichoderinae, “FOR,” Formicidae, “MYR,” Myrmicinae, “PON,” Ponerinae). Proportional trap incidence data were arcsine square-root transformed. Asterisks denote significant harvest effects after adjusting for multiple comparisons.

could have directly or indirectly altered ant community composition. We observed a lower occurrence of ants in the harvest sites, particularly species of intermediate dominance belonging to the subfamily Myrmicinae. Furthermore, we observed a reduction in the abundances of closed-habitat specialists (e.g., *Brachymyrmex depilis* and *Myrmica fracticornis*) with the harvest treatment. Biomass removal may have created unfavorable environmental conditions for these ant species preventing colonization and population growth. While we did not see any difference in the trap occurrence of the two common species (*Formica montana* and *Lasius neoniger*), we did observe increases in the number of individuals captured with harvest (Appendix S3: Table S1). The

increased number of individuals per colony could have allowed these two ant species to increase in competitive dominance. Other studies have found similar results of disturbance maintaining or facilitating competitive dominance in ants (Arnan et al. 2013, Moranz et al. 2013). For example, in the southeastern United States, disturbance to soil via tillage facilitated the establishment of the invasive fire ant (*Solenopsis invicta*) thus enhancing their competitive dominance over native ant species (King and Tschinkel 2008). Similarly, in tall-grass prairies in the central United States, disturbances such as grazing and burning allowed the competitively dominant *F. montana* to establish and exclude subordinate species by reducing vegetation cover and increasing soil

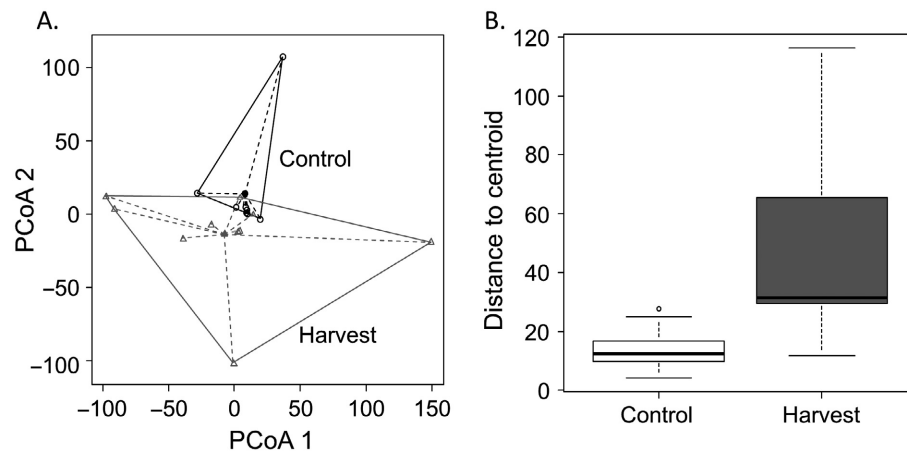


Fig. 4. Community composition and dissimilarity in control and harvest sites for β_{dev} -diversity. Community composition depicted using PCoA scores from a Bray-Curtis dissimilarity matrix (A) and dissimilarity in community composition depicted as the distances to centroid (B). Circles represent PCoA scores from control sites; triangles represent PCoA scores from harvest sites. Solid symbols represent centroid values of each treatment cluster, and polygons are the boundaries of each cluster.

Table 2. The effects environmental gradients on β_{dev} -diversity using distance-based redundancy analyses.

Variables	df	Variance	F	P
Proportion of sand	1	2415.7	1.39	0.01
Patch size	1	2117.1	1.22	0.05
Landscape diversity	1	1802.4	1.04	0.34
Residual	16	27854.5		

Notes: Environmental variables included the proportion of sand, habitat size, and landscape diversity within landscapes (1 km radii from field centers). Boldface denotes significant effects ($P \leq 0.05$).

temperature (Moranz et al. 2013). In our study, harvest sites also had fewer closed-habitat specialists which may have been a direct result of biomass removal or an indirect effect through the competitive effects of *F. montatna* and *L. neoniger*. While disentangling the magnitude of the direct and indirect effects of harvest on ant communities is beyond the scope of this study, both pathways could be affecting α diversity within managed prairie grasslands.

Harvest increased β diversity of ants in grasslands

In contrast to α diversity, β_{dev} -diversity (our unbiased estimate of β diversity) was higher in harvested sites indicating that ant communities among harvest sites were more dissimilar than ant communities among control sites. Dissimilarity in

ant community composition was largely driven by rare species (e.g., *B. depilis*, *F. incerta*, and *M. americana*) and small-sized nesters (e.g., *M. fracticornis* and *F. vinculans*). One possibility is that, contrary to our initial hypothesis, harvesting may have increased environmental heterogeneity among sites, rather than having a homogenizing effect on community composition. While the removal of biomass was conducted similarly across all experimental sites, repeated harvesting may have altered environmental conditions in ways that allowed for differential rates of mortality, colonization, and varied strength of competition for newly open space, resulting in large differences in community composition among harvested sites (Myers et al. 2015). Indeed, previous work in this system has found that, even though control sites had greater litter biomass and less bare ground cover (Kim et al. 2017), variation in vegetation structure and soil temperature was lower among the control sites. The greater similarity among control sites (i.e., lower variance in vegetation structure and the lack of repeated disturbances) may have impacted the ant communities by allowing them to converge in species composition. In contrast, repeated disturbance events within harvest sites may have required ant communities to continuously reestablish and reset, resulting in greater community dissimilarity among sites (Gotelli and Arnett 2000,

Sanders et al. 2003, Badano et al. 2005). Because we controlled for harvest-mediated changes in ant abundances with our null modeling approach, dissimilarity in community composition among sites (i.e., β_{dev} -diversity) was not due to random sampling effects.

In both the harvest and control sites, β_{dev} -diversity was positive indicating that niche-processing affecting the spatial distribution of ant species was strong in these landscapes (Chase et al. 2011, Myers et al. 2015). Variation in community composition could be due to dispersal limitation, environmental filtering, or sizes of the regional species pool (Andersen 2008, Chase and Myers 2011). We found that dispersal limitation did not influence community dissimilarity as the spatial variables (UTM coordinate) did not affect β_{dev} -diversity. Instead, we found that β_{dev} -diversity was affected by the proportion of sand and habitat size suggesting that community assembly was due to environmental filtering and species pool. Preference for different soil types and vegetation cover in ants is well known (Kaspari and Weiser 1999, Tschinkel et al. 2012), particularly in disturbance adapted systems such as prairie grasslands. Therefore, differences in soil composition between sites could have created environmental filters by which only few species can persist thus influencing community dissimilarity. The effects of patch size on community dissimilarity could be due to differences in species pool sizes. For example, larger grassland patches can generally support more and different types of species compared to smaller patches (e.g., species–area relationship, MacArthur and Wilson 1967, Badano et al. 2005) resulting in greater β_{dev} -diversity. These results suggest that local factors (e.g., proportion of sand) and larger-scale factors (e.g., patch size) can both have effects on the assembly of ant communities within grasslands.

CONCLUSIONS

Understanding how disturbance affects α and β diversities has conservation and restoration implications. Harvesting can have similar effects on biodiversity as other disturbances such as fire and grazing and can be used to manage biodiversity at both local and regional scales. While many studies have focused on α diversity in restoration (Arnan et al. 2015, Trager et al. 2017), ignoring

other components of diversity (e.g., β diversity) and can lead to conflicting management advice (Concepción et al. 2012). In our study, annual harvest decreased α diversity by lowering the occurrence of intermediately dominant ant species and increasing the number of individuals of the two dominant ant species. For land managers interested in implementing management practices aimed at increasing ant diversity *within* a site, harvesting may not be recommended. In our study, greater α diversity in the control sites came at the cost of β diversity loss which may be favored if land managers prefer homogeneous habitats for management or aesthetic reasons. If harvesting is a necessary component of land management (e.g., as a substitute for fire, haying, or biofuel production), then harvesting does not necessarily have negative consequences for biodiversity as our study found that harvested grasslands increased β diversity by potentially increasing environmental heterogeneity among sites. Understanding the consequences of harvesting for α and β diversities can help target subsequent land management and restoration efforts. For example, if land managers want to increase α -diversity to compensate for species losses following harvest, land managers might consider maintaining refuges nearby harvested sites. These undisturbed portions of the habitat may allow rarer species to persist locally (thus maintaining α diversity) while increasing heterogeneity among sites (thus increasing β diversity). While our study did not test for interactions with harvest treatment and environmental gradients on α and β diversities, other studies have found that different community assembly mechanisms can predominate in disturbed vs. undisturbed habitats (e.g., arthropods: Clough et al. 2007, birds: Karp et al. 2012, plants: Myers et al. 2013). Therefore, special consideration must be given to how these mechanisms might interact with disturbance in efforts to effectively maintain diversity at all spatial scales (Dauber et al. 2006, Underwood and Fisher 2006, Moranz et al. 2013).

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