

GRASSHOPPER AND BEE COMMUNITIES ON MISSOURI PRAIRIES:
COMPARING RECONSTRUCTIONS AND REMNANTS

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COMPARING RECONSTRUCTIONS AND REMNANTS

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ABSTRACT

Tallgrass prairies once occupied a large swath of central North America, but now face the combined challenges of habitat loss and fragmentation. In Missouri, where less than 1% the historical prairie remains, prairies are being reconstructed from agricultural or wooded land. The success of reconstructed grasslands is often assessed based on the extent to which native prairie plants have reestablished. Invertebrates, which make up a large portion of prairie biodiversity, are often assumed to colonize reconstructions if native vegetation returns. However, the limited mobility of many invertebrates, the isolation of many tallgrass remnants, and the difficulty in establishing prairie plants raises serious questions as to whether invertebrate communities on reconstructed prairies are and will be equivalent to those found on remnant prairies. To evaluate the effectiveness of prairie reconstructions in restoring grassland invertebrate communities, we sampled two guilds of terrestrial invertebrates: native bees (*Anthophila*) and grasshoppers (*Acrididae*). The first objective of this project was to compare grasshopper and bee communities on reconstructions to those on remnants by evaluating species richness, diversity, and community composition. We sought to identify species or functional groups associated with remnants or reconstructions that could be used to monitor invertebrate communities on reconstructions and remnants in the future. The second objective was to evaluate the effects of prairie reconstruction age on grasshopper and bee communities to determine if communities on reconstructions are converging with remnants.

We sampled invertebrates from four pairs of reconstructed and remnant prairies in Missouri in 2016 and 2017. We captured bees with bee bowls and grasshoppers with sweep nets, identifying individuals to the lowest taxonomic level possible. Shannon diversity of grasshoppers was higher on reconstructions than remnants at three of the four locations, and 10 of the 33 taxa were unique to remnants. In contrast, we detected no differences between reconstructions and remnants in bee species richness nor diversity. Community composition of bees and grasshoppers was different on reconstructions was different from that of remnants. Bee communities differed between the prairie types largely because of relative abundance of taxa; remnants and reconstructions shared all but three of the 60 taxa.

Grasshopper communities on reconstructed prairies were characterized by a few long-winged, generalist species that are typically successful in agroecosystems. Two short-winged grasshoppers that preferred either forbs or grasses were associated with remnant prairie. The species that characterized reconstructions became less abundant with reconstruction age, although they were still more common on the oldest reconstructions than remnants. The differences between remnant and reconstructed grasshopper communities likely reflects the disparities in dispersal ability between grasshopper taxa, as well as the differences in food resources between prairie types.

There were several taxa that contributed to the differences between bee communities on reconstructions and remnants. There were two ground-nesting halictids that were more abundant on remnant prairie, one of which is considered to be strongly associated with remnants. On reconstructions, one soil-nesting generalist species and one stem-nesting genus were more abundant than on remnants. Twig nesters were more

common on reconstructions than remnants, suggesting that there may be more nesting opportunities for stem and twig nesters on reconstructions. Although several taxa appeared to change in abundance across reconstruction ages, only one of them belonged to the group of taxa that differentiated reconstructions from remnants. Bee communities on older reconstructions were distinct from those on remnants, and reconstructions do not appear to be trending toward convergence with remnants. The proportion of the bee community captured was probably small, and we did not capture enough oligolectic and kleptoparasitic bees to draw any inferences about their prevalence on reconstructed versus remnant prairies.

Our results show that prairie reconstructions in Missouri do not support the same communities of bees and grasshoppers found on remnants. Grasshoppers appear to be more diverse on remnants, and there are many species that seemingly have not colonized nearby reconstructions. Further investigation into the habitat disparities driving their failure to colonize reconstructions could help restore the entire grasshopper community to reconstructions. More intensive sampling is necessary to fully understand how the rarer members of bee communities respond to prairie reconstruction. Grasshopper and bee communities on reconstructions may require many decades and continual, intensive management to fully converge with remnant communities.

CHAPTER 1

Introduction

As human populations, cities and agricultural lands expand, traditional “passive” conservation consisting of protecting large blocks of wild land is becoming largely untenable. Conservation efforts are instead shifting from preservation and management of remnant ecosystems, to active reclamation of disturbed land and subsequent ecosystem restoration and reconstruction (Dobson et al. 1997, Török and Helm 2017). Large-scale ecosystem reconstruction may be the best conservation strategy for many species in decline today. Ecosystem reconstruction takes time, in part because the plants that form the base of any terrestrial reconstruction effort often require years to reach maturity (Vesk and Mac Nally 2006, Vesk et al. 2008). It is imperative to understand the fastest and most effective ways of reconstructing ecosystems before fragmentation and local extinctions make historical ecosystems irretrievable.

Reconstructing any ecosystem is a daunting task not just because of the enormous complexity of most ecosystems, but also because it can be quite challenging to identify exactly what the end product should be. Ecological communities are often dynamic, and the community of interest on a habitat remnant one year may be quite different the next (Simberloff 1990). Furthermore, it may be impossible to know whether remaining remnant communities actually represent desired historical communities, depending on how well they have been studied and catalogued. The nebulous nature of reconstruction goals makes monitoring, both target communities in remnant habitats and communities

post-reconstruction, essential to assessing the effectiveness of ecosystem reconstruction (Kremen et al. 1994, Thom 2000, Block et al. 2001, Benayas et al. 2009).

Monitoring ecosystems requires identifying target taxa that provide information on the status of the ecosystem (Török and Helm 2017). Typically species that are dependent on the type of habitat being reconstructed, referred to as “conservative,” make the most cost-effective monitoring subjects (Block et al. 2001, Török and Helm 2017). Plants are commonly used (Panzer and Schwartz 1998, Walker et al. 2004, McLachlan and Knispel 2005), in part because most ecosystem reconstructions initially focus on trying to reestablish a plant community, and also because plant diversity and community composition can be effective predictors of animal diversity (Scott et al. 1993, Panzer and Schwartz 1998). However, a fundamental limitation of only monitoring plants in a reconstruction setting is that, while plants are actively placed on the landscape, other taxa must colonize from existing remnants. To accurately assess reconstruction of the entire ecosystem, it is necessary to track whether taxa that are not introduced will eventually colonize and persist in reconstructed sites. Vertebrates, in particular birds and mammals that people find charismatic, are often monitored because they are easily recognizable and in some cases reflect ecosystem functioning (Sergio et al. 2006, Fleishman and Murphy 2009). Tracking plant, mammal, and bird populations, however, still neglects the large portion of prairie ecosystems composed of invertebrates (New 1993, Panzer and Schwartz 1998).

Invertebrates’ enormous diversity, which includes many conservative, specialist, or sensitive species, suggests a high potential to serve as indicators of ecosystem function and reconstruction progress. In fact, invertebrates are already used as bioindicators, both

in aquatic (Bonada et al. 2006) and terrestrial systems (Andersen and Majer 2004). Despite the surfeit of species available, monitoring of terrestrial invertebrates has often focused on large, charismatic species such as butterflies (Dunn 2005, Fleishman and Murphy 2009). Other than a general lack of charisma, invertebrate focused conservation or reconstruction monitoring may also be hindered by dramatic population fluctuations (Fleishman and Murphy 2009) and the considerable challenge of identifying such a speciose group.

We investigated invertebrate communities in tallgrass prairies, an imperiled ecosystem in North America that has been the subject of considerable restoration and reconstruction research in the past two decades (Schwartz and Whitson 1987, McLachlan and Knispel 2005, Shepherd and Debinski 2005, Rowe 2010, Larson et al. 2011). Tallgrass prairie reconstruction in Missouri is an excellent example of ongoing efforts to rebuild an ecosystem based on information from only small fragments of remnant habitat. Tallgrass prairie once covered close to a third of Missouri but has since been reduced by over 99% (Christisen 1972) due to mechanized agriculture, urbanization, and forest expansion (Samson and Knopf 1994). The remaining tallgrass prairie in Missouri consists of small patches (Christisen 1972, Solecki and Toney 1986). Conservation organizations such as the Missouri Prairie Foundation and the Nature Conservancy, as well public agencies including the Missouri Department of Conservation, have responded by converting agricultural or wooded land back to prairie, a process of unknown duration and with significant challenges.

Scientists and managers reconstructing tallgrass prairie generally attempt to create a plant community that corresponds to those found in local remnant prairies (Kurtz 2013).

Seeding and continually reseeding with the appropriate native seed mixes will theoretically create the diverse mix of forbs and grasses that comprise tallgrass prairie vegetation communities. Determining the correct seed mixes is a science in and unto itself; the ideal mix may vary regionally (Diboll 1997, Larson et al. 2011), and in many cases is still undetermined. Burning, mowing, grazing, and spraying for invasive species are all common post-planting management practices that can have substantial impacts on vegetative communities in tallgrass prairies, whether they be reconstructed or remnant (Kruess and Tschardtke 2002, Panzer 2002, Walker et al. 2004, Shochat et al. 2005, Humbert et al. 2010, Debinski et al. 2011). Plant communities are commonly used to evaluate reconstruction success in tallgrass prairies (Kindscher and Tieszen 1998, Martin et al. 2005). Particular taxa like milkweed (*Asclepias*) have received attention in recent years; as monarch butterfly (*Danaus plexippus*) populations have declined (Brower et al. 2012, Pleasants and Oberhauser 2013), milkweed specific planting efforts have intensified (Bowles et al. 2015, Pleasants 2017). Active reconstruction of the animal communities in prairie ecosystems, or species reintroduction, has been limited to only a few endangered species, most famously in Missouri the Greater prairie chicken (*Tympanuchus cupido*). The American burying beetle (*Nicrophorus americanus*) remains the only example of which we are aware of an insect purposely reintroduced to a prairie reconstruction in Missouri. Many insects will colonize a reconstructed grassland or prairie independently (Mortimer et al. 1998, Moreira et al. 2007), but it would be unreasonable to assume that the entire target insect community will immediately return to prairie reconstructions given disparities between insects in colonization ability (Thomas 2000, Zalewski and Ulrich 2006, Lester et al. 2007).

Colonization ability in insects is tied to dispersal ability (Zera and Denno 1997, Thompson 1999, Lester et al. 2007, Picaud and Petit 2008) and habitat specificity (Piechnik et al. 2008, Dennis et al. 2011). The best colonizers should be strong dispersers and generalists capable of surviving in a broad range of habitats (Lester et al. 2007, Dennis et al. 2011). Insects have very different dispersal abilities, with flightless insects usually being more dispersal-limited than strong fliers. Even within species, individuals can vary greatly in wing length and flight ability, usually matched with varied reproductive abilities (Steenman et al. 2014). Species that lack mobility, and are thus poor dispersers, are more likely to go locally extinct than more mobile species (Kotiaho et al. 2005, Reinhardt et al. 2005, Marini et al. 2010), which could be related to their delayed colonization of new habitats (Picaud and Petit 2008). Habitat specificity also contributes to colonization ability, as well as extinction risk (Dennis et al. 2011). Specialists may be less likely to survive dispersal because of the lack of resources in the matrix surrounding their habitats (Bonte et al. 2003, Tischendorf et al. 2003, Kuefler et al. 2010). Additionally, habitat reconstructions may lack certain resources present on remnants, at least early in the reconstruction process, making persistence following immigration less likely for some specialists (Piechnik et al. 2008). Previous studies have found that specialist species tend to colonize new habitat after generalists (Baur and Bengtsson 1987, Picaud and Petit 2008) and also tend to go locally extinct more frequently (Reinhardt et al. 2005, Dennis et al. 2011). Dispersal ability and habitat specificity can play an important role in determining what species can survive on remnant habitat and colonize reconstructed habitat.

We chose two groups of insects from different feeding guilds to evaluate communities on tallgrass prairie reconstructions and compare them to communities on remnants. Multispecies or multiguild approaches to monitoring grasslands using vertebrates are thought to be more informative for evaluating grassland ecosystem health (Brennan and Kuvlesky Jr 2005), and there is reason to believe the same is true for invertebrates. Different insect taxa, even within the same guild, can respond differently to prairie habitat components (Swengel 2001, Engle et al. 2008, Woodcock et al. 2009), and drawing conclusions from just one taxon could be misleading. For example, bee and butterfly diversity were found to be inversely related on Iowa's prairies (Davis et al. 2007), suggesting that including insect groups with different ecosystem roles is an important step in obtaining a broad picture of communities on reconstructions. We investigated grasshoppers (Acrididae) and bees (clade Anthophila). Bees are pollinators that provide considerable ecosystem services to humans (Losey and Vaughan 2006). Grasshoppers are also economically important, but as a crop pest (Davis et al. 1992). They are major aboveground herbivores in grasslands that serve as a food source for numerous other animals, from birds to snakes to spiders (Belovsky et al. 1990). Both groups contain species suspected to be closely associated with healthy prairie ecosystems (Reed 1996), as well as species found in a broad range of habitats.

The overall purpose of the study was to compare the bee and grasshopper communities on tallgrass prairie reconstructions to those on remnants in order to evaluate the progress made toward recreating tallgrass prairie invertebrate communities. We had two specific objectives. First, to compare bee and grasshopper communities in reconstructions to remnants by examining species richness, diversity, and community

composition of the two taxa at four pairs of reconstructed and remnant prairies in Missouri. We also identified species or functional groups associated with remnants or reconstructions that could potentially be monitored to assess invertebrate community health and change over time on prairie reconstructions and remnants in the future. Second, we evaluated reconstructions of different ages to determine whether bee and grasshopper communities on reconstructions are converging with communities on remnants over time, or whether they are remaining distinct.

CHAPTER 2

Grasshopper communities in Missouri's reconstructed and remnant prairies

Introduction

Grasslands are in decline globally due to intensification of land use by humans (Ceballos et al. 2010). Species that rely on grassland habitat have, predictably, declined as well, in some cases precipitously (Brennan and Kuvlesky Jr 2005, Pleasants and Oberhauser 2013). Besides traditional conservation of remaining fragments of native grassland, there are also efforts to reconstruct grassland from agricultural or otherwise disturbed land (Dobson et al. 1997, Török and Helm 2017). Grasslands in the form of prairies once covered the Great Plains of North America, but very little remains (Whiles and Charlton 2006). On par with national trends in prairie habitat loss, Missouri now contains less than 1% its historical tallgrass prairie (Christisen 1972). Reconstruction efforts to bolster the remaining acreage have been underway for nearly 20 years.

The process of tallgrass prairie reconstruction is often quite extensive (Smith 2010, Kurtz 2013). After removing the vegetation occupying the land, whether it be forest, crops, or pasture, managers plant a diverse native seed mix containing grasses and forbs (Smith 2010, Kurtz 2013). Management can be intensive, involving spraying herbicides, burning, mowing, and grazing. Ascertaining whether reconstructions and management practices have effectively restored tallgrass prairie communities requires monitoring animal and plant communities of reconstructions as well remnant prairies (Kremen et al. 1994, Thom 2000, Block et al. 2001, Benayas et al. 2009). Remnant

prairies represent the best examples of historical tallgrass prairie ecosystems, thus they serve as target communities for reconstruction efforts. In general, habitat specialists, species that require conditions specific to the habitat of interest, make the most effective monitoring subjects (Block et al. 2001, Török and Helm 2017). Concern for charismatic species like prairie chickens (*Tympanuchus cupido*), quail (*Colinus virginianus*), and monarchs (*Danaus plexippus*) often drives management and conservation efforts on Missouri prairies, but there are other ecologically important taxa that warrant more extensive monitoring. Of particular interest are taxa that may not be able to surmount the obstacles to colonization posed by habitat fragmentation, one of which is grasshoppers (Acrididae) (Hjermann and Ims 1996, Heidinger et al. 2010, Ortego et al. 2015).

Grasshoppers do not typically garner extensive conservation attention.

Restoration or reconstruction studies focusing on grasshoppers are less common than on economically beneficial insects like bees (Harmon-Threatt and Hendrix 2015, Griffin et al. 2017, Tonietto et al. 2017), or publicly popular insects such as butterflies (Ries et al. 2001, Swengel 2001, Davis et al. 2007, Vogel et al. 2007, Brückmann et al. 2010, Kuefler et al. 2010). Several grasshopper species are serious agricultural pests that receive intensive insecticidal control (Lockwood et al. 1988). One common misconception, based on the resilience of some pest grasshoppers to concerted extermination efforts, is that pest grasshoppers are safe from the loss of populations and declining biodiversity affecting pollinators. However, considering the sudden extinction of the Rocky Mountain locust, *Melanoplus spretus*, which once rivaled the bison in terms of animal biomass on North American prairies (Lockwood 2004), along with the endemism found in some grasshopper genera (Hilliard Jr 2001, Knowles 2001, Otte

2012), losing grasshopper diversity is a distinct possibility. Fifteen species are already listed as species of concern by the Missouri Department of Conservation, and it is difficult to know how currently undescribed or recently described species are faring. The Order in which grasshoppers belong, Orthoptera, is also a good indicator of overall species richness in agricultural and grassland areas (Sauberer et al. 2004), meaning that grasshoppers could hold the potential to gauge prairie reconstruction health.

We can make some general hypotheses about grasshopper community response to environmental change, such as the creation of a reconstructed tallgrass prairie, based on succession and colonization trends. One of the most widely used and basic community metrics is species richness, or the number of species of a particular taxon found in a habitat. The assumption that insect species richness on remnants should be greater than on the presumably lower quality reconstructions is often proved wrong (Davis et al. 2007, Williams 2011, Diepenbrock et al. 2013). Another important descriptor of communities on tallgrass prairie reconstructions is species composition. Much of the research describing grasshopper community composition on tallgrass prairies has occurred on Konza Prairie (Joern 1986, Evans 1988). However, studies on Konza Prairie are of limited use for evaluating or predicting grasshopper communities found on prairie reconstructions in Missouri because Konza is entirely remnant prairie.

Colonization ability in insects is tied to dispersal ability (Zera and Denno 1997, Thompson 1999, Lester et al. 2007, Picaud and Petit 2008) and habitat specificity (Piechnik et al. 2008, Dennis et al. 2011). Grasshopper species display widely different dispersal capabilities. Some species possess long wings and powerful flight muscles that allow them to disperse long distances, hundreds of miles in the case of the migratory

grasshopper *Melanoplus sanguipines* (Pfadt 1994). Other grasshoppers have poorly developed wings and can only disperse by hopping distances measured in yards rather than miles. Grasshoppers with strong dispersal abilities may be better colonizers because they are better able to reach new habitats. In fragmented landscapes, like grasslands in the United States or much of Europe, differences in mobility affect grasshopper community composition and persistence (Marini et al. 2010, Marini et al. 2012), with low mobility grasshoppers being more likely to go extinct than high mobility grasshoppers (Reinhardt et al. 2005). In France, wing length to body length ratios of grasshopper species decreased with succession in old fields, suggesting that better dispersing species colonize new habitats before poor dispersers (Picaud and Petit 2008). There is also some genetic confirmation that grasshoppers considered more sedentary are less successful dispersers (Blanchet et al. 2012), although other studies have found that populations of less mobile grasshoppers showed no distinct genetic structure (Keller et al. 2013). Grasshoppers are usually not considered specialists because of their broad diets relative to other insect taxa, but they still display a range of diet breadths (Joern 1979). Grasshoppers with broad diets may be better colonizers because they can survive and reproduce under a variety of resource conditions (Peterson and Denno 1998, Piechnik et al. 2008).

We hypothesized that long-winged grasshoppers and grasshoppers with generalist diets, that is, those feeding on a mixture of grasses and forbs, would be more common on reconstructions than remnants because they are more likely to successfully colonize new habitat. We also hypothesized that smaller, short-winged, specialist species would be more common on remnants than reconstructions because they are not as likely to colonize new habitat. Grasshopper surveys from Wisconsin prairies offer strong support for the

first hypothesis. Reconstructed prairies were occupied by a suite of mobile, generalist species that persisted in older reconstructions (Bomar 2001).

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

Methods

Site Selection

We sampled four areas containing prairies managed by the Missouri Department of Conservation. Three of the areas, all located within St. Clair County in the Upper Osage Grasslands of southwestern Missouri (Fig. 2.1), contain contiguous remnant and reconstructed prairies. They were Wah’Kon-Tah Prairie (Fig. 2.2), Linscomb (Fig. 2.3), and Schell-Osage (hereafter Schell; no figure available). The remaining area is located 135 miles northeast in the Central Dissected Plains in Calloway County (Fig. 2.1) consisting of one remnant (Fig. 2.4) and reconstructed (Fig. 2.5) prairie, which are considered one location in our analyses although they are separated by almost 20 miles. The reconstructed prairies at Wah’Kon-Tah, Linscomb, and North contained reconstructions of different ages. There were ten individual reconstructions at Wah’Kon-

Tah initiated from 2002 from 2008. Linscomb contained two reconstructions, one from 2007 and the other from 2013. The North location had the greatest range of reconstruction ages. The earliest was initiated in 2004, and the most recent in 2016. Schell had only one reconstructed site from 2014. For analyses, reconstruction age was calculated as the years since planting until sampling year.

Various grassland management practices form a mosaic of treatments that could potentially confound invertebrate surveys. Therefore, we excluded tracts scheduled to be hayed, grazed, mowed, or high-clipped in 2016 or 2017 because those practices could alter the invertebrate community during summer months (Humbert et al. 2010). Burning also affects invertebrate communities (Panzer 2002), but we included burned patches in our site selection because the burns were scheduled for the dormant season, outside of the sampling window.

Due to the fragmented nature of the native prairie patches available for sampling and the heterogeneity of the landscape, we chose to sample transects at locations randomly generated in each remnant and reconstructed prairie. We used ArcMap 10.3.1 (ESRI 2015) to randomly generate points (Figs. 2.2, 2.3, 2.4, 2.5). Points were regenerated after 2016 for sampling in 2017. Each point, which represented the center of a transect, was located greater than 40m from the edge of the prairie and at least 75m from another transect. In 2016 we sampled 134 transects, 75 on reconstructions and 59 on remnants. In 2017, we reduced sampling intensity at the North location, which lowered the total transects to 116, 63 on reconstructions and 53 on remnants.

Collecting

We collected grasshoppers by two methods, standardized sweeping and targeted capture. We performed standardized sweeping, generally accepted as the best method of grasshopper collection (Evans et al. 1983, Larson et al. 1999), along 60m transects centered on the randomly generated points. We performed 10 sweeps perpendicular to the transect with a 38cm diameter net at four spots along the transect, located 15m and 30m from the center of the transect in both directions. The four subsamples were combined into a single sample, thus each transect consisted of a total of 40 sweeps (Fig. 2.6). By necessity, seven different people performed the sweeping over the two years. Different sweeping techniques can bias the grasshoppers collected (O'Neill et al. 2002), therefore we agreed upon and practiced the same sweeping motion and made an effort to assign sweepers to different prairie types throughout the season. One researcher conducted 45% of the sweeps (Fig. 2.7).

In 2016, sampling occurred once in June, once in July, and once in August/September. Sweeps were conducted on days without consistent precipitation or winds over 15mph. In 2017, we restricted standardized sweeping to one visit in August/September. In 2017, we replaced the early-season standardized sweeps with targeted capture in order to increase the number of adult grasshoppers captured. Targeted capture entailed walking slowly and capturing every adult grasshopper that we observed or flushed. We spent equal time conducting targeted captures at remnant and reconstructed prairies and alternated sampling between the two prairie types several times per day. We spent approximately 100 hours conducting targeted capture from June to September 2017.

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

Vegetation

We measured vegetation density and estimated forb to grass ratio during the standardized sweeping in August/September of 2017. We measured vegetation density with a modified Robel pole (Benkobi et al. 2000, Uresk and Benzon 2007) at three of the four sweeping points along each transect (Fig. 2.8). At each location we recorded the lowest visible decameter on the Robel pole from a distance of four meters and a height of 1 meter (Fig. 2.8). We estimated the forb to grass coverage ratio of a 1.0 x 0.5m plot at the same places we measured vegetation density.

Statistical analyses

Diversity and Total Abundance

We compared taxon richness (species plus genera that were not identified further) and diversity in reconstructed and remnant prairies at each location using a combination of asymptotic and non-asymptotic techniques. The non-asymptotic approach consisted of rarefaction/extrapolation (Weibull et al. 2003, Gotelli and Colwell 2011, Colwell et al. 2012), which resamples species data to estimate the richness or diversity at other sample sizes. We performed rarefaction/extrapolation using the package iNEXT (Hsieh et al. 2016). Although there are two types of rarefaction/extrapolation, individual-based and sample-based (Gotelli and Colwell 2011), we were limited to individual-based rarefaction

because of the addition of the targeted capture grasshopper observations in 2017. Grasshoppers from 2017 represented captures from two different methods but were combined together for analyses. We conducted all analyses using R version 3.4.0 (R Core Team 2017).

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

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

abundant species, making it a good measure of the diversity of dominant species (Keylock 2005, Chao et al. 2014).

In the asymptotic approach, we used nonparametric estimators, which typically utilize count data for rare species to estimate species richness without making assumptions about the underlying distribution of species. We generated *jack1*, *jack2*, *Chao1*, and *iChao1* estimators with the package SpadeR (Chao and Chiu 2016). *Chao1* (Colwell and Coddington 1994) and *iChao1* (Chiu and Chao 2016) are best at estimating lower bounds of species richness (Chao and Chiu 2016). *Chao1* is based on rare species, defined as species observed only once (singletons), or twice (doubletons); *iChao1* includes tripletons and quadruplets in the estimation of undetected rare species. *jack1* and *jack2* use jackknife techniques, which reduce bias by successively deleting observations from the data to estimate species richness (Chao and Chiu 2016).

We modeled total abundance and species richness of grasshoppers using univariate generalized linear models with a negative binomial distribution including the effects of *status* (reconstruction or remnant), *location* (Wah'Kon-Tah, Linscomb, Schell, or North) and an interaction between the two. Only grasshopper data from 2016 were included in the model because we did not collect a sufficient number of grasshoppers from standardized sweeping in 2017. We started with a model including all variables and interactions, then removed interactions and variables one at a time. We conducted analyses of variance (ANOVA) on models with and without variables to determine whether the variables improved the model fit, discarding those that did not ($p > 0.05$) (Blakey et al. 2016, Clarke-Wood et al. 2016). We used the function *glm.nb* in the package MASS (Ripley et al. 2017).

Community analysis

To visualize community data, we ordinated the grasshopper communities using non-metric multidimensional scaling (NMS) with a Bray-Curtis dissimilarity matrix (Paton et al. 2009, Clarke-Wood et al. 2016). NMS ordination compresses the abundance and species information from each sample and constructs a space of k dimensions based on the differences between samples. Taxa abundances were summed at each transect. Only taxa that occurred in over 5% of transects were included in the ordination, thus we included only the 15 most common grasshopper taxa in the ordination. There was an insufficient number of grasshoppers from standardized sweeping in 2017 to run a NMS ordination, therefore we only present the ordination of grasshopper communities from 2016. Eight transects (four remnant, four reconstruction) with zero individuals were removed before analysis. We used the function *metaMDS* in package *vegan* (Oksanen et al. 2016) to run NMS. We used the function *dimcheckMDS* to choose the number of dimensions and viewed the resulting ordination with the *ordirgl* function found in the package *ordiplot3d*.

To test whether reconstruction and remnant communities were distinct, we modeled abundances of the same taxa used in the ordinations. Models were generated in the package *mvabund*, which handles multivariate count data with generalized linear models. The response variable was the abundance of a taxa summed across sample dates for each transect and we used a negative binomial distribution for all models. Explanatory variables included *status* (remnant or reconstructed), *location* (Wah'Kon-Tah, Linscomb, Schell, and North), *edge proximity* (distance from transect to closest prairie edge, measured in ArcMAP) and all interactions between them. We started with a model

including all variables and interactions, then removed interactions and variables one at a time. We conducted ANOVA on models with and without variables to determine whether the variables improved the model fit, discarding those that did not ($p > 0.05$) (Blakey et al. 2016, Clarke-Wood et al. 2016). Because of a significant *status x location* interaction, we ran individual multivariate models for each location as well. We examined the multivariate model coefficients for each taxon to identify which taxa contributed to differences between communities. For ease of interpretation, all coefficients presented are from models without interaction terms and coefficients with very large standard errors were excluded.

We grouped grasshoppers by wing length (*short, long*) and by preferred diet (*grass, forb, mixed*) (Table 2.1). We considered grasshoppers to be short-winged if the species' wings typically do not extend more than 2/4 of abdomen length. Information on grasshopper diet and wing length was taken from Pfadt (1994), Otte (1981), and Capinera and Sechrist (1982). Using the package *mvabund*, we created multivariate models of abundance and richness for each functional group. Explanatory variables in this analysis included *status, location, and edge proximity* and all interactions among them. Due to a significant *status x location* interaction, we also modeled functional group abundance for each prairie separately.

Age effects

We evaluated effects of reconstruction age on grasshopper communities using NMS and multivariate abundance models. We used the 12 most abundant grasshopper taxa on reconstructions with a Bray-Curtis dissimilarity index to ordinate the grasshopper communities on reconstructions. To quantitatively assess community change over time,

we used multivariate abundance models (*mvabund*) of the same taxa used in the ordination of reconstructions.

We assessed effects of reconstruction age on the functional composition, based on wing length and diet, of grasshopper communities with multivariate models of abundance and richness. Explanatory variables included *age*, *location*, and *edge proximity* and all interactions among them. We started with a model including all variables and interactions, then removed interactions and variables one at time. We conducted ANOVA on models with and without variables to determine whether the variables improved the model fit, discarding those that did not ($p > 0.05$) (Blakey et al. 2016, Clarke-Wood et al. 2016). We also modeled prairies separately because of significant *age x location* interactions, and the importance of location. We modeled overall abundance and richness using generalized linear models with a negative binomial distribution and selected from the same variables and in the same manner as for the functional group models.

The above methods were used to determine the effects of prairie reconstruction age on grasshopper communities. The ultimate goal of investigating age in a reconstruction context, however, is to determine if reconstruction communities are converging with the target communities on remnants. To visualize whether grasshopper communities converge with remnants over time, we used the same ordination generated from comparing reconstructions to remnants, only with a different coloring and grouping scheme to emphasize reconstructions of different ages. We also divided reconstructions into two age classes, ≤ 5 years and > 5 years, and performed the same multivariate model analyses of abundance for taxa and functional groups as described in the community

analysis section above. We repeated those analyses for the reconstruction groups split into ≤ 9 years and > 9 years.

Vegetation

We averaged the three measures of vegetation density and forb/grass ratio per transect in 2017 and compared vegetation on remnants to vegetation on reconstructions with linear models (function *lm* in package Stats). To investigate relationships between vegetation characteristics and insect species' abundances, we ran separate models with only 2017 data that included vegetation measurements, with the same methods as described in the community composition analysis.

Results

Diversity and total abundance

We collected 2435 grasshoppers representing 33 species in 2016 and 2017 combined (Table 2.1). There was one grasshopper species of note. *Melanoplus inconspicuous* represents, to our knowledge, a northern range expansion into Missouri. We found the short-winged, early-hatching species at Wah'Kon-Tah Prairie and Linscomb Wildlife Area. At the three locations where sampling effort was equal over both years (Wah'Kon-Tah, Linscomb, Schell), remnants had greater raw species richness than reconstructions (Fig. 2.9). Rarefaction/extrapolation curves of species richness suggest higher species richness on remnants than reconstructions at two of the locations, Wah'Kon-Tah and Linscomb, based on the lack of overlap in the 95% confidence interval (Fig. 2.10). Extrapolated and rarefied Shannon diversities were higher, with no overlap in 95% confidence intervals, on remnants than reconstructions at Wah'Kon-Tah,

Linscomb, and Schell. Simpson diversity confidence intervals overlapped at all locations except Linscomb, where remnants were more diverse. This suggests that the other prairies contained similar numbers and frequencies of the most common species. Asymptotic estimates of species richness did not differ between remnants and reconstructions at any of the locations (Fig. 2.11).

The final model for grasshopper abundance included a *location* by *status* interaction ($\chi^2 = 4.33$, $p < 0.0001$). When locations were modeled separately, *status* was significant at two of the locations, Linscomb ($\chi^2 = 15.094$, $p < 0.001$) and Wah'Kon-Tah ($\chi^2 = 11.41$, $p < 0.001$). There was a greater abundance of grasshoppers on reconstructions than remnants at Linscomb ($z = 4.00$, $p < 0.001$), while there were more grasshoppers on remnants than reconstructions at Wah'Kon-Tah ($z = -3.37$, $p < 0.001$).

Community analysis

Remnant and reconstruction grasshopper communities from 2016 appeared distinct based on 3-D ordinations (Fig. 2.12; stress = 0.169, $k = 3$). Multivariate abundance models of the same species used in ordination contained a significant *status* by *location* interaction ($\chi^2 = 122.5$, $p < 0.0001$), indicating the effect of reconstruction on abundances varied by location. When locations were analyzed separately, remnant and reconstruction grasshopper communities were different at Wah'Kon-Tah ($\chi^2 = 79.4$, $p < 0.001$), Linscomb ($\chi^2 = 75.76$, $p < 0.001$), and North ($\chi^2 = 28.43$, $p = 0.013=6$) but not at Schell ($\chi^2 = 16.53$, $p = 0.287$). Univariate tests showed that two taxa, *Campylacantha olivacea* and the genus *Orphulella*, contained significant *status* by *location* interactions. The multivariate model without the interaction supported the visual evidence that remnant and reconstruction communities were distinct ($\chi^2 = 87.76$, $p < 0.001$).

Communities also differed by location ($\chi^2 = 273.6$, $p < 0.001$). *Status* coefficients representing the effect of reconstruction on abundance from the multivariate model without the interaction are presented in Figure 2.13. We refrained from interpreting the overall *status* coefficient for the two taxa responsible for the significant interaction. *Melanoplus femurrubrum*, *M. differentialis*, *Hesperotettix*, and *Syrbula admirabilis* were all more abundant on reconstructions, while *P. nebrascensis* and *M. gracilis* were more abundant on remnants (Fig. 2.13). The most common grasshopper across sites was *Melanoplus scudderi*. Counting all grasshoppers captured with standardized sweeps and targeted capture over both years, twelve species were unique to remnants, and two species were found only on reconstructions (Table 2.2).

Long-winged grasshoppers and mixed diet grasshoppers were more abundant on reconstructions (Fig. 2.14, Wald $\chi^2 = 3.09$, $p = 0.021$; Fig. 2.15, Wald $\chi^2 = 5.01$, $p < 0.001$). Grass-eating and short-winged grasshopper abundances were strongly associated with remnant prairie at Wah'Kon-Tah, but not at the other locations. The proportion of long-winged to short-winged grasshoppers differed greatly by location and by year (Fig. 2.16). We captured more short-winged than long-winged grasshoppers at Wah'Kon-Tah Prairie, and more long-winged than short-winged at Linscomb and our Northern sites in 2016 and in 2017 (Fig. 2.16). The proportion of long-winged grasshoppers was greater in reconstructions at all four locations in 2016, but only at two locations in 2017 (Fig. 2.16). Overall proportions of grasshoppers by diet also varied considerably by location (Fig. 2.17). At all four locations, grasshoppers with mixed diets made up greater proportion of total captures on reconstructions than on remnants in both years (Fig. 2.17).

Age effects

Ordination of only reconstruction communities ($k = 3$, stress = 0.146) indicated very young reconstructions, those five years and younger, were distinct from the oldest reconstructions, those over nine years, but communities corresponding to all other reconstruction ages appeared to have considerable overlap (Fig. 2.18). The best multivariate abundance model contained a significant interaction between *age* and *location* ($\chi^2 = 42.84$, $p = 0.009$), but univariate tests found that the interaction was only significant for one species, *Dichromorpha viridis* ($\chi^2 = 11.636$, $p = 0.043$). The model without an interaction showed that grasshopper communities differed by *age* ($\chi^2 = 42.57$, $p < 0.001$) and *location* ($\chi^2 = 161.3$, $p < 0.001$). *M. femurrubrum*, *M. bivitattus*, and first instar *Melanoplus* (thought to be mainly *M. femurrubrum*) abundances were negatively associated with reconstruction age (Fig. 2.19).

The best model for total grasshopper abundance included *age* ($\chi^2 = 13.291$, $p = 0.0003$) and *location* ($\chi^2 = 50.615$, $p < 0.0001$). The grasshopper richness model also included *age* ($\chi^2 = 14.63$, $p = 0.0001$) and *location* ($\chi^2 = 33.16$, $p < 0.0001$). *Age* was negatively associated with grasshopper abundance and richness, meaning grasshopper abundance was lower on older reconstructions (Fig. 2.20)

The best model for grasshopper abundance on reconstructions grouped by wing length contained *age* ($\chi^2 = 16.15$, $p = 0.002$) and *location* ($\chi^2 = 59.55$, $p < 0.001$). The richness model contained the same terms. Long-winged grasshoppers were more abundant and taxon-rich on younger reconstructions overall and at the three prairies that contained reconstructions of different ages (Fig. 2.20). There was no effect of reconstruction age on the abundance of short-winged grasshoppers.

The best abundance and richness models of grasshoppers according to diet contained *age* ($\chi^2 = 20.5$, $p = 0.002$; $\chi^2 = 15.36$, $p < 0.001$) and *location* ($\chi^2 = 110.8$, $p < 0.001$; $\chi^2 = 43.08$, $p < 0.001$). Mixed and grass diet grasshoppers were more abundant and taxa rich on younger reconstructions than older reconstructions (Fig. 2.21).

Because the same species associated with reconstructions were also more common on younger reconstructions, specifically long-winged generalists such as *M. femurrubrum* and *M. bivitattus*, determining whether older reconstructions were still distinct from remnants becomes particularly important. The ordination with remnants included and reconstruction age displayed indicated grasshopper communities at older reconstructions tended to be closer to the remnants in ordination space than the younger reconstructions (Fig. 2.22). The multivariate models of those same taxa split at five and nine years contained a significant interaction between *age group (including remnant prairies)* and *location* ($\chi^2 = 109.1$, $p < 0.001$; $\chi^2 = 110.1$, $p < 0.001$), which once again was only significant in univariate tests for *Campylacantha olivicea* ($\chi^2 = 17.731$, $p = 0.031$; $\chi^2 = 16.534$, $p = 0.034$). The models from either age split without the interaction showed that older reconstructions were still distinct from remnants (Wald $\chi^2 = 7.65$, $p < 0.001$; Wald $\chi^2 = 6.55$, $p < 0.001$) after accounting for location ($\chi^2 = 238.4$, $p < 0.001$; $\chi^2 = 266.7$, $p < 0.001$). Examining the individual taxa did not yield many significant differences between reconstructions and remnants for either age class at either break point (Figs. 2.23). The reduction in sample size severely limited our ability to discern differences in the abundance of taxa. However, *M. femurrubrum* was consistently more abundant on reconstructions than remnants in any age group (Figs. 2.23). *Syrbula admirabilis* appears to be a species that differentiates reconstructions of five or less years

from remnants, while the abundance of *P. nebrasensis* was significantly greater on remnants than on older reconstructions (Figs. 2.23). Models of wing length and diet, which contained *age group (including remnant prairies)* ($\chi^2 = 30.18$, $p < 0.001$; $\chi^2 = 53.63$, $p < 0.001$) and *location* ($\chi^2 = 73.18$, $p < 0.001$; $\chi^2 = 105.6$, $p < 0.001$), gave further clues on how reconstruction communities of different ages relate to remnants. When examining the trends in total abundance (Fig. 2.24), it is apparent not only that grasshopper abundance is lower on older reconstructions than younger reconstructions, but that older reconstructions, specifically those over nine years old, have fewer grasshoppers than remnants. These results suggest that there are more grasshoppers on reconstructions than remnants for the first nine years, after which abundance decreases to less than remnants. Decreased grasshopper abundance on older reconstructions is partly due to decreases in the common generalists *M. femurrubrum* and *M. bivitattus*, but there must be other taxa responsible, as there were still more of those two species on older reconstructions than on remnants (Fig. 2.23). The diet model showed that the abundance of generalist grasshoppers on older reconstructions did not differ from remnants, although the abundance on younger reconstructions did differ from remnants (Fig. 2.25). Grass preferring grasshoppers were more abundant on remnants than on older reconstructions, while forb preferring grasshoppers were more common on younger reconstructions than remnants (Fig. 2.25).

Vegetation

There was no overall effect of *status* or *location* on forb percentage, although there was a significant interaction ($F = 3.1881$, $p = 0.027$) (Fig. 2.26) due to the reconstruction at Schell having a higher forb percentage than the remnant.

Reconstructions had a higher vegetation density than remnants ($t = 4.831$, $p < 0.0001$), and density differed by location as well (Fig. 2.26; $F = 5.3377$, $p = 0.0017$). Vegetation density and forb percentage were not significantly associated with total abundance or richness of grasshoppers ($\chi^2 = 0.433$, $p = 0.80$; $\chi^2 = 0.298$, $p = 0.84$). Vegetation measurements were not related to the abundance of grasshoppers in diet groups or wing length categories.

Statistical Notes

An underlying assumption of the statistical analyses is that the transects (replicates) are spatially independent. For the transects to be spatially independent, the grasshoppers caught at one transect should not affect the grasshoppers at any other transects. We assumed this to be the case for our transects because most of the grasshoppers we caught at the transects were either nymphs or short-winged, meaning their ability to traverse the minimum of 75m to a nearby transect is limited. However, the grasshopper rarefaction/extrapolation analyses were unique in that the level of replication was the individual, and not the transect. For these analyses, we can say with certainty that the independence assumption was violated (as it often is), because some individuals came from the same transects.

We were ultimately interested in comparisons of communities from different remnant and reconstructed prairies; however, we were limited in the number of available comparisons due to the extreme loss of tallgrass prairie habitat in Missouri. Therefore, while we present analyses comparing remnant and restored communities, our study design actually randomized replicates at the level of the prairie location. Therefore, our scope of inference is technically at the level of prairie location. That is part of the

reason for modeling and displaying results for the prairie locations as well as the overall model.

Discussion

Tallgrass prairies have been depleted more than any other ecosystem in North America. Those attempting to restore tallgrass prairies can plant native vegetation and monitor the plant community over time, adjusting seed mixes and management practices as necessary. However, animal communities must colonize restored habitat from other areas, and therefore must be monitored in order to determine if reconstructions provide the appropriate habitat for colonization. Invertebrates make up a large portion of the tallgrass prairie community, and may require very specific habitat characteristics typically only found on remnant prairies. Our first objective was to compare the grasshopper communities of reconstructions and remnants and identify species or functional groups that can be used to evaluate prairie reconstruction progress.

Grasshopper communities on remnant and reconstructed prairies were distinct, and remnants appeared to contain more species than reconstructions. Of the eleven species only found on remnants, eight of them are known to be associated with prairie habitat. Two of them *P. brunneri*, and *S. obscura* are associated to some degree with field edges or woodlands. The predominance of the prairie-associated species found on the remnants, but not on the reconstructions, provides some evidence that remnant prairies host a more diverse community of grasshoppers because they offer prairie habitat that is superior to the nearby reconstructions, and not merely because they have more types of habitat.

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

Reconstructions and remnant grasshopper communities also differed in the abundance of dominant species. Three long-winged generalists (mixed diet) were more abundant on reconstructions (*M. femurrubrum*, *M. bivittatus* and *M. differentialis*) and two short-winged species (*P. nebrascensis*, *M. gracilis*) with a diet preference for grass or forbs were more abundant on remnants. This supports our hypothesis that remnants would be characterized by more sedentary specialists. The higher abundance of all long-winged and generalist grasshoppers on reconstructions supports our hypothesis that

reconstructions should be characterized by highly mobile generalists. Communities from both methods of grasshopper had higher proportions of grasshoppers with mixed diets on reconstructions. Our findings align with those from succession studies (Picaud and Petit 2008) and prairie reconstructions that showed that generalist grasshoppers dominate newly created grassland habitats (Bomar 2001). A comparison of reconstructed and remnant prairies in Wisconsin also found that *M. femurrubrum* was a dominant species on reconstructions (Bomar 2001).

Our second objective was to evaluate the effect of reconstruction age on grasshopper communities. Older reconstructions, although still distinct from remnants, were closer to remnants than young reconstructions were, and many of the functional groups and taxa that identified reconstructions decreased in abundance with reconstruction age. *M. femurrubrum* decreased in abundance with reconstruction age, but remained more common on older reconstructions than remnants. Bomar (2001) sampled from reconstructions as old as 50 years, and found that *M. femurrubrum* remained the dominant grasshopper on reconstructions. We are cautious in interpreting the effects of reconstruction age because of the cross-sectional nature of the study. Reconstruction and management practices have changed over the last twenty years, meaning older reconstructions were not necessarily managed or restored in the same manner as younger reconstructions. Those changes in treatment could affect how grasshopper communities changed over time on reconstructions of different ages. Additionally, we cannot know the composition of the early grasshopper communities on the older reconstructions. That said, it appears that reconstruction grasshopper communities start out dominated by long-winged generalists, and that over time those taxa diminish in numbers until they are

similar to remnants. However, at least on reconstructions under 15 years of age, grasshoppers associated with remnants do not replace the early colonizers.

The conservation implications of differences in diversity and community composition of prairie grasshoppers between remnants and reconstructions are fairly clear. Reconstructions are not home to some of the prairie grasshopper species, and thus may not be able to bolster the small grasshopper populations of nearby remnants. There are two, non-mutually exclusive explanations for this: grasshopper species on remnants cannot disperse to the new habitats, or they do not survive and reproduce on reconstructions if they are able to reach them (Peterson and Denno 1998, Beck and Kitching 2007). Seven of the eleven grasshoppers unique to remnants were long-winged and probably capable of dispersing the short distances between remnants and reconstructions at the three locations in the Osage Plains. Furthermore, *P. nebrascensis*, although short-winged, was very abundant on some of the remnant prairies and should have by chance dispersed onto the adjacent reconstructions. This, in addition to lack of convincing evidence that, overall, short-winged grasshoppers were more abundant or diverse on remnants than reconstructions, suggests that dispersal ability is not the sole reason that reconstructions were less diverse than remnants. Habitat differences on reconstructions must play at least some part in the differing grasshopper communities. We attempted to discover some of the habitat characteristics responsible for the difference in communities by measuring forb/grass ratio and vegetation density. However, neither differed between remnants and reconstructions, nor were they significant predictors of grasshopper abundance. These results are not entirely unexpected, as past studies have also failed to find consistent links between grasshopper

populations and environmental variables (Anderson 1964, Hastings and Pepper 1964, Evans 1988). There were various characteristics that we did not measure, such plant community composition and soil properties, that could also impact grasshopper community composition on reconstructions and remnants. Plant community composition is a likely suspect, since grasshoppers are herbivores and reconstructions are known to differ from remnants in plant composition and structure (Kindscher and Tieszen 1998, Olechnowski et al. 2009). Soil, too, is a distinct possibility. Grasshoppers deposit their eggs in the soil, and many require fairly specific soil types or temperatures for egg deposition (Uvarov 1966). From a conservation perspective, making reconstructions hospitable to rare grasshoppers may be more important at this point than attempting to aid species' dispersal from isolated habitat patches.

Habitat characteristics, vegetative or soil related, almost certainly play a direct role in determining the grasshopper communities of reconstructed prairies, but they may also act indirectly through species interactions. Competition between grasshopper species (Ritchie and Tilman 1992), mediated by vegetation or soil, might alter grasshopper communities. Size is known to be an important factor in grasshopper interspecific competition (Belovsky 1986, Whitman 2008). Larger grasshoppers are thought to suppress midsize grasshoppers, which in turn suppress small grasshoppers (Belovsky and Slade 1993). Reconstructions that support large populations of generalist, long-winged grasshoppers, which in this study consisted of two large species, *M. differentialis* and *M. bivittatus*, and one midsize species, *M. femurrubrum*, may not be hospitable homes for midsize grasshoppers due to direct competition.

Reconstruction habitat may have direct and indirect effects on grasshopper communities, but grasshoppers may also have an effect on reconstruction vegetation. Grasshoppers are major herbivores, and with the low grazing pressure that the reconstructions we sampled face, they may be the major source of herbivory on reconstructed prairies. Elevated numbers of generalist species on reconstructions could impact efforts to restore prairie plant species. That was the case for a glade restoration in Missouri; grasshoppers of the genus *Melanoplus* suppressed growth of planted forbs, which limited restoration success (Van Zandt et al. 2005). We are not aware of any evidence of grasshoppers inhibiting prairie reconstruction efforts, but the idea of grasshoppers devouring certain desirable plants is hardly a far-fetched idea (Ritchie and Tilman 1992, Pfadt 1994). *M. femurrubrum* and *M. bivittatus* can suppress plants they prefer to feed on, and boost un-preferred plant species (Ritchie and Tilman 1992). There are some promising solutions should generalist grasshoppers like *M. femurrubrum* be found to hinder plant restoration. Installing log piles for lizard habitat effectively reduced grasshopper populations on glades and allowed the desired plants to flourish (Van Zandt et al. 2005). Similar habitat manipulation might work on smaller scale prairie reconstructions.

Conclusion

Our study produced results that can help future reconstruction projects in two ways. Monitoring can be more effective by focusing on certain taxa. The eleven species not found on reconstructions, as well species that were simply less abundant on reconstructions, such as *P. nebrascensis*, warrant further monitoring and investigation into their habitat requirements. The species that were very abundant on reconstructions

could also influence the reconstruction process itself. Their impact on other parts of highly dynamic reconstruction ecosystems should be clarified for future reconstruction projects. Grasshopper monitoring studies should continue to incorporate a community level perspective. It may be tempting to focus on some of the species that studies like this suggest are particularly important, but grasshopper populations are highly variable, meaning the dominant species may change frequently (Campbell et al. 1974, Capinera and Thompson 1987, Evans 1988).

Table 2.1. Grasshopper taxa captured in 2016 and 2017.

Grasshopper taxa	Diet	Wing length
<i>Amphitornus coloradus</i>	grass	long
<i>Arphia sulphurea</i>	mixed	long
<i>Arphia xanthoptera</i>	grass	long
<i>Campylacantha olivacea</i>	mixed	short
<i>Chortophaga viridifasciata</i>	grass	long
<i>Dichromorpha viridis</i>	grass	short
<i>Dissosteira carolina</i>	mixed	long
<i>Encoptolophus sordidus</i>	grass	long
<i>Hesperotettix</i>	forbs	long
<i>Hippiscus ocelote</i>	grass	long
<i>Hypochlora alba</i>	forbs	short
<i>Melanoplus bivittatus</i>	mixed	long
<i>Melanoplus confusus</i>	mixed	long
<i>Melanoplus differentialis</i>	mixed	long
<i>Melanoplus femurrbrum</i>	mixed	long
<i>Melanoplus flavidus</i>	forbs	long
<i>Melanoplus gracilis</i>	grass	short
<i>Melanoplus inconspicuous</i>	forbs	short
<i>Melanoplus keeleri</i>	forbs	long
<i>Melanoplus sanguipines</i>	mixed	long
<i>Melanoplus scudderi</i>	forbs	short
<i>Mermiria bivittata</i>	grass	long
<i>Orphulella pelidna</i>	grass	long
<i>Orphulella speciosa</i>	grass	long
<i>Paratylotropidia brunneri</i>	unknown	short
<i>Phoetaliotes nebrascensis</i>	grass	short
<i>Pseudopomala brachyptera</i>	grass	short
<i>Schistocerca alutacea</i>	forbs	long
<i>Schistocerca americana</i>	mixed	long
<i>Schistocerca obscura</i>	mixed	long
<i>Stethophyma celata</i>	grass	long
<i>Syrbula admirabilis</i>	grass	long

Table 2.2. Numbers of grasshoppers captured in 2016 and 2017.

	Wah'Kon-Tah	North	Linscomb	Schell
Remnant	556	171	249	101
Reconstruction	340	348	532	138

Table 2.3 Grasshopper species only found on remnants or reconstructions.

Remnant	Reconstruction
<i>Hypochlora alba</i>	<i>Hippiscus ocelote</i>
<i>Melanoplus inconspicuus</i>	<i>Dissosteira carolina</i>
<i>Melanoplus confusus</i>	
<i>Melanoplus flavidus</i>	
<i>Mermiria bivittata</i>	
<i>Orphulella speciosa</i>	
<i>Paralytropidia brunneri</i>	
<i>Pseudopomala brachyptera</i>	
<i>Schistocerca obscura</i>	
<i>Stethophyma celata</i>	

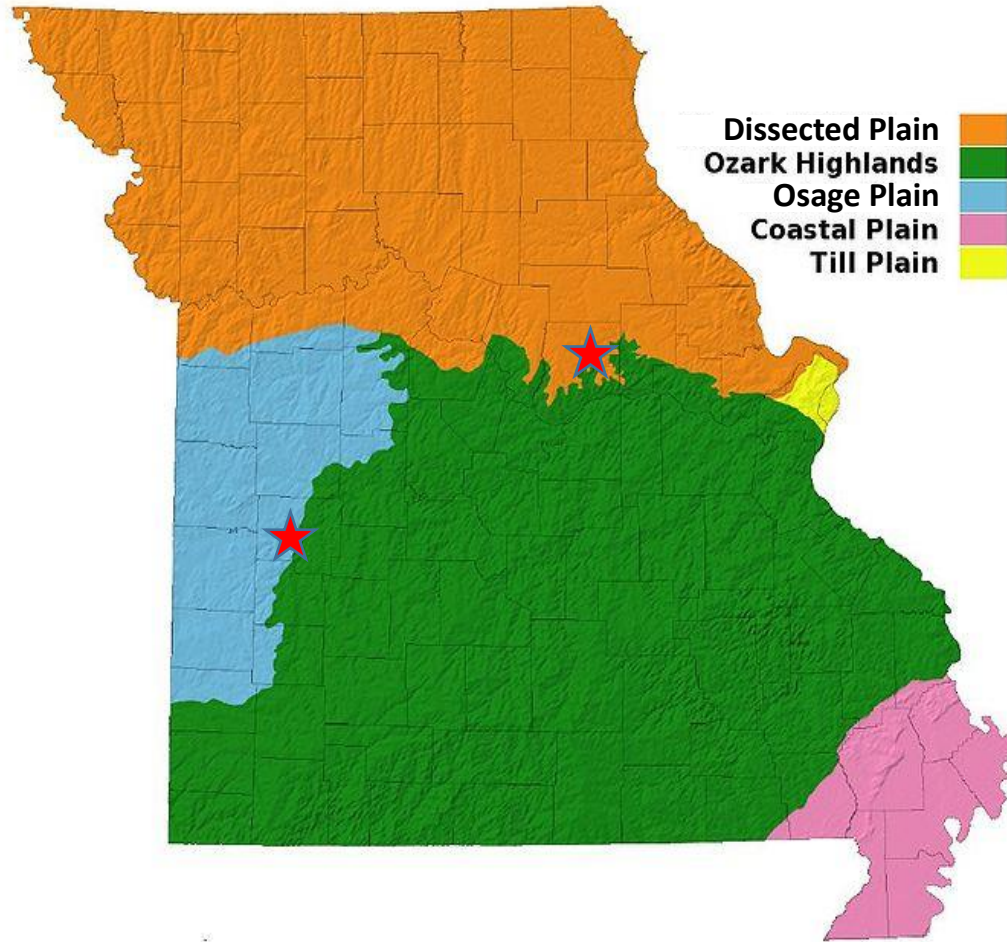


Figure 2.1. Ecoregions of Missouri. Wah’Kon-Tah, Linscomb, and Schell-Osage prairies, indicated by the red star in the Osage Plains, are located in St. Clair County. The North prairies, located in Calloway County, are indicated by the red star in the Dissected Plains. Figure, with the exception of the stars, created by Kbh3rd at Wikipedia using Missouri Spatial Data Information.

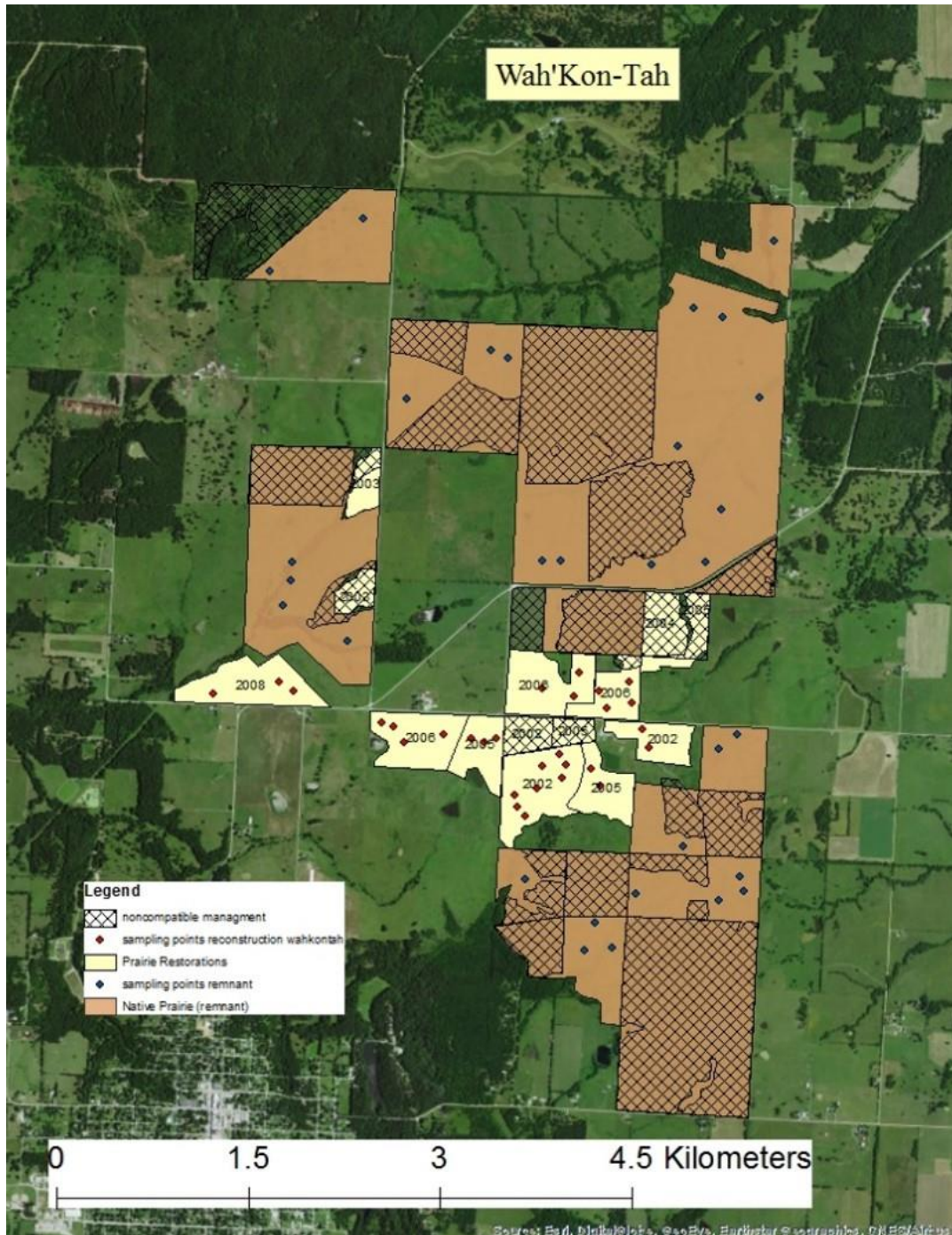


Figure 2.2. Wah’Kon-Tah Prairie, with transects from 2016 displayed as dots. Remnant prairie is brown, reconstructions are tan. Hashed areas were not sampled due to management practices. ArcMap 10.3.

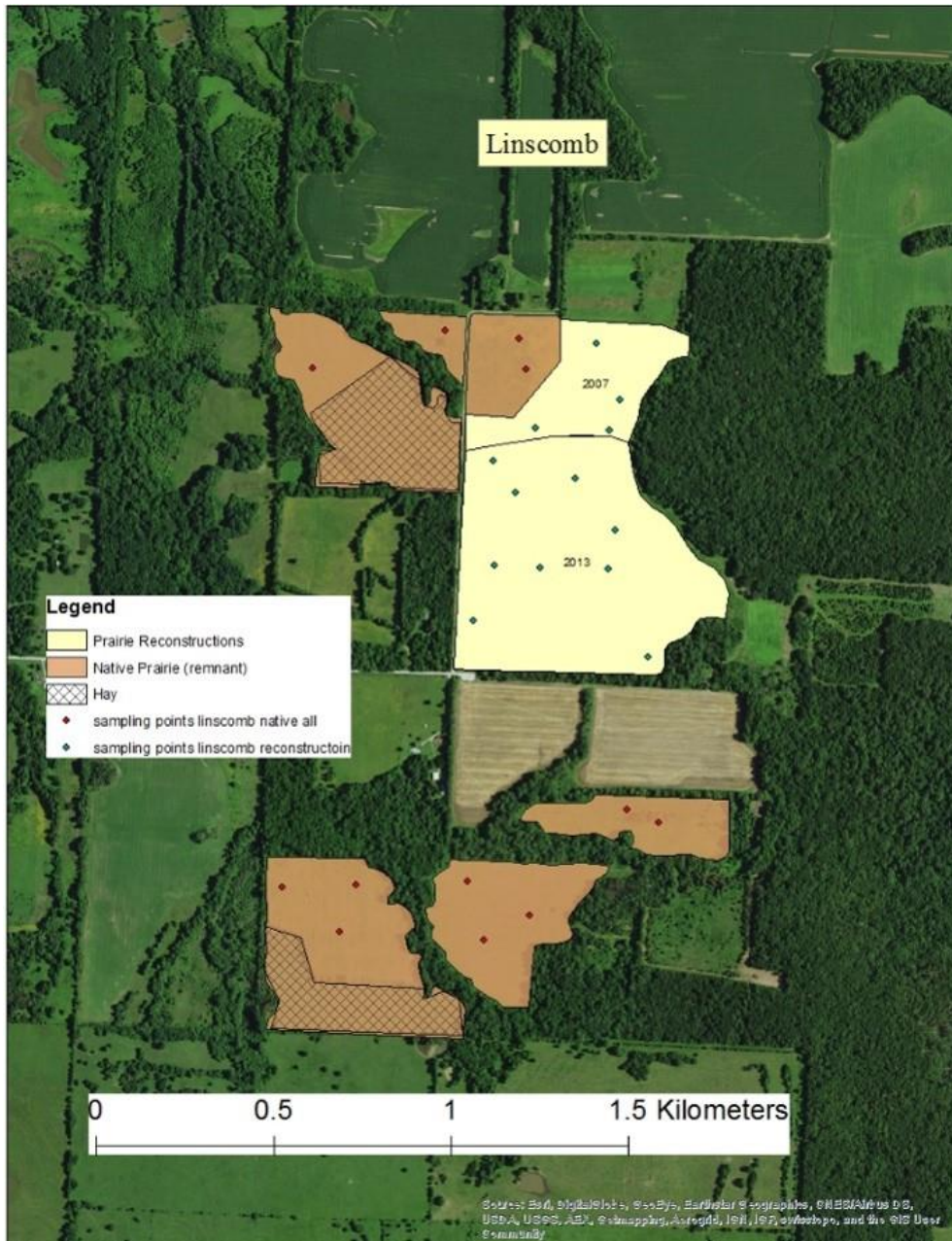


Figure 2.3. Prairie at Linscomb Wildlife Area, with transects from 2016 displayed as dots. Remnant prairie is brown, reconstructions are tan. Hashed areas were not sampled due to management practices. ArcMap 10.3.

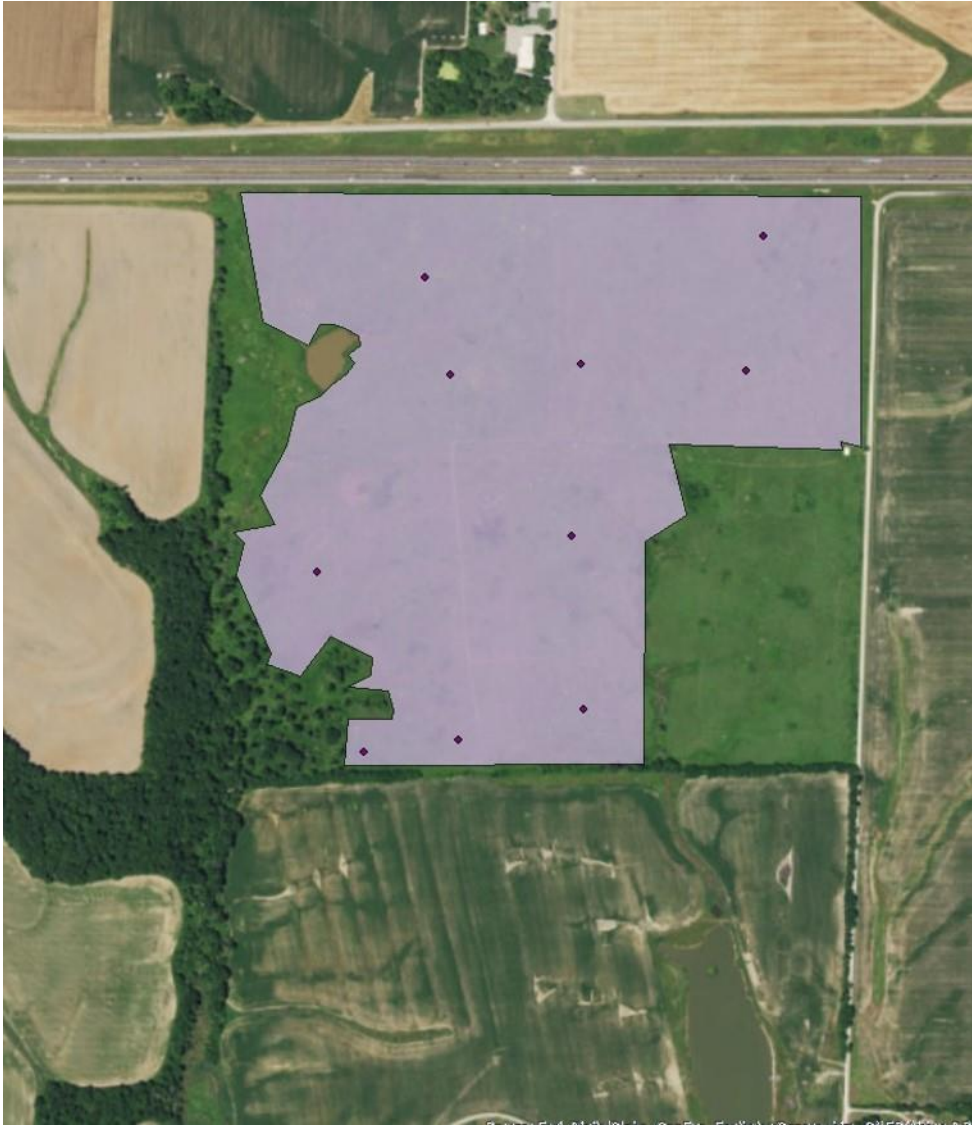


Figure 2.4. North remnant, Tucker Prairie, with transects from 2017 displayed as dots. ArcMap 10.3.



Figure 2.5. North reconstruction, Prairie Fork Conservation Area, with transects from 2016 displayed as dots. ArcMap 10.3.

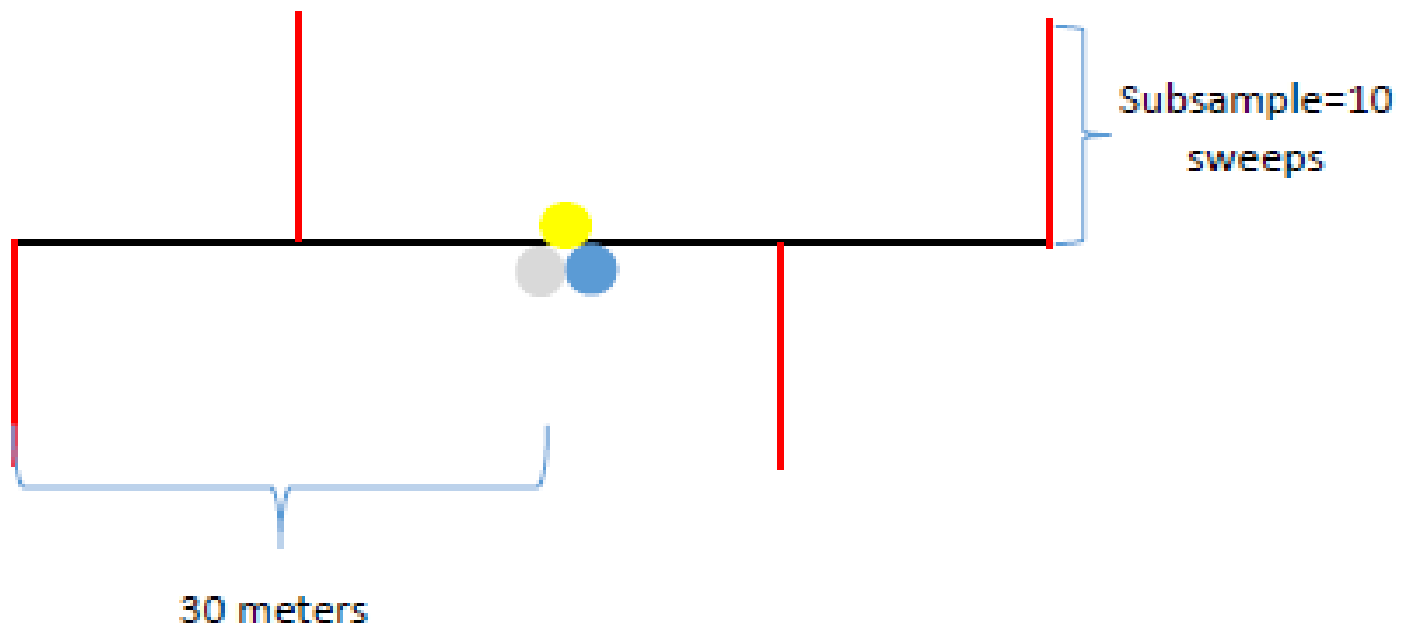


Figure 2.6. Diagram of a transect. Red lines mark where we conducted sweeps. No sweeping was done at the center of the transect because bee bowls were placed there at Wah'Kon-Tah and North prairies.



Figure 2.7. Sweeping at Schell.



Figure 2.8. Measuring vegetation density with a Robel pole. The observer, positioned 4 meters from the pole at a height of 1 meter, records the lowest visible decameter on the pole.

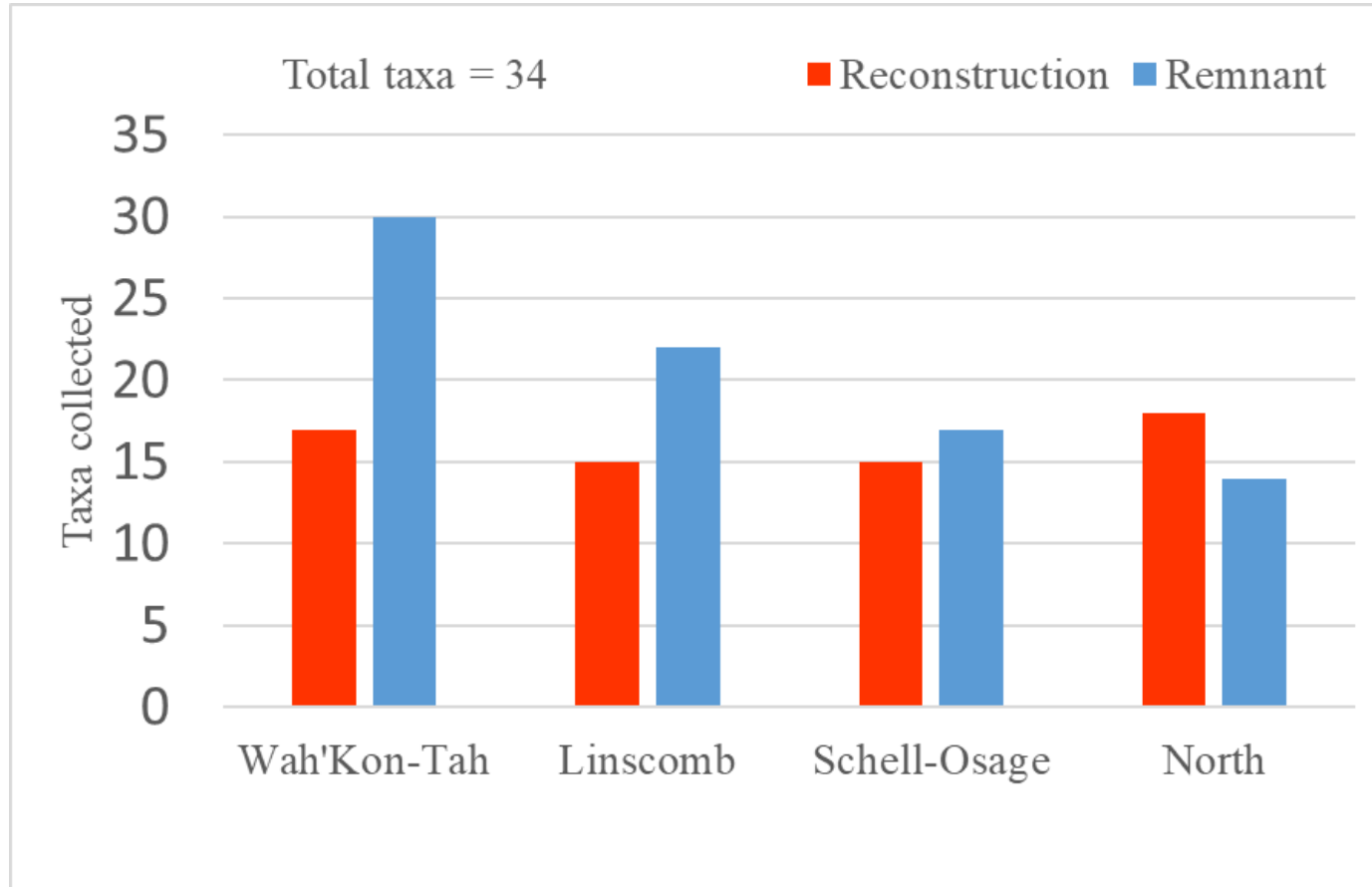


Figure 2.9. Number of grasshopper taxa (lowest possible identification: species or genus) from 2016 and 2017.

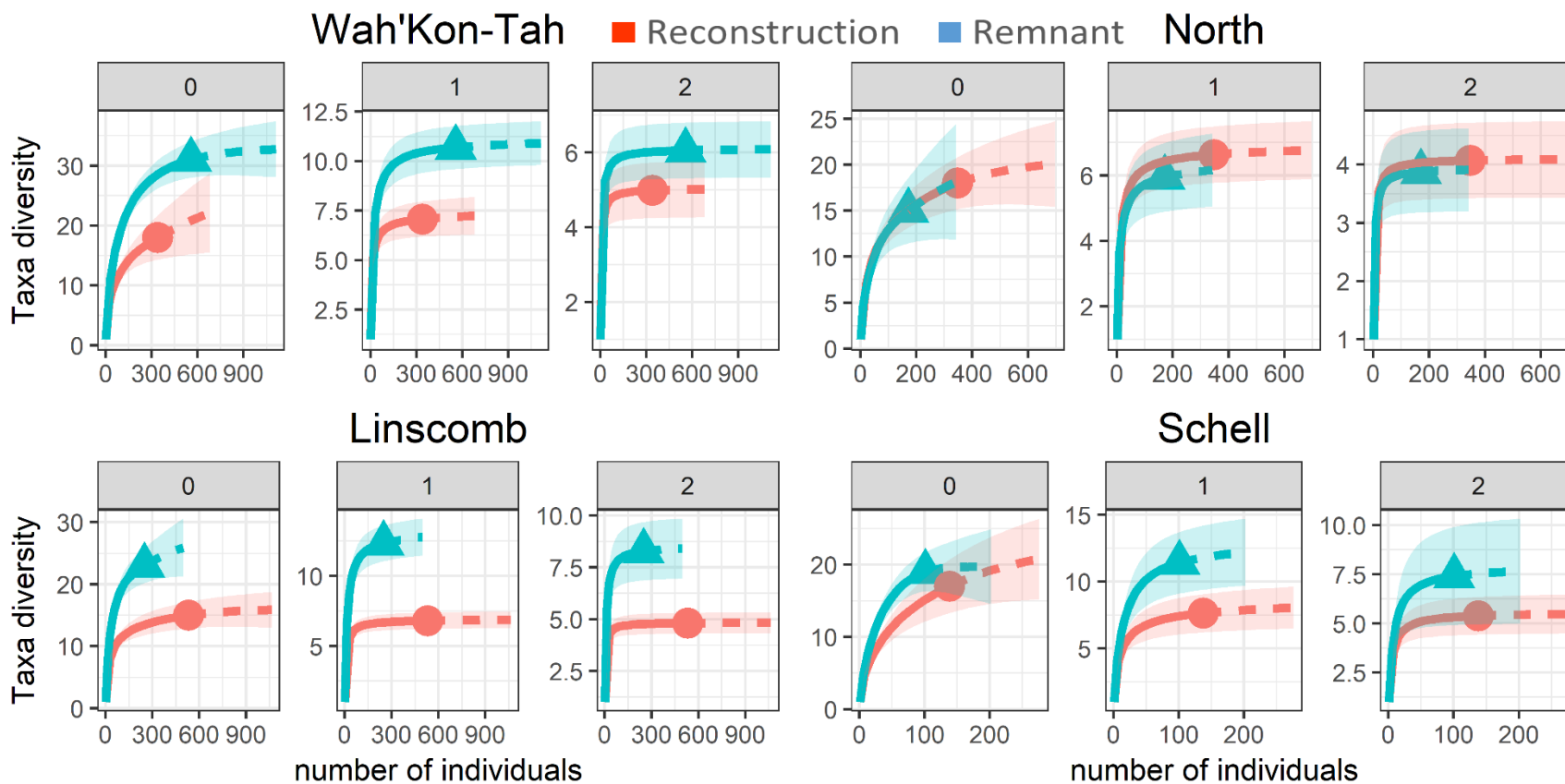


Figure 2.10. Sample-based rarefaction and extrapolation of Hill number diversity. 0 = species richness, 1 = Shannon diversity, and 2 = Simpson diversity. Shaded areas represent 95% confidence intervals.

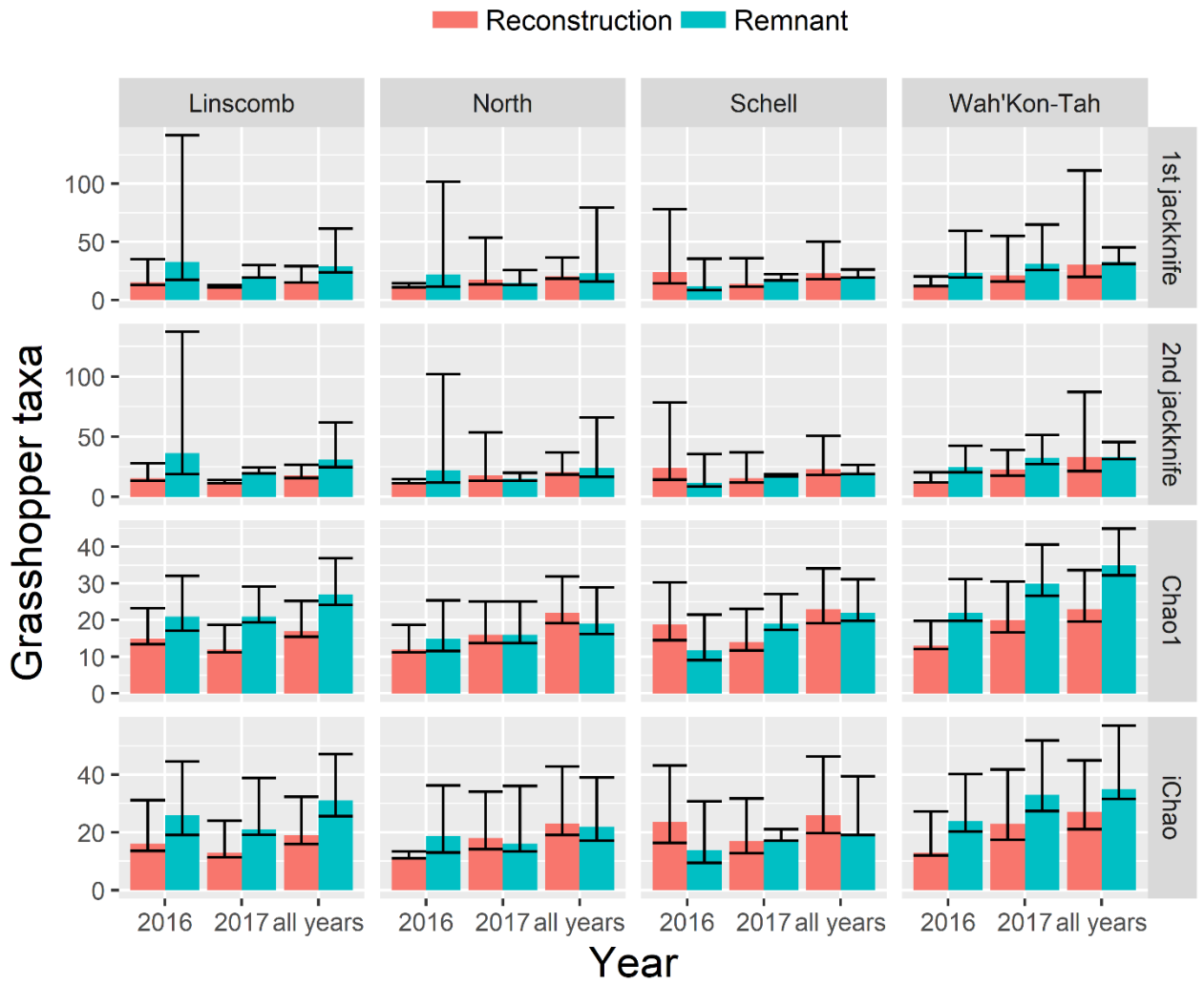


Figure 2.11. Asymptotic, non-parametric estimates of grasshopper taxa richness. Bars represent 95% confidence intervals.

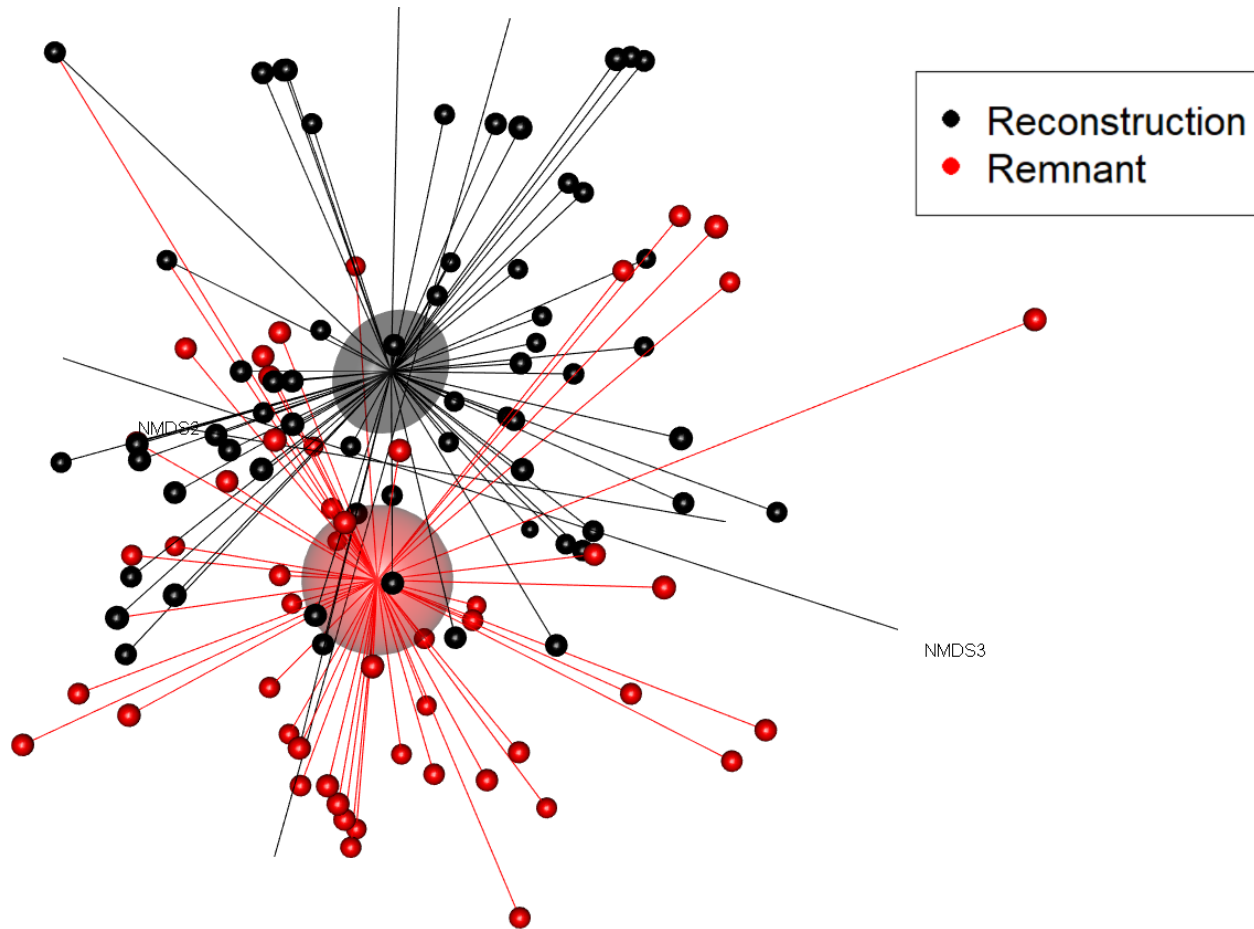


Figure 2.12. NMS ordination (3-dimensional) of grasshopper communities. Dots represent communities at transects. Spheres represent 95% confidence intervals around the centroids of reconstructions (black) and remnants (red).

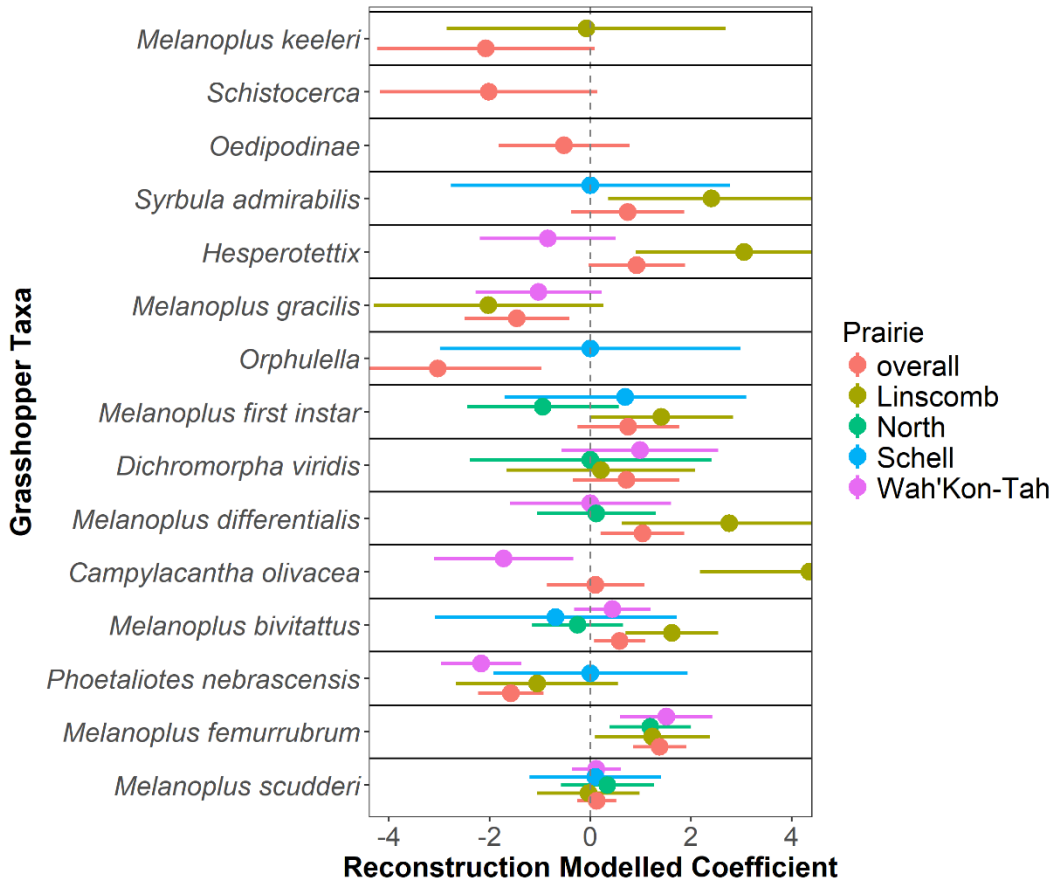


Figure 2.13. Coefficients, with 95% confidence intervals, of the effect of prairie *status* (reconstruction or remnant) from multivariate models of the abundance of taxa used in ordination. Positive coefficients signify a higher abundance on reconstructions, negative coefficients signify higher abundance on remnants. There are up to five coefficients for each species, representing models for Wah’Kon-Tah, North, Linscomb, Schell and the prairies combined with no interaction (overall). Model coefficients with very large standard errors are not shown. There was a significant interaction in univariate abundance models for *Campylacantha olivea* and *Orphulella*.

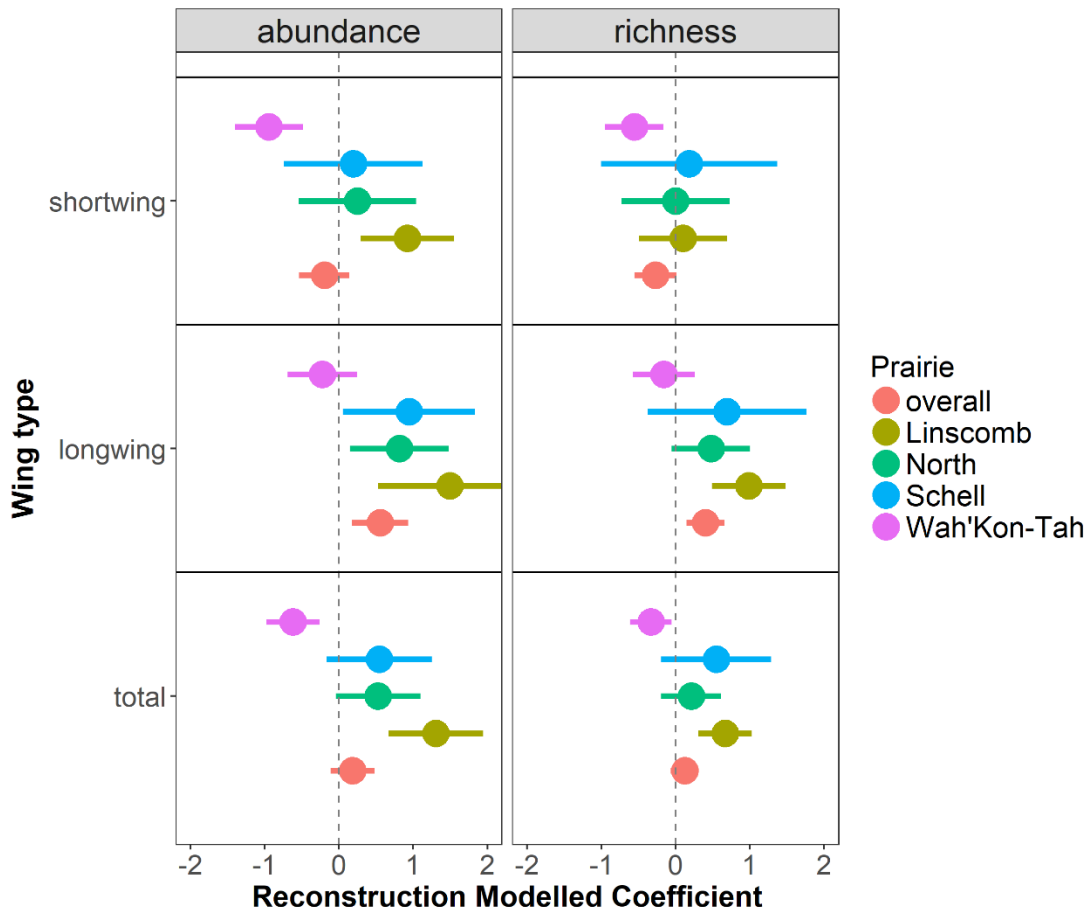


Figure 2.14. Coefficients, with 95% confidence intervals, for the effect of prairie *status* (reconstruction or remnant) from multivariate models of grasshopper abundance and richness according to wing length. Positive coefficients signify a higher abundance on reconstructions, negative coefficients signify higher abundance remnants. There are up to four coefficients for each species, representing models for Wah'Kon-Tah, North, Linscomb and the prairies combined with no interaction (overall).

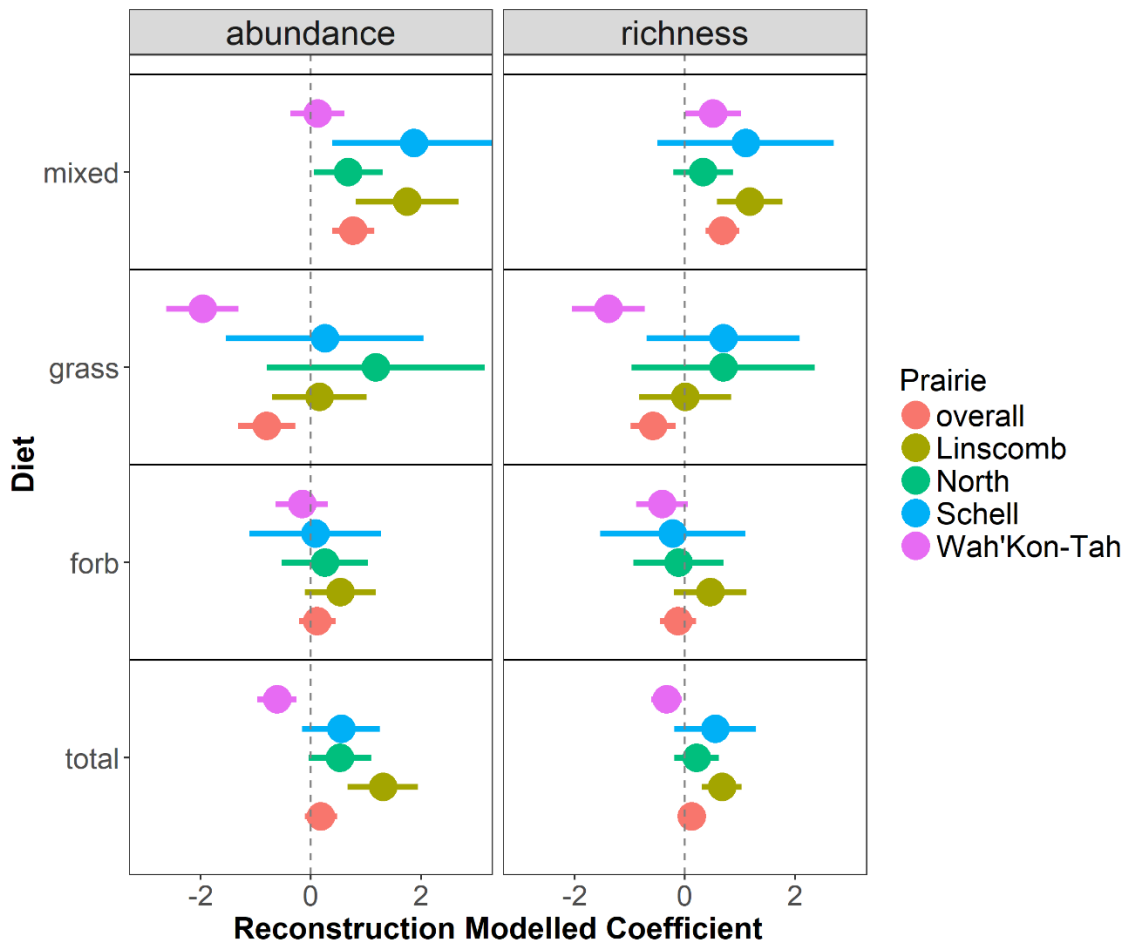


Figure 2.15. Coefficients, with 95% confidence intervals, for the effect of prairie *status* (reconstruction or remnant) from multivariate models of grasshopper abundance and richness according to diet. Positive coefficients signify a greater abundance on reconstructions, negative coefficients signify greater abundance remnants. There are up to five coefficients for each species, representing models for Wah’Kon-Tah, North, Linscomb, Schell and the prairies combined with no interaction (overall).

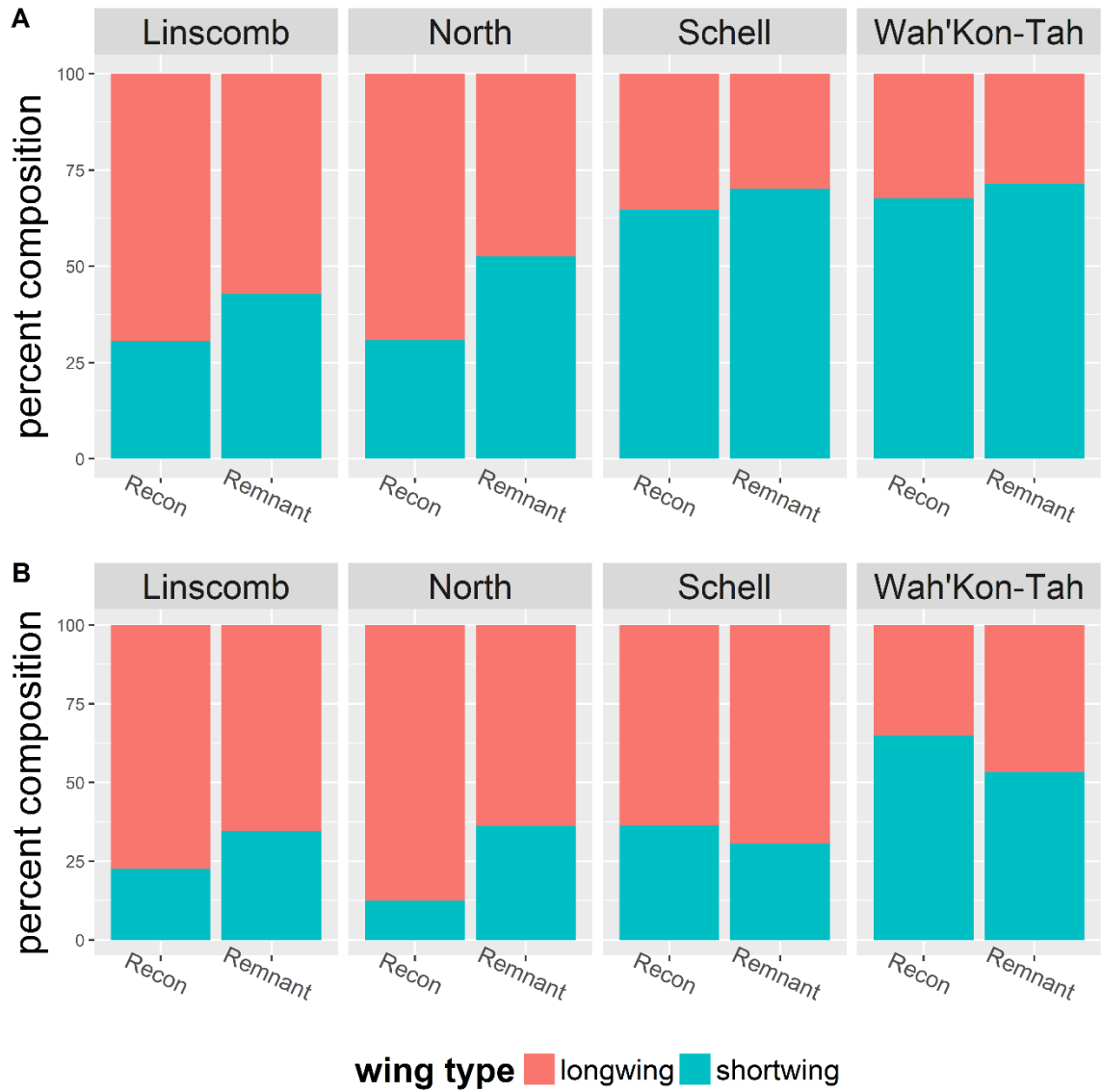


Figure 2.16. Proportions of grasshoppers captured representing different wing length categories in 2016 (A), and 2017 (B).

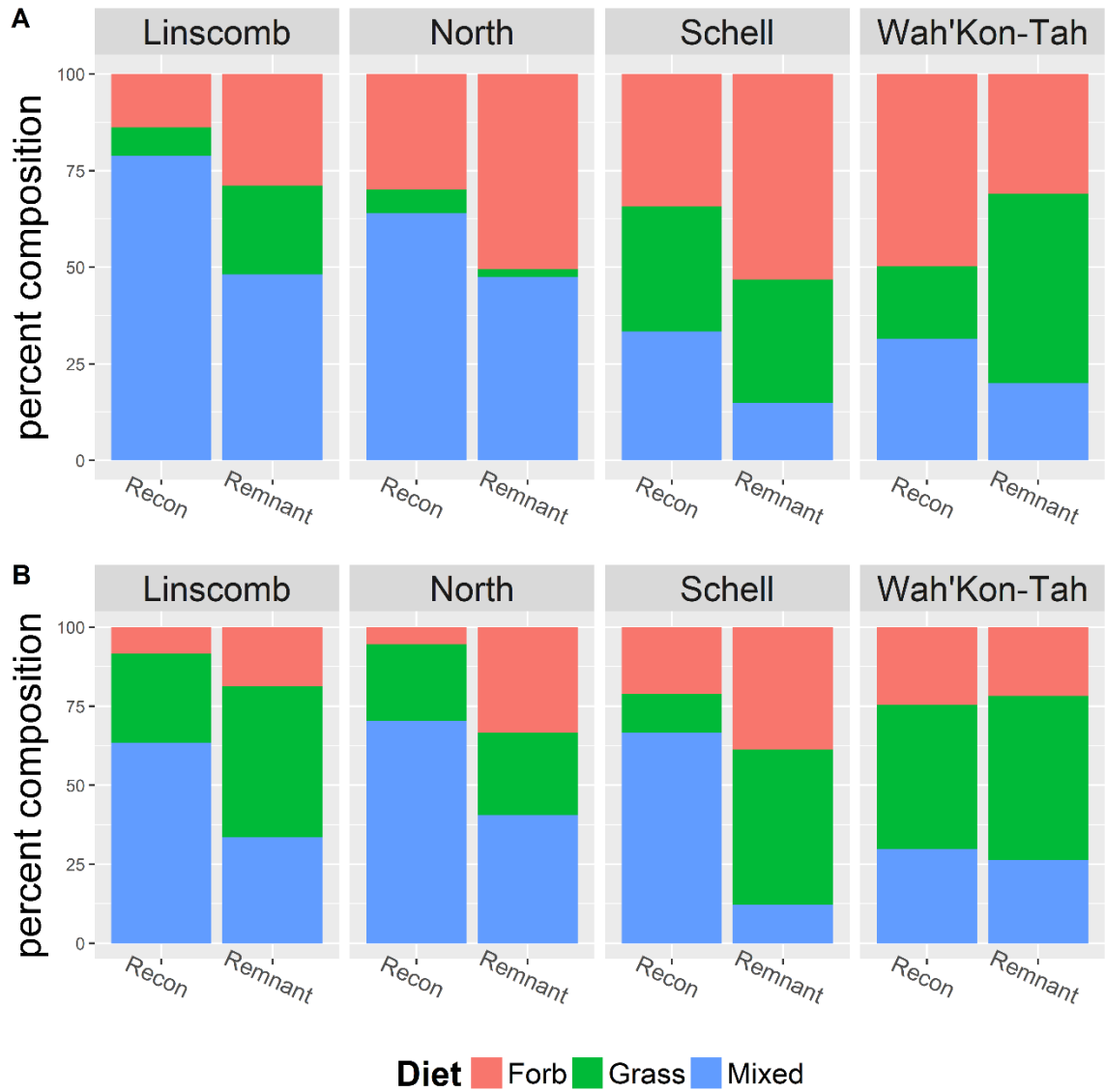


Figure 2.17. Proportions of grasshoppers captured representing different diet categories in 2016 (A), and 2017 (B).

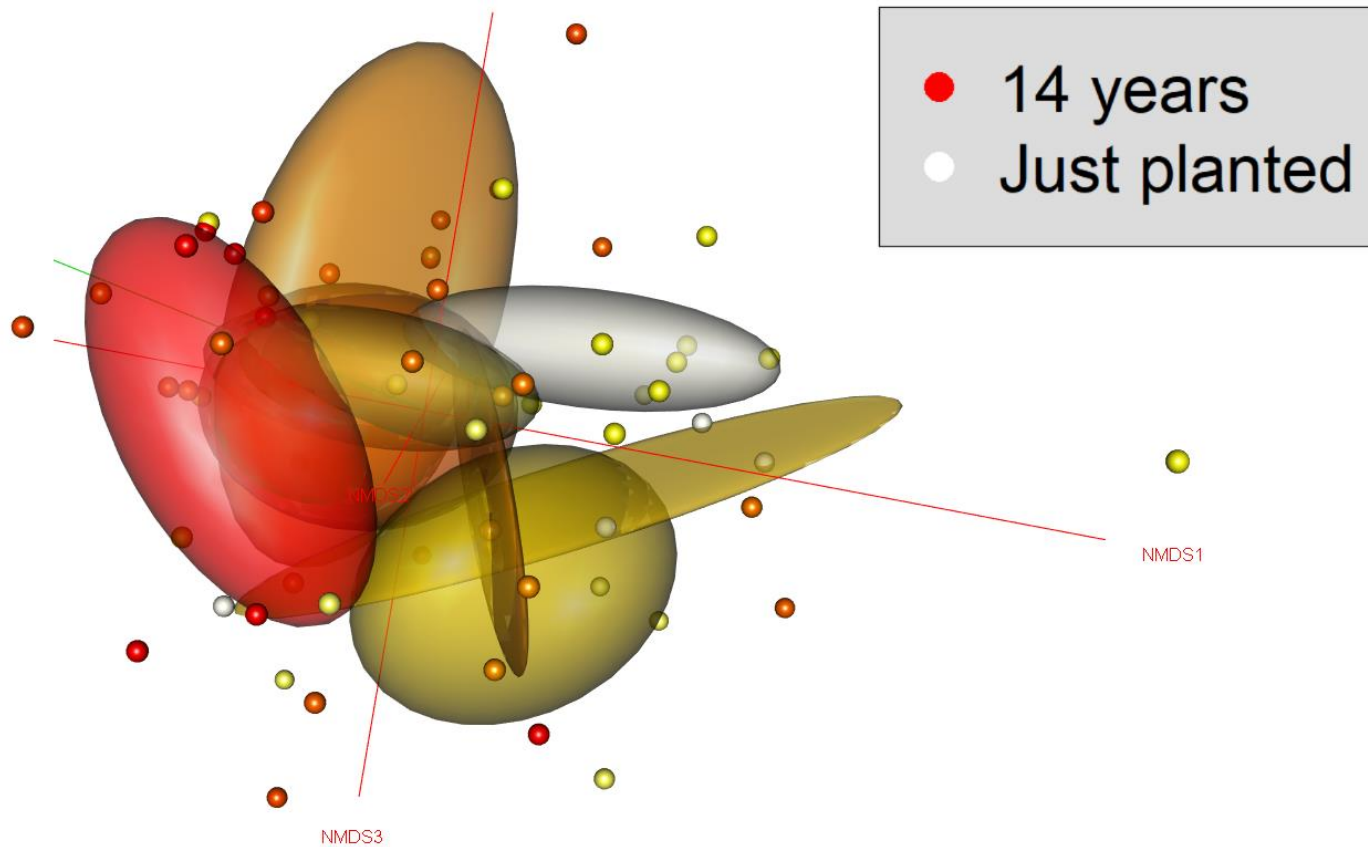


Figure 2.18. NMS ordination ($k = 3$, stress = 0.146) of grasshopper communities on reconstructions. Dots represent communities at transects. Spheres represent 95% confidence intervals around the centroids of reconstructions of the same age. The color of dots and centroids moves from white to yellow, to orange, then to red with increasing age.

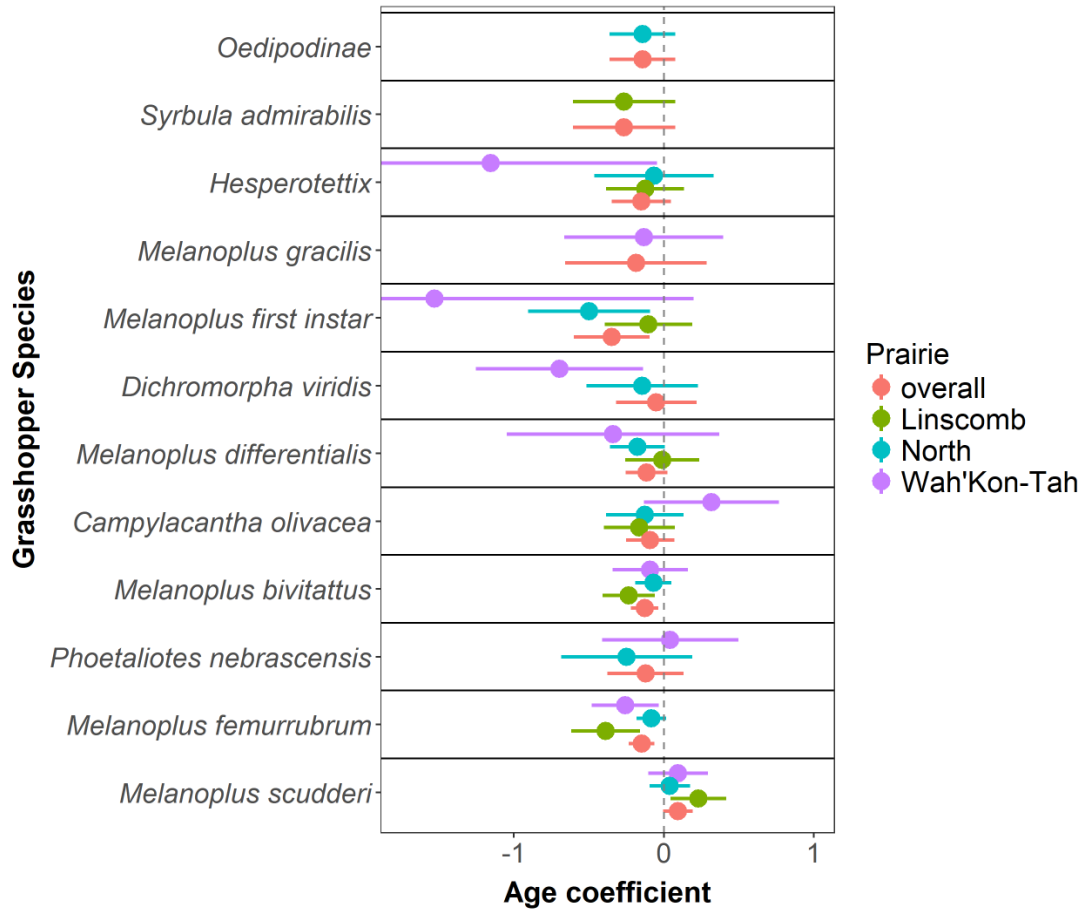


Figure 2.19. Coefficients with 95% confidence intervals of *age* from multivariate abundance model on the grasshopper taxa used in ordination. Positive coefficients signify a greater abundance on older reconstructions, negative coefficients signify greater abundance on younger reconstructions. There are up to four coefficients for each species, representing models for Wah’Kon-Tah, North, Linscomb and the prairies combined with no interaction (overall). Model coefficients with very large standard errors are not shown.

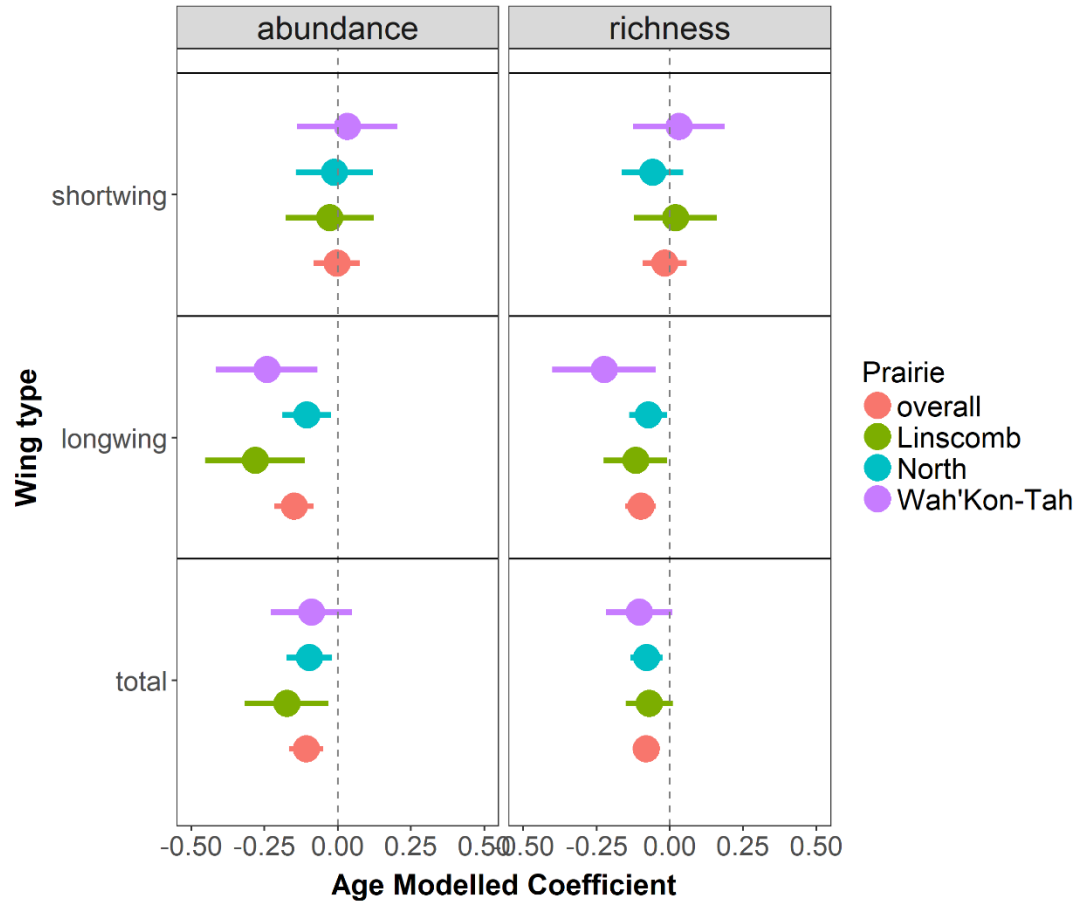


Figure 2.20. Coefficients for *age* from multivariate models of grasshopper abundance and richness according to wing length, and total abundance. Positive coefficients signify increasing abundance with age of a reconstruction, negative coefficients signify decreasing abundance with age. There are up to four coefficients for each species, representing models for Wah'Kon-Tah, North, Linscomb and the prairies combined with no interaction (overall).

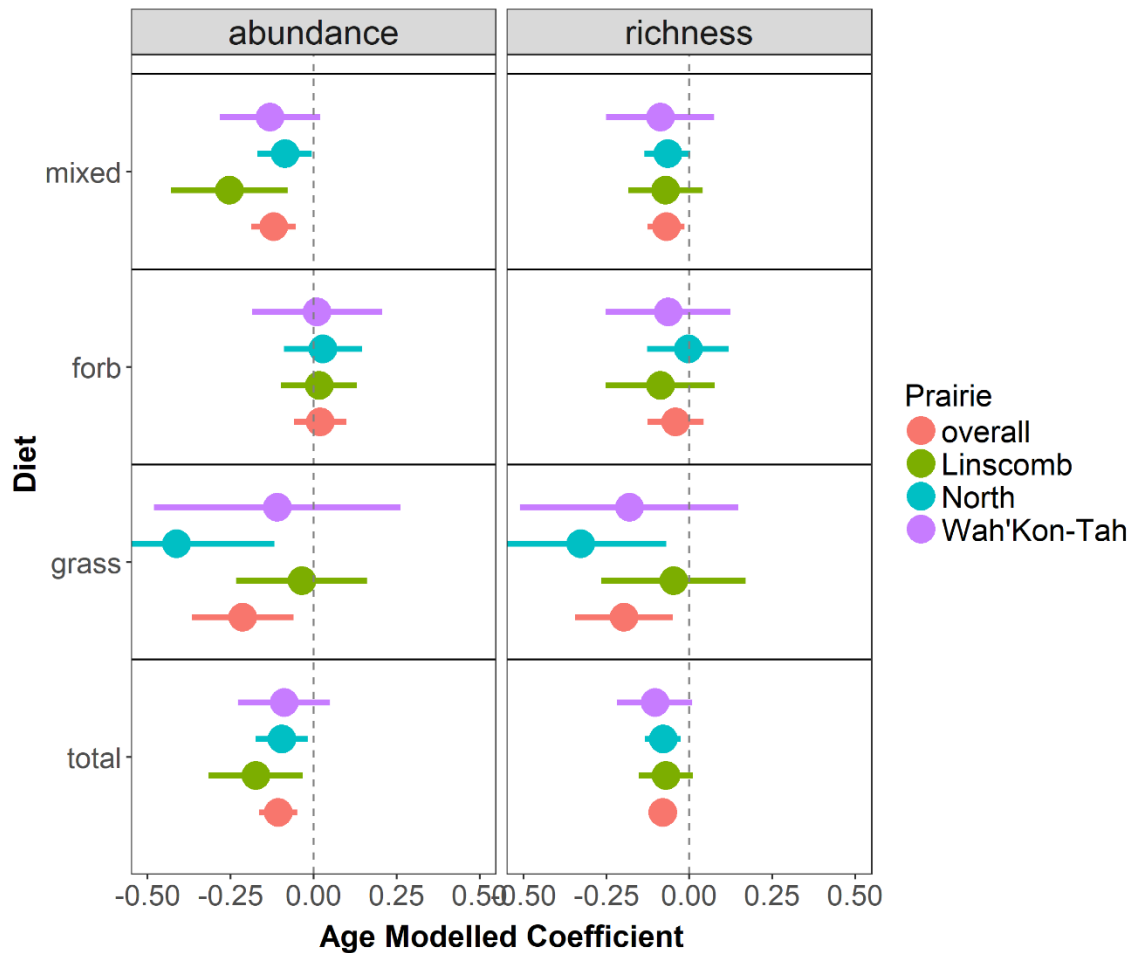


Figure 2.21. Coefficients for the effect of reconstruction age from multivariate models of grasshopper abundance and richness according to diet, and total abundance. Positive coefficients signify increasing abundance with age of a reconstruction, negative coefficients signify decreasing abundance with age. There are up to four coefficients for each species, representing models for Wah'Kon-Tah, North, Linscomb and the prairies combined with no interaction (overall).

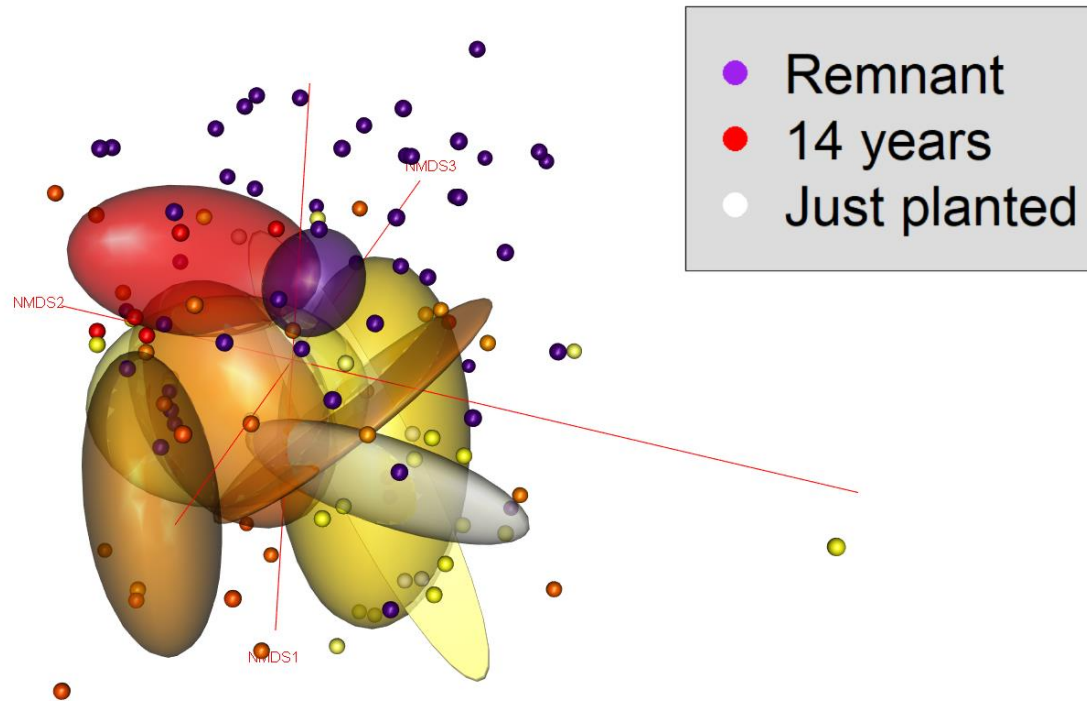


Figure 2.22. NMS ordination (3-dimensional) of grasshopper communities. Dots represent communities at transects. Spheres represent 95% confidence intervals around the centroids of reconstructions of the same age, and of remnants. For reconstructions, the color of dots and centroids moves from white to yellow, to orange, then to red with increasing age. Remnants are purple.

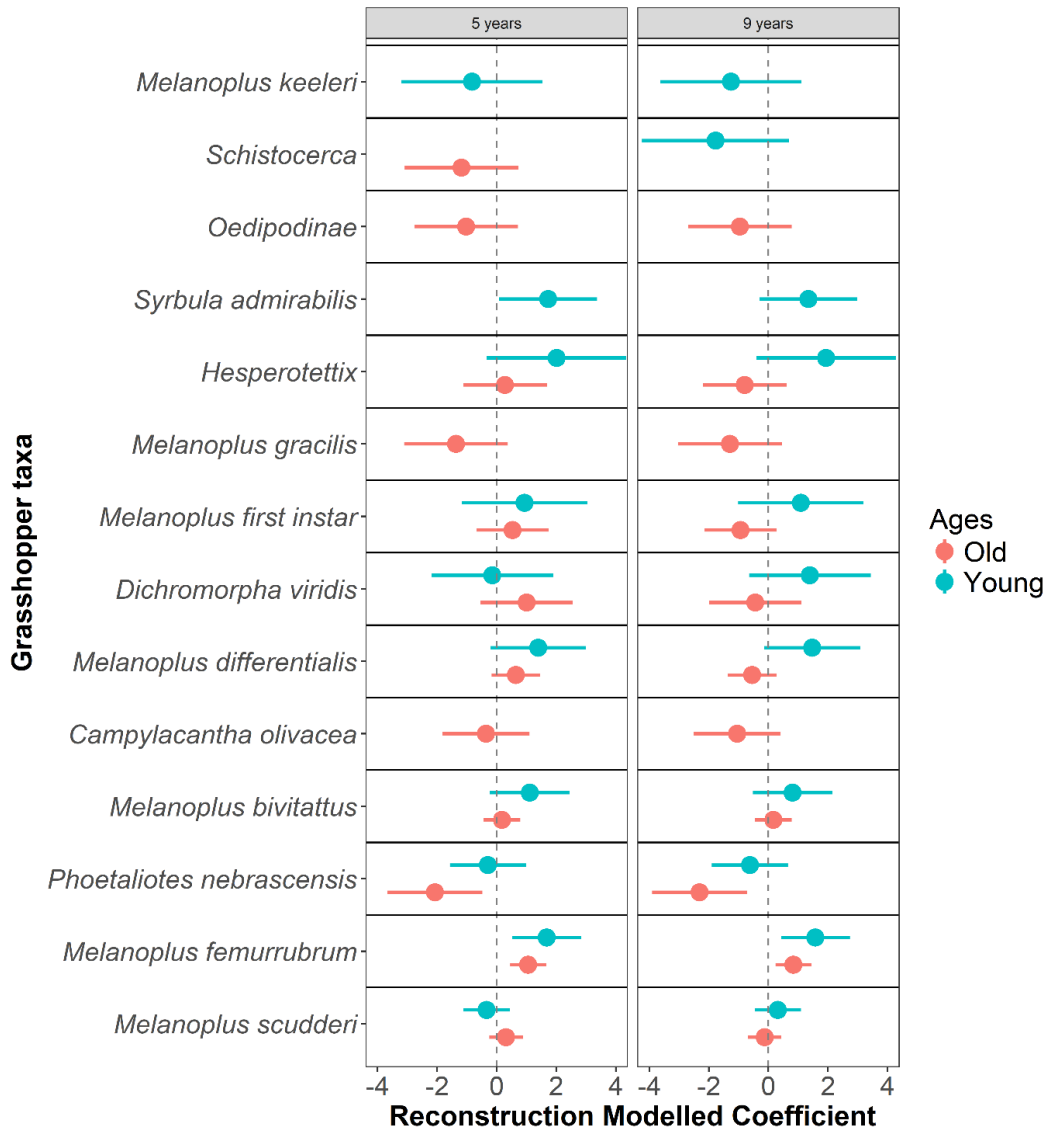


Figure 2.23. Coefficients with 95% confidence intervals of *age group* from the multivariate abundance model on the grasshopper taxa used in the ordination. Reconstructions were split into two age groups at five and nine years. Positive coefficients signify a greater abundance on reconstructions, negative coefficients signify greater abundance on remnants. Model coefficients with very large standard errors are not shown.

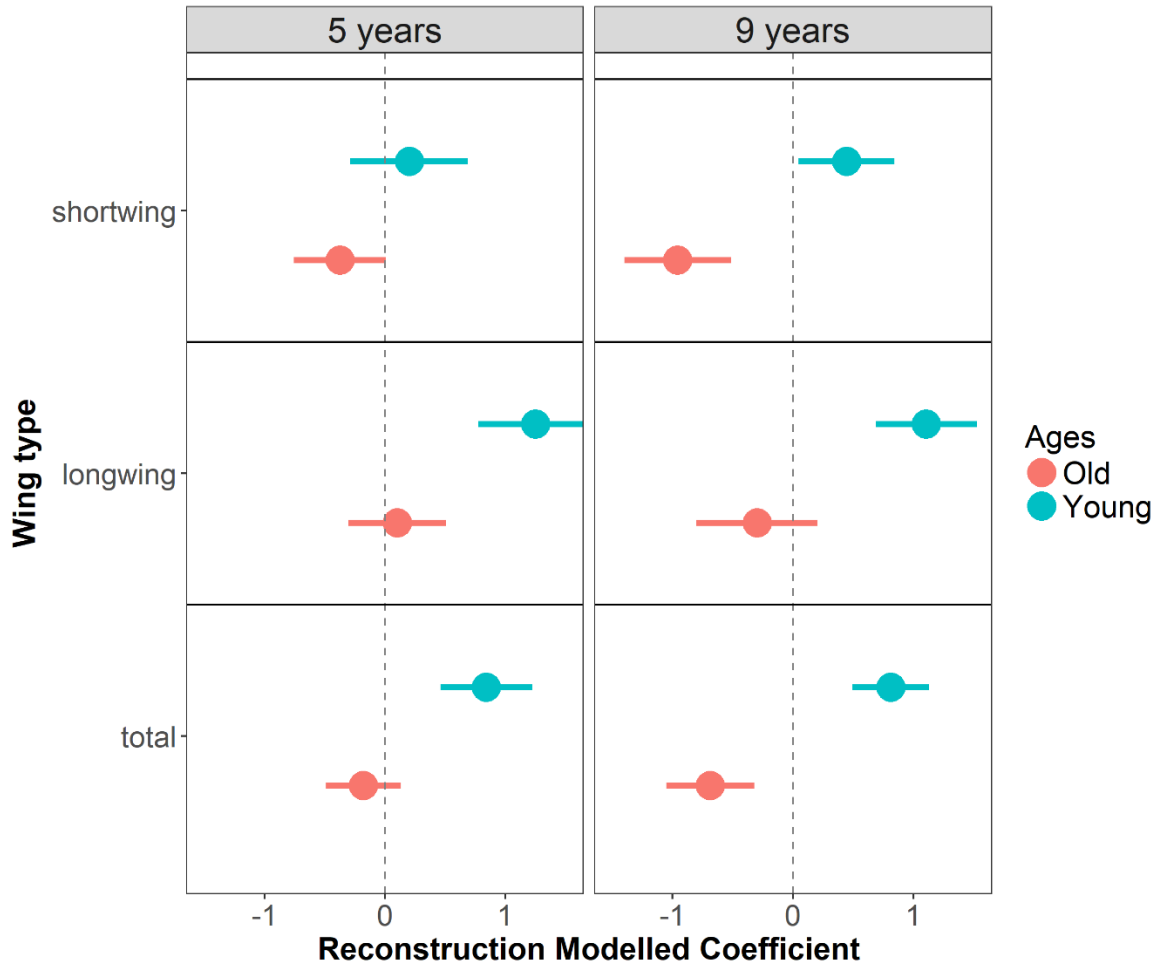


Figure 2.24. Coefficients for *age group* from multivariate models of grasshopper abundance according to wing length, and total abundance. Positive coefficients signify greater abundance on reconstructions, negative coefficients signify greater abundance on remnants.

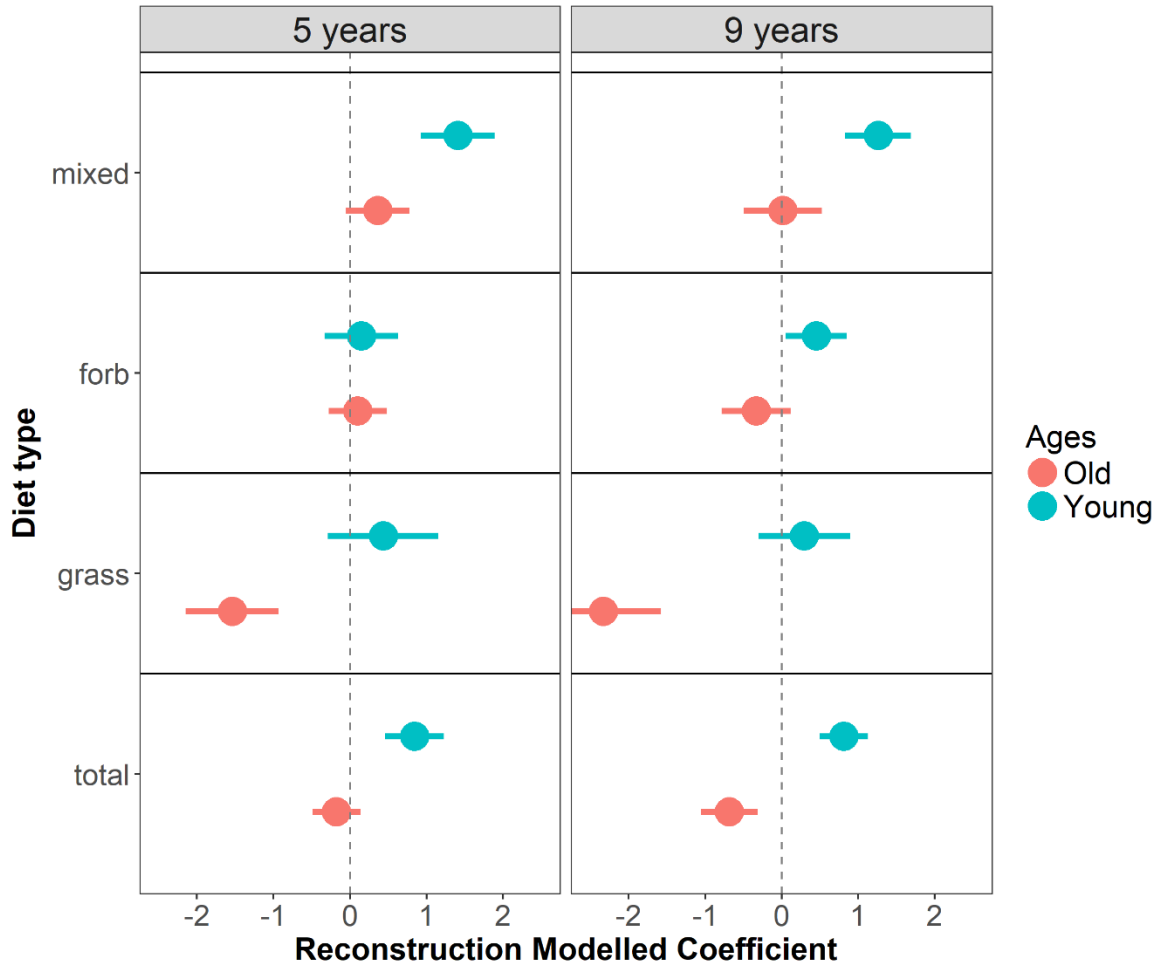


Figure 2.25. Coefficients for *age groups* from multivariate models of grasshopper abundance according to wing length, and total abundance. Positive coefficients signify greater abundance on reconstructions, negative coefficients signify greater abundance on remnants.

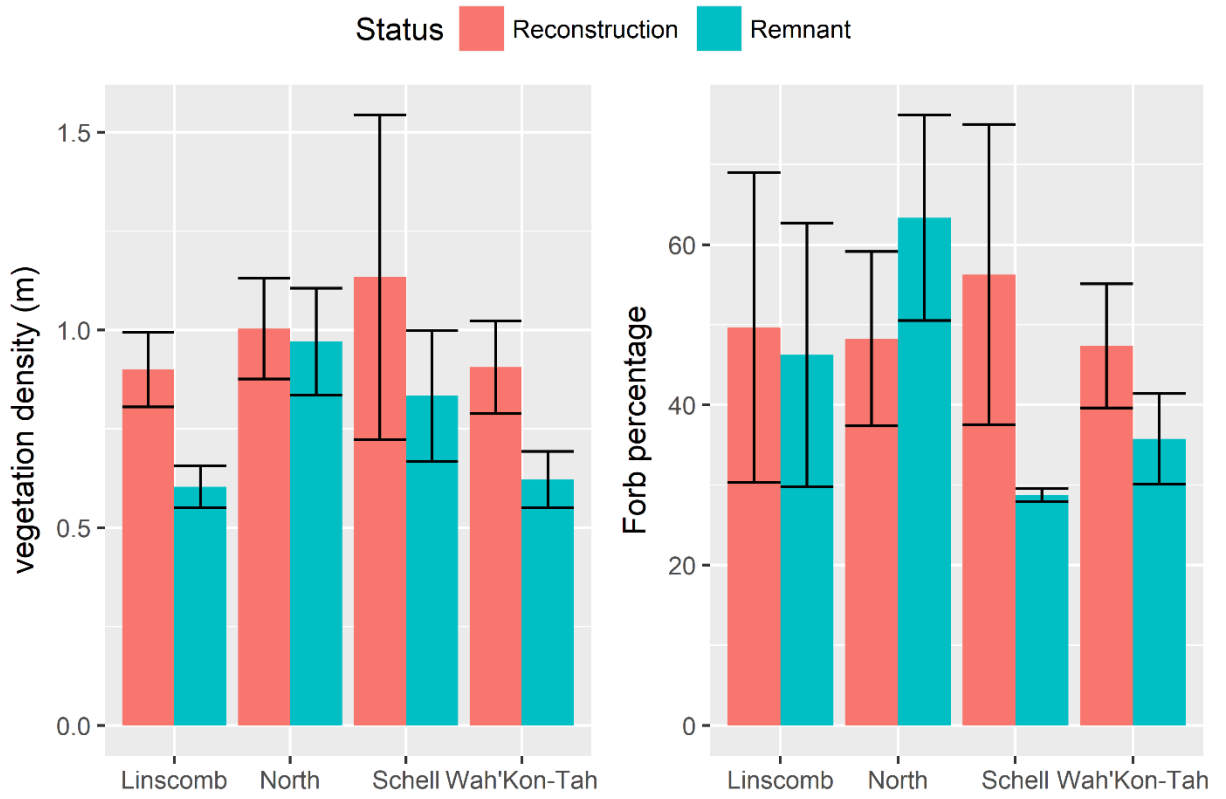


Figure 2.26. Mean vegetation measurements with 95% confidence intervals.

CHAPTER 3

Bee communities on reconstructed and remnant prairies

Introduction

Grasslands are one of the most threatened ecosystems in the world. North America has seen a tremendous amount of prairie converted to agricultural use, leaving less than 5% of prairies intact (Samson and Knopf 1994). Various grassland animals and plants have experienced population declines over the last 100 years as well, due in part to habitat loss and fragmentation (New 1993, Brennan and Kuvlesky Jr 2005). When habitat conservation fails, as it clearly did for North American prairies, habitat restoration can toss a lifeline to imperiled species drowning in a sea of corn and soy. There are plenty of floundering insects, birds, mammals, and plants that deserve a spot on the restoration rescue raft, but one group stands out because of their beneficial impact on the very agricultural matrix that threatens them: bees.

Alarming losses in the diversity and abundance of some native bees (Colla and Packer 2008) alongside declines in their economically valued imported cousin, the honeybee (*Apis mellifera*), have led to increased research and conservation initiatives for bees and pollinators. Habitat loss no doubt plays some role in bee decline (Grixti et al. 2009, Cameron et al. 2011), meaning remaining tallgrass prairies may act as vital reservoirs of bee diversity. There are several examples from the midwestern United States that highlight the importance of remnant prairie habitat for bee diversity and conservation. Compared to ruderal areas, prairies in Iowa contained more bee species, more rare species, and overall more bees (Kwaiser and Hendrix 2008). In Illinois, prairie

remnants and old fields contained similar bee abundances, but remnants were more diverse and differed in community composition (Tonietto et al. 2017). Efforts to improve bee habitat outside remnant prairies generally fall into one of two strategies. The first strategy is integrating bee friendly practices on agricultural or urban environments. Habitat enhancements in agricultural systems, such as leaving untilled ground for soil nesters, putting out nest boxes for cavity of stem nesters, and planting wildflowers on field margins are effective in boosting wild bee diversity and abundance (Tonietto et al. 2018). Similar practices can work in urban environments as well (Hernandez et al. 2009, Tonietto et al. 2018). Implementing bee friendly practices in agricultural and urban ecosystems may be beneficial for many native bees, but there remain conservative species that appear to be linked to high quality prairie remnants. For species such as the blue sage bee (*Tetraloniella cressoniana*) (Arduser 2016), which are strongly linked to healthy prairie ecosystems, preserving and expanding prairies are the only way to secure their persistence. The only way to expand prairie habitat is through restoration.

Restoration is the second strategy for boosting and protecting bee diversity. Restoration can range from the rehabilitation of grazing lands to the full scale rebuilding of prairie from agricultural fields, which is referred to as reconstruction. Scientists and managers reconstructing tallgrass prairie generally attempt to create a plant community that corresponds to those found in local remnant prairies (Kurtz 2013). Seeding and continually reseeding with the appropriate native seed mixes will theoretically create the diverse mix of forbs and grasses that comprise tallgrass prairie vegetation communities (Kurtz 2013). Determining the correct seed mixes is a science in and unto itself, as the ideal mix may vary regionally (Diboll 1997, Larson et al. 2011), and in many cases is still

unknown. Reseeding reconstructions is likely necessary, as native plants can go locally extinct even after a decade or more (McLachlan and Knispel 2005). Burning, mowing, grazing, and spraying for invasive species are all common post-planting management practices on reconstructed prairies that can have unintended consequences for insects and other prairie animals (Kruess and Tschardtke 2002, Panzer 2002, Walker et al. 2004, Shochat et al. 2005, Humbert et al. 2010, Debinski et al. 2011). Habitat restoration is theoretically promising for rescuing imperiled species (Török and Helm 2017) and has been effective in practice both for plants (McLachlan and Knispel 2005), the usual proximate target of reconstruction, and for native bees (Tonietto et al. 2018).

Assessing the efficacy of restorations for native bees can be challenging due to the variable nature of insect populations (Fleishman and Murphy 2009), which can confound studies that only last a few years, and the substantial regional variation in bee community composition (Williams 2011). Additionally, tallgrass prairie ecosystems are dynamic (Evans 1988, Whiles and Charlton 2006), representing moving targets for restoration (Simberloff 1990). Studies examining bee communities on restorations have yielded somewhat inconsistent results. There is fairly strong evidence that bees colonize newly restored habitats quickly, resulting in species richness and abundances similar to remnant habitat within five years (Exeler 2009, Williams 2011, Griffin et al. 2017). Bee community composition on restorations, however, may converge with that found on remnants over time (Griffin et al. 2017), or remain distinct (Williams 2011; Tonietto et al. 2017). Although theoretically interesting, the trends in community composition are only useful to improving the restoration process if we connect the bee community to habitat characteristics, particularly those that can be managed. Consolidating species into

functional groups by their role in the ecosystem, or by their habitat requirements, can accomplish that.

Bees can be divided into functional groups based on nesting habitat and foraging requirements (Potts et al. 2003, Tonietto et al. 2017). Foraging groups include oligolectic, polylectic, and kleptoparasitic bees. Oligolectic bees can be considered pollen specialists because they only collect pollen from related plant taxa, while polylectic bees are considered generalists because they collect pollen from a wide range of unrelated plant families. Kleptoparasitic bees, sometimes referred to simply as parasitic, visit flowers to consume nectar and pollen but do not collect pollen to provision nests, instead depositing eggs in nests already provisioned by other species. Kleptoparasitic bees have been shown to be good indicators of high-quality grassland habitat (Sheffield et al. 2013). Specialist bees may also be good indicators because their populations suffer more than generalists in fragmented landscapes like Midwestern prairies (Brückmann et al. 2010). In Missouri, there is some evidence that remnant sites support more specialist and kleptoparasitic species than reconstructions (Arduser, unpublished data). Floral resources should be a major habitat influence on foraging functional group composition, and indeed there is evidence of significant impacts of floral abundance and diversity on bee communities (Potts et al. 2003). Linking bees with floral resources could lead to restorations with better plant communities for pollinators, which is already under investigation (Harmon-Threath and Hendrix 2015). In some cases, however, floral resources were not responsible for observed differences in bee communities (Williams 2011).

Another habitat characteristic that can affect bee community composition is the availability of nesting resources (Potts et al. 2003). Native bee species may nest in the

soil, plant stems, wood, or cavities (Ascher and Pickering 2017), and the availability of these resources can differ across landscapes, often due to management practices. Grazing and frequent fire can increase the abundance of soil nesting bees by exposing bare ground (Potts et al. 2003, Kimoto et al. 2012), whereas some stem and twig nesting bees appear to benefit from less frequent fire and more dead wood (Cane and Neff 2011) and stems for nesting (Cane et al. 2007). Soil properties and the availability of stems and wood for nesting can differ between reconstructions and remnants. Prairie reconstructions that were previously cultivated fields likely contain more homogenous, shallower soils than remnants (Baer et al. 2005) as well as greater soil compaction and less organic matter (Six et al. 1998). Stem nesting habitat may also differ between remnants and reconstructions because of differences in plant communities (Kindscher and Tieszen 1998, McLachlan and Knispel 2005, Middleton et al. 2010). More research involving simultaneous sampling of different locations and different ages of reconstructions is necessary to better understand bee communities on prairie reconstructions, and whether reconstructions can actually rescue declining bee species.

We had two objectives for our study. First, we compared bee (*Anthophila*) communities on reconstructions to those on remnants by evaluating species richness, diversity, and community composition at paired reconstructed and remnant prairies in Missouri. We sought to identify species or functional groups associated with remnants or reconstructions that could be used to monitor reconstructions and remnants in the future. Our second objective was to evaluate the effect of prairie reconstruction age on bee communities to determine if bee communities on reconstructions are converging with remnant bee communities. We hypothesized that bee communities of remnant and

reconstructed prairies would not differ in the number of species and diversity, but would differ in community composition. The community composition of bee nesting groups should differ between reconstructions and remnants because of soil and vegetation differences. Those community differences should diminish over time, with older reconstruction communities converging with remnants.

Methods

Site Selection

We sampled two areas containing prairies managed by the Missouri Department of Conservation. Wah'Kon-Tah Prairie was located within St. Clair County in the Upper Osage Grasslands of southwestern Missouri (Fig. 2.1) and contained contiguous remnant and reconstructed prairies (Fig. 2.2). The other area was located 135 miles northeast in the Central Dissected Plains in Calloway County (Fig. 2.1). This area consisted of two prairies: one remnant, Tucker Prairie, (Fig. 2.4) and one reconstructed, Prairie Fork Conservation Area (Fig. 2.5). These prairies were considered one location in our analyses although they were separated by almost 20 miles. The reconstructed prairies contained reconstructions of different ages. There were ten individual reconstructions at Wah'Kon-Tah initiated from 2002 from 2008. The North location contained reconstructions started as early as 2004, and as recent as 2016.

Various grassland management practices form a mosaic of treatments that might confound invertebrate surveys. We excluded areas that were scheduled to be hayed, grazed, mowed, or high-clipped in the sampling year because those practices might alter the invertebrate community during the summer months (Humbert et al. 2010). Burning

also affects invertebrate communities (Panzer 2002), but we included burned patches in our sampling because burns occurred during the dormant season, outside our sampling window.

Due to the fragmented nature of remnant prairie patches available for sampling and the heterogeneity of the landscape, we chose to place bee bowls at randomly selected locations within each remnant and reconstructed prairie. We used ArcMap 10.3.1 (ESRI 2015) to randomly generate points (Figs. 2.2, 2.3, 2.4, 2.5). There were 30 generated on the Wah'Kon-Tah remnants, 30 on the Wah'Kon-Tah reconstructions, 30 on the North reconstruction, and 15 on the North remnant. Each point, representing the location of three bee bowls, was located at least 40m from the edge of the prairie and 75m from another point. Points were regenerated after 2016 for sampling in 2017. Four bee bowl sampling spots in 2016, and two in 2017, were excluded because of access difficulties. In 2016 we sampled at 101 points, 58 on reconstructions and 43 on remnants. In 2017, we reduced sampling intensity at the North location, which lowered the points to 49 on reconstructions and 39 on remnants (88 total).

Collecting

We sampled bees using bee bowls made with clear 9oz cups (SOLO[®]) and fluorescent paint (Droege 2012). We placed three bowls, one white (white spray paint, Valspar[®]), one yellow, and one blue (Fluorescent Blue, Fluorescent Yellow, mixed with Silica Flat, Guerra Paint & Pigment Corporation), at the randomly generated points. Bowls sat in rings of PVC that were glued to each other and then mounted on a ½ inch dowel rod, which allowed us to change the height of bee bowls (Fig. 3.1). We positioned the bee bowls at half vegetation height to track flower height. Bee bowls are only

effective if they are visible (Tuell and Isaacs 2009), thus they must be placed higher later in the growing season to keep up with plant height. We filled the bowls with soapy water, and they remained in the field for 48 hours each sampling period (Droege 2015). The contents of the three bowls were combined into a single sample for each sampling period. In 2016, we sampled with bee bowls once each in June, July, and August. In 2017, we sampled monthly from April to August. Occasionally, we caught bees in our standardized sweeping for grasshoppers (see Chapter 2), which were identified and added to the bees captured with bee bowls at that transect for analyses.

Bees were identified to species, or in some cases genus or subgenus, using Arduer (2016) and discoverlife.org (Ascher and Pickering 2017). We grouped bees by family and nesting habitat (Table 3.1). All bees were either pinned or frozen. Pinned specimens will be stored in the Enns Entomological Museum at the University of Missouri, Columbia.

Vegetation

We took four vegetation measurements in 2017. We counted flower abundance and diversity at every bee bowl location during each sample period. One observer walked a 30 meter transect, with the bee bowls at the halfway point, and counted all plant stems that had at least one flower on them within a 1.2 meter swath along the entire length of the transect. We also counted the number of discernable plant species in bloom encountered in the same swath. We averaged the abundance and richness of plants with flowers observed per transect over the sampling periods in 2017. We measured vegetation density and estimated forb to grass ratio once in August/September. We measured vegetation density with a modified Robel pole (Benkobi et al. 2000, Uresk and

Benzon 2007) at three locations along a 60 meter transect centered on the bee bowls (see chapter 2, Fig. 2.6). At each location we recorded the lowest visible decameter on the Robel pole from a distance of four meters and a height of 1 meter (Fig. 2.8). We estimated the forb to grass coverage ratio of a 1.0 x 0.5 meter rectangle at the same locations where we measured density. The three measurements per transect were averaged to yield a single vegetation density and forb/grass ratio value for each transect.

Statistical analyses

Diversity and total abundance

We compared taxon richness (species plus genera that were not identified further) and diversity in reconstructed and remnant prairies at each location using a combination of asymptotic and non-asymptotic techniques. The non-asymptotic approach consisted of rarefaction/extrapolation (Weibull et al. 2003, Gotelli and Colwell 2011, Colwell et al. 2012), which resamples species data to estimate the richness or diversity at other sample sizes. We performed rarefaction/extrapolation using the package iNEXT (Hsieh et al. 2016). There are two types of rarefaction/extrapolation: individual-based and sample-based (Gotelli and Colwell 2011). Sample-based is generally preferred over individual based if it is available, thus we performed sample-based rarefaction, treating each bee bowl location as a sample. We conducted all analyses using R version 3.4.0 (R Core Team 2017).

The rarefaction/extrapolation curves depict Hill numbers, which are measures of diversity that combine species richness and abundance. The curves show the estimated Hill numbers at hypothetical sample sizes, ranging from zero to two-times the actual

sample size. We generated rarefaction/extrapolation of Hill curves for each year separately as well as lumped together. We plotted the curves using 95% confidence intervals, calculated with the bootstrap method (Colwell et al. 2012).

One of the parameters in Hill number equations is q , which determines the sensitivity to relative frequencies (Chao et al. 2014). Hill numbers were calculated for $q = 0, 1, \text{ and } 2$. The resulting estimates are species richness ($q = 0$), Shannon diversity ($q = 1$), and Simpson diversity ($q = 2$). Shannon diversity estimates are presented as the exponentials of Shannon indices, and Simpson diversity estimates are presented as inverses of Simpson concentration, such that larger numbers represent greater diversity (Hsieh et al. 2016). The three diversity metrics are influenced differently by relative frequencies of species (Chao et al. 2014). Species richness is not influenced by relative frequency, and only refers to the presence of a species. Shannon diversity weights species according to their relative frequencies (Peet 1975, Routledge 1979, Chao et al. 2014), meaning communities with highly skewed relative abundances will have lower Shannon diversity than communities with the same number of evenly abundant species (Peet 1975, Keylock 2005). Simpson diversity discounts rare species and places more emphasis on abundant species, making it a good measure of the diversity of dominant species (Peet 1974, 1975).

In the asymptotic approach, we used nonparametric estimators, which typically utilize count data for rare species to estimate species richness without making assumptions about the underlying distribution of species. We generated *jack1*, *jack2*, *Chao1*, and *iChao1* estimators with the package SpadeR (Chao and Chiu 2016). *Chao1* (Colwell and Coddington 1994) and *iChao1* (Chiu and Chao 2016) are best at estimating

lower bounds of species richness (Chao and Chiu 2016). *Chao1* is based on rare species, defined as species observed only once (singletons), or twice (doubletons); *iChao1* includes tripletons and quadrupletons in the estimation of undetected rare species. *jack1* and *jack2* use jackknife techniques, which reduce bias by successively deleting observations from the data to estimate species richness (Chao and Chiu 2016).

We modeled total abundance and species richness of bees using univariate generalized linear models with a negative binomial distribution including the variable *status* (reconstruction or remnant), *location* (Wah'Kon-Tah or North) and *year* (2016 or 2017). We started with a model including all variables and interactions, then removed interactions and variables one at time. We conducted analyses of variance (ANOVA) on models with and without variables to determine whether the variables improved the model fit, discarding those that did not ($p > 0.05$) (Blakey et al. 2016, Clarke-Wood et al. 2016). We used the function *glm.nb* in the package *MASS* (Ripley et al. 2017).

Community analysis

To visualize community data, we ordinated the bee communities using non-metric multidimensional scaling (NMS) with a Bray-Curtis dissimilarity matrix (Paton et al. 2009, Clarke-Wood et al. 2016). NMS ordination compresses the abundance and species information from each sample and constructs a space of k dimensions based on the differences between samples. Taxa abundances were summed across sampling periods for bee bowl locations for each year separately. Only species that occurred in over 5% of bee bowl samples were included in the ordination, thus we used the 24 most common bee taxonomic groups (mostly species and a few genera). Bee bowl samples with zero individuals were removed before analysis. We used the function *metaMDS* in package

vegan (Oksanen et al. 2016) to run NMS. We used the function *dimcheckMDS* to choose the number of dimensions and viewed the resulting ordination with the *ordirgl* function found in the package *ordiplot3d*.

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

We grouped bees by nesting substrate using information from Discover Life (Ascher and Pickering 2017). Nesting categories included *wood* (bees that nest in logs or tree cavities), *twig* (twig and stem nesters), and *soil*. Using the package *mvabund*, we created multivariate models of abundance and richness for each functional group and family. Explanatory variables in this analysis included *status*, *location*, *edge proximity*,

year, and all interactions among them. Due to a significant *status x location* interaction, we also modeled functional group abundance and richness for each prairie separately.

Age effects

We evaluated the effects of reconstruction age on bee communities using NMS and multivariate abundance models. We used the 23 most common bee taxa on reconstructions with a Bray-Curtis dissimilarity index to ordinate the bee communities on reconstructions. We chose the 23 most abundant taxa by selecting taxa that were present at greater than 10% of transect locations. To quantitatively assess community change over time, we used multivariate abundance models (*mvabund*) of the same taxa used in the ordination of reconstructions.

We assessed the impact of reconstruction age on family representation and functional composition, based on nesting habitat, with multivariate models of abundance and richness. The possible variables included *age*, *location*, *edge proximity*, and *year*. We started with a model including all variables and interactions, then removed interactions and variables one at a time. We conducted ANOVA on models with and without variables to determine whether the variables improved the model fit, discarding those that did not ($p > 0.05$) (Blakey et al. 2016, Clarke-Wood et al. 2016). We also modeled prairies separately because of significant *age x location* interactions. We modeled overall abundance and richness using generalized linear models with a negative binomial distribution and selected from the same variables and in the same manner as for the functional group models.

The above methods can determine whether reconstruction bee communities differ between reconstructions of different ages. However, the ultimate goal of investigating age in a reconstruction context is to determine if reconstruction communities are converging with the target communities on remnants. To visualize whether bee communities converge with remnants over time, we used the same ordination generated from comparing reconstructions to remnants, only with a different coloring and grouping scheme to emphasize reconstructions of different ages. We also divided reconstructions into two age classes, ≤ 5 years and > 5 years, and performed the same multivariate model analyses of abundance for taxa and functional groups as described in the community analysis section above. We repeated those analyses for the reconstruction groups split into ≤ 9 years and > 9 years.

Vegetation

We compared each of the four vegetation measurements on remnants to reconstructions in a linear model. To investigate relationships between vegetation characteristics and insect species' abundances, we ran separate models with only 2017 data that included vegetation measurements, with the same methods as described in the community composition analysis.

Results

Diversity and total abundance

We collected 3647 bees (Table 3.2) from 60 identified species or genera in 2016 and 2017 combined. The Wah'Kon-Tah remnant had the highest raw species richness (Fig. 3.2). 95% confidence intervals from sample-based rarefaction/extrapolation curves

comparing species richness, Shannon diversity, and Simpson diversity between reconstruction and remnant habitats at Wah'Kon-Tah and North overlapped in 2016, 2017 (data not shown), and when both years were combined (Fig. 3.3), with one exception. Simpson diversity was greater on reconstructions than the remnant in the North (Fig. 3.3). Asymptotic estimators did not detect any differences between species richness of remnant and reconstructed prairies at either Wah'Kon-Tah or the Northern Prairies (Fig. 3.4).

The best generalized linear model of total bee abundance contained *year* ($\chi^2 = 7.87$, $p = 0.005$) and an interaction between *status* and *location* ($\chi^2 = 11.27$, $p < 0.001$). When locations were modeled separately, bees were more abundant on reconstructions than remnants at the North location ($z = 4.53$, $p < 0.0001$), but not at Wah'Kon-Tah ($\chi^2 = 1.05$, $p = 0.306$). Bees were more abundant in 2016 than in 2017. The best bee richness model only included *location* ($\chi^2 = 6.69$, $p = 0.0097$), suggesting that species richness only differed between locations, not between remnants and reconstructions.

Community analysis

Remnant and reconstruction bee communities appeared somewhat distinct in 3-D ordinations (Fig. 3.5; stress = 0.19; $k = 3$). However, communities were clearly different by location (Fig. 3.6) and year (Fig. 3.7), indicating that *year* and *location* were more important sources of variation in the bee communities than *status*. The best multivariate model of species abundances contained *year* ($\chi^2 = 314.9$, $p < 0.001$) and a significant interaction between *location* and *status* ($\chi^2 = 78.87$, $p < 0.001$); therefore we ran separate models for each location. Remnant and reconstruction communities were distinct at Wah'Kon-Tah Prairie ($\chi^2 = 101.5$, $p < 0.001$) and the North prairies ($\chi^2 = 92.58$, $p <$

0.001). Based on model coefficients representing the effect of reconstruction on species abundance, *Eucera hamata* (Apidae), *Ceratina* (Apidae), *Apis mellifera* (Apidae), *Melissodes comptooides* (Apidae), *Agapostemon texanus* (Halictidae), and *Hylaeus mesillae* (Colletidae) were more common on reconstructions than remnants overall (Fig. 3.8). However, *A. texanus* and *M. comptooides* were mainly found on Wah'Kon-Tah or North respectively. *Melissodes communis* (Apidae), *Halictus parallelus* (Halictidae), and *Augochlorella persimilis* (Halictidae) were more abundant on remnants (Fig. 3.8). *H. parallelus*, and *M. communis* were mainly found at Wah'Kon-Tah. Outside of the common species used in the ordination and multivariate abundance models, there was one rare species only found on remnants, and three species only found on reconstructions (Table 3.3).

Most of the bees captured (71%) belonged to the family Halictidae, while Apidae was the second most common bee family observed (Fig. 3.9). The best multivariate model of family abundances contained a significant *location x status* interaction ($\chi^2 = 29.21$, $p < 0.001$). The model without the interaction showed that Apidae and Colletidae, which in this case was comprised entirely of the genus *Hylaeus*, were more abundant on reconstructions (Fig. 3.10; $z = 0.266$, $p < 0.001$). Richness did not differ between remnants and reconstructions for any of the families except for Colletidae, which was more species rich on reconstructions (Fig. 3.10; $\chi^2 = 8.22$, $p = 0.031$).

The most abundant nesting functional group was soil, followed by twig/stem nesters (Fig. 3.11). Overall twig/stem nester abundance was greater on reconstructions than remnants (Fig. 3.12; $\chi^2 = 12.14$, $p = 0.022$). Based on separate models for each prairie, twig nesters were more abundant only on reconstructions at Wah'Kon-Tah ($z = -$

2.02, $p = 0.043$). The genus *Ceratina* and *H. messillae*, identified in the multivariate abundance model as more common on reconstructions, were most likely responsible for the greater twig/stem nester abundance on reconstructions. Soil nesters were more common on reconstructions at the North location (Fig. 3.12; $\chi^2 = 2.059$, $p = 0.039$). The proportion of the community made up of soil nesters differed only slightly between remnants and reconstructions. (Fig. 3.11).

Age effects

Ordination ($k = 4$, stress = 0.171) revealed no obvious trends based on reconstruction age, but the centroids of newer reconstructions did tend to cluster on one side of the NMS space (Fig. 3.13). The best multivariate abundance model contained a significant interaction between *age* and *location* ($\chi^2 = 76.04$, $p < 0.001$), and an interaction between *location* and *year* ($\chi^2 = 58.85$, $p = 0.002$). Univariate tests revealed the interaction was significant for only three bee species, *Augochloropsis metallica* ($\chi^2 = 14.6$, $p = 0.006$), *Melissodes bimaculata* ($\chi^2 = 12.26$, $p = 0.012$), and *Halictus parallelus* ($\chi^2 = 9.826$, $p = 0.064$). For this reason, and ease of interpretation, we excluded the *age* \times *location* interaction term. The model without that interaction included *age* ($\chi^2 = 61.29$, $p < 0.001$) and *year* \times *location* ($\chi^2 = 73.7$, $p < 0.001$), indicating that bee communities differed by reconstruction age. There were four taxa that showed a significant abundance response to age (Fig. 3.14). *A. metallica* was not considered because of the significant interaction, which left the subgenus *Dialictus*, *A. aurata*, and the genus *Ceratina*. *Dialictus* abundance decreased with reconstruction age. *A. aurata* was the most common native bee captured on reconstructions and its abundance increased with reconstruction age. *Ceratina* also increased in abundance with reconstruction age (Fig. 3.14).

The best bee abundance model for reconstructions included *age* ($\chi^2 = 5.81$, $p = 0.016$), and a *location x year* interaction ($\chi^2 = 9.99$, $p = 0.0015$). The model without an interaction contained *age* ($\chi^2 = 5.81$, $p < 0.0001$) and *location x year* ($\chi^2 = 9.99$, $p = 0.0016$), which showed that bee abundance was negatively associated with reconstruction age (Fig. 3.15). That relationship appears to be driven by the North location (Fig. 3.15). None of the explanatory variables or interactions were significant predictors of bee richness, however.

The best multivariate model of bee family abundance contained *location x year* ($\chi^2 = 33.41$, $p = 0.002$), and although it had weak explanatory power, *age* ($\chi^2 = 17.29$, $p = 0.093$). Bees belonging to the family Halictidae were more abundant on younger reconstructions (Fig. 3.15). The best model of nesting group abundances contained *age* ($\chi^2 = 17.44$, $p = 0.003$) and an interaction between *location* and *year* ($\chi^2 = 19.52$, $p < 0.001$). Twig nester abundance was positively associated with reconstruction age, whereas soil nester abundance was negatively associated with reconstruction age (Fig. 3.16). There was no effect of *age* on the species richness of any of the bee families or nesting groups on reconstructions, and so the response of richness is not shown in Figures 3.15 or 3.16.

It was difficult to determine whether bee communities on older reconstructions had converged with those on remnants. The NMS ordination (Fig. 3.17) of different age groups and remnant prairies did not show clear signs of convergence or lack of convergence over time. There was extensive overlap between communities of various ages and remnants. The best multivariate abundance models for both age divisions contained a significant interaction between *location* and *age group* ($\chi^2 = 124.5$, $p < 0.001$;

$\chi^2 = 123.9$, $p < 0.001$), and *location* and *year* ($\chi^2 = 108.1$, $p < 0.001$; $\chi^2 = 106.1$, $p < 0.001$). The only species for which the interaction was remotely significant on univariate tests was *Melissodes comptoides* ($\chi^2 = 11.861$, $p = 0.07$; $\chi^2 = 11.190$, $p = 0.07$). Models without the *location x age group* interaction indicated that older and younger reconstructions split at either five or nine years were still distinct from remnants (Wald $\chi^2 = 10.852$, $p < 0.001$; Wald $\chi^2 = 8.755$, $p < 0.001$). The taxa that contributed to the difference between older reconstructions and remnants were the same taxa that contributed to the overall difference between reconstructions and remnants (Fig. 3.18). The taxa that differentiated overall reconstructions from remnants, *Ceratina*, *E. hamata*, *A. persimilis*, *H. mesillae*, and *H. paralellus* were still different when comparing remnants and older reconstructions. *Dialictus* abundance decreased over reconstruction time (Fig 3.18). *Dialictus* was more abundant on younger reconstructions than remnants, but abundance did not differ between older reconstructions and remnants.

The best generalized linear models for bee abundance with the reconstruction age groups split at five and nine years included a significant effect of *year* ($\chi^2 = 10.51$, $p < 0.0001$; $\chi^2 = 8.152$, $p < 0.0001$) and an interaction between *age group* (including remnant prairies) and *location* ($\chi^2 = 14.82$, $p < 0.0001$; $\chi^2 = 19.309$, $p < 0.0001$). However, we plotted coefficients from the models, which contained *age group* ($\chi^2 = 13.34$, $p = 0.001$; $\chi^2 = 13.34$, $p = 0.001$) and *year* ($\chi^2 = 11.07$, $p < 0.001$, $\chi^2 = 8.15$, $p = 0.003$), without the interaction. Overall bee abundance was greater on younger reconstructions than remnants (Figs. 3.18; $z = 3.45$, $p < 0.001$; $z = 3.22$, $p = 0.001$); however, abundance on older reconstructions did not differ from remnants ($z = 0.27$, $p = 0.81$; $z = -0.29$, $p = 0.77$). The best multivariate models for nesting group abundance without the *age group x location*

interaction ($\chi^2 = 18.74$, $p = 0.004$; $\chi^2 = 17.18$, $p = 0.026$), contained *age group* ($\chi^2 = 35.06$, $p < 0.001$; $\chi^2 = 32.99$, $p < 0.001$) and *location x year* ($\chi^2 = 19.53$, $p < 0.001$; $\chi^2 = 21.51$, $p < 0.001$). The best multivariate models for abundance by family without the *age group x location* interaction ($\chi^2 = 20.07$, $p = 0.003$; $\chi^2 = 30.94$, $p = 0.003$), contained *age group* ($\chi^2 = 50.96$, $p < 0.001$; $\chi^2 = 61.22$, $p < 0.001$) and *year x location* ($\chi^2 = 24.33$, $p = 0.002$; $\chi^2 = 27.73$, $p = 0.002$).

Greater bee abundances on younger reconstructions were likely due in part to the abundance trends in soil nesting bees (Fig. 3.19), which were more abundant on younger reconstructions than remnants, but not on older reconstructions. Conversely, twig nesters on older reconstructions were more abundant than on remnants, while younger reconstructions did not differ from remnants (Fig. 3.19). Bee family analyses showed that Apidae were consistently more abundant on reconstructions of any age than remnants, while Halictids were more common on reconstructions aged five years or less than on remnants (Fig. 3.20). Halictids were less abundant on older reconstructions than remnants, however (Fig. 3.20).

Vegetation

Neither flower abundance nor richness differed significantly between remnants and reconstructions, or between locations (Fig. 3.21; $F = 0.8787$, $p = 0.456$). Forb percentage differed between remnants and reconstructions according to location ($F = 8.15$, $p = 0.005$), due to the Schell reconstruction having a greater forb percentage than the Schell remnant. Reconstructions had a greater vegetation density than remnants ($t = 3.53$, $p < 0.0001$), and density was greater at the North location than at Wah'Kon-Tah (Fig. 3.21; $F = 10.18$, $p = 0.002$). Vegetation density, forb percentage, flower abundance

and flower richness were not significantly associated with total abundance or richness of bees ($\chi^2 = 5.58$, $p = 0.23$; $\chi^2 = 2.41$, $p = 0.45$). None of the vegetation measurements were associated with the abundance of bee families or the abundance of nesting habitat functional groups.

Statistical Notes

The analyses performed here have an underlying assumption that transects (replicates) are independent of each other. For the transects to be spatially independent, the bees caught at one transect should not affect the bees caught at any other transects. There is some reason to believe this is not true for bees, potentially leading to pseudoreplication (Hurlbert 1984). Some bees have foraging ranges of a mile or larger (Greenleaf et al. 2007), meaning that transects located closer than that could capture bees that might have been caught at a different location during the same sampling period.

We were ultimately interested in comparisons of communities from different remnant and reconstructed prairies; however, we were limited in the number of available comparisons due to the extreme loss of tallgrass prairie habitat in Missouri. Therefore, while we present analyses comparing remnant and restored communities, our study design actually randomized replicates at the level of the prairie location. Therefore, our scope of inference is technically at the level of prairie location. That is part of the reason for modeling and displaying results for the prairie locations as well as the overall model.

Discussion

Our first objective was to compare bee communities of reconstructions and remnants, and identify species or functional groups that can be used to evaluate prairie reconstruction progress. Bee communities on remnant and reconstructed prairies shared nearly all species, but were distinct due to differing abundances for some taxa. We found little evidence that remnant and reconstructed prairies differed in bee species richness or diversity, similar to what several studies on restorations have found (Exeler 2009, Williams 2011, Griffin et al. 2017, Tonietto et al. 2017). Our second objective was to evaluate the effect of reconstruction age on bee communities. Our results suggest that the composition of reconstruction communities remains distinct from the community found on remnants even 15 years after reconstruction. Williams (2011) also found that the composition of bee communities on reconstructions remained distinct from remnants after six years. Tonietto et al. (2017) found that bee communities in Illinois were most different from remnants a few years after reconstruction, but became quite similar to remnants after 20 years. Griffin et al. (2017), however, found that bee community composition converged with that of remnants after only 2-3 years in Illinois.

We identified several bee taxa that were significantly more abundant on reconstructions or remnants and could hold potential as long term monitoring subjects. Of the taxa associated with reconstructions in this study, two of them could offer insight into why reconstruction communities differ from remnants. *Ceratina* and *Hylaeus mesillae* are both stem or twig nesters and are likely driving the greater abundance of twig/stem nesters on reconstructions. *Ceratina* and *Hylaeus* are also partly responsible for the greater abundances of Apidae and Colletidae, respectively. There are few studies that

directly link stem density or abundance with stem-nesting bees, but prescribed fire, which eliminates stems and twigs available for nesting, has been shown to negatively impact stem-nesting bees (Eickwort et al. 1981, Cane et al. 2007, Cane and Neff 2011). The amount of dead wood has also been found to influence bee community structure (Grundel et al. 2010). Reconstruction vegetation was significantly denser than that of remnants, which may indicate an increased availability of stems for nesting on reconstructions, although vegetation density did not add any explanatory power to any of the abundance models. It is possible that the methods we used to measure vegetation density simply did not provide an accurate enough estimate of stem nesting availability to predict stem nester abundance.

Plant community composition could also influence bee community composition on remnant and reconstructed prairies. Reconstructions can differ from remnants in plant community composition (McLachlan and Knispel 2005, Hansen and Gibson 2014), and thus may contain more plants suitable for stem nesting, even if the vegetation on reconstructions is not denser than on remnants. Many reconstructions appeared more “weedy” than remnants (personal observation), and it is possible that *Ceratina* and *H. mesillae*, which are common generalists, are more successful on these widespread, early colonizing plants. Interestingly, the trend in *Ceratina* abundance on reconstructions of different ages is counter-intuitive if one assumes that reconstructions are eventually converging with remnants (Foster et al. 2007, Watts et al. 2008, Carter and Blair 2012, Tonietto et al. 2017). *Ceratina* were more abundant on reconstructions than remnants, leading to the hypothesis that *Ceratina* abundance should decrease with reconstruction age. However, *Ceratina* abundance actually increased with reconstruction age, and was

different from remnant abundance on older reconstructions. One possible explanation is that stem and twig density accumulate over several growing seasons on reconstructions. There may be woody or stem-dense habitats available on older reconstructions that do not exist on remnants and have not had the time to accumulate on newer reconstructions.

Ceratina was the by far the most abundant group of stem nesters in our samples, which makes it difficult to interpret trends across all stem and twig nesters. There were two other major groups of stem nesters, *Hylaeus* (Family: Colletidae) and Megachilidae. The abundance of bees in genus *Hylaeus* did not respond to reconstruction age. Megachilids were more abundant, but not significantly so, on older reconstructions. The lack of a response in Megachilids and Colletids make us hesitant to generalize the trend we found in *Ceratina* abundance to all stem or twig nesters.

The abundance of *E. hamata* on reconstructions may be related to plant community composition as well, since it belongs in the soil nesting functional group and is therefore likely not related to stem abundance. *E. hamata* is a common, widespread generalist (Arduser 2016, Ascher and Pickering 2017). It may outperform more conservative grassland bees on reconstructions because they more closely resemble weedy fields common in the rest of Missouri. The same logic may apply to *A. texanus* and *M. comptoides*, but we cannot speculate as to why those particular generalists, and not closely related generalists like *A. virescens*, were more common on reconstructions. Soil is another potential factor explaining the greater abundance of ground nesters like *E. hamata* on reconstructions. One of the stronger clues that soil affects reconstruction community composition in our study comes from the observed trend in *Dialictus* abundance. *Dialictus* abundance decreased with reconstruction age (Fig. 3.14) and was

greater on younger reconstructions than remnants (Fig. 3.18). The genus *Lasioglossum*, and in particular its subgenus *Dialictus*, are associated with disturbed soil (Kim et al. 2006). Recently reconstructed prairies have been, by definition, recently disturbed, and probably offer more nesting habitat for bees like *Dialictus*. The trend in *Dialictus* abundance was particularly strong at the North location. The North reconstruction contained parcels that were still being planted with native seed and may have provided the disturbed soil where *Dialictus*, and possibly other soil nesting species, thrived. *Lasioglossum*, *A. virescens*, *E. hamata*, and *M. comptoides* are all other soil nesting bees that were more abundant on the North reconstruction than the remnant, and are common bees that can be found on frequently disturbed agricultural sites (Ascher and Pickering 2017). There appear to be taxa associated with young reconstructions, possibly because of soil conditions, but there were also soil nesters that were more abundant on older reconstruction. *A. aurata* was more abundant on older reconstructions than younger reconstructions. *A. aurata* may require soil that has been disturbed less recently than taxa like *Dialictus* or *E. hamata*.

Species or functional groups closely associated with remnants have the potential to be good indicators of reconstruction success. There were three candidate species based on the multivariate models: *A. persimilis*, *M. communis*, and *H. parallelus*. The first two offer few clues on why they were more abundant on remnants. *H. parallelus* is a conservative prairie species found mainly on remnants in Missouri (Arduser, personal communication), and could serve as a useful indicator species on prairies in the Osage Plains, where almost all our specimens were collected. All three species are ground nesting generalists. *M. communis* and *H. parallelus* are large bees while *A. persimilis* is

one of the smallest bees that we captured. Although we have no direct evidence from the locations we sampled to support such speculation, soil condition may be responsible for prevalence of these ground nesting species on remnants. Reconstruction soils, which are recently disturbed and usually altered by agricultural activity (Kindscher and Tieszen 1998), may lack some bees' ideal soil nesting conditions.

We expected remnants to have more rare, specialist species. That was not the case however, as there was only one rare specialist, *M. nivea*, that was unique to remnants. We were not able to compare specialist diversity or abundance between remnants and reconstructions because we caught too few specialists representing only a small proportion of the species thought to inhabit Missouri's prairies (Arduser 2011). This could mean two things, that Wah'Kon-Tah and the North prairies do not contain the rare, specialist species that have been recorded within the last ten years, or that our methods failed to detect them. The former is unlikely because, although there is some evidence that specialist bees are more sensitive to habitat loss like Missouri's prairies have undergone (Bommarco et al. 2010), over 30 bee species would have had to go extinct in less than ten years (Arduser 2011). Therefore we speculate that the lack of specialist species captured was due to the capture method. Bee bowls are biased toward small bees (Geroff et al. 2014), particularly soil-nesting Halictidae such as *Dialictus* or *Augochlorella aurata*, the two most abundant bee in our samples (Geroff et al. 2014). The bee community we collected was made up of mostly small Halictidae, meaning we lacked the sample size required to examine other groups. The family *Megachilidae*, stem and twig nesters of which many are oligolectic, were particularly underrepresented in our samples. Some *Megachilidae* genera, such as *Osmia* and *Megachile*, are known to be

underrepresented in bee bowl surveys (Geroff et al. 2014, Arduser 2016); we caught only one individual in two years. We also probably under-sampled the parasitic bee community, especially non-halictid parasites. Parasitic bees are usually present in communities at low abundances (Sheffield et al. 2013), but besides a few *Lasioglossum* kleptoparasites (Family: Halictidae), we captured no parasitic bees in the bowls. A mixture of sampling methods, or use of a malaise trap, would likely provide a more complete picture of bee communities on prairies.

Conclusion

Our results show that bee communities on remnant and reconstructed prairies are distinct. The distinction was due to different relative abundances of bees, not necessarily the identity, because remnants and reconstructions shared almost all bee taxa. We identified several bee taxa that were significantly more abundant on reconstructions or remnants, and thus hold potential as long-term monitoring subjects. Detailed information on the habitat requirements and life history of some of those bees is lacking and could help identify the differences between remnants and reconstructions that are influencing bee communities. Our results suggest that bee communities may require longer than 15 years to converge with remnant communities. Further monitoring will be required to determine if and when composition of the more common, soil nesting bees caught with our methods on reconstructions matches that on remnants. More extensive and varied sampling is likely required to determine when the entire bee community on reconstructions reaches the target composition found on remnants.

Table 3.1. Bee taxa captured in 2016 and 2017 with family, nesting habitat and diet specialism.

Taxa	Family	Nest habitat	Diet
<i>Andrena (Andrena)</i>	Andrenidae	Soil	Unknown
<i>Andrena (Derandrena)</i>	Andrenidae	Soil	Unknown
<i>Andrena (Melandrena)</i>	Andrenidae	Soil	Unknown
<i>Andrena (Plastandrena)</i>	Andrenidae	Soil	Oligolectic
<i>Andrena (Ptilandrena)</i>	Andrenidae	Soil	Unknown
<i>Andrena (Rhacandrena)</i>	Andrenidae	Soil	Unknown
<i>Andrena (Scapteropsis)</i>	Andrenidae	Soil	Unknown
<i>Andrena (Trachandrena)</i>	Andrenidae	Soil	Unknown
<i>Andrena arabis</i>	Andrenidae	Soil	Oligolectic
<i>Andrena cressoni</i>	Andrenidae	Soil	Polylectic
<i>Andrena rudbeckia</i>	Andrenidae	Soil	Oligolectic
<i>Andrena violae</i>	Andrenidae	Soil	Oligolectic
<i>Pseudopanurgus albitarsis</i>	Andrenidae	Soil	Oligolectic
<i>Agapostemon sericeus</i>	Apidae	Soil	Polylectic
<i>Andrena carlini</i>	Apidae	Soil	Unknown
<i>Apis mellifera</i>	Apidae	Cavity	Polylectic
<i>Bombus auricomus</i>	Apidae	Soil	Polylectic
<i>Bombus bimaculata</i>	Apidae	Soil	Polylectic
<i>Bombus griseocolis</i>	Apidae	Soil	Polylectic
<i>Bombus impatiens</i>	Apidae	Soil	Polylectic
<i>Bombus pennsylvanicus</i>	Apidae	Soil	Polylectic
<i>Ceratina</i>	Apidae	Stem/twig	Polylectic
<i>Eucera hamata</i>	Apidae	Soil	Polylectic
<i>Eucera rosae</i>	Apidae	Soil	Polylectic
<i>Melissodes agilis</i>	Apidae	Soil	Oligolectic
<i>Melissodes bimaculata</i>	Apidae	Soil	Polylectic
<i>Melissodes boltoniae</i>	Apidae	Soil	Oligolectic
<i>Melissodes communis</i>	Apidae	Soil	Polylectic
<i>Melissodes comptoides</i>	Apidae	Soil	Polylectic
<i>Melissodes dentriventris</i>	Apidae	Soil	Oligolectic
<i>Melissodes nivea</i>	Apidae	Soil	Oligolectic
<i>Melissodes trinodis</i>	Apidae	Stem/twig	Oligolectic
<i>Melissodes veronia</i>	Apidae	Soil	Oligolectic
<i>Nomada</i>	Apidae	Kleptoparasite	kleptoparasite
<i>Ptilothrix bombiformis</i>	Apidae	Soil	Oligolectic
<i>Xylocopa virginica</i>	Apidae	Wood	Polylectic
<i>Hylaeus fedorica</i>	Colletidae	Stem/twig	Polylectic
<i>Hylaeus illinoisensis</i>	Colletidae	Stem/twig	Polylectic
<i>Hylaeus mesillae</i>	Colletidae	Stem/twig	Polylectic
<i>Agapostemon texanus</i>	Halictidae	Soil	Polylectic
<i>Agapostemon virescens</i>	Halictidae	Soil	Polylectic
<i>Augochlora pura</i>	Halictidae	Wood	Polylectic
<i>Augochlorella aurata</i>	Halictidae	Soil	Polylectic
<i>Augochlorella persimilis</i>	Halictidae	Soil	Polylectic
<i>Augochloropsis fulgida</i>	Halictidae	Soil	Polylectic
<i>Augochloropsis metallica</i>	Halictidae	Soil	Polylectic
<i>Dialictus</i>	Halictidae	Soil	Polylectic
<i>Halictus ligatus</i>	Halictidae	Soil	Polylectic
<i>Halictus parallelus</i>	Halictidae	Soil	Polylectic
<i>Lasioglossum</i>	Halictidae	Soil	Polylectic
<i>Lasioglossum paralictus</i>	Halictidae	Kleptoparasite	kleptoparasite
<i>Megachile brevis</i>	Megachilidae	Stem/twig	Polylectic
<i>Megachile montivaga</i>	Megachilidae	Soil	Polylectic
<i>Megachile parallela</i>	Megachilidae	Stem/twig	Polylectic
<i>Megachile petulans</i>	Megachilidae	Stem/twig	Polylectic
<i>Megachile relativa</i>	Megachilidae	Stem/twig	Polylectic

Table 3.2. Numbers of bees captured in 2016 and 2017 on remnants and reconstructions.

	Wah'Kon-Tah	North
Remnant	1130	346
Reconstruction	948	1223

Table 3.3. Bee species only found on remnants or reconstructions.

Remnant	Reconstruction
<i>Melissodes nivea</i>	<i>Agapostemon sericeus</i>
	<i>Melissodes dentriventris</i>
	<i>Melissodes elegans</i>



Figure 3.1. Bee bowls in their PVC holders placed at half vegetation height.

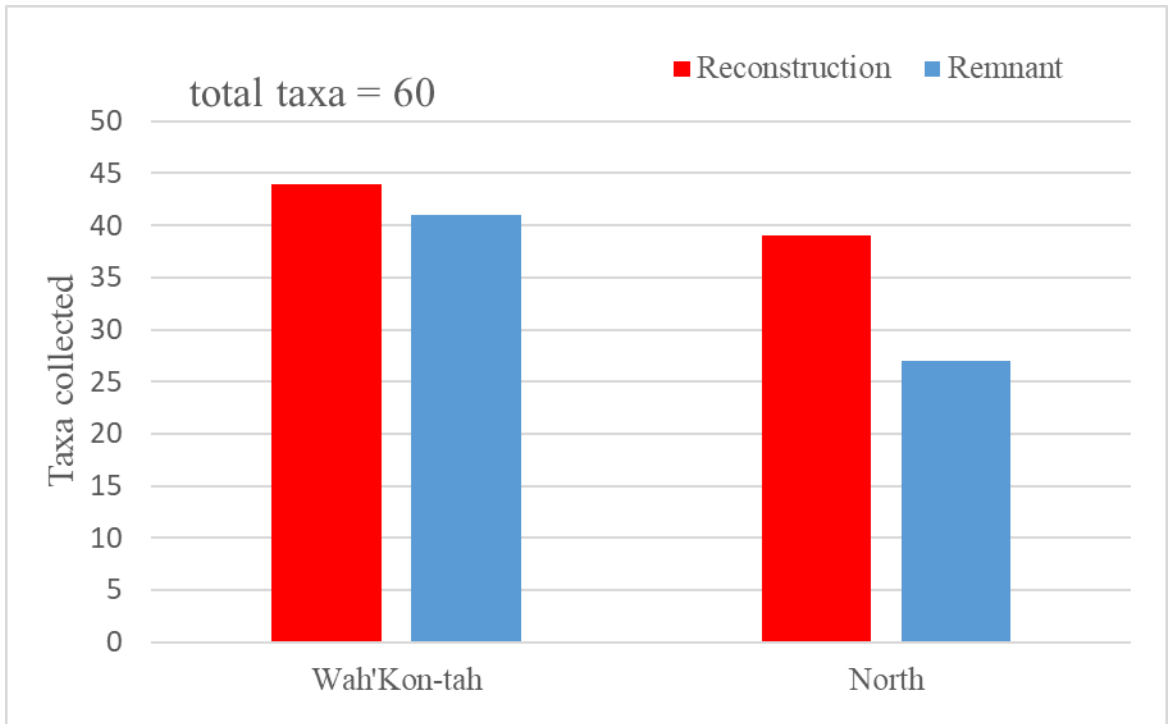


Figure 3.2. Number of bee taxa (lowest possible identification: species, subgenus, or genus) captured on remnants and reconstructions in 2016 and 2017.

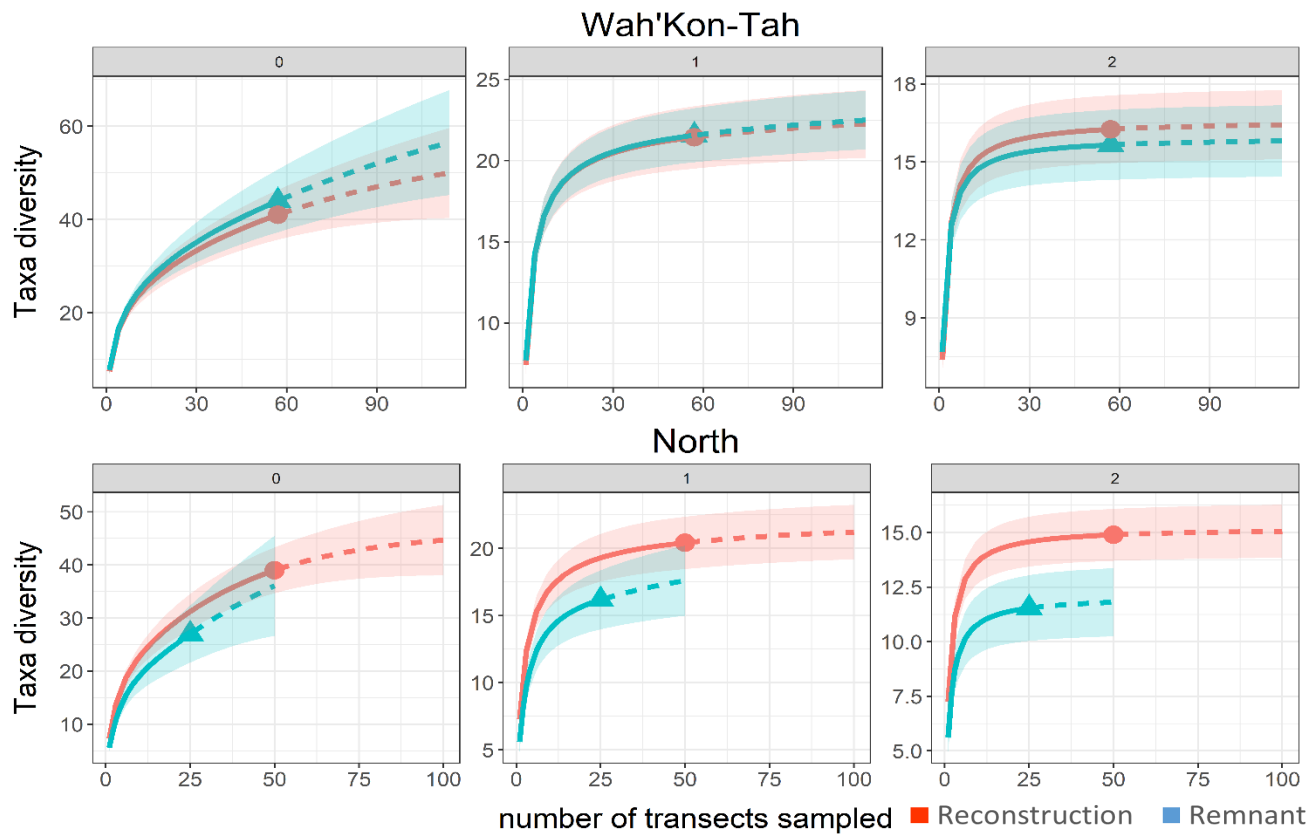


Figure 3.3. Sample-based rarefaction and extrapolation of bee Hill number diversity generated in iNEXT. 0 = species richness, 1 = Shannon diversity, and 2 = Simpson diversity. Shaded areas represent 95% confidence intervals.

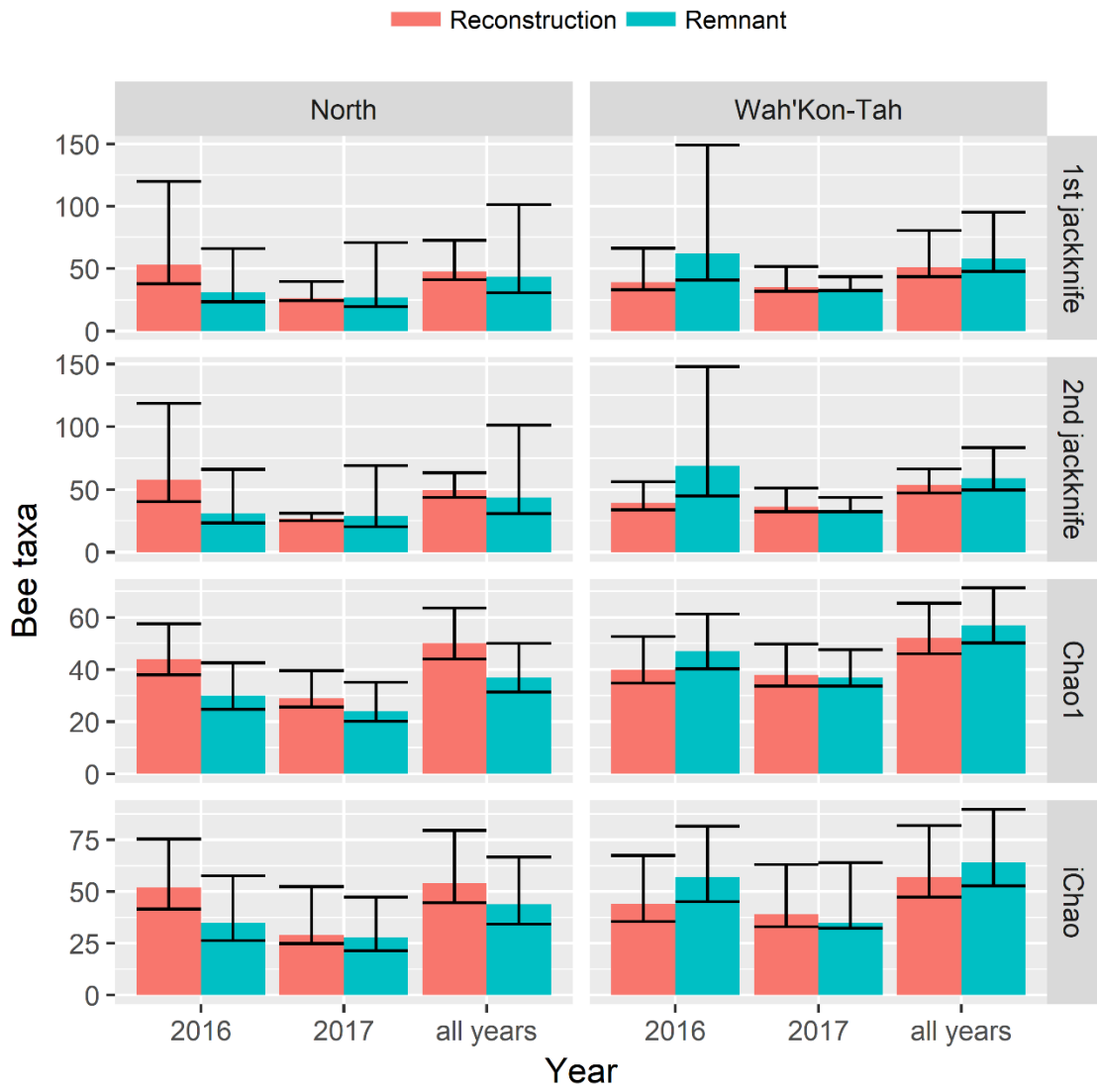


Figure 3.4. Asymptotic, non-parametric estimates of bee taxa richness. Bars represent 95% confidence intervals.

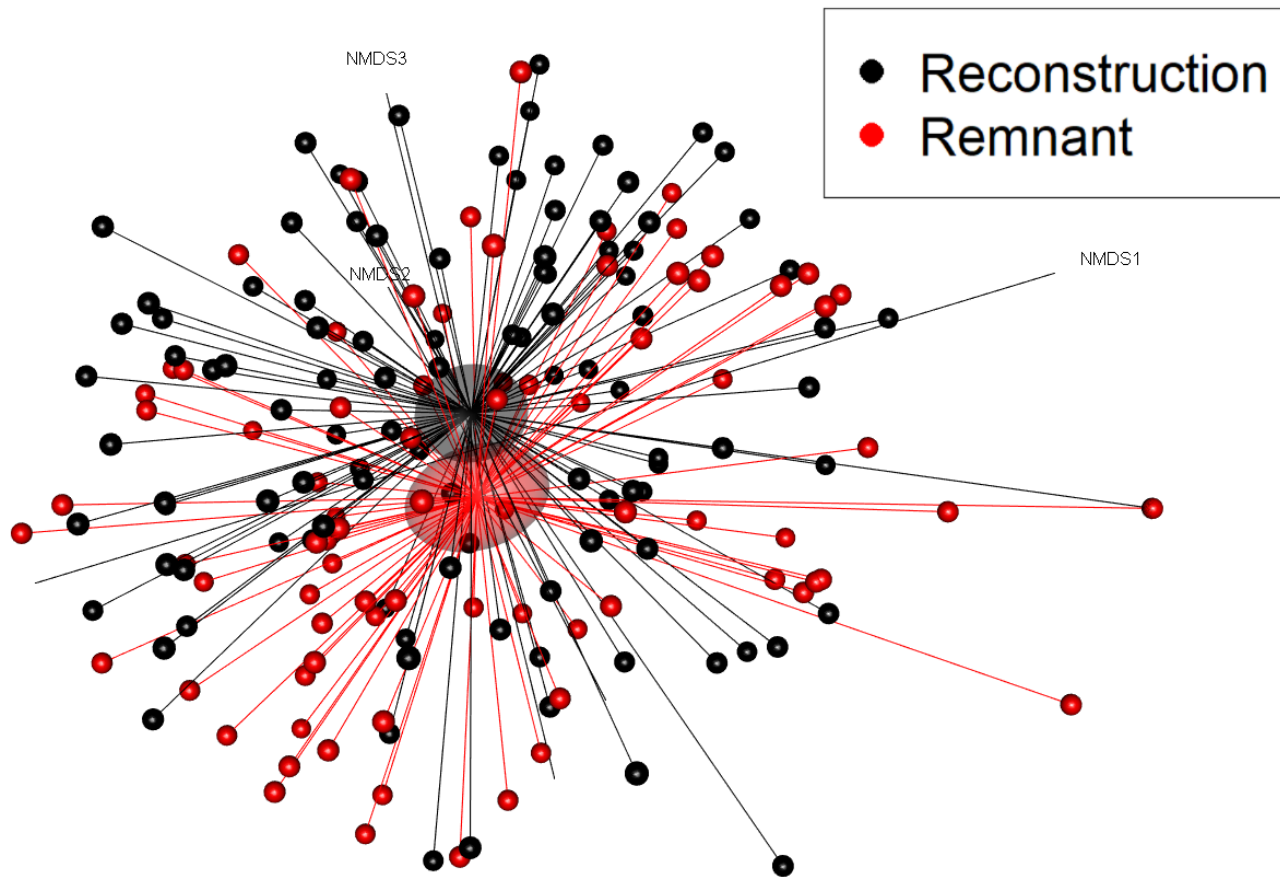


Figure 3.5. NMS ordination ($k = 4$, stress = 0.18) of bee communities. Dots represent communities at bee bowl locations. Spheres represent 95% confidence intervals around the centroid of reconstructions and remnants.

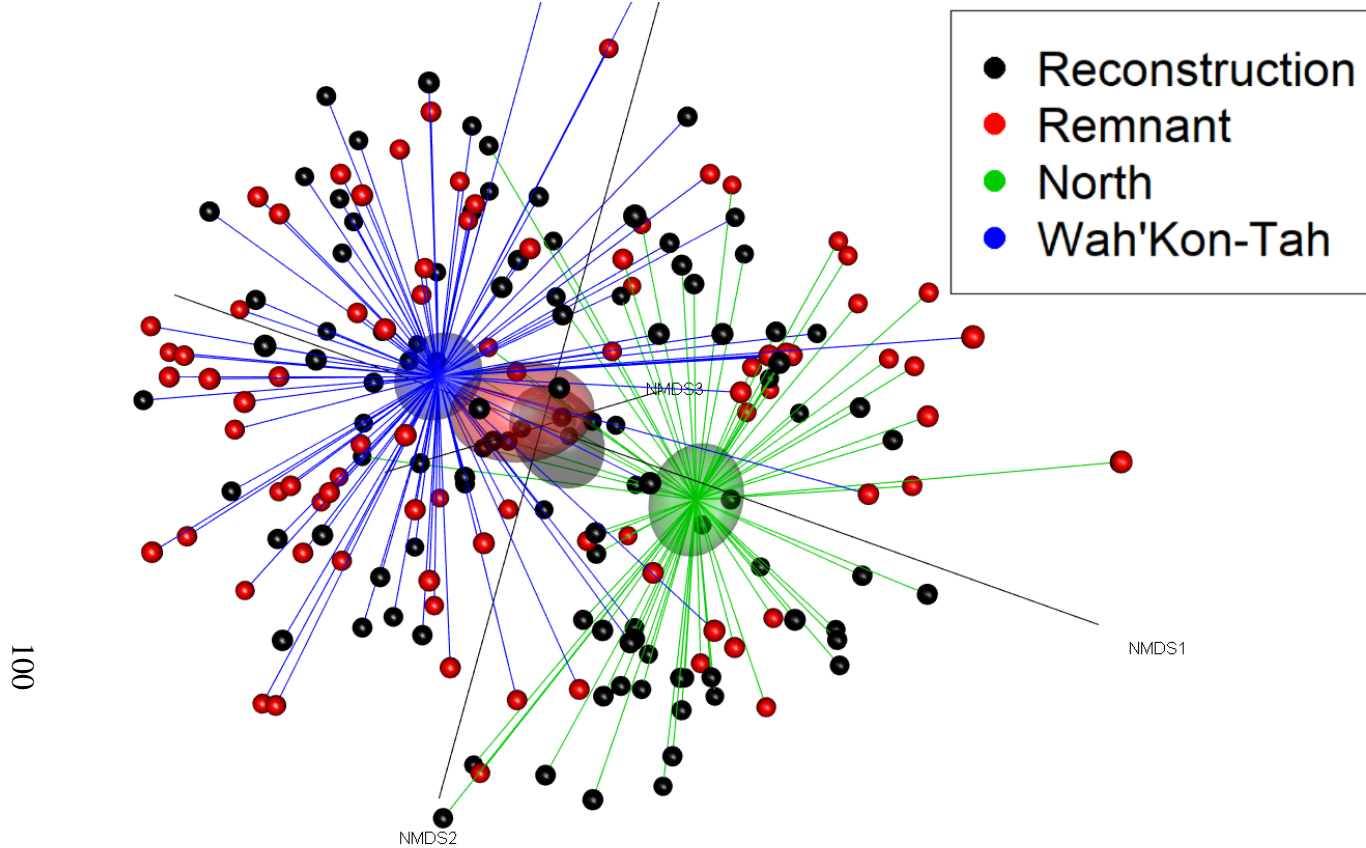


Figure 3.6. NMS ordination ($k = 4$, stress = 0.18) of bee communities. Dots represent communities from bee bowl samples. Spheres represent 95% confidence intervals around the centroids of reconstructions and remnants at each location, as well as centroids of all remnants and all reconstructions.

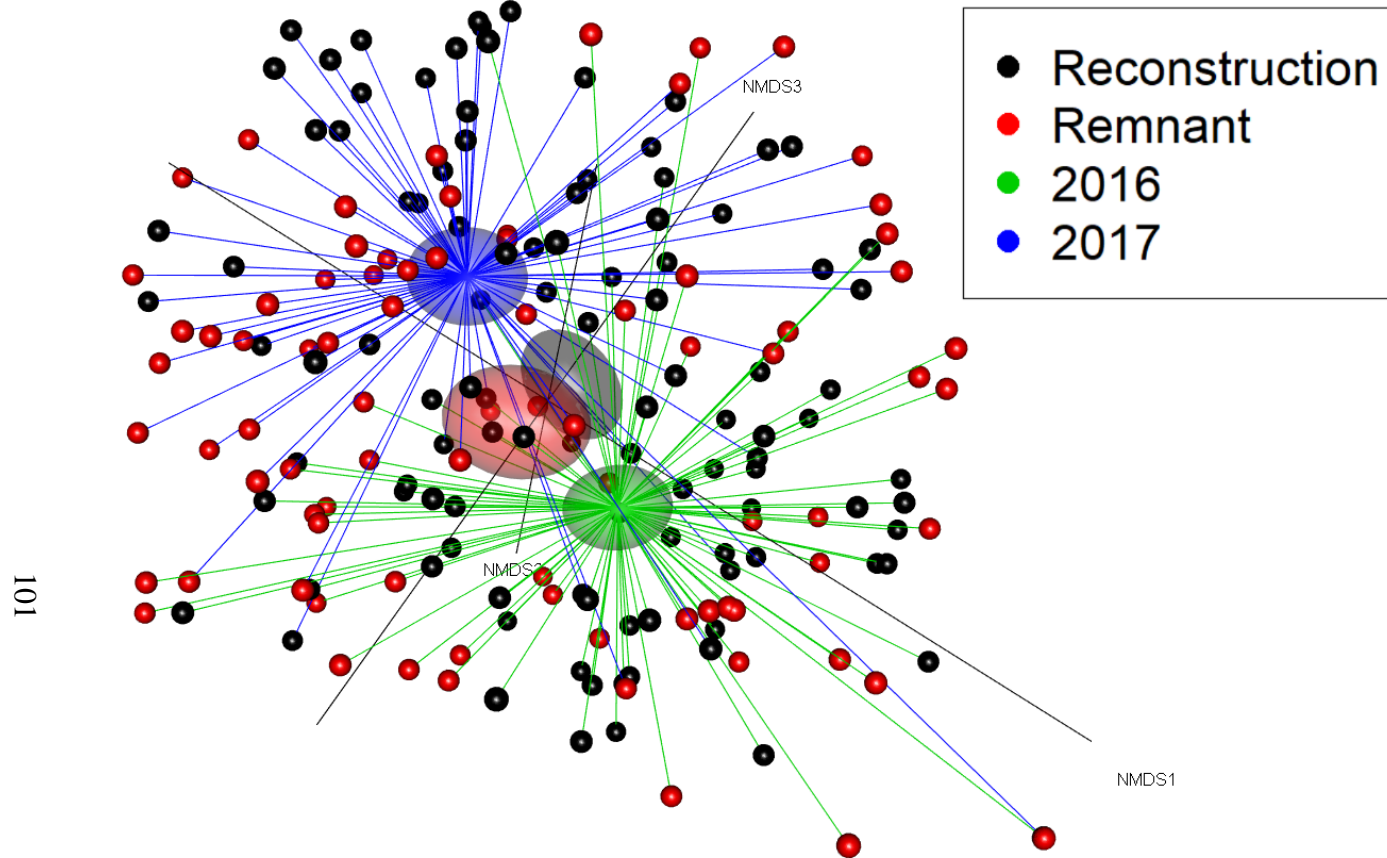


Figure 3.7. NMS ordination ($k = 4$, stress = 0.18) of bee communities. Dots represent communities from bee bowl samples. Spheres represent 95% confidence intervals around the centroid of years, as well as centroids of all remnants and all reconstructions.

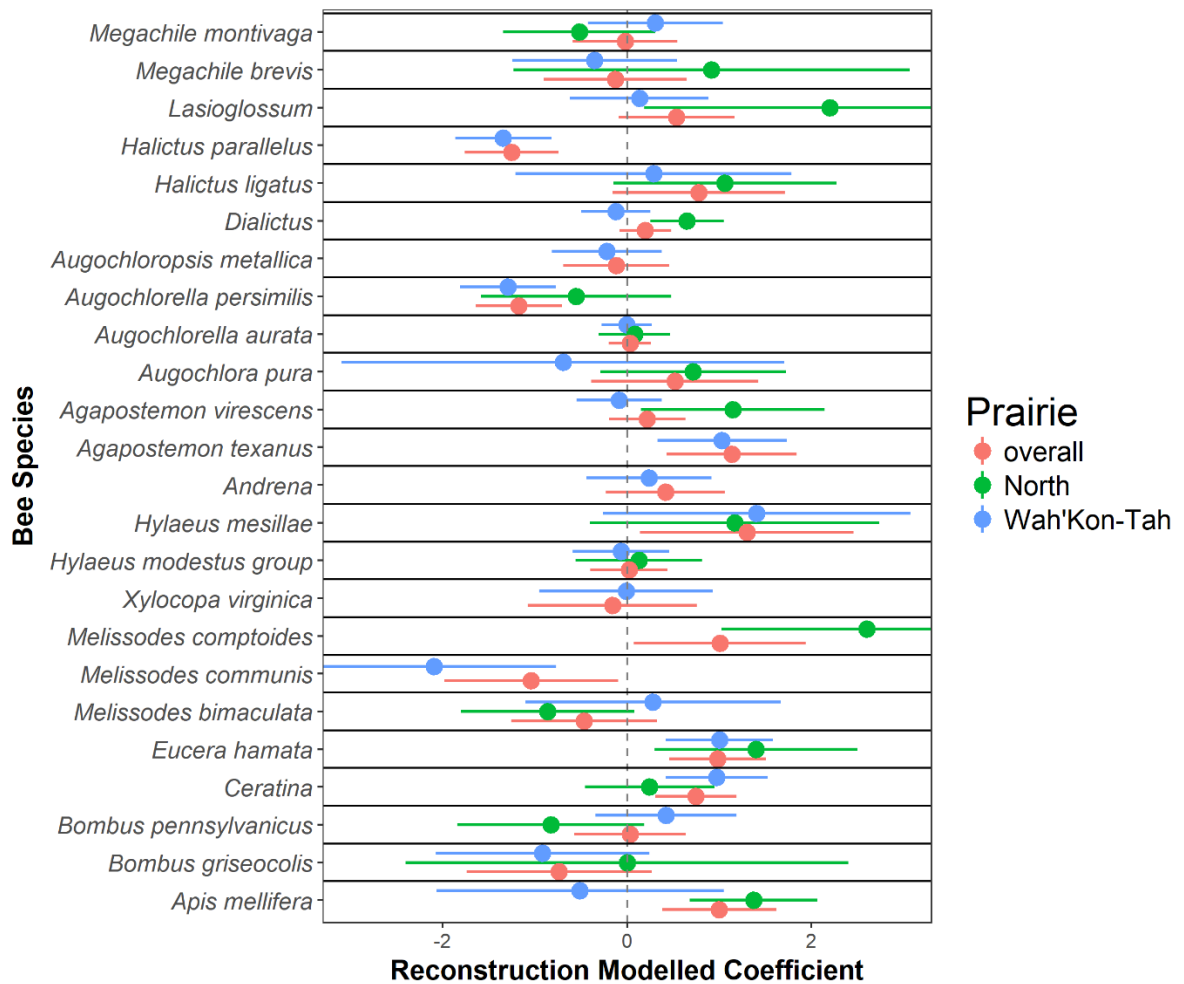


Figure 3.8. Coefficients, with 95% confidence intervals, of the effect of prairie *status* (reconstruction or remnant) from multivariate abundance model on taxa used in ordination. Positive coefficients signify greater abundance on reconstructions, negative coefficients signify greater abundance on remnants. There are up to three coefficients for each species, representing models for Wah'Kon-Tah, North, and the prairies combined with no interaction (overall). Model coefficients with very large standard errors are not shown.

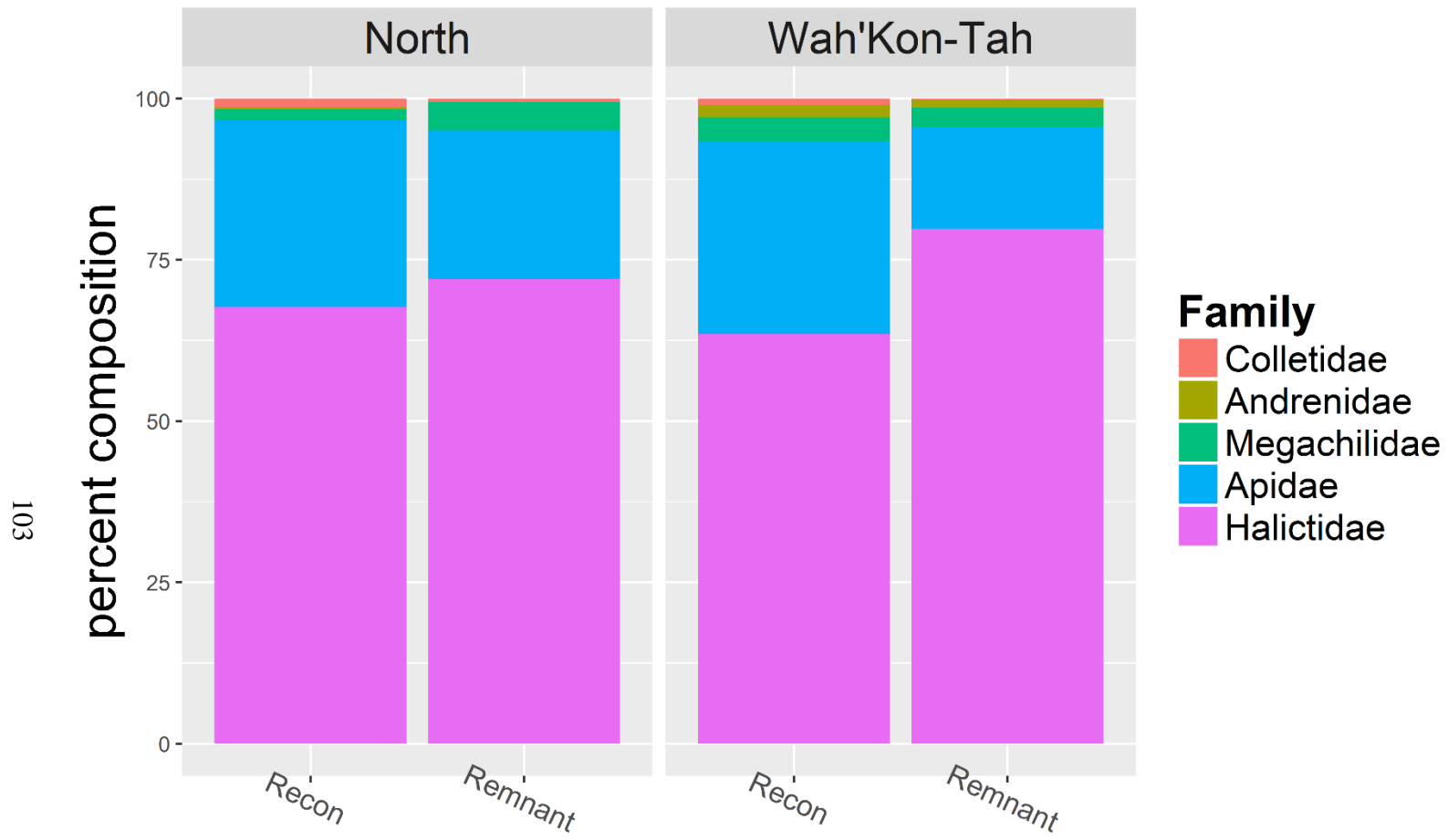


Figure 3.9. Proportions of bees from different families captured over both years.

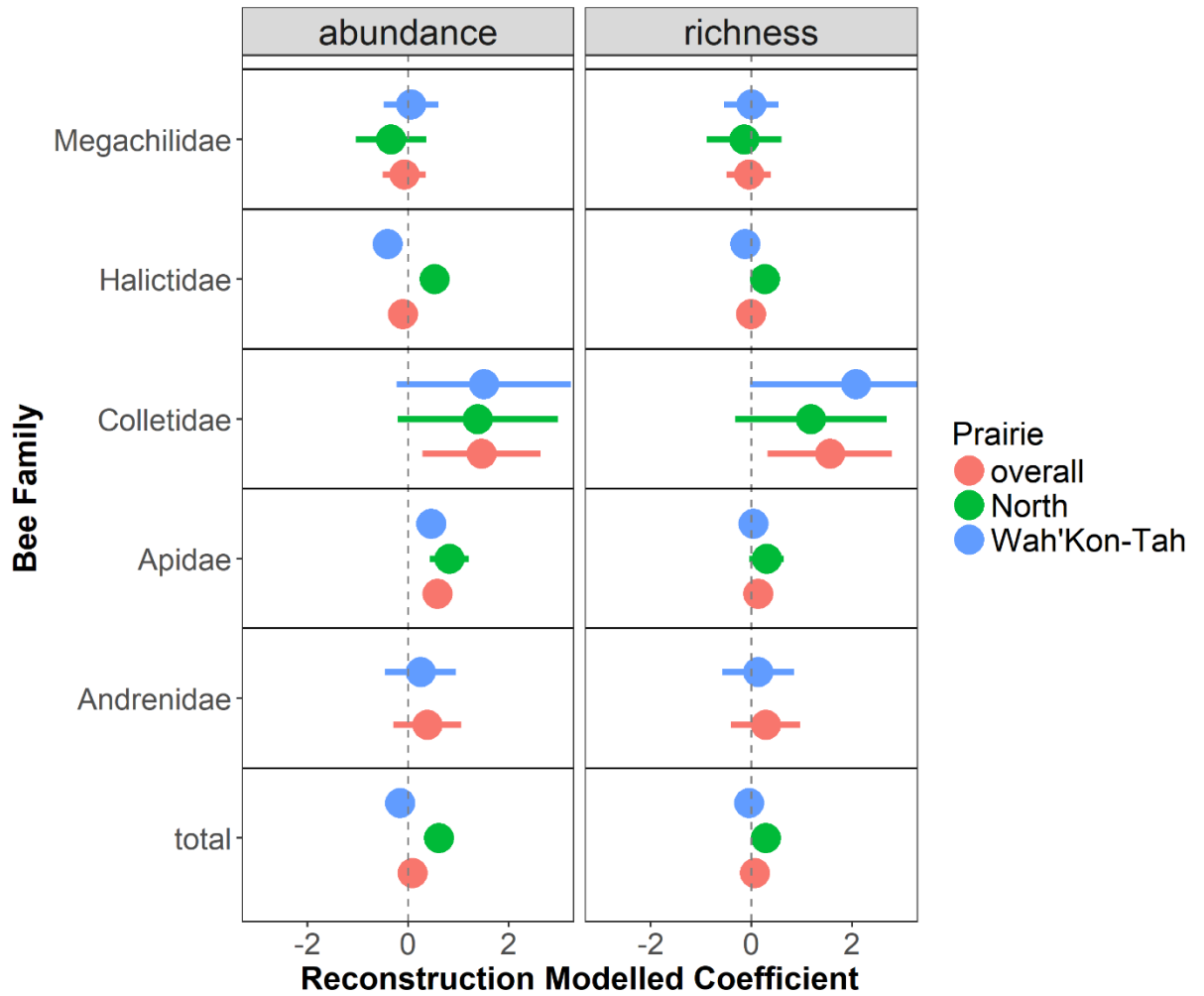


Figure 3.10. Coefficients, with 95% confidence intervals, for the effect of prairie *status* (reconstruction or remnant) from multivariate models of bee abundance and richness according to family. Positive coefficients signify a greater abundance on reconstructions, negative coefficients signify greater abundance remnants. There are up to three coefficients for each species, representing models for Wah'Kon-Tah, North, and the prairies combined with no interaction (overall). Model coefficients with very large standard errors are not shown.

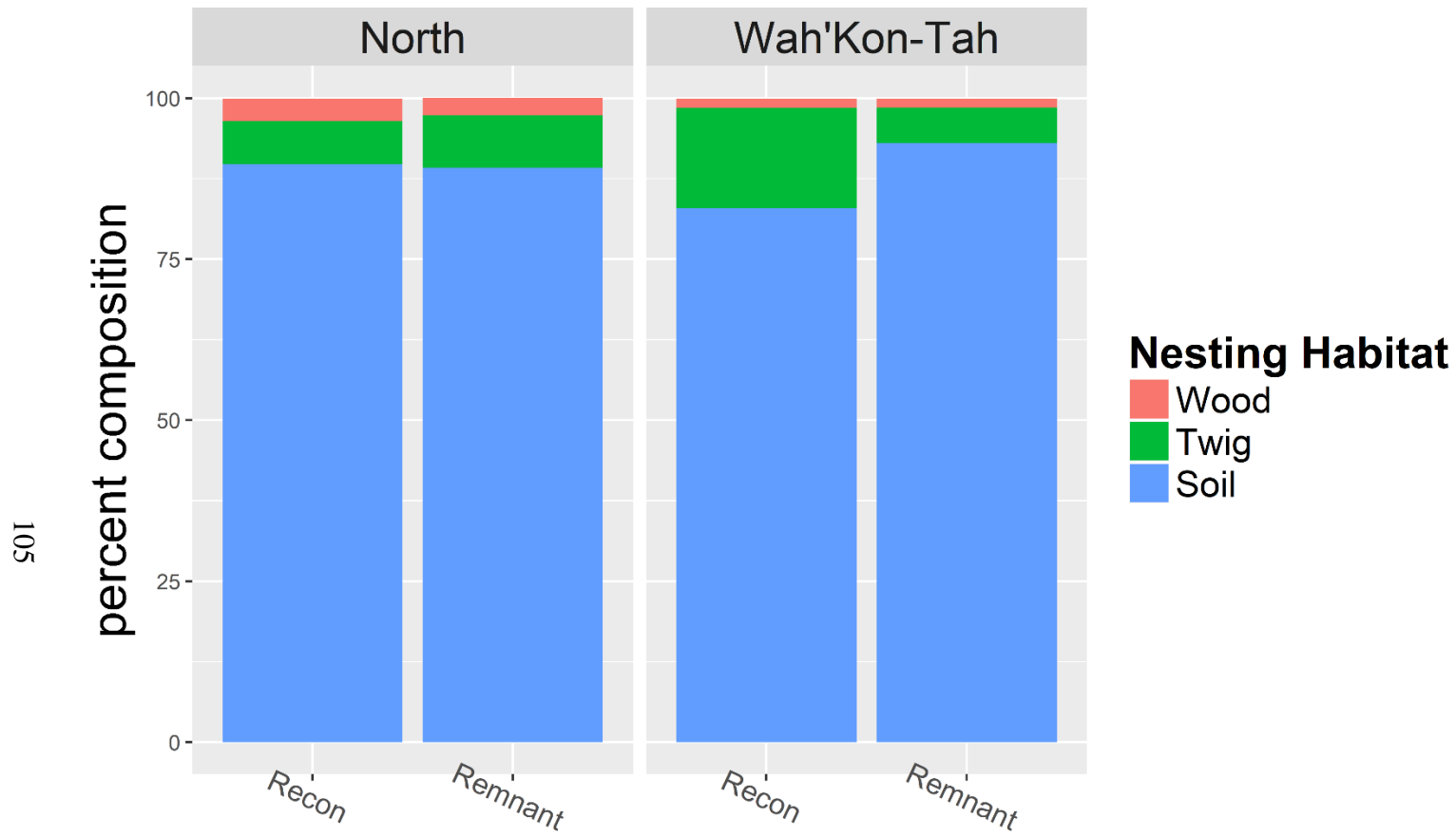


Figure 3.11. Proportions of bees captured over both years that utilize different nesting habitats.

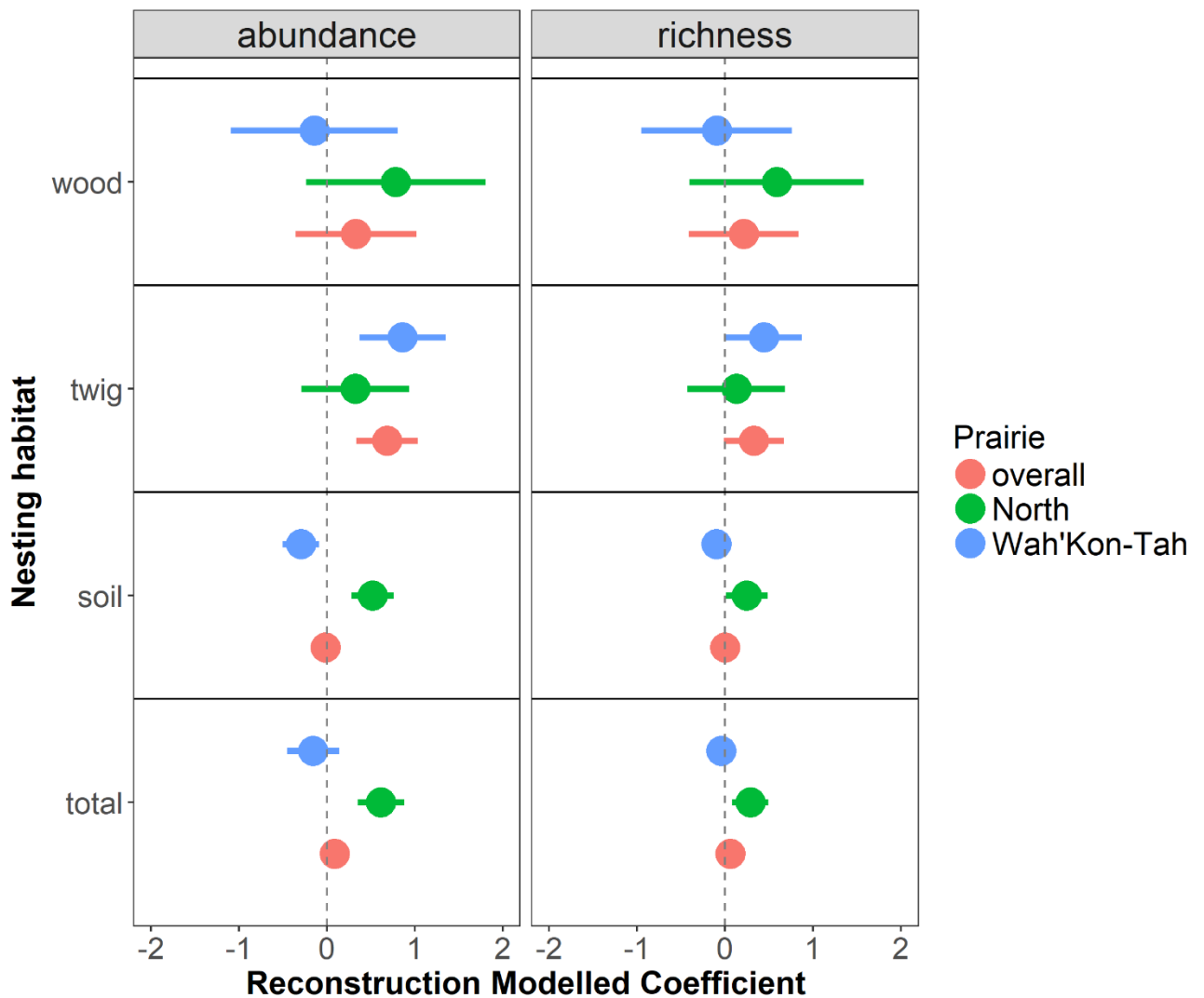


Figure 3.12. Coefficients, with 95% confidence intervals, for the effect of prairie *status* (reconstruction or remnant) from multivariate models of bee abundance and richness according to nesting habitat. Positive coefficients signify a greater abundance on reconstructions, negative coefficients signify greater abundance remnants. There are up to three coefficients for each species, representing models for Wah'Kon-Tah, North, and the prairies combined with no interaction (overall). Model coefficients with very large standard errors are not shown.

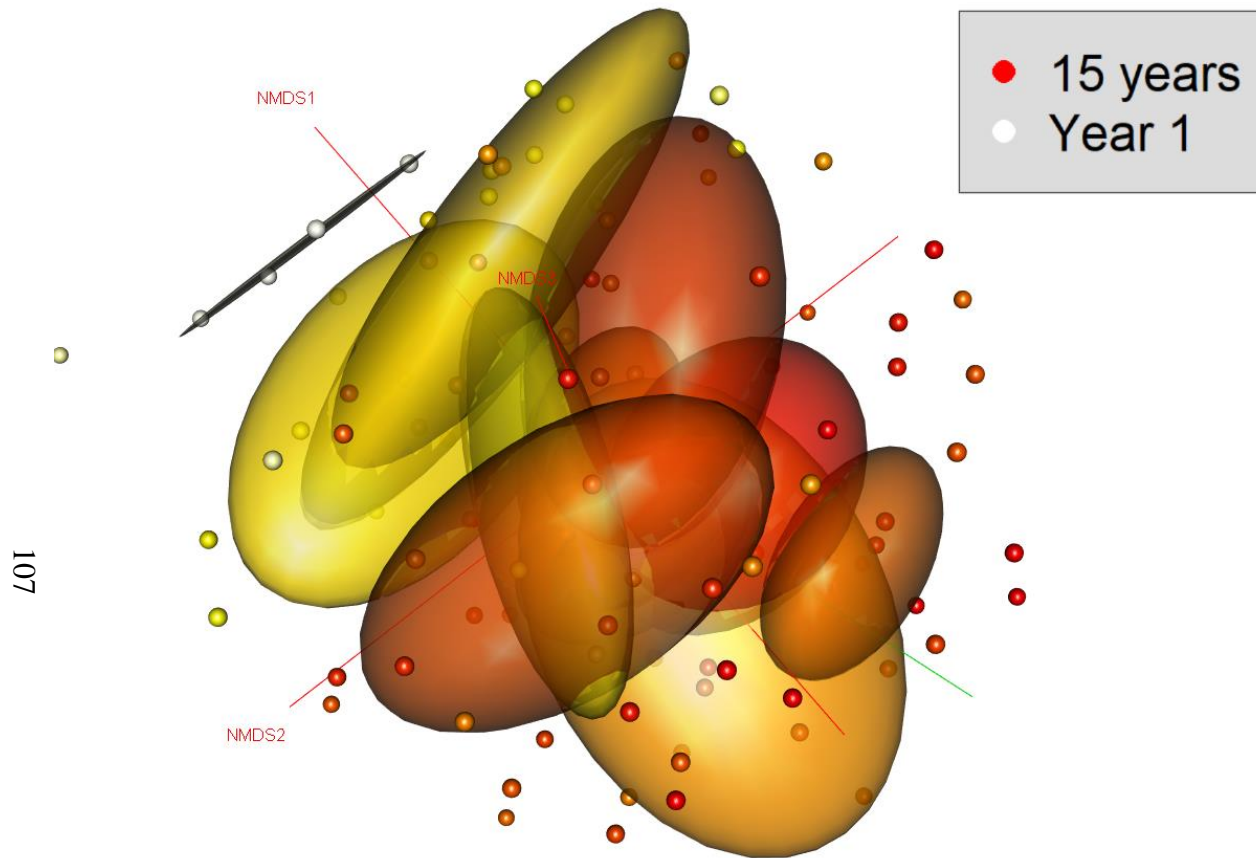


Figure 3.13. NMS ordination (3-dimensional) of bee communities. Dots represent communities from bee bowl samples. Spheres represent 95% confidence intervals around the centroids of reconstructions of the same age. The color of dots and centroids moves from white to yellow, to orange, then to red with increasing age. In this figure, Year 1 appears black because of the angle of the plane.

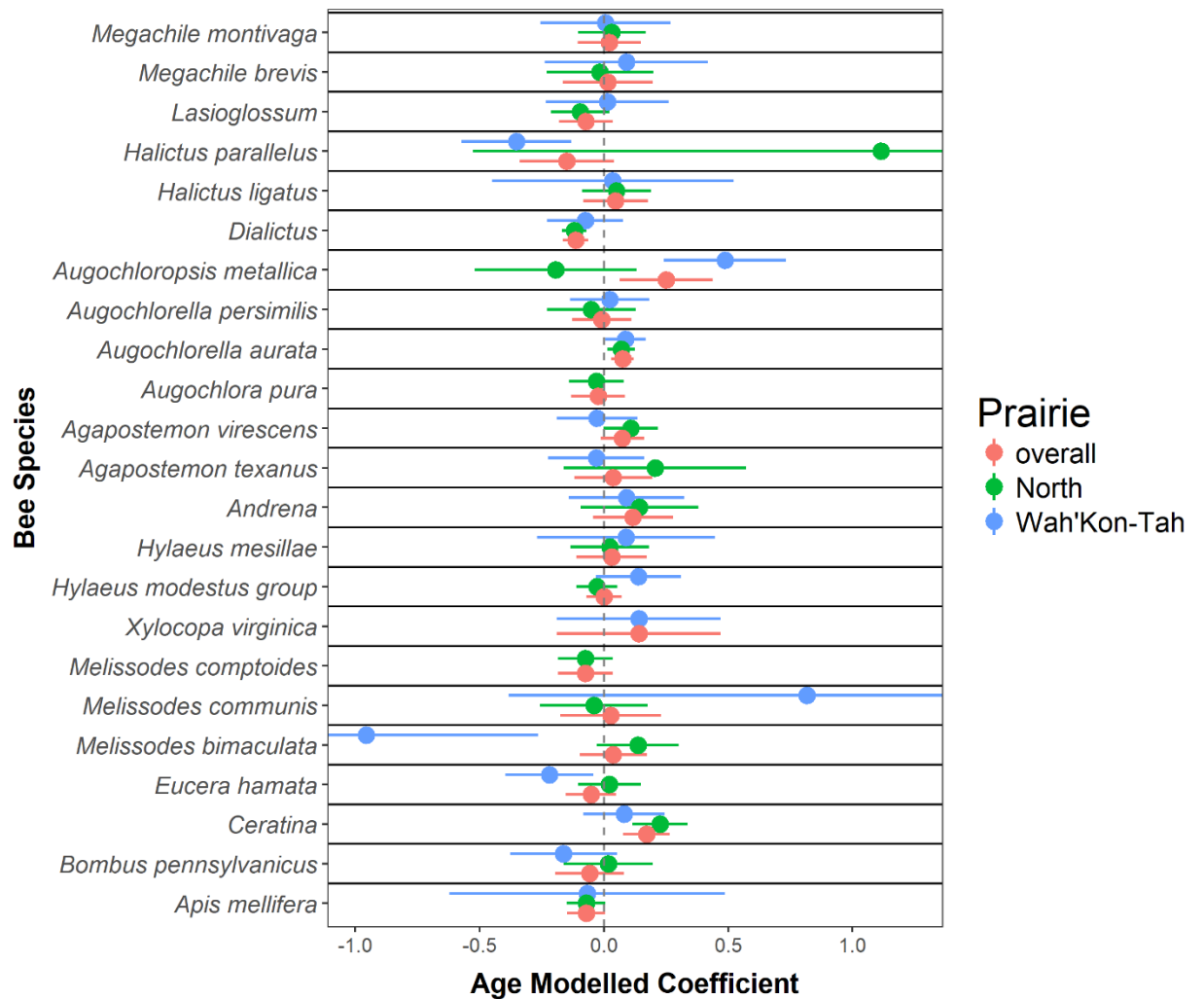


Figure 3.14. Coefficients, with 95% confidence intervals, of *age* from multivariate abundance model on the bee taxa used in ordination. Positive coefficients signify a greater abundance on older reconstructions, negative coefficients signify greater abundance on younger reconstructions. There are up to three coefficients for each species, representing models for Wah'Kon-Tah, North, and the prairies combined with no interaction (overall). Model coefficients with very large standard errors are not shown.

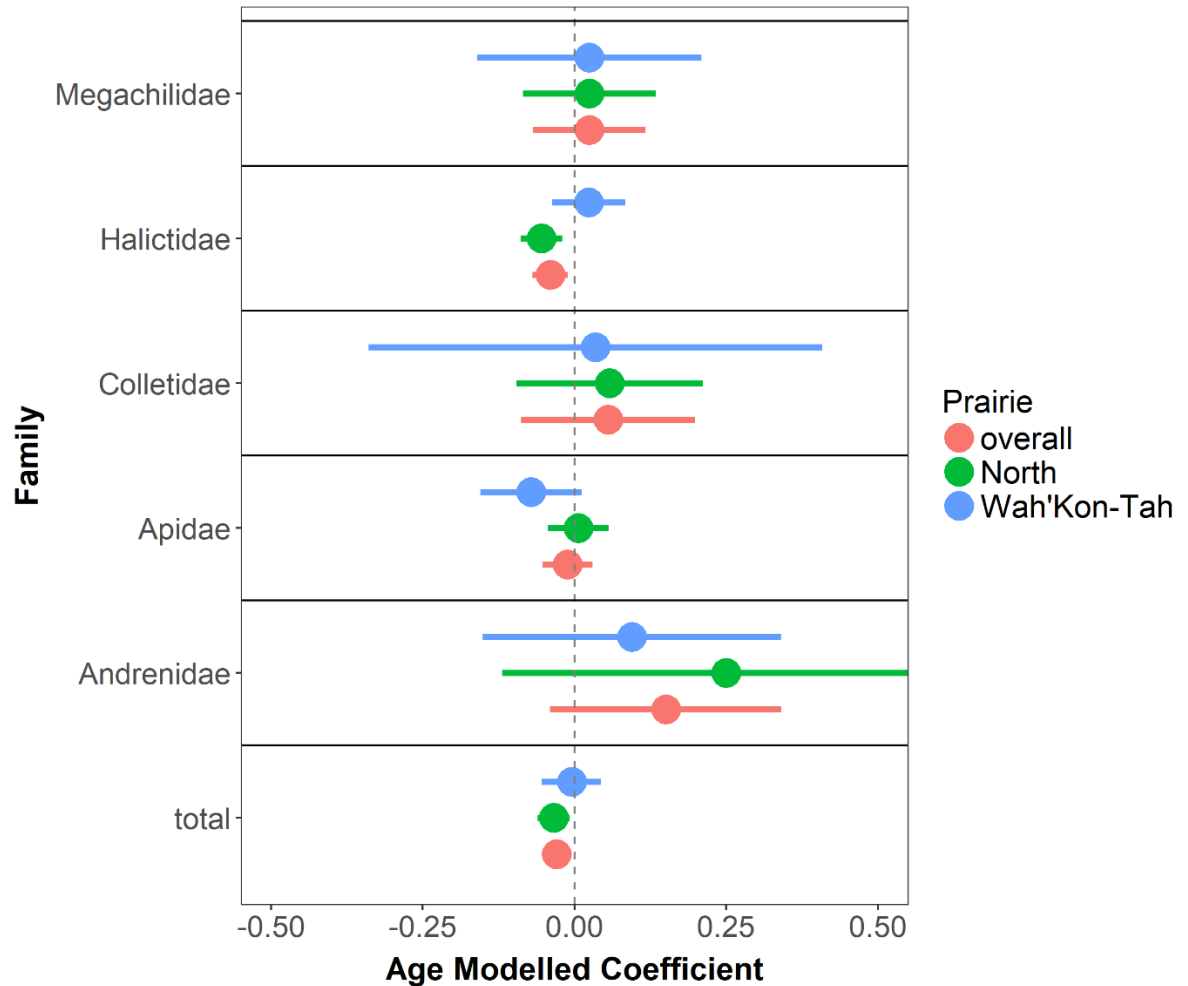


Figure 3.15. Coefficients, with 95% confidence intervals, for the effect of reconstruction age from multivariate models of bee abundance according to family. Positive coefficients signify increasing abundance with age of a reconstruction, negative coefficients signify decreasing abundance with age. There are up to three coefficients for each species, representing models for Wah'Kon-Tah, North, and the prairies combined with no interaction (overall). Model coefficients with very large standard errors are not shown.

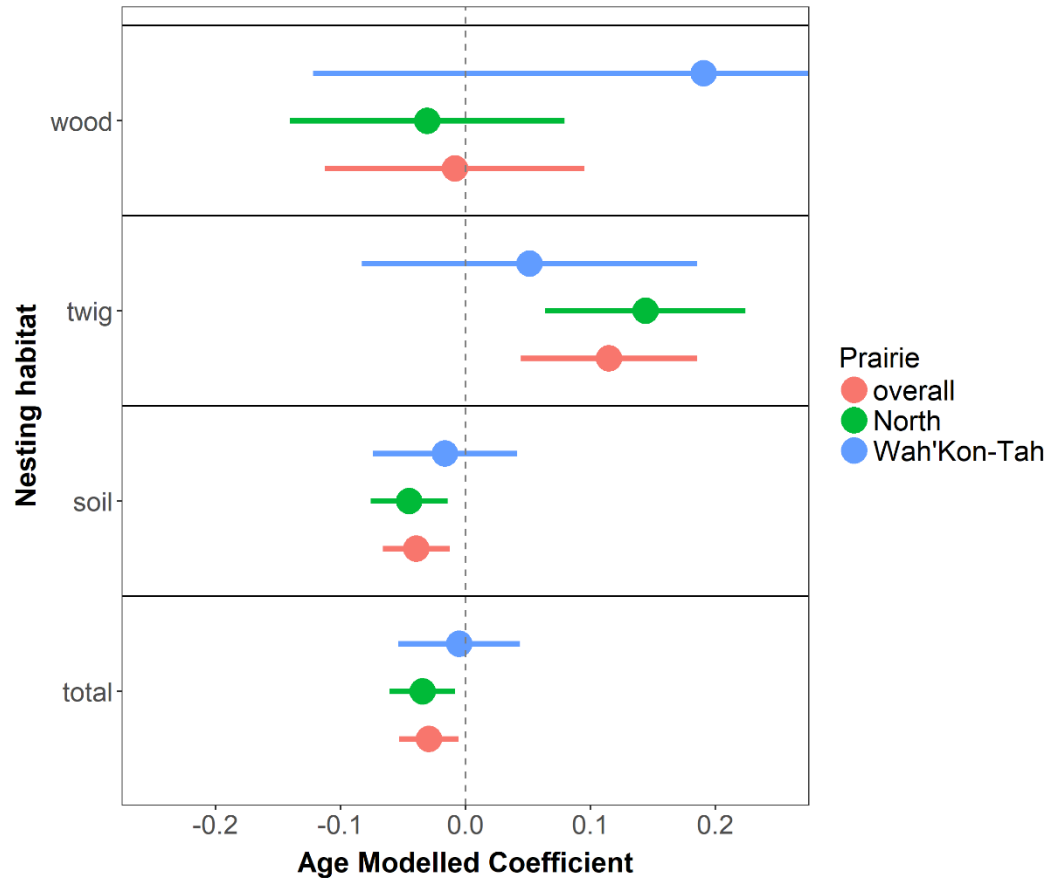


Figure 3.16. Coefficients, with 95% confidence intervals, for *age* from multivariate models of bee abundance according to nesting habitat. Positive coefficients signify increasing abundance with age of a reconstruction, negative coefficients signify decreasing abundance with age. There are up to three coefficients for each species, representing models for Wah'Kon-Tah, North, and the prairies combined with no interaction (overall). Model coefficients with very large standard errors are not shown.

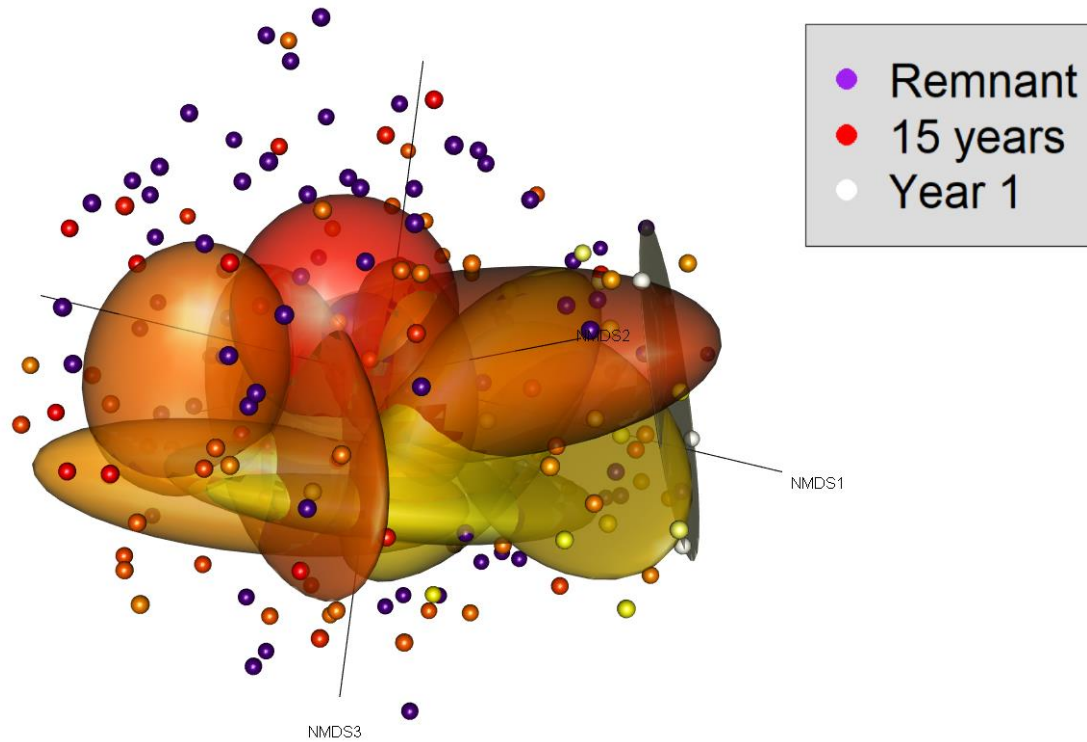


Figure 3.17. NMDS ordination (3-dimensional) of bee communities. Dots represent communities at locations. Spheres represent 95% confidence intervals around the centroids of reconstructions of the same age, and of remnants. The color of dots and centroids moves from white to yellow, to orange, then to red with increasing age. The centroid of the remnants (purple) is located near the center of the space. In this figure, Year 1 appears black because of the angle of the plane.

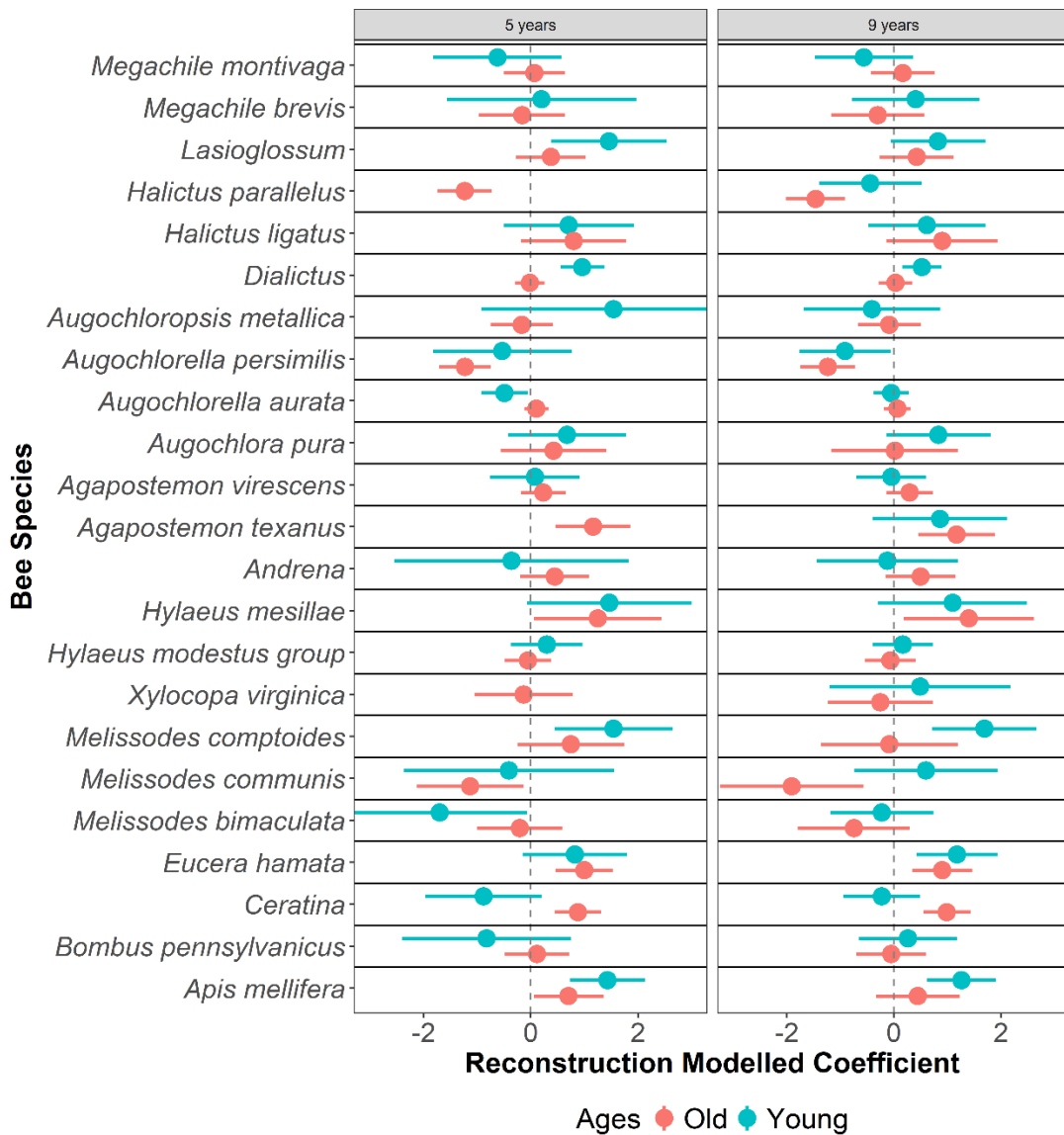


Figure 3.18. Coefficients with 95% confidence intervals for *age group* split at five and nine years from multivariate abundance model on the bee taxa used in ordination.

Positive coefficients signify a greater abundance on reconstructions, negative coefficients signify greater abundance on remnants.

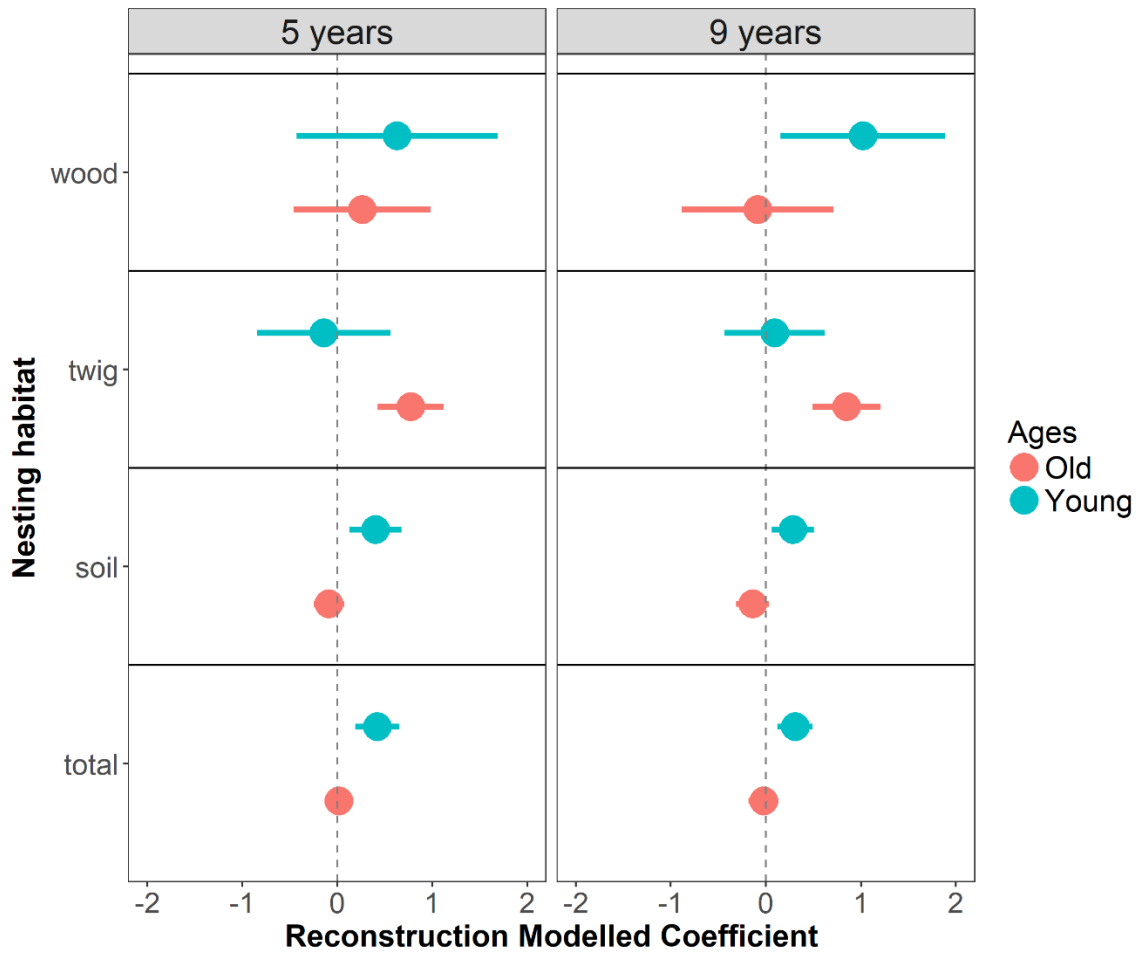


Figure 3.19. Coefficients, with 95% confidence intervals, for *age group* from multivariate models of bee abundance according to nesting habitat. Positive coefficients signify greater abundance on reconstructions, negative coefficients signify greater abundance on remnants.

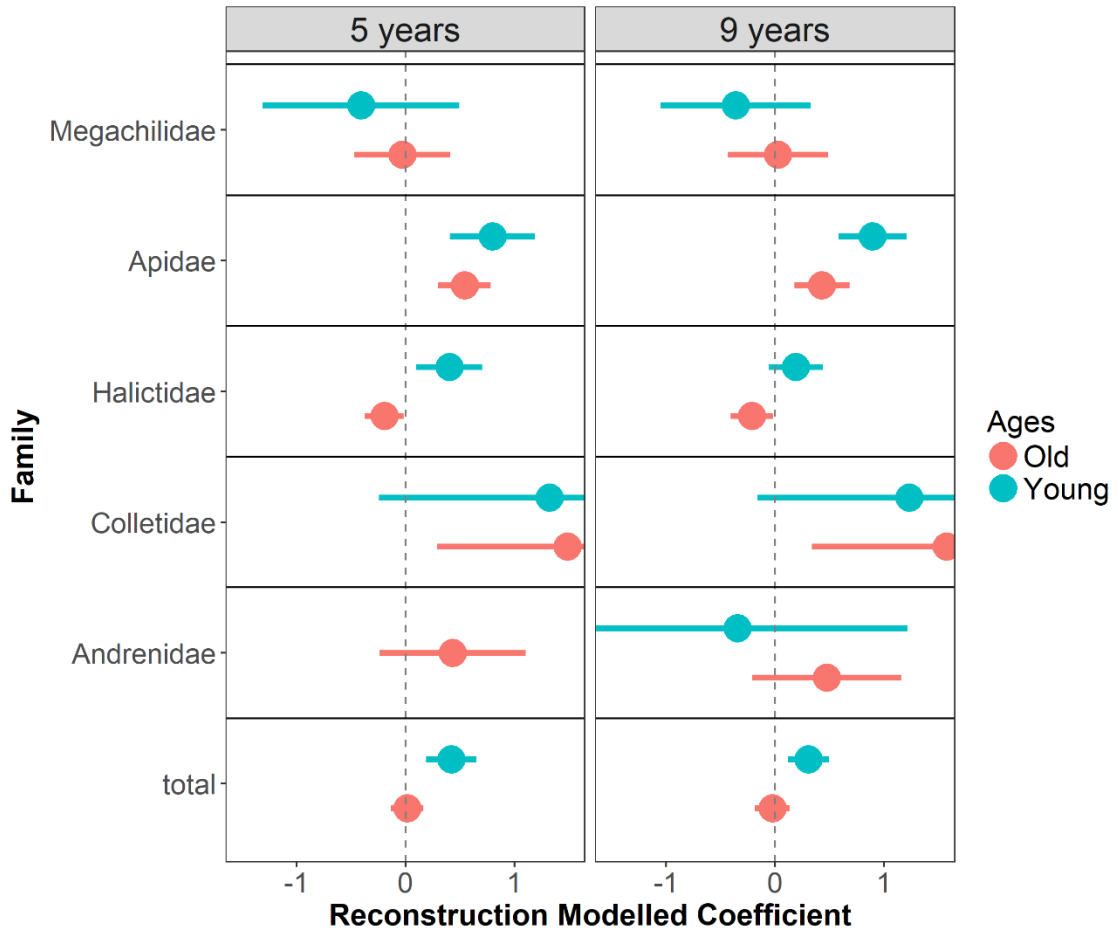


Figure 3.20. Coefficients, with 95% confidence intervals, for *age group* from multivariate models of bee abundance according to family. Positive coefficients signify greater abundance on reconstructions, negative coefficients signify greater abundance on remnants.

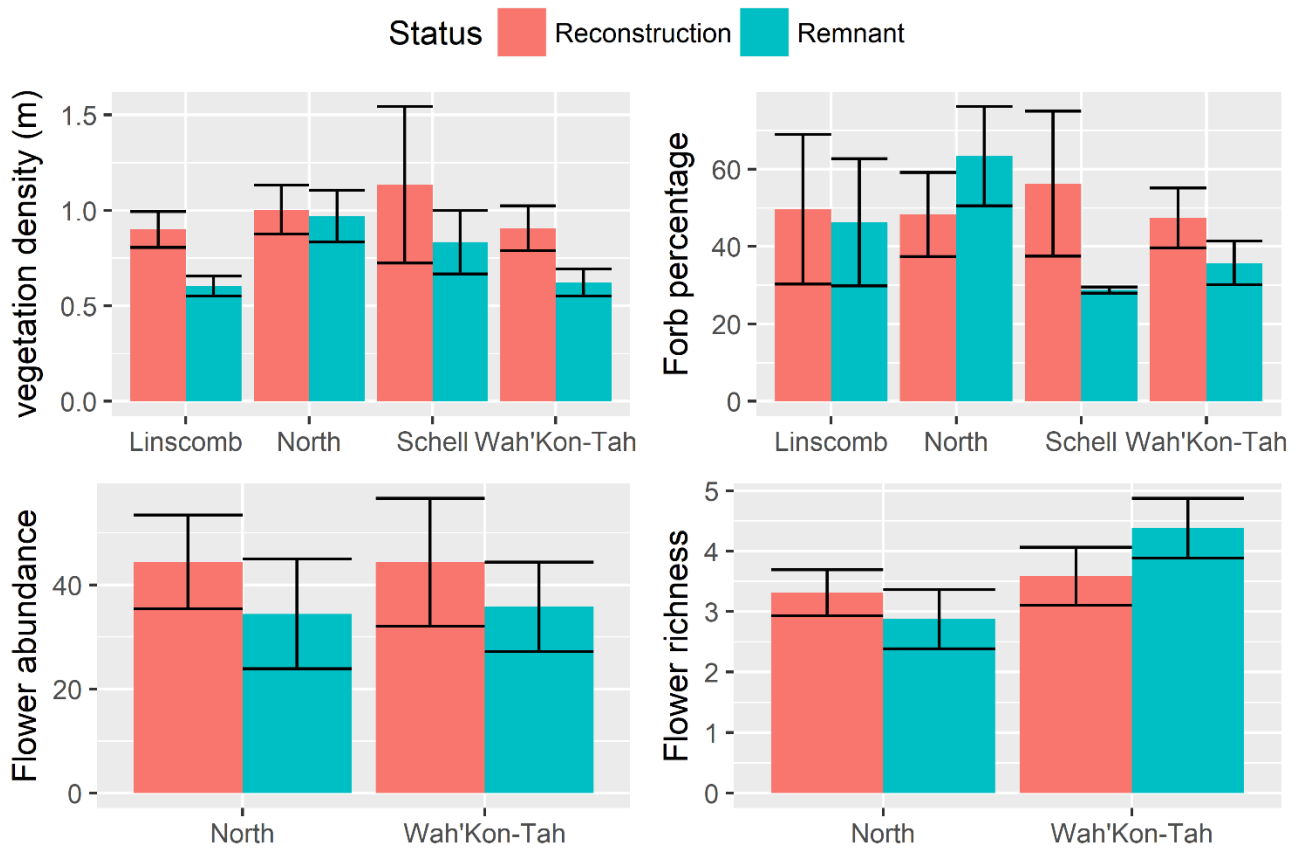


Figure 3.21. Vegetation density, forb percentage, flower abundance, and flower richness means with 95% confidence intervals.

CHAPTER 4

Conclusions and future monitoring

Conclusions

Habitat reconstruction, and specifically tallgrass prairie reconstruction, is a relatively new phenomenon. The methods involved in reconstructing and managing prairies have changed with our growing understanding of disturbance and succession (Anderson 2011). Reconstruction success is gauged using a variety of taxa, from fungi (Tipton 2016) to animals (Cullen and Wheeler 1993, Kennedy et al. 2009). We sought to determine whether reconstructed tallgrass prairies contained similar bee and grasshopper communities as remnant prairies in Missouri. We did not see identical patterns in the two different taxa, which should make one cautious about drawing conclusions about invertebrate restoration from one guild or taxon, especially considering other studies that found even more substantial differences in communities (Davis et al. 2007). Reconstructions hosted similar bee diversity and richness, and generally the same bee species as remnants. However, certain bee taxa were more common on remnants or reconstructions, meaning reconstructed bee communities remained distinct from remnants. Grasshoppers, on the other hand, were more diverse on remnants at three out of the four prairies from which we sampled. Nearly a third of all grasshopper species captured were absent from reconstructions. Reconstructions were characterized by two or three long-winged, generalist species that are strong dispersers (Pfadt 1994).

Clearly, at least two of the many invertebrate guilds on prairies do not recover by themselves in less than twenty years. Reconstructed prairies should continue to be monitored in order to determine if and when communities will converge with remnants.

Deeper knowledge of the habitat requirements of certain taxa associated with remnants or reconstructions could aid managers in creating the appropriate habitat on reconstructions. To acquire that knowledge, monitoring must be efficient and effective. This study can also assist in crafting those monitoring protocols, helping to avoid the difficulties we encountered. Parts of this study can be applied to restoration research and monitoring in other locations, while other parts should not be used far from the prairies we sampled. The species level information from this study is relevant mostly to Missouri prairies, as well as parts of neighboring prairie states. Other states, and even locations in northern Missouri, will probably only share some of the species we found, for both grasshoppers and bees. However, the functional group data can likely be used across the tallgrass prairie region, and perhaps on grassland restorations of other types as well, as long as the methods are similar.

Future monitoring

Bees

The limited portion of the bee community captured in the bee bowls was not entirely surprising based on comparisons of sampling techniques (Roulston et al. 2007). Our goal at the start of the study was to catch specialists and kleptoparasites that appear to be related to prairie ecosystem health (Sheffield et al. 2013). Even with two years of considerable effort focused on just two locations, we did not capture enough rare bees to determine whether remnants were home to more kleptoparasites or specialists. There are two solutions to that problem, increasing the sample size by catching more bees through more intensive sampling, or targeting specific bees using a net. More intensive sampling

could entail more bee bowls, or the use of other types of traps. Blue vane traps catch a greater diversity of bees, but might also remove too many of the rare bees, such as bumble bee queens, that we are trying to protect and restore (Geroff et al. 2014). Malaise traps would provide the most complete picture of bee communities with the least effort, but also cause the greatest bee carnage (Geroff et al. 2014). Regardless of the method, year after year of removing thousands of bees may damage the very community that we are trying to conserve and restore. Additionally, accurate bee identification to species level is very time-consuming; catching more bees only extends the processing stage. Focusing on rare specialists and kleptoparasites, in particular, requires considerable expertise in bee taxonomy and can result in unreliable identifications. The alternative, more targeted capture of oligolectic and kleptoparasitic bees, solves the excessive capture problem but compounds identification issues. Formidable expertise and skill are needed to identify and net rare bees on the wing. Additionally, it becomes difficult to draw conclusions from sampling that is heavily dependent on individual prowess with a net.

Sampling rare bee species on prairies may be prohibitively difficult in the long-term barring new developments in sampling technology. Therefore it may be that common taxa, like those we caught in bee bowls, are more useful in monitoring the convergence, or lack thereof, of reconstructed and remnant bee communities. We identified three taxa found on both the Osage Plains and the Central Dissected Plains that, because of their association (Niemi et al. 1997) with reconstructions or remnants, could be used to monitor bee communities without excessive sampling. To be practical monitoring subjects, these species should be relatively identifiable (Dale and Beyeler 2001). *E. hamata* and *Ceratina*, which were more common on reconstructions, are easily

identified. *A. persimilis*, which holds greater potential than the others because it is associated with remnants, is rather difficult to differentiate from its ubiquitous congener *A. aurata*. Discerning the two species could be learned with some repetition. A fourth and bona fide conservative prairie species, *H. parallelus*, might be particularly useful in Southern Missouri, where it was quite common on remnants. All four are abundant enough that effective sample sizes could be small and oversampling unlikely. If MDC does commit to long-term monitoring of bee communities, including rare species of interest, the cost of frequently removing thousands of bees from prairies, or training net-wielding bee experts, makes non-fatal sampling techniques worth investigating. Creative applications of existing technology, whether it be buzz recording (Heise et al. 2017), eDNA (Bohmann et al. 2014), camera traps (Qing et al. 2012, Yu et al. 2013), or machine learning (Acevedo et al. 2009), could make bee monitoring cheap, informative, and safe.

Grasshoppers

Capturing grasshoppers seems to be a simple undertaking compared to bees. They are large, usually earthbound, and rather conspicuous. Children can catch them quite easily. We chose to sample grasshoppers, however, by standardized sweeping. The technique is quite common in grasshopper research (Evans et al. 1983, Evans 1988, Larson et al. 1999, O'Neill et al. 2002), and is a good tool for community analysis since it measures community composition quite well (Larson et al. 1999). Yet standardized sweeping should be avoided in Missouri monitoring for efficiency reasons. Tallgrass prairie is not always tall, but when it is, it defeats even the most determined of sweep netters. Beating head-high gramminoids savagely with a piece of canvas is, admittedly, cathartic, but doing so while high-stepping it through patches of merciless blackberry

thorns is a soul-sapping struggle. It is also a poor way to catch adult grasshoppers, which have the means and practically an eternity to escape the blundering scientist intent on sweeping in a straight line. Future grasshopper monitors in Missouri would be well-advised to return to their childhood ways and catch them as we did in the second year of the study. We moved slowly through the prairie and netted grasshoppers that flushed from their feeding sites, putting them into a kill jar immediately. It was an efficient way of catching the most number of species. We caught several species that we had not caught with the standardized sweeps in 2016, and the wider sample of the grasshopper community may have allowed us to detect greater richness on remnants than reconstructions in 2017. This targeted capture method also has the potential to be non-fatal if the person catching grasshoppers has some expertise in grasshopper identification. Catching grasshoppers in a simple, intuitive way could be a useful way to monitor grasshopper communities, and determine if reconstructions eventually host some of the species only found on remnants in this study.

Management recommendations

This study can provide some practical management recommendations, but these recommendations should be seen as preliminary because we did not measure many environmental variables, or assess specific management practices other than reconstruction itself. Current management appears to be diverse on the prairies I sampled, which is ideal for insects (Panzer 2002). Burning will definitely alter invertebrate communities in the short-term by eliminating species that live or nest above ground, like stem nesting bees, and insects with poor mobility, like shortwinged grasshoppers. Providing refugia in the form of unburned patches can allow those invertebrates to persist

(Panzer 2002). Managers should seek to promote landscape heterogeneity in order to support insect diversity. Prairies may seem homogenous at a distance, but actually contain a large number of microhabitats. Insects have evolved to fill those various niches. Reconstructions in general appeared more uniform than remnants, probably because the same seed-mix was spread over the entire area. Over time, the plant differentiate according to microhabitat conditions, but to speed the process for invertebrates, efforts could be taken to create heterogeneity earlier in the reconstruction process. Differing the seed mixes according to the location, or even somewhat randomly, could promote insect diversity. Allowing for more bare ground and woodier sections might also provide habitat for predators that could bring stability to the invertebrate community (see Chapter 2 discussion).

I believe the two largest factors responsible for differences in invertebrate communities between reconstructions and remnants are the plant community and soil. I am aware that there is plenty of research and management attention on restoring the plant community, and do not feel qualified to suggest any different practices. Reconstructions appear more weedy and less grassy, but I do not possess the expertise to suggest how to speed plant restoration. The other factor is soil. The two taxa that I studied are considered above ground invertebrates, yet both are directly influenced by soil condition because of nesting habits. Further research and monitoring of soil health on reconstructions compared to remnants could help elucidate the role of soil in the success of reconstruction efforts.

Other taxa

There are several good options for further invertebrate monitoring work on prairie reconstructions and remnants. Our study covered one taxa of aboveground herbivores, and one pollinator taxa. It would be useful to investigate other taxa in each of those guilds because there might be different responses. Of particular importance though would be a guild we did not cover, below-ground herbivores. Grassland cicadas, prairie mole crickets, and earthworms are all examples of belowground herbivores that could struggle to colonize reconstructions because of differing soil conditions. These taxa might also have critical impacts on reconstruction progress through nutrient cycling (Wheeler et al. 1992). Finally, it would be very informative to examine insects occupying a higher trophic level, in other words predators. As with the other guilds, bottom-up effects of the environment might influence which prairie invertebrates are able to occupy reconstructions, and insect predators might affect reconstruction efforts through top-down effects on herbivores and plants (Carson and Root 1999).

Larger implications

Many tallgrass prairie insects are probably at risk of at least local extinction in Missouri. There is simply no way to completely nullify a 99% loss in habitat in less than 150 years. Restoring the complete tallgrass prairie ecosystem would involve restoring the entire historical range, a fantasy. However, there are still ways of mitigating the loss of tallgrass prairies, through intensive management of remnants, localized but intensive reconstruction, or widespread but minor improvement of degraded land (Myers et al. 2000, Reinhardt et al. 2005, Davies et al. 2009, Török and Helm 2017). The last option may be the most impactful given how much more land is in agriculture than tallgrass prairie. Even without complete reconstruction, minor improvements of degraded or

intensely cultivated land could have major consequences for grassland species. For some taxa, common species are just as likely to go locally extinct as rare species (Steck et al. 2007). Agricultural deintensification could boost diversity and preserve some of the more common, versatile grassland species (Steck et al. 2007, Tonietto et al. 2018). Agricultural land use was not, however, the topic of my research. I focused on remnant and reconstructed prairies in Missouri, which represent the other two paths toward protecting tallgrass prairie ecosystems. Remnants will likely not become more scarce given that they are largely owned by the state's natural resource management agencies, or by organizations dedicated to conservation. Thus continued and improved management of the remaining prairies is necessary to minimize further loss of conservative prairie species.

The second option, reconstruction, can help preserve tallgrass prairie communities by rescuing rare species surviving only on the remnants. Expanding habitat area allows for more durable populations with greater connectivity between prairies (MacArthur and Wilson 2016). If managers can successfully replicate the vegetation and soil conditions found on remnants, we will likely see similar insect communities on reconstructions, and a lower probability of extinction for prairie obligates (Fahrig 1997). The end goal is a healthy, functioning prairie ecosystem replete with the insect species that would have occupied it before the conversion to cropland. Expectations, however, should still be tempered by two factors: the difficulty of identifying target historical communities, and the possible existence of extinction debt.

Identifying target communities requires knowledge of past and present species distributions and populations. We can track local extinctions and range-wide declines in

some of the larger and charismatic species such as monarchs (Brower et al. 2012, Pleasants 2017) or bumblebees (Grixti et al. 2009) because people naturally take notice of them (Fleishman and Murphy 2009), and have for many years. But the extinctions, expansions, and fluctuations of the vast majority of insect species have gone largely unnoted (Dunn 2005). This is true for non-insect taxa as well (Clark and May 2002, Nielsen et al. 2009), making it unclear what represents the historic, baseline community, and what represents an artifact of a century of habitat fragmentation and changes in ecosystem function (Thorpe and Stanley 2011). This, in turn, makes evaluating tallgrass reconstructions complicated. After all, how can we go about rebuilding an ecosystem when we do not know what species should inhabit it? In the absence of a time machine, we must base our reconstruction efforts on the remaining examples of tallgrass prairies, remnants. Remnants are the best examples of historical tallgrass prairies, but we should not jump to the conclusion that they are accurate and unchanged representatives of that ecosystem. Remnants have experienced a different disturbance cycle since European colonization. Cattle grazing and haying replaced burning and bison grazing.

Even if we make the shaky assumption that remnants represent the historic tallgrass prairie ecosystems, preserving and replicating remnants in order to expand tallgrass prairie may not yield the expected result. Remnants may represent irreproducible relics from a destroyed ecosystem (Steck et al. 2007), headed toward a degraded state despite our best efforts. Habitat losses do not always immediately translate to extinctions, and species distributions can mirror past historical landscapes closer than current ones (Lindborg and Eriksson 2004, Debinski et al. 2011, Essl et al. 2015). In essence, there is a delay between habitat alteration and species' responses to it, resulting in a mismatch

between the species that ecosystem should support, and those it actually supports. This idea is called extinction debt (Kuussaari et al. 2009).

Depending on the organisms in question and the severity of the habitat destruction, extinction debt can last practically no time at all, to thousands of years (Kuussaari et al. 2009, Holland 2013). The geologically instantaneous destruction of tallgrass prairie in North America suggests a large extinction debt that will be paid off quickly for insects (Hylander and Ehrlén 2013), which are short-lived compared to other taxa. In practice, knowing whether extinction debt still exists is quite difficult. On one hand, tallgrass prairie communities on remnants may have already adjusted to fragmentation. On the other, it is quite possible that even decades after tallgrass prairie was converted to agricultural fields in Missouri, insect species doomed to extinction are still surviving on scattered patches of unconnected prairie. Extinction debt for insects has been detected after fifty years in other grassland systems (Sang et al. 2010). There is some evidence of extinction debt for the taxa targeted in this study. Small specialist bees showed no response to habitat loss on fragmented prairies, even though larger bodied, better dispersing specialists did (Bommarco et al. 2010). That finding could mean that extinction debt has been paid in poor dispersing bees, but not in large bees. Community composition and diversity may change considerably as stochastic events and inbreeding suppression snuff out some of the remaining species. This raises the rather depressing question of whether reconstructions and remnant communities will converge not because we have boosted prairie species on reconstructions, but because we have lost them on remnants.

Conserving the prairie communities found on remnants may require more than simply reproducing historical disturbance regimes through proper management techniques. Reintroduction and assisted migration of invertebrates is probably necessary in order to preserve functioning metapopulations and form new metapopulations that can prevent regional or statewide extinctions. There is much to be learned about reintroduction and assisted migration in insects. The two terms are quite similar, but for the purpose of this discussion I am distinguishing them thus: assisted migration is the simple act of relocating insects from one remnant prairie to a nearby remnant in hopes of introducing genetic variation and protecting the species from stochastic extinction events. Reintroduction is a more extreme version of assisted migration that involves the addition of a species to a new environment that has not hosted the species for many years. Reintroduction science is its own field already (Sarrazin and Barbault 1996, Armstrong and Seddon 2008), but very little has attempted let alone researched in invertebrates.

There are several species for which I believe reintroduction holds great promise, both as a learning tool and as a conservation strategy. Prairie mole crickets (*Gryllotalpa major*) are potentially important below-ground herbivores whose range has shrunk to but a few prairie remnants in Missouri (Figg and Calvert 1987). They are such a conservative species that there is little to no chance of them escaping to rampage across people's lawns. Prairie mole crickets are also about as capable of capturing the public's interest as any insect without big pretty wings. They are quite large and their springtime leks are a riveting auditory experience. Burrowing crayfish are another prairie invertebrate for which reintroduction seems appropriate. They are critical for the survival of the declining Northern Crawfish Frog (*Lithobates areolatus*) (Heemeyer et al. 2012) and are

themselves declining due to habitat loss and pressure from invasive species of crayfish. Reintroducing burrowing crayfish could save several species simultaneously.

Assisted migration should be a priority for highly fragmented landscapes like Missouri's tallgrass prairie. At this point, I can only speculate as to the best way to move insects between prairies. Vacuuming them at random and redistributing them might be a cost effective way of relocating above ground invertebrates, although there is the potential for spreading undesirable species as well, or homogenizing prairie communities. Targeting specific species might be safer and easier to gauge the success or failure of assisted migration, with the downside being the considerable time and expertise needed to identify and capture individual insects.

It is important to acknowledge the possibility that losses in species richness and extinctions may occur in spite of dedicated reconstruction efforts and conservation on remnants. While discouraging, this notion does not mean that reconstruction efforts are for naught, for they can still limit the loss of prairie biodiversity. It does make monitoring of great importance on remnants and reconstructions. Studies like this one will be vital for tracking the moving targets that are remnant communities, keeping reconstruction goals realistic, and identifying species that stand the best chance of being rescued.

REFERENCES

- Acevedo, M. A., C. J. Corrada-Bravo, H. Corrada-Bravo, L. J. Villanueva-Rivera, and T. M. Aide. 2009. Automated classification of bird and amphibian calls using machine learning: A comparison of methods. *Ecological Informatics* 4:206-214.
- Andersen, A. N., and J. D. Majer. 2004. Ants show the way Down Under: invertebrates as bioindicators in land management. *Frontiers in Ecology and the Environment* 2:291-298.
- Anderson, M. J. 2011. Navigating the multiple meanings of beta diversity: a roadmap for the practicing ecologist (vol 14, pg 19, 2011). *Ecology Letters* 14:210-210.
- Anderson, N. L. 1964. Some relationships between grasshoppers and vegetation. *Annals of the Entomological Society of America* 57:736-742.
- Arduser, M. 2011. Bees known from Osage Plains prairies in Missouri. unpublished report. Missouri Department of Conservation.
- Arduser, M. 2016. Identificaiton and ecology of tallgrass prairie bees. Arduser, (n.p.).
- Ascher, J. S., and J. Pickering. 2017. Discover Life bee species guide and world checklist.
- Baer, S. G., S. L. Collins, J. M. Blair, A. K. Knapp, and A. K. Fiedler. 2005. Soil heterogeneity effects on tallgrass prairie community heterogeneity: an application of ecological theory to restoration ecology. *Restoration Ecology* 13:413-424.
- Ballard, H. E. 1992. Keys to known and potential Missouri Orthoptera. The Nature Conservancy.
- Baur, B., and J. Bengtsson. 1987. Colonizing ability in land snails on Baltic uplift archipelagos. *Journal of Biogeography* 14:329-341.
- Beck, J., and I. J. Kitching. 2007. Correlates of range size and dispersal ability: a comparative analysis of sphingid moths from the Indo-Australian tropics. *Global Ecology and Biogeography* 16:341-349.
- Belovsky, G. E. 1986. Generalist herbivore foraging and its role in competitive interactions. *American Zoologist* 26:51-69.
- Belovsky, G. E., and J. B. Slade. 1993. The role of vertebrate and invertebrate predators in a grasshopper community. *Oikos* 68:193-201.
- Belovsky, G. E., J. B. Slade, and B. A. Stockhoff. 1990. Susceptibility to predation for different grasshoppers - an experimental-study. *Ecology* 71:624-634.

- Benayas, J. M. R., A. C. Newton, A. Diaz, and J. M. Bullock. 2009. Enhancement of biodiversity and ecosystem services by ecological restoration: a meta-analysis. *Science* 325:1121-1124.
- Benkobi, L., D. W. Uresk, G. Schenbeck, and R. M. King. 2000. Protocol for monitoring standing crop in grasslands using visual obstruction. *Journal of Range Management* 53:627-633.
- Blakey, R. V., B. S. Law, R. T. Kingsford, J. Stoklosa, P. Tap, K. Williamson, and J. Minderman. 2016. Bat communities respond positively to large-scale thinning of forest regrowth. *Journal of Applied Ecology* 53:1694-1703.
- Blanchet, E., M. Lecoq, G. A. Sword, K. Berthier, C. Pages, C. Billot, R. Rivallan, A. Foucart, J. M. Vassal, A. M. Risterucci, and M. P. Chapuis. 2012. A comparative analysis of fine-scale genetic structure in three closely related syntopic species of the grasshopper genus *Calliptamus*. *Canadian Journal of Zoology* 90:31-41.
- Block, W. M., A. B. Franklin, J. P. Ward, J. L. Ganey, and G. C. White. 2001. Design and implementation of monitoring studies to evaluate the success of ecological restoration on wildlife. *Restoration Ecology* 9:293-303.
- Bohmann, K., A. Evans, M. T. P. Gilbert, G. R. Carvalho, S. Creer, M. Knapp, W. Y. Douglas, and M. De Bruyn. 2014. Environmental DNA for wildlife biology and biodiversity monitoring. *Trends in Ecology & Evolution* 29:358-367.
- Bomar, C. R. 2001. Comparison of grasshopper (Orthoptera: Acrididae) communities on remnant and reconstructed prairies in western Wisconsin. *Journal of Orthoptera Research* 10:105-112.
- Bommarco, R., J. C. Biesmeijer, B. Meyer, S. G. Potts, J. Poyry, S. P. Roberts, I. Steffan-Dewenter, and E. Ockinger. 2010. Dispersal capacity and diet breadth modify the response of wild bees to habitat loss. *Proceedings of the Royal Society B-Biological Sciences* 277:2075-2082.
- Bonada, N., N. Prat, V. H. Resh, and B. Statzner. 2006. Developments in aquatic insect biomonitoring: a comparative analysis of recent approaches. *Annual review of entomology* 51:495-523.
- Bonte, D., N. Vandenbroecke, L. Lens, and J.-P. Maelfait. 2003. Low propensity for aerial dispersal in specialist spiders from fragmented landscapes. *Proceedings of the Royal Society of London B: Biological Sciences* 270:1601-1607.
- Bowles, M., J. McBride, and T. Bell. 2015. Long-term processes affecting restoration and viability of the federal threatened Mead's milkweed (*Asclepias meadii*). *Ecosphere* 6:1-22.

- Brennan, L. A., and W. P. Kuvlesky Jr. 2005. North American grassland birds: an unfolding conservation crisis? *Journal of Wildlife Management* 69:1-13.
- Brower, L. P., O. R. Taylor, E. H. Williams, D. A. Slayback, R. R. Zubieta, and M. I. Ramirez. 2012. Decline of monarch butterflies overwintering in Mexico: is the migratory phenomenon at risk? *Insect Conservation and Diversity* 5:95-100.
- Brückmann, S. V., J. Krauss, and I. Steffan-Dewenter. 2010. Butterfly and plant specialists suffer from reduced connectivity in fragmented landscapes. *Journal of Applied Ecology* 47:799-809.
- Brust, M., J. Thurman, C. Reuter, L. Black, R. Quartarone, and A. J. Redford. 2014. Grasshoppers of the Western U.S. USDA APHIS Identification Technology Program (ITP).
- Cameron, S. A., J. D. Lozier, J. P. Strange, J. B. Koch, N. Cordes, L. F. Solter, and T. L. Griswold. 2011. Patterns of widespread decline in North American bumble bees. *Proceedings of the National Academy of Sciences* 108:662-667.
- Campbell, J. B., W. H. Arnett, J. Lambley, O. K. Jantz, and H. Knutson. 1974. Grasshoppers (Acrididae) of the Flint Hills native tallgrass prairie in Kansas.
- Cane, J. H., T. Griswold, and F. D. Parker. 2007. Substrates and materials used for nesting by North American *Osmia* bees (Hymenoptera: Apiformes: Megachilidae). *Annals of the Entomological Society of America* 100:350-358.
- Cane, J. H., and J. L. Neff. 2011. Predicted fates of ground-nesting bees in soil heated by wildfire: thermal tolerances of life stages and a survey of nesting depths. *Biological Conservation* 144:2631-2636.
- Capinera, J. L., and T. Sechrist. 1982. Grasshoppers (Acrididae) of Colorado: identification, biology and management. *Bulletin (Colorado Agricultural Experiment Station)*; 584S.
- Capinera, J. L., and D. C. Thompson. 1987. Dynamics and structure of grasshopper assemblages in shortgrass prairie. *The Canadian Entomologist* 119:567-575.
- Carson, W. P., and R. B. Root. 1999. Top-down effects of insect herbivores during early succession: influence on biomass and plant dominance. *Oecologia* 121:260-272.
- Carter, D. L., and J. M. Blair. 2012. Recovery of Native Plant Community Characteristics on a Chronosequence of Restored Prairies Seeded into Pastures in West-Central Iowa. *Restoration Ecology* 20:170-179.

- Ceballos, G., A. Davidson, R. List, J. Pacheco, P. Manzano-Fischer, G. Santos-Barrera, and J. Cruzado. 2010. Rapid decline of a grassland system and its ecological and conservation implications. *Plos One* 5:e8562.
- Chao, A., and C. H. Chiu. 2016. Nonparametric estimation and comparison of species richness, Chichester.
- Chao, A., N. J. Gotelli, T. C. Hsieh, E. L. Sander, K. H. Ma, R. K. Colwell, and A. M. Ellison. 2014. Rarefaction and extrapolation with Hill numbers: a framework for sampling and estimation in species diversity studies. *Ecological Monographs* 84:45-67.
- Chiu, C.-H., and A. Chao. 2016. Estimating and comparing microbial diversity in the presence of sequencing errors. *PeerJ* 4:e1634.
- Christisen, D. M. 1972. Prairie preservation in Missouri. Pages 42-46 in L. C. Hulbert, editor. *Proceedings of the Third Midwest Prairie Conference*. Division of Biology, Kansas State University, Manhattan, KS.
- Clark, J. A., and R. M. May. 2002. Taxonomic bias in conservation research. *Science* 297:191-192.
- Clarke-Wood, B. K., K. M. Jenkins, B. S. Law, and R. V. Blakey. 2016. The ecological response of insectivorous bats to coastal lagoon degradation. *Biological Conservation* 202:10-19.
- Colla, S. R., and L. Packer. 2008. Evidence for decline in eastern North American bumblebees (Hymenoptera: Apidae), with special focus on *Bombus affinis* Cresson. *Biodiversity and Conservation* 17:1379.
- Colwell, R. K., A. Chao, N. J. Gotelli, S. Y. Lin, C. X. Mao, R. L. Chazdon, and J. T. Longino. 2012. Models and estimators linking individual-based and sample-based rarefaction, extrapolation and comparison of assemblages. *Journal of Plant Ecology* 5:3-21.
- Colwell, R. K., and J. A. Coddington. 1994. Estimating terrestrial biodiversity through extrapolation. *Philosophical Transactions of the Royal Society of London B* 345:101-118.
- Cullen, W., and C. P. Wheater. 1993. The flora and invertebrate fauna of a relocated grassland at Thrislington Plantation, County Durham, England. *Restoration Ecology* 1:130-137.
- Dale, V. H., and S. C. Beyeler. 2001. Challenges in the development and use of ecological indicators. *Ecological Indicators* 1:3-10.

- Davies, B., J. Biggs, P. Williams, and S. Thompson. 2009. Making agricultural landscapes more sustainable for freshwater biodiversity: a case study from southern England. *Aquatic Conservation: Marine and Freshwater Ecosystems* 19:439-447.
- Davis, J. D., S. D. Hendrix, D. M. Debinski, and C. J. Hemsley. 2007. Butterfly, bee and forb community composition and cross-taxon incongruence in tallgrass prairie fragments. *Journal of Insect Conservation* 12:69-79.
- Davis, R. M., M. D. Skold, J. S. Berry, and W. P. Kemp. 1992. The economic threshold for grasshopper control on public rangelands. *Journal of Agricultural and Resource Economics* 17:56-65.
- Debinski, D. M., R. A. Moranz, J. T. Delaney, J. R. Miller, D. M. Engle, L. B. Winkler, D. A. McGranahan, R. J. Barney, J. C. Trager, A. L. Stephenson, and M. K. Gillespie. 2011. A cross-taxonomic comparison of insect responses to grassland management and land-use legacies. *Ecosphere* 2:art131.
- Dennis, R. L., L. Dapporto, S. Fattorini, and L. M. Cook. 2011. The generalism–specialism debate: the role of generalists in the life and death of species. *Biological Journal of the Linnean Society* 104:725-737.
- Diboll, N. 1997. Designing seed mixes. Pages 135-150 in P. S. and C. F. Mutel, editors. *The Tallgrass Restoration Handbook: For Prairies, Savannas and Woodlands*. Island Press, Washington DC.
- Diepenbrock, L. M., D. L. Finke, A. Stewart, and N. Littlewood. 2013. Refuge for native lady beetles (Coccinellidae) in perennial grassland habitats. *Insect Conservation and Diversity* 6:671-679.
- Dobson, A. P., A. Bradshaw, and A. á. Baker. 1997. Hopes for the future: restoration ecology and conservation biology. *Science* 277:515-522.
- Droege, S. 2012. Handy Bee Manual. US Geological Survey Native Bee Inventory and Monitoring Lab, Beltsville, MD.
- Droege, S. 2015. Tips on How to Use Bee Bowls to Collect Bees. US Geological Survey Native Bee Inventory and Monitoring Lab, Beltsville, MD.
- Dunn, R. R. 2005. Modern insect extinctions, the neglected majority. *Conservation Biology* 19:1030-1036.
- Eickwort, G. C., R. W. Matthews, and J. Carpenter. 1981. Observations on the nesting behavior of *Megachile rubi* and *M. texana* with a discussion of the significance of soil nesting in the evolution of megachilid bees (Hymenoptera: Megachilidae). *Journal of the Kansas Entomological Society* 54:557-570.

- Engle, D. M., S. D. Fuhlendorf, A. Roper, and D. M. Leslie Jr. 2008. Invertebrate community response to a shifting mosaic of habitat. *Rangeland Ecology & Management* 61:55-62.
- Essl, F., S. Dullinger, W. Rabitsch, P. E. Hulme, P. Pysek, J. R. Wilson, and D. M. Richardson. 2015. Delayed biodiversity change: no time to waste. *Trends in Ecology and Evolution* 30:375-378.
- Evans, E. W. 1988. Community dynamics of prairie grasshoppers subjected to periodic fire: predictable trajectories or random walks in time? *Oikos* 52:283-292.
- Evans, E. W., R. A. Rogers, and D. J. Opfermann. 1983. Sampling grasshoppers on burned and unburned tallgrass prairie: night trapping vs. sweeping. *Environmental Entomology* 12:1449-1454.
- Exeler, N. 2009. Wild bee communities in restored sand ecosystems in north-western Germany: Community structure, population genetics and habitat preferences. Dissertation. University of Osnabrück, Germany, Osnabrück.
- Fahrig, L. 1997. Relative effects of habitat loss and fragmentation on population extinction. *The Journal of Wildlife Management* 61:603-610.
- Figg, D., and P. Calvert. 1987. Status, distribution, and life history of the prairie mole cricket (*Gryllotalpa major*). Missouri Department of Conservation, Jefferson City, MO.
- Fleishman, E., and D. D. Murphy. 2009. A realistic assessment of the indicator potential of butterflies and other charismatic taxonomic groups. *Conservation Biology* 23:1109-1116.
- Foster, B. L., C. A. Murphy, K. R. Keller, T. A. Aschenbach, E. J. Questad, and K. Kindscher. 2007. Restoration of prairie community structure and ecosystem function in an abandoned hayfield: a sowing experiment. *Restoration Ecology* 15:652-661.
- Geroff, R. K., J. Gibbs, and K. W. McCravy. 2014. Assessing bee (Hymenoptera: Apoidea) diversity of an Illinois restored tallgrass prairie: methodology and conservation considerations. *Journal of Insect Conservation* 18:951-964.
- Gotelli, N. J., and R. K. Colwell. 2011. Estimating species richness. Pages 39-54 in A. E. Magurran and B. McGill, editors. *Biological diversity: frontiers in measurement and assessment*. Oxford University Press, New York.
- Greenleaf, S. S., N. M. Williams, R. Winfree, and C. Kremen. 2007. Bee foraging ranges and their relationship to body size. *Oecologia* 153:589-596.

- Griffin, S. R., B. Bruninga-Socolar, M. A. Kerr, J. Gibbs, and R. Winfree. 2017. Wild bee community change over a 26-year chronosequence of restored tallgrass prairie. *Restoration Ecology* 25:650-660.
- Grixti, J. C., L. T. Wong, S. A. Cameron, and C. Favret. 2009. Decline of bumble bees (*Bombus*) in the North American Midwest. *Biological Conservation* 142:75-84.
- Grundel, R., R. P. Jean, K. J. Frohnapple, G. A. Glowacki, P. E. Scott, and N. B. Pavlovic. 2010. Floral and nesting resources, habitat structure, and fire influence bee distribution across an open-forest gradient. *Ecological Applications* 20:1678-1692.
- Hansen, M. J., and D. J. Gibson. 2014. Use of multiple criteria in an ecological assessment of a prairie restoration chronosequence. *Applied Vegetation Science* 17:63-73.
- Harmon-Threatt, A. N., and S. D. Hendrix. 2015. Prairie restorations and bees: The potential ability of seed mixes to foster native bee communities. *Basic and Applied Ecology* 16:64-72.
- Hastings, E., and J. Pepper. 1964. Population studies on the big-headed grasshopper *Aulocara elliotti*. *Annals of the Entomological Society of America* 57:216-220.
- Heemeyer, J. L., P. J. Williams, and M. J. Lannoo. 2012. Obligate crayfish burrow use and core habitat requirements of crawfish frogs. *The Journal of Wildlife Management* 76:1081-1091.
- Heidinger, I. M. M., S. Hein, and D. Bonte. 2010. Patch connectivity and sand dynamics affect dispersal-related morphology of the blue-winged grasshopper *Oedipoda caerulescens* coastal grey dunes. *Insect Conservation and Diversity* 3:205-212.
- Heise, D., N. Miller-Struttman, C. Galen, and J. Schul. 2017. Acoustic detection of bees in the field using CASA with focal templates. Pages 1-5 *Sensors Applications Symposium (SAS), 2017 IEEE*. IEEE Xplore Digital Library, Glassboro, NJ.
- Hernandez, J. L., G. W. Frankie, and R. W. Thorp. 2009. Ecology of urban bees: a review of current knowledge and directions for future study. *Cities and the Environment* 2:3.
- Hilliard Jr, J. R. 2001. Two new grasshopper species in the Texanus group of the genus *Melanoplus* (Orthoptera: Acrididae: Melanoplinae) with biological notes on the group. *Transactions of the American Entomological Society* 127:31-68.
- Hjermann, D. O., and R. A. Ims. 1996. Landscape ecology of the wart-biter *Decticus verrucivorus* in a patchy landscape. *Journal of Animal Ecology* 65:768-780.

- Holland, S. 2013. Relaxation time and the problem of the pleistocene. *Diversity* 5:276-292.
- Hsieh, T. C., K. H. Ma, A. Chao, and G. McNerny. 2016. iNEXT: an R package for rarefaction and extrapolation of species diversity (Hill numbers). *Methods in Ecology and Evolution* 7:1451-1456.
- Humbert, J. Y., J. Ghazoul, G. J. Sauter, and T. Walter. 2010. Impact of different meadow mowing techniques on field invertebrates. *Journal of Applied Entomology* 134:592-599.
- Hurlbert, S. H. 1984. Pseudoreplication and the design of ecological field experiments. *Ecological Monographs* 54:187-211.
- Hylander, K., and J. Ehrlén. 2013. The mechanisms causing extinction debts. *Trends in Ecology & Evolution* 28:341-346.
- Joern, A. 1979. Feeding patterns in grasshoppers (Orthoptera: Acrididae): factors influencing diet specialization. *Oecologia* 38:325-347.
- Joern, A. 1986. Experimental study of avian predation on coexisting grasshopper populations (Orthoptera: Acrididae) in a sandhills grassland. *Oikos* 46:243-249.
- Keller, D., R. Holderegger, and M. J. Strien. 2013. Spatial scale affects landscape genetic analysis of a wetland grasshopper. *Molecular Ecology* 22:2467-2482.
- Kennedy, P. L., S. J. DeBano, A. M. Bartuszevige, and A. S. Lueders. 2009. Effects of native and non-native grassland plant communities on breeding passerine birds: Implications for restoration of northwest bunchgrass prairie. *Restoration Ecology* 17:515-525.
- Keylock, C. 2005. Simpson diversity and the Shannon–Wiener index as special cases of a generalized entropy. *Oikos* 109:203-207.
- Kim, J., N. Williams, and C. Kremen. 2006. Effects of cultivation and proximity to natural habitat on ground-nesting native bees in California sunflower fields. *Journal of the Kansas Entomological Society* 79:309-320.
- Kimoto, C., S. J. DeBano, R. W. Thorp, R. V. Taylor, H. Schmalz, T. DelCurto, T. Johnson, P. L. Kennedy, and S. Rao. 2012. Short-term responses of native bees to livestock and implications for managing ecosystem services in grasslands. *Ecosphere* 3:1-19.
- Kindscher, K., and L. L. Tieszen. 1998. Floristic and soil organic matter changes after five and thirty-five years of native tallgrass prairie restoration. *Restoration Ecology* 6:181-196.

- Kirk, K., and C. R. Bomar. 2003. Guide to the Grasshopper of Wisconsin. Wisconsin Department of Natural Resources, Madison, WI.
- Knowles, L. L. 2001. Genealogical portraits of speciation in montane grasshoppers (genus *Melanoplus*) from the sky islands of the Rocky Mountains. *Proceedings of the Royal Society of London B: Biological Sciences* 268:319-324.
- Kotiaho, J. S., V. Kaitala, A. Komonen, and J. Paivinen. 2005. Predicting the risk of extinction from shared ecological characteristics. *Proceedings of the National Academy of Sciences* 102:1963-1967.
- Kremen, C., A. M. Merenlender, and D. D. Murphy. 1994. Ecological monitoring: a vital need for integrated conservation and development programs in the tropics. *Conservation Biology* 8:388-397.
- Kruess, A., and T. Tschardt. 2002. Grazing intensity and the diversity of grasshoppers, butterflies, and trap-nesting bees and wasps. *Conservation Biology* 16:1570-1580.
- Kuefler, D., B. Hudgens, N. M. Haddad, W. F. Morris, and N. Thurgate. 2010. The conflicting role of matrix habitats as conduits and barriers for dispersal. *Ecology* 91:944-950.
- Kurtz, C. 2013. A practical guide to prairie reconstruction. University of Iowa Press.
- Kuussaari, M., R. Bommarco, R. K. Heikkinen, A. Helm, J. Krauss, R. Lindborg, E. Ockinger, M. Partel, J. Pino, F. Roda, C. Stefanescu, T. Teder, M. Zobel, and I. Steffan-Dewenter. 2009. Extinction debt: a challenge for biodiversity conservation. *Trends in Ecology and Evolution* 24:564-571.
- Kwaiser, K. S., and S. D. Hendrix. 2008. Diversity and abundance of bees (Hymenoptera: Apiformes) in native and ruderal grasslands of agriculturally dominated landscapes. *Agriculture, Ecosystems & Environment* 124:200-204.
- Larson, D. L., J. B. Bright, P. Drobney, J. L. Larson, N. Palaia, P. A. Rabie, S. Vacek, and D. Wells. 2011. Effects of planting method and seed mix richness on the early stages of tallgrass prairie restoration. *Biological Conservation* 144:3127-3139.
- Larson, D. P., K. M. O'Neill, and W. P. Kemp. 1999. Evaluation of the accuracy of sweep sampling in determining grasshopper (Orthoptera : Acrididae) community composition. *Journal of Agricultural and Urban Entomology* 16:207-214.
- Lester, S. E., B. I. Ruttenberg, S. D. Gaines, and B. P. Kinlan. 2007. The relationship between dispersal ability and geographic range size. *Ecology Letters* 10:745-758.
- Lindborg, R., and J. Eriksson. 2004. Historical landscape connectivity affects present plant species diversity. *Ecology* 85:1840-1845.

- Lockwood, J. A. 2004. Locust: the devastating rise and mysterious disappearance of the insect that shaped the American frontier. Wiley Online Library.
- Lockwood, J. A., W. P. Kemp, and J. A. Onsager. 1988. Long-term, large-scale effects of insecticidal control on rangeland grasshopper populations (Orthoptera: Acrididae). *Journal of Economic Entomology* 81:1258-1264.
- Losey, J. E., and M. Vaughan. 2006. The economic value of ecological services provided by insects. *Bioscience* 56:311-323.
- MacArthur, R. H., and E. O. Wilson. 2016. *The theory of island biogeography*. Princeton University Press.
- Marini, L., R. Bommarco, P. Fontana, and A. Battisti. 2010. Disentangling effects of habitat diversity and area on orthopteran species with contrasting mobility. *Biological Conservation* 143:2164-2171.
- Marini, L., E. Ockinger, A. Battisti, and R. Bommarco. 2012. High mobility reduces beta-diversity among orthopteran communities - implications for conservation. *Insect Conservation and Diversity* 5:37-45.
- Martin, L. M., K. A. Moloney, and B. J. Wilsey. 2005. An assessment of grassland restoration success using species diversity components. *Journal of Applied Ecology* 42:327-336.
- McLachlan, S. M., and A. L. Knispel. 2005. Assessment of long-term tallgrass prairie restoration in Manitoba, Canada. *Biological Conservation* 124:75-88.
- Middleton, E. L., J. D. Bever, and P. A. Schultz. 2010. The effect of restoration methods on the quality of the restoration and resistance to invasion by exotics. *Restoration Ecology* 18:181-187.
- Moreira, R. G., G. W. Fernandes, E. D. Almada, and J. C. Santos. 2007. Gallling insects as bioindicators of land restoration in an area of Brazilian Atlantic Forest. *Lundiana* 8:107-112.
- Mortimer, S. R., J. A. Hollier, and V. K. Brown. 1998. Interactions between plant and insect diversity in the restoration of lowland calcareous grasslands in southern Britain. *Applied Vegetation Science* 1:101-114.
- Myers, N., R. A. Mittermeier, C. G. Mittermeier, G. A. Da Fonseca, and J. Kent. 2000. Biodiversity hotspots for conservation priorities. *Nature* 403:853.
- New, T. R. 1993. Angels on a pin: dimensions of the crisis in invertebrate conservation. *American Zoologist* 33:623-630.

- Nielsen, S. E., D. L. Haughland, E. Bayne, and J. Schieck. 2009. Capacity of large-scale, long-term biodiversity monitoring programmes to detect trends in species prevalence. *Biodiversity and Conservation* 18:2961-2978.
- Niemi, G. J., J. M. Hanowski, A. R. Lima, T. Nicholls, and N. Weiland. 1997. A critical analysis on the use of indicator species in management. *The Journal of Wildlife Management*:1240-1252.
- O'Neill, K. M., D. P. Larson, and W. P. Kemp. 2002. Sweep sampling technique affects estimates of the relative abundance and community composition of grasshoppers (Orthoptera : Acrididae). *Journal of Agricultural and Urban Entomology* 19:125-131.
- Oksanen, J., F. Blanchet, R. Kindt, and P. Legendre. 2016. others (2010) vegan: community ecology package. R package version:2.0-5.
- Olechnowski, B. F., D. M. Debinski, P. B. Drobney, K. Viste-Sparkman, and W. T. Reed. 2009. Changes in vegetation structure through time in a restored tallgrass prairie ecosystem and implications for avian diversity and community composition. *Ecological Restoration* 27:449-457.
- Ortego, J., M. P. Aguirre, V. Noguerales, and P. J. Cordero. 2015. Consequences of extensive habitat fragmentation in landscape-level patterns of genetic diversity and structure in the Mediterranean esparto grasshopper. *Evolutionary applications* 8:621-632.
- Otte, D. 1981. *The North American Grasshoppers: Acrididae: Oedipodinae*. Harvard University Press.
- Otte, D. 2012. Eighty new melanoplus species from the United States (Acrididae: Melanoplinae). *Transactions of the American Entomological Society* 138:73-167.
- Panzer, R. 2002. Compatibility of prescribed burning with the conservation of insects in small, isolated prairie reserves. *Conservation Biology* 16:1296-1307.
- Panzer, R., and M. W. Schwartz. 1998. Effectiveness of a vegetation-based approach to insect conservation. *Conservation Biology* 12:693-702.
- Paton, D., D. Rogers, B. Hill, C. Bailey, and M. Ziembicki. 2009. Temporal changes to spatially stratified waterbird communities of the Coorong, South Australia: implications for the management of heterogeneous wetlands. *Animal Conservation* 12:408-417.
- Peet, R. K. 1974. The measurement of species diversity. *Annual Review of Ecology and Systematics* 5:285-307.

- Peet, R. K. 1975. Relative diversity indices. *Ecology* 56:496-498.
- Peterson, M. A., and R. F. Denno. 1998. The influence of dispersal and diet breadth on patterns of genetic isolation by distance in phytophagous insects. *The American Naturalist* 152:428-446.
- Pfadt, R. E. 1994. *Field Guide to Common Western Grasshoppers*. University of Wyoming.
- Picaud, F., and D. P. Petit. 2008. Body size, sexual dimorphism and ecological succession in grasshoppers. *Journal of Orthoptera Research* 17:177-181.
- Piechnik, D. A., S. P. Lawler, and N. D. Martinez. 2008. Food-web assembly during a classic biogeographic study: Species' "trophic breadth" corresponds to colonization order. *Oikos* 117:665-674.
- Pleasants, J. 2017. Milkweed restoration in the Midwest for monarch butterfly recovery: estimates of milkweeds lost, milkweeds remaining and milkweeds that must be added to increase the monarch population. *Insect Conservation and Diversity* 10:42-53.
- Pleasants, J. M., and K. S. Oberhauser. 2013. Milkweed loss in agricultural fields because of herbicide use: effect on the monarch butterfly population. *Insect Conservation and Diversity* 6:135-144.
- Potts, S. G., B. Vulliamy, A. Dafni, G. Ne'eman, and P. Willmer. 2003. Linking bees and flowers: How do floral communities structure pollinator communities? *Ecology* 84:2628-2642.
- Qing, Y., L. Jun, Q.-j. Liu, G.-q. Diao, B.-j. Yang, H.-m. CHEN, and T. Jian. 2012. An insect imaging system to automate rice light-trap pest identification. *Journal of Integrative Agriculture* 11:978-985.
- R Core Team. 2017. *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Reed, C. 1996. *List of Insect Species which May Be Tallgrass Prairie Specialists Final Report to the USFWS Cooperating Agencies July 1, 1996*.
- Reinhardt, K., G. Kohler, S. Maas, and P. Detzel. 2005. Low dispersal ability and habitat specificity promote extinctions in rare but not in widespread species: the Orthoptera of Germany. *Ecography* 28:593-602.
- Ries, L., D. M. Debinski, and M. L. Wieland. 2001. Conservation value of roadside prairie restoration to butterfly communities. *Conservation Biology* 15:401-411.

- Ritchie, M. E., and D. Tilman. 1992. Interspecific competition among grasshoppers and their effect on plant abundance in experimental field environments. *Oecologia* 89:524-532.
- Roulston, T. a. H., S. A. Smith, and A. L. Brewster. 2007. A comparison of pan trap and intensive net sampling techniques for documenting a bee (Hymenoptera: Apiformes) fauna. *Journal of the Kansas Entomological Society* 80:179-181.
- Routledge, R. 1979. Diversity indices: Which ones are admissible? *Journal of theoretical Biology* 76:503-515.
- Rowe, H. I. 2010. Tricks of the trade: techniques and opinions from 38 experts in tallgrass prairie restoration. *Restoration Ecology* 18:253-262.
- Samson, F., and F. Knopf. 1994. Prairie conservation in north america. *Bioscience* 44:418-421.
- Sang, A., T. Teder, A. Helm, and M. Pärtel. 2010. Indirect evidence for an extinction debt of grassland butterflies half century after habitat loss. *Biological Conservation* 143:1405-1413.
- Sarrazin, F., and R. Barbault. 1996. Reintroduction: challenges and lessons for basic ecology. *Trends in Ecology & Evolution* 11:474-478.
- Sauberer, N., K. P. Zulka, M. Abensperg-Traun, H.-M. Berg, G. Bieringer, N. Milasowszky, D. Moser, C. Plutzer, M. Pollheimer, and C. Storch. 2004. Surrogate taxa for biodiversity in agricultural landscapes of eastern Austria. *Biological Conservation* 117:181-190.
- Schwartz, O. A., and P. D. Whitson. 1987. A 12-year study of vegetation and mammal succession on a reconstructed tallgrass prairie in Iowa. *American Midland Naturalist* 117:240-249.
- Scott, J. M., F. Davis, B. Csuti, R. Noss, B. Butterfield, C. Groves, H. Anderson, S. Caicco, F. D'Erchia, and T. C. Edwards Jr. 1993. Gap analysis: a geographic approach to protection of biological diversity. *Wildlife Monographs* 123:3-41.
- Sergio, F., I. Newton, L. Marchesi, and P. Pedrini. 2006. Ecologically justified charisma: preservation of top predators delivers biodiversity conservation. *Journal of Applied Ecology* 43:1049-1055.
- Sheffield, C. S., A. Pindar, L. Packer, and P. G. Kevan. 2013. The potential of cleptoparasitic bees as indicator taxa for assessing bee communities. *Apidologie* 44:501-510.

- Shepherd, S., and D. M. Debinski. 2005. Evaluation of isolated and integrated prairie reconstructions as habitat for prairie butterflies. *Biological Conservation* 126:51-61.
- Shochat, E., M. A. Patten, D. W. Morris, D. L. Reinking, D. H. Wolfe, and S. K. Sherrod. 2005. Ecological traps in isodars: effects of tallgrass prairie management on bird nest success. *Oikos* 111:159-169.
- Simberloff, D. 1990. Reconstructing the ambiguous: can island ecosystems be restored. Pages 37-51 in Towns, D.R., Daugherty, C. H., and Atkinson, I. A. E., editors. *Ecological restoration of New Zealand islands*. Conservation Sciences Publication, Department of Conservation, Wellington, NZ.
- Six, J., E. Elliott, K. Paustian, and J. Doran. 1998. Aggregation and soil organic matter accumulation in cultivated and native grassland soils. *Soil Science Society of America Journal* 62:1367-1377.
- Smith, D. 2010. *The Tallgrass Prairie Center guide to prairie restoration in the Upper Midwest*. University of Iowa Press.
- Solecki, M., and T. Toney. 1986. Characteristics and management of Missouri's public prairies. Pages 168-171 in *Proceedings of the North American Prairie Conference*.
- Song, H. 2009. Taxonomic Identification Key to *Schistocerca* species. <http://www.schistocerca.org/key.htm>.
- Steck, C. E., M. Bürgi, J. Bolliger, F. Kienast, A. Lehmann, and Y. Gonthier. 2007. Conservation of grasshopper diversity in a changing environment. *Biological Conservation* 138:360-370.
- Steenman, A., A. W. Lehmann, and G. U. C. Lehmann. 2014. Life-history trade-off between macroptery and reproduction in the wing-dimorphic pygmy grasshopper *Tetrix subulata* (Orthoptera Tetrigidae). *Ethology Ecology & Evolution* 27:93-100.
- Swengel, A. B. 2001. A literature review of insect responses to fire, compared to other conservation managements of open habitat. *Biodiversity & Conservation* 10:1141-1169.
- Thom, R. M. 2000. Adaptive management of coastal ecosystem restoration projects. *Ecological Engineering* 15:365-372.
- Thomas, C. D. 2000. Dispersal and extinction in fragmented landscapes. *Proceedings of the Royal Society B-Biological Sciences* 267:139-145.

- Thompson, J. D. 1999. Population differentiation in Mediterranean plants: insights into colonization history and the evolution and conservation of endemic species. *Heredity* 82:229.
- Thorpe, A. S., and A. G. Stanley. 2011. Determining appropriate goals for restoration of imperilled communities and species. *Journal of Applied Ecology* 48:275-279.
- Tipton, A. G. 2016. Restoration at the roots: mycorrhizal interactions and habitat restoration in glades and prairies. Dissertation. University of Missouri--Columbia.
- Tischendorf, L., D. J. Bender, and L. Fahrig. 2003. Evaluation of patch isolation metrics in mosaic landscapes for specialist vs. generalist dispersers. *Landscape Ecology* 18:41-50.
- Tonietto, R. K., J. S. Ascher, and D. J. Larkin. 2017. Bee communities along a prairie restoration chronosequence: similar abundance and diversity, distinct composition. *Ecological Applications* 27:705-717.
- Tonietto, R. K., D. J. Larkin, and S. Diamond. 2018. Habitat restoration benefits wild bees: A meta-analysis. *Journal of Applied Ecology* 55:582-590.
- Török, P., and A. Helm. 2017. Ecological theory provides strong support for habitat restoration. *Biological Conservation* 206:85-91.
- Tuell, J. K., and R. Isaacs. 2009. Elevated pan traps to monitor bees in flowering crop canopies. *Entomologia Experimentalis et Applicata* 131:93-98.
- Uresk, D. W., and T. A. Benzon. 2007. Monitoring with a modified Robel pole on meadows in the central Black Hills of South Dakota. *Western North American Naturalist* 67:46-50.
- Uvarov, B. P. 1966. Grasshoppers and Locusts: A Handbook of General Acridology. Vol. 1, Anatomy, Physiology, Development, Phase Polymorphism, Introduction to Taxonomy. Published for the Anti-Locust Research Centre at the University Press.
- Van Zandt, P. A., E. Collins, J. B. Losos, and J. M. Chase. 2005. Implications of food web interactions for restoration of Missouri Ozark glade habitats. *Restoration Ecology* 13:312-317.
- Vesk, P. A., and R. Mac Nally. 2006. The clock is ticking—Revegetation and habitat for birds and arboreal mammals in rural landscapes of southern Australia. *Agriculture, Ecosystems & Environment* 112:356-366.

- Vesk, P. A., R. Nolan, J. R. Thomson, J. W. Dorrrough, and R. M. Nally. 2008. Time lags in provision of habitat resources through revegetation. *Biological Conservation* 141:174-186.
- Vogel, J. A., D. M. Debinski, R. R. Koford, and J. R. Miller. 2007. Butterfly responses to prairie restoration through fire and grazing. *Biological Conservation* 140:78-90.
- Walker, K. J., P. A. Stevens, D. P. Stevens, J. O. Mountford, S. J. Manchester, and R. F. Pywell. 2004. The restoration and re-creation of species-rich lowland grassland on land formerly managed for intensive agriculture in the UK. *Biological Conservation* 119:1-18.
- Watts, C. H., B. R. Clarkson, and R. K. Didham. 2008. Rapid beetle community convergence following experimental habitat restoration in a mined peat bog. *Biological Conservation* 141:568-579.
- Weibull, A.-C., Ö. Östman, and Å. Granqvist. 2003. Species richness in agroecosystems: the effect of landscape, habitat and farm management. *Biodiversity & Conservation* 12:1335-1355.
- Wheeler, G., K. Williams, and K. Smith. 1992. Role of periodical cicadas (Homoptera: Cicadidae: Magicicada) in forest nutrient cycles. *Forest Ecology and Management* 51:339-346.
- Whiles, M. R., and R. E. Charlton. 2006. The ecological significance of tallgrass prairie arthropods. *Annual Review of Entomology* 51:387-412.
- Whitman, D. W. 2008. The significance of body size in the Orthoptera: a review. *Journal of Orthoptera Research* 17:117-134.
- Williams, N. M. 2011. Restoration of nontarget species: bee communities and pollination function in riparian forests. *Restoration Ecology* 19:450-459.
- Woodcock, B. A., S. G. Potts, T. Tscheulin, E. Pilgrim, A. J. Ramsey, J. Harrison-Cripps, V. K. Brown, and J. R. Tallowin. 2009. Responses of invertebrate trophic level, feeding guild and body size to the management of improved grassland field margins. *Journal of Applied Ecology* 46:920-929.
- Yu, X., J. Wang, R. Kays, P. A. Jansen, T. Wang, and T. Huang. 2013. Automated identification of animal species in camera trap images. *EURASIP Journal on Image and Video Processing* 2013:52.
- Zalewski, M., and W. Ulrich. 2006. Dispersal as a key element of community structure: the case of ground beetles on lake islands. *Diversity and Distributions* 12:767-775.

Zera, A. J., and R. F. Denno. 1997. Physiology and ecology of dispersal polymorphism in insects. *Annual Review of Entomology* 42:207-230.