RH: Bee responses to prairie restoration

Bee communities along a prairie restoration chronosequence: similar abundance and diversity, distinct composition

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Abstract

Recognition of the importance of bee conservation has grown in response to declines of managed honey bees and some wild bee species. Habitat loss has been implicated as a leading cause of declines, suggesting that ecological restoration is likely to play an increasing role in bee conservation efforts. In the Midwestern USA, restoration of tallgrass prairie has traditionally targeted plant community objectives without explicit consideration for bees. However, restoration of prairie vegetation is likely to provide ancillary benefits to bees through increased foraging and nesting resources. We investigated community assembly of bees across a chronosequence of restored eastern tallgrass prairies and compared patterns to those in control and reference habitats (old fields and prairie remnants, respectively). We collected bees for three years and measured diversity and abundance of in-bloom flowering plants, vegetation structure, ground cover, and surrounding land use as predictors of bee abundance and bee taxonomic and functional diversity. We found that site-level variables, but not site type or restoration age, were significant predictors of bee abundance (bloom diversity: $p = 0.004$, bare ground cover: $p = 0.02$) and bee diversity (bloom diversity: $p = 0.01$). There were significant correlations between overall composition of bee and blooming plant communities (mantel test: $p = 0.002$), and both plant and bee assemblages in restorations were intermediate between those of old fields and remnant prairies. Restorations exhibited high bee beta diversity, i.e., restored sites' bee assemblages were taxonomically and functionally differentiated from each other. This pattern was strong in younger restorations (< 20 years old), but absent from older restorations (> 20 years), suggesting restored prairie bee communities become more similar to one another and more similar to remnant prairie bee communities over time with the arrival of more species and functional groups of bees. Our results indicate that old fields, restorations, and remnants provide habitat for diverse and abundant bee communities, but continued restoration of old fields will help support and conserve bee communities more similar to reference bee communities characteristic of remnant prairies.

Introduction

Bees are the most effective pollinators in many systems, and the most important on a global scale (Winfree et al. 2011). In North America, declines of managed and feral European Honey Bees (*Apis mellifera*), and some wild species of North American bumble bees (*Bombus* spp.), have been documented in recent decades (Grixti et al. 2009, Cameron et al. 2011, Cornman et al. 2012). Despite the services they provide, the majority of wild bee species' current conservation status is largely unknown, as studies containing taxonomically detailed, long-term data have been few (National Research Council 2007). Available evidence suggests widespread persistence despite taxon-specific declines (Colla et al. 2012, Bartomeus et al. 2013), but more localized "extinction" of bee-plant interactions have been reported in the Midwestern USA (Burkle et al. 2013).

Concerted efforts to conserve wild bees are necessary given their biological diversity and importance as pollinators in natural and agricultural systems. Habitat loss, and associated reductions in foraging and nesting resources, is one of the main threats to wild bees (e.g., Scheper et al. 2014, Baude et al. 2016). To mitigate resource losses in human-dominated landscapes, such as agricultural fields, conservation approaches include enhancing foraging opportunities by planting native forbs in hedgerows, field margins, or fallow fields and increasing nesting opportunities by placing nesting boxes or reducing tilling (Scheper et al. 2013). These approaches have been effective in the decades-long agri-environment schemes implemented across Europe, though efforts have mainly been shown to support generalist species (Shepherd et al. 2003, Scheper et al. 2013) a set of species important for delivering pollination services but of lesser interest with respect to biodiversity conservation (Kleijn et al. 2015). Historically, bees, or pollinators in general, were only rarely the direct target of conservation activity in natural systems (Dicks et al. 2010, Menz et al. 2011), instead they were often the presumed beneficiaries of "umbrella" conservation or "field of dreams" restoration, i.e., it was

thought that if habitat structure was restored, bee and other species "will come" (Hilderbrand 2005). Over the past years, bee conservation has been more actively pursued by governments, non-government organizations and others (Stine et al. 2015).

Large-scale habitat restoration could increase the quantity and quality of native bee habitat by improving access to foraging resources and diverse nesting sites, as restoration of grassland and other vegetation often targets forbs (non-graminoid, herbaceous flowering plants) and results in greater habitat heterogeneity (Packard 1997, Apfelbaum and Haney 2012). Positive correlations between taxonomic diversity of forbs and bees in restored sites, such heathlands (Forup et al. 2008), roadside verges along highways (Hopwood 2008), and restored riparian forests (Williams 2011) and following habitat reclamation, i.e., restoration of habitats that have been completely destroyed or transformed, in former strip mines (Cusser and Goodell 2013) and landfills (Rutgers-Kelly and Richards 2013, Tarrant et al. 2013) suggest potential for synergistic goals in plant and pollinator-focused restoration efforts.

Ecological restoration likely confers net long-term benefits to bees, yet the restoration process itself could simultaneously act as a filter, influencing bee community composition by excluding disturbance-sensitive bees from colonizing restored sites. For example, bees are known to exhibit trait-mediated responses to disturbances such as burning or mowing. Williams et al. (2010) found that above-ground nesting bee species were approximately nine-times more sensitive to such disturbances than belowground-nesting species. In prairie restoration, mowing and return of historic fire regimes through prescribed burns are commonly employed; burning is also key for maintaining the quality of remnant prairies. Regular fire return is critical for reducing litter accumulation, preventing woody and invasive plant encroachment, and conserving prairie specialists (Hobbs and Huenneke 1992, Bowles and Jones 2013). However, this important component of the natural disturbance regime could act as a filter on bee assemblages. For example bee communities in fire-managed systems could be rich in individuals and species (reflecting increases in disturbance-tolerant species) but depauperate in the *types* of bees that are represented if certain traits are associated with greater sensitivity to fire (*sensu* Mouillot et al. 2013).

The few studies evaluating bee outcomes in restored natural sites have investigated bee abundance and species richness or other forms of taxonomic alpha diversity (Forup et al. 2008, Hopwood 2008, Bried and Dillon 2011, Golet et al. 2011, Hanula and Horn 2011, Fielder et al. 2012), sometimes including traits-based analyses or community composition (but see Exeler et al. 2009, Williams 2011). Though most studies have found positive effects of restoration on bees, that is not always the case, e.g., Russel et al. (2005) found deleterious effects of too much mowing, and filtering could be masked if bee communities are assessed only based on abundance and richness rather than composition and associated traits or functional groups (Golet et al. 2011, Williams 2011).

We evaluated the effects of restoration on native bee communities using a tallgrass prairie restoration chronosequence, with unmanaged old fields as controls and prairie remnants as reference sites, in the greater Chicago area of northeastern Illinois, USA. In this region, conversion of former agricultural fields (old fields) back to tallgrass prairie, the dominant pre-settlement ecosystem represents the majority of restoration work. We investigated bees' responses in terms of abundance, alpha diversity, community composition, and beta diversity, using both taxonomic and functional (trait-based) measures. We related bee community patterns to abundance, diversity, and composition of blooming plants, and other habitat characteristics, such as proportion of natural area in the surrounding landscape.

We predicted that bee assemblages in restorations would differ with site age, be intermediate in their characteristics between old fields and remnants, and reflect parallel trends with respect to flowering plant communities (Exeler et al. 2009, Williams 2011). Specifically, we hypothesized that a) blooming plant abundance, bee abundance, bee taxonomic alpha diversity and bee functional alpha diversity would increase with restoration age; b) restorations would be intermediate in these measures relative to control (lower) and reference sites (higher); and c) restorations would be intermediate between control and reference sites with respect to community taxonomic composition of blooming plants and taxonomic and functional composition of bees. Finally, because restorations are *de novo* habitats subject to management actions that can function as disturbances, we expected d) restored sites to host a limited subset of relatively tolerant and rapidly dispersing bees, which would be reflected in

restorations having lower taxonomic and functional beta diversity (differentiation among restored sites) than longer-established, less actively managed old fields and remnants.

Methods

Study system

In Illinois, less than 0.01% of land area covered historically by tallgrass prairie, the dominant pre-settlement ecosystem, remains intact (Iverson 1988). Prairie remnants tend to be small, isolated parcels of land that were never farmed or otherwise developed. The restoration of former agricultural fields to tallgrass prairie constitutes a large proportion of restoration efforts in the Chicago region (Chicago Region Biodiversity Council 1999).

We collected data from 18 sites, including former agricultural fields (hereafter referred to as old fields) that had never been restored that served as unmanaged controls ($n = 4$), botanically high-quality remnant prairies used as reference sites for restoration efforts ($n = 4$), and restorations in former agricultural fields that comprised a prairie-restoration chronosequence ranging from $3 - 37$ years of active management ($n = 10$) (Figure 1). Of the 10 restored prairies, 5 restorations were > 20 years old (younger restorations) and 5 restorations were < 20 years old (older restorations).

Prairie restorations were overseen by county forest preserve districts using broadly similar techniques that are representative of prairie restoration efforts in the region (Packard 1997). Early on in prairie restoration projects, aggressive management includes disturbances like whole-site tilling or disking, drilling for seed application, reintroduction of fire on an annual basis, and removal or breakage of drainage tiles (Packard 1997). These efforts often include heavy machinery. In contrast, older restorations and remnant prairies are also subject to management, but these tend to involve less generalized disturbance. For example, site managers perform localized physical and chemical targeting of woody and invasive plant species and will often burn in patches to provide refugia for plant and animal recolonization (Packard and Ross 1997).

Each of our study sites constituted a designated 1-ha within a larger preserve chosen by a county-level land manager as being representative of typical old fields, restored prairies, or high-quality reference sites under their jurisdiction. All of the study sites had substantial areas of adjacent natural land cover as potential sources of colonization by native bees. To account for differences in preserve size and surrounding land cover, we characterized the surrounding landscape of each site within a 1-km radius and quantified surrounding land cover to include in later analyses. We imported Google Earth version 7.1.2.2041 (Google Inc. 2009) images into ArcMap version 10.1 (ESRI 2010) and quantified land area for the following categories: natural and unmanaged areas, industrial parks, impermeable surfaces, turf grass, water, high- or low-density residential, sand beaches, golf courses, and agricultural fields.

Field sampling

We sampled sites three times between June and October in each of three study years: 2010, 2011 and 2012. In 2010, only 12 sites were sampled, after which 6 additional sites were added. We used a modified version of The Bee Inventory Plot to survey each site (LeBuhn et al. 2003). Each site visit took one day, and we rotated orders of visits between years. We arrived at a site by 8:00 AM to set up bee bowls—modified pan traps painted with UV-reflective fluorescent paint (yellow, blue, or white). We added soapy water to each bowl and left them out until collection at 3:00 PM. We used 30 bowls in each site, 10 of each color, with half of the bowls mounted on 1-m dowels to approximate the height of the prairie canopy in mid-summer. A bowl of the same color was placed at the base of each dowel. We also used aerial nets to collect bees we saw while walking haphazardly throughout the site for 60 minutes of collection effort (one person for 60 mins. or two people for 30 mins.) in the morning and again in the afternoon (for a total of 2 h of netting time per site per visit). We recorded weather data during each sampling event (sky condition, wind speed, and temperature) and cancelled data collection if mean wind speeds exceeded 3 mps for 30 s, if the sky was too overcast to see our shadow, or if the afternoon high temperature was below 15.5°C.

To quantify potential foraging and nesting resources, we sampled 35 1-m^2 quadrats in a grid within each site. Within each quadrat, we recorded identity and cover of every forb and woody plant in bloom (hereafter referred to as "blooming plants"), using an arcsine-square root cover class system (McCune et al. 2002): 0 = 0% cover, 1 = >0%, 2 = >1%, 3 = >5%, 4 = >25%, 5 = >50%, 6 = >75%, 7 = >95%, and 8 = >99%. We also recorded total cover of forbs (blooming or not), graminoids, woody plants, bare ground, herbaceous litter, fine and coarse woody debris, moss, and rocks using the same cover classes.

All bees were returned to a laboratory at the Chicago Botanic Garden, where they were washed, dried and pinned. Bee species were identified by J.S.A., and functional traits were assigned based on the literature and by J.S.A.

Statistical analyses

All statistical analyses were performed in R, version 3.2.3 (R Development Core Team 2010). We tested for differences in surrounding natural/unmanaged area as a function of restoration age and site type using linear regression and ANOVA, respectively. We quantified alpha diversity of blooming plants and bees at each site using the Simpson diversity index (Simpson 1949).

To compare bee abundance and alpha diversity by site type, we used linear mixed-effects (LME) models in the nlme package in R (Pinheiro et al. 2014). The saturated model included site type, blooming plant abundance, blooming plant diversity, the proportion of natural area within the surrounding 1-km radius, mean bare-ground cover, and year of data collection, with site as a random error term. Abundance data were square-root transformed to meet assumptions of normality. We tested for multicollinearity of model predictor variables; all variance inflation factors (VIF) were < 3, and VIF$^{(1/(2*d.f.))}$ were all < 2. We then used backward elimination and model comparisons by ANOVA to find the minimal adequate model (Crawley 2005). To test effects of restoration age on bee abundance and diversity, we included restored sites and old fields (as a restoration age of 0), but excluded remnant sites, and repeated LME models and model selection procedures.

To evaluate bee and blooming plant species composition, we used non-metric multidimensional scaling (NMDS) ordination in the vegan package in R (Oksanen et al. 2010). For these and subsequent multivariate analyses, we calculated relative abundance of blooming plants and bee species for each site × year combination, i.e., calculated means across the three June to October sampling events. Data were relativized by species and site maxima to account for high variation in abundance across sites and species, and NMDS was performed using three axes. To test for differences in blooming plant and bee composition by site type, we performed permutational multivariate analysis of variance (PERMANOVA, Anderson 2005). Analyses were based on Bray-Curtis dissimilarity with 10,000 permutations for each test and pair-wise comparisons performed between site types. Having found significant differences by PERMANOVA, we evaluated which species were most responsible for differentiating communities using similarity percentage (SIMPER) analysis in the vegan package, which evaluates the contribution of each species to Bray-Curtis dissimilarity between groups (site types). We conducted a Mantel test to determine whether blooming plant and bee community composition were significantly correlated.

To compare the trait space occupied by bee communities in different site types, we constructed a matrix of bee species' traits that included: native status (native or not), nest location (ground or aboveground), lecty (oligolectic or not), sociality (cleptoparasite, eusocial, or non-eucosial), size (mean male and female lengths from Mitchell (1960, 1962)), and flight phenology (spring, spring to summer, spring to fall, summer, summer to fall, and fall). Flight phenology was initially assigned based on collection dates and then verified by J.S.A. with consideration of additional data including regional specimen records. Next, we calculated community-weighted mean (CWM) trait values for each site. To prevent traits divided into multiple classes (e.g., flight phenology) from having undue influence on multivariate analyses, we used weights to standardize the relative importance of each variable, i.e., a binary trait like native status had a weight of 1.0 while length, which was subdivided into two classes, was weighted as 0.5 for male length and 0.5 for female length. These data were then used as the basis for a two-axis NMDS ordination. We again used

PERMANOVA to test for differences in community composition and evaluated which traits were most responsible for differentiating communities using SIMPER.

To characterize the multivariate trait space occupied by bee communities, we calculated functional dispersion (FDis) using the FD package in R (Laliberté and Legendre 2010, Laliberté et al. 2014). In multi-dimensional trait space, FDis is the mean distance of individual species to the centroid of all species. We started with the same species × traits matrix described above and calculated Gower distance among species (a measure of dissimilarity where the "distance" between two units is the sum of all variable-specific distances), with qualitative traits that divided into multiple classes down-weighted as described above. We performed principle coordinates analysis (PCoA) of Gower dissimilarity to assign multivariate trait scores to each species. The resulting PCoA axes were then used to calculate FDis values for each site, with weighting by species' relative abundances.

We followed the approach of Hardy and Senterre (2007) to evaluate taxonomic and functional differentiation (beta diversity) among sites of the same type using the spacodiR package in R (Eastman et al. 2011). This involved calculating metrics that partition diversity into within-site (alpha) vs. among-site (beta) components in a manner analogous to classic population genetic coefficients (e.g., F_{ST} and N_{ST}): I_{ST} is based solely on taxonomic composition; T_{ST} combines taxonomic and trait measures of composition; and U_{ST} and τ_{ST} are based solely on trait composition and use abundance-weighted and presence-absence data, respectively. Thus these metrics differ in the weight given to trait-based indicators of community composition (highest for U_{ST} and τ_{ST}) and rare species (highest for τ_{ST}).

Permutation tests were used to determine if sites of a given category were more differentiated from one another than expected by chance. Distributions of expected values for T_{st}, U_{st}, and τ_{st} were calculated using 1,000 permutations of null '1a' (Hardy 2008). This null model constrains permutations within groups of species of similar abundance so that interspecific differences in abundances of species do not confound detection of trait differences. This null model was appropriate

for our data given that high variation in abundance is typically observed among bee species, with many species seeming to be naturally rare (Williams et al. 2001).

Results

We collected 6,561 bees comprising 115 species and 32 genera (Supplemental Information). The amount of natural and unmanaged area in the surrounding landscape was not correlated with restoration age (d.f. = 108, $p = 0.17$) but did differ by site type ($F_{2, 143} = 54.96$, $p < 0.0001$). In general, remnants had less surrounding natural area than restorations or old fields. Likewise, restoration age was not a predictor of mean bare ground cover ($F_{1, 95} = 0.05$, $p = 0.81$), but bare ground cover different by site type ($F_{2, 15} = 4.03$, $p = 0.03$), with more bare ground available in remnants, followed by restorations.

Blooming plant abundance and diversity significantly differed by site type ($F_{2, 143} = 20.53$, $p < 0.0001$ and $F_{2, 143} = 10.16$, $p < 0.0001$, respectively). Overall, there was greater blooming plant abundance and diversity in remnants than restorations or old fields. Blooming plant abundance was similar by restoration age ($F_{1, 108} = 0.016$, $p = 0.89$), but blooming plant diversity differed ($F_{1, 108} = 7.15$, $p = 0.008$), with older restorations tending to have greater diversity of blooming plants.

Bee abundance

Bee abundance was similar across site types ($F_{2, 14} = 1.93$, $p = 0.18$, Figure 2a), but significantly correlated with blooming plant diversity ($F_{1, 126} = 8.53$, $p = 0.004$) and mean bare ground cover ($F_{1, 126} = 4.83$, $p = 0.02$). Likewise, bee abundance was similar across restoration age ($F_{1, 90} = 2.99$, $p = 0.08$), yet blooming plant diversity ($F_{1, 94} = 4.05$, $p = 0.04$) and mean bare ground cover ($F_{1, 94} = 3.66$, $p = 0.05$) were again significant predictors of bee abundance. We collected the most bees in a single day (332 individuals) from the youngest prairie restoration site (3 years old), which was covered in peak-blooming whorled milkweed (*Asclepias verticillata*), and featured the highest overall blooming plant cover and abundance observed during the study.

Bee taxonomic diversity and community composition

Bee taxonomic Simpson diversity did not significantly differ by site type ($F_{2, 14} = 1.59$, $p = 0.23$) or restoration age ($F_{1, 90} = 0.15$, $p = 0.69$, Figure 2b). Overall, blooming plant Simpson diversity was a significant predictor of bee diversity ($F_{91, 127} = 6.51$, $p = 0.01$), but not when remnants were excluded to analyze the effect of restoration age ($F_{1, 90} = 2.35$, $p = 0.12$). The two sites that had the highest bee taxonomic Simpson diversity were restorations, as was the site with the lowest.

Blooming plant community composition and taxonomic bee community composition differed by site type (PERMANOVA, d.f. = 2, $F = 2.53$, $p = 0.001$ and d.f. = 2, $F = 1.50$, $p = 0.002$, respectively; Figure 3a, b). Sites' bee and blooming plant community composition were correlated (Mantel test: r = 0.12, $p = 0.002$). We found 12 bee species to be responsible for a large proportion (60%) of the differentiation among site types (Table 1). Bee taxonomic beta diversity (I_{ST}) was greater among restorations than among old fields or remnants; this was driver by younger restorations (< 20 years), which were more differentiated from each other than were older restorations (> 20 years) (Figure 4).

Bee functional diversity and community composition

Bee alpha functional diversity (FDis) was similar across site types ($F_{2, 14} = 1.74$, $p = 0.21$, Figure 2c), and by restoration age ($F_{1, 90} = 1.42$, $p = 0.23$). Analyses based on community-weighted mean values of individual traits also showed little differences among site types, with the exception of bees active summer-to-fall (d.f. = 3, $F = 3.24$, $p = 0.03$, Figure 3), which were more likely to be found in older restorations than in remnants (Tukey's HSD, $p = 0.03$.).

Functional composition of bee communities differed by site type (PERMANOVA, d.f = 2, $F = 2.32$, $p = 0.03$, Figure 2c). Mean lengths of males and females explained most of the multivariate differences in trait composition by site type (SIMPER > 60%), with larger bees being more abundant in remnants (Table 1).

Functional-trait beta diversity was greater in restorations than in other site types (Figure 4). Only younger restorations (< 20 years old) exhibited beta diversity higher than expectations under null models; this was the case for a combined taxonomic/functional metric ($T_{ST} = 0.089$, 95% CI [0.043 - 0.082]) and an abundance-weighted functional metric ($U_{ST} = 0.034$, 95% CI [-0.021, 0.022]), but not a functional metric based on species' presence-absence ($\tau_{ST} = 0.011$, 95% CI [-0.005, 0.014]). In contrast, old fields, older restorations, and remnants were not significantly differentiated from one another (within site types) based on any metric.

Bee species of interest

We collected four individuals of *Bombus affinis*, a bumble bee in decline regionally (Colla and Packer 2008, Grixti et al. 2009) with at least one individual collected from all site types. Other bees of interest included six cleptoparasitic species as well as several specialist foraging species (Figure 5, *Supplemental Information*).

Discussion

Restored prairies support diverse and abundant bee assemblages, including cleptoparasitic species indicative of high-quality habitat (Sheffield et al. 2013) and the rusty patched bumble bee (*B. affinis*), a species of concern currently found in less than 10% of its former range (Cameron et al. 2011). Our findings highlight the value of prairie restoration for wild bee communities while also indicating that even unmanaged old fields constitute significant bee habitat. Though unrestored old fields contained similar abundances and diversity of bees, bee communities of restorations were more compositionally similar to remnants, increasingly structurally so with restoration age. Overall, regardless of habitat type, bee abundance, diversity and community composition tracked blooming plant diversity and composition, and bee abundance was predicted by availability of bare ground; increases in which are indirect effects of prairie restoration and management techniques such as burning and mowing.

Our study is one of the few to explore bee responses to overall prairie restoration as currently implemented (Petersen 1997) as opposed to bees responses to specific land-management techniques such as grazing (Sjödin 2007, Sjödin et al. 2008, Grundel et al. 2010, Redpath et al. 2010), mowing (Russell et al. 2005, Noordjik et al. 2009), burning (Potts et al. 2006, Moretti et al. 2009), invasive plant removal (Hanula and Horn 2011, Fiedler et al. 2012), or the effect of restoration in agricultural or grazing lands (Pywell et al. 2012, Scheper et al. 2013, M'Gonigle et al. 2015). By working within a chronosequence of tallgrass prairie restorations, our findings have direct relevance for land managers in the region interested in pollinator conservation as these techniques are applied in concert in natural lands.

We initially predicted disturbances associated with restoration (e.g., burning) would act as a filter, selecting for a non-random subset of bees able to colonize and persist in relatively young, disturbed habitats. We found the opposite—bee communities of restorations were more differentiated from one another than those of old fields or remnants, a pattern illuminated by high beta diversity in younger restorations undergoing the most active management (Figure 4). Our findings indicate that, early on, bees represented in restorations comprise a stochastic subset of local species. As restorations develop and more bee species colonize, initial differences in bee communities among sites diminish. As a result, older restorations (> 20 years) had bee communities structurally more similar to those of older control and reference habitats, and compositionally more similar to reference sites. These community-level changes could not have been detected based on analyses of bee abundance, richness, or alpha diversity—the metrics most commonly used to evaluate bee-community responses to habitat change and conservation efforts (Winfree 2009, Williams et al. 2010). Our findings highlight the importance of older restoration sites for native bee conservation. Those implementing large-scale prairie restoration should not expect to find the full suite of bees the site will eventually support within the first few years of restoration.

We predicted that bee diversity would increase with restoration age, with bee assemblages tracking "maturation" of the plant community over time. However, we did not find evidence of this pattern. It may be that our expectation that sites would exhibit a relatively linear developmental

trajectory was flawed (Zedler and Lindig-Cisneros 2000). Empirical data from restoration monitoring frequently shows more complex patterns of site development, with non-linearity, time lags, persistent alternative states, and other patterns countering the expectation of steady progress (Zedler and Callaway 1999, Suding et al. 2004).

In addition, our use of a chronosequence approach, i.e., space-for-time substitution, may be confounded by improvements in restoration practice. Restoration techniques rapidly evolve through sharing of professional experience (Apfelbaum and Haney 2012). Over the past 50+ years of tallgrass prairie restoration efforts, methods have improved (Packard and Mutel 1997). Thus, younger restorations in our dataset may have achieved better plant community results. Alternatively, older restorations may have reached an earlier peak of vegetation quality (e.g., based on floristic quality index (Swink and Wilhelm 1994)) and then declined under less active management. Regardless, our data are consistent with direct effects of blooming plant composition on bee communities.

Our results bolster the established evidence across multiple habitat types that sites with greater floral resources support greater bee diversity and abundance (e.g. Steffan-Dewenter 2001, Knop et al. 2006, Murray et al. 2009, Bried and Dillon 2011, Weiner et al. 2011). Our old field control sites, though of low quality from a botanical perspective, were not poor-quality habitat in terms of native bee abundance. Plants that were abundant in old fields, such as non-native clover species (*Trifolium* and *Melilotus* spp.) and relatively disturbance-tolerant Asteraceae (e.g., *Leucanthemum vulgare*, *Solidago canadensis*, *Erigeron strigosus*), provide ample foraging resources for many wild bee species. Collectively, these and other forbs provide blooming resources throughout spring, summer, and fall, providing overlapping bloom time recommended for native bee conservation (Shepherd et al. 2003). We second the recommendation of Harmon-Threatt and Hendrix (2014) to use design of restoration seed mixes as an opportunity to maximize support for native bee communities in prairies. We encourage restoration practitioners interested in native bee conservation to target forb diversity as a management goal, specifically to insure blooming resources are available from late-April – early-October while bees are actively foraging locally (Shepherd et al. 2003).

The majority of bees we collected were solitary soil-dwellers (*Supplemental Information*); females of these species require undisturbed bare ground to construct their nests (Michener 2000). It is not surprising then that sites with more bare ground and tended to have more bees. Sites with the greatest average bare ground cover were remnant and restored prairies, again reflecting reinstatement of the historic burn cycle, removing buildup of standing and matted dead vegetation and debris (Packard 1997). Though burning may constitute a negative disturbance to bees in some systems (Moretti et al. 2009, Williams et al. 2010), it is a critical component of the Midwestern prairie that appears to be positively associated with bee abundance. Compared to other systems, grasslands have relatively low fuel loads and short burn times (Beyers et al. 2005). Research on ground nesting bees' tolerance of fire indicates that many bee species are capable of withstanding belowground temperature profiles associated with grassland burning at the egg, larval, and adult stages (Pearson 1933, Cane and Neff 2011). Additionally, in our study region it is typical that after larger, more frequent (i.e., annual) burns during the first few years of restoration, prescribed burns are performed using a purposeful patchwork design, leaving a mosaic of burned and unburned patches (Packard 1997), which may provide refugia for above-ground nesting species. The landscape context of our study—high availability of natural land cover within bee flight ranges—further buffers potentially harmful effects of fire on bees. It was perhaps for these reasons that we did not find consistent differences among bee nesting types (Table 1, Figure 5). In the early years of a large-scale restoration project, when large burns are more frequent, we encourage site managers to consider pollinators habitat needs, making sure there is unburned natural area available within flight range (Greenleaf et al. 2007). If not available, plantings along edges of the burned patch could serve as a designed refuge. This area would be functionally similar to hedgerows in the agricultural matrix, restoration of which increases colonization and between-season persistence of wild bees (M'Gonigle et al. 2015).

The landscape context within which our sites happened to be located may have resulted in conservative estimates for bee diversity and abundance in remnants due to their lesser connectivity with natural areas, and old-field bee assemblages may have been boosted by greater connectivity to natural areas. Though natural area in the surrounding landscape was not a significant predictor of bee

abundance or diversity, remnant sites had significantly less surrounding natural area than restorations or old fields. Old fields and restorations tended to be part of larger preserves managed by county forest preserve districts, therefore, several old fields were within flight ranges of higher quality prairie habitat, and bees' needs may have been met in aggregate from a larger mosaic of land cover types. Regardless, seemingly degraded old fields provided valuable habitat support for a diverse suite of native bees.

Over 90% of bee species we recorded from each habitat type were native (Figure 3). Of the non-honeybee exotics, only *Andrena wilkella* was numerous, which occurred in roughly equal numbers across site types (*Supplemental information*). In our study, three above-ground nesting species (*Hylaeus affinis*, *Xylocopa virginica*, *and Ceratina dupla*) were responsible for much of the differentiation among site types (Table 1). Other species in similar functional groups also had variable relative abundances across site types, (e.g., species in the genera *Bombus*, *Lasioglossum*, and *Melissodes*) suggesting systematic filtering was not experienced by bees based on functional groups. Finally, though ongoing discovery of new state records is routine in much of North America, it is noteworthy for Illinois given that its fauna has long been studied in exceptional detail (e.g., Robertson 1929, Pearson 1933, Tonietto 2008, Grixti et al. 2009, Tonietto and Ascher 2009, Tonietto et al. 2011, Molumby and Przybylowicz 2012, Burkle et al. 2013, Ksiazek et al. 2014, Lowenstein et al. 2014).

Our findings show that tallgrass prairie restoration is an important component of wild bee conservation. From an analytical perspective, our findings implicate the importance of including community compositional metrics and other dimensions of biodiversity when analyzing effects of habitat restoration on native bees, as high levels of taxonomic diversity and frequency of singletons may mask effects. From a management perspective, our results highlight the importance and potential of prairie restoration in bee conservation strategy to support bee communities similar to those found in remnant prairie habitat.

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Supporting Information

Additional supporting information may be found in the online version of this article at http://onlinelibrary.wiley.com/doi/10.1002/eap.xxxx/suppinfo

Data Availability

Data associated with this paper have been deposited in a Dryad digital repository http://dx.doi.org/10.5061/dryad.34n83

Table 1. The relative abundances and cumulative contributions of species and traits responsible for

60% of the taxonomic and functional differentiation, respectively, of site types (SIMPER analysis).

Bee species or trait	Old fields	Restorations	Cumulative contribution %
Lasioglossum sp.	24.63	17.23	0.10
Augochlorella aurata	12.36	9.92	0.17
Bombus impatiens	8.36	10.11	0.24
Lasioglossum albipenne	12.81	4.57	0.31
Halictus ligatus	13.00	6.26	0.38
Hylaeus affinis	5.81	7.76	0.43
Lasioglossum anomalum	6.72	2.34	0.47
Bombus griseocollis	6.63	5.84	0.50
Ceratina dupla	3.63	3.80	0.53
Melissodes trinodis	2.54	4.57	0.31
Lasioglossum hitchensi	5.00	1.00	0.59
Ceratina calcarata	2.36	4.15	0.62
Mean male length	8.11	8.62	0.35
Mean female length	8.32	8.70	0.65

	Old fields	Remnants	Cumulative contribution %
Augochlorella aurata	12.36	25.50	0.11
Lasioglossum sp.	24.63	21.16	0.18
Bombus impatiens	8.36	11.91	0.24
Halictus ligatus	13.00	10.50	0.31
Lasioglossum albipenne	12.81	0.91	0.37
Hylaeus affinis	5.81	7.83	0.41
Melissodes trinodis	2.45	8.83	0.45
Ceratina dupla	3.63	4.58	0.53
Lasioglossum anomalum	6.72	3.91	0.56
Melissodes agilis	2.09	6.00	0.59
Melissodes bimaculata	0.72	5.25	0.62
Mean female length	8.32	8.97	0.34
Mean male length	8.11	8.58	0.66

	Restorations	Remnants	Cumulative contribution %
Augochlorella aurata	9.92	25.50	0.12
Lasioglossum sp.	17.23	21.16	0.20
Bombus impatiens	10.11	11.91	0.26
Halictus ligatus	6.26	10.50	0.31
Hylaeus affinis	7.76	7.83	0.04
Melissodes trinodis	4.57	8.83	0.42
Melissodes agilis	1.46	6.00	0.45
Ceratina dupla	3.80	7.75	0.49
Xylocopa virginica	2.23	4.58	0.52
Melissodes bimaculata	0.80	5.25	0.56
Bombus griseocollis	5.84	4.75	0.59
Lasioglossum anomalum	2.34	3.91	0.61
Mean female length	8.70	8.97	0.33
Mean male length	8.62	8.58	0.67

Figure 1. Map of field collection sites. The box in the larger map of the eastern United States outlines the region in northeastern Illinois where sites were located. The 18 sites consist of old fields (n=4), restored prairies of former agricultural fields (n=10) and remnant prairies (n=4).

Figure 2. Bee alpha diversity by site type and years restored for a) abundance, b) taxonomic diversity (Simpson index), and c) functional diversity (FDis). Each point represents one site × year combination and data for remnants are included for reference. Site type and restoration age were not significant predictors of taxonomic or functional diversity ($p > 0.05$).

Figure 3. Nonmetric multidimensional scaling (NMDS) ordinations of study sites. Site types significantly differed in terms of a) blooming plant composition (PERMANOVA: $p = 0.001$), b) bee species composition ($p = 0.002$), and c) bee trait composition ($p = 0.03$). Ellipses show the standard deviation around the centroid for each site type.

Figure 4. Bee taxonomic and functional beta diversity by site type. Restorations are split into younger (< 20 years, $n = 5$) and older sites (> 20 years, $n = 5$). Points represent observed means. Gray bands and dashed lines represent 95% confidence intervals and means, respectively, for null models. Coefficients represent differences among communities in taxonomic composition (I_{ST}), taxonomic and trait composition (T_{ST}), and abundance-weighted and presence-absence trait composition (U_{ST} and τ_{ST}).

Figure 5. Mean proportion of bee traits represented in each site type. Restorations are split into younger (< 20 years, $n = 5$) and older sites (> 20 years, $n = 5$). Points represent observed means and error bars are ± 1 SE. Significant differences between site types within each trait are annotated by different an asterisk. Y-axes vary per trait.

a

b

c

Old fields

Restored prairies

Remnant prairies