



Comparing grasshopper (Orthoptera: Acrididae) communities on tallgrass prairie reconstructions and remnants in Missouri

JOSEPH P. LAROSE,¹ ELISABETH B. WEBB² and DEBORAH L. FINKE¹ ¹Division of Plant Sciences, University of Missouri, Columbia, MO, USA and ²U.S. Geological Survey, Missouri Cooperative Fish and Wildlife Research Unit, University of Missouri, Columbia, MO, USA

Abstract. 1. Tallgrass prairies, which once occupied a large swath of central North America, face the combined challenges of habitat loss and fragmentation. In Missouri, where less than 1% the historical prairie remains, prairies are being reconstructed from agricultural or wooded land.

2. Invertebrates are often assumed to colonise reconstructions if native vegetation returns; however, the limited mobility of many invertebrates, the isolation of many tallgrass remnants, and the difficulty in establishing prairie plants raise serious questions as to whether invertebrate communities on reconstructed prairies are and will be equivalent to those found on remnant prairies.

3. Grasshoppers (Acrididae) display a range of dispersal capabilities and may be valuable for assessing the success of prairie restoration for invertebrates.

4. Our first objective was to compare grasshopper communities on reconstructed and remnant prairies and, if differences existed, identify species or functional groups associated with each habitat type. The second objective was to evaluate the effect of time because prairie reconstruction on grasshopper communities to determine if communities on reconstructions are converging with communities on remnants.

5. Our results suggest that prairie reconstructions in Missouri do not support the same communities of grasshoppers as prairie remnants.

6. Grasshopper diversity was generally greater on remnants. Many species had not colonised nearby reconstructions.

7. Communities on prairie reconstructions were characterised by a few long-winged, generalist species that are typically successful in agroecosystems.

8. Further investigation into the habitat disparities driving low grasshopper diversity on reconstructions could help restore the grasshopper community of reconstructions.

Key words. Dispersal, Ecology, Grassland, Orthoptera, Prairies, Restoration, Succession.

Introduction

Grassland ecosystems are in decline globally due to intensification of land use by humans (Ceballos *et al.*, 2010). Predictably, species that rely on grassland habitat have declined as well, in some cases precipitously (Brennan & Kuvlesky Jr, 2005; Pleasants & Oberhauser, 2013). Besides traditional conservation

of remaining fragments of native grassland, there are also efforts to reconstruct grassland from agricultural or otherwise disturbed land (Dobson *et al.*, 1997; Török & Helm, 2017). Tallgrass prairie reconstruction in Missouri is an excellent example of the ongoing effort to rebuild ecosystems based on information from only small fragments of remnant habitat. Tallgrass prairie once covered close to a third of Missouri but has since been reduced by over 99% (Christisen, 1972) due to mechanised agriculture, urbanisation, and forest expansion (Samson & Knopf, 1994; Wright & Wimberly, 2013). The remaining tallgrass prairie in Missouri consists of small patches within a landscape of row

Correspondence: Deborah L. Finke, Division of Plant Sciences, 1-33 Agriculture Building, University of Missouri, Columbia, MO 65211, Tel: 573.884.5125, Fax: 573.882.1469. E-mail: finked@missouri.edu

crops, pasture, and woodland (Christisen, 1972; Solecki & Toney, 1986). Conservation organisations such as the Missouri Prairie Foundation and The Nature Conservancy, as well as public natural resource agencies including the Missouri Department of Conservation, have responded by converting agricultural or wooded land back to prairie, a process of unknown duration and with substantial challenges.

The process of tallgrass prairie reconstruction is often quite extensive (Smith, 2010; Kurtz, 2013). Following removal of existing vegetation occupying the land, whether forest, crops, or pasture, managers plant a diverse native seed mix containing grasses and forbs (Smith, 2010; Kurtz, 2013). Management can be intensive, often involving spraying herbicides, burning, mowing, and grazing (Smith, 2010). Ascertaining the effectiveness of prairie reconstruction and management practices requires monitoring animal and plant communities of reconstructions as well as remnant prairies (Kremen *et al.*, 1994; Thom, 2000; Block *et al.*, 2001; Benayas *et al.*, 2009). Remnant prairies represent the best examples of historical tallgrass prairie ecosystems, and thus often serve as target communities for reconstruction efforts. Of particular interest for monitoring and conservation are taxa that may not be able to surmount the obstacles to colonisation posed by habitat fragmentation, such as grasshoppers (Acrididae) (Hjermann & Ims, 1996; Reinhardt *et al.*, 2005; Schultz *et al.*, 2008; Heidinger *et al.*, 2010; Ortego *et al.*, 2015).

Grasshoppers do not typically garner extensive conservation attention. Restoration or reconstruction studies focusing on grasshoppers are less common than on economically beneficial insects like bees (Harmon-Threatt & Hendrix, 2015; Griffin *et al.*, 2017; Tonietto *et al.*, 2017) or publicly popular insects such as butterflies (Ries *et al.*, 2001; Swengel, 2001; Davis *et al.*, 2007; Vogel *et al.*, 2007; Brückmann *et al.*, 2010; Kuefler *et al.*, 2010). Several grasshopper species are abundant, serious agricultural pests that receive intensive insecticidal control (Lockwood *et al.*, 1988). Despite some species' abundance, the loss of grasshopper diversity in prairie ecosystems is a distinct possibility considering the sudden extinction of the Rocky Mountain locust, *Melanoplus spretus* (Scudder) (Acrididae: Melanoplineae), which once rivalled the bison in terms of animal biomass on North American prairies (Lockwood, 2004), along with the endemism found in some grasshopper genera (Hilliard Jr, 2001; Knowles, 2001; Otte, 2012). Indeed, 15 grasshopper species are already listed as species of concern by the Missouri Department of Conservation (Missouri Natural Heritage Program, 2018) and the status of currently undescribed or recently described species is largely unknown. We evaluated grasshopper communities not only for the sake of grasshopper conservation, but also because of their potential as indicators of overall prairie reconstruction health as orthopterans are known to be good indicators of biodiversity in agricultural and grassland areas (Sauberer *et al.*, 2004; Bazelet & Samways, 2011; Alignan *et al.*, 2018).

Colonisation ability in insects is tied to dispersal ability (Zera & Denno, 1997; Thompson, 1999; Lester *et al.*, 2007; Picaud & Petit, 2008) and habitat specificity (Piechnik *et al.*, 2008; Dennis *et al.*, 2011). Grasshopper species display widely variable dispersal capabilities. Some species possess long wings and powerful flight muscles that allow them to disperse long distances; the migratory grasshopper *Melanoplus sanguipines* (Fabricius) (Acrididae:

Melanoplineae) is capable of dispersing hundreds of kilometres (Pfadt, 1994). Other grasshoppers have poorly developed wings and are only capable of short distance dispersal by hopping (Pfadt, 1994), such as *Melanoplus gracilis* (Bruner) (Acrididae: Melanoplineae). Grasshoppers with strong dispersal abilities may be better colonisers because they are more capable of immigrating to new habitats. In fragmented landscapes, such as grasslands in the United States and much of Europe, differences in mobility can affect grasshopper community composition and persistence (Marini *et al.*, 2010; Marini *et al.*, 2012), with low mobility grasshoppers being more likely to go extinct than high mobility grasshoppers (Reinhardt *et al.*, 2005). In France, wing length to body length ratios of grasshopper species decreased over succession in old fields, suggesting that better dispersing species colonise new habitats before poor dispersers (Picaud & Petit, 2008). A survey of Wisconsin prairies found that reconstructed prairies were occupied by a suite of mobile species (Bomar, 2001). Those mobile species were also habitat generalists. Their relative abundance on reconstructions may reflect the role of habitat generalism in colonisation. Diet is a major part of habitat specificity. Grasshoppers display a range of diet breadths (Joern, 1979), and species with broad diets may be better colonisers because they can survive and reproduce under a variety of resource conditions and habitats (Peterson & Denno, 1998; Piechnik *et al.*, 2008).

There were two objectives of our study. First, we compared grasshopper communities on reconstructions to those on remnants by evaluating species richness, diversity, and community composition at four pairs of reconstructed and remnant prairies in Missouri. We sought to identify species or functional groups associated with remnants or reconstructions for use in monitoring these reconstructions and remnants in the future. Second, we evaluated the effect of prairie reconstruction age on grasshopper communities to determine if grasshopper communities on reconstructions were converging with communities on remnants.

We hypothesised that grasshopper species richness and diversity would be greater on remnants than on reconstructions, although we were aware that insect species richness on remnants is not always greater than on the presumably lower quality reconstructions (Davis *et al.*, 2007; Williams, 2011; Diepenbrock *et al.*, 2013) because of differences in restoration practices and remnant health. In accordance with results from the Wisconsin prairie survey from Bomar (2001), we hypothesised that long-winged grasshoppers and grasshoppers with generalist diets, those feeding on a mixture of grasses and forbs, would be more common on reconstructions than remnants because of increased probability of successfully colonising new habitat. We also hypothesised that smaller, short-winged, specialist species would be more common on remnants than reconstructions because they are not as likely to colonise newly formed habitat patches.

Materials and methods

Site selection

We sampled four areas (locations) containing both reconstructed and remnant prairies managed by the Missouri

Department of Conservation (Supporting Information Fig. S1). Wah'Kon-Tah Prairie, Linscomb Wildlife Area, and Schell-Osage Conservation Area (hereafter Schell), all within St. Clair County in the Upper Osage Grasslands of southwestern Missouri, contained contiguous remnant and reconstructed prairies. Wah'Kon-Tah's remnant prairie covers 756 ha and its reconstruction covers 160. Linscomb had 41 ha of remnant and 32 of reconstruction. Schell had approximately 1.5 ha of each. The remaining location, approximately 200 km northeast in the Central Dissected Plains in Calloway County, consisted of one remnant, the University of Missouri's Tucker Prairie (59 ha), and one reconstructed prairie, Prairie Fork Conservation Area (142 ha). These two prairies are one location in our analyses (hereafter North) even though they were separated by 32 km. We included the North location in order to generalise our conclusions for reconstructions in various parts of Missouri.

The reconstructed prairies at Wah'Kon-Tah, Linscomb, and North contained reconstructions of different ages. There were ten individual reconstructions at Wah'Kon-Tah initiated between 2002 and 2008. Linscomb contained two reconstructions, one reconstructed in 2007 and the other in 2013. The North location had the greatest range of reconstruction ages: 2004 to 2016. Schell had only one reconstruction site, initiated in 2014. For analyses, reconstruction age was calculated as the years since planting until sampling year.

There are various grassland management practices that could potentially confound invertebrate surveys. We sought to identify patterns independent of management practices, therefore, we excluded tracts scheduled to be hayed, grazed, mowed, or high-clipped in 2016 or 2017 because those practices could alter invertebrate communities during summer months (Humbert *et al.*, 2010). Prescribed burning also affects invertebrate communities (Panzer, 2002), but we included burned patches in our site selection because the burns were scheduled for the dormant season, outside of the sampling window.

Due to the heterogeneous and fragmented nature of the native prairie patches available for sampling, we chose to sample transects at locations randomly generated in each remnant and reconstructed prairie. We generated the same number of points on remnants and reconstruction at each location except for North. There were double the number of transects on the North reconstruction because it was larger than the remnant and contained the widest range of reconstruction ages, which we were particularly interested in sampling. We used ArcMap 10.3.1 (ESRI 2015) to randomly generate transect sampling points, which were regenerated after 2016 for sampling in 2017. Each point, which represented the centre of a transect, was located >40 m from the prairie edge and > 75 m from another transect. We assumed that a minimum of 75 m between points ensured independence, because nymphs, which made up the vast majority of grasshoppers captured in standardised sweeps, are incapable of flight. Adult long-winged grasshoppers however, may be capable of traveling distances >75 m (Pfadt, 1994). In 2016 we sampled along 134 transects: 75 on reconstructions and 59 on remnants. In 2017, we reduced sampling intensity at the North location, the most intensely sampled location, by a third in order to redirect effort to another method of collection described in the next section. This lowered total transects to 116: 63 on

reconstructions and 53 on remnants. A summary of transects sampled at each location in 2016 and 2017 are located in Supporting Information Table S1.

Collecting

We collected grasshoppers using two methods: standardised sweeping and targeted capture. We performed standardised sweeping, generally accepted as the best grasshopper collection method (Evans *et al.*, 1983; Larson *et al.*, 1999), along 60 m transects centred on the randomly generated points. We performed 10 sweeps perpendicular to each transect with a 38 cm diameter net at four spots along the transect, located 15 m and 30 m from the centre of the transect in both directions. The four subsamples were combined into a single sample; thus, each transect consisted of 40 total sweeps. By necessity, seven people performed the sweeping over the 2 years. Different sweeping techniques can bias the grasshoppers collected (O'Neill *et al.*, 2002); therefore researchers used and practised the same standardised sweeping motion and made an effort to assign sweepers to different prairie types throughout the season. One researcher conducted 45% of the sweeps.

In 2016, sampling occurred once in June, once in July, and once in August/September. Sweeps were conducted on days without consistent precipitation, after dew had evaporated sufficiently, when temperature was above 21 °C, and winds were under 15 km/h. The majority of individuals caught in 2016 were nymphs. In 2017, we restricted standardised sweeping to one visit in August/September and we replaced the early-season standardised sweeps with targeted capture to catch more adult grasshoppers. Targeted capture entailed walking slowly and capturing every adult grasshopper that we observed or flushed. We spent equal time conducting targeted captures at remnant and reconstructed prairies and alternated sampling between the two prairie types several times per day. We spent approximately 100 h conducting targeted capture from June to September 2017. The same temperature, wind, and precipitation requirements applied to targeted capture.

Grasshoppers were identified to species, or genus for some nymphs and females, using Pfadt (1994), Kirk and Bomar (2003), Ballard (1992), and Song (2009). Voucher specimens were pinned or frozen. Pinned specimens are stored in the Enns Entomological Museum at the University of Missouri, Columbia.

Vegetation

We measured vegetation density and estimated forb to grass ratio during standardised sweeping in August/September of 2017. We measured vegetation density with a modified Robel pole (Benkobi *et al.*, 2000; Uresk & Benzon, 2007) at three randomly chosen sweeping points along each transect. At each location we recorded the lowest decameter on the Robel pole visible from a distance of 4 m and a height of 1 m. We visually estimated the forb to grass coverage ratio of a 1.0 × 0.5 m plot at the locations where we measured vegetation density.

Statistical analyses

Do communities on reconstructions differ from those on remnants?

Diversity. We compared taxon richness (species plus genera that were not identified further) and diversity in reconstructed and remnant prairies at each location using rarefaction/extrapolation (Weibull *et al.*, 2003; Gotelli & Colwell, 2011; Colwell *et al.*, 2012), which resamples species data to estimate richness or diversity at other sample sizes. We conducted all analyses using R version 3.4.0 (R Core Team, 2017). We performed individual-based rarefaction instead of sample-based (Gotelli & Colwell, 2011) using the package iNEXT (Hsieh *et al.*, 2016) because of the addition of the targeted capture grasshopper observations in 2017. Individual-based rarefaction assumes independence for each individual, which is often violated because some individuals are caught at the same location, thus failing to account for clumping. This was the case for the individual-based rarefaction we performed.

The rarefaction/extrapolation curves depict Hill numbers, which are measures of diversity that combine species richness and abundance (Hsieh *et al.*, 2016). The curves show the estimated Hill numbers at hypothetical sample sizes, ranging from zero to two-times the actual sample size. We generated rarefaction/extrapolation of Hill curves for each year separately as well as lumped together. We plotted the curves using 95% confidence intervals, calculated with the bootstrap method (Colwell *et al.*, 2012).

One of the parameters in Hill number equations is q , which determines the sensitivity to relative frequencies of species (Chao *et al.*, 2014). Hill numbers were calculated for $q = 0$, 1, and 2. The resulting estimates are species richness ($q = 0$), Shannon diversity ($q = 1$), and Simpson diversity ($q = 2$). The three diversity metrics are influenced differently by relative frequencies of species (Chao *et al.*, 2014). Species richness is not influenced by relative frequency, and only refers to the presence of a species. Shannon diversity weights species according to their relative frequencies (Peet, 1975; Routledge, 1979; Chao *et al.*, 2014), meaning communities with highly skewed relative abundances will have lower Shannon diversity than communities with the same number of evenly abundant species (Peet, 1975; Keylock, 2005). Simpson diversity discounts rare species and places greater emphasis on abundant species, making it a good measure of the diversity of dominant species (Keylock, 2005; Chao *et al.*, 2014). Shannon diversity estimates are presented as the exponentials of Shannon indices, and Simpson diversity estimates are presented as inverses of Simpson concentration, such that larger numbers represent greater diversity (Hsieh *et al.*, 2016).

Total abundance. We modelled total abundance of grasshoppers using univariate generalised linear models. A mixed effect model was not appropriate because there were less than the five levels necessary to estimate the among-population variance accurately (Harrison *et al.*, 2018); in this case there were only four locations. We used a negative binomial distribution, which was the best fit for the data based on Dunn-Smyth residual plots. We evaluated the effects of *status* (reconstruction or remnant),

location (Wah'Kon-Tah, Linscomb, Schell, or North) and the *status* \times *location* interaction. Only grasshopper data from 2016 were included in the models because we did not collect enough grasshoppers from standardised sweeping in 2017. We started with a model including all variables and interactions, then removed interactions and variables one at a time. We conducted analyses of variance (ANOVA) on models with and without variables to determine whether variables improved model fit, discarding those that did not ($P > 0.05$) (Blakey *et al.*, 2016; Clarke-Wood *et al.*, 2016). We used the function *glm.nb* in the package MASS (Venables & Ripley, 2002). We did not perform similar analyses comparing diversity and richness between reconstructions and remnants because grasshopper abundance, diversity, and richness were strongly correlated at each transect.

Community composition. The following analyses were performed only on grasshoppers collected in 2016 because of the low number of grasshoppers collected from transects in 2017. Individuals belonging to the genera *Orphulella* (Acrididae: Gomphocerinae) and *Hesperotettix* (Acrididae: Melanoplinae) were not identified to species because all individuals captured in 2016 were nymphs that were difficult to identify past genera. To visualise community data, we ordinated grasshopper communities using non-metric multidimensional scaling (NMS) with a Bray–Curtis dissimilarity matrix (Paton *et al.*, 2009; Clarke-Wood *et al.*, 2016). NMS ordination compresses the abundance and species information from each sample and constructs a space of k dimensions based on the differences between samples. Taxa abundances were summed at each transect. Only taxa that occurred in $>5\%$ of transects were included in the ordination, thus we included only the 15 most common grasshopper taxa in the ordination. Eight transects (four remnant, four reconstruction) with zero individuals were removed prior to analysis. We used the function *metaMDS* in package *vegan* (Oksanen *et al.*, 2016) to run NMS. We used the function *dimcheckMDS* to choose the number of dimensions (k) and viewed the resulting ordination with the *ordirgl* function.

To test whether grasshopper communities on reconstructed and remnant prairies were statistically distinct, we constructed multivariate models of 2016 grasshopper abundances using the same 15 taxa used in the ordinations. Models were generated in the package *mvabund* (Wang *et al.*, 2012), which handles multivariate count data with generalised linear models. The response variables were the abundances of each taxa summed across sampling dates for each transect and we used a negative binomial distribution for all models. Explanatory variables included prairie *status* (remnant or reconstructed), *location* (Wah'Kon-Tah, Linscomb, Schell, and North), *edge proximity* (distance from transect to closest prairie edge, measured in ArcMAP) and all possible interactions. We started with a model including all variables and interactions, then removed interactions and variables sequentially. We conducted ANOVA on models with and without variables to determine whether variables improved the model fit, discarding those that did not ($P > 0.05$) (Blakey *et al.*, 2016; Clarke-Wood *et al.*, 2016). Because of a significant *status* \times *location* interaction, we ran individual multivariate models for each location as well. We examined the multivariate model

coefficients for each taxon to identify which taxa contributed to differences between locations.

Functional groups. We grouped grasshoppers by wing length (*short, long*) and by preferred diet (*grass, forb, mixed*) (Table 1), according to Pfadt (1994), Otte (1981), and Capinera and Sechrist (1982). We considered grasshoppers to be short-winged if the species' wings typically do not extend more than half of abdomen length. Using the package *mvabund*, we created multivariate models of abundance for each functional group to look for differences between reconstructions and remnants as well between reconstructions of different ages. We again used only the grasshoppers collected at transects from 2016. Explanatory variables for the reconstruction versus remnant analysis included prairie *status, location*, and *edge proximity* and all possible interactions. We conducted ANOVA on models with and without variables to determine whether the variables improved the model fit, discarding those that did not ($P > 0.05$) (Blakey *et al.*, 2016; Clarke-Wood *et al.*, 2016). Due to a significant *status* × *location* interaction, we also modelled functional group abundance for each prairie separately.

Does reconstruction age affect grasshopper communities? We used the same methods as those described earlier to analyse the effect of reconstruction age on grasshopper communities, with a few modifications. We modified the ordination comparing remnants and reconstructions by adding a heat-map of colour that was scaled to reconstruction age. Only reconstructed transects were used in models and prairie *status* was replaced with reconstruction *age*. Only the 12 most abundant grasshopper taxa found on reconstructions were used in the multivariate models of age effect.

Are grasshopper communities on older reconstructions converging with remnants? To determine if older reconstructions have converged with remnants, we also classified reconstructions into two broad age classes: ≤5 years and >5 years, and performed the same multivariate model analyses of abundance for taxa and functional groups as described in the community composition and functional group sections above. We repeated those analyses for the reconstruction groups split into ≤9 years and >9 years. Five and nine were chosen as breaks because they represented roughly the bottom and top third of the age range, which ensured a sufficient number of transects to perform analyses.

Did vegetation density or the forb:grass ratio affect grasshopper communities? We averaged the three measures of vegetation density and forb:grass ratio for transects in 2017 and compared vegetation on remnants to vegetation on reconstructions with linear models (function *lm* in package *Stats*). To evaluate relationships between vegetation characteristics and grasshopper species abundances, we ran separate models for each vegetation measurement, using the same methods as described in the community composition analysis.

Table 1. Grasshopper taxa captured in 2016 and 2017. Species typically associated with prairies are denoted with an asterisk.

Grasshopper taxon	Unique to	Diet	Wing length
<i>Amphitornus coloradus</i> (Thomas)	-	Grass	Long
<i>Arphia sulphurea</i> (Fabricius)*	-	Mixed	Long
<i>Arphia xanthoptera</i> (Burmeister)*	-	Grass	Long
<i>Campylacantha olivacea</i> (Scudder)	-	Mixed	Short
<i>Chortophaga viridifasciata</i> (DeGeer)	-	Grass	Long
<i>Dichromorpha viridis</i> (Scudder)*	-	Grass	Short
<i>Dissosteira carolina</i> (Linnaeus)	Reconstrn	Mixed	Long
<i>Encoptolophus sordidus</i> (Burmeister)*	-	Grass	Long
<i>Hesperotettix</i>	-	Forbs	Long
<i>Hippiscus ocelote</i> (Saussure)	Reconstrn	Grass	Long
<i>Hypochlora alba</i> (Dodge)*	Remnant	Forbs	Short
<i>Melanoplus bivittatus</i> (Say)	-	Mixed	Long
<i>Melanoplus confusus</i> (Scudder)	Remnant	Mixed	Long
<i>Melanoplus differentialis</i> (Thomas)	-	Mixed	Long
<i>Melanoplus femurrubrum</i> (DeGeer)	-	Mixed	Long
<i>Melanoplus flavidus</i> (Scudder)*	Remnant	Forbs	Long
<i>Melanoplus gracilis</i> (Bruner)	-	Grass	Short
<i>Melanoplus inconspicuus</i> (Caudell)*	Remnant	Forbs	Short
<i>Melanoplus keeleri</i> (Thomas)	-	Forbs	Long
<i>Melanoplus sanguipines</i> (Fabricius)	-	Mixed	Long
<i>Melanoplus scudderii</i> (Uhler)	-	Forbs	Short
<i>Mermiria bivittata</i> (Serville)*	Remnant	Grass	Long
<i>Orphulella pelidna</i> (Burmeister)*	-	Grass	Long
<i>Orphulella speciosa</i> (Scudder)*	Remnant	Grass	Long
<i>Paratylotropidia brunneri</i> (Scudder)*	Remnant	Unknown	Short
<i>Phoetaliotes nebrascensis</i> (Thomas)*	-	Grass	Short
<i>Pseudopomala brachyptera</i> (Scudder)*	Remnant	Grass	Short
<i>Schistocerca alutacea</i> (Harris)	-	Forbs	Long
<i>Schistocerca americana</i> (Drury)	-	Mixed	Long
<i>Schistocerca obscura</i> (Fabricius)	Remnant	Mixed	Long
<i>Stethophyma celata</i> (Otte)*	Remnant	Grass	Long
<i>Syrbula admirabilis</i> (Uhler)*	-	Grass	Long

Results

We collected 2435 grasshoppers, 1044 on remnants and 1391 on reconstructions, representing 33 species in 2016 and 2017

combined (Table 1). There was one grasshopper species of note, *Melanoplus inconspicuus* (Caudell) (Acrididae: Melanoplineae) represents, to our knowledge, a northern range expansion into Missouri. We found the short-winged, early-hatching species at Wah'Kon-Tah Prairie and Linscomb Wildlife Area.

Do communities on reconstructions differ from those on remnants?

Diversity. At the three locations where sampling effort (i.e., number of transects) was equal (Wah'Kon-Tah, Linscomb, Schell), remnant prairies had greater raw taxa richness compared to reconstructions. At the fourth location (North), where sampling effort was greater on the reconstructed prairie than the remnant, raw species richness was greater on the reconstruction than on the remnant. Rarefaction/extrapolation curves of species richness indicate greater species richness on remnants compared to reconstructions at two locations, Wah'Kon-Tah and Linscomb, based on the lack of overlap in the 95% confidence interval (Supporting Information Fig. S2). Extrapolated and rarefied Shannon diversities were greater, with no overlap in 95% confidence intervals, on remnants than reconstructions at Wah'Kon-Tah, Linscomb, and Schell. Simpson diversity confidence intervals overlapped at all locations except Linscomb, where remnants were more diverse. This suggests that the other prairies contained similar numbers and frequencies of the most common species.

Total abundance. The final model for grasshopper abundance included a *location* \times *status* interaction ($\chi^2_3 = 30.91$, $P < 0.001$). When abundance was modelled separately at each location, *status* was significant at Linscomb ($\chi^2_1 = 15.09$, $P < 0.001$) and Wah'Kon-Tah ($\chi^2_1 = 11.41$, $P < 0.001$). Grasshopper abundance was greater on reconstructions than remnants at Linscomb (Wald $\chi^2_1 = 4.00$, $P < 0.001$), while there were more grasshoppers on remnants than reconstructions at Wah'Kon-Tah (Wald $\chi^2_1 = -3.37$, $P < 0.001$).

Community composition. Remnant and reconstruction grasshopper communities from 2016 appeared distinct based on ordinations (Fig. 1; stress = 0.169, $k = 3$). Multivariate abundance models of the same species used in ordination contained a significant *status* \times *location* interaction ($\chi^2_3 = 122.5$, $P < 0.0001$), indicating differences in grasshopper community composition between reconstructed and remnant prairies varied by location. When locations were analysed separately, grasshopper communities on remnant and reconstruction prairies differed at Wah'Kon-Tah ($\chi^2_1 = 79.4$, $P < 0.001$), Linscomb ($\chi^2_1 = 75.76$, $P < 0.001$), and North ($\chi^2_1 = 28.43$, $P = 0.013$) but not at Schell ($\chi^2_1 = 16.53$, $P = 0.287$). Univariate models of the abundance of two taxa, *Campylacantha olivacea* (Scudder) (Acridae: Gomphocerinae) and the genus *Orphulella* (Acrididae: Gomphocerinae), contained significant *status* \times *location* interactions. The multivariate model without the interaction term supported

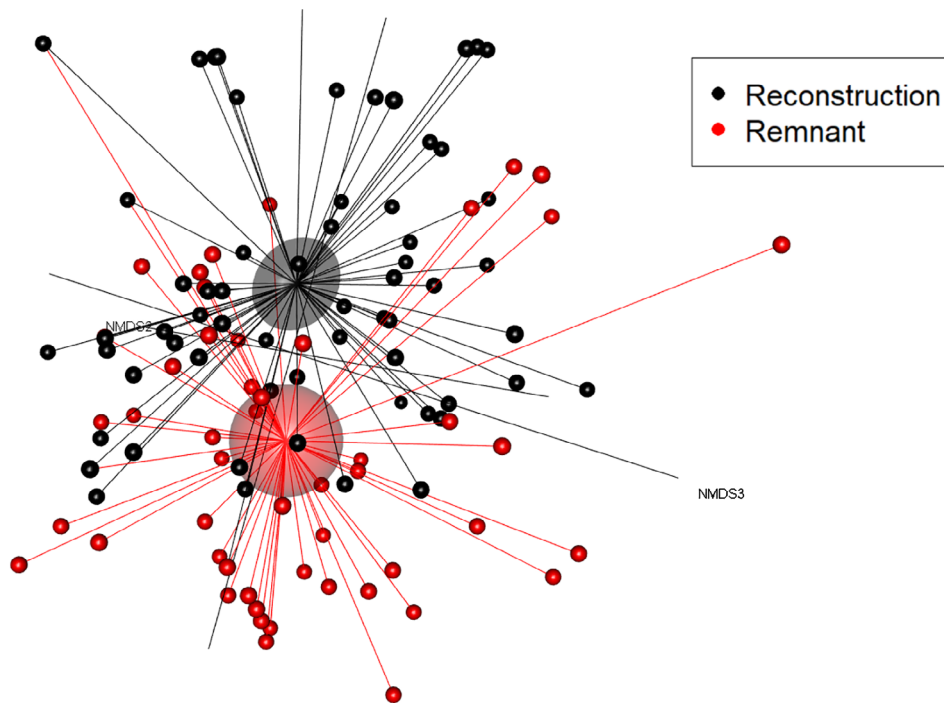


Fig. 1. NMS ordination ($k = 3$) of grasshopper communities. Dots represent communities at transects. Spheres represent 95% confidence intervals around the centroids of reconstructions (black) and remnants (red). [Color figure can be viewed at wileyonlinelibrary.com]

evidence from the ordination that remnant and reconstruction grasshopper communities were distinct ($\chi^2_1 = 87.76$, $P < 0.001$).

Communities also differed by location ($\chi^2_1 = 273.6$, $P < 0.001$). *Status* coefficients representing the effect of reconstruction on abundance from the multivariate model without the interaction are presented in Fig. 2. We refrained from interpreting the overall *status* coefficient for the two taxa responsible for the significant interaction. *Melanoplus femurrubrum* (Acrididae: Melanoplineae), *Melanoplus differentialis* (Thomas) (Acrididae: Melanoplineae), *Hesperotettix* (Acrididae: Melanoplineae), and *Syrbula admirabilis* (Uhler) (Acrididae: Gomphocerinae) were all more abundant on reconstructions, while *Phoetaliotes nebrascensis* (Thomas) (Acrididae: Melanoplineae) and *Melanoplus gracilis* were more abundant on remnants (Fig. 2). The most common grasshopper across sites was *Melanoplus scudderi* (Uhler) (Acrididae: Melanoplineae). Among all grasshoppers captured with standardised sweeps and targeted capture over both years, 10 species were unique to remnants, and two species were found only on reconstructions (Table 1).

Functional groups. Long-winged grasshoppers and mixed diet grasshoppers were more abundant on reconstructions

(Fig. 3, Wald $\chi^2_1 = 3.09$, $P = 0.021$; Fig. 3, Wald $\chi^2_1 = 5.01$, $P < 0.001$). Grass-eating and short-winged grasshopper abundances were strongly associated with remnant prairie at Wah'-Kon-Tah, but not at the other locations (Fig. 3). At all four locations, grasshoppers with mixed diets made up greater proportion of total captures (15–79%) on reconstructions than on remnants in both years.

Does reconstruction age affect grasshopper communities?

Ordination (Supporting Information Fig. S3; stress = 0.169, $k = 3$) indicated that grasshopper communities on reconstructions 5 years and younger were distinct from those over 5 years old, but communities corresponding to all other reconstruction ages appeared to have considerable overlap. The best multivariate abundance model contained a significant interaction between *age* and *location* ($\chi^2_3 = 42.84$, $P = 0.009$), but univariate tests found the interaction was only significant for one species, *Dichromorpha viridis* (Scudder) ($\chi^2_1 = 11.636$, $P = 0.043$). The model without an interaction showed that grasshopper communities differed by *age* ($\chi^2_1 = 42.57$, $P < 0.001$) and *location*

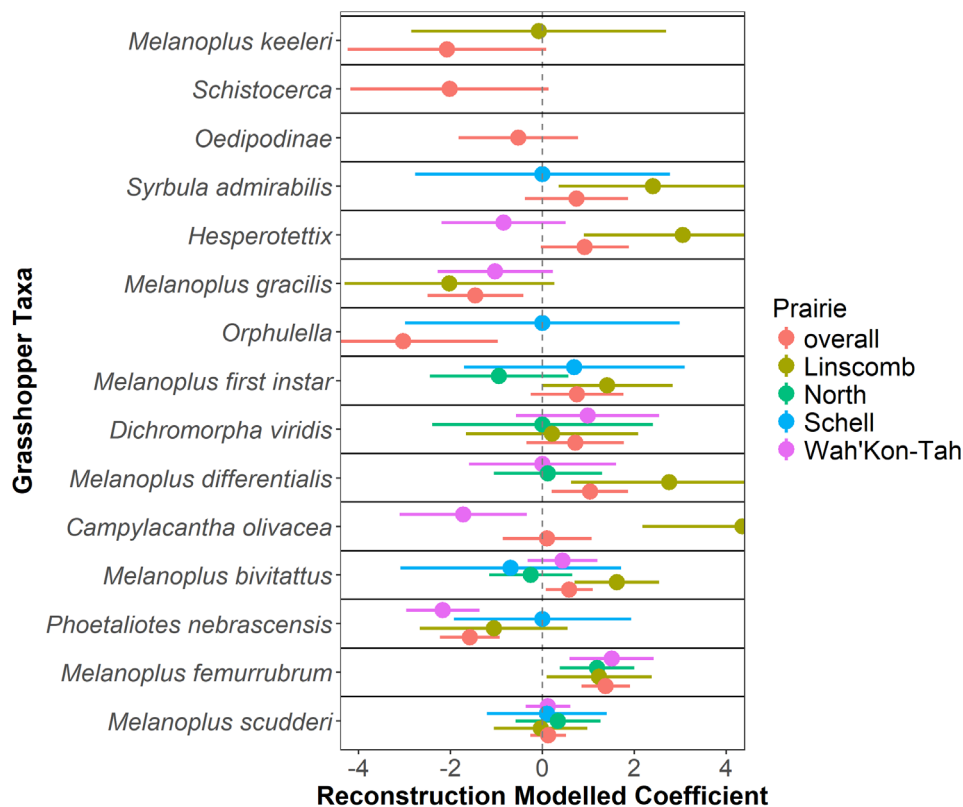


Fig. 2. Coefficients, with 95% confidence intervals, of the effect of prairie *status* (reconstruction or remnant) from multivariate models of the abundance of taxa used in ordination. Taxa are listed by abundance, with the most abundant at the bottom. Positive coefficients signify a greater abundance on reconstructions, negative coefficients signify greater abundance on remnants. There are up to five coefficients for each species, representing models for Wah'-Kon-Tah, North, Linscomb, Schell, and the prairies combined with no interaction (overall). Model coefficients with very large standard errors are not shown. There was a significant interaction in univariate abundance models for *Campylacantha olivacea* and *Orphulella*. [Color figure can be viewed at wileyonlinelibrary.com]

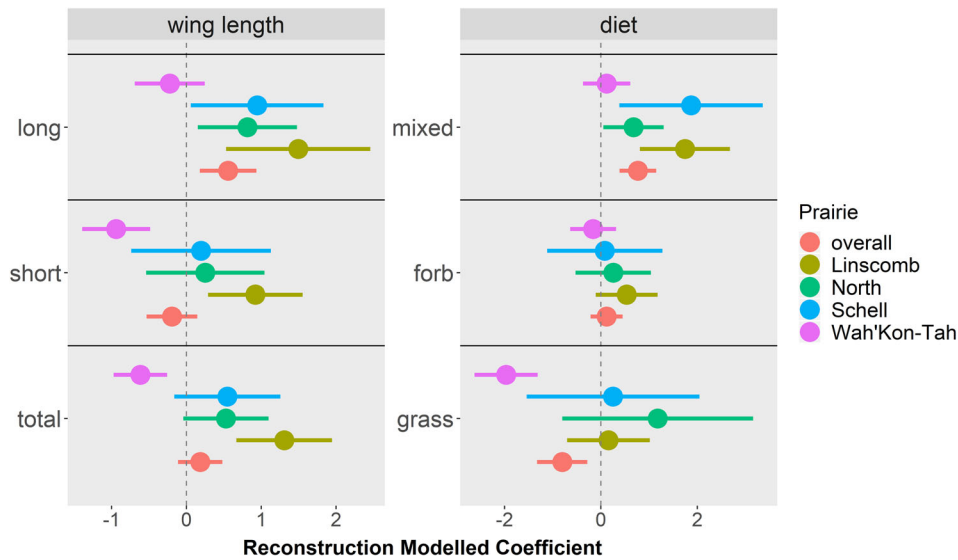


Fig. 3. Coefficients, with 95% confidence intervals, of the effect of prairie status (reconstruction or remnant) from multivariate models of the abundance of functional groups. Positive coefficients signify a greater abundance on reconstructions, negative coefficients signify greater abundance on remnants. There are up to five coefficients for each species, representing models for Wah'Kon-Tah, North, Linscomb, Schell, and the prairies combined with no interaction (overall). [Color figure can be viewed at wileyonlinelibrary.com]

($\chi^2_1 = 161.3$, $P < 0.001$). *M. femurrubrum*, *Melanoplus bivittatus* (Say), and first instar *Melanoplus* (thought to be mainly *M. femurrubrum*) abundances were negatively associated with reconstruction age (Supporting Information Fig. S4).

The best model for total grasshopper abundance included *age* ($\chi^2_1 = 13.291$, $P = 0.0003$) and *location* ($\chi^2_1 = 50.615$, $P < 0.0001$). *Age* was negatively associated with grasshopper abundance, meaning grasshopper abundance was lower on older reconstructions. The best model for grasshopper abundance on reconstructions grouped by wing length contained *age* ($\chi^2_1 = 16.15$, $P = 0.002$) and *location* ($\chi^2_1 = 59.55$, $P < 0.001$). Long-winged grasshoppers were more abundant on more recent reconstructions overall and at the three prairies that contained reconstructions of different ages (Supporting Information Fig. S5). There was no effect of reconstruction age on the abundance of short-winged grasshoppers (Supporting Information Fig. S5). The best grasshopper abundance models based on diet contained *age* ($\chi^2_1 = 20.5$, $P = 0.002$) and *location* ($\chi^2_1 = 110.8$, $P < 0.001$). Grasshoppers with mixed and grass diets were more abundant on more recent reconstructions compared to older reconstructions (Supporting Information Fig. S5).

Are grasshopper communities on older reconstructions converging with remnants?

Species that differentiated reconstructions from remnants, specifically long-winged generalists such as *M. femurrubrum* and *M. bivittatus*, were more common on younger reconstructions than older reconstructions; therefore, it was important to determine whether older reconstructions were distinct from

remnants. Ordination plots displaying reconstruction age indicated grasshopper communities on older reconstructions tended to be more similar to remnants in ordination space than younger reconstructions (Supporting Information Fig. S3). The multivariate models of those same taxa split at 5 and 9 years contained a significant interaction between *age group* (including remnant prairies) and *location* ($\chi^2_1 = 109.1$, $P < 0.001$; $\chi^2_1 = 110.1$, $P < 0.001$), which once again was only significant in univariate tests for *Campylacantha olivacea* ($\chi^2_1 = 17.731$, $P = 0.031$; $\chi^2_1 = 16.534$, $P = 0.034$). The models from either age split without the interaction indicated older reconstructions were still distinct from remnants (Wald $\chi^2_1 = 7.65$, $P < 0.001$; Wald $\chi^2_1 = 6.55$, $P < 0.001$) after accounting for location ($\chi^2_1 = 238.4$, $P < 0.001$; $\chi^2_1 = 266.7$, $P < 0.001$). Examining individual taxa did not yield many significant differences between reconstructions and remnants for either age class at either break point. The reduction in sample size substantially limited our ability to discern differences in abundance. However, *M. femurrubrum* was consistently more abundant on reconstructions than remnants in any age group. *S. admirabilis* appears to be a species that differentiates reconstructions of 5 or less years from remnants, whereas abundance of *P. nebrascensis* was significantly greater on remnants than on older reconstructions.

Grasshopper abundance on young reconstructions was greater than on remnants, but decreased with age. Reconstructions older than 9 years had fewer grasshoppers than remnants. Decreased grasshopper abundance on older reconstructions was partly due to fewer common generalists, specifically *M. femurrubrum* and *M. bivittatus*. However, there must be other taxa contributing to this trend, as there were still more of those two species on older reconstructions than on remnants. Models of wing length

and diet, which contained *age group* (including remnant prairies) ($\chi^2_1 = 30.18, P < 0.001$; $\chi^2_1 = 53.63, P < 0.001$) and *location* ($\chi^2_1 = 73.18, P < 0.001$; $\chi^2_1 = 105.6, P < 0.001$). The diet model did not detect a difference in abundance of generalist grasshoppers on older reconstructions and remnants, although the abundance on younger reconstructions did differ from remnants. Grasshoppers that preferred grass were more abundant on remnants than on older reconstructions, whereas forb-preferring grasshoppers were less common on remnants than on younger reconstructions.

Did vegetation density or the forb:grass ratio affect grasshopper communities?

There was no overall effect of *status* or *location* on forb percentage, although there was a significant interaction ($F_{3,125} = 3.1881, P = 0.027$) due to the reconstruction at Schell having a greater forb percentage compared to the remnant. Reconstructions had greater vegetation density than remnants ($t_{65} = 4.831, P < 0.0001$), and density differed by location as well ($F_{3,125} = 5.3377, P = 0.0017$). Vegetation density and forb percentage were not significantly associated with total abundance of grasshoppers ($\chi^2_2 = 0.433, P = 0.80$). Vegetation measurements were not related to the abundance of grasshoppers in diet groups or wing length categories.

Discussion

Tallgrass prairies have been degraded more than any other ecosystem in North America (Samson & Knopf, 1994). Those attempting to restore tallgrass prairies can plant native vegetation and monitor the plant community over time, adjusting seed mixes and management practices (Rowe, 2010); however, animal communities must independently colonise restored habitat from other areas, and therefore must be monitored in order to determine if reconstructions provide the appropriate habitat. Invertebrates make up a large portion of the tallgrass prairie community and may require very specific habitat characteristics typically only found on remnant prairies (Opler, 1981).

Our first objective was to compare the grasshopper communities of reconstructions and remnants and identify species or functional groups that can be used to evaluate prairie reconstruction progress. Grasshopper communities on remnant and reconstructed prairies were distinct, and remnants appeared to contain more species than reconstructions. Of the ten species only found on remnants, eight of them are known to be associated with prairie habitat (Pfadt, 1994; Reed, 1996; Kirk & Bomar, 2003). The two other species, *Paratylotropidia brunneri* (Scudder) and *Schistocerca obscura* (Fabricius), are associated to some degree with field edges or woodlands. The presence of prairie-associated species found on the remnants, but not on the reconstructions, provides some evidence that remnant prairies host a more diverse community of grasshoppers because reconstructions lack certain prairie habitat characteristics which deserve further investigation.

Landscape heterogeneity may be responsible for the one example of greater grasshopper diversity on reconstructions in

our study. Three of the locations offered convincing evidence that grasshopper communities were more diverse on remnants than reconstructions. The North location was the exception to a trend of greater Shannon diversity and raw species richness on remnants, which could be explained by landscape differences. Wah'Kon-Tah, Linscomb, and Schell prairies have a remnant adjacent to a reconstruction, and they are similar in terms of landscape heterogeneity. The North location consisted of a square patch of remnant prairie bordered by an interstate highway and corn fields, and a reconstruction 32 km away consisting of alternating patches of reconstruction and forest, bordered by roads, cornfields, and drainages. The discrepancy in habitat heterogeneity between remnant and reconstruction at the North location, absent at the other prairie locations, may be responsible for greater grasshopper diversity on the reconstruction. Further support for this hypothesis comes from the two species unique to reconstructions, both found at the North location; *Hippiscus ocelote* (Saussure) prefers open patches within woodlands (Brust *et al.*, 2014), and *Dissosteira carolina* (Linnaeus) prefers crop field edges and disturbed sites (Pfadt, 1994). Those habitats were much more common at the North reconstruction than the remnant.

Grasshopper communities on reconstructions and remnants differed in the abundance of functional groups. Three long-winged generalists (mixed diet) were more abundant on reconstructions than on remnants (*M. femurrubrum*, *M. bivittatus*, and *M. differentialis*), which supports our hypothesis that reconstructions would be characterised by highly mobile generalists. Two short-winged species (*P. nebrascensis*, *M. gracilis*) with a diet preference for grass or forbs were more abundant on remnants. This supports our hypothesis that remnants would be characterised by more sedentary specialists, which aligns with two studies that showed that generalist grasshoppers tend to dominate newly created grassland habitats (Bomar, 2001; Picaud & Petit, 2008). A comparison of reconstructed and remnant prairies in Wisconsin also found that *M. femurrubrum* was a dominant species on reconstructions (Bomar, 2001).

Our second objective was to evaluate the effect of reconstruction age on grasshopper communities. Older reconstructions, although still distinct from remnants, were closer in community composition to remnants than young reconstructions and many of the functional groups and taxa that identified reconstructions decreased in abundance with reconstruction age. *M. femurrubrum* decreased in abundance with reconstruction age but remained more common on older reconstructions than remnants. Bomar (2001) sampled from reconstructions as old as 50 years and found that *M. femurrubrum* remained the dominant grasshopper on reconstructions. We are cautious in interpreting the effects of reconstruction age because reconstruction and management practices have changed over the last 20 years, including seeding a greater diversity and ratio of forb seeds in comparison to grasses, which could affect how grasshopper communities changed over time on reconstructions of different ages. Nevertheless, it appears that grasshopper communities on reconstructed prairies are initially dominated by long-winged generalists and that over time those taxa diminish in numbers until communities are similar to remnants. However, at least on

reconstructions <15 years of age, grasshoppers associated with remnants do not replace the early colonisers.

Differences in the diversity and community composition of prairie grasshoppers between remnants and reconstructions have important conservation implications. Eight prairie grasshopper species associated with prairies were not found on reconstructions, and thus reconstructions may not be able to bolster the small grasshopper populations of nearby remnants. There are two, non-mutually exclusive explanations for this finding: grasshopper species on remnants cannot disperse to the new habitats or they do not survive and reproduce on reconstructions if they are able to reach them (Peterson & Denno, 1998; Beck & Kitching, 2007). Seven of the 10 grasshoppers unique to remnants were long-winged and probably capable of dispersing the short distances between remnants and reconstructions at the three locations in the Osage Plains. This suggests that dispersal ability is not the sole reason that reconstructions were less diverse than remnants.

Habitat suitability differences between remnants and reconstructions likely contributed to the differing grasshopper communities. We investigated some possible habitat characteristics responsible for the difference in communities by measuring forb:grass ratio and vegetation density. However, neither vegetation metric was a significant predictor of grasshopper abundance. Other studies have also failed to find consistent links between grasshopper populations and environmental variables (Anderson, 1964; Hastings & Pepper, 1964; Evans, 1988). Other characteristics, including plant community composition and soil properties, could impact grasshopper community composition on reconstructions and remnants. Plant community composition is likely a contributing factor, as grasshopper species' diets vary and reconstructions are known to differ from remnants in plant composition and structure (Kindscher & Tieszen, 1998; Olechnowski *et al.*, 2009). Soil characteristics could also have impacted grasshopper community composition. Grasshoppers deposit their eggs in the soil, and many require fairly specific soil conditions or temperatures for egg deposition (Uvarov, 1966). Plant and soil characteristics may also influence interspecific competition among grasshoppers, which is commonly size-dependent (Belovsky, 1986; Whitman, 2008). Reconstructions that support large populations of generalist, long-winged grasshoppers, which in this study consisted of two large species, *M. differentialis* and *M. bivittatus*, and one midsize species, *M. femurrubrum*, may not be supportive habitat for midsize grasshoppers due to direct competition. From a conservation perspective, making reconstructions hospitable to rare grasshoppers may be more important than attempting to aid species' dispersal from isolated habitat patches.

Our study produced results that can aid future reconstruction projects and grasshopper conservation. Monitoring can be more effective by focusing on certain taxa, such as the 10 prairie remnant species not found on reconstructions, as well as species that were simply less abundant on reconstructions, such as *P. nebrascensis*. All of those species warrant further monitoring and investigation into their habitat requirements to determine why they were not abundant on reconstructions. The long-winged generalist species that were very abundant on reconstructions could be influencing the reconstruction process itself and

their impact should be investigated. Additionally, it is important that grasshopper monitoring efforts continue to incorporate a community level perspective. Monitoring that only focuses on certain species suggested by previous studies as particularly important can lead to inconsistent findings because grasshopper populations are dynamic and exhibit frequent shifts in the dominant species (Campbell *et al.*, 1974; Capinera & Thompson, 1987; Evans, 1988). Continued monitoring will be necessary to determine if grasshopper communities on reconstructions eventually align with those on remnants.

Acknowledgements

The Missouri Department of Conservation, Wildlife Division was the primary funder of this project. Prairie Fork Charitable Endowment Trust and Prairie Biotic also provided grant support. We thank Paul Lenhart for assistance in identification and Rachel Blakey for advice on analyses. The authors have no conflicts of interest. The Missouri Cooperative Fish and Wildlife Research Unit is jointly sponsored by the MDC, the University of Missouri, the U.S. Fish and Wildlife Service, the U.S. Geological Survey, and the Wildlife Management Institute. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

Supporting information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Appendix S1. Supporting Information.

References

- Alignan, J.-F., Debras, J.-F. & Dutoit, T. (2018) Orthoptera prove good indicators of grassland rehabilitation success in the first French Natural Asset Reserve. *Journal for Nature Conservation*, **44**, 1–11.
- Anderson, N.L. (1964) Some relationships between grasshoppers and vegetation. *Annals of the Entomological Society of America*, **57**, 736–742.
- Ballard, H.E. (1992) Keys to known and potential Missouri Orthoptera. The Nature Conservancy.
- Bazelet, C.S. & Samways, M.J.J.E.I. (2011) Identifying grasshopper bioindicators for habitat quality assessment of ecological networks. *Ecological Indicators*, **11**, 1259–1269.
- Beck, J. & Kitching, I.J. (2007) Correlates of range size and dispersal ability: a comparative analysis of sphingid moths from the Indo-Australian tropics. *Global Ecology and Biogeography*, **16**, 341–349.
- Belovsky, G.E. (1986) Generalist herbivore foraging and its role in competitive interactions. *American Zoologist*, **26**, 51–69.
- Benayas, J.M.R., Newton, A.C., Diaz, A. & Bullock, J.M. (2009) Enhancement of biodiversity and ecosystem services by ecological restoration: a meta-analysis. *Science*, **325**, 1121–1124.

- Benkobi, L., Uresk, D.W., Schenbeck, G. & King, R.M. (2000) Protocol for monitoring standing crop in grasslands using visual obstruction. *Journal of Range Management*, **53**, 627–633.
- Blakey, R.V., Law, B.S., Kingsford, R.T., Stoklosa, J., Tap, P., Williamson, K. & Minderman, J. (2016) Bat communities respond positively to large-scale thinning of forest regrowth. *Journal of Applied Ecology*, **53**, 1694–1703.
- Block, W.M., Franklin, A.B., Ward, J.P., Ganey, J.L. & White, G.C. (2001) Design and implementation of monitoring studies to evaluate the success of ecological restoration on wildlife. *Restoration Ecology*, **9**, 293–303.
- Bomar, C.R. (2001) Comparison of grasshopper (Orthoptera: Acrididae) communities on remnant and reconstructed prairies in western Wisconsin. *Journal of Orthoptera Research*, **10**, 105–112.
- Brennan, L.A. & Kuvlesky, W.P., Jr. (2005) North American grassland birds: an unfolding conservation crisis? *Journal of Wildlife Management*, **69**, 1–13.
- Brückmann, S.V., Krauss, J. & Steffan-Dewenter, I. (2010) Butterfly and plant specialists suffer from reduced connectivity in fragmented landscapes. *Journal of Applied Ecology*, **47**, 799–809.
- Brust, M., Thurman, J., Reuter, C., Black, L., Quartarone, R., & Redford, A.J. (2014) Grasshoppers of the Western U.S. *USDA APHIS Identification Technology Program (ITP)*.
- Campbell, J.B., Arnett, W.H., Lambley, J., Jantz, O.K. & Knutson, H. (1974) Grasshoppers (Acrididae) of the Flint Hills native tallgrass prairie in Kansas. *Kansas State Agricultural Experiment Station Research Paper*, **19**(147).
- Capinera, J.L., & Sechrist, T.S. (1982) *Grasshoppers (Acrididae) of Colorado: Identification, Biology and Management*. Colorado Agricultural Experiment Station, Fort Collins, CO.
- Capinera, J.L. & Thompson, D.C. (1987) Dynamics and structure of grasshopper assemblages in shortgrass prairie. *The Canadian Entomologist*, **119**, 567–575.
- Ceballos, G., Davidson, A., List, R., Pacheco, J., Manzano-Fischer, P., Santos-Barrera, G. & Cruzado, J. (2010) Rapid decline of a grassland system and its ecological and conservation implications. *PLoS One*, **5**, e8562.
- Chao, A., Gotelli, N.J., Hsieh, T.C., Sander, E.L., Ma, K.H., Colwell, R. K. & Ellison, A.M. (2014) Rarefaction and extrapolation with Hill numbers: a framework for sampling and estimation in species diversity studies. *Ecological Monographs*, **84**, 45–67.
- Christisen, D.M. (1972) Prairie preservation in Missouri. *Proceedings of the Third Midwest Prairie Conference* (ed. by (ed. by L.C. Hulbert), pp. p. 42–46. Division of Biology, Kansas State University, Manhattan, KS.
- Clarke-Wood, B.K., Jenkins, K.M., Law, B.S. & Blakey, R.V. (2016) The ecological response of insectivorous bats to coastal lagoon degradation. *Biological Conservation*, **202**, 10–19.
- Colwell, R.K., Chao, A., Gotelli, N.J., Lin, S.Y., Mao, C.X., Chazdon, R. L. & Longino, J.T. (2012) Models and estimators linking individual-based and sample-based rarefaction, extrapolation and comparison of assemblages. *Journal of Plant Ecology*, **5**, 3–21.
- Davis, J.D., Hendrix, S.D., Debinski, D.M. & Hemsley, C.J. (2007) Butterfly, bee and forb community composition and cross-taxon incongruence in tallgrass prairie fragments. *Journal of Insect Conservation*, **12**, 69–79.
- Dennis, R.L., Dapporto, L., Fattorini, S. & Cook, L.M. (2011) The generalism–specialism debate: the role of generalists in the life and death of species. *Biological Journal of the Linnean Society*, **104**, 725–737.
- Diepenbrock, L.M., Finke, D.L., Stewart, A. & Littlewood, N. (2013) Refuge for native lady beetles (Coccinellidae) in perennial grassland habitats. *Insect Conservation and Diversity*, **6**, 671–679.
- Dobson, A.P., Bradshaw, A. & Baker, A.á. (1997) Hopes for the future: restoration ecology and conservation biology. *Science*, **277**, 515–522.
- Evans, E.W. (1988) Community dynamics of prairie grasshoppers subjected to periodic fire: predictable trajectories or random walks in time? *Oikos*, **52**, 283–292.
- Evans, E.W., Rogers, R.A. & Opfermann, D.J. (1983) Sampling grasshoppers on burned and unburned tallgrass prairie: night trapping vs. sweeping. *Environmental Entomology*, **12**, 1449–1454.
- Gotelli, N.J. & Colwell, R.K. (2011) Estimating species richness. *Biological Diversity: Frontiers in Measurement and Assessment* (ed. by (ed. by A.E. Magurran and B. McGill)), pp. p. 39–54. Oxford University Press, New York.
- Griffin, S.R., Bruninga-Socolar, B., Kerr, M.A., Gibbs, J. & Winfree, R. (2017) Wild bee community change over a 26-year chronosequence of restored tallgrass prairie. *Restoration Ecology*, **25**, 650–660.
- Harmon-Threatt, A.N. & Hendrix, S.D. (2015) Prairie restorations and bees: the potential ability of seed mixes to foster native bee communities. *Basic and Applied Ecology*, **16**, 64–72.
- Harrison, X.A., Donaldson, L., Correa-Cano, M.E., Evans, J., Fisher, D. N., Goodwin, C.E., Robinson, B.S., Hodgson, D.J. & Inger, R.J.P. (2018) A brief introduction to mixed effects modelling and multi-model inference in ecology. *PeerJ*, **6**, e4794.
- Hastings, E. & Pepper, J. (1964) Population studies on the big-headed grasshopper *Aulocara elliotti*. *Annals of the Entomological Society of America*, **57**, 216–220.
- Heidinger, I.M.M., Hein, S. & Bonte, D. (2010) Patch connectivity and sand dynamics affect dispersal-related morphology of the blue-winged grasshopper *Oedipoda caerulea* coastal grey dunes. *Insect Conservation and Diversity*, **3**, 205–212.
- Hilliard, J.R., Jr. (2001) Two new grasshopper species in the Texanus group of the genus *Melanoplus* (Orthoptera: Acrididae: Melanoplinae) with biological notes on the group. *Transactions of the American Entomological Society*, **127**, 31–68.
- Hjermann, D.O. & Ims, R.A. (1996) Landscape ecology of the wart-biter *Decticus verrucivorus* in a patchy landscape. *Journal of Animal Ecology*, **65**, 768–780.
- Hsieh, T.C., Ma, K.H., Chao, A. & McInerny, G. (2016) iNEXT: an R package for rarefaction and extrapolation of species diversity (Hill numbers). *Methods in Ecology and Evolution*, **7**, 1451–1456.
- Humbert, J.Y., Ghazoul, J., Sauter, G.J. & Walter, T. (2010) Impact of different meadow mowing techniques on field invertebrates. *Journal of Applied Entomology*, **134**, 592–599.
- Joern, A. (1979) Feeding patterns in grasshoppers (Orthoptera: Acrididae): factors influencing diet specialization. *Oecologia*, **38**, 325–347.
- Keylock, C. (2005) Simpson diversity and the Shannon–Wiener index as special cases of a generalized entropy. *Oikos*, **109**, 203–207.
- Kindscher, K. & Tieszen, L.L. (1998) Floristic and soil organic matter changes after five and thirty-five years of native tallgrass prairie restoration. *Restoration Ecology*, **6**, 181–196.
- Kirk, K. & Bomar, C.R. (2003) *Guide to the Grasshoppers of Wisconsin*. Wisconsin Department of Natural Resources, Madison, WI.
- Knowles, L.L. (2001) Genealogical portraits of speciation in montane grasshoppers (genus *Melanoplus*) from the sky islands of the Rocky Mountains. *Proceedings of the Royal Society of London B: Biological Sciences*, **268**, 319–324.
- Kremen, C., Merenlender, A.M. & Murphy, D.D. (1994) Ecological monitoring: a vital need for integrated conservation and development programs in the tropics. *Conservation Biology*, **8**, 388–397.
- Kuefler, D., Hudgens, B., Haddad, N.M., Morris, W.F. & Thurgate, N. (2010) The conflicting role of matrix habitats as conduits and barriers for dispersal. *Ecology*, **91**, 944–950.

- Kurtz, C. (2013) *A Practical Guide to Prairie Reconstruction*. University of Iowa Press, Iowa City, IA.
- Larson, D.P., O'Neill, K.M. & Kemp, W.P. (1999) Evaluation of the accuracy of sweep sampling in determining grasshopper (Orthoptera : Acrididae) community composition. *Journal of Agricultural and Urban Entomology*, **16**, 207–214.
- Lester, S.E., Ruttenberg, B.I., Gaines, S.D. & Kinlan, B.P. (2007) The relationship between dispersal ability and geographic range size. *Ecology Letters*, **10**, 745–758.
- Lockwood, J.A. (2004) *Locust: The Devastating Rise and Mysterious Disappearance of the Insect that Shaped the American Frontier*. Basic Books, New York, NY.
- Lockwood, J.A., Kemp, W.P. & Onsager, J.A. (1988) Long-term, large-scale effects of insecticidal control on rangeland grasshopper populations (Orthoptera: Acrididae). *Journal of Economic Entomology*, **81**, 1258–1264.
- Marini, L., Bommarco, R., Fontana, P. & Battisti, A. (2010) Disentangling effects of habitat diversity and area on orthopteran species with contrasting mobility. *Biological Conservation*, **143**, 2164–2171.
- Marini, L., Ockinger, E., Battisti, A. & Bommarco, R. (2012) High mobility reduces beta-diversity among orthopteran communities - implications for conservation. *Insect Conservation and Diversity*, **5**, 37–45.
- Missouri Natural Heritage Program (2018) *Missouri Species and Communities of Conservation Concern Checklist*. Missouri Department of Conservation, Jefferson City, MO.
- Oksanen, J., Blanchet, F., Kindt, R., & Legendre, P. (2016) *Vegan: Community Ecology Package. R Package Version 2.0-5*. <<https://CRAN.R-project.org/package=vegan>> 12th October 2016.
- Olechnowski, B.F., Debinski, D.M., Drobney, P.B., Viste-Sparkman, K. & Reed, W.T. (2009) Changes in vegetation structure through rime in a restored tallgrass prairie ecosystem and implications for avian diversity and community composition. *Ecological Restoration*, **27**, 449–457.
- O'Neill, K.M., Larson, D.P. & Kemp, W.P. (2002) Sweep sampling technique affects estimates of the relative abundance and community composition of grasshoppers (Orthoptera : Acrididae). *Journal of Agricultural and Urban Entomology*, **19**, 125–131.
- Opler, P.A. (1981) Management of prairie habitats for insect conservation. *Journal of the Natural Areas Association*, **1**, 3–6.
- Ortego, J., Aguirre, M.P., Noguerales, V. & Cordero, P.J. (2015) Consequences of extensive habitat fragmentation in landscape-level patterns of genetic diversity and structure in the Mediterranean esparto grasshopper. *Evolutionary Applications*, **8**, 621–632.
- Otte, D. (1981) *The North American Grasshoppers: Acrididae: Oedipodinae*. Harvard University Press, Cambridge, MA.
- Otte, D. (2012) Eighty new melanoplus species from the United States (Acrididae: Melanoplinae). *Transactions of the American Entomological Society*, **138**, 73–167.
- Panzer, R. (2002) Compatibility of prescribed burning with the conservation of insects in small, isolated prairie reserves. *Conservation Biology*, **16**, 1296–1307.
- Paton, D., Rogers, D., Hill, B., Bailey, C. & Ziembicki, M. (2009) Temporal changes to spatially stratified waterbird communities of the Coorong, South Australia: implications for the management of heterogeneous wetlands. *Animal Conservation*, **12**, 408–417.
- Peet, R.K. (1975) Relative diversity indices. *Ecology*, **56**, 496–498.
- Peterson, M.A. & Denno, R.F. (1998) The influence of dispersal and diet breadth on patterns of genetic isolation by distance in phytophagous insects. *The American Naturalist*, **152**, 428–446.
- Pfadt, R.E. (1994) *Field Guide to Common Western Grasshoppers*. University of Wyoming, Laramie, WY.
- Picaud, F. & Petit, D.P. (2008) Body size, sexual dimorphism and ecological succession in grasshoppers. *Journal of Orthoptera Research*, **17**, 177–181.
- Piechnik, D.A., Lawler, S.P. & Martinez, N.D. (2008) Food-web assembly during a classic biogeographic study: species' "trophic breadth" corresponds to colonization order. *Oikos*, **117**, 665–674.
- Pleasants, J.M. & Oberhauser, K.S. (2013) Milkweed loss in agricultural fields because of herbicide use: effect on the monarch butterfly population. *Insect Conservation and Diversity*, **6**, 135–144.
- R Core Team (2017) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria. <<http://www.R-project.org/>>. 10th March 2017.
- Reed, C. (1996) *List of Insect Species Which May Be Prairie Specialists: Final Report to the USFWS Cooperating Agencies*. Minnesota Department of Natural Resources, St. Paul, MN.
- Reinhardt, K., Kohler, G., Maas, S. & Detzel, P. (2005) Low dispersal ability and habitat specificity promote extinctions in rare but not in widespread species: the Orthoptera of Germany. *Ecography*, **28**, 593–602.
- Ries, L., Debinski, D.M. & Wieland, M.L. (2001) Conservation value of roadside prairie restoration to butterfly communities. *Conservation Biology*, **15**, 401–411.
- Routledge, R. (1979) Diversity indices: which ones are admissible? *Journal of Theoretical Biology*, **76**, 503–515.
- Rowe, H.I. (2010) Tricks of the trade: techniques and opinions from 38 experts in tallgrass prairie restoration. *Restoration Ecology*, **18**, 253–262.
- Samson, F. & Knopf, F. (1994) Prairie conservation in north america. *BioScience*, **44**, 418–421.
- Sauberer, N., Zulka, K.P., Abensperg-Traun, M., Berg, H.-M., Bieringer, G., Milasowszky, N., Moser, D., Plutzer, C., Pollheimer, M. & Storch, C. (2004) Surrogate taxa for biodiversity in agricultural landscapes of eastern Austria. *Biological Conservation*, **117**, 181–190.
- Schultz, C.B., Russell, C. & Wynn, L. (2008) Restoration, reintroduction, and captive propagation for at-risk butterflies: a review of British and American conservation efforts. *Israel Journal of Ecology and Evolution*, **54**, 41–61.
- Smith, D. (2010) *The Tallgrass Prairie Center Guide to Prairie Restoration in the Upper Midwest*. University of Iowa Press, Iowa City, USA.
- Solecki, M. & Toney, T. (1986) Characteristics and management of Missouri's public prairies. *Proceedings of the North American Prairie Conference*, **9**, 168–171.
- Song, H. (2009) *Taxonomic Identification Key to Schistocerca Species*. <<http://www.schistocerca.org/key.htm>> 1st May 2017.
- Swengel, A.B. (2001) A literature review of insect responses to fire, compared to other conservation managements of open habitat. *Biodiversity & Conservation*, **10**, 1141–1169.
- Thom, R.M. (2000) Adaptive management of coastal ecosystem restoration projects. *Ecological Engineering*, **15**, 365–372.
- Thompson, J.D. (1999) Population differentiation in Mediterranean plants: insights into colonization history and the evolution and conservation of endemic species. *Heredity*, **82**, 229–236.
- Tonietto, R.K., Ascher, J.S. & Larkin, D.J. (2017) Bee communities along a prairie restoration chronosequence: similar abundance and diversity, distinct composition. *Ecological Applications*, **27**, 705–717.
- Török, P. & Helm, A. (2017) Ecological theory provides strong support for habitat restoration. *Biological Conservation*, **206**, 85–91.
- Uresk, D.W. & Benzou, T.A. (2007) Monitoring with a modified Robel pole on meadows in the central Black Hills of South Dakota. *Western North American Naturalist*, **67**, 46–50.
- Uvarov, B.P. (1966) *Grasshoppers and Locusts: A Handbook of General Acridology*, Vol. 1. Cambridge University Anti-Locust Research Centre, Cambridge, UK.
- Venables, W.N. & Ripley, B.D. (2002) *Modern Applied Statistics with S*. Springer, New York.
- Vogel, J.A., Debinski, D.M., Koford, R.R. & Miller, J.R. (2007) Butterfly responses to prairie restoration through fire and grazing. *Biological Conservation*, **140**, 78–90.

- Wang, Y., Naumann, U., Wright, S.T., Warton, D.I. & J.M.i.E., & Evolution (2012) mvabund—an R package for model-based analysis of multivariate abundance data. *Methods in Ecology and Evolution*, **3**, 471–474.
- Weibull, A.-C., Östman, Ö. & Granqvist, Å. (2003) Species richness in agroecosystems: the effect of landscape, habitat and farm management. *Biodiversity & Conservation*, **12**, 1335–1355.
- Whitman, D.W. (2008) The significance of body size in the Orthoptera: a review. *Journal of Orthoptera Research*, **17**, 117–134.
- Williams, N.M. (2011) Restoration of nontarget species: bee communities and pollination function in riparian forests. *Restoration Ecology*, **19**, 450–459.
- Wright, C.K. & Wimberly, M.C. (2013) Recent land use change in the Western Corn Belt threatens grasslands and wetlands. *Proceedings of the National Academy of Sciences*, **110**, 4134–4139.
- Zera, A.J. & Denno, R.F. (1997) Physiology and ecology of dispersal polymorphism in insects. *Annual review of entomology*, **42**, 207–230.

Accepted 18 May 2019

Editor: Alan Stewart
Associate editor: Philip Barton