The Prairie Naturalist Great Plains Natural Science Society

2020

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Joseph LaRose

Elisabeth B. Webb

Deborah Finke

The Prairie Naturalist 52:33-44; 2020

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JOSEPH LAROSE, ELISABETH B. WEBB, AND DEBORAH FINKE

Division of Plant Sciences, University of Missouri, Columbia, Missouri 65211, USA (JL, DF)
U.S. Geological Survey, Missouri Cooperative Fish and Wildlife Research Unit, Department of Fisheries and Wildlife Sciences, University of Missouri, Columbia, Missouri 65211, USA (EBW)

ABSTRACT The tallgrass prairie of North America is an imperiled ecosystem that has been the subject of considerable restoration effort and research in the past two decades. While native prairie plant species are purposely introduced during restoration, prairie invertebrates, including native bees (Anthophila), are not and must colonize from surrounding remnants. Prairie restorations may not support the same bee communities as remnant prairies because of habitat differences and dispersal limitations. We sampled native bees on reconstructed and remnant prairies in Missouri in the summers of 2016 and 2017 and compared the communities by evaluating species richness, diversity, and community composition. We detected no differences in bee species richness or diversity between reconstructions and remnants; remnants and reconstructions shared all but three of the 57 taxa observed. Community composition of bees on reconstructions was different from that of remnants because of differences in the relative abundance of taxa. Several species were associated with either reconstructed or remnant prairies. At a functional level, stem nesters were more common on reconstructed than remnant prairie. We also examined whether bee communities on reconstructions converged with those observed on remnants over time by comparing bee communities across restorations of different ages and found that reconstruction communities did not appear to be converging with remnants. Reconstructing prairie bee communities may depend on restoring soil conditions and disturbance regimes that influence bee nesting habitat.

KEY WORDS Anthophila, community, diversity, grasslands, monitoring, pollinators, restoration.

Substantial losses in the diversity and abundance of native bees in North America (Colla and Packer 2008) have led to increased research and conservation initiatives for bees and other insect pollinators. Habitat loss undoubtedly plays some role in bee decline (Grixti et al. 2009, Cameron et al. 2011), and this is almost certainly true in prairie ecosystems, most of which have been converted to agricultural land (Samson and Knopf 1994). The remaining prairie habitat, though small, is important for conserving bee diversity. Remnant prairies in Iowa contained more bee species, including more rare species, and greater bee abundance than ruderal areas (Kwaiser and Hendrix 2008). In Illinois, while prairie remnants and old fields contained similar bee abundances, bee communities in remnant prairie were more diverse and differed in composition than those in old fields (Tonietto et al. 2017). The growth of restoration science and ecology has opened another potential avenue for bee conservation through the restoration or reconstruction of prairies.

Prairie restoration can range from the rehabilitation of grazing lands to the full-scale reconstruction of prairie from agricultural fields. Scientists and managers reconstructing tallgrass prairie generally attempt to establish a plant community that corresponds to those found in local remnant prairies (Kurtz 2013). Prairie restoration appears to be a promising strategy for native bee conservation; it has been effective in practice for plants (McLachlan and Knispel 2005), the usual proximate target of reconstruction, and restoration of a variety of habitats has been successful for native bees (Tonietto et al. 2018).

Assessing how well restoration works for native bees can be challenging due to the variability exhibited by insect populations (Fleishman and Murphy 2009) and the substantial regional variation in bee community composition (Williams 2011). Additionally, tallgrass prairie ecosystems are dynamic (Evans 1988, Whiles and Charlton 2006), representing moving targets for restoration (Simberloff 1990). This dynamism makes simultaneously monitoring restored and remnant habitats critical. Studies examining bee communities on restorations have yielded somewhat inconsistent results. There is substantial evidence that bees colonize newly restored habitats quickly, resulting in species richness and abundance similar to remnant habitat within five years (Exeler 2009, Williams 2011, Griffin et al. 2017). The community composition of bees on restorations, however, may converge with that found on remnants over time (Griffin et al. 2017) or remain distinct (Williams 2011, Tonietto et al. 2017). The habitat differences responsible for the difference in bee communities are not entirely known.

Examining functional groups can provide information about the habitat characteristics important to bees on prairie restorations. Assigning bees to groups based on nesting habitat requirements (Potts et al. 2003, Tonietto et al. 2017) is one useful way of using functional groups. Native bee species may nest in the soil, plant stems or twigs, wood, or cavities (Ascher and Pickering 2017), and the availability of these resources can vary across habitat types and landscapes. Soil and stem nesting habitat may differ between remnant and reconstructed prairies because of differences in plant communities (Kindscher and Tieszen 1998, McLachlan and Knispel 2005, Middleton et al. 2010). The legacy of a site may also affect nesting resources, especially soil nesting habitat. Prairie reconstructions that were previously cultivated fields likely contain more homogenous, shallower soils than remnants (Baer et al. 2005) as well as greater soil compaction and less organic matter (Six et al. 1998). Finally, prairie management can greatly alter the availability of nesting resources. Grazing and frequent fire can increase the abundance of soil nesting bees by exposing bare ground (Potts et al. 2003, Kimoto et al. 2012), whereas less frequent fire benefits some stem and twig nesting bees by providing more stems and twigs (Cane et al. 2007, Cane and Neff 2011).

Research involving simultaneous sampling of different locations and different ages of reconstructions is important to better understand bee communities on prairie reconstructions and whether reconstructions can rescue declining bee species. We had two objectives for our study. First, we compared native bee (Anthophila) communities on reconstructions to those on remnants by evaluating species richness, diversity, and community composition at paired reconstructed and remnant prairies in Missouri. We sought to identify species or functional groups associated with remnants or reconstructions that could be used in future monitoring. Our second objective was to compare native bee communities across prairie reconstructions of different ages to determine if bee communities on reconstructions were converging with those on remnants over time. We hypothesized that bee communities of remnant and reconstructed prairies would not differ in species richness or diversity. We also thought community composition would likely differ between reconstructions and remnants, but as the soil and plant community converge over time with those found on remnants, those community differences would diminish on older reconstructions.

STUDY AREA

We sampled two locations containing prairies managed by the Missouri Department of Conservation. The Wah'Kon-Tah Prairie location, situated in St. Clair County in the Upper Osage Grasslands region of southwestern Missouri, contained remnant (756 ha) and reconstructed (160 ha) prairie (Fig. 1). Prairie reconstruction at Wah'Kon-Tah was initiated in ten parts from 2002 to 2008. The second location was 333 km northeast in the Central Dissected Plains region in Calloway County. This North location consisted of two distinct prairies: one remnant (Tucker Prairie, 59 ha) and one reconstructed (Prairie Fork Conservation Area, 142 ha), separated by 32 km (Fig. 1). Reconstruction of prairie patches at Prairie Fork Conservation Area in the North location started in 2004 and was ongoing at the start of this study in 2016.

There were various grassland management practices that could confound invertebrate surveys. Therefore, we excluded areas that were scheduled to be hayed, grazed, mowed, or high-clipped in the sampling year because those practices might alter the invertebrate community during the summer months (Humbert et al. 2010). Burning also affects invertebrate communities (Panzer 2002); however, we included burned patches in our sampling because burns were scheduled during the dormant season, outside of the sampling window.

METHODS

Sampling Scheme

We sampled bee communities using bee bowls placed at randomly selected locations within each remnant and reconstructed prairie in 2016 and 2017. We used ArcMap 10.3.1 (ESRI 2015) to randomly generate points each year. There were 30 sampling points generated on the Wah'Kon-Tah reconstructions and 30 points on the remnant prairie. At the North location, there were 30 points on the reconstructions and 15 on the remnant in 2016 and 20 points on the reconstruction and 10 on the remnant in 2017. We reduced the samples in the North in 2017 to increase distances between bee bowls and better match sampling intensity with the larger Wah'Kon-Tah. Each sample point was located at least 40 m from the prairie edge to limit edge effects. The two closest sampling points were 120 m apart, and the average nearest neighbor distance was 250 m. Independence in this case means that the bees caught at one sampling point should not have affected bees caught at any other location. However, while we assumed independence among samples, native bee species differ considerably in body size and flight range, with some bees having foraging ranges of 1.5 km or larger (Greenleaf et al. 2007). As some of the samples in this study were located closer than 1.5 km, samples may better reflect bee foraging preference than nest location, especially for larger bees with large flight ranges. Sample independence is a challenge in many bee studies (Davis et al. 2007, Kwaiser and Hendrix 2008, Kimoto et al. 2012). Our experimental design and distance between sampling locations is similar to previous research (Briggs et al. 2013).

Collecting

We sampled bees using bee bowls made with clear 0.27 L (9-oz) cups (SOLO®) and fluorescent paint (Droege 2012). We placed three bowls, one yellow, one blue (Fluorescent

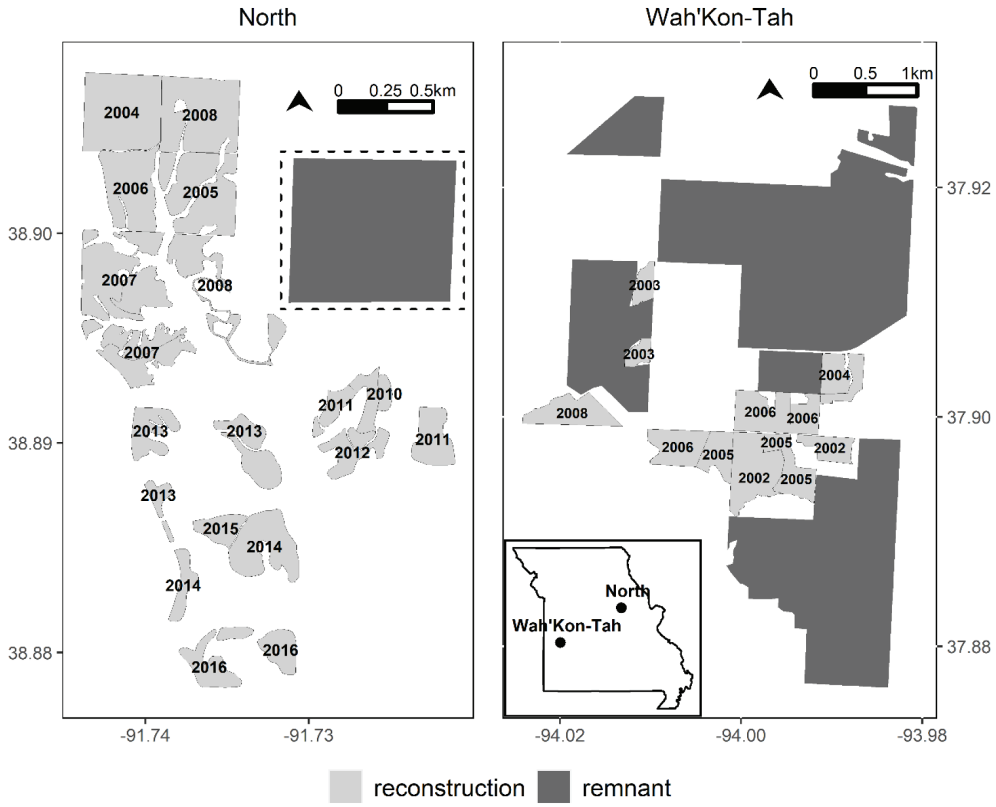

Figure 1. Maps of Wah'Kon-Tah and North prairies in Missouri, USA. The remnant prairie at the North location is 32 km away from the reconstructed pictured, therefore it is displayed to scale as an inset (dashed border). Reconstructed portions of prairie are labeled with the year in which they were seeded.

Yellow, Fluorescent Blue, mixed with Silica Flat; Guerra Paint & Pigment Corporation), and one white (white spray paint; Valspar®), at each randomly generated point. Bowls sat in plastic (PVC) rings that were glued to each other and then mounted on a 12.7 mm dowel rod, which allowed us to modify bee bowl height with growing vegetation. We positioned the bee bowls at half vegetation height to track flower height. Bee bowls are only effective if they are visible (Tuell and Isaacs 2009), thus they must be placed higher later in the growing season to correspond with plant growth. We filled bee bowls with soapy water, and they remained in the field for 48 hr during each sampling period (Droege 2015). The contents of the three bowls were combined into a single sample for each sampling period. In 2016, we sampled monthly from June to August. In 2017, we sampled monthly from April to August. We also caught bees through standardized sweeping as part of a concurrent study on grasshoppers (LaRose et al. 2019). We conducted 40 sweeps along a 60-m transect centered at every bee bowl location concurrent with bee bowl use. Any bees captured were identified and added to bees captured with bee bowls for analyses.

Bees were identified to species, or in cases where species could not be reliably determined, to genus or subgenus, using Arduser (2016) and discoverlife.org (Ascher and Pickering 2017). We grouped bees by family and nesting habitat (Table 1). Representative specimens of every taxon were pinned and stored in the Enns Entomological Museum at the University of Missouri, Columbia.

Statistical analyses

Bee diversity and total abundance. We compared bee taxon richness (species plus genera and subgenera that were not identified further) and diversity in reconstructed and remnant prairies at each location (Wah'Kon-Tah and North) using non-asymptotic techniques. The non-asymptotic approach consisted of rarefaction/extrapolation (Weibull et al. 2003, Gotelli and Colwell 2011, Colwell et al. 2012), which resamples species data to estimate the richness or diversity at other sample sizes. We performed sample-based rarefaction/extrapolation on the locations separately using the package iNEXT (Hsieh et al. 2016), treating each bee bowl location as a sample. We conducted all analyses using R version 3.4.0 (R Core Team 2017).

We generated rarefaction/extrapolation curves for three Hill numbers (Hsieh et al. 2016), which are measures of diversity that combine species richness and abundance. The curves represented the estimated Hill numbers at

Table 1. Bee taxa captured in on Missouri prairies in 2016 and 2017 with family and nesting habitat information. Single asterisk (*) indicates taxa was unique to remnant prairies; double asterisk (**) indicates taxa was unique to reconstructed prairie.

Taxa	Family	Nest Habitat
Andrena (Andrena)	Andrenidae	Soil
Andrena (Derandrena)	Andrenidae	Soil
Andrena (Melandrena)	Andrenidae	Soil
Andrena (Plastandrena)	Andrenidae	Soil
Andrena (Ptilandrena)	Andrenidae	Soil
Andrena (Rhacandrena)	Andrenidae	Soil
Andrena (Scapteropsis)	Andrenidae	Soil
Andrena (Trachandrena)	Andrenidae	Soil
Andrena arabis	Andrenidae	Soil
Andrena cressoni	Andrenidae	Soil
Andrena rudbeckia	Andrenidae	Soil
Andrena violae	Andrenidae	Soil
Andrena carlini	Andrenidae	Soil
Pseudopanurgus albitarsis	Andrenidae	Soil
Apis mellifera	Apidae	Cavity
Bombus auricomus	Apidae	Soil
Bombus bimaculata	Apidae	Soil
Bombus griseocolis	Apidae	Soil
Bombus impatiens	Apidae	Soil
Bombus pennsylvanicus	Apidae	Soil
Ceratina	Apidae	Stem/twig
Eucera hamata	Apidae	Soil
Eucera rosae	Apidae	Soil
Melissodes agilis	Apidae	Soil
Melissodes bimaculata	Apidae	Soil
Melissodes boltoniae	Apidae	Soil
Melissodes communis	Apidae	Soil
Melissodes comptoides	Apidae	Soil
*Melissodes dentriventris***	Apidae	Soil
*Melissodes elegans***	Apidae	Soil
*Melissodes nivea**	Apidae	Soil
Melissodes trinodis	Apidae	Stem/twig

Taxa	Family	Nest Habitat
Melissodes veronia	Apidae	Soil
Nomada	Apidae	Kleptoparasite
Ptilothrix bombiformis	Apidae	Soil
Xylocopa virginica	Apidae	Wood
Hylaeus fedorica	Colletidae	Stem/twig
Hylaeus illinoisensis	Colletidae	Stem/twig
Hylaeus mesillae	Colletidae	Stem/twig
Agapostemon sericeous	Halictidae	Soil (sand)
Agapostemon texanus	Halictidae	Soil
Agapostemon virescens	Halictidae	Soil
Augochlora pura	Halictidae	Wood
Augochlorella aurata	Halictidae	Soil
Augochlorella persimilis	Halictidae	Soil
Augochloropsis fulgida	Halictidae	Soil
Augochloropsis metallica	Halictidae	Soil
Halictus ligatus	Halictidae	Soil
Halictus parallelus	Halictidae	Soil
Lasioglossum	Halictidae	Soil
Lasioglossum (Dialictus)	Halictidae	Soil
Lasioglossum paralictus	Halictidae	Kleptoparasite
Megachile brevis	Megachilidae	Stem/twig
Megachile montivaga	Megachilidae	Soil
Megachile parallela	Megachilidae	Stem/twig
Megachile petulans	Megachilidae	Stem/twig
Megachile relativa	Megachilidae	Stem/twig

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 collectively. We plotted the Hill curves using 95% confidence intervals, calculated with the bootstrap method (Colwell et al. 2012).

We compared bee abundance on remnants and reconstructions by modeling the total abundance of bees summed across sampling periods using univariate generalized linear models with a negative binomial distribution. Variables included *status* (reconstruction or remnant), *location* (Wah'Kon-Tah or North) and *year* (2016 or 2017). We started with an initial model that included all variables and interactions and then removed interactions and variables individually. We conducted analyses of variance (ANOVA) on models with and without variables and discarded those variables that did not improve model fit ($P > 0.05$) (Blakey et al. 2016, Clarke-Wood et al. 2016). We used the function *glm.nb* in the package *MASS* (Ripley et al. 2017). We compared the abundance of bees across reconstructions of different ages to determine if bee abundance on reconstructions was changing over time. For these analyses, we used the same ANOVA methods but only included data from reconstructed prairies, replacing *status* with *age* (years since initial reconstruction).

Community analysis. To visualize community data, we ordinated the bee communities using non-metric multidimensional scaling (NMS) with a Bray-Curtis dissimilarity matrix (Paton et al. 2009, Clarke-Wood et al. 2016). Taxa abundances were summed across sampling periods for bee bowl locations for each year separately. Only species that occurred in more than 5% of bee bowl samples were included in the ordination in order to reduce noise that rare species can contribute (Gauch 1982) and to reduce ordination stress, a measure of goodness of fit, to interpretable levels (<0.20) (Clarke 1993). Therefore we used the 24 most common bee taxonomic groups (primarily species and a few genera). Bee bowl samples with zero individuals were removed before analysis for the same reason. 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) according the stress value and visualized the resulting ordination with the *ordirgl* function.

To test whether bee communities in reconstruction and remnant prairies were distinct, we modeled abundances of the same taxa used in the ordinations. Multivariate models were generated in the package *mvabund* (Wang et al. 2012), which incorporates multivariate count data into generalized linear models. The response variables were the abundances of a taxa summed across sample dates for each bee bowl sample; we used a negative binomial distribution for all models. Explanatory variables included *status* (remnant or reconstructed), *location* (Wah'Kon-Tah, and North), *edge proximity* (distance from bee bowl location to closest prairie edge, measured in ArcMAP), *year* (2016 or 2017), and all interactions among them. We tested the significance of variables and interactions with an ANOVA comparing the full model to a model without each variable (Blakey et al. 2016, Clarke-Wood et al. 2016). Because of a significant *status* × *location* interaction, we ran multivariate models for each location as well. To identify which taxa contributed to differences between communities we examined the multivariate model coefficients for each taxon. Coefficients with a P-value <0.05 were considered significant.

We used the same methods to compare bee community composition across reconstructions of different ages by removing remnant sampling points (and therefore *status*) and adding *age* as a variable for remaining reconstruction sites. Only the 23 most abundant bees found on reconstructions were used in the models for age effect.

Functional groups. We grouped bees by nesting habitat using information from discoverlife.org (Ascher and Pickering 2017) and Arduser (2016). Nesting categories included *wood* (bees that nest in logs or tree cavities), *stem* (twig and stem nesters, hereafter stem nesters), and *soil*. Using the package *mvabund*, we created multivariate models of abundance for each functional group. Explanatory variables in this analysis included *status*, *location*, *edge proximity*, *year*, and all possible interactions. Due to a significant *status* × *location* interaction, we also modeled functional group abundance for each location separately. We used the same methods to compare functional groups across reconstructions of different ages by removing remnant sampling points (and therefore *status*) and adding *age*.

RESULTS

Did bee communities on reconstructions differ from those on remnants?

Diversity and total abundance. We collected 3,647 bees from 57 identified species or genera in 2016 and 2017 combined (Table 1). Most of the bees captured were in family Halictidae (71%); Apidae (20%) was the second most common bee family observed. There was little difference in diversity between remnants and reconstructions based on rarefaction/extrapolation curves for species richness, with Shannon diversity and Simpson diversity 95% confidence intervals of reconstruction and remnant diversity overlapping for all three Hill numbers (Fig. 2). At the North location, Simpson diversity was greater on reconstructions than the remnant (Fig. 2).

The best generalized linear model of total bee abundance contained year ($\chi^2 = 7.87$, $P = 0.005$) and an interaction between status and location ($\chi^2 = 11.27$, $P < 0.001$). When locations were modeled separately, bees were more abundant on reconstructions than remnants at the North location ($\zeta = 4.53$, $P < 0.0001$), but not at Wah'Kon-Tah ($\chi^2 = 1.05$, $P = 0.306$). Bees were more abundant in 2016 than in 2017.

Community composition. Remnant and reconstruction bee communities appeared somewhat distinct in 3-D ordinations (Fig. 3A; stress = 0.19; k = 3), with some overlap in 95% confidence intervals on the centroids. However, communities were clearly different by location (Fig. 3B) and year, indicating that *year* and *location* were more important sources of variation in the bee communities than *status*. The best multivariate model of species abundances contained *year* ($\chi^2 = 314.9$, $P < 0.001$) and an interaction between *location* and *status* ($\chi^2 = 78.87$, $P < 0.001$). However, univariate tests showed that the interaction was only significant for two species, *Melissodes communis* ($\chi^2 = 11.17$, $P < 0.03$) and *Melissodes comptoides* ($\chi^2 = 17.44$, $P < 0.002$). Therefore we focus on results from a model without the interaction term that included *location* ($\chi^2 = 394.8$, $P < 0.001$), *year* ($\chi^2 = 313.3$, $P < 0.001$), and status ($\chi^2 = 145.7$, $P < 0.001$). Remnant and reconstruction communities were distinct at Wah'Kon-Tah Prairie ($\chi^2 = 101.5$, $P < 0.001$) and the North prairies ($\chi^2 = 92.58$, $P < 0.001$). Based on model coefficients representing the effects of reconstruction on species abundance, *Eucera hamata*, *Ceratina*, *Apis mellifera*, *Agapostemon texanus*, and *Hylaeus mesillae* were more common on reconstructions than remnants. *Halictus parallelus* and *Augochlorella persimilis* were more abundant on remnants. Beyond the common species used in the ordination and multivariate abundance models, there was one rare species only found on remnants, *Melissodes nivea*, and three species found

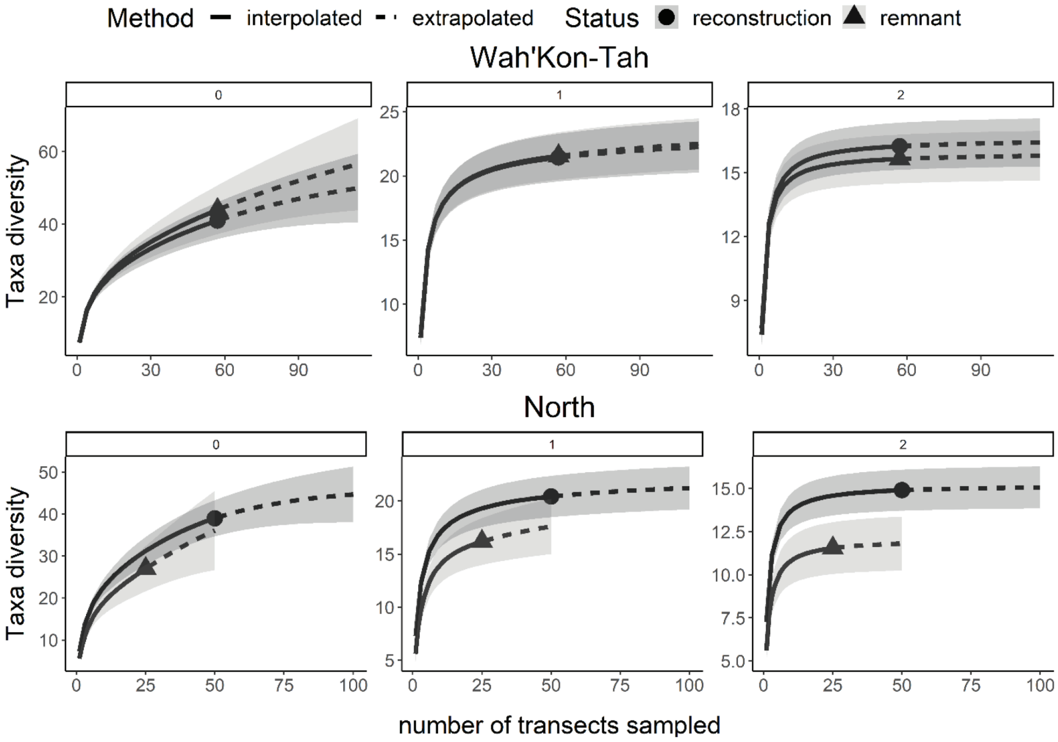

Figure 2. Sample-based rarefaction and extrapolation of Hill number diversity of bees captured on Missouri prairies in 2016 and 2017. 0 = species richness, 1 = Shannon diversity, and 2 = Simpson diversity. Shaded areas represent 95% confidence intervals. Shannon diversity estimates are presented as the exponentials of Shannon indices, and Simpson diversity estimates are presented as inverse of Simpson concentration, such that larger numbers represent greater diversity.

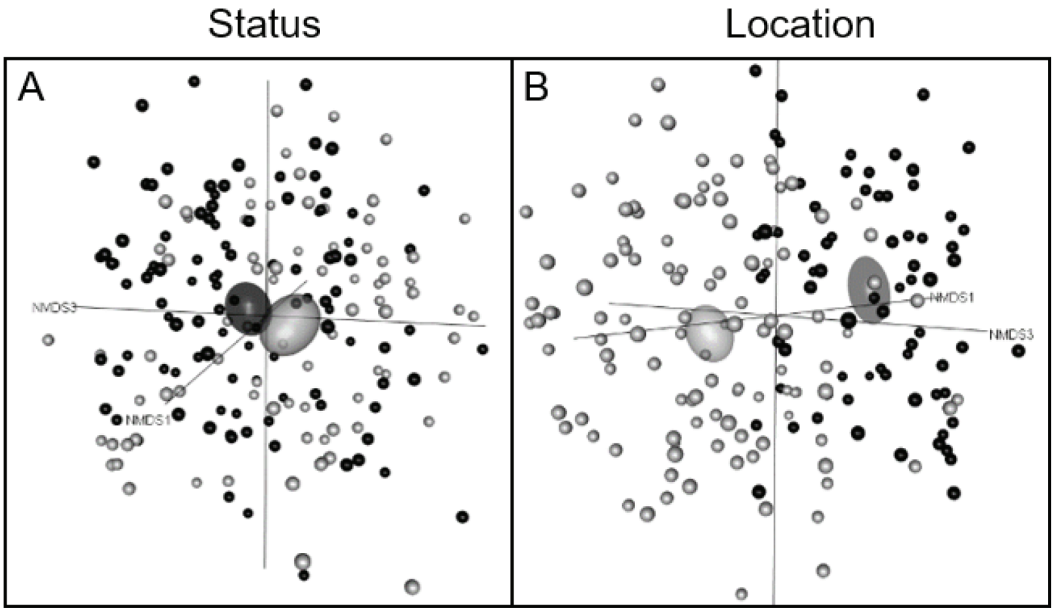

Figure 3. NMS ordination (k = 4, stress = 0.18) of bee communities from Missouri prairies in 2016 and 2017. Dots represent communities from individual bee bowl samples. Spheres represent 95% confidence intervals around the centroids. A: Remnants (black) and reconstructions (grey). B: Wah’Kon-Tah (black) and North (grey) locations.

only on reconstructions, *Agapostemon sericeus*, *Melissodes dentriventris*, and *Melissodes elegans*.

Functional groups. Among nesting functional groups, soil nesters were most abundant (90.5%), followed by stem nesters (7.0%). Overall abundance of stem nesters was greater on reconstructions than remnants (Fig. 4; χ^2 = 12.14, P = 0.022); this response was likely driven by the abundance of stem nesters on reconstructions at Wah'Kon-Tah (ζ = -2.02, P = 0.043). The genus *Ceratina* and *H. messillae*, identified in the multivariate abundance model as more common on reconstructions, were likely responsible for the greater stem nester abundance on reconstructions. In the North location, soil nesters were more common on reconstructions than on remnants (Fig. 4; χ^2 = 2.059, P = 0.039).

Did reconstruction age affect community composition?

Ordination (k = 4, stress = 0.171) revealed no obvious trends based on reconstruction age, but the centroids of newer reconstructions clustered on one side of the NMS space. The best multivariate abundance model contained a interaction between *age* and *location* (χ^2 = 76.04, P < 0.001), but univariate tests revealed the interaction was significant for only two bee species, *Augochloropsis metallica* (χ^2 = 14.6, P = 0.006) and *Melissodes bimaculata* (χ^2 = 12.26, P = 0.012), as well as marginally significant for *Halictus parallelus* (χ^2 = 9.826, P = 0.064). Consequently, and for ease of interpretation, we excluded the *age* × *location* interaction term. The model without an *age* × *location* interaction included *age* (χ^2 = 61.29, P < 0.001) and *year* × *location* (χ^2 =73.7, P < 0.001), indicating that bee communities differed across reconstruction age. Excluding *A. metallica* because of a signification interaction, there were three taxa that showed a significant abundance response to reconstruction age: *Lasioglossum* subg. *Dialictus*, *A. aurata*, and the genus *Ceratina. Dialictus* abundance decreased with reconstruction age. *A. aurata*, which was the most common native bee captured on reconstructions, and *Ceratina* abundance increased with reconstruction age.

The best bee abundance model for reconstructions included an *age* × *location* interaction (χ^2 = 5.81, P = 0.016), which was due to a negative relationship between bee abundance and reconstruction age at the North location (χ^2 = 9.99, P < 0.002) (Fig. 4).

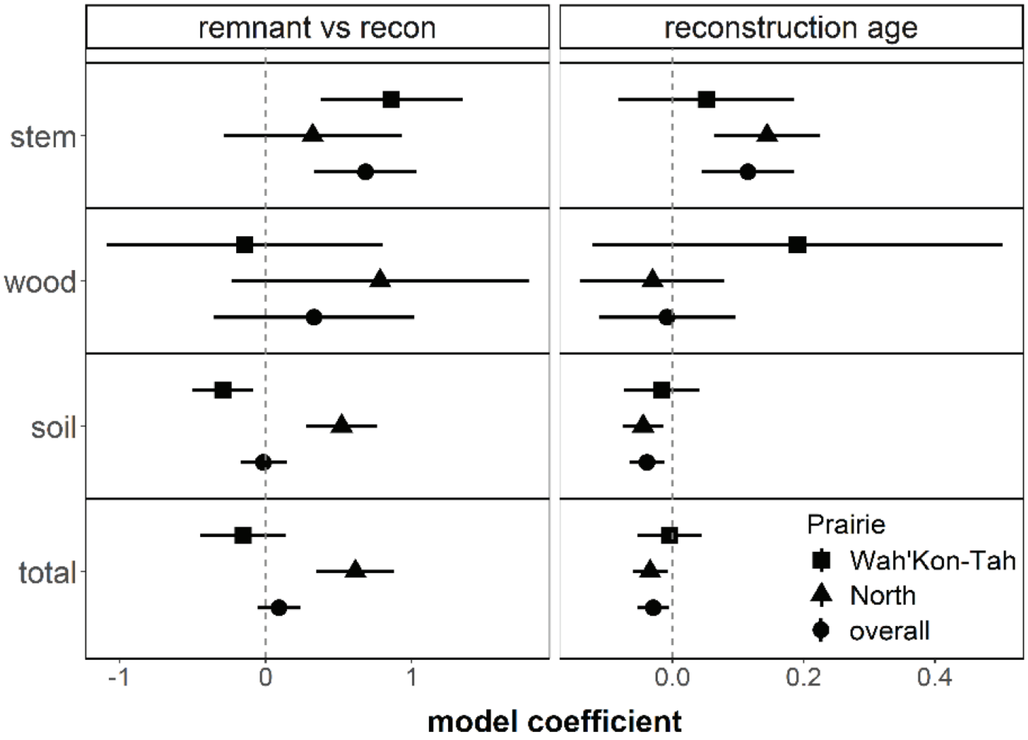

Figure 4. The effect of prairie *status* (left) and *age* (right) on the abundance of three bee nesting groups as well as total bee abundance on Missouri prairies in 2016 and 2017. Symbols represent coefficients, with 95% confidence intervals, from a multivariate abundance model. Positive coefficients signify greater abundance on reconstructions (recon) than remnants (left), or increasing abundance with age (right). There are up to three coefficients for each species, representing the response of taxa for the Wah'Kon-Tah and North areas separately, and for both prairie areas combined with no interaction (overall). Model coefficients with very large standard errors are not shown.

Functional groups

The best model of nesting group abundances contained age (χ^2 = 17.44, P = 0.003) and an interaction between location and year (χ^2 = 19.52, P < 0.001). Stem nester abundance was positively associated with reconstruction age, whereas soil nester abundance was negatively associated with reconstruction age (Fig. 4).

DISCUSSION

Our first objective was to compare bee communities of prairie reconstructions and remnants and identify species or functional groups that can be used to evaluate prairie reconstruction progress and effectiveness. Bee communities on remnant and reconstructed prairies shared nearly all species but were distinct due to differing abundances for some taxa. Although remnants and reconstructions were statistically distinct, communities differed much more between locations and between years. Similar to what studies on restorations have found on Central European grasslands (Exeler 2009), riparian habitats in California (Williams 2011), and Illinois prairies (Tonietto et al. 2017), we found little evidence that remnant and reconstructed prairies in Missouri differed in bee species richness or diversity. It is important to note the possible effect of sample independence and geography in our study when interpreting the observed differences in remnant and reconstructed bee communities. Because the distance between some sampling locations was less than some bees' flight ranges, it is possible that bees nested near one sample location and foraged at another. In this case, we sampled foragers and their foraging preference, not just nesters. As for geography, the reconstruction and the remnant were farther apart at the North location. It is possible that the differences we observed at the North location arise at least partly from differences in background bee communities at the remnant and reconstruction sites, and not necessarily differences between the types of prairie.

Our second objective was to evaluate the effect of reconstruction age on bee communities. Our results suggest that reconstruction bee communities differ along an age gradient, and not necessarily in ways that show convergence with remnant communities. Past studies do not show consistent convergence either. In California, bee communities on restorations remained distinct from remnants after six years (Williams 2011), whereas restoration bee community composition converged with that of remnants after only 2–3 years in Illinois (Griffin et al. 2017). Another study in Illinois reported that bee communities were most different from remnants for several years after reconstruction but became similar to remnants after 20 years (Tonietto et al. 2017).

We identified several bee taxa that were more abundant on either reconstructions or remnants and could hold potential as long-term monitoring subjects. *Ceratina* and *Hylaeus mesillae* are both relatively common twig or stem nesters that were more abundant on reconstructions. Interestingly, *Ceratina* abundance actually increased with reconstruction age, which is the opposite of what we would expect if reconstructions were converging with remnants, as past studies have shown (Foster et al. 2007, Watts et al. 2008, Carter and Blair 2012, Tonietto et al. 2017). The trends in *Ceratina* and *H. mesillae* abundance could result from amount of stems available for nesting, although without plant community data we are limited to speculation. There are few studies that directly link stem density or abundance with stem-nesting bees; however, prescribed fire, which eliminates stems and twigs, has been shown to negatively impact presence of stem-nesting bees (Eickwort et al. 1981, Cane et al. 2007, Cane and Neff 2011). *Ceratina* and *H. mesillae*, which are generalists, may be more successful nesting in the stems of plants that dominate early reconstructions, some of which are widespread exotics such as wild mustard (*Sinapis arvensis*) and dandelion (*Taraxacum officinale*) (McLachlan and Knispel 2005).

Some of the species associated with reconstructions were ground nesters. Like plant community composition, soil characteristics are potential factors in explaining the greater abundance of ground nesters such as *E. hamata* on reconstructions. One of the stronger indicators that soil affects reconstruction community composition in our study comes from the observed trend in *Dialictus* abundance. The genus *Lasioglossum*, and in particular its subgenus *Dialictus*, is associated with disturbed soil (Kim et al. 2006). *Dialictus* abundance decreased with reconstruction age. Recently reconstructed prairies have been recently disturbed and thus likely offer more nesting habitat for soil nesting bees such as *Dialictus*. The trend in *Dialictus* abundance was particularly strong at the North location. There were some soil-nesting taxa whose abundance increased with reconstruction age, such as *A. aurata* that may thrive in soil that has been disturbed less recently than taxa like *Dialictus* or *E. hamata*.

Species or functional groups closely associated with remnants have the potential to be good indicators of reconstruction success and our study identified two candidate species based on results of the multivariate models: *A. persimilis*, and *H. parallelus*. *H. parallelus* is a thought to be a prairie specialist because it has been found mainly on remnants in Missouri (Arduser 2016), and our results provide quantitative support for that hypothesis. Both *H. parallelus* and *A. persimilis* are ground nesting generalists, but *H. parallelus* is a large bee while *A. persimilis* is one of the smallest bees that we captured. Reconstruction soils, which are generally recently disturbed and usually altered by agricultural activity (Kindscher and Tieszen 1998), may lack the ideal soil nesting conditions for those species.

Our results indicated that bee communities on remnant and reconstructed prairies were distinct. The distinction was due to differences in relative abundances of bees, not necessarily the identity, because remnants and reconstructions shared almost all bee taxa. We identified several bee taxa that were more abundant on reconstructions or remnants and thus hold potential as long-term monitoring subjects. Trends in nesting group abundances emphasize the impacts of management and potential importance of soil characteristics and function on bee communities. More extensive and varied sampling is likely necessary to determine when the entire bee community on reconstructions reaches the target composition found on prairie remnants.

MANAGEMENT IMPLICATIONS

Prairie restoration and reconstruction efforts that are focused on achieving remnant-like bee communities would likely benefit from considering community measures other than species richness and diversity, as these may not differ between restorations and remnants. Restoration efforts aimed at providing habitat for prairie bees could consider incorporating nesting habitat availability, particularly soil and plant stems, because of its strong association with bee community composition.

ACKNOWLEDGEMENTS

We thank M. Arduser for assistance in identification. We thank two anonymous reviewers for comments on an earlier version of this manuscript. Rachel Blakey gave valuable statistical advice. The Missouri Department of Conservation's (MDC) Wildlife Division was the primary funder of this project, which was supervised by M. Alleger. Prairie Fork Charitable Endowment Trust and Prairie Biotic also provided grant support. The Missouri Cooperative Fish and Wildlife Research Unit is jointly sponsored by the MDC, University of Missouri, U.S. Fish and Wildlife Service, U.S. Geological Survey, and 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.

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Submitted 7 October 2019. Accepted 18 June 2020.
Associate Editor: Keith Geluso