

WILD BEE COMMUNITY CHANGE OVER A 26-YEAR
CHRONOSEQUENCE OF RESTORED TALLGRASS PRAIRIE

By

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ABSTRACT OF THE THESIS

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Restorations require diverse communities of non-target organisms for important ecosystem functions and meeting restoration goals, yet little is known about how communities of non-target organisms such as wild bees develop over time. We sampled bee communities along a 26 year chronosequence of restored tallgrass prairie in north-central Illinois to evaluate whether bee abundance, richness, and community composition in restored habitat converges on that of remnant prairie, and to study the processes that shape community development over time. Restoration increased bee abundance and richness 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 maintained high abundance and richness throughout the entire restoration chronosequence. Bee richness peaked at the oldest restored sites of 22-26 yrs, in which it surpassed that of even prairie remnants. Bee community composition of the youngest restored sites differed from that of remnants in terms of relative species abundances, but the community composition of prairie restorations converged on remnants by 5-7 years after restoration. Changes in

community composition of restorations over the chronosequence progressed predominantly through the gradual accumulation of species, rather than species replacement. We conclude that tallgrass prairie restoration is successful in restoring bee communities when examined over long timeframes.

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INTRODUCTION

Successful restoration of degraded habitats to functional, self-sustaining ecosystems requires reestablishing a diverse set of species across a range of taxa (Young 2000, Jordan et al. 1999, Palmer et al. 2006). However, restoration efforts are rarely able to target entire ecological communities, and often focus on reinstating plants and vegetative structure with the assumption that non-target organisms such as arthropods, fungi, and birds will colonize on their own (Dobson et al. 1997, Young 2000, Williams 2011, Harmon-Threatt and Hendrix 2014). Many non-target organisms provide necessary ecological functions such as decomposition, seed dispersal, and pollination; thus successful reestablishment of non-target populations is important to restoration goals of achieving pre-degradation diversity (Young 2000). Despite this, up to two-thirds of all studied restorations lack information on the status of non-target organisms (Ruiz-Jaen and Aide 2005), and the responses of many taxa to habitat restoration remain largely unknown (Dobson et al. 1997, Burkhalter et al. 2013). A better understanding of non-target communities in ecological restorations is important for assessing restoration efforts and improving management (Longcore 2003).

Long-term study of non-target communities can provide significant insight into restoration success and aid in the understanding of how communities develop in restored habitat. The goal of most ecological restorations is to create a self-sustaining system in which the abundance, richness and community composition of restored habitat converges on that of remnant habitat and persists over time (Jordan et al. 1999, Palmer et al. 2006). Long-term study can be used to elucidate the trajectories of colonization and community

change, and reveal whether communities of restorations become increasingly similar to those of remnant habitat over time (Sluis 2002, Brady and Noske 2010). In addition, long-term study can allow a greater understanding of the processes that shape community composition over time. For example, community composition may experience shifts in the relative abundances of species, as well as changes in the identity of species present in the habitat (Olsgard et al. 1997, Williams 2011). Further, changes in species identity along a temporal gradient can be shaped by two different processes: species replacement, in which one species is substituted by a different species, and richness effects, in which species are gained or lost over time (Carvalho et al. 2012, Carvalho et al. 2013). The relative importance of these processes may be very important in structuring communities over increasing restoration age (Carvalho et al. 2012, Carvalho et al. 2013). Though many studies have followed the development of restored plant communities (e.g. Sluis 2002, Baer et al. 2002, Camill et al. 2004, Willand et al. 2013), little is known about how the communities of non-target taxa change over time in restorations.

Pollinators are one group of non-target organisms that provide a necessary function to restored ecosystems through their role in plant reproduction (Handel 1997, Dixon 2009). With over 87% of all flowering plant species dependent on animal-mediated pollination for reproduction (Ollerton et al. 2011), most terrestrial ecosystems require pollinators for natural plant composition and structure. Wild bees are the most important pollinators worldwide of most terrestrial ecosystems (Neff and Simpson 1993). Ecological restorations may therefore require the establishment of diverse bee communities in order to meet restoration goals.

Few studies have examined the response of wild bees to ecological restoration, and there remains a significant gap in knowledge regarding long-term patterns of bee community development in restored habitat. Some previous studies have shown that wild bees may be able to rapidly colonize restored habitat (Exceler et al. 2009). Further, restorations habitats can harbor bee abundance and richness similar to that of undegraded remnant habitat (Forrup and Memmot 2005, Forrup et al. 2007, Exceler et al. 2009, Williams 2011, Fiedler et al. 2012, Tarrant et al. 2013). Bee communities of restored habitat may differ significantly from those of remnant habitat in terms of species composition, containing sets of species distinct from those in undegraded habitat (Forrup et al. 2008, Exceler et al. 2009, Williams 2011). In addition, the interaction networks of restored habitat are variable, with some restored habitats with similar complexity to remnants (Forrup and Memmot 2005, Williams 2011), and others with significantly lower complexity than remnants (Forrup and Memmot 2008). Almost all previous studies have compared the bee communities of restored habitat to remnants at a single point in time, rather than following community development over many years. It remains unknown whether bee diversity and composition is maintained over longer timeframes, and how bee community composition develops in restored habitat.

In this study, we examined wild bee communities along a chronosequence of restored habitat and remnants at the Nachusa Grasslands, a large tallgrass prairie restoration run by the Nature Conservancy 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 looked at how abundance, richness, and community composition of bee communities change over

time in a prairie restoration and explored the processes that drive community development. We asked the following questions: 1) Does bee richness and abundance change with time since prairie restoration, and do the communities of restorations ever reach the richness and abundance of those in prairie remnants? 2) Does the bee community composition of restored prairie converge on that of remnants over time, and what processes shape bee community development?

METHODS

Study site

Nachusa Grasslands, a tallgrass prairie preserve owned and managed by the Nature Conservancy in north-central Illinois (41°89' N, 89°34' W), comprises over 1,900 ha of restored prairie plantings, prairie remnants, and other habitats such as wetlands and oak savanna (Jones and Cushman 2004, Hansen and Gibson 2013, Willand et al. 2013).

Historically, most of the original tallgrass prairie in the area was converted to agricultural cropland by 1940, with only small, scattered prairie remnants on unfarmable land remaining when the Nature Conservancy began acquiring land in 1986 (Hansen and Gibson 2013). Since then, the Nature Conservancy has created 115 restoration plantings with the goal of establishing a large tract of continuous tallgrass prairie habitat for the protection of prairie biodiversity and preservation of the once-common Illinois prairie ecosystem. 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 and Gibson 2013, Willand et al. 2013). The surrounding landscape remains predominantly agricultural and planted with corn and soybean row-crops.

Data collection

To study patterns of pollinator abundance and diversity along a chronosequence of restoration plantings, we sampled pollinator communities between April and August

2014 from 3 agricultural fields (corn) representing the pre-restoration state, 13 restoration plantings ranging in age (time since seeding) from 2 to 26 years, and 3 remnant prairie sites that had never been converted to agriculture (Table 1 and Figure 1). Sites ranged in size from about 2.55 to 19 hectares, and were distributed across the landscape such that sites of similar ages were not significantly clustered (Mantel $r=0.10$, p value= 0.107). Prior to analysis, we separated sites into six categorical age groups: agricultural, restored for 2-3 yrs, restored for 5-7 yrs, restored for 11-13 yrs, restored for 22-26 yrs, and remnants (Table 1). We used Q-GIS (QGIS Development Team 2014) to determine the percentage of the surrounding landscape devoted to the two dominant non prairie landcover types, agricultural and wooded, within a 500 m radius from the sample transect at each site. Land cover was hand digitized from aerial photos (41°89' N and 89°34' W, Google Earth, September 9, 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 (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. Each array consisted of a clover-shaped arrangement of three 3.25 ounce soufflé cups (Solo Brand P325), one each of fluorescent blue, yellow, or white, and filled with soapy water (~0.5 % Dawn Blue dishwashing detergent in tap water) (Droege et al. 2010). Each array was given stability by a stand made of 3 PVC pipe couplings and was mounted on a T rebar fencepost. Vane traps 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 (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.

We placed three pan traps and one vane trap at each study site, arranged along a 30 meter transect and positioned 60 meters from a non-prairie edge (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 sample sites visited in a single day to standardize sampling conditions. We collected insects from traps into ethanol and stored the specimens in labeled Whirl-Paks. We conducted 8 sampling rounds between April and August 2014. Specimens were processed and fully curated, and are deposited in Rachael Winfree's laboratory at Rutgers University in New Brunswick, NJ. All specimens were identified to the species level by Jason Gibbs, a professional taxonomist at Michigan State University.

Analysis

Patterns of Abundance and Richness

We looked at the effects of restoration age, sample date, and surrounding land cover on two response variables, wild bee abundance and richness, using generalized linear mixed models (GLMMs). For each of the two response variables, we created a set of models with site as a random effect and every combination of the following fixed effects: restoration age, sample date, and percentage agricultural and wooded land within 500 m. The negative binomial distribution was used for abundance models and the Poisson distribution for richness models based on the overdispersion of the Pearson residuals. We

then used AICc model selection (Akaike 1973) to determine the best models for the each of the response variables (Table 2). 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). Models were created using package lme4 (Bates et al. 2014) and package glmmADMB (Skaug et al. 2015), and AICc model selection was conducted with AICcmodavg (Mazerolle 2015) and MuMIn (Barton 2015). Effect sizes were estimated using package afex (Singmann et al. 2015), and contrasts were conducted with the glht function in package multcomp (Hothorn et al. 2008).

Bee Community Composition

To visualize differences in community composition between sites, we used nonmetric multidimensional scaling (NMDS), which plots the dissimilarities between community compositions of sites into two dimensional space. We first calculated dissimilarity using the Bray-Curtis metric, which compares sites using relative abundance of species. We used a PERMANOVA test (Anderson 2001) with SS Type II for unequal group sizes to statistically determine whether dissimilarity between restoration ages was significant, as well as the effect of percentage agricultural and wooded within a 500 m radius. To determine whether bee community composition in restored sites became more similar to those in remnants over time, we conducted pairwise PERMANOVAs between the remnants and each restoration age of restored sites. To determine the effect of species identity on structuring community composition over time, we removed relative

abundances by converting data to presence-absence and repeating NMDS plotting, PERMANOVA tests and contrasts. All sites were used in these analyses, including agricultural, restored, and remnant sites. All ordination and PERMANOVAs were conducted using package *vegan* (Oksanen et al. 2015).

We next examined patterns of change in species composition across the temporal gradient of restoration age by separating overall dissimilarity between sites into its two components, species replacement and richness effects. To do this, we conducted beta diversity partitioning analysis with the methods outlined by Carvalho et al. 2012. Beta diversity, broadly defined as the degree of change in species composition along environmental gradients, is shaped by two different processes: species replacement, in which a species at one site is substituted by a different species in another site, and richness effects, in which one site contains a subset of the species of the other site (Carvalho et al. 2012, Legendre 2014). Species replacement and richness effects can occur along gradients in different proportions, often in opposing directions, such that species replacement and richness effects may change along the gradient even if overall beta diversity remains stable. Compositional changes can be separated into their replacement and richness components by calculating presence-absence dissimilarity with metrics that take only these components of beta diversity into account. Three measures are used to calculate presence-absence dissimilarity between two sites: (a) the number of species found in both sites, (b) the number of species unique to the first site, and (c) the number of species unique to the second site. Using this notation, we calculated overall beta diversity using the Jaccard dissimilarity metric (β_{cc}), as in Carvalho et al. 2012. Jaccard dissimilarity between sites can be defined as $\beta_{cc} = (b+c)/a+b+c$, in which total

compositional difference ($b+c$) is given as a proportion of the total number of species ($a+b+c$). Species replacement (β_{-3}) can be defined as $\beta_{-3}=2 (\min(b,c)/a+b+c)$, 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. Richness effects (β_{rich}) can be defined as $\beta_{rich}= |b-c|/a+b+c$, in which $|b-c|$ represents absolute difference in richness between sites (a schematic explanation of these equations can be found in Carvalho et al. 2012). We used each of these three measures of beta diversity to create pairwise presence-absence dissimilarity matrices, which we plotted against a matrix of pairwise age differences between our sites. 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_{cc} , β_{-3} , 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 data set 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 (Carvalho et al. 2012, Lichstein 2006) in package *ecodist* (Goslee and Urban 2007).

RESULTS

Over the course of our study, we collected a total of 2,254 specimens of 87 bee species in 24 different genera. In total, 103 bee individuals of 22 species were collected from the 3 agricultural sites, 1582 individuals of 77 species collected from the 13 restored prairie sites, and 569 individuals of 53 species collected from the 3 remnant prairie sites.

Patterns of abundance and richness

Both abundance and richness of bee communities showed a strong response to restoration age (Figure 2). The model chosen by AIC model selection for abundance included restoration age, date of sampling and percentage wooded, while the model chosen for richness included only restoration age and date of sampling. Likelihood ratio tests of generalized linear mixed models reported a highly significant effect of restoration age and date of sampling on both bee abundance and richness (Table 2). Percentage wooded had a significant effect on bee abundance, but was not included in the best richness model.

Tukey-Kramer contrasts between restoration ages revealed that restorations and remnant prairie sites had significantly higher abundance and richness than agricultural sites (Figure 2). Further, restored sites maintained levels of abundance and richness similar to that of remnants throughout the entire restoration chronosequence. The oldest restored sites of 22-26 yrs showed higher richness even than the remnants, although the difference was non-significant.

Bee community composition

Bee community composition including relative species abundances was significantly affected by restoration age ($R^2=0.31$, $p=0.020$), but not by landscape cover within a 500 m radius, including both percentage agricultural ($R^2=0.04$, $p=0.496$) and percentage wooded ($R^2=0.06$, $p=0.118$). Further, pairwise PERMANOVAs revealed that bee communities of remnants were significantly different from those in agricultural sites ($R^2=0.19$, $p=0.001$) and the youngest restored sites of 2-3 yrs ($R^2=0.10$, $p=0.026$), but that communities of remnants were not significantly different from those of restored sites of older ages (5-7 yrs ($R^2=0.05$, $p=0.453$), 11-13 yrs ($R^2=0.06$, $p=0.244$), or 22-26 yrs ($R^2=0.04$, $p=0.706$)).

When NMDS and PERMANOVAs were repeated using presence-absence data to look at species identities, overall dissimilarity between sites was not significantly affected by restoration age ($R^2=0.26$, $p=0.144$), percentage agricultural within 500 m ($R^2=0.04$, $p=0.373$), or percentage wooded within 500 m ($R^2=0.05$, $p=0.250$). Pairwise PERMANOVAs showed that while the community composition of remnants remained significantly different from those of agricultural sites ($R^2=0.19$, $p=0.002$), communities of remnants were not significantly different from those of restored sites of 2-3 yrs ($R^2=0.06$, $p=0.366$), 5-7 yrs ($R^2=0.04$, $p=0.641$), 11-13 yrs ($R^2=0.04$, $p=0.707$), or 22-26 yrs ($R^2=0.05$, $p=0.561$). Overall dissimilarity between restoration sites therefore did not change significantly over time in terms of species identities.

Fitting with the results of the presence-absence NMDS and PERMANOVA analysis, the plot of overall beta diversity (β_{cc}) against the age difference between sites showed that dissimilarity increased only slightly with increasing difference in site ages

(Figure 3 and Table 3). However, partitioning overall beta diversity into its two separate components, species replacement ($\beta_{\text{.3}}$) and richness effects (β_{rich}), revealed that species replacement and richness effects showed strong and opposing trends over time.

Dissimilarity due to species replacement decreased with increasing age difference, while richness effects increased. The high y intercept of $\beta_{\text{.3}}$ and low y intercept of β_{rich} indicate that species replacement was much more important to structuring differences between sites of similar age than richness differences. However, richness effects became increasingly important and species replacement less important with increasing age difference between sites, indicating that community change over time operates primarily through the gradual accumulation of new species. The lack of strong change over time in overall beta diversity is due to the fact that the opposing trends of species replacement and richness largely cancel out.

DISCUSSION

Using a chronosequence to examine how bee communities of tallgrass prairie restorations develop over 26 years, we found that ecological restoration of tallgrass prairie plant communities successfully increased both bee abundance and richness to the target level of the remnant prairie. Bee abundance and richness reached similar levels to remnant sites even within the first 2-3 years after initial restoration, indicating rapid colonization of restored prairie habitat by bee communities. Similar rates of bee colonization have been previously found in both restored (Exeler et al. 2009) and unrestored successional communities (Steffan-Dewenter and Tschardtke 2001, Potts et al. 2003, Alanen et al. 2011). In several studies of unrestored habitat, bees reached peak abundance and richness only 1-2 years after the habitat first became available (Steffan-Dewenter and Tschardtke 2001, Potts et al. 2003, Alanen et al. 2011), indicating that bees are able to quickly occupy and establish populations in newly created favorable habitat. Bees, which are highly mobile (Greenleaf et al. 2007), may be able to colonize restored habitat much more quickly than some other non-target taxa such as birds and moths, which have been shown to take many years to reach the abundance and richness of remnants (Brady and Noske 2010, Summerville et al. 2007). Our results support the assumption that non-target organisms will occupy newly restored habitat unaided, and indicates that plants may have access to pollinators even within the early years of a restoration.

In addition to rapidly colonizing restored habitat, bee communities maintained high abundance and richness throughout the entire restoration chronosequence. These results are especially intriguing because they contrast strongly with the trend often found

for restored prairie plant communities, in which initial peaks in plant richness within the first few years after restoration are followed by gradual declines in richness over time due to replacement of rare plants by dominant species (Sluis 2002, Camill et al. 2004, McLachlan and Knipspel 2005, Hansen and Gibson 2013, Willand et al. 2013). This indicates that non-target organisms may be responding to restoration differently than the actual targets of restoration, the plant communities. Therefore, restorations that do not successfully maintain high plant diversity may still be successful in restoring diverse communities of non-target organisms. The fact that bees may respond differently to restoration than plants also demonstrate the importance of evaluating both target and non-target organisms when assessing restoration success.

We found some evidence that bee richness increased over increasing restoration age, with the oldest restored sites (22-26 yrs) containing even higher bee richness than that of prairie remnants. This increase in richness may be due to changes in habitat structure or resources over time (Menz et al. 2011), or the gradual accumulation of bee species that colonize slowly due to rarity or low dispersal rates. Higher richness in old restorations than in remnants may reflect differences in management history; remnants were historically positioned on marginal land and developed naturally, while restorations were seeded with a highly diverse native plant mixes (Hansen and Gibson 2013, Willand et al. 2013). Understanding these trends more clearly requires future analysis of the vegetative cover and species identity of flowering plants across prairie sites.

Like bee abundance and richness, bee community composition in restored prairie habitat converged on that of remnants over time, but took longer to do so. The bee communities of agricultural sites and the youngest restorations of 2-3 yrs were

significantly different from those of remnants, but restorations of 5 yrs and older were compositionally similar to remnants. Further, the youngest restored sites of 2-3 yrs were only significantly different from remnants in terms of relative abundances of species, rather than species identity. This indicates that although bee relative abundance distributions change over time, there is no distinct set of species associated with restorations of any age compared to remnant prairie. Separating changes in community composition into its two components, species replacement and richness effects, further showed that richness effects rather than species replacement were important in structuring compositional differences between sites of different ages. Therefore, change over time primarily operates through the addition of rare species rather than a turnover in bee community composition. Previous studies of successional changes in unrestored glacier foreland have found some evidence for turnover in pollinator communities, likely due to long term successional changes in associated plant communities (Albrecht et al. 2010). In contrast, our results indicate a lack of successional stages in bee communities of restored prairie.

The landscape context of our study, in which restored sites and remnants were located within a larger expanse of prairie, has important implications for the interpretation of our results. Because the restorations and remnants in our study were part of a large tract of tallgrass prairie preserve located within a highly agricultural landscape, the majority of bee species likely originated from the remnant prairies. In contrast, other restoration projects in which patches of restored habitat are more isolated from remnants may contain bee communities primarily composed of species originating from other surrounding habitats. This could explain differences in our results and those of

another study, which found that restored habitat contained sets of bee species distinct from those found in remnants (Williams 2011). The distance of our sites to other restored prairie may also impact rates of colonization and the identity of colonizing bee species. Distance between restored habitat and remnants can affect the bee diversity of new restorations (Cusser and Goodell 2013), and some bee species are able to disperse greater distances than other species based on body size and more easily colonize new habitats (Greenleaf et al. 2007). Therefore, studies of restorations that have greater spatial separation from remnant habitat may expect greater degrees of filtering than found in our study (Cusser and Goodell 2013), and thus potentially slower rates of colonization and community development. Further, close distance between our sites and surrounding prairie means that the bees captured at our sites may nest elsewhere due to the high mobility of many bee species. Our study thus examines bee presence and foraging location rather than providing an absolute measure of nesting populations at study sites. Bee presence is an important measure because it reveals where foraging bees go in response to habitat characteristics and resources (Bennet et al. 2014), and also where bees are providing pollination function. Studying restorations in landscape contexts such as ours, in which restored areas are spatially connected, may be especially valuable because restorations are often established at the landscape scale rather than in isolated patches (Hobbs and Norton 1996).

The reestablishment of wild bees in restored habitat may be important to overall restoration success due to their functional role as pollinators (Handel 1997, Dixon 2009). Our results indicate that diverse communities of bees colonize restored prairie by 2-3 years after restoration and persist over at least 26 years. Restored plant communities

therefore have access to pollinators during both the initial years of restoration as well as over the long term. These results may be especially encouraging to restoration practitioners, as they suggest that functional non-target organisms sufficiently reestablish diverse communities under current restoration management.

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Table 1. Description of sites used in the study. Sites were divided into six groups for analysis, with the restored sites categorized according to the age of the restoration. % ag and % wooded describes the percentage of land within a 500m radius occupied by agricultural land or forest cover.

Age Group	Site name	Year planted	% ag	% wooded
Agricultural	Corn 1	NA	100.00	0
	Corn 2	NA	93.57	4.99
	Corn 3	NA	94.17	0
Restored for 2-3 yrs	2012/HPN	2012	14.50	1.51
	103/L	2011	6.74	8.77
Restored for 5-7 yrs	94/SB	2009	50.38	0
	85/CCKWest	2008	25.16	0
	86/HPW	2008	11.22	31.73
	66/CCKEast	2007	32.33	0
	73/FC	2007	23.66	14.59
	81/TC	2007	42.63	2.35
Restored for 11-13 yrs	57/TC	2003	52.66	3.01
	50/HPE	2001	0	38.84
	49/SF	2001	20.09	11.89
Restored for 22-26 yrs	37/WH	1992	5.82	49.53
	24/25/MU	1988	0	23.13
Remnant	HLREM	NA	4.56	3.25
	MUREM	NA	14.09	6.32
	TCREM	NA	54.32	3.13

Table 2. Results of generalized linear mixed models. The best models selected by AICc model selection for a) abundance and b) richness are shown with their degrees of freedom, AICc values and fixed effects. X^2 and p values of fixed effects were obtained through the use of likelihood ratio tests.

	d.f.	AICc	Restoration age	Date	% ag	% wood
(a) Abundance						
Best model	16	1033.29	+	+		+
X^2			28.85	67.58		6.05
p value			<0.0001	<0.0001		0.01
(b) Richness						
Best model	14	750.07	+	+		
X^2			39.90	24.13		
p value			<0.0001	0.001		

Table 3. Results of beta diversity partitioning analysis for restored sites. Intercept and slope are shown for linear least squares regressions of overall Jaccard beta diversity (β_{cc}), species replacement (β_{-3}), and richness effects (β_{rich}) by age difference between sites. Mantel tests were used to test the significance of the relationship between community dissimilarity and age difference, and Mantel's r and significance are reported.

Dissimilarity metric	Intercept	Slope	Mantel's r	p value
β_{cc}	0.535	0.0037	0.3549	0.007
β_{-3}	0.465	-0.0063	-0.4785	0.001
β_{rich}	0.07	0.0099	0.6479	0.002

Figure 1. Map of sample transects at the Nachusa Grasslands in north-central Illinois.

Land owned by The Nature Conservancy is shown in light grey, and Illinois Department of Natural Resources land is pictured in dark grey. For this study, we used 3 agricultural fields (corn), 13 restored prairies ranging in age from 2-26 yrs, and 3 remnant prairies.

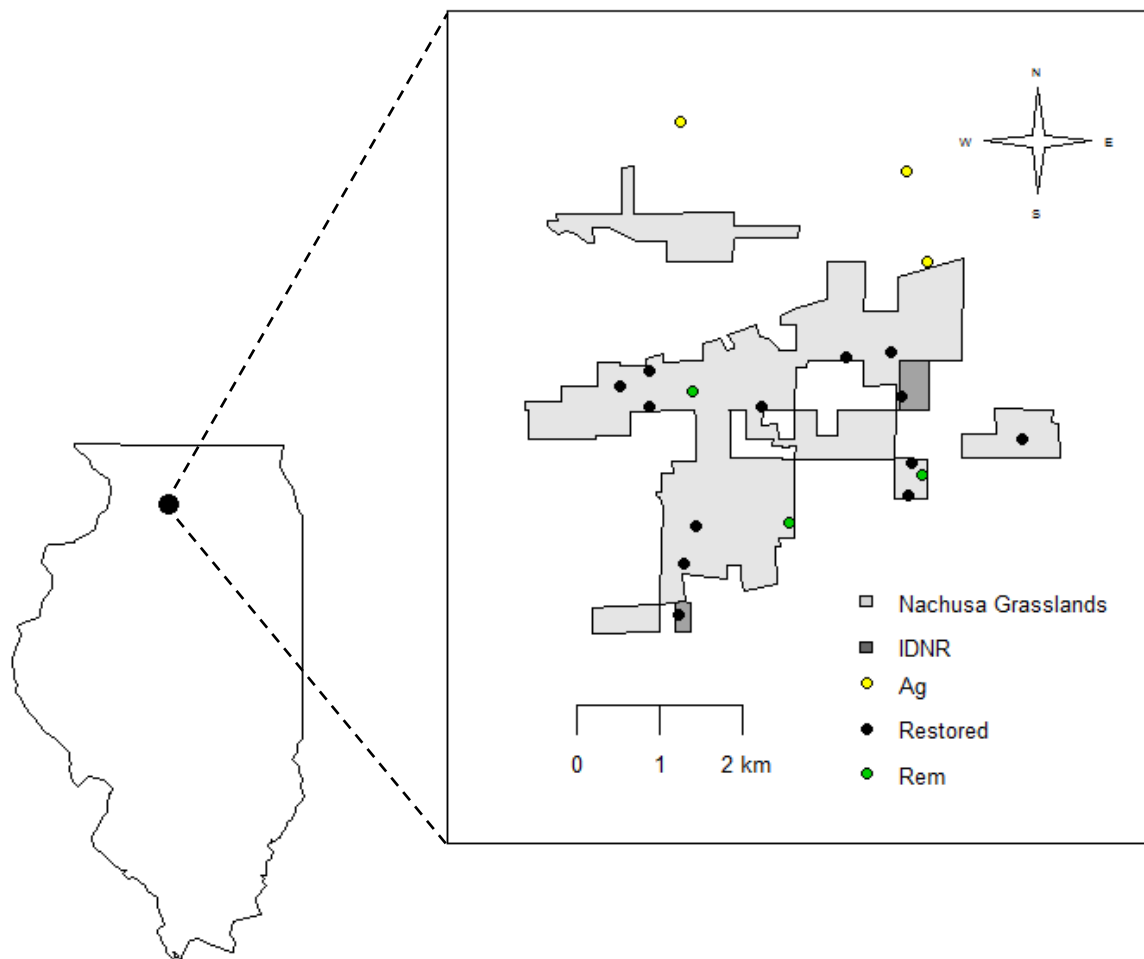


Figure 2. Model estimated means and standard errors of bee community A) abundance and B) richness. Means represent expected abundance and richness at sites on a single sample date. Letters indicate significant differences calculated using Tukey-Kramer contrasts.

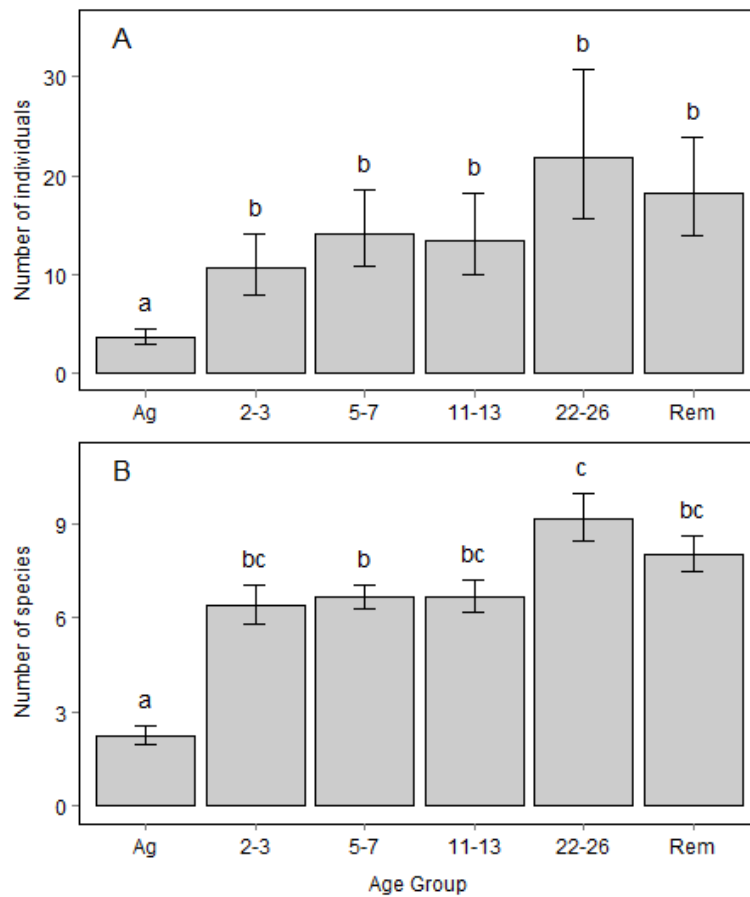


Figure 3. Nonmetric multidimensional scaling (NMDS) ordination plots for bee communities. Ordinations in A) are based on relative abundances with Bray-Curtis distances (stress=0.14) and ordinations in B) are based on presence-absence Bray-Curtis distances (stress=0.15). Sites are colored according to restoration age.

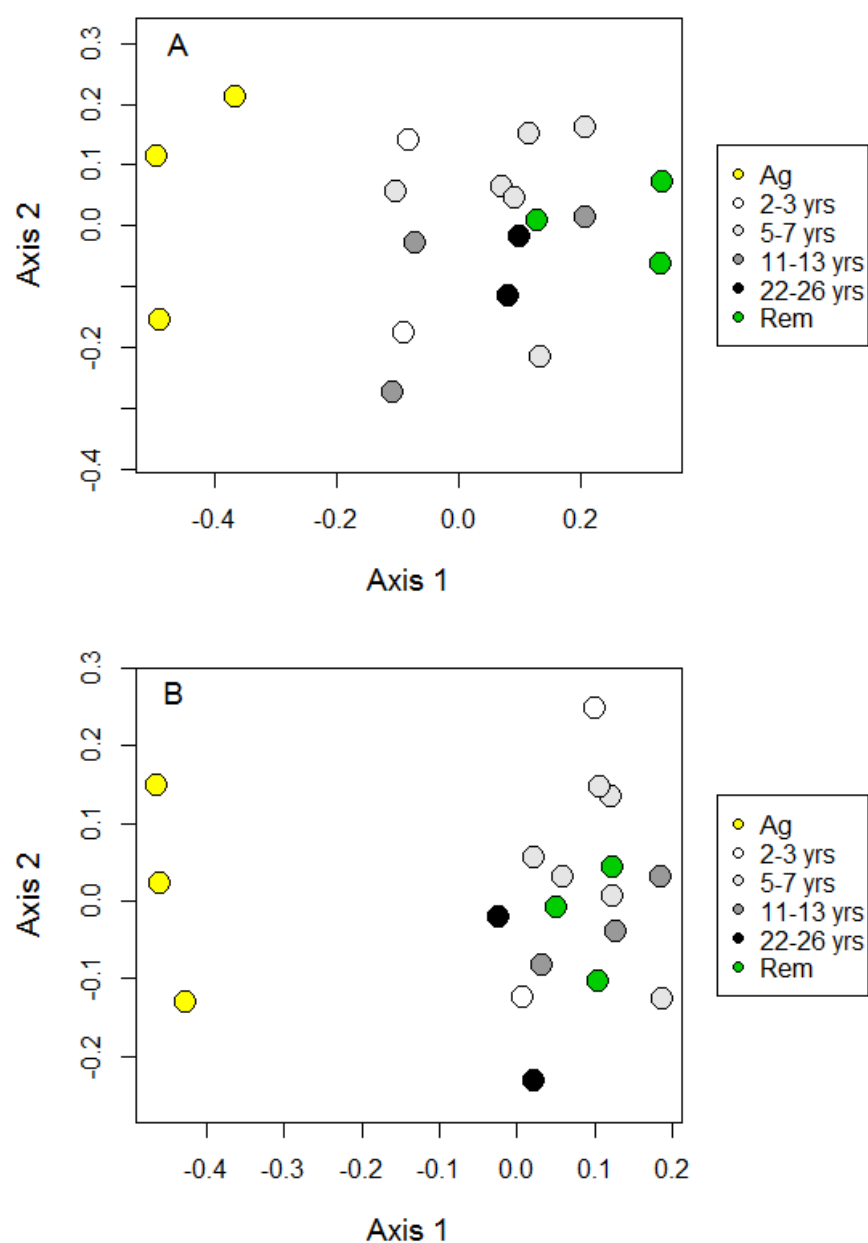


Figure 4. Plots of beta diversity partitioning analysis for restored sites. Pairwise dissimilarity of bee communities are plotted against pairwise dissimilarity in age for total beta diversity (β_{cc}), as well as partitioned into the two components of overall beta diversity, species replacement (β_{-3}) 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. Linear regressions were fitted to assess the relationship between community dissimilarity and age difference (see Table 3).

