

RESEARCH ARTICLE

Wild bee community change over a 26-year chronosequence of restored tallgrass prairie

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Restoration efforts often focus on plants, but additionally require the establishment and long-term persistence of diverse groups of nontarget organisms, such as bees, for important ecosystem functions and meeting restoration goals. We investigated long-term patterns in the response of bees to habitat restoration by sampling bee communities along a 26-year chronosequence of restored tallgrass prairie in north-central Illinois, U.S.A. Specifically, we examined how bee communities changed over time since restoration in terms of (1) abundance and richness, (2) community composition, and (3) the two components of beta diversity, one-to-one species replacement, and changes in species richness. Bee abundance and raw richness increased with restoration age from the low level of the pre-restoration (agricultural) sites to the target level of the remnant prairie within the first 2–3 years after restoration, and these high levels were maintained throughout the entire restoration chronosequence. Bee community composition of the youngest restored sites differed from that of prairie remnants, but 5–7 years post-restoration the community composition of the restored prairie converged with that of remnants. Landscape context, particularly nearby wooded land, was found to affect abundance, rarefied richness, and community composition. Partitioning overall beta diversity between sites into species replacement and richness effects revealed that the main driver of community change over time was the gradual accumulation of species, rather than one-to-one species replacement. At the spatial and temporal scales we studied, we conclude that prairie restoration efforts targeting plants also successfully restore bee communities.

Key words: beta diversity, community composition, nontarget organisms, pollinators, prairie remnants

Implications for Practice

- Current prairie restoration efforts that target plant communities can also successfully restore diverse communities of nontarget bee pollinators, at least in interconnected prairie landscapes through which bees can easily disperse.
- Bee abundance and richness increase to near reference (prairie remnant) levels within the first few years of restoration. Thus, restored plants are likely to have access to pollinators in the early years of a restoration.
- Over the remainder of the time series, bee communities develop through the gradual accumulation of species rather than through species replacement.
- The prairie restoration chronosequence we studied was located in a large expanse of remnant and restored prairie sites, which may have facilitated the rapid colonization and establishment of bees in our study.

Introduction

The most commonly stated goal of ecological restoration projects is the reestablishment of a habitat or ecosystem to reference conditions (Hallett et al. 2013). Thus, the long-term success of such reestablishments depends on the successful restoration of a diverse set of species across a range of taxa (Jordan et al. 1990; Young 2000; Palmer et al. 2006). However,

in practice restoration efforts are rarely able to target multiple taxonomic groups, and often focus on reinstating vegetative structure and diversity, with the assumption that nontarget organisms such as arthropods, fungi, and birds colonize on their own (Dobson et al. 1997; Young 2000; Suding 2011; Williams 2011; Harmon-Threatt & Hendrix 2015). These nontarget organisms provide necessary ecological functions such as decomposition, seed dispersal, and pollination; thus their successful reestablishment is essential for the restoration of self-sustaining ecosystems (Young 2000). Despite this, up to two-thirds of all studied restorations lack information on the status of nontarget organisms (Ruiz-Jaen & Aide 2005) and the responses of many taxa to habitat restoration remain largely

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unknown (Dobson et al. 1997; Burkhalter et al. 2013). Better understanding of nontarget species in ecological restorations is needed to assess the true success of restoration efforts and improve management (Longcore 2003).

A second common goal of ecological restoration is long-term persistence of the reestablished community (Jordan et al. 1990; Palmer et al. 2006; Hallett et al. 2013). Thus time series studies are needed to measure changes in community composition and how it converges (or not) on target conditions (Sluis 2002; Brady & Noske 2010). Communities can change through shifts in relative abundances of species, as well as changes in species identity (Olsgard et al. 1998; Williams 2011). Similarly, changes in species identity over time can be shaped by two different processes: species replacement, in which a species present in one year is substituted by a different species in another year, and richness effects, in which the total number of species changes over time (Carvalho et al. 2012, 2013). These two processes are components of beta diversity, broadly defined as the degree of change in species composition along environmental gradients of space or time (Carvalho et al. 2012; Legendre 2014; Socolar et al. 2016). Though a number of studies have followed the development of restored plant communities over time series of 8–19 years (e.g. Baer et al. 2002; Sluis 2002; Camill et al. 2004; McLachlan & Knispel 2005; Carter & Blair 2012; Hansen & Gibson 2013), few studies have similarly explored communities of nontarget organisms over long time scales.

One group of nontarget organisms that may be essential to the long-term success of habitat restoration efforts are wild bees (Ambrose & Kevan 1990; Handel 1997; Dixon 2009; Menz et al. 2011), which provide a critical function as the primary pollinators of most terrestrial ecosystems (Neff & Simpson 1993). Previous studies have found that bees can colonize newly available habitat quickly (Steffan-Dewenter & Tschardt 2001; Potts et al. 2003; Exeler et al. 2009) and establish communities on restored habitat with similar richness and abundance to that of remnant habitat (Forup & Memmott 2005; Forup et al. 2007; Hopwood 2008; Exeler et al. 2009; Williams 2011; Tarrant et al. 2013), but that the bee communities of restored habitats may remain dissimilar in composition from those of remnants even 6 years after restoration (Williams 2011). Further, there is evidence that pollinator communities may exhibit significant species turnover in response to successional plant communities over long time frames, indicating that species replacement may play a strong role in bee compositional changes in unrestored systems (Albrecht et al. 2010). However, of the handful of studies that looked at bee communities in restorations, none has tracked the development of bee communities over time frames greater than 5 years, or explored the processes that govern changes in bee communities over time in restored habitat.

In this study, we used a space-for-time substitution to examine the long-term response of wild bee communities to restoration of a tallgrass prairie in north-central Illinois. Tallgrass prairie is one of the most threatened biomes in the world, and in Illinois only about 0.01% of the original undegraded tallgrass prairie remains (White 1978; Taft et al. 2006). We sampled bee communities along a 26-year chronosequence of restored habitat and prairie remnants to investigate the patterns of change

in three aspects of communities over time: (1) abundance and richness, (2) community composition, and (3) the two components of beta diversity, species replacement and richness effects. Based on previous studies of bees in restored habitat, we hypothesized that we would see rapid increases in bee abundance and richness, but that community composition of restorations would only converge on that of remnants over very long time frames. Further, we hypothesized that species replacement would be more important than richness effects in determining shifts in community composition, such that species identities would change with time since restoration, similar to successional change, but that total richness would not increase significantly after initial colonization.

Methods

Study Site

The Nachusa Grasslands (41°89'N, 89°34'W) is a large tallgrass prairie run and managed by The Nature Conservancy in north-central Illinois, and consists of over 1,900 ha of restored prairie plantings, prairie remnants, and other habitats such as wetlands and oak savanna (Jones & Cushman 2004; Hansen & Gibson 2013). As is characteristic of North American tallgrass prairies, the area is generally mesic with an average annual precipitation of 975 mm, and most precipitation occurs during the growing season (Steinauer & Collins 1996; Wodika et al. 2014). The tallgrass prairie vegetation at the Nachusa Grasslands is dominated by many perennial forbs including *Solidago rigida* and *Ratibida pinnata*, as well as C₄ grasses including big bluestem (*Andropogon gerardii*) and Indian grass (*Sorghastrum nutans*) (Steinauer & Collins 1996; Hansen & Gibson 2013; Goldblum et al. 2014). The prairie generally has flowers blooming from early April to October, with peak bloom occurring in July and August. Historically, most of the original tallgrass prairie in the area was converted to agricultural cropland by 1940, with only small, scattered prairie remnants in unfarmable areas remaining when The Nature Conservancy began acquiring land in 1986 (Hansen & Gibson 2013). Since then, The Nature Conservancy has created 115 interconnected restoration plantings and thus established a large tract of continuous tallgrass prairie habitat. Restoration plantings are seeded with mixes of native prairie plants obtained from remnant prairie patches, existing restoration plantings, and local nurseries. Restoration management has varied somewhat over time, but has generally included the removal of exotic plant species, yearly prescribed burning, and supplemental seeding as needed (Hansen & Gibson 2013). The surrounding landscape remains predominantly agricultural and planted with corn and soybean row crops.

Data Collection

We sampled pollinator communities between May and August 2014 from three agricultural fields (corn) representing the pre-restoration state, 12 restoration plantings ranging in age (time since seeding) from 2 to 26 years, and three remnant prairie sites that had never been converted to agriculture

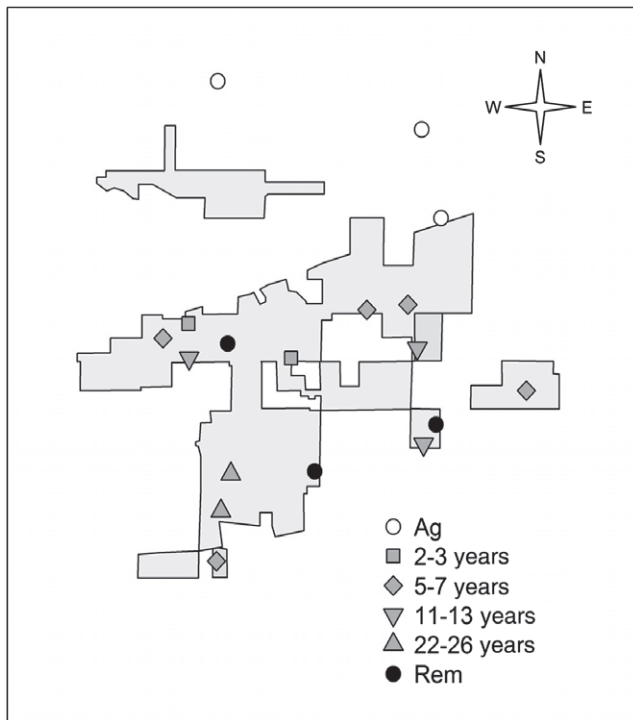


Figure 1. Map of study system showing the data collection transects in three agricultural fields, 12 restored prairies ranging in age from 2 to 26 years, and three remnant prairies. Light gray indicates Nachusa Grasslands land.

(Table S1, Supporting Information; Fig. 1). We selected restored sites that were rated as high-quality by the Nachusa Grasslands land managers (B. Kleiman 2014, Nachusa Grasslands Project Director, personal communication). All sites in our study were between 0.37 and 8.08 km from each other and distributed across the landscape such that sites of similar ages were not spatially clustered (Mantel $r = 0.09$, p value = 0.126). Restoration plantings and remnants were between 5.61 and 25.32 ha in size. Prior to analysis, we separated sites into six categorical groups: agricultural, restored for 2–3 years, restored for 5–7 years, restored for 11–13 years, restored for 22–26 years, and remnants (Table S1). We used QGIS (QGIS Development Team 2014) to determine land cover within a 500 m radius from the data collection transect at each site. This spatial scale minimized overlap among sites because most sites were at least 1 km apart, and a 500 m radius encompasses the typical foraging ranges of solitary bees (Gathmann & Tscharntke 2002; Zurbuchen et al. 2010). Within this radius, we determined percentage of the surrounding landscape devoted to the two dominant non-prairie landcover types: agriculture, which represented between 0 and 100% of the land within a 500 m radius of our sites, and woodlands, which represented between 0 and 50% (Table S1). Land cover was hand-digitized from aerial photos (41°89'N and 89°34'W, Google Earth, 9 September 2013) at the 1:7,000 scale.

We collected bees using two methods of passive sampling: pan traps and vane traps. Pan traps use bright coloration to

attract bees into shallow dishes filled with soapy water, in which they drown and can later be collected (Leong & Thorp 1999; Droege et al. 2010). For this study, we created pan trap arrays that could be raised or lowered to the height of the vegetation, the level at which bees usually forage; raised pan trap arrays have been shown to catch a more diverse bee community in grassland habitats (Geroff et al. 2014). Each array consisted of a clover-shaped arrangement of three 0.096 L soufflé cups (Solo Brand P325), one each painted fluorescent blue, fluorescent yellow, or white, and filled with soapy water (approximately 0.5% Dawn Blue dishwashing detergent in tap water) (Droege et al. 2010). Each array was given stability by a stand made of three polyvinyl chloride plastic (PVC) pipe couplings and was mounted on a T rebar fencepost (Fig. S1). The vane traps we used operate by attracting flying pollinators to a bright blue “vane” of plastic, which causes them to fall through a funnel into an attached bowl from which they cannot escape. Vane traps are known to be very effective at catching large bee species, which may not be well sampled by pan traps (Kimoto et al. 2012; Geroff et al. 2014). As with the pan traps, we attached the vane traps to T rebar fence posts and set them at the level of the vegetation.

Within each study site, we placed three pan trap arrays and one vane trap along a 30 m transect, positioned 60 m from an edge in which the site bordered non-prairie land (agricultural or wooded). During each round of sampling, we set up traps in the early morning of warm, sunny days, and collected the traps 24 hours later, with all transects studied in a single day to standardize weather conditions across restoration age classes. We collected insects from traps into ethanol and stored the specimens in labeled Whirl-Paks. We conducted eight rounds of sampling, with one sampling round roughly every 2 weeks, between May and August 2014. Specimens were processed and fully curated, and are deposited in R.W.’s Laboratory at Rutgers University in New Brunswick, NJ, U.S.A. All specimens were identified to the species level by J.G. based on taxonomic revisions (Mitchell 1960, 1962; LaBerge 1961, 1971, 1973, 1980, 1989; Ribble 1968; LaBerge & Bouseman 1970; Bouseman & LaBerge 1979; McGinley 1986; Gibbs 2010, 2011; Rehan & Sheffield 2011; Gibbs et al. 2013) and comparison to material deposited at Rutgers and Michigan State Universities.

Analysis

Patterns of Abundance and Richness. Using generalized linear mixed models (GLMMs), we looked at the effects of restoration age, site size, and surrounding land cover on three response variables: wild bee abundance, species richness, and richness rarefied to the lowest sample size among our sites to control for differences in abundance. For each of the three response variables, we created a set of models with site as a random effect and every combination of the following fixed effects: restoration age, site size, percentage wooded land within 500 m, and percentage agricultural land within 500 m. Sampling round was also included as a fixed effect in the abundance and raw richness models to account for the effect of timing in our eight sample periods, because bee communities are well known

to fluctuate throughout the growing season due to variation in bee phenology and population dynamics (Williams et al. 2001). Richness was lumped across all sample periods for the rarefied richness models in order to obtain sufficient sample sizes for rarefaction. The negative binomial distribution was used for abundance models and the Poisson distribution for richness models based on the overdispersion of the Pearson residuals, and the normal distribution was used for the rarefied richness models. We then used Akaike's information criterion corrected for small sample sizes (AICc) to determine the best models for each of the response variables, rejecting all models that had a ΔAICc score greater than 2 (Table S2). Overall significances of fixed effects were estimated for the best models using likelihood ratio tests. To determine the effects of each restoration age in our chosen models, we conducted global contrasts using the Tukey–Kramer method, which is robust to unequal group sizes (Kramer 1956). All analyses used in this study were conducted in the statistical program R, version 3.1.2 (R Core Team 2014). Richness was rarefied using the package *iNEXT* (Hsieh et al. 2016). Models were created using the package *lme4* (Bates et al. 2014) and the package *glmmADMB* (Skaug et al. 2015), and AICc model selection was conducted with *AICcmodavg* (Mazerolle 2015) and *MuMIn* (Barton 2015). Significances of fixed effects were estimated using the package *afex* (Singmann et al. 2015), and contrasts were conducted with the *glht* function in the package *multcomp* (Hothorn et al. 2008).

Bee Community Composition. To determine whether spatial distance between study sites significantly affected community dissimilarity, we used a Mantel test to look at the correlation between distance and community dissimilarity. We calculated dissimilarity using the Bray–Curtis metric, which compares sites using the identity and relative abundance of species. We excluded agricultural sites from this analysis because they were positioned outside the main restoration area and contained very different bee communities from those of restored and remnant sites, and thus would obscure the relationship between distance and community dissimilarity between the rest of our sites.

To visualize differences in community composition between sites, we used nonmetric multidimensional scaling (NMDS), which ordines sites in bee community space. For compositional analyses, we combined bees collected from all sample periods across the entire season per site. We used a permutational multivariate analysis of variance (PERMANOVA) test (Anderson 2001) with SS Type II for unequal group sizes to determine whether remnants and restorations of different ages and surrounding land cover differed significantly in their bee community composition. For these overall PERMANOVA tests, we again excluded agricultural sites because they would obscure the patterns of community composition due to their highly dissimilar bee communities and landscape context. To determine if bee community composition in restorations converged with remnants over time, we conducted contrasts in which we used pairwise PERMANOVAs to separately compare the agricultural sites and sites in each restoration age category to the remnants. We also repeated the above analyses (NMDS plotting, overall PERMANOVA, and pairwise PERMANOVAs) using

Bray–Curtis dissimilarity based on species presence–absence only (also known as the Sorensen index). A comparison of these two sets of results indicates the importance of relative abundance in driving the changes in community composition over time. Species that were only represented by a single individual over the course of the summer were excluded from all compositional analyses. Ordination and PERMANOVAs were conducted using the R package *vegan* (Oksanen et al. 2015).

Components of Beta Diversity. We decomposed the changes in bee community composition over time, as measured above, into their two components, species replacement and richness effects. To accomplish this, we used the beta diversity partitioning analysis described by Carvalho et al. (2012). This analysis is based on presence–absence data and uses the Jaccard index of dissimilarity rather than presence–absence Bray–Curtis, which has been shown to overestimate species replacement and underestimate richness effects (Carvalho et al. 2012). Total Jaccard dissimilarity (β_{tot}) is defined for each pairwise comparison of restorations of different ages as the proportion of species that are not shared between the two sites:

$$\beta_{\text{tot}} = (b + c) / (a + b + c),$$

where a is the number of species found in both sites, b is the number of species unique to the first site, and c is the number of species unique to the second site. The species replacement component (β_{repl}) is defined as:

$$\beta_{\text{repl}} = 2(\min(bc) / (a + b + c)),$$

in which the number of substitutions between sites is the minimum number of unique species $\min(b,c)$, multiplied by two because substitution involves two species. Finally, richness effects (β_{rich}) can be defined as:

$$\beta_{\text{rich}} = |b - c| / (a + b + c),$$

in which $|b - c|$ represents absolute difference in richness between sites. Thus, β_{repl} and β_{rich} are additive and sum to β_{tot} . A more detailed explanation of these equations can be found in Carvalho et al. (2012).

We used each of these three measures to create pairwise dissimilarity matrices, which we plotted against a matrix of pairwise age differences between our sites using code from Ensing (2011). We only used restored sites in this analysis, because agricultural sites and remnants did not have definable ages. For each of our three plots (β_{tot} , β_{repl} , and β_{rich} vs. age difference), we fitted least square regressions and examined the y -intercept and slope of each. These regressions were used to compare intercepts and slopes in a heuristic way only, because the plotted points were calculated from all possible pairwise comparisons within the dataset and thus not independent from each other. To statistically assess the significance of the relationship between dissimilarity and age difference for each of the three dissimilarity metrics, we used a Mantel test (Lichstein 2006; Carvalho et al. 2012) in the package *ecodist* (Goslee & Urban 2007).

Results

Over the course of our study, we collected a total of 2,097 specimens of 85 bee species in 23 different genera (Table S3). In total, 102 individuals of 21 species were collected from the three agricultural sites, 1,429 individuals of 76 species collected from the 13 restored prairie sites, and 566 individuals of 51 species were collected from the three remnant prairie sites.

Patterns of Abundance and Richness

Both abundance and raw richness of bee communities showed a strong response to restoration age (Figs. 2A, 2B, & S2). The model chosen by AICc model selection for abundance included restoration age ($\chi^2 = 27.38$; $p < 0.0001$) and percentage of wooded land ($\chi^2 = 6.67$; $p = 0.01$), while the two equivalent models chosen for raw richness both included restoration age ($\chi^2 = 37.31$, $p < 0.0001$; $\chi^2 = 36.43$, $p < 0.0001$), with one model also including percentage of wooded land ($\chi^2 = 1.07$; $p = 0.30$) (Table S2). As expected, sampling round was highly significant for both abundance ($\chi^2 = 61.97$; $p < 0.0001$) and raw richness ($\chi^2 = 22.79$, $p = 0.002$; $\chi^2 = 22.95$, $p = 0.002$), likely due to the phenology of bee communities throughout the growing season. However, when richness across the season was rarefied to the lowest sample size among our sites (28 individuals), we found that neither of the two equivalent best models included restoration age. Both rarefied richness models included percentage of wooded land ($\chi^2 = 5.84$, $p = 0.02$; $\chi^2 = 11.15$, $p = 0.0008$), and one model included percentage of agricultural land ($\chi^2 = 3.38$, $p = 0.07$), indicating that rarefied richness primarily responded to the landscape context of our sites (Fig. 2D).

Tukey–Kramer contrasts between restoration ages in our abundance and raw richness models revealed that restorations and remnant prairie sites had significantly higher abundance and raw richness than agricultural sites (Fig. 2A & 2B). Further, restored sites achieved the target state of the prairie remnants within 2–3 years and maintained levels of abundance and richness that were not significantly different from that of remnants throughout the entire restoration chronosequence, though the abundance showed an increasing trend over the restoration chronosequence with remnant sites having the highest richness. Bee abundance and richness were very variable within all age groups, likely contributing to the lack of statistically significant differences in abundance between age groups. The oldest restored sites of 22–26 years showed higher richness than that of the remnants, although the difference was nonsignificant. We did not conduct contrasts between restoration ages for rarefied richness (Fig. 2C), because restoration age was not included in the best models.

Bee Community Composition

Using a Mantel test, we found no significant correlation between bee community composition and the distance between study sites (Mantel $r = 0.069$, $p = 0.538$).

In PERMANOVA analysis using relative species abundances, we found that composition was significantly affected by restoration age ($R^2 = 0.33$, $p = 0.045$), and the percentage of wooded

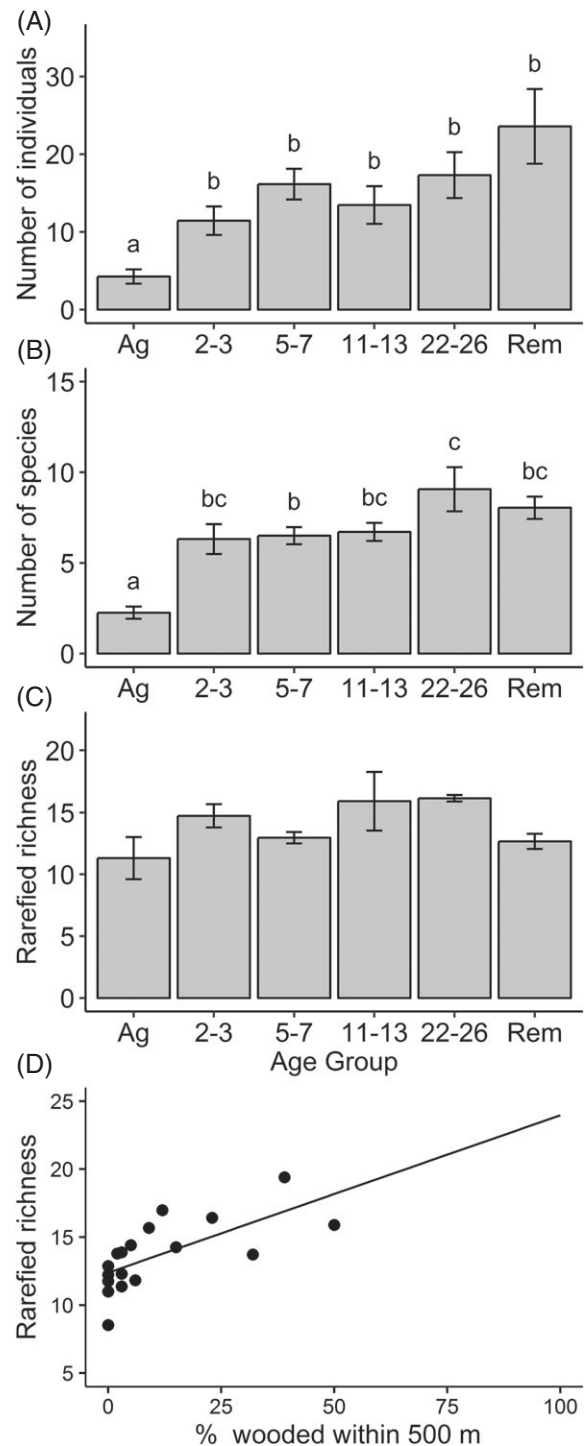


Figure 2. Arithmetic means (\pm SE) of three indices, bee (A) abundance, (B) richness, and (C) rarefied richness by sample size. Means for (A) and (B) are calculated with counts per sample date, but (C) rarefied richness represents cumulative values over the course of the entire season. Letters indicate significant differences calculated using Tukey–Kramer contrasts on the top models in Table S2. (D) Rarefied richness plotted against percentage wooded land within 500 m, with a trend line predicted from a model with only percentage wooded included as a fixed effect (rarefied richness Model 2).

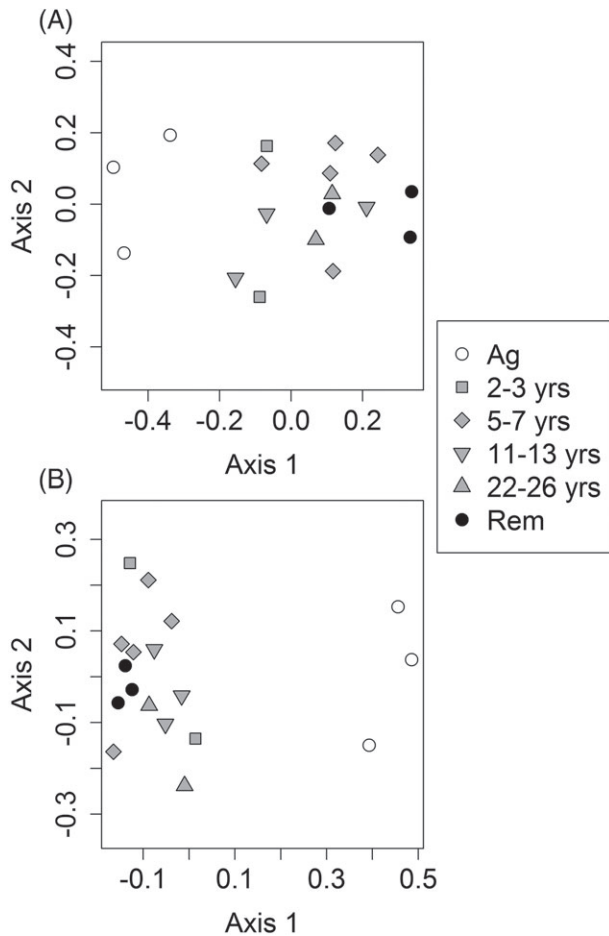


Figure 3. Nonmetric multidimensional scaling ordination plots for bee communities with ordinations based on Bray–Curtis distances, which include relative abundances (A, stress = 0.13) and presence–absence Bray–Curtis distances (B, stress = 0.14). The switch in x-axis orientation between A and B is arbitrary.

land within a 500-m radius ($R^2 = 0.11$, $p = 0.033$), but not by the percentage of agricultural land ($R^2 = 0.10$, $p = 0.084$). Pairwise PERMANOVAs found that bee communities of remnants were significantly different from those in agricultural sites ($R^2 = 0.20$, $p = 0.001$) and the youngest restored sites of 2–3 years ($R^2 = 0.10$, $p = 0.037$), but that communities of remnants were not significantly different from those of restored sites of older ages (5–7 years, $R^2 = 0.06$, $p = 0.391$; 11–13 years, $R^2 = 0.07$, $p = 0.279$; and 22–26 years, $R^2 = 0.04$, $p = 0.762$). Bray–Curtis dissimilarity between sites, with 0 representing identical species composition and 1 representing total dissimilarity, ranged from 0.38 to 0.85 (mean = 0.59 ± 0.11) indicating high variation between sites. Visual analysis in NMDS was consistent with PERMANOVAs (Fig. 3A).

When PERMANOVAs were repeated using presence–absence data (Sorensen instead of Bray–Curtis index), community composition no longer differed significantly in response to any of our predictor variables. Specifically, overall dissimilarity between sites was not significantly affected by restoration age ($R^2 = 0.28$, $p = 0.518$), percentage of wooded land within

Table 1. Results of linear least squares regression of three dissimilarity metrics, Jaccard dissimilarity (β_{tot}), species replacement (β_{repl}), and richness effects (β_{rich}), against the age difference between sites. As data points represent all pairwise comparisons between sites and thus are not independent, significance was evaluated using Mantel tests, which are robust to nonindependence.

| Dissimilarity Metric | Intercept | Slope | Mantel's r | p Value |
|-----------------------|-----------|--------|------------|---------|
| β_{tot} | 0.523 | 0.003 | 0.23 | 0.146 |
| β_{repl} | 0.430 | −0.004 | −0.30 | 0.040 |
| β_{rich} | 0.095 | 0.006 | 0.45 | 0.009 |

500 m ($R^2 = 0.11$, $p = 0.164$), or percentage of agricultural land within 500 m ($R^2 = 0.1$, $p = 0.201$). Pairwise PERMANOVAs showed that while the community composition of remnants remained significantly different from those of agricultural sites ($R^2 = 0.21$, $p = 0.004$), communities of remnants were not significantly different from those of restored sites of any age class (2–3 years, $R^2 = 0.06$, $p = 0.388$; 5–7 years, $R^2 = 0.05$, $p = 0.544$; 11–13 years, $R^2 = 0.04$, $p = 0.75$; 22–26 years, $R^2 = 0.05$, $p = 0.607$) (Fig. 3B). Sorensen dissimilarity between sites ranged from 0.21 to 0.70 (mean = 0.43 ± 0.11).

Components of Beta Diversity

Partitioning differences in community composition into its components, species replacement (β_{repl}) and richness effects (β_{rich}), revealed that both showed clear directional effects over time. However, the slopes were in opposite directions with a β_{repl} slope of −0.004 and a β_{rich} slope of 0.006, meaning that dissimilarity between two sites due to species replacement decreased with increasing age difference between the sites, while dissimilarity due to richness effects increased (Table 1; Fig. 4). The two terms therefore largely canceled each other, such that the slope of overall dissimilarity (β_{tot}) was only 0.003, leading to little change in dissimilarity overall. Replacement was the stronger effect, and its higher intercept indicated that differences in species composition between sites of similar ages were strongly driven by species replacement, such that even sites of similar ages were highly variable in terms of species composition. In contrast, the compositional differences between the oldest and youngest sites were driven roughly equally by species replacement and richness effects.

Discussion

We found that prairie restorations that exclusively targeted plants also successfully and quickly restored a critical nontarget functional group, native bee pollinators. These results confirm and extend the findings of previous studies in different habitat types, which found that restored habitats can harbor bee abundance and richness similar to that of remnant habitat (Forup & Memmott 2005; Forup et al. 2007; Hopwood 2008; Exeler et al. 2009; Williams 2011; Tarrant et al. 2013). These other studies compared the bee communities of restored habitat to remnants at single points in time ranging from 1 to 14 years, but ours is the first to our knowledge that has followed the development of

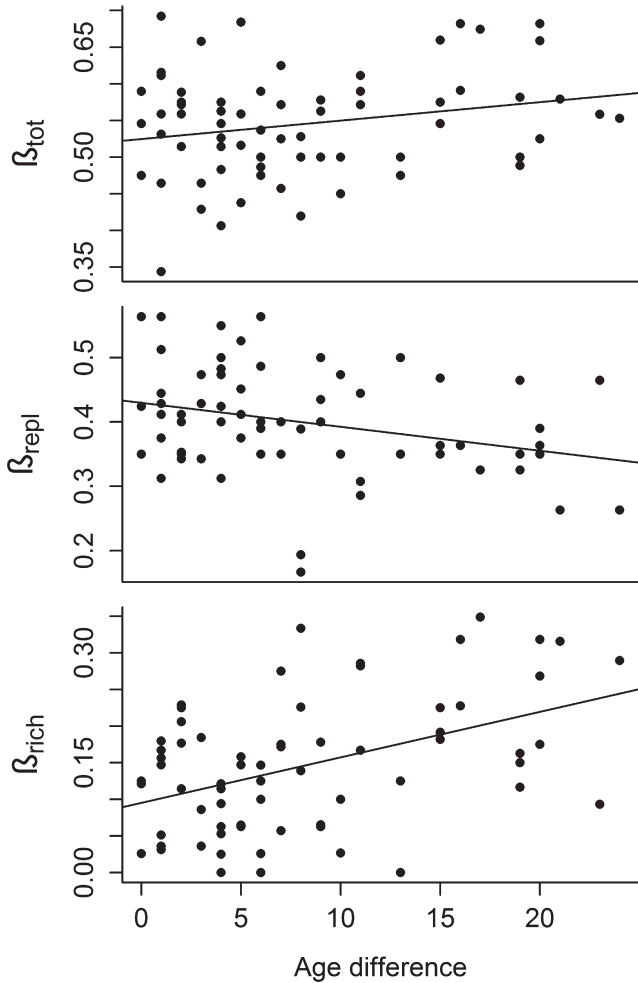


Figure 4. Pairwise dissimilarity of bee communities plotted against pairwise dissimilarity in age for total Jaccard dissimilarity (β_{cc}), as well as partitioned into the two components of total dissimilarity, species replacement (β_{-3}), and richness effects (β_{rich}). Each point represents a pair of sites, plotted by dissimilarity in composition against difference in age, ranging from 0 years for sites of identical age to a maximum age difference of 24 years between the youngest and oldest sites. Regression lines are shown only for visual interpretation and measurement of slope and intercept. Because the data points represent all pairwise comparisons between sites, they are not independent, and our statistical tests were based on a Mantel test which accounts for this nonindependence (Table 1).

bee communities over long time frames (>5 years). Our results are encouraging to restoration practitioners as they suggest that pollinators sufficiently reestablish diverse communities under current restoration management and maintain them over time. However, because the rapid establishment of bee communities we observed was likely influenced by the large, highly interconnected prairie landscape of our study, our findings may be most applicable to other large restoration projects.

Patterns of Abundance and Richness

Fitting with our predictions that bees would rapidly colonize restored prairie habitat, we found that bee abundance and raw

richness reached comparable levels to remnant prairie patches within the first 2–3 years after initial restoration, though abundance showed a nonsignificant upward trend over the chronosequence. Such rapid colonization by bees has previously been seen in restored sand dune habitat, where bee abundance and richness reached that of remnant habitat within a single year after restoration (Exeler et al. 2009), as well as in unrestored successional plant communities, in which bees reached peak abundance and richness within 2 years (Steffan-Dewenter & Tscharntke 2001; Potts et al. 2003). The rapid restoration we observed for bee pollinators is particularly important because bees provide an essential ecosystem service to plants through pollination, and bee abundance and richness are good predictors of pollination function across multiple plant species (Garibaldi et al. 2013; Kleijn et al. 2015). In the context of a prairie restoration, rapid colonization by bees may mean that prairie plants have access to pollinators even in the early years of a restoration project.

When we controlled for abundance in our richness models by rarefying raw richness to the lowest sample size among our sites, we found that landscape factors rather than age group were responsible for differences in richness among sites. Specifically, the percent of nearby wooded land had a strong effect on rarefied richness. Wooded land was also included in the top model for abundance, indicating that wooded land can add both individuals and species to a restoration site. This is likely due to the fact that forested areas provide additional and different nesting resources compared to other habitats (Grundel et al. 2010; Wray et al. 2014), thus allowing the establishment of bees that otherwise would not be found in the prairie. Further, wooded areas are often low in floral resources for bees due to their vegetation structure (Winfree et al. 2007), meaning that bees that nest in the forest may predominantly forage in nearby prairie habitats that contain a greater density of flowers. The importance of landscape context to rarefied richness differs from our finding that restoration age determines raw richness. We present both analyses because our finding that older restored prairie sites reach the raw richness of remnant prairie is important to prairie conservation and restoration practitioners, despite being confounded by abundance.

Previous studies of restored tallgrass prairie plant communities have found that initial peaks in plant species richness after restoration are often followed by gradual declines in richness over time (Sluis 2002; Camill et al. 2004; McLachlan & Knispel 2005; but see Carter & Blair 2012). In contrast, the bee communities in our study did not show any significant decreases in either raw richness or rarefied richness over the 26-year chronosequence. We did not collect plant data and therefore cannot examine the patterns of change in plant communities at our sites, but a study by Hansen and Gibson (2013) on plant diversity in our same study system (the Nachusa Grasslands) found that following initial restoration, plant richness decreased over the course of 19 years due to the replacement of rare forbs by dominant grasses. Pollinator diversity has been shown to be highly correlated with the diversity of flowering plants (Steffan-Dewenter & Tscharntke 2001; Potts et al. 2003; Albrecht et al. 2010), so we would expect pollinator richness to

follow the trajectory of the plant community. We do not know why the bees in our study followed a different trajectory than that of the plant communities, but we speculate that it is because most bee species captured at our sites were generalist foragers, and thus may be responding more strongly to total floral abundance than to the number of plant species. Bee species richness may also rely on other factors, such as nesting habitat and bee dispersal ability, that are little related to plant richness.

Bee Community Composition

Contrary to our expectations, the composition of bee communities at restorations rapidly converged on the composition of remnants over time. In terms of relative species abundances, only the bee communities of agricultural sites and the youngest restorations of 2–3 years were significantly different from those of remnants, and when only bee species identity was considered, only the agricultural (corn field) sites clustered independently. These results differ from those of Williams (2011), who found that the species composition of bee communities in restored riparian habitat remained dissimilar from those in remnants even after 6 years since restoration. In addition, several studies of invertebrate communities other than pollinators have reported that though abundance and species diversity increased significantly within the first few years after restoration, communities in restorations remained quite different in composition from those in remnants after more than 10 years (Davis et al. 2003; Nichols & Nichols 2003; Wassenaar et al. 2005; Grimbacher & Catterall 2007).

Our findings may have been influenced by the landscape context of our study, in which restored sites and remnants were located within a larger expanse of highly interconnected prairie habitat. Many studied restorations are located in highly fragmented landscapes and may not be connected to large expanses of similar habitat. Isolation from source habitat is a major barrier to colonization of restorations by nontarget organisms, and highly isolated restorations are often colonized more slowly or by a different set of species than those found in remnant habitat (Armitage & Fong 2004; Watts et al. 2008; Cusser & Goodell 2013). In spatially isolated restorations, nontarget organisms may disperse from areas other than the target habitat, such as the surrounding agricultural matrix, and thus contribute to longstanding differences in nontarget community composition between remnants and restorations (Williams 2011). In the case of bees, restorations that have greater spatial separation from remnant habitat may also expect greater degrees of filtering (Cusser & Goodell 2013) due to the strong positive relationship between body size and dispersal distance (Greenleaf et al. 2007). This means that only larger bees with strong dispersal ability may be able to reach isolated restorations from distant remnant habitats. In our study, high connectivity between prairie patches and a lack of correlation between bee community composition and spatial distance between sites further supports the conclusion that bees were able to easily disperse through the landscape, which may not be the case for small or isolated prairie restorations. Our results are therefore most applicable to large preserves, which may become increasingly common;

there is an ongoing effort among restoration managers to make larger, more connected restored areas that can support and protect greater biodiversity (J. Walk 2016, The Nature Conservancy, IL, personal communication).

We found that the surrounding habitat type also had a significant effect on bee community composition, such that the relative abundances of species also responded to the wooded area within 500 m of the sites. As discussed above, this is likely because patches of forest can support a different set of species than grassland habitats (Brosi et al. 2007; Grundel et al. 2010; Wray et al. 2014), and thus impact the suite of species found foraging in nearby prairie patches.

It is important to note that community composition was quite variable overall, even between sites of similar ages. Given that sites only shared between 31 and 79% of their species and only 15–62% of their relative species abundances, even sites that clustered together in our analysis had highly variable sets of species. Further, pairwise site dissimilarity did not correlate with the distance between sites, meaning that bees in restored sites were not simply originating from the sites directly around them. Other studies have found that bee communities are variable across even local-spatial scales, which can make the detection of trends in community composition difficult (see Williams et al. 2001 for a review of bee community variability). For example, in a study which compared restored heathland sites to nearby remnant habitat, Forup et al. (2007) found high variability in bee communities even between spatially adjacent sites. Variability may therefore be due to specific characteristics of the sites and landscape context, but can also be influenced by chance events and natural population fluctuations (Williams et al. 2001; Forup et al. 2007).

Components of Beta Diversity

Though we did not find evidence for significant change in overall community composition across the restoration time series, decomposing the overall beta diversity into its two components of species replacement and richness effects revealed that both had directional effects that were not distinguishable from measurements of community dissimilarity alone (Carvalho et al. 2012, 2013). In particular, we found that species replacement became less important and richness effects more important with increasing differences in site ages, such that the opposing slopes largely canceled each other out and led to little change in overall beta diversity. Therefore, though community dissimilarity between sites of similar ages was due mainly to species replacement, dissimilarity between the youngest and oldest restored sites was due to species replacement and richness effects in almost equal parts.

The increasing importance of richness effects over the time series indicates that pairs of sites with higher dissimilarity in age were also more dissimilar in terms of the numbers of species they contained. Our beta diversity partitioning analysis did not indicate directionality of richness changes, but based on the non-significant upward trend found in our earlier analysis of richness over time, we conclude that this relationship was driven by higher richness in older restored sites compared to younger

sites. Changes in site community composition over time thus likely progressed through the gradual accumulation of species. Further, the accompanying decrease in species replacement with increasing age difference was likely due to increased nestedness, such that to some degree younger sites contained a nested subset of species found in the older sites. Though compositional changes in bee communities over time series have been largely unexplored, Albrecht et al. (2010) provided a comparable study by looking at pollinator communities over a 130-year chronosequence of glacier foreland undergoing natural plant succession. They found that pollinator richness increased over time, but that unlike our findings, there was also evidence of distinct successional stages in pollinator communities in response to strong turnover of the plant communities. The trajectories of richness effects and species replacement in our study suggest that this dissimilarity in results is not a product of differences in time scale, but rather differences in the study systems. As restorations, the sites in our study were heavily seeded and managed for rapid recovery of the plant community, and thus may have missed the early successional plant communities that might attract a different set of pollinators.

In summary, although our previous results showed that the community composition of restored sites rapidly converged on that of remnants, partitioning overall beta diversity into its two components revealed that restored sites in fact continued to change across the time series in ways that were not otherwise observable. Our results indicate that diverse communities of bees colonize restored prairie within 2–3 years after restoration and persist over the long term with slight increases in species richness. These results illustrate the value of examining communities over long time frames, in order to detect trends that cannot be determined from restoration studies set at a single point in time.

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Supporting Information

The following information may be found in the online version of this article:

Table S1. Description of sites, divided into six age groups including agricultural sites, restored sites lumped by age (time since year planted), and remnants.

Table S2. Fixed effects included in the best (A) abundance, (B) richness, and (C) rarefied richness models selected by AICc model selection, with all models with $\Delta AICc$ within two of the top model counted as equivalent.

Table S3. List of species and total number of specimens collected across all 18 sites.

Figure S1. Picture of elevated pan trap array.

Figure S2. Raw data, displayed as arithmetic means (\pm SE) of two indices, bee (A) abundance and (B) richness as a function of restoration age group.

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