THE IMPACTS OF EXOTIC SPECIES ON NATIVE BEE COMMUNITIES AND INTERACTIONS IN NOVEL NORTHERN GREAT PLAINS GRASSLANDS

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Title

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The Supervisory Committee certifies that this ***disquisition*** complies with North Dakota State University's regulations and meets the accepted standards for the degree of

DOCTOR OF PHILOSOPHY

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ABSTRACT

Human alterations to landscapes impose novel conditions on native plant and animal species. Exotic plants are among these changes and are presently common and prevalent across Northern Great Plains (NGP) grasslands. Their introductions alter plant communities and influence the wildlife species that rely on the resources provided by plant communities. Exotic plants displace native plant species, but we do not understand how or if some exotic plants can provide resources to pollinating insects requiring floral resources. Considering the spread of exotic plants and the important ecological services bees provide, it is important to understand how native bees value and interact with exotic plants, and how exotic plants may shape bee communities in the NGP. To address this, we employ a unique dataset built from a statewide survey of bees and associated plant species across North Dakota grasslands to investigate the broad questions of how bees select between native and exotic floral resources, how exotic grasses may indirectly affect bee diversity through the plant community, and how exotic species dominance changes the interaction structure between bees and plants. From our selection analyses, we found native bumble bees selected for native plants and plant diversity over exotic plants whenever significant selection occurred, while European honey bees selected for exotic plants and floral resource density. However, both benefited from floral resource diversity, indicating that common management may exist for both groups. Invasive grasses did not affect bee richness at a broad scale but negatively influenced particular bees, such as ground-nesting species. We found litter accumulation to be influential over plant communities and particular types of bees based on their life history traits, indicating the need for grassland management practices that prevent homogenous plant structure. Finally, we found that exotic bees and plants influenced bee-plant interaction network properties through their dominance over contemporary pollination networks. This implicates that managing exotic species may be needed to reduce effects on the complex bee-plant interactions and consequent pollination services. Broadly, this work provides further evidence of exotic species effects on ecological communities and the first large-scale assessment of their impacts on bee communities in NGP grasslands.

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DEDICATION

For what it may be worth, I dedicate my dissertation work to the remaining Great Plains grasslands. It was not a fair trade, but I also dedicate this dissertation research to the native bees that died as a result of this work in optimistic hopes that its results and implications are in turn able to benefit bees in the future. As always, everything is for London. My faithful and spunky canine companion is the only one who knew the hours I worked identifying bees and processing data and always kept me company during long nights.

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Abstract

The ubiquitous presence of anthropogenic pressures on native ecosystems has resulted in numerous functional and compositional changes that often result in novel ecosystems. It is necessary to understand how native species interact with these novel systems, especially if those species provide essential ecosystem services or are of conservation concern. Exotic plants and European honey bees are prevalent across the Northern Great Plains region (NGP) and contribute to the novelty of interactions between native bees and altered grasslands. Honey bees are known to benefit from exotic flowering forbs but less is known on how native species view these novel resources, especially compared to native forbs. Using data from a statewide survey of bees across North Dakota grasslands, we compared seasonal floral selection of honey bees and bumble bees. Additionally, we determined which floral characteristics best explained the abundance of both groups. Both bee groups had substantial visitations to exotic plant species, but selection analyses, which incorporates both the use and availability of resources, revealed that honey bees and native bumble bees differed in selection between native and non-native floral resources. However, this depended on the seasonal period and the bumble bee species examined. Honey bees selected for exotic resources in the middle and late seasonal periods and grouped bumble bees selected for native resources in the mid-seasonal period. Native forb presence and floral richness best explained the variation in bumble bee abundance, while honey bee abundance was associated with flowering densities in the early and mid-seasons and floral richness in both the early and late seasons. Our results imply that honey bee and native bumble bee management and conservation should differ based on their associations with native and exotic floral resources. However, floral species diversity was important to both groups at certain points in the growing season, providing a common management target. As such, we support focused management for floral diversity on landscapes to provision native bumble bees and honey bees.

Introduction

Human globalization accommodated intentional and incidental non-native species introductions (Hobbs et al. 2006). The resulting novel interactions between native and non-native species are, however, highly dependent on the system (Van Riper and Larson 2010) and species considered (Simberloff et al. 2013). These interactions vary greatly from being beneficial or benign (Schlaepfer et al. 2011; Nelson et al. 2017), to negative interactions that affect native species' fitness (Rodewald 2011; Woods et al. 2012; Gibson et al. 2013; Pyšek et al. 2020). It is important that research focus on such impacts of species' functions rather than their origin (Davis et al. 2011), but some exotic species have significant consequences for ecosystem function and human interests with nearly $20 billion USD spent on managing invasive-exotic species annually (Fantle-Lepczyk et al. 2022). Thus, more research is necessary to understand how exotic species interactions with other species affect biodiversity and how species in higher trophic levels are utilizing these novel resources.

Many grasslands in North America can be considered novel systems due to interactions between native species, introduced species, and the prescribed management (or lack thereof) that differs from those maintained by historical disturbances (e.g. fire, grazing patterns; Hobbs et al. 2006; Ellis-Felege et al. 2013; Toledo et al. 2014; Gasch et al. 2020). For example, invasions of cheatgrass, *Bromus tectorum* Linnaeus, are prevalent across the Great Basin region and have increased fire frequencies that threatens native sagebrush communities (Rottler et al. 2015;

Bradley et al. 2018). Additionally, in tallgrass prairies, exotic plant-dominated grasslands had homogenized functional traits and lower biodiversity than native tallgrass prairie (Martin et al. 2014). Some exotic forb species present in North American grasslands were intentionally cultivated for agricultural benefits, but have reduced native plant species in their unintended, yet invasive, spread into grasslands (Varriano et al. 2020). Regardless of the manner of their introduction, exotic plant species have transformed the composition and structure of North America’s grasslands with consequence on ecological interactions.

Irrespective of potentially invasive characteristics, some exotic plant species have the prospect to benefit native wildlife species. For example, exotic forbs may serve as a pollen or nectar resource for ecologically important species such as pollinating bees (Tepedino et al. 2008). However, exotic plant species must be morphologically, spatially, and temporally available, and have nutritious pollen or nectar to be considered beneficial to native bees (Stout and Morales 2009). Significant concessions to these standards may limit the value of exotic plants to bees. Aside from being physically accessible and of some nutritive value, these direct benefits may only be available to pollen-generalist bees; those that specialize on pollen from particular native plants are not likely to use exotic plant pollen sources (Vanbergen et al. 2018). Even if introduced forb species are beneficial for some bee species, those with invasive qualities can also have indirect negative effects on bees through their replacement of native host plants (Stout and Morales 2009; Van Riper and Larson 2009). However, because of their persistent establishment throughout many grasslands, there is a need to evaluate whether and/or how exotic plant species support ecologically important species.

The pollination services bees provide in both agricultural and natural systems make them important conservation targets. Greater pollinator diversity enhances the seed set and fruit yield in plants including crops making pollinator populations and diversity valuable to most systems (Garibaldi et al. 2014; Blitzer et al. 2016). However, their populations are subject to compounding risks such as floral resource loss, pathogens, and intensive pesticide use (Goulson et al. 2015). Population declines are difficult to assess for this diverse group of insects but there is growing evidence that bumble bees (*Bombus* Latreille) in North America have undergone dramatic decreases across their historic ranges (Cameron et al. 2011; Colla et al. 2012), with multiple bumble bee species proposed for federal protection (U.S. Fish and Wildlife Service 2016, 2017, 2019). Grasslands in the Northern Great Plains (hereafter, NGP) region contain a high diversity of bumble bees, but how they have adapted to the change in the amount and composition of resources in this region is largely unknown.

Contemporary grasslands in the NGP are novel ecosystems due to the interactions between exotic and native species together with anthropogenic alterations to landscapes and historical disturbances (Toledo et al. 2014). Introduced forb species also accompany these changes, with species such as leafy spurge (*Euphorbia esula* Linnaeus) and Canada thistle (*Cirsium arvense* (L.) Scop.) having advantageous growth over native plant species, reducing biodiversity, and reducing palatable forage for livestock (Belcher and Wilson 1989; Duncan et al. 2004). Other introduced forb species such as sweet clovers (*Melilotus* spp. Miller) and alfalfa (*Medicago sativa* Linnaeus) are planted as part of soil conservation projects and as food or cover for wildlife species (Ogle et al. 2008). However, these can spread into unintended areas (Lesica and DeLuca 2000; Ogle et al. 2008). These legume species are excellent nitrogen fixers which can benefit plant establishment and growth in degraded soils but may facilitate the competitive growth of other exotic plant species over native species (Lesica and DeLuca 2000; Van Riper and Larson 2009; Dornbusch et al. 2018).

In addition to non-native plant species introductions, the NGP region has a high density of non-native bees that contributes to these novel grassland communities. European honey bees (*Apis mellifera* Linneaus) are of great economic importance in the NGP with honey product in 2020 valued at over $61.5 million USD in North Dakota alone (USDA 2021). Honey bees have received much attention from the public and researchers due to the increasing difficulties in maintaining hives in the apiary industry (Goulson et al. 2015). In addition to challenges such as hive diseases and pests (Genersch 2010), managed honey bees in North America are also negatively affected by the loss of suitable pollen and nectar forage, primarily from agricultural practices that remove floral resources (Decourtye et al. 2010). However, the resources important to honey bees in the NGP may differ from those important to native bees (Otto et al. 2017). Many of the exotic plant species prevalent across the NGP region (i.e., sweet clover) have benefited the honey industry (Westgate and Vinall 1912; Johnston 1923) and are promoted by state and federal agencies for use in seed mixes for general pollinator benefits (USDA 2011; Otto et al. 2020). Previous work in the NGP has shown similarities in large-scale land-use valuation to both honey bees and bumble bees (Evans et al. 2018), but perspective into how each bee group use resources at a finer scale is needed before we can assume that honey bees and native bees value similar resources.

Comparing the relative value of exotic plant species between honey bees and native bees would provide perspective into how both groups interact with the novel plant community and can inform management and conservation for each. However, proportional visitation to different flowers alone does not infer preference because the ratio of the resource visited to how much of the resource was available needs to be considered. Relatively few studies incorporate bee use of floral resources against their availability scaled at the level of floral species, but they can identify valuable floral species to bees and can provide crucial and locally-relevant information for conservation (Loffland et al. 2017; Cole et al. 2020; Simanonok et al. 2021). Bumble bees are well-suited to examine the differences and similarities of exotic plant use compared to honey bees because they are the most similar native bee species to honey bees with regards to phylogeny in the NGP (Bossert et al. 2019). Additionally, both groups (excluding cuckoo bumble bee species in *Bombus*: Subgenus *Psithyrus*) can be broadly categorized as generalist and eusocial foragers that are most likely to visit non-native floral resources (Bartomeus et al. 2016), but differ with regards to both classifications. The importance of honey-production and high density of honey bees present in the growing seasons of the NGP (U.S. Department of Agriculture 2020) coupled with plant communities that are novel to native bee species necessitates examination to explore whether they differ from a managed and non-native bee species. To address this, we use data from a statewide effort to sample bees on the grasslands of North Dakota. Our first objective was to 1) compare the selection of native and exotic floral resources between honey bees and their most similar native components, bumble bees. We explored this objective treating bumble bees as a group and by individual species. Our second objective was to 2) determine the floral community characters that influence the abundance of both honey bees and bumble bees.

Methods

Study System

Our study takes place at grassland sites across North Dakota (ND) in ecosystems that span from tallgrass to mixed-grass prairie. The eastern border of ND is historically characterized by tallgrass prairie with mixed-grass prairie describing the majority of grassland ecosystems to the west (Whitman and Wali 1975). Tallgrass prairie was comprised largely of native grasses such as big bluestem (*Andropogon gerardii* Vitman), little bluestem (*Schizachyrium scoparium* Michaux), indiangrass (*Sorghastrum nutans* Linnaeus), and switchgrass (*Panicum virgatum* Linnaeus) while common grasses in mixed-grass systems often included little bluestem, green needlegrass (*Nassella viridula* Trinius), blue grama (*Bouteloua gracilis* Willd. ex Kunth), and western wheatgrass (*Elymus smithii* (Rydb.) Gould; DeKeyser et al. 2009). However, invasive cool-season grasses such as Kentucky bluegrass (*Poa pratensis* Linnaeus) and smooth brome (*Bromus inermis* Leyssera) have replaced native grasses in many grasslands in North Dakota (Grant et al. 2009). In addition, cropland expansion has dramatically reduced the amount of grasslands in the state which are also largely fragmented and under differing management goals. Native forb composition varies across the state and within the growing season with chickweeds (*Cerastium* spp. Linnaeus), onions (*Allium* spp. Linnaeus), legumes (Fabaceae), and anenomes (*Anemone* spp. Linnaeus) common in the early growing season, many Asteraceae species, western snowberry (*Symphoricarpos occidentalis* Hooker), legume species (Fabaceae) abundant throughout the middle and late season, and goldenrods (*Solidago* spp. Linnaeus), asters (*Symphyotrichum* spp. Nees), and blazing stars (*Liatris* spp. Gaertn. ex Schreb.) common in the late growing season. Non-native forb species such as alfalfa (*Medicago sativa* Linnaeus), sweet clover (*Melilotus* spp. Miller) and exotic thistle species (*Cirsium* Miller and *Carduus* Linnaeus) are commonly found in ND grasslands throughout the growing season.

We used honey bee and bumble bee capture data and floral survey data from a 2017-2020 statewide survey effort across North Dakota. We established three sites per 53 ND counties every year during the growing season from the end of May to mid-September. We kept one site per county the same for all four years while we replaced two sites per county annually, bringing the total number of sites surveyed to 477. We selected sites that were grassland tracts of at least

20 contiguous hectares. We intentionally targeted sites that varied in ownership and management to account for land diversity in ND. As a result, our sites were comprised of: federal (n=159), state (n=187), other agency (n=7), and privately-owned (n=124) lands. Publicly-owned grasslands were managed for wildlife conservation, livestock grazing, and haying while private lands included rangelands, idle grasslands, hayland, and those enrolled in US Department of Agriculture conservation programs such as the Conservation Reserve Program, Conservation Reserve Enhancement Program, and Wetlands Reserve Program. We established two study areas per site and two observers would perform separate bee and floral surveys in their corresponding study area at each site visit. Each study area included one 50-m^2 plot for bee surveys and a set of transects for floral surveys. The two study areas were randomly-placed at least 100-m apart. Observers visited each site twice each growing season to account for phenological changes while incorporating the large number of sites for a total of 2,544 paired bee and floral surveys over the course of the study. The first site visit occurred before July 15th with the second visit being after.

Surveys

Collectors conducted 30-min active netting surveys for bees in their respective 50-m^2 plots located in each study area of each site. We split bee surveys into a 15-minute search restricted to three evenly-placed 50-m transects located within the survey plot. In this restricted portion, observers would net any bee encountered along each transect, with special focus for those on flowers. Bees were collected, killed, and stored in labeled containers with survey information including the flower species the bee was captured on when applicable. Collectors paused survey time during specimen handling. During the next 15 minutes, collectors could survey within the plot for bees freely in order to focus on areas of the plot likely to maximize bee capture, such as patches of flowers. Collectors processed captured bees and survey time in the same manner as described previously. All netting surveys occurred between 9:00-18:00 hours in temperatures between 21–36 C° on days with sustained winds under 25 km/h and lower cloud cover. Bumble bee and honey bee specimens were stored in alcohol until identification by C. K. Pei at the end of the season.

Each bee survey was accompanied with floral transect surveys in order to quantify flowering resources available to bees at the time of surveys. In 2017-2018, the study area included three 100-m long floral survey transects while in 2019-2020, there were two 200-m long transects. This methodological change was an effect of modifications to another aspect of the statewide survey effort. Surveyors counted all flowering stems originating from the ground for each forb species within a 5-m wide belt transect. We were then able to employ floral count data from the two differing transect methodology between years by calculating floral density and density-richness (hereafter referred as floral richness) from floral survey areas (1500-m^2 in 2017 and 2018, 2000-m^2 in 2019 and 2020.

Analysis

The available floral community undergoes compositional changes over the course of the growing season due to variable flowering phenology of the various plant species (Cole et al. 2020). To accommodate this, we split our data for both selection and bee abundance analyses into three different growing periods based on the date range of our surveys in all years: the "early-season" period included surveys conducted from May 23rd to July 9th, the "mid-season" period from July 10th to August 13th, and "late-season" from August 13th to September 17th. In addition, we limited the data to include only worker bumble bees to increase the fairness of comparisons, as all honey bees captured were also workers. In addition, workers may exhibit more selection of floral resources than other classes of bumble bees (Harmon-Threatt et al. 2017).

Bee Selection

For comparisons between honey bees and bumble bees as a group, we limited the data for selection analyses to include surveys that captured both honey bees and bumble bees so that selection could be compared for surveys where both groups were present. Similarly, for the comparisons between honey bees and individual bumble bee species, we only included surveys that captured both honey bees and the corresponding bumble bee species. Additionally, we included bumble bee species that had at least 20 workers captured per season to ensure adequate sample size for our interpretations (Aebischer et al. 1993).

Pollinator selection data from netting surveys is a special case of typical wildlife selection studies because we would obtain only single observations per animal if we organized the data by bee specimen (Manly et al. 2002). Insect communities vary greatly in space and time so we treated our data at the survey level within each seasonal period because we wanted to acknowledge that floral availability between surveys were different and meet the assumption that resources were available to all animals (Alldredge and Griswold 2006). In doing this, we formatted our data for both honey bee and bumble bees similarly to traditional Design III selection datasets where we measured habitat availability (in our case, floral species availability) for each animal (survey, in our case; Manly et al. 2002).

Our interest was primarily in how both bee groups differed in their selection of native and exotic floral species, but we also wanted to provide a plant species-specific perspective to inform the region of important resources for both bee groups. To accommodate this, we first performed compositional analysis for honey bee and grouped bumble bee selection between grouped native and exotic floral species (Jha et al. 2013). Compositional analyses tests for the random use of resources that are defined by several categories (such as plant species) using log-ratios of use and availability data, provides a ranking of these resources, and may be more robust to issues such as low sample sizes and non-independence of data than other selection methods (Aebischer et al. 1993). We also performed compositional analysis for each bumble bee species against honey bees captured in coinciding surveys. To perform compositional analyses, we used the *compana* function in *adehabitatHS* package in R Studio v.1.3.1093 and replaced surveys with 0 in a resource category with the default 0.01 as suggested in Aebischer et al. (1993) (Calenge 2006).

We accompanied compositional analyses with eigenalanlyses of selection ratios to improve our ability to interpret bee selection (Calenge and Dufour 2006). This method is similar to principal components and correspondence analyses. Eigenanalysis of selection ratios additively and linearly partitions inertia and shows the variability in resource selection ratios which is maximized on the first factorial axis. Scores of individual surveys and floral resource type are projected on two axes. If the variation of bee floral selection between surveys was more similar, the first factorial axes would explain most of the variation. However, if inertia is more distributed between axes, there is greater dissimilarity in floral selection between bees in different surveys. In this case, we are able to determine the ecological mechanisms behind this variation in habitat selection within a group.

We calculated honey bee and grouped bumble bee selection ratios for plant species that had at least five visitations as well as selection ratios for each bumble bee species (Manly et al. 2002; Simanonok et al. 2021) to grant a perspective of how bumble bees and honey bees selected individual floral species. Selection ratios $\widehat{w}_{ij}$ for a plant species i during survey j were calculated in Equation 1.

$$\widehat{w}_{ij} = \frac{(u_{ij}/u_{+j})}{\pi_{ij}} \qquad \text{(Equation 1)}$$

In Equation 1, u_{ij} is the proportion of used units in plant species i during survey j, u_{+j} is the total proportion of used units for survey j, and π_{ij} is the ratio of the proportion available in plant species i in survey j to the total proportion of available floral units across survey j (Manly et al. 2002). Bees select for a resource, against its availability, if $\widehat{w}_{ij}$ is greater than 1 and selected against if between 0 and 1. We chose to display these selection ratios for plant species that bees interacted with at least 5 times per seasonal period but did not average these because availability was unique for each survey and we expected considerable variability between surveys at different sites (Calenge and Dufour 2006).

Floral Community Measures

We used honey bee and worker bumble bee data at the survey level to determine relationships between each bee group and measures of the floral community in each seasonal period. We did this by fitting negative binomial generalized linear mixed models with a univariate fixed effect approach to explain bumble bee and honey bee abundance captured in our netting surveys (function *glmer.nb* in R package *lme4*; Bates et al. 2015). Fixed effects included floral density, floral richness, native floral density, and exotic floral density and we used site as random factors in each model. We evaluated model fit using AIC-based model selection and model weights (*AICcmodavg* package; Mazerolle 2020). We selected best models as those with the highest AICc values but considered any with ΔAICc values of 2 and under as comparably strong (Burnham and Anderson 2002).

Results

We used capture data from 17.7% of total netting surveys that had both honey bees and bumble bee workers present with 87 worker bumble bees in the early-season, 971 in the mid-season, and 404 in the late-season. The bumble bees were from eight species with sufficient sample size for selection analyses. We captured 598 honey bees in the early-seasons, 2,512 in mid-seasons, and 1,264 in late-seasons.

Qualitatively, bumble bees visited a higher proportion of native flowers over all three seasonal periods (Fig. 1.1A-C; Fig. 1.3B). Honey bees across seasonal periods had higher relative visitation to exotic plants in the early and middle seasons but visited slightly more native plant species in the late seasonal period only (Fig. 1.1A-C; Fig. 1.4B). We observed 247 flowering forb species at locations that had both honey bees and bumble bees present across years and seasonal periods. While total floral densities were highest in the early season, this was largely due to the higher proportion of exotic floral densities in 2017 and 2018. Besides these instances, the mid-seasonal period had the greatest floral densities across years, with the lowest floral densities in the late season.

Bee Selection

Grouped bumble bees disproportionately selected for native over exotic floral species in the mid-season period but not in the other seasonal periods (Table 1.1A). Despite the availability of and their visitation to both native and exotic plants, honey bees selected for exotic floral resources in both the mid-season and late-season periods but demonstrated no selection between floral species in the early-season periods (Table 1.1B). However, eigenanalysis of the selection ratios showed there was a notable amount of variation in honey bee and bumble bee selection between floral groups, indicating that other sources of variation drive selection between bees in different surveys (Figs. A1-A3).

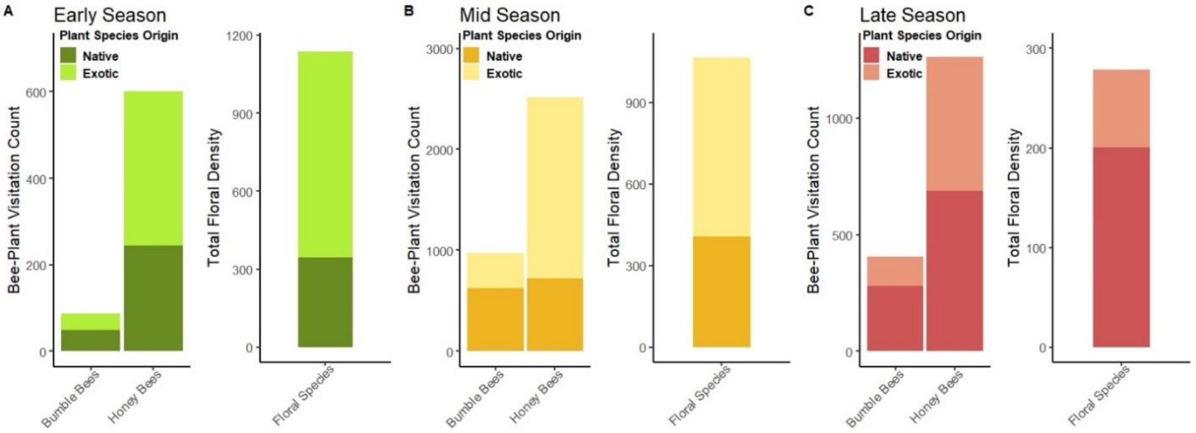


Figure 1.1. Bumble bee and honey bee visitation to native and exotic floral species and the availability of native and exotic floral species in the early (A), mid (B), and late (C) seasonal periods combined across surveys and years. Bee-plant visitation counts are from netting surveys in North Dakota from 2017-2020. Floral densities (flowering stems/m^2) were measured in floral surveys that accompanied each netting survey for bees.

Selection between honey bees and specific bumble bee species captured at the same sites differed between seasonal period and bumble bee species, with significant bumble bee selection for native plant species and significant honey bee selection for exotic species (Fig. 1.2). Eigenanalysis of selection ratios between individual bumble bee species and honey bees showed bees selected more similarly within each bee group, signifying the variation found in the grouped analyses may be largely due to variation between species (Figs. A4-A11). However, variation was still considerable between surveys of *Bombus griseocollis*, *B. rufocinctus*, and *B. ternarius* which are all common species with wide diet breadths (Figs. A7, A9, A10). Three bumble bee species selected for native flowers in the mid-season period while honey bees in the mid-season disproportionately selected for exotic species except when compared against surveys containing *B. bimaculatus*, *B. ternarius*, and *B. vagans* (Fig. 1.2). *Bombus vagans* visited native plants significantly higher than exotic plants in the mid-season period, but they did not select differently between exotic and native plants (Fig. 1.2). In the late-season period, *Bombus griseocollis* selected native flowers more than exotic flowers. Honey bees did not disproportionately visit either plant group in the late-season periods for each bumble bee species pairing (Fig. 1.2).

Table 1.1. Compositional analyses results for grouped bumble bees (A) and honey bees (B) in 2017-2020 bee surveys in North Dakota across seasonal periods. Wilks lambda and p-values are from a test of random selection between native and non-native floral species. Ranks are determined if native or non-native floral resources are used significantly more. Both tests provide different perspectives but show the relative importance of floral resources to either bee group. Non-significant results are denoted by “ns”.

Bumble Bees		Early-Season	Mid-Season	Late-Season
Survey Count (n)		54	257	123
Wilks Lambda		0.991	0.974	0.984
p-value		0.470	0.020	0.182
Rank	1	ns (Native)	Native	ns (Native)
	2	ns (Exotic)	Exotic	ns (Exotic)
Honey Bees		Early-Season	Mid-Season	Late-Season
Survey Count (n)		54	257	123
Wilks Lambda		0.932	0.891	0.938
p-value		0.052	0.002	0.018
Rank	1	ns (Exotic)	Exotic	Exotic
	2	ns (Native)	Native	Native

Twelve native forb and five exotic forb species had sufficient grouped bumble bee visitations for use-availability selection ratio interpretations (Fig. 1.3A). Bumble bees selected for native thistles (*Cirsium* spp. Miller), lead plant (*Amorpha canascens* Pursch), purple prairie clover (*Dalea purpurea* Ventenat), bee balm (*Monarda fistulosa* Linnaeus), and prairie blazing star (*Liatris punctata* Hooker) despite their availability. Exotic forbs Canada thistle (*Cirsium*

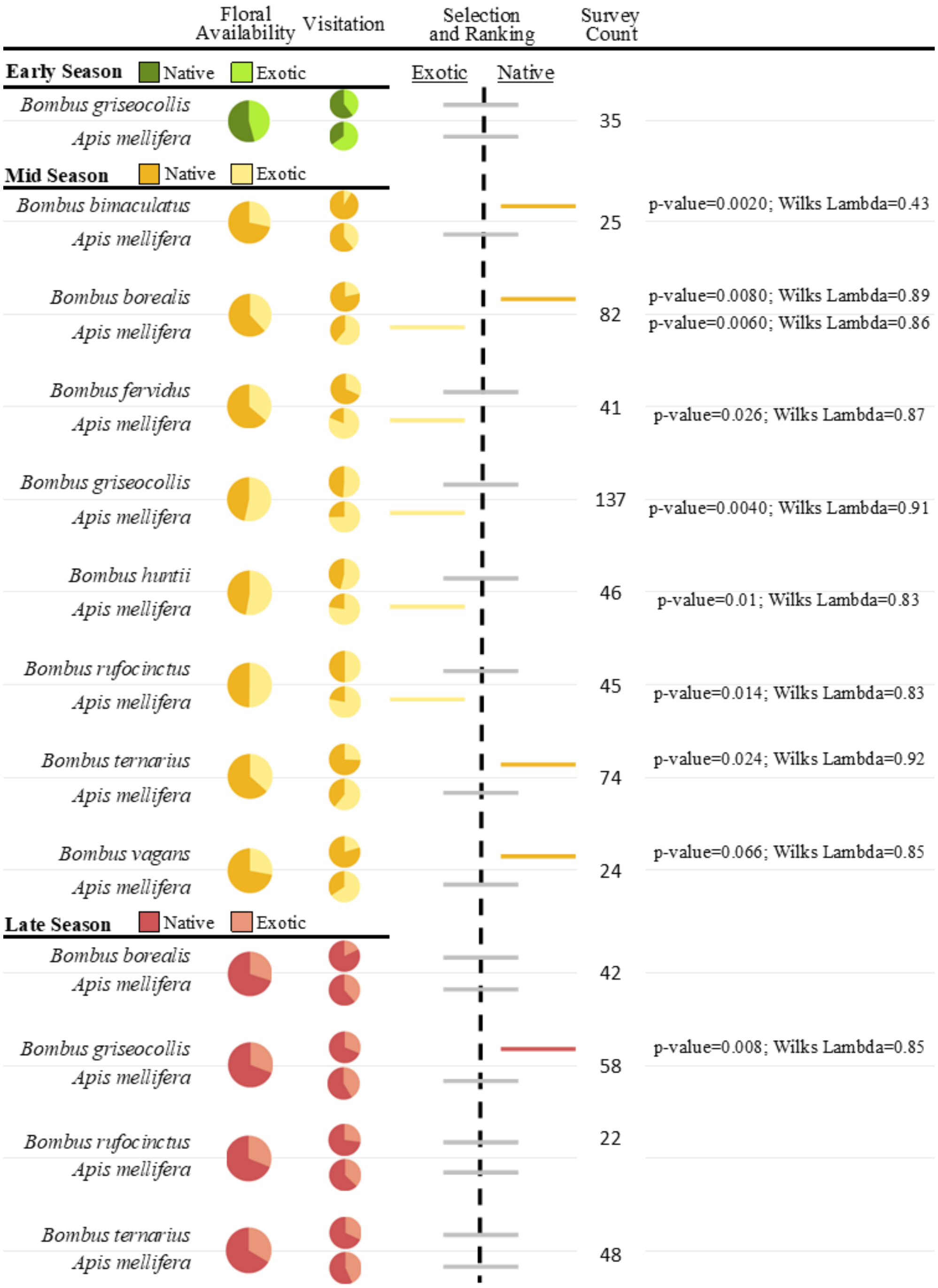
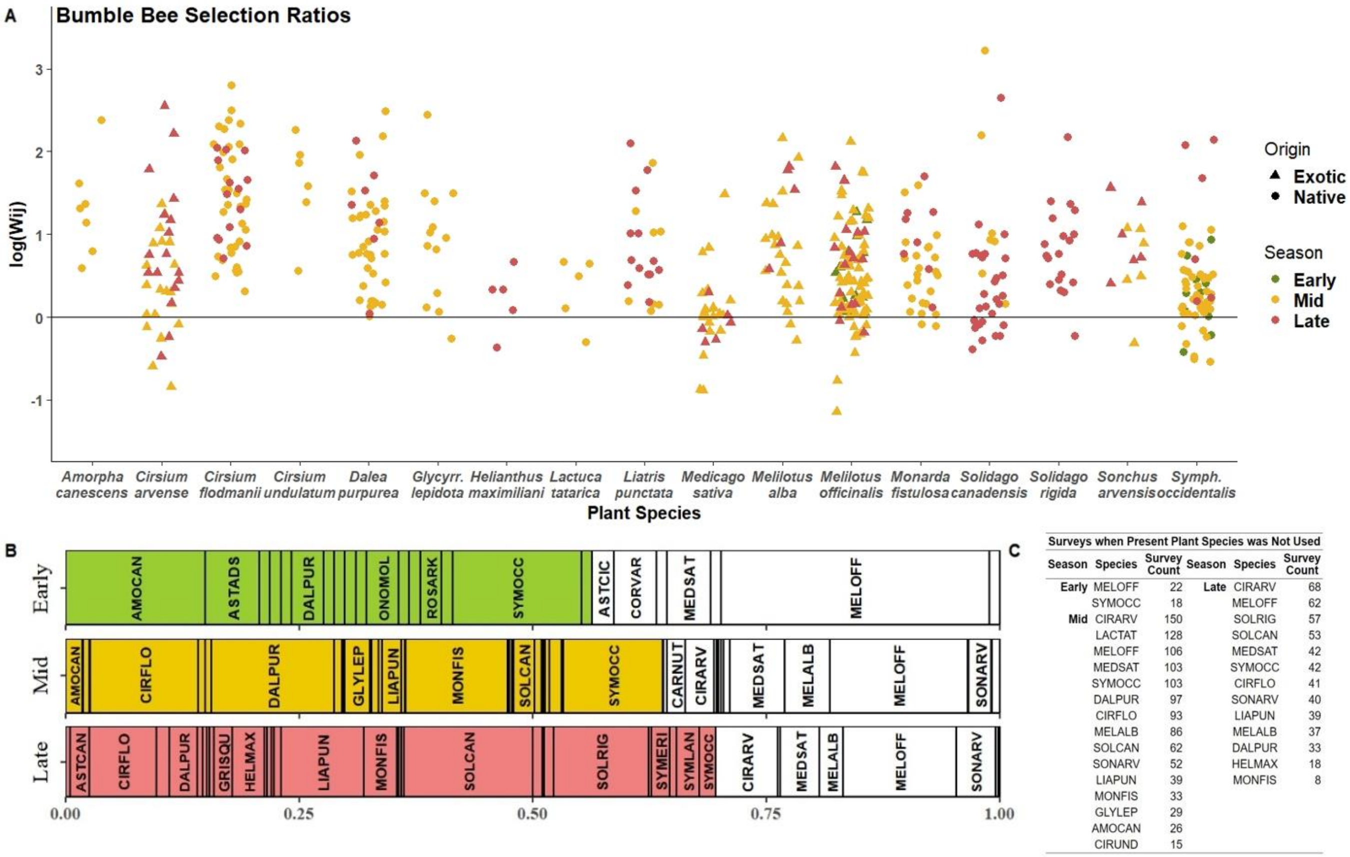


Figure 1.2. Compositional analyses results for paired comparisons of bumble bee species and honey bees captured in mutual surveys in North Dakota across seasonal periods to show both the visitation to and selection of native and exotic floral species. Wilks lambda and p-values are from a test of random selection between native and exotic floral species. Selection is significant if bars do not overlap the dotted vertical line. The side of the line the bar falls for each species in each pairing shows which floral type is ranked significantly higher. *Selection was not significant between native and exotic floral species but native was ranked significantly higher than exotic floral species.

arvense (L.) Scop.), yellow sweet clover (Melilotus officinalis (L.) Lam.), alfalfa (*Medicago sativa* Linnaeus), and native forbs Canada goldenrod (*Solidago canadensis* Linnaeus) and western snowberry (*Symphoricarpos occidentalis* Hooker) had high bumble bee visitation and selection in many surveys but had a considerable number of surveys where these species were selected against (Fig. 1.3A, points below 0). Moreover, Canada thistle, yellow sweet clover, blue lettuce (*Lactuca tatarica* (L.) C.A. Mey), western snowberry, and goldenrod species were plants that were most often present but unused by bumble bees (Fig. 1.3C).

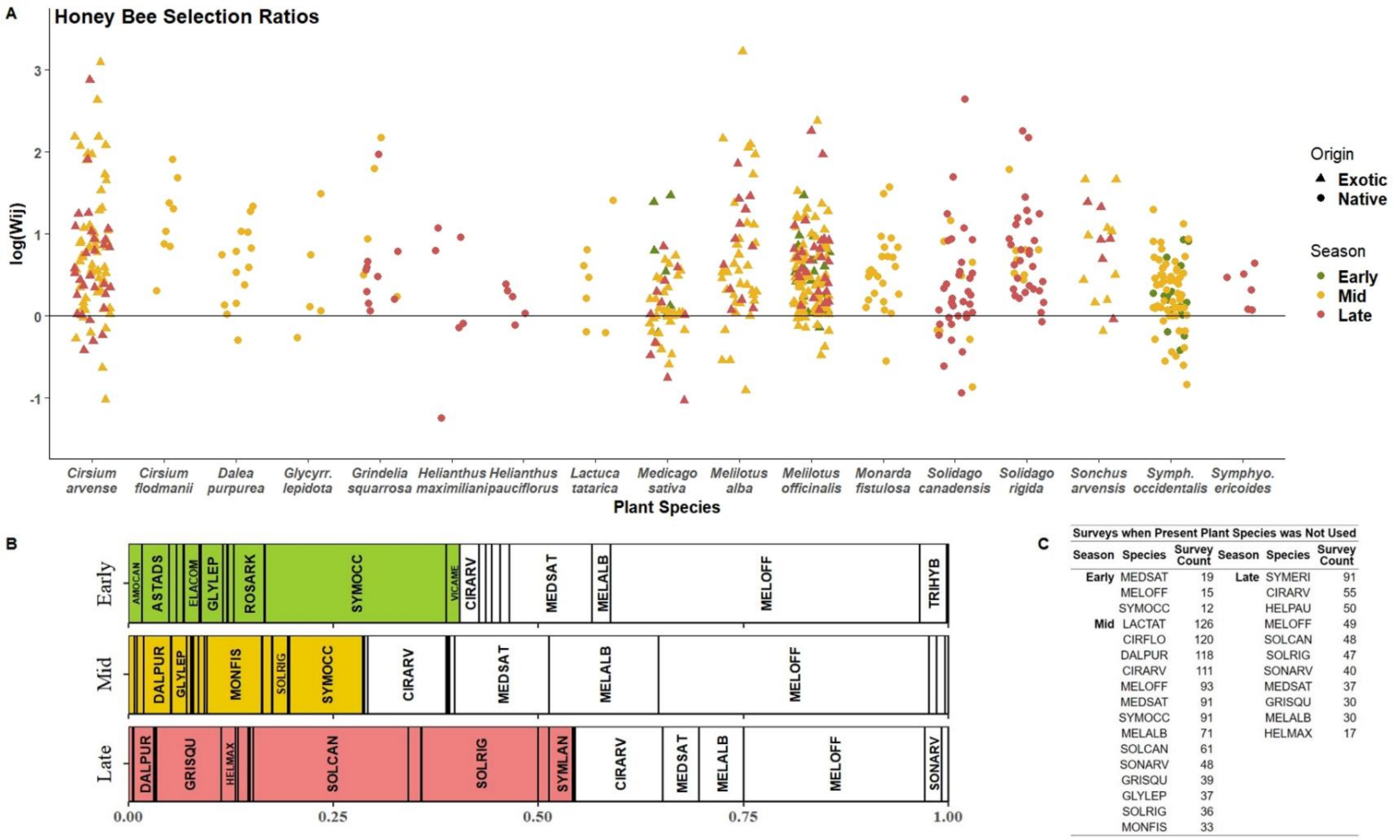
Honey bees visited twelve native forb species that had at least five interactions in a seasonal period and five species of exotic forbs (Fig. 1.4A). Though with relatively fewer visitations, honey bees also selected for particular native plant species especially in the late season, such as curlycup gumweed (*Grindelia squarrosa* (Pursh) Dunal), stiff goldenrod (*Solidago rigida* Linnaeus), and heath aster (*Symphyotrichum ericoides* (L.) G.L. Nesom). Honey bees selected for yellow sweet clover in many surveys and numerous visitations to Canada thistle (*Cirsium arvense* (L.) Scop.), alfalfa (*Medicago sativa* Linnaeus), Canada goldenrod (*Solidago canadensis* Linnaeus), and western snowberry (*Symphoricarpos occidentalis* Hooker), but similarly to bumble bees, there were many surveys where honey bees selected against them despite their higher availabilities in a survey (Fig. 1.4A). Blue lettuce, Flodman’s thistle, purple prairie clover, and Canada thistle were most often present but not visited by honey bees in surveys (Fig. 1.4C).



Surveys when Present Plant Species was Not Used

Season	Species	Survey Count	Season	Species	Survey Count
Early	MELOFF	22	Late	CIRARV	68
	SYMOCC	18		MELOFF	62
Mid	CIRARV	150		SOLRIG	57
	LACTAT	128		SOLCAN	53
	MELOFF	106		MEDSAT	42
	MEDSAT	103		SYMOCC	42
	SYMOCC	103		CIRFLO	41
	DALPUR	97		SONARV	40
	CIRFLO	93		LIAPUN	39
	MELALB	86		MELALB	37
	SOLCAN	62		DALPUR	33
	SONARV	52		HELMAX	18
	LIAPUN	39		MONFIS	8
	MONFIS	33			
	GLYLEP	29			
	AMOCAN	26			
	CIRUND	15			

Figure 1.3. Selection and visitation of grouped bumble bees to flowering plant species in North Dakota from 2017-2020. (A) Log-transformed selection ratios (W_{ij}) of bumble bees for plant species with at least 5 visitations in each seasonal period denoted as native (circles) and exotic (triangles) and early, middle, and late seasonal periods (green, yellow, red). Selection is for plant species if greater than 0 (horizontal line is placed at y=0) and against plant species if below 0. Instances where the plant was present but not visited ($W_{ij}=0$) were removed for clarity. (B) Proportional visitation to plant species in the early, middle, and late seasonal periods. Colored bars quantify visitation to native species and white bars are visitation to non-native species. (C) The amount of W_{ij} values of 0 per plant species per flowering period to convey the number of surveys where plant species were present but unused by bumble bees. Six-letter species codes refer to the first three letters of the plant genus and first three letters of the specific epithet of plant species.



Surveys when Present Plant Species was Not Used

Season	Species	Survey Count	Season	Species	Survey Count
Early	MEDSAT	19	Late	SYMERI	91
	MELOFF	15		CIRARV	55
	SYMOCC	12		HELPAU	50
Mid	LACTAT	126		MELOFF	49
	CIRFLO	120		SOLCAN	48
	DALPUR	118		SOLRIG	47
	CIRARV	111		SONARV	40
	MELOFF	93		MEDSAT	37
	MEDSAT	91		GRISQU	30
	SYMOCC	91		MELALB	30
	MELALB	71		HELMAX	17
	SOLCAN	61			
	SONARV	48			
	GRISQU	39			
	GLYLEP	37			
	SOLRIG	36			
	MONFIS	33			

Figure 1.4. Selection and visitation of honey bees to flowering plant species in North Dakota from 2017-2020. (A) Log-transformed selection ratios (W_{ij}) of honey bees for plant species with at least 5 visitations in each seasonal period denoted as native (circles) and exotic (triangles) and early, middle, and late seasonal periods (green, yellow, red). Selection is for plant species if greater than 0 (horizontal line is placed at y=0) and against plant species if below 0. Instances where the plant was present but not visited (W_{ij}=0) were removed for clarity. (B) Proportional visitation to plant species in the early, middle, and late seasonal periods. Colored bars quantify visitation to native species and white bars are visitation to non-native species. (C) The amount of W_{ij} values of 0 per plant species per flowering period to convey the number of surveys where plant species were present but unused by honey bees. Six-letter species codes refer to the first three letters of the plant genus and first three letters of the specific epithet of plant species.

Floral Community Measures

In the early-seasons, bumble bee abundance was higher at sites with greater native floral availability (β: 0.517; 95% CI: 0.256, 0.779) and flowering forb richness (β: 0.146.501; 95% CI: 88.220, 204.782; Table 1.2A), but was not affected by exotic floral availability or total floral resource density (Fig. 1.5A). Honey bee abundance in the early season was best predicted by flowering forb richness (β:134.458; 95% CI: 84.848, 184.069) and total floral resource density (β: 0.128; 95% CI: 0.0929, 0.164; Table 1.2A). Honey bee abundance was also significantly higher with increasing native (β: 0.560; 95% CI: 0.349, 0.770) and exotic floral availability (β: 0.0927; 95% CI: 0.0562, 0.129 ; Fig. 1.5A), however those terms were not part of the best models.

Flowering forb richness best explained bumble bee abundance in the mid-seasons (β: 114.976; 95% CI: 105.631, 184.321; Table 1.2B) but surveys with higher native floral density also had significantly higher bumble bee abundance (β: 0.417; 95% CI: 0.239, 0.596; Fig. 1.5B). Bumble bee abundance did not have a significant relationship with either exotic floral density or the total forb density present in our surveys (Fig. 1.5B). In the mid-season, honey bee abundance was higher at sites with greater native (β: 0.441; 95% CI: 0.246, 0.636) and exotic floral availability (β: 0.238; 95% CI: 0.180, 0.296) and with overall greater total flowering forb density (β: 0.268; 95% CI: 0.213, 0.324) and richness (β: 45.971; 95% CI: 2.302, 89.639). However, total flowering forb density best explained honey bee abundance (Table 1.2B).

In the late-seasons, the species richness of flowering plants best explained bumble bee abundance (Table 1.2C) which was significantly higher in surveys with greater floral richness (β: 126.250; 95%CI: 72.332, 180.169; Fig. 1.5C). Bumble bee abundance in the late-season was also significantly higher during surveys with greater total floral density (β: 0.252; 95% CI: 0.0647,

Table 1.2. Akaike's information criterion-based model selection results of univariate negative binomial generalized linear mixed models of bumble bee abundance and honey bee abundance in early (a), mid (b), and late (c) seasonal periods between 2017 and 2020 in North Dakota. Models within 2 ΔAICc are considered competitive. Only results from significant models are displayed.

Early-Season				
Bumble Bee Abundance	K	AICc	ΔAICc	Weight
Native Forb Density	4	865.54	0.00	0.54
Forb Density Richness	4	865.90	0.36	0.46
Honey Bee Abundance	K	AICc	ΔAICc	Weight
Forb Density Richness	4	3416.42	0.00	0.47
Total Forb Density	4	3416.63	0.21	0.42
Native Forb Density	4	3419.27	2.85	0.11
Exotic Forb Density	4	3428.29	11.87	0.00
Mid-Season				
Bumble Bee Abundance	K	AICc	ΔAICc	Weight
Forb Density Richness	4	3176.16	0.00	1
Native Forb Density	4	3222.29	46.12	0
Honey Bee Abundance	K	AICc	ΔAICc	Weight
Total Forb Density	4	4651.47	0.00	0.99
Exotic Forb Density	4	4660.89	9.41	0.01
Native Forb Density	4	4680.45	28.97	0.00
Forb Density Richness	4	4687.24	35.76	0.00
Late-Season				
Bumble Bee Abundance	K	AICc	ΔAICc	Weight
Forb Density Richness	4	1324.43	0.00	1
Total Forb Density	4	1341.83	17.40	0
Native Forb Density	4	1343.62	19.19	0
Honey Bee Abundance	K	AICc	ΔAICc	Weight
Forb Density Richness	4	1718.22	0.00	1
Total Forb Density	4	1733.86	15.63	0
Native Forb Density	4	1736.32	18.10	0
Exotic Forb Density	4	1748.82	30.60	0

0.440) and native floral availability (β: 0.283; 95% CI: 0.0149, 0.551) but was not significantly affected by exotic floral densities (Fig. 1.5C). Floral species richness best explained the variance of honey bee abundance in the late season (Table 1.2C) with more honey bees captured during surveys at sites with greater floral richness (β: 225.346; 95% CI: 146.188, 304.505; Fig. 1.5C). Surveys with higher total floral density (β: 0.642; 95% CI: 0.375, 0.909), native floral density (β: 0.714; 95% CI: 0.342, 1.085), and exotic floral density (β: 0.429; 95% CI: 0.0311, 0.827) also resulted in greater honey bee capture (Fig. 1.5C).

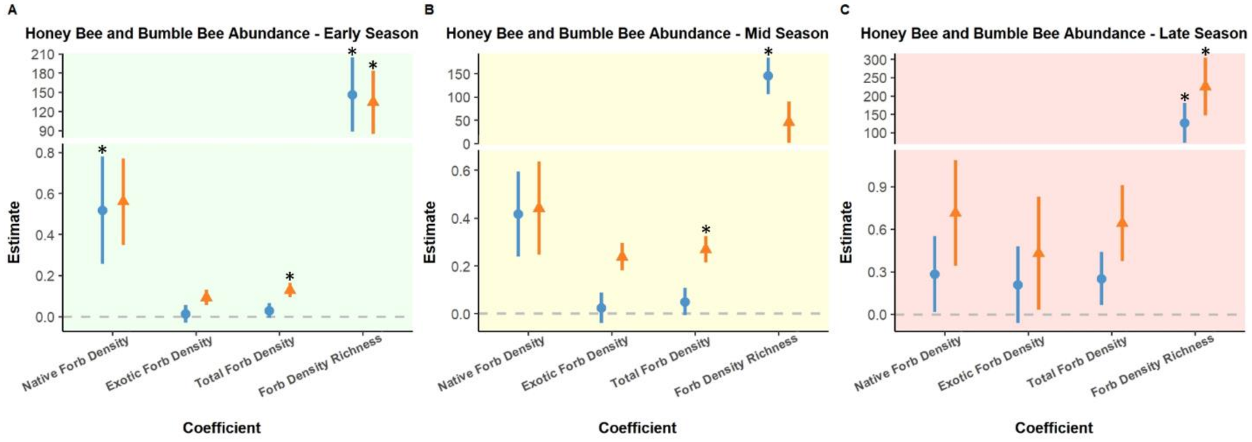


Figure 1.5. Estimated coefficients and 95% confidence intervals of native and exotic forb density, total forb density, and forb density-richness from univariate generalized linear mixed models with random factors from surveys explaining bumble bee (blue circle, blue line) and honey bee (orange triangle, orange line) abundance. Relationships between predictor variables and bee abundance was considered significant if the confidence interval did not include 0. Best models are denoted with asterisks. Scale breaks in the estimate axis was included to accommodate the different scale of forb-density richness.

Discussion

Changes in the availability and composition of floral resources are among the most substantial risks to native bumble bees (Cameron and Sadd 2020). Honey bee presence in the NGP is artificially-managed, but their economic importance in this region requires understanding of how they value grassland resources. Despite both groups' notable usage of native and non-native plants, we found selection between the two groups differed, especially in the middle seasonal period (from July 10th to August 13th). However, these comparisons were more meaningful when considering species-specific bumble bee variation. In addition, we found that native floral resource density and overall floral richness was most important in explaining bumble bee abundance. Overall floral richness was also an important determinant of honey bee abundance at the beginning and end of growing seasons, but the overall density of floral resources was of particular importance in the mid-seasonal period. Despite differences, both honey bee and native bumble bee abundances were higher with increasing floral resource richness at particular seasonal periods, highlighting the importance of floral resource diversity in supporting both bee groups.

We found high visitation to non-native plants by both groups due to their pollen-generalism (Figs. 1.3b and 1.4b; Tepedino et al. 2008; Stout and Morales 2009; Gillespie et al. 2017), but the mechanisms behind why honey bees and bumble bees visit non-native flowers may differ between the two groups (Leonhardt and Blüthgen 2012). For example, bumble bees may be more likely to visit non-native flowers when native choices are less present (Harmon-Threatt and Kremen 2015) and therefore non-native floral visitation by bumble bees may reflect the quantity of non-native flowers available compared to natives during a specific survey. This may show the potential value of non-native species, which often occur in disturbed areas (Wood et al. 2018). However, we found no evidence of relationships between bumble bee abundances and exotic floral densities which may caution that floral communities largely comprised of non-native species may do little for local bumble bee populations (Fig. 1.5). The densities of flowers available, can drive honey bee visitation, regardless of origin, which may be largely due to their social foraging strategy (Hung et al. 2019; Urbanowicz et al. 2020). This difference of valuing identity versus density (Leonhardt and Blüthgen 2012; Fowler et al. 2016; Bendel et al. 2019) may be why bumble bees in our surveys never significantly selected for non-native species regardless if we measured bumble bees as a group or by species, despite the high availability of non-native plants (Tables 1.1a and 1.2).

The divergence of selection and important floral community characters between bumble bees and honey bees was most apparent in the mid-season period, when both native and non-native floral resources had the highest availability. In the mid-seasonal period, honey bees selected for dense floral stands while bumble bees selected for the richness of floral resources, which is largely driven by native plants. Forage in the mid-seasonal period may be important for colony growth but floral resource use and availability at the early and late seasonal periods is also critical for bumble bee fitness (Rotheray et al. 2017; Smart et al. 2021). Bumble bees as a group did not have a significant selection of native or exotic resources in either seasonal period, though they were associated with native plant density and species richness. The overall floral abundance is lower in the early and late season periods which may have the potential to suppress selective preferences in bumble bees (Drossart et al. 2017; Roger et al. 2017; Maebe et al. 2021) and if nutritive value between native and non-native plants is similar, bumble bees may utilize either floral resource types when needed (Harmon-Threatt and Kremen 2015).

It is necessary to acknowledge other sources that contribute to floral resource selection in addition to plant species. Pollen nutrition is important for bee health (Di Pasquale et al. 2013) and though bumble bees do select for pollen quality (Somme et al. 2015; Ruedenauer et al. 2016), it may not be as important a factor in honey bee foraging decisions, which may more greatly concern the quantity over resource (Pernal and Currie 2001; Leonhardt and Blüthgen 2012; Corby-Harris 2018). Pollen quality would likely only affect selection if there are differences between native and exotic pollen quality but exotic plants can have similar, and in some species, superior nutritive value to other plants (Harmon-Threatt and Kremen 2015; Russo et al. 2019). In addition, the presence of other floral-visitors can cause resource partitioning in bee communities (Wilms and Wiechers 1997; Goulson and Darvill 2004; Spiesman and Gratton 2016; but see Tepedino and Stanton 1981). This may be a concern for the NGP region especially, due to the high densities of honey bees during the growing season. Studies involving the competitive effects of honey bees on native bees often use bumble bees due to their similarity but there has not been research on whether honey bee presence affects bumble bee foraging or fitness in the NGP. Honey bee effects on native pollinators are difficult to determine due to variation between systems but there is evidence that high densities of honey bees cause native bee avoidance of resources (Rogers et al. 2013; Angelella et al. 2021; Bommarco et al. 2021) and reduced bumble bee fitness (Thomson 2004; Goulson and Sparrow 2009; Elbgami et al. 2014). If honey bee presence affects bumble bee foraging and fitness in the NGP, it will likely be most impactful in low diversity systems (Herbertsson et al. 2016; Franklin et al. 2018).

Our study uses floral visitation as the measure of selection but it is important to interpret this as selection of pooled pollen and nectar rewards. Pollen-use data may offer an improved perspective on biological associations between bees and plant species (Cane and Sipes 2007). However, we limited our data to bumble bee worker visitation which maximizes the biological meaningfulness that is possible for our dataset. We also offer caution in interpreting selection results as true preference which can only be obtained in controlled environments where animals have choice of resources in equal proportions (Alldredge and Griswold 2006). It would be inappropriate to assume that bees absolutely prefer one type of resource over another because it must be recognized that their presence in a system with a less-preferred resource already includes selection at a larger scale, such as a site with those resources (Johnson 1980). This means, that if a bumble bee selected for native floral resources over exotic resources, there still may be value in those exotic resources that contributed to the bee's selection of that particular grassland area. For example, bumble bees as a group selected native flowers over non-native flowers in the mid-seasonal period, but floral richness in this seasonal period was the most important floral community character to bumble bee abundance. Though to a smaller extent, non-native species still contribute to floral richness and therefore may influence bumble bee selection at a larger scale.

The novel assemblage of floral resources in the NGP combined with the high densities of a non-native and social pollinator warrants further investigation to how native pollinators interact in this novel system. Specifically, our results would benefit from understanding why both bee groups selected against certain plant species more often than others, especially with regards to nutritional factors. Whether honey bees affect the foraging or fitness of their bumble bee relatives is also of particular importance because of the compounding risks to declining bumble bee populations. Considering the species-dependent nature of plant selection, this should be done with regards to individual bumble bee species. Additionally, future research should explore network analyses to identify possible property changes in pollination networks due to the high amount of exotic species present in this region.

Our results show that use of fine-scale floral resources differ between honey bees and bumble bees. This determination is important for grassland managers seeking to enhance pollinator resources because management for honey bees in the form of dense stands of exotic plant species is not equally supportive of native bees (Urbanowiscz et al. 2020). Sufficient native floral resources, such as the availability of native thistles (Simanonok et al. 2021), purple prairie clover (Otto et al. 2017), and blazing stars, is necessary to support native bumble bees, but enhanced diversity of floral species seems important to both groups. Honey bees are economically eminent in North Dakota, but it is necessary to include native bees in pollinator management because bee diversity drives the pollination services provided by bees and the stability of those services (Winfree et al 2007). Further, exotic species are present and persisting components of the NGP. A better understanding of floral resource use in novel grassland systems can guide conservationists and grassland managers in supporting declining bumble bee populations (Hanberry et al. 2021) while simultaneously sustaining apiary industry interests.

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CHAPTER 2: INVASIVE GRASS AND LITTER ACCUMULATION CONSTRAIN BEE AND PLANT DIVERSITY IN ALTERED GRASSLANDS

Abstract

Ecologists consider biological invasions one of the primary drivers of global change. Many remaining grasslands in North America have extensive invasions of exotic grass species that have replaced native plant species. In the Northern Great Plains, exotic cool-season grasses Kentucky bluegrass (Poa pratensis) and smooth brome (Bromus inermis), paired with human alterations to the landscape and historical disturbance regimes, have resulted in functionally and structurally altered grassland plant communities. These changes may extend to impact species that rely on these plant communities, such as bees. Bees are ecologically diverse and serve important pollinator roles but are at risk from the loss and change of floral and nesting resources in plant communities. Our objectives were to determine whether Kentucky bluegrass and smooth brome alter the bee and forb species richness in invaded Northern Great Plains grasslands and how litter accumulation, grass cover, and the amount of bare ground interact with bee functional traits. To do this, we surveyed 67 grassland sites from 2017-2020 with two bee-sampling methods (268 netting and bee bowl surveys total) and vegetation cover surveys at each site. We collected 20,111 bees from 182 bee species and observed 249 forb and shrub species in vegetation surveys. Bee richness was higher with greater forb richness, but the latter was significantly lower with thicker litter depths and higher with a greater coverage of all grasses other than Kentucky bluegrass and smooth brome. Bee trait analyses showed varying relationships with plant community variables. Of these, litter depth and Kentucky bluegrass cover reduced ground-nesting bee abundance while small-bodied bees increased with bare ground. While our results support the close relationship between bee and plant diversity, we also

found litter depth, in particular, influenced the structure of these two communities. Specifically, Kentucky bluegrass and smooth brome are two exotic grass species associated with thatch-forming litter layers, especially under idle management that appear to simplify bee and forb communities. Our results make apparent the importance in maintaining structural and compositional diversity in invaded grasslands to support diverse bee communities.

Introduction

Biodiversity drives the stability of ecosystem services and function (Tilman et al. 2006; Hautier et al. 2015; Pennekamp et al. 2018). This is largely due to the complement of differing species responses to environmental variation (Loreau and de Mazancourt 2013). However, biodiversity faces threats that impact the amount, structure, and composition of resources required by and available to species (Chapin et al. 2000; Brooks et al. 2002; Fahrig 2003; Krauss et al. 2010). These threats to ecosystem stability are primarily due to anthropogenic sources, making it necessary to understand the factors that shape biodiversity in human-altered ecosystems (Cardinale 2014).

Human-facilitated spread of exotic-invasive species has the ability to impact biodiversity by reducing and changing resources available to native species in impacted ecosystems (Pyšek et al. 2020). Additionally, invasive species can take advantage of environmental alterations already in place (Didham et al. 2005) and can cause alterations to historic processes, threatening species dependent on those processes (Mack and D’Antonio 1998). For example, cheatgrass (Bromus tectorum L.) invasions in the Great Basin region of North America have changed sagebrush plant community structure and have led to increased fire frequencies that threaten sagebrush and wildlife that specialize on shrubland resources (Bradley et al. 2018).

Exotic species with invasive attributes, along with other human alterations to historical processes and landscapes, have changed North American grasslands (Fuhlendorf et al. 2012; Martin et al. 2014; Toledo et al. 2014). Dominant exotic grass species in particular have changed plant species composition in many grasslands (Grant et al. 2009). These changes are achieved through nutrient cycle alterations, advantageous growth conditions, and altered grassland disturbances necessary to plant diversity (Christian and Wilson 1999; Davis et al. 2000; Stotz et al. 2017). Plant community composition and structure mediates resources for many animal species making it important to understand the direct and indirect effects of exotic-invasive species and how native species interact in novel grasslands (Ruehmann et al. 2011; Rosenkranz and McGonigle 2020).

Exotic-invasive plant species may indirectly interact with pollinating insects, such as bees, through their relationships with flowering forb species (Cane 2011). For example, abundances of the cool-season, invasive-exotic grasses smooth brome (Bromus inermis Leys.) and Kentucky bluegrass (Poa pratensis L.), have been associated with lower native plant species diversity (Stotz et al. 2017; Hendrickson et al. 2021). Those relationships are important because bee species richness is linked with floral resource diversity, likely due to their reliance on floral resources at all life stages and their diversity in pollen diet requirements (Potts et al. 2003; Ebeling et al. 2008; Papanikolaou et al. 2017).

Additionally, invasive grasses under idle or low-disturbance management can form thick litter layers, influencing grassland structure and nutrient cycling (Sanderson et al. 2017; Hendrickson et al. 2021). Litter layers in grasslands are dead plant matter senesced from previous growing seasons but persistent and thick litter layers can impact native plant species growth with varying effects on pollinators (Toledo et al. 2014). For example, thick litter layers may harm ground-nesting bees that require bare soil (Harmon-Threatt 2020; Olynyk et al. 2021) but bees in other systems have been shown to benefit from litter cover (Grundel et al. 2010; Smith DiCarlo et al. 2019). Bees may respond differently to conditions created from introduced species and other human alterations due to the great diversity in bee resource requirements

Bee diversity is crucial to maintain and improve pollination services as greater bee functional diversity yields enhanced seed or fruit set in plants (Hoehn et al. 2008; Blitzer et al. 2016). Bees are key pollinators in agroecosystems and natural systems but have subject to risks associated with the loss of floral resource availability and diversity and threats such as pathogens and pesticides (Potts et al. 2010). Bees are diverse in their phylogeny, morphology, and life history requirements associated with nesting, sociality, and pollen diet breadths (Michener 2007). However, this diversity complicates assessments of their responses to environmental changes (Bartomeus et al. 2017). Their inherent diversity and vulnerability to anthropogenic changes, including those created by invasive plants, necessitate research that acknowledges functional trait responses to novel plant community conditions in addition to the perspectives provided by broader measurements of bee diversity.

Exotic grasses are prevalent in Northern Great Plains (NGP) grasslands of North America and have replaced native grasses and forbs in many grasslands. Exotic grass dominance reduces floral diversity depended on by insect pollinators (Kral-O’Brien et al. 2019), but how the altered conditions created by these exotic grasses shape bee communities has not been investigated in this region, despite calls for the subject (Toledo et al. 2014; Hanberry et al. 2021). Employing data from a statewide survey of bees across North Dakota (ND), USA, we address this knowledge gap by determining 1) which local-scale plant community characteristics associated with exotic grasses influence bee and forb species richness and 2) which contribute to shaping both bee and forb communities. We also seek to provide another perspective to 3) determine how these characteristics relate to bees' varying functional traits. The results from these objectives are crucial in informing bee conservation in the NGP but also provide further empirical evidence of biodiversity impacts of exotic species.

Methods

Study System

We collected data on bee and plant communities through surveys across a range of ND grasslands from 2017-2020. Grasslands on the eastern and northern regions of ND are historically glaciated landscapes characterized by tallgrass prairie on the eastern border (Lake Agassiz Plain ecoregion) and mixed-grass prairie throughout the center and northern portions of the state (Fig. 2.1; Northwestern and Northern Glaciated Plains ecoregions; Bryce et al. 1998). The historically unglaciated southwest region of the state is part of the Northwestern Great Plains ecoregion primarily characterized by mixed-grass prairie (Fig. 2.1). Historical tallgrass species include *Andropogon gerardii* Vitman, *Schizachyrium scoparium* Michx., and *Panicum virgatum* L., while mixed-grass prairie communities had grass species such as *Schizachyrium scoparium* Michx., *Nassella viridula* Trin., *Bouteloua gracilis* Willd. ex Kunth, *Elymus smithii* (Rydb.) Gould (Dekeyser et al. 2009). Native forb and shrub communities go through phenological changes throughout the growing season with many of the most common forb and shrub species belonging to plant families Asteraceae and Fabaceae. Contemporary ND grasslands have widespread invasions of exotic grass species Kentucky bluegrass and smooth brome (Fig. 2.1, using data from vegetation surveys described below) along with commonly-found introduced forb species such as leafy spurge (*Euphorbia esula* L.), Canada thistle (*Cirsium arvense* L.), sweet clovers (*Melilotus* Mill. spp.), and alfalfa (*Medicago sativa* L.; Belcher and Wilson 1989; Murphy and Grant 2005; Toledo et al. 2014).

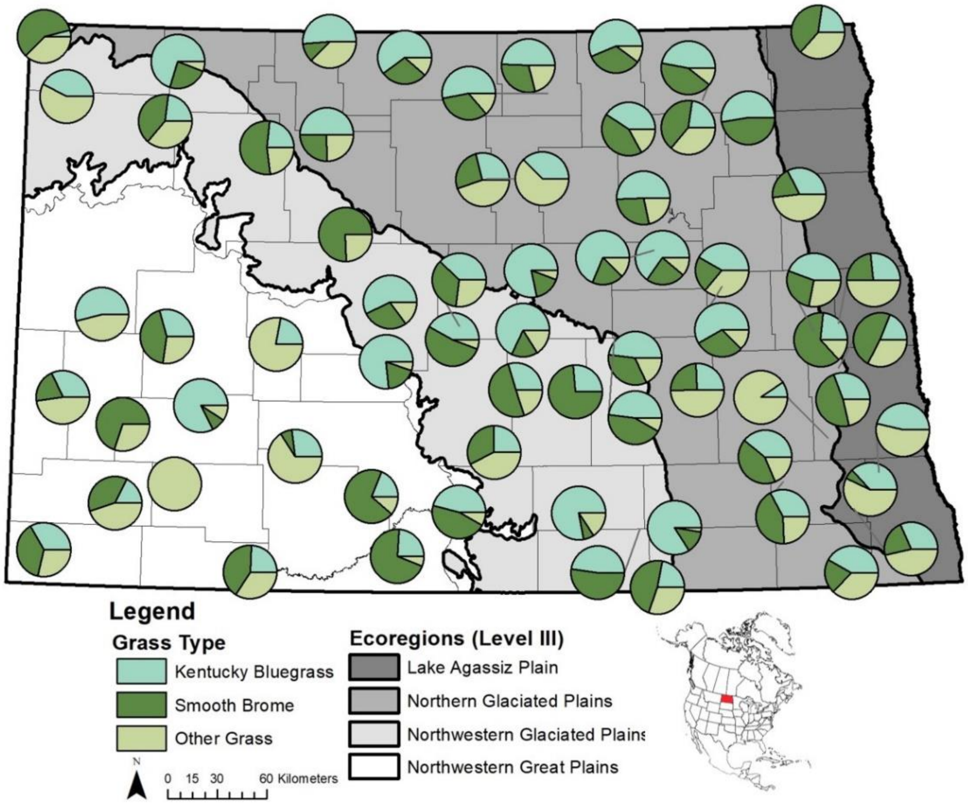

Figure 2.1. Grass composition including Kentucky bluegrass (Poa pratensis), smooth brome (Bromus inermis), and other grass species (primailry native grasses but could include less problematic exotic grasses) across vegetation cover surveys in North Dakota from 2017-2020 at 67 grassland sites. Ecoregion spatial data sourced from Bryce et al. 1998.

We conducted data collection on contiguous grasslands tracts of at least 20 hectares to accommodate our study areas at each site. We established two study areas at each site, spaced at least 100-m apart. Sites were managed by a variety of federal, state, and non-governmental agencies as well as private landowners for diverse land-uses such as for rangeland, hayland, or wildlife conservation. We sampled at 21 sites in 2017, 16 sites in 2018, and 15 sites in both 2019 and 2020 for a total of 67 sites. This study uses a subset of 67 sites from the greater statewide survey effort to include only sites that were sampled with two bee-sampling methods. Bee-sampling methods may represent different community compositions, making it necessary to include a complement of methods (Rhoades et al. 2017; Pei et al. 2022). We sampled each site twice throughout the growing season, each with both bee-sampling methods to help account for phenological changes between June and the end of August annually bringing the total number of paired survey instances to 134. We sampled vegetation cover once within the middle to late growing season at each site to allow sufficient warm-season plant growth. Surveys were conducted by graduate students and trained field technicians.

Bee Surveys

We surveyed bee communities at each site using active netting and passive bee bowl sampling. We conducted netting surveys between 9:00-18:00 hours at temperatures between 21-36 C°, sustained wind speeds under 25 km/hr and low cloud cover. At each site visit, two collectors conducted netting surveys at two 50-m^2 plots, each located within a study area at a site. Netting surveys were split into two portions, a 15-minute portion that restricted collectors to three parallel and evenly spaced 50-m long transects within the plot and the other portion allowing collectors to move freely within the plot for an additional 15-minutes. The restricted portion ensured collectors spent time evenly within the plot while the free-search portion allowed collectors to maximize their bee capture by moving to areas of the plot most likely to encounter bees such as floral patches. When a collector captured a bee in their net, they paused survey time to securely move bees to kill tubes labeled with the floral species or other material the bee was captured on. Collectors then stored specimens in alcohol until specimen identification.

Passive pan traps, known as bee bowls, are colored cups or bowls filled with soapy water and deployed at a site to passively collect bees that are attracted to the colored traps. At each site visit, we deployed bee bowls along two transects of 15 bowls, with each transect located in each study area at a site for a total of 30 bee bowls per site visit (Shapiro et al. 2014). Bowls in each transect were spaced 5-m apart, creating approximately 75-m long transects at each study area. We used blue, white, and yellow-colored 16-oz plastic stadium cups as our bee bowls and placed them on ring stands created from steel strips and garden stakes (Pei et al. 2022). Ring stands were adjustable and lowered to the height of surrounding vegetation to reduce attractiveness of bees from outside the study area as well as grazing cattle. Bee bowls were left to collect bees for a targeted 24 hours. After collectors retrieved bee bowl samples, bee specimens were stored in alcohol until identification. We combined the collected bees from both netting and bee bowl surveys across observers and surveys at each site.

C.K. Pei identified all bee specimens to species or morphospecies when species could not be reliably assigned using taxonomic revisions and reviews and other credible publications (Table B1). After identification, bee species were sorted into traits defined by their sociality, nesting habit, diet breadth, and body size using bionomic information found in natural history studies and taxonomic literature (Table B2). We categorized bee sociality as ‘eusocial’ for species that are structured with a main egg-laying female and working castes, including many primitively eusocial Halictid bees (Eickwort 1986), ‘solitary’, for species that provision nests alone, and ‘communal/semisocial’ for species documented to have flexible sociality (Michener 2007). Sociality is complex in many Hymenopterans, and we acknowledge there can be variation in sociality between individuals but use these categorizations based on known species trends (Wcislo 1997). We categorized bees as ‘ground-nesting’ if they dug nests in ground substrate, ‘ground-cavity’ nesters for bumble bees that generally nested in or on pre-existing ground cavities, ‘cavity-nesting’ for species that nest in wood, pithy stem, or other cavities, and ‘hive’ for honey bees. We assigned 'polylectic' to bees that provision nests with pollen from many plant species, 'oligolectic' for species that specialize on pollen from within a single plant family. We categorized bees that parasitized on nest provisioning by other bees as 'cleptoparasitic'. We measured average inter-tegular distances (ITD; Cane 1987) of five females (workers, if bumble bees) when possible to the nearest 1/4th-mm to determine body size groupings. Bees were classified as 'small' if ITD was between 0.75-2.49mm, 'medium' if between 2.50-4.24mm and 'large' if between 4.25-6.00mm. If we were unable to assign a species a trait in all four categories, we omitted them from fourth-corner analyses. This included morphospecies, unless we could classify them with a genus-wide characteristic (e.g. bees in *Sphecodes* Latreille are cleptoparasitic).

Plant Surveys

We sampled the plant community at each site using vegetation cover surveys. We surveyed each site with a total of 50 1-m^2 sampling quadrats. At each study area of a site location, we laid out 25 quadrats in a quincunx pattern of 5 groups of 5 quadrats in order to include variation in the plant community. We estimated percent bare ground and abundance of Kentucky bluegrass, smooth brome, other grasses, and forbs and shrubs to species with percent canopy cover classes modified from the Daubenmire method: 0-5, 5-10, 10-20, 20-30, 30-40, 40-50, 50-60, 60-70, 70-80, 80-90, 90-95, 95-100% (Daubenmire 1959). Other grasses were composed of primarily native grass species but could also include exotic grasses that were not Kentucky bluegrass or smooth brome. If forbs or shrubs could not be identified to species, they were assigned as a morphospecies. We use plant taxonomic species and family names according to the USDA PLANTS Database (http://plants.usda.gov/). At each quadrat, we also recorded litter depth to the nearest centimeter. We recorded cover estimates as midpoints which we then averaged the estimated midpoints and litter depths between study areas at a site. For purposes in this study, our mentioning of "forbs" will include smaller woody shrubs such as Rosa spp. and western snowberry.

Analyses

Our first objective was to identify whether invasive grasses, and other conditions associated with invasive grass spread affect the number of bee and floral species at our sites. Preliminarily, we checked for possible collinearity between variables by ensuring variance inflation factors were low (<2; O'Brien 2007; Zuur et al. 2010). We determined the relationship between bee richness captured between both methods at each site and explanatory variables bare ground, Kentucky bluegrass cover, smooth brome cover, other grass cover, litter depth, and forb richness using univariate generalized linear mixed models with site included as random factors (R package *lme4* v.1.1-28; Bates et al. 2015). We fitted models with Poisson distributions and checked model fit with simulated residuals created with the *DHARMa* package (v.0.4.5; Hartig 2022). We used this methodology to also determine the relationships between forb species richness at the site level and bare ground, Kentucky bluegrass cover, smooth brome cover, other grass cover, and litter depth. Species richness alone cannot define biodiversity but we used species richness in our responses for simpler biological interpretations (Hurlbert 1971). In addition, rare species make large contributions in bee and plant species pools, making richness a representative measure in these groups (Morris et al. 2014). As species diversity can regulate processes such as pollination (Harrison et al. 2014), determining these relationships can provide increased understanding of invasive grass impacts on grassland pollination communities.

While species richness can give broad perspectives, our second objective was to determine how local-scale plant community characteristics associated with invasive grasses relate to particular bee groups and floral species at our survey sites. We used non-metric multidimensional scaling to calculate Bray-Curtis distances between bee abundances per genera captured at each site with both methods (R package *vegan* v.2.5-7; Oksanen et al. 2020). We then fitted environmental vectors (bare ground, Kentucky bluegrass, smooth brome, other grass species cover, litter depth and forb richness) to the resulting ordination scores to display multiple linear regression relationships with bee genera and assessed their significance (p-value<0.05) with permutation testing (n=999; *envfit* function in *vegan*; Oksanen et al. 2020). We repeated this procedure with the distances between individual forb species cover that had totals of at least 20% across all surveys to limit the data to relatively abundant forb species throughout the state (Table B3).

Further, communities can be assessed with different measures that provide complementary perspectives. Bee trait analyses not only group phylogenetically distant bees based on common morphology or life history requirements, but may be more informative of the functional roles of bees have, especially pertaining to their pollination services (Petchey and Gaston 2002; Fruend et al. 2013). To address how plant community conditions associated with invasive grasses affect bees with varying traits (third objective), we used fourth-corner analysis to model relationships between bee social, diet breadth, nesting, and body size traits and bare ground, Kentucky bluegrass, smooth brome, other grass cover, litter depth, and forb richness. The fourth-corner method associates three matrices: environmental variables by site, species by site, and species traits by species to determine relationships between individual species traits and individual environmental variables (Brown et al. 2014). These relationships are determined through generalized linear models with negative binomial distributions to better accommodate count data (Wang et al. 2022). To simplify results to meaningful models, we fitted these models with least absolute shrinkage and selection operator (LASSO) penalties (Brown et al. 2014; Wang et al. 2022). In doing this, coefficients of interactions that do not explain bee species abundance are reduced to zero. We used the *mvabund* package (v.4.2.1) in R to compute fourth-corner analyses and visualize the strength of the associations between traits and plant community variables by plotting standardized coefficients (Wang et al. 2022).

Results

We captured 20,111 individuals comprised of 182 bee species (Fig. 2.2B, Fig. 2.2C) and estimated the cover of 249 forb species (Fig. 2.2A). Bee richness was greater at sites with increasing forb richness but was not associated with any of the other environmental factors (p=0.0019, SE=0.0027; Fig. 2.3A, Table B4). Forb richness was significantly greater with

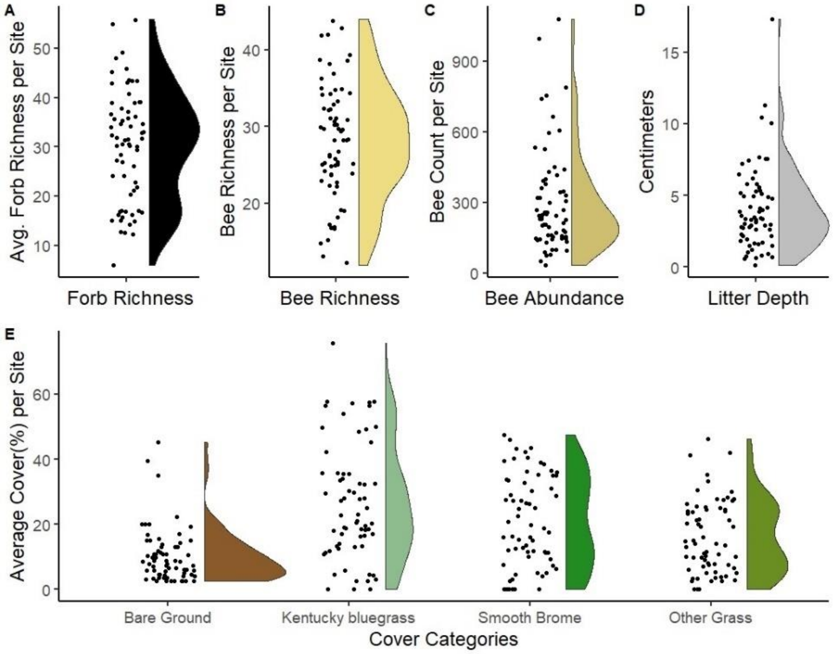

Figure 2.2. Distribution of average forb richness (A), litter depths (D), and vegetation cover groups E), across sites. Plotted distribution of bee species richness (B) and abundance (C) captured at each site in North Dakota from 2017-2020. Plots can be interpreted similarly to boxplots but include a half violin plot showing the smoothed density distribution of each variable and the discrete data depicted by the points for that variable below each half violin plot. Bee measures are obtained from both netting and bee bowl surveys.

increasing cover of grasses other than Kentucky bluegrass or smooth brome ($p>0.05$, SE=0.0039) but lower at sites with higher litter depths ($p=0.036$, SE=0.016; Fig. 2.3B, Table B5) with no strong correlations between litter depth and native/other grass cover.

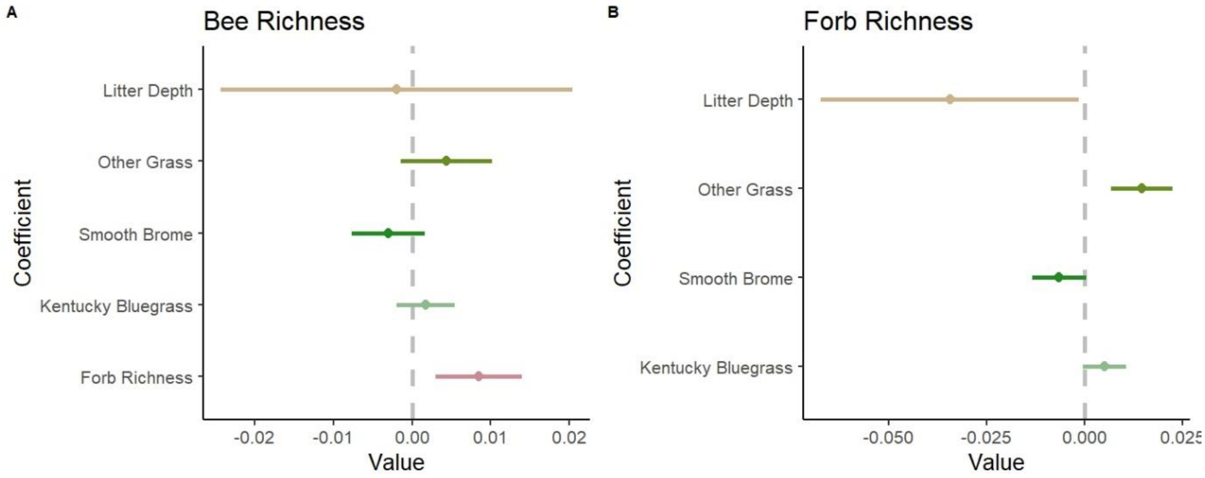

Figure 2.3. Plotted estimated coefficients and 95% confidence intervals from generalized linear mixed models of bee richness (A) and forb richness (B) from surveys in North Dakota from 2017-2020. Models are significant if the confidence intervals do not include zero. Coefficients to the right of the zero lines are positive relationships while those that fall to the left negatively affect richness.

Smooth brome cover ($r^2=0.14$, $p=0.024$) and forb species richness ($r^2=0.13$, $p=0.020$) were significantly correlated with the bee community when grouped by bee genus. Bee genera *Hoplitis* Klug, *Lasioglossum* Curtis, and *Halictus* Latreille were marginally associated with increasing smooth brome while bees in *Augochloropsis* Cockerell, *Anthophora* Latreille, *Colletes* Latreille, *Heriades* Spinola, *Sphecodes* Latreille, and *Nomada* Scopoli were most associated with increasing forb species richness (Fig. 2.4; axes=3, stress=0.188). Litter depth ($r^2=0.13$, $p=0.031$) and smooth brome ($r^2=0.17$, $p=0.0080$) were significantly correlated with the forb community. Both environmental vectors were associated with common exotic forb species such as yellow sweet clover (*M. officinalis* L.), alfalfa, field bindweed (*Convolvulus arvensis* L.), dandelion

(*Taraxacum officinale* F.H. Wigg.), and absinth wormwood (*Artemisia absinthium* L.; Fig. 2.5; axes=3, stress=0.182).

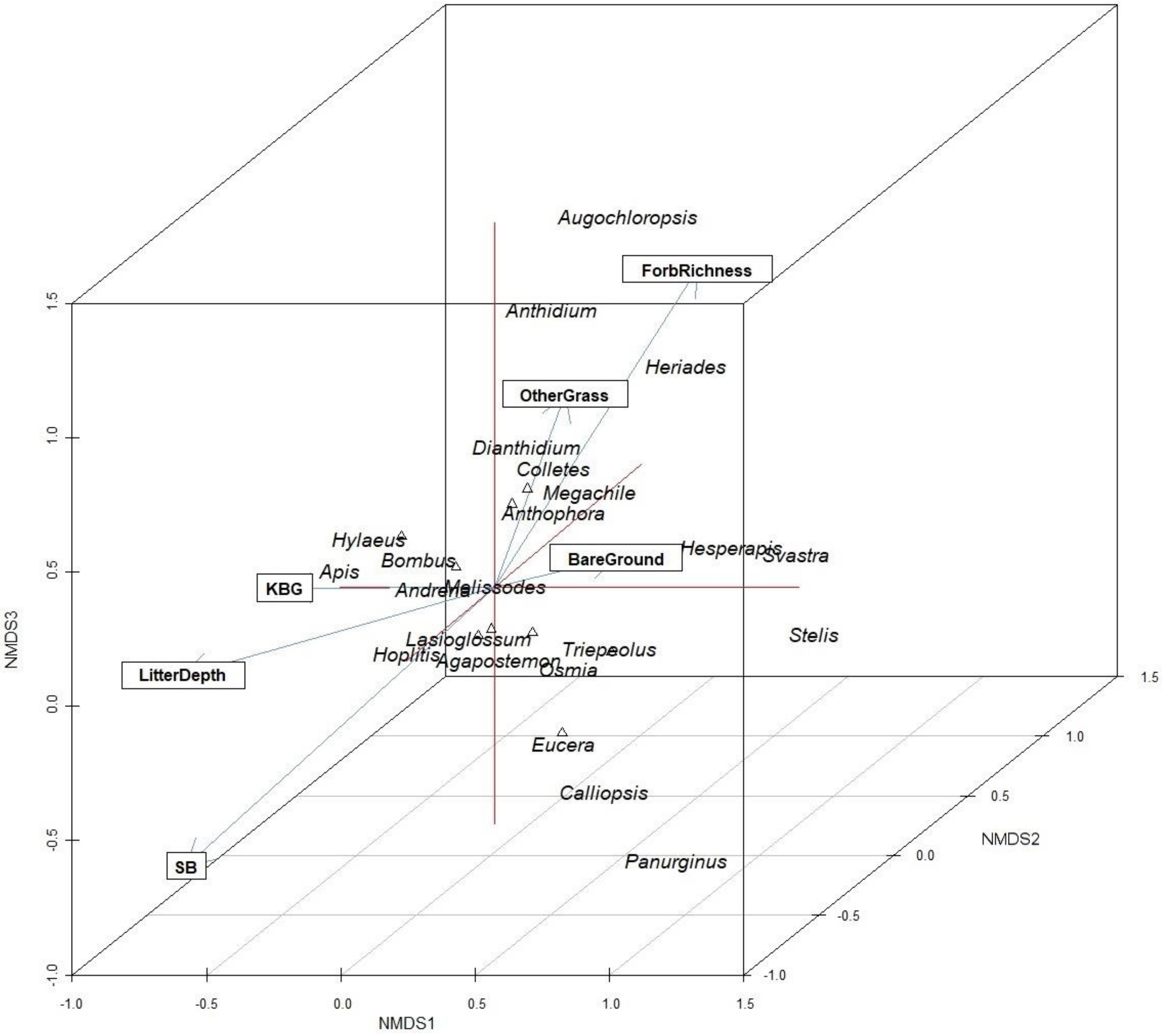

Figure 2.4. Ordination results of the bee genera surveyed in North Dakota between 2017 and 2020 as plotted on three axes (red). Environmental vectors (blue) show envfit results in relation to the plant community. Longer vectors convey a stronger linear influence over the bee community. Triangles depict bee genera names that are not labeled for legibility. Abbreviations: KBG=Kentucky bluegrass; SB= Smooth brome; Stress=0.188, k=3.

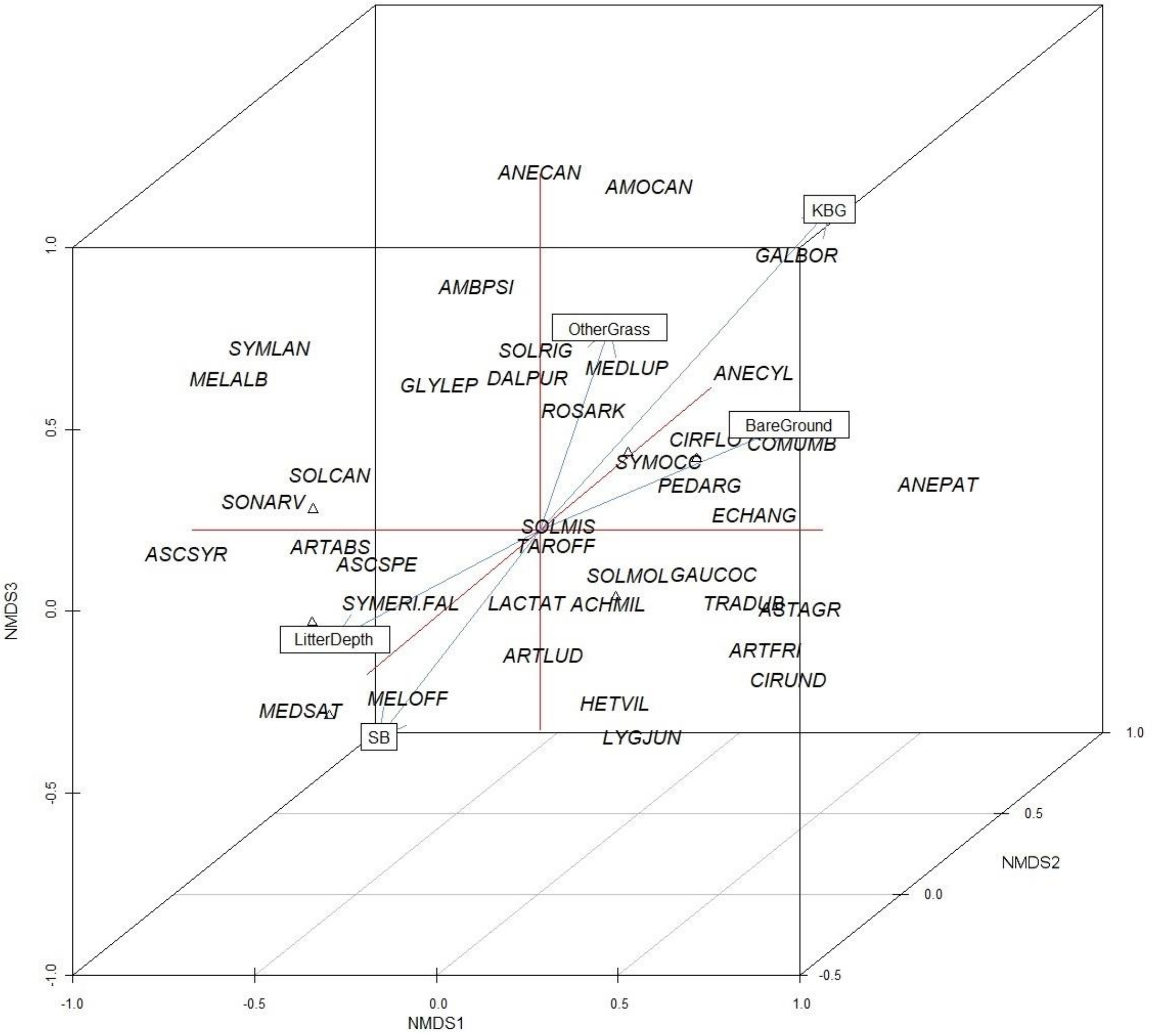

Figure 2.5. Ordination results of the forb species surveyed in North Dakota between 2017 and 2020 as plotted on three axes (red). Environmental vectors (blue) show envfit results in relation to the plant community. Longer vectors convey a stronger linear influence over the plant community. Only plant species that had at least 20% coverage from all surveys combined were included to show most abundant species. Triangles depict plant species names that are not labeled for legibility. Abbreviated codes for forb species can be found in Table B3. Stress=0.182, k=3.

Fourth-corner coefficients revealed variable associations between bee traits and plant community variables (Fig. 2.6). Increasing forb species richness was associated with higher large, polylectic, and cavity nesting bee abundances but lower honey bee and medium-sized bee abundances. Increasing litter depth had a strong negative relationship with ground-nesting bee abundance and a weaker negative relationship with primitively eusocial bees, but increased cavity-nesting bee abundance. Bare ground had a positive relationship with small, primitively eusocial, and polylectic bees, but weakly reduced cleptoparasitic bee abundance. Ground nesting bee abundance was lower with increasing Kentucky bluegrass cover but eusocial bees had a weak positive association with Kentucky bluegrass cover. Increasing native grasses and other grass cover that was not Kentucky bluegrass or smooth brome increased solitary and cavity-nesting bee abundances but decreased small bee abundances.

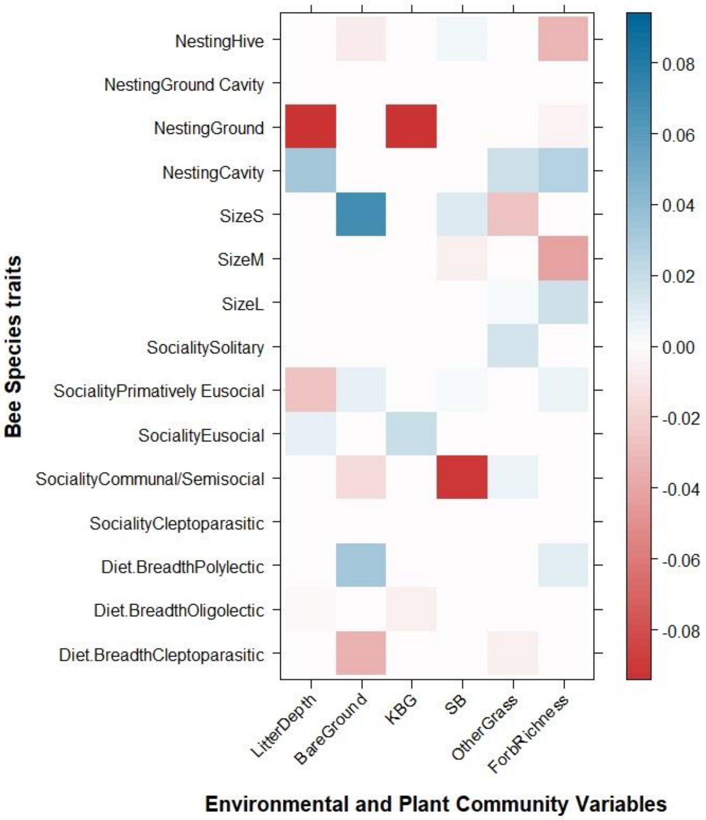

Figure 2.6. Summary matrix of bee species traits and environmental variable relationships. Standardized regression coefficients from generalized linear models with LASSO penalties are plotted. Blue cells signify positive relationships while red cells show negative relationships. The strength of the interaction is symbolized by the shade of color.

Discussion

Exotic grass invasions are prevalent in many contemporary grasslands, especially those in the NGP region. Invasions homogenize grassland structure and biotic compositions causing great concern for conservation and grassland management (Ellis-Felege et al. 2013; Toledo et al. 2014). These results are some of the first to inform of bee community responses to conditions specifically associated with invasive grass spread and the first in the NGP. Though we found no significant relationships with bee species richness and grass cover and litter depth, invasive grasses have varying relationships with bees of particular life history traits, depending on the invasive grass species and plant community characteristic. Agreeing with results from different studies in other systems, the number of bee species we observed was dependent on the richness of surrounding forb species (Ebeling et al. 2008; Grundel et al. 2010; Blaauw and Isaacs 2014; Carson et al. 2016). However, higher forb richness was determined by lower litter depths and higher coverage of native grasses and grasses other than Kentucky bluegrass and smooth brome, both of which are known to be affected by invasive grasses (Printz and Hendrickson 2015; Palit et al. 2021). Our results provide further evidence that invasions have varying effects on diverse groups of organisms and that preventing homogenous plant communities created by invasive grasses is important for grassland bee conservation.

Higher floral richness was important in supporting bee richness in our study and significantly contributed to shaping the bee community. This is likely, in part, due to the varying pollen requirements needed by different bees; a site with higher floral richness availability may accommodate a wider variety of bee diet breadths (Woodard and Jha 2017). However, floral richness alone may not be of great importance if the floral host species of a particular specialist bee is not present (Fründ et al. 2010). Some bees may not primarily value floral diversity due to their foraging strategy (Leonhardt and Blüthgen 2012). For instance, honey bees (*Apis mellifera* L.), which were classified as hive-nesting, medium-sized, social bees in our study had a negative association with floral diversity. Honey bees are social foragers and may value the quantity or density of floral resources more than their identity (Leonhardt and Blüthgen 2012; Hung et al. 2019). Floral richness is important in supporting bee diversity but it alone cannot explain bee communities due to other resource requirements, such as nesting resources.

Aside from floral diversity, we found that litter depth is influential in structuring bee communities. Importantly, litter depth reduced the abundance of ground-nesting bees that burrow into soil substrate, agreeing with another study that included litter depth effects on bees in the NGP (Olynyk et al. 2021). However, cavity-nesting bees and social bees had positive associations with litter depths. Many cavity-nesting bee species require access to pithy stems for nesting and likely benefit from increased litter availability (Potts et al. 2005). Litter layers may be associated with social bees in our study region through the plant communities that are associated with increasing litter depths, but this may be a regionally dependent relationship due to contrasting findings in other regions (Carvell 2002; Williams et al. 2019; Olynyk et al. 2021). These communities had higher amounts of sweet clover and alfalfa (Fig. 2.4), exotic plants with high visitation by social honey bees and bumble bees. Bees with different life history requirements respond differently to litter depths, indicating that homogenous litter layers across a landscape would have adverse effects on bee community diversity.

Beyond litter management, our results show bee diversity may be best enhanced through managing for local-scale heterogeneity in the plant community structure due to the differing resource needs between bee species (Kruess and Tscharntke 2002; Black et al. 2011). For example, many bee species rely on bare ground, however, others need sufficient herbaceous or litter cover (Kimoto et al. 2012). Integrative grassland management strategies can achieve mosaic grassland structure that benefits biodiversity (Swengel 1998; Fuhlendorf et al. 2006; Black et al. 2011; Ponisio et al. 2016). While invasive grasses are now integrated components of NGP grasslands, managers should place priority in preventing further spread and interrupting structural and compositional homogeneity within invasive grass-dominated grasslands (Grant et al. 2009; Ellis-Felege et al. 2013; Gasch et al. 2020). Specifically, fire-grazing interactions can reduce thick litter layers created by exotic grasses, but grassland managers can manipulate the pattern and timing of these disturbances to create a diversity of plant community structure (Ashton et al. 2016; Powell et al. 2018) that may support bees with different life history requirements (Ponisio et al. 2016). Enhancing flowering forb diversity on a landscape is, however, critical to supporting bee diversity, as found in our study and across other systems (Potts et al. 2003; Grundel et al. 2010; Sutter et al. 2017) but grassland management practices can also directly influence grassland bee community diversity (Griffin et al. 2021). Disrupting competitive effects of invasive grasses can provide opportunity for native species growth (Printz and Hendrickson 2015), but restorative seeding may be required in some grasslands to increase plant diversity (Baer et al. 2002; Gaskin et al. 2021).

Our results demonstrate the direct and indirect influences of invasive grasses on bee communities and floral resources. Our study grants a perspective on the plant community through local plant community characteristics associated with invasive grasses, but we recommend future bee-plant network analyses to provide a more holistic understanding on invasive plant influence over bee communities, given the relationships between forb and bee species. It is important that researchers and grassland managers understand the impacts of invasive grasses, especially considering their extent in regions like the NGP and their varying effects on abiotic processes and biodiversity. In altered grasslands, managers can focus efforts on promoting diverse floral resources with the accompanying goal of interrupting structural homogenization of invaded plant communities. Though our study most directly implicates bees in NGP grasslands, our results may also contribute to understanding invasive species effects in other altered grassland systems with similar bee species pool sizes (Pärtel et al. 2016).

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CHAPTER 3: INTRODUCED SUPER-GENERALISTS INFLUENCE BEE-PLANT NETWORK PROPERTIES ON NOVEL GRASSLANDS

Abstract

Species interactions are foundational in defining and maintaining biodiversity and its consequent ecosystem services. However, anthropogenic changes, such as exotic species introductions, alter species interaction networks with various consequences on ecosystem stability and resilience. The Northern Great Plains grasslands have a high prevalence of exotic plant species, in addition to high densities of European honey bees *Apis mllifera*, but we do not understand how these exotic-generalist species influence the structure of pollination networks in the region. We addressed three objectives to provide a broad assessment of exotic species' roles in bee-plant networks in North Dakota, USA. First, we determined the modularity and central species in broad ecoregional networks. Considering the context-specific variation of exotic species' impacts, our second objective was determining the relatedness of common network properties that provide different perspectives on network structure, diversity, and stability. Finally, we assessed the relationships of network properties with floral richness, total floral density, native and exotic floral density, and the abundance of honey bees at our survey sites. We created networks from bee-plant associations from a statewide survey dataset across North Dakota grasslands that spanned four years and all 53 counties. Several species had highly centralized roles in each ecoregion, including exotic honey bees and plants, as well as certain native bee and plant species that can serve as important conservation targets. The relatedness of properties in our system were largely influenced by the abundance of honey bees and we found varying relationships regarding the floral characters and honey bee abundances with network properties. Of these, exotic species decreased the number of compartments, interaction diversity,

and diversity of bee partners for plants. Conserving the structure of pollination networks is crucial to maintaining biodiversity and pollination services, making it important to understand exotic species impacts, especially in regions with high species introductions. We determined that bee-plant networks in this region are largely novel due to exotic bee and plant introductions. Managing against exotic species dominance may lessen their effects over network interaction structure and may be critical to maintain pollination services on altered grasslands.

Introduction

Biological communities and the ecological interactions that support ecosystem resilience and function are at risk from various factors of global change (Chapin et al. 2000). However, the conservation of species interaction networks receives less attention than species-specific conservation efforts but offers enhanced information on particular species' roles in an ecological community (McCann 2007; Tylianakis et al. 2010). Additionally, interaction networks provide a view on ecosystem diversity and resilience, while also providing informative measures for conservation goals (Elle et al. 2012). Networks do so by broadly synthesizing the numerous species interactions, or the lack thereof, that ultimately affect ecosystem processes and services (e.g. pollination; Tylianakis et al. 2010; Hagen 2012; Tylianakis and Morris 2017).

Species introductions are pervasive global concerns with various, yet often substantial, effects on biodiversity and ecological interactions (Bascompte and Jordano 2007). Among other global change factors, introduced species are widely human-facilitated through direct and purposeful introductions in addition to unintentional ones (Simberloff et al. 2013). For example, human alterations to biodiversity and ecological processes, in addition to climatic changes, can open niches and favor introduced species that have properties that allow them to integrate into ecological communities (MacDougall and Turkington 2005). Such colonizing species can change the amount and composition of interactions in an existing community by reordering, and sometimes eliminating interactions or species in existing antagonistic and mutualistic relationships with varying consequences (Frost et al. 2019). These changes can also impact the ecosystem processes upheld by existing network interactions in various ways. For example, in some systems an introduced generalist plant may facilitate pollination to native species by attracting more pollinators, whereas in another system, an introduced plant may detract conspecific pollen transfer (Morales and Traveset 2009; Ferrero et al. 2013). Such consequences of species introductions and their influence on network interactions are complicated to synopsize as they are largely dependent on the existing community, ecosystem, and the introduced species' traits (Bartomeus et al. 2008; Frost et al. 2019). This however, emphasizes the need for further study especially in regions that have undergone or are at risk of many species introductions.

Introduced species generally fill roles in new communities that are similar to their role in their native ecosystems (Emer et al. 2016; Frost et al. 2019). As such, species with greater influence over networks through their high degree of interactions are likely to form many interactions in a novel community. Super-generalist species, those with the broadest degree of interactions with other species, may then incur the greatest changes to the new interaction network when introduced to a new community (Tylianakis et al. 2010; Russo et al. 2014). The integration of new species into a community is thus dependent on the introduced species' role, resulting in complicated consequences for the stability and persistence of networks to perturbations. For example, a topological view of a network with an introduced generalist can exhibit stabilizing properties (e.g. higher nestedness; Stouffer et al. 2014). However, purely topological perspectives may require further scrutiny as high stability in an ecological network can be associated with severely degraded biological communities in the same way a community with a high number and diversity of intact and regulatory ecological links is (Tylianakis et al. 2010; Heleno et al. 2012). In addition, properties associated with stability can be greatly influenced by super-abundant species (Suweis et al. 2013). With the context-dependent nature of species introductions, incorporating multiple properties in network analyses may provide an enhanced understanding of the effects of introduced species on network structure and diversity, and a more holistic perspective on network stability (Lewinsohn et al. 2006).

Many contemporary grasslands in North America are composed of novel communities largely due to exotic species introductions and anthropogenic changes to natural disturbance processes (Martin et al. 2014). The replacement of native grassland plant species by exotic plant species can incur functional, structural, and compositional changes in grassland communities which may alter native animal species interactions with native plants (Van Riper and Larson 2009; Toledo et al. 2014). For example, in the Northern Great Plains (NGP) region, exotic leafy spurge (*Euphorbia esula*) and Russian thistle (*Salsola tragus*) in grasslands can decrease the amount of conspecific pollen transfer, presumably by distracting floral visitors from surrounding native plants (Larson et al. 2006; Larson et al. 2014). Though their integration into pollinator networks is less investigated, the NGP hosts several other exotic floral species that occur in high densities such as sweet clover (*Melilotus* spp.), alfalfa (*Medicago sativa*), and Canada thistle (*Cirsium arvense*). Few studies have reported pollination networks in the NGP (Otto et al. 2017; Bendel et al. 2019; Vilella-Arnizaut et al. 2021) with fewer investigating exotic species effects on structural network properties (Larson et al. 2014; Larson et al. 2016). However, study of the novel interactions is particularly warranted and highly applicable in the NGP given the prevalence of exotic plants and an introduced pollinator species.

Within the NGP, North Dakota hosts the highest densities of an introduced super-generalist pollinator, the European honey bee *Apis mellifera* L. (Otto et al. 2020). Honey bees are economically important to the NGP region, with a $61.5 million USD honey production value in North Dakota alone in 2020 and further utility in crop pollination in other regions (USDA 2021). Their high degree of pollen-generalism, foraging efficiency, and broad influence in their native range suggests dramatic consequences for native pollinators and both native and exotic floral species in their introduced range (Valdovinos et al. 2018; Frost et al. 2019). Few studies in North America have investigated these effects, but some have identified reductions of native bee abundance and diversity due to honey bees (Thomson 2004; Thomson 2016; Angelella et al. 2021). However, there is considerable evidence from South America that shows honey bees as dominant in pollinator communities, causing structural changes to pollination networks (M. de M. Santos et al. 2012; Martins et al. 2013). It is important to understand their influence on interactions that affect pollination services in agricultural and natural systems, especially in regions with atypically high honey bee concentrations, but no investigations concerning potential network effects of honey bees exist in the NGP region despite its high honey bee densities.

The prevalence of exotic species (both plant and pollinator) and new bee-plant interactions in the NGP region may validate our expectation that the structure of pollination networks in this region is novel. However, these novel conditions are relatively unassessed, and we therefore have no broad understanding of how exotic species might be affecting pollination services on agriculturally and ecologically important grasslands in the NGP. We used data from a statewide survey of bee communities across the state of North Dakota (ND), USA to investigate novel pollination network structure in the NGP. North Dakota presents a gradient of plant communities across the state, a high prevalence of exotic plants, and is the largest honeyproducing state in the United States. Overarchingly, our goal is to present an empirical and comprehensive illustration of the status of bee-plant interactions in novel grasslands through multiple approaches that may enhance our understanding of network dynamics altered with introduced species. Our first objective is to determine the modularity and influential species in bee-plant networks across North Dakota's four primary ecoregions. Secondly, we present the relationships of network properties with floral community characters and honey bee abundances to provide a first report of their relatedness in altered NGP grasslands and to empirically inform the relationships tested in our third objective where we test the relationships between floral community characters and honey bee abundances with both the structure and diversity of network interactions. For this, we predict that exotic plant and bee species will influence some network properties, especially those related to the diversity of interactions. However, with evidence of exotic mutualisms formed between exotic plants and honey bees in other systems (Morales and Aizen 2006), we also expect the amount of exotic floral species and honey bees may influence how NGP pollination networks are compartmentalized.

Methods

Study System

We sourced our data from a statewide survey of grassland bee and plant communities in North Dakota from 2017-2020. North Dakota is delineated into four level III ecoregions with the Lake Agassiz Plain (LAP) ecoregion bordering the east of ND, the Northern Glaciated Plain (NGLP) in the east-central region of the state, the Northwestern Glaciated Plain (NWGLP) ecoregion following the Missouri River across in a south-central to northwest diagonal, and the Northwestern Great Plains (NWGP) ecoregion characterizing the southwest region of the state (CEC 1997; Bryce et al. 1998). Tallgrass prairie communities historically characterized the LAP region, while the NGLP and NWGLP regions can be characterized as mixed-grass prairie plant communities. The historically unglaciated NWGP region is predominately mixed-grass prairie with short-grass prairie on the far western border. However, cool-season exotic grass species Kentucky bluegrass (*Poa pratensis*), smooth brome (*Bromus inermis*) are prevalent in most grasslands in North Dakota (Murphy and Grant 2005). Additionally, exotic forbs are present in many grasslands across the regions including sweet clovers (*Melilotus* spp.), alfalfa (*Medicago sativa*), leafy spurge (*Euphorbia esula*), and Canada thistle (*Cirsium arvense*; Ellis-Felege et al. 2013).

We established 53 grassland sites, one located in each ND county. Sites were at least 20 hectares of contiguous grassland managed by both state and federal agencies for rangeland and wildlife production. At each site, we established two 50-m^2 survey plots, spaced at least 100-m apart, each accompanied with a set of transects for floral surveys. We visited each site two times per year (eight total visits) with two observers conducting independent netting surveys for bees and floral surveys every year of the survey bringing the total number of paired surveys to 424. Our surveys occurred twice at each site each year to account for phenological changes while balancing the number of survey sites. We conducted surveys during the growing season, starting from May 27th to Sept 14th.

We performed netting surveys for bees during the daytime with temperatures between 21-36 C°, low cloud cover (<50%), and sustained wind speeds of $\leq$ 25 km/hr. Collectors would perform netting surveys for bees in their respective 50-m^2 plot for a total of 30 minutes (Pei et al. 2022). When collectors securely netted a bee, they paused survey time, transferred the specimen to a kill tube, and recorded the floral species the bee was on. Collectors transferred bee specimens from kill tubes to labeled tubes filled with 95% alcohol until they could be identified.

Specimens were identified to species or morphospecies when species could not be confidently assigned using taxonomic revisions, revisions, and other credible taxonomic sources (Table C1).

We accompanied each bee survey with floral surveys to estimate the amount and type of floral resource availability to bees at the time of a survey. During floral surveys, observers walked along a transect and recorded the number of flowering stems per floral species within a five-meter belt along the transect. For surveys between 2017-2018, each study plot at a site was accompanied with three 100-m long transects spaced approximately 50-m apart. In 2019-2020, we accompanied both bee survey plots at each site with two 200-m transects spaced 100-m apart. This change to the transect lengths and numbers was due to methodological changes associated with another objective of the larger statewide survey project. However, we were able to standardize between methods by calculating floral density and floral density-richness (hereafter, floral richness) values.

From netting surveys, we filtered the data to include only associations between female bees and floral species to exclude differences in male foraging (Roswell et al. 2019; Kishi and Kakutani 2020). We also excluded interactions involving plants in Apocynaceae (two genera) because of the pollinium form of their pollen. Bees do not purposefully collect or provision nests with this form of pollen and these plants could only offer nectar rather than nectar or pollen (Michener 2007). Even though our data does not differentiate between nectar and pollen collection, bees had the ability to potentially collect pollen and/or nectar from the other plants.

Analysis

To address our objectives, we selected properties that are often associated with the conservation of network stability and functionality (Tylianakis et al. 2010; Elle et al. 2012). Our objectives each included particular network properties, but we include a list of all properties we considered throughout and a brief descriptions here:

Network-wide Properties

- *Modularity and Compartments:* Modularity is the degree of block organization in species interactions (Olesen et al. 2007). Modules are sets of interacting species that interact more closely with each other than with species of other modules. Higher modularity infers a network with a greater number of specialized interactions (Elle et al. 2012; Olesen et al. 2017). Compartments are extreme form of modules that are formed with no connection between compartments (Lewinsohn et al. 2006). Where modularity incorporates the degree of interactions, the number of compartments is simply measured as the number of distinct sets of interactions. Inferences of network stability and modularity are debated, complicated, and likely circumstantial with different arguments showing modularity with either destabilizing or stabilizing influences in mutualistic networks (Thébault and Fontaine 2010; Grilli et al. 2016).
- *Weighted Connectance*: Connectance is the proportion of realized links from the total number of possible links (Jordano 1987). As such, connectance is affected by network size (the number of species in the network; Dunne et al. 2002). Weighting connectance by network size reduces the effects of this relationship (Dunne et al. 2002). Higher connectance can describe a complex network, but connectance cannot always be an inference of a network’s resilience to perturbation because the identity of species that influence connectance may have differing implications to the network’s conservation (Heleno et al. 2012).

- *Weighted Nestedness (NODF)*: Nestedness overlap and decreasing fill (NODF) is based on the degree to which specialist species interact with generalist species and vice versa (Almeida-Neto et al. 2008). Highly nested networks exhibit high degrees in this interaction asymmetry between generalist and specialist species. Nestedness typically shows a positive relationship with network size and is therefore weighted to the number of species to reduce these effects. Greater nestedness is generally considered to increase network stability.
- *Interaction Evenness:* Shannon evenness of interactions with higher values indicate that interactions are evenly distributed between species in a network (Dormann et al. 2009.
- Specialization (H2´): H2´ is the degree to which the interaction frequency between species differs from the expected number of interactions (Blüthgen et al. 2006). High H2´ values indicate a higher degree of specialization (Dormann et al. 2009). Specialization in this case does not inform on life history-associated connections between species (e.g. diet breadth).
- Network Shannon Diversity: Interaction diversity is measure based on the Shannon index that considers interaction richness and evenness (Dormann et al. 2009).

Trophic-level Properties

- Generality and Vulnerability: Generality in our pollination networks refers to the plant partner diversity of bees. Vulnerability is the diversity of bee partners a plant species has. Higher generality and vulnerability are considered to increase network stability because the loss of specialized interactions will not likely have cascading effects on the remaining network (Kaiser-Bunbury and Blüthgen 2015). These measures are typically used in antagonistic relationships but can identify the group (plant or pollinator) at risk of low partner diversity (Kaiser-Bunbury and Blüthgen 2015; Dormann et al. 2009).

To address our first objective, we pooled survey data from across all surveys within each ecoregion. We expect these ecoregion networks to differ as ecoregions themselves differ in both biological and physical properties (Omernik 1995). We determined the degree of modularity in each of these pooled interactions to identify groups of closely interacting species using the edge betweenness clustering method in the *igraph* package available in the R statistical environment (Newman and Girvan 2004; Csardi 2006; R Core Team 2020). The maximum modularity value is 1, but values ≥ 0.3 are considered strongly modular (Clauset et al. 2004; Newman and Girvan 2004). We visualized the networks to view the composition of these modules using the *edgebundleR* package (v.0.1.4; Bostock et al. 2016). In addition to modularity, we determined influential species, or the degree a species contributes to a network, in each ecoregional network with eigenvector centrality in *igraph* (v. 1.3.0; Bonacich 1987; Csardi 2006). In this method, well-connected species will have a higher centrality value, especially if they interact with other highly-connected species (Delmas et al. 2019).

To address our second objective, we built bee-plant interaction networks at the site-level and determined the relative distances between network properties with floral community characters and the amount of honey bees captured at each site. For floral community characters, we included the total floral density, native and exotic floral density, and floral species richness that we measured from all floral surveys at each site. We calculated the properties for weighted connectance, compartmentalization, weighted nestedness, specialization, Shannon diversity at the network level, and generality/vulnerability at the group level to describe the networks from all surveys per site using the bipartite package (v. 2.17; Dormann 2008). We excluded any networks that were too small to calculate any of the properties. To visualize the relatedness of the network properties and floral characters and honey bees, we first used non-metric multidimensional scaling ordination to show the relative Bray-Curtis distances between floral characters and honey bees using the *vegan* package in R (v. 2.5-7; Oksanen et al. 2020). Then, we used the *envfit* function to fit the properties to the ordination space created with the floral characters and honey bees in order to determine which properties had significant relationships with shaping ordination scores.

We then tested the relationships between the network properties and floral community characters (floral richness, floral density, and native and exotic floral density) and honey bee abundances at each site, while acknowledging variation in year and ecoregion in our third objective. Using the methodology to obtain network properties and other variables from our second objective, we fitted a set of eight models (linear or generalized linear models) to explain each property using each environmental variable alone, with the addition of year variation, with an interaction between each environmental variable and year, with the addition of ecoregional variation, with an ecoregion interaction with each environmental variable, with the addition of both year and ecoregional variation, with a year and ecoregion interaction with each environmental variable, and a null model (Table C2). To determine which model best explains the relationship between the network properties and each environmental variable, we performed model selection based on Akaike information criterion adjusted for small sample sizes (AIC_c), considering the best model(s) as those with a ΔAIC_c of 2 and under as the best model(s) (Burnham and Anderson 2002). We fitted linear regression models to test weighted connectance, number of compartments, H2´, generality (removed outliers), vulnerability, and network

Shannon diversity. For interaction evenness, we removed outliers and fit generalized linear models with a Gaussian log link function. Generalized linear models explaining weighted NODF showed substantial residual overdispersion and we therefore did not include analyses here with weighted NODF. To show the relationships between the network properties and floral community characters and honey bee abundances at each site, we plotted the estimated coefficients of these relationships with 95% confidence intervals. If there was more than one ‘best model’, we averaged the estimated coefficients for those models in order to incorporate that variability that may come from year or ecoregion (Burnham and Anderson 2004).

Results

We captured a total of 5,175 bees from 151 species from across all networks and sites. Captured bees interacted with 136 floral species. Broadly, native bees had higher relative visitation to native plants, while honey bees visited both native and exotic plants similarly (Fig. 3.1).

Objective 1

Most ecoregion networks were strongly modular with modularity from the edge betweenness clustering method being 0.55 in the LAP region, 0.43 in the NWGLP region, and 0.40 in the NWGP region (Fig. 3.2). However, the network from all sites and surveys in the NGLP region had a modularity value of 0.28, which indicates a weaker community structure (Newman and Girvan 2004). Though the bee and plant species with the highest centrality in each ecoregion’s network differed with ecoregion, there were species that commonly had high connectivity to other species in the network (Table 3.1). Of these, honey bees and Bombus griseocolllis had high connection to other species in each ecoregion’s total network. Species that had the highest centrality scores were expectedly generalist species, such as plants that were visited by many bee species, and bees that visited many plant species.

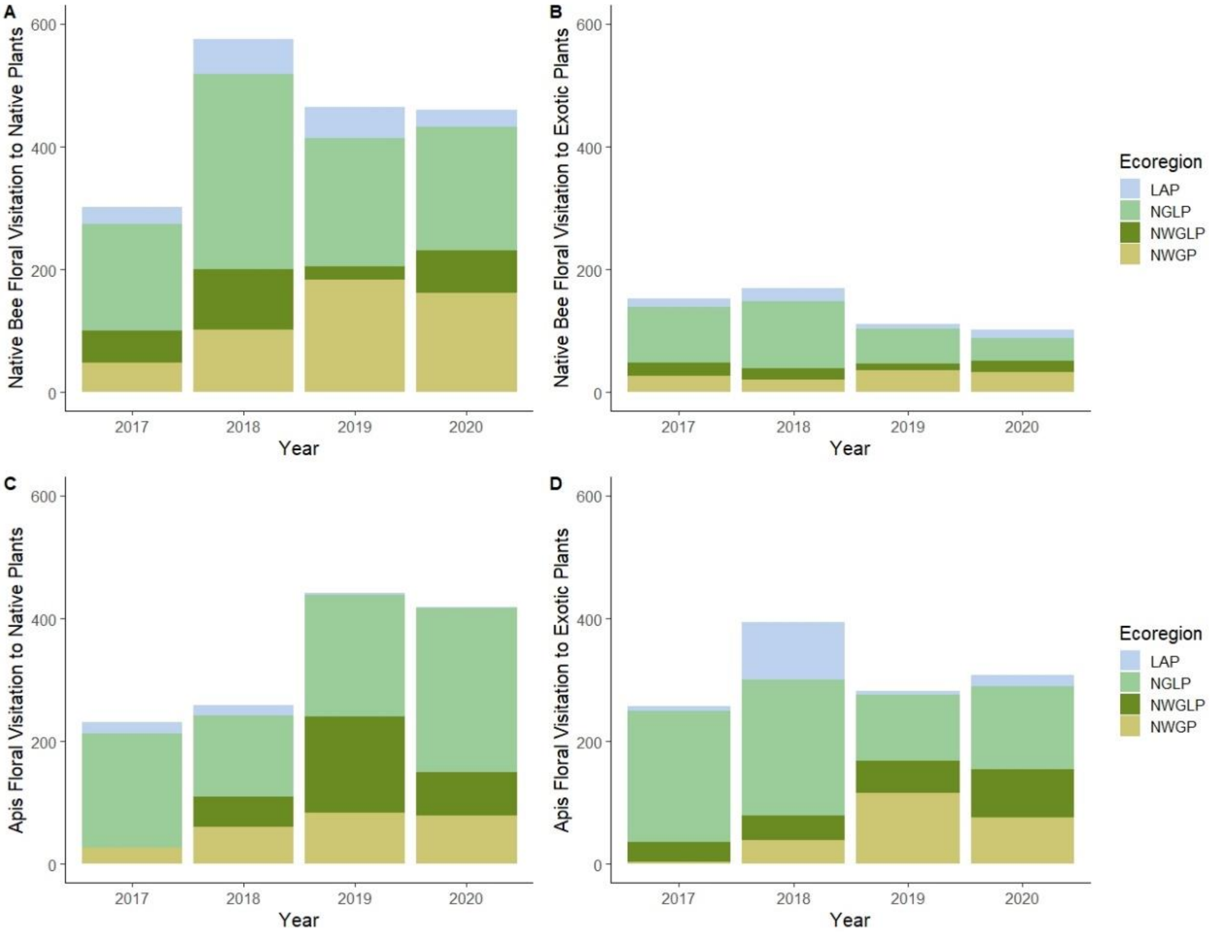

Figure 3.1. Number of native bee visitations to native (a) and exotic (b) floral species and the number of honey bee (Apis mellifera) visitations to both native (c) and exotic (d) floral species by ecoregion and year in North Dakota between 2017 and 2020. LAP: Lake Agassiz Plain ecoregion; NGLP: Northern Glaciated Plain ecoregion; NWGLP: Northwestern Glaciated Plain ecoregion; NWGP: Northwestern Great Plain ecoregion.

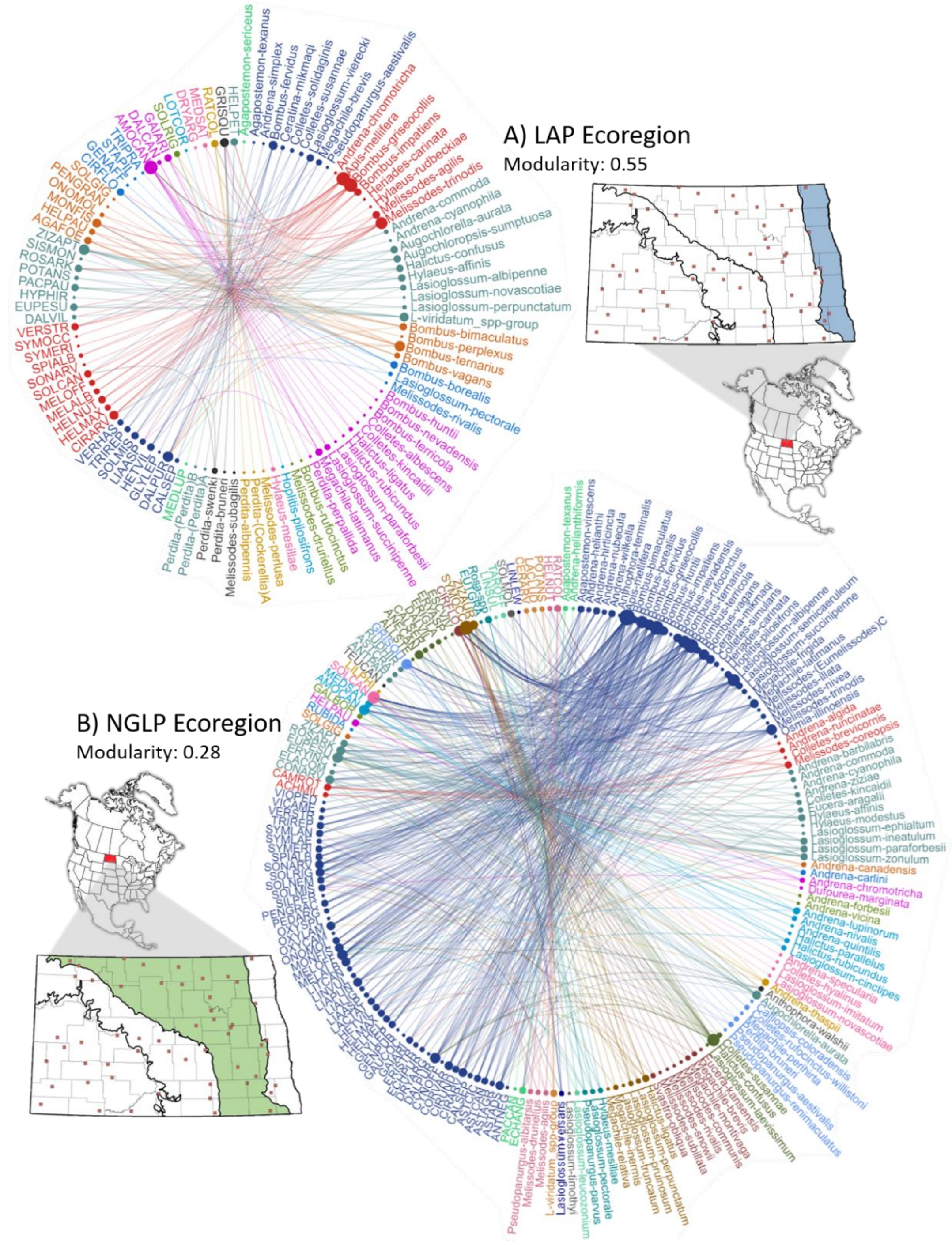

Figure 3.2. Bee-plant networks across the Lake Agassiz Plain (A; LAP) and Northern Glacial Plain (B; NGLP) ecoregions in North Dakota from 2017-2020. Each network consists of bee species with species names written out and the plant species denoted with species codes found in Table C3. Lines connecting species signify an observed interaction between species from surveys while the size of the circles refer to the weight of those species interactions. Modularity values and the colors of species denote the community membership measured by edge betweenness clustering which determines modules through the shortest paths.

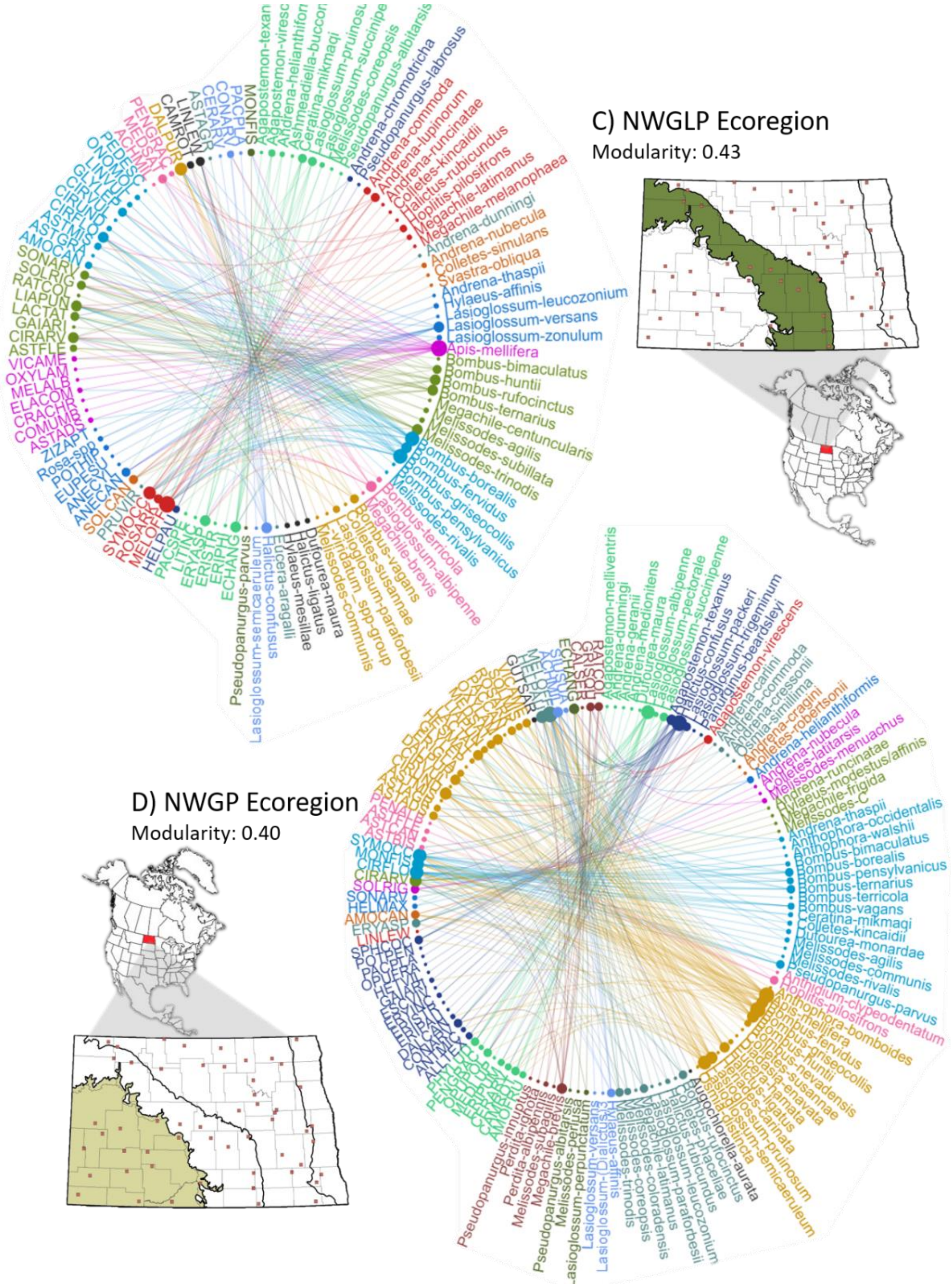

Figure 3.2. Bee-plant networks across the Northwestern Glaciated Plain (C; NWGLP) and Northwestern Great Plains (D; NWGP) ecoregions in North Dakota from 2017-2020 (continued). Each network consists of bee species with species names written out and the plant species denoted with species codes found in Table C3. Lines connecting species signify an observed interaction between species from surveys while the size of the circles refer to the weight of those species interactions. Modularity values and the colors of species denote the community membership measured by edge betweenness clustering which determines modules through the shortest paths.

Table 3.1. Top 15 species in each North Dakota ecoregion with the highest degree of eigenvector centrality. Bee species names are written out while plant species are denoted with a six-letter code (see Table C3 for codes). Exotic species are denoted with an asterisk. LAP: Lake Agassiz Plain ecoregion; NGLP: Northern Glaciated Plain ecoregion; NWGLP: Northwestern Glaciated Plain ecoregion; NWGP: Northwestern Great Plain ecoregion.

Ecoregion	Species	Centrality	Ecoregion	Species	Centrality
LAP	*Bombus griseocollis*	1	NGLP	*Apis mellifera**	1
	AMOCAN	0.88		*Bombus griseocollis*	0.81
	*Apis mellifera**	0.76		*Bombus ternarius*	0.73
	DALPUR	0.57		*Bombus rufocinctus*	0.67
	Bombus ternarius	0.56		SYMOCC	0.66
	CIRARV*	0.55		MELOFF*	0.62
	MONFIS	0.50		*Bombus borealis*	0.60
	ZIZAPT	0.47		SOLCAN	0.53
	ROSARK	0.38		DALPUR	0.52
	Melissodes trinodis	0.37		*Halictus confusus*	0.46
	AGAFOE	0.36		*L. albipenne*	0.45
	Halictus confusus	0.35		*Bombus fervidus*	0.44
	MELALB*	0.35		MELALB*	0.43
	MELOFF*	0.35		AMOCAN	0.42
	L. vierecki	0.31		CIRFLO	0.42
NWGLP	*Apis mellifera**	1	NWGP	MELOFF*	1
	MELOFF*	0.90		*Apis mellifera**	0.92
	Bombus griseocollis	0.79		*Bombus griseocollis*	0.84
	SYMOCC	0.70		SYMOCC	0.82
	Bombus borealis	0.67		*L. semicaeruleum*	0.76
	DALPUR	0.60		*Halictus confusus*	0.69
	Bombus ternarius	0.60		CIRFLO	0.67
	LIAPUN	0.58		*Bombus huntii*	0.67
	CIRARV*	0.57		*L. albipenne*	0.59
	Bombus fervidus	0.51		*L. pruinosum*	0.58
	CIRFLO	0.49		*Bombus fervidus*	0.56
	L. albipenne	0.46		DALPUR	0.54
	Halictus confusus	0.42		CIRUND	0.52
	GLYLEP	0.42		CIRARV*	0.52
	SOLRIG	0.41		LACTAT	0.51

Objective 2

In our second objective, most of the site-level network properties we used showed some relatedness to each other in the ordination space (stress=0.18; axes=2). Interaction evenness (r^2=0.41; p=0.001), number of compartments (r^2=0.089; p=0.001), network Shannon diversity (r^2=0.10; p=0.001), vulnerability (r^2=0.089; p=0.0030), generality (r^2=0.20; p=0.001), and nestedness (r^2=0.19; p=0.001) significantly shaped to the ordination space of floral characters and honey bee abundances. Interaction evenness, number of compartments, network Shannon diversity, and vulnerability had negative relationships with nestedness and generality (Fig. 3.3). H2´ and connectance did not have significant linear relationships with the community space created by the floral characters and honey bee abundances (Fig. 3.3). The richness of floral species was closely associated with increasing interaction evenness, network Shannon diversity, and the diversity of plant visitors while honey bees were tightly associated with increasing nestedness and the diversity of plants that bees visited (generality).

Objective 3

Weighted Connectance

Floral richness, total floral density, exotic floral density, and honey bee abundance did not have significant relationships with network connectance, regardless of best models (Fig. 3.4A). Both the univariate and additive year models with native floral density were selected as the best model, indicating some importance of yearly variation in native flowering density and connectance (Table C4). When the estimated coefficients were averaged, native floral density had a negative relationship with network connectance (β: -0.0072; 95% CI: -0.013, -0.0019; Fig. 3.4A).

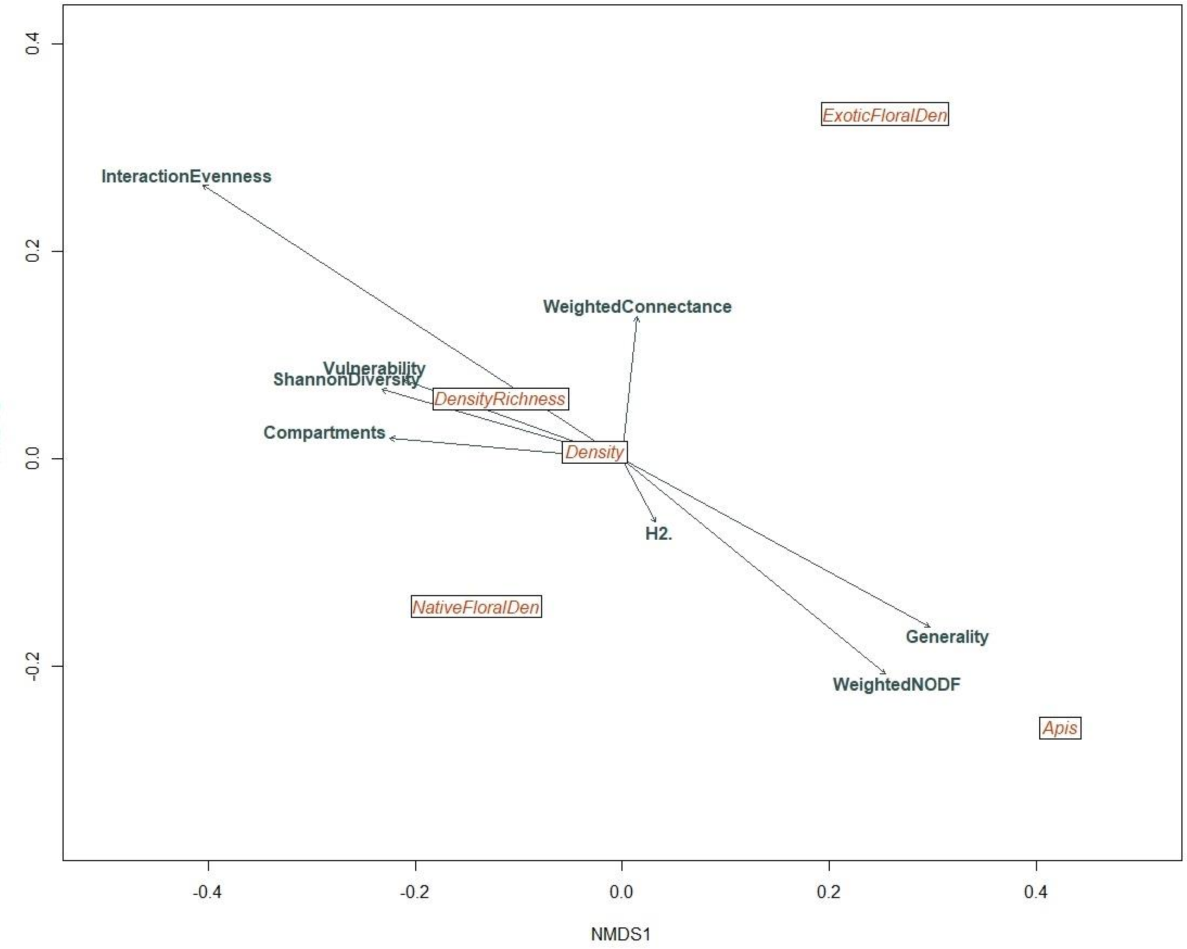

Figure 3.3. Ordination results of the floral richness, floral density, and honey bee abundance values observed in North Dakota between 2017 and 2020 and their relatedness to eight network properties, represented by the blue vectors. The length and direction of the vectors convey the strength and relationship with other vectors and the ordination space created by the floral and honey bee characters (stress=0.18; k=2).

Number of Compartments

The univariate floral richness model was selected as the best model in explaining the relationship between floral richness and the number of compartments in the networks at each site per year (Table C5). Higher floral species richness at each site was significantly associated with more network compartments (β: 13.28; 95%CI: 6.21, 20.36; Fig. 3.4B). The model with exotic floral density alone, and with the addition of ecoregional variation were selected as

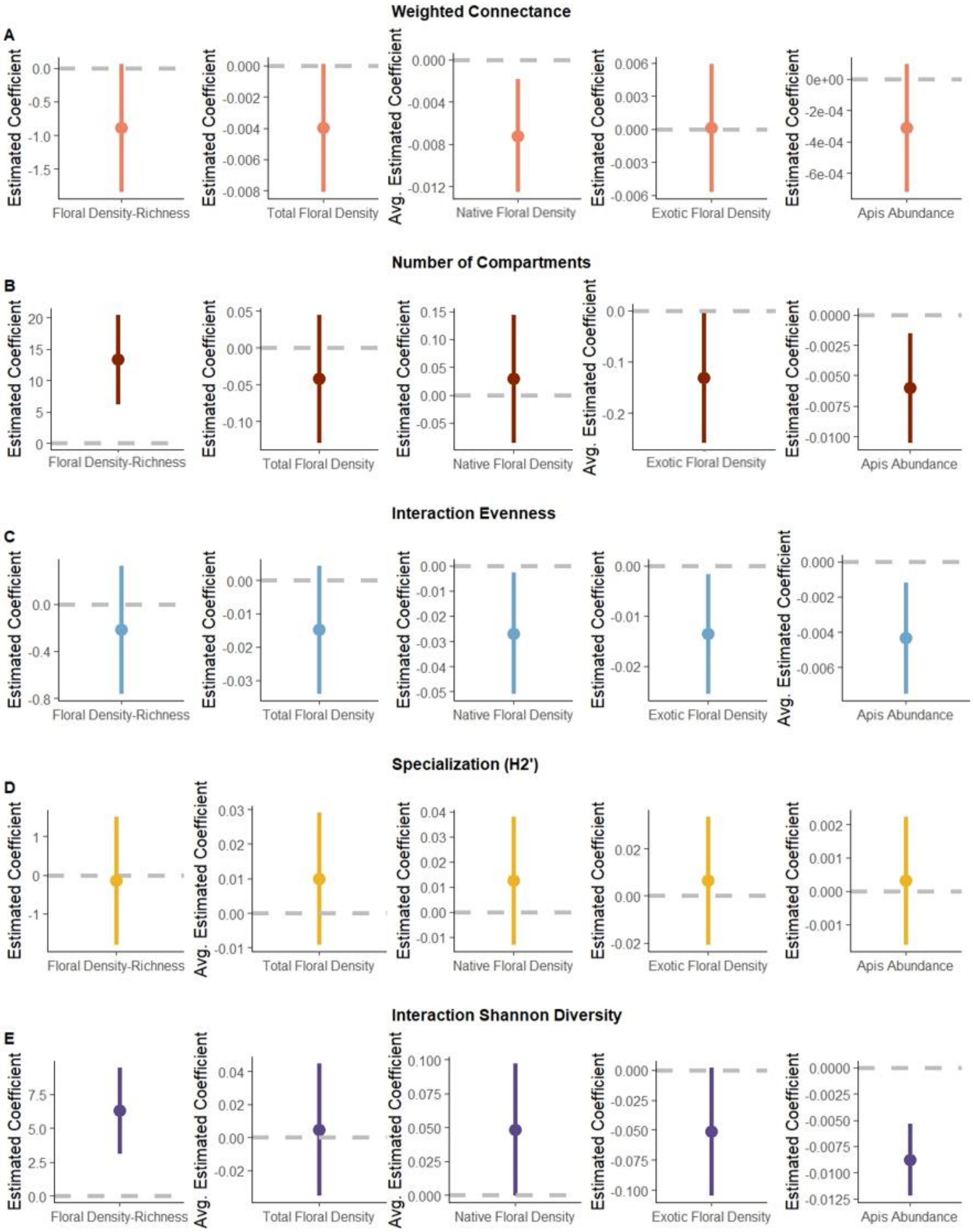

Figure 3.4. Plotted estimated coefficients and their 95% confidence intervals from linear models explaining weighted connectance, number of compartments, specialization, and interaction diversity (A, B, D, E) and generalized linear models explaining interaction evenness (C). Models are significant between the floral variable or honey bee abundance if confidence intervals do not include zero. Coefficients and confidence intervals above zero convey significant positive relationships while those below zero describe negative relationships.

best models explaining the relationship between exotic floral density and network compartments, indicating importance of the variation in honey bees and network compartments due to ecoregion (Table C6). Additionally, averaged models showed a significant negative relationship between the density of exotic floral resources at each site and the number of network compartments (β: -0.13; 95% CI: -0.26, -0.0023; Fig. 3.4B). The univariate model with honey bee abundance alone was the best model explaining the relationship between network compartments and the amount of honey bees captured at each site with the number of network compartments being significantly lower at sites with more honey bees (β: -0.0060; 95% CI: -0.010, -0.0016; Fig. 3.4B; Table C7). The total and native floral densities did not have any significant relationships with the number of network compartments (Fig. 3.4B).

Interaction Evenness

Total floral density and floral richness did not have significant relationships with network interaction evenness. The model with an ecoregional interaction was selected as best in explaining the relationship between native floral densities at each site and interaction evenness while the model with the addition of ecoregion was selected as best for explaining the relationship between exotic floral densities and interaction evenness at each site (Table C8). From these best models, both native (β: -0.027; 95% CI: -0.050, -0.0033) and exotic floral densities (β: -0.014; 95% CI: -0.025, -0.0019) had a significant negative association with the evenness of interactions (Fig. 3.4C). Three models were competitive in explaining the relationship between honey bees and interaction evenness, including the univariate with honey bee abundance alone, the model with the addition of ecoregion, and the model with an interaction between honey bee abundance and ecoregional variation (Table C9). The averaged estimated coefficients from these models showed sites with higher honey bee abundances had a lower degree of network interaction evenness (β: -0.0044; 95% CI: -0.0075, -0.0012; Fig. 3.4C).

H2´

Floral density, native and exotic floral densities, floral richness, and honey bee abundances did not have significant relationships with specialization (H2´; Fig. 3.4D).

Network Shannon Diversity

Total, native, and exotic floral densities did not have any significant relationships with the Shannon diversity of interactions at each site. The most competitive models to explain the relationship between floral richness at a site and interaction Shannon diversity as well as honey bee abundance and interaction Shannon diversity were the models that included the additions of year and ecoregion, indicating the importance of variation in both in determining these relationships (Tables C10, C11). Overall, higher floral richness at each site had a significantly higher diversity of interactions (β: 6.27; 95% CI: 3.13, 9.40) while the amount of honey bees at each site significantly lowered the diversity of network interactions (β: -0.0088; 95% CI: -0.012, -0.0055; Fig. 3.4E).

Generality

The degree of generality among bees was not significantly related to the floral richness, exotic floral density, and honey bee abundance at a site (Fig. 3.5A). The two competitive models that best explained the relationship between native floral densities and bee generality included both the model with an interaction of yearly variation and the univariate model of native floral density (Table C12). Upon averaging both models, the degree of generality was significantly higher at a site with greater native floral density (β: 0.072; 95% CI: 0.0039, 0.14; Fig. 3.5A). Similarly, two competitive models best explained the relationship of total floral densities at each site with the level of generality, including the univariate model with total floral density and the additive model with yearly variation (Table C13). Greater total floral density at a site had a significantly higher degree of generality in bees (β: 0.035; 95% CI: 0.010, 0.060; Fig. 3.5A).

Vulnerability

Only the amount of honey bees at a site influenced the degree of vulnerability of plant partners (Fig. 3.5B). The best model explaining this relationship included the additive yearly variation, indicating the importance of yearly variation in honey bee abundances in explaining vulnerability at each site (Table C14). In this model, plants at sites with higher honey bee abundances had significantly lower degree of partner diversity (β: -0.012; 95% CI: -0.018, -0.0058; Fig. 3.5B).

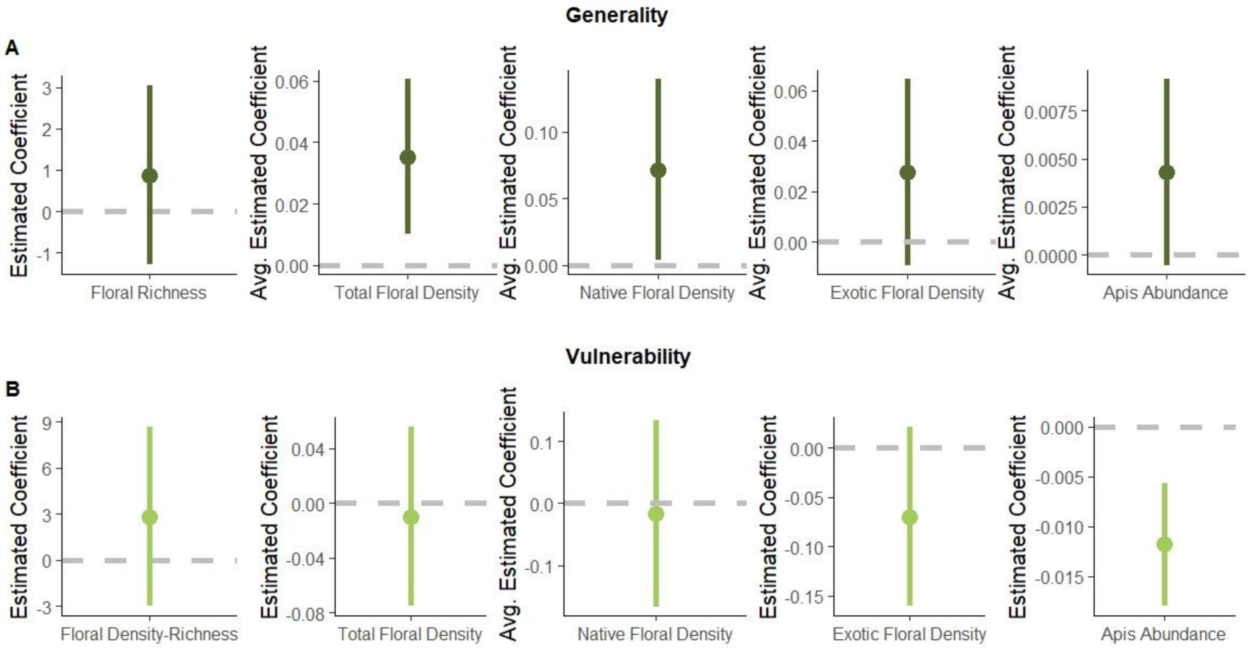

Figure 3.5. Plotted estimated coefficients and their 95% confidence intervals from linear models explaining the generality (A) and vulnerability (B) in bee-plant networks in North Dakota from 2017-2020. Models are significant between the floral variable or honey bee abundance if confidence intervals do not include zero. Coefficients and confidence intervals above zero convey significant positive relationships while those below zero describe negative relationships.

Discussion

We demonstrate how exotic species influence network properties in a region with a high prevalence of exotic species, contributing to the greater understanding of the ecological impacts of species introductions. In doing this, we also provided a first broad assessment of NGP bee-plant networks and identified factors that influence network structure and the distribution of interactions. Our results provide further evidence that the integration of generalist exotic species is complex, and therefore benefits from multiple perspectives using multiple network properties. The perspectives granted from our primary objectives first establish that across North Dakota's ecoregions, exotic plant and bee species play highly central roles in contemporary pollination networks in addition to native species. In our second objective, we also establish that the degree of nestedness and bee generality were negatively associated with several other properties including interaction evenness, vulnerability, network diversity, and the number of structural compartments in our systems, but that the strength in this relationship may be largely due to honey bees. Finally, we found varying relationships between network properties and plant community characters and honey bee abundances. We found that while honey bees increased the nestedness of networks, they lowered the number of compartments, reduced the diversity of network interactions, and decreased the number of bee partners that plants had. Similarly, the density of exotic floral resources at a site decompartmentalized networks. These relationships add to the complex understanding of network structure in novel communities and how properties relate to network stability (Traveset et al. 2013).

Our broad scale view of bee-plant networks showed that exotic plant and bee species are integrated and also central in contemporary pollination networks in the NGP. Similar to other regions with high densities of introduced honey bees, we found that honey bees acted as highly central species in all ND ecoregions (Aizen et al. 2008; M. de M. Santos 2012; Martins et al. 2013). Generalist native bumble bee species were also highly integrated in each ecoregional network as well as some sweat bee species particularly in the NWGP ecoregion. However, this similarity in the degree of connectedness cannot necessarily translate to the influence each species has on overall network structure because non-native generalists can have different effects than ecologically similar native counterparts (Giannini et al. 2015). Additionally, exotic sweet clovers and Canada thistle were highly central in broad ecoregional networks, likely due to their accessibility to bees in space and time but also in morphology (Bjerknes et al. 2007). However, we also identified native plant species with highly centralized roles in ecoregion networks which may serve as important conservation targets. Conserving these generalist native plant species may be crucial in maintaining many pollinator species interactions (Campbell et al. 2012; Hagen 2012).

Ecological network analyses have overarching goals of understanding the structure, stability, and resilience of species interactions to various perturbations (e.g. species removals and additions) but the relationships between descriptive network properties and these themes are complicated to generalize across systems (Rohr et al. 2014; Landi et al. 2018; Delmas et al. 2019). For example, studies from regions with dense honey bee introductions found that honey bees increased network nestedness, a structural property often associated with stability (Bascompte et al. 2003; M. de M. Santos 2012; Traveset et al. 2013; Giannini et al. 2015). This positive relationship between honey bees and nestedness supported by our results. Although we did not find any clear relationships between exotic generalist plants and nestedness, other studies have also found increases in nestedness due to exotic generalist plants (Traveset et al. 2013; Russo et al. 2014; Stouffer et al. 2014; Hernández-Castellano et al. 2020). Nestedness is expected to increase stability in mutualistic networks due to their natural asymmetry and because a nested structure facilitates the interaction breadths of both generalists and specialists (Bascompte et al. 2006; Stouffer et al. 2014), but the stabilizing properties of nestedness is debated to be over-saturated by the abundance and connectance of particular species (James et al. 2012; Saavedra and Stouffer 2013; Suweis et al. 2013). The degree to which nestedness can imply stability may be dependent on a trade-off of the degree and strength of interactions of a species (Rohr et al. 2014). Considering this, honey bees may promote the persistence of a network through nestedness only if they do not have few, intense interactions. In our system, honey bees can promote stability though nestedness if they interact evenly between plant species, but our other results, such as those concerning interaction diversity, agree with other findings that suggest they do not evenly distribute their interactions (Aizen et al. 2008). This highlights the conclusion that nestedness cannot necessarily convey stability alone without perspectives from other properties.

Compartmentalization also has complex implications for the stability and resilience of species interactions in mutualistic networks (Olesen et al. 2007). In our system, sites with higher exotic species presence had fewer network structural compartments. This may be due to the super-generalism of the introduced species, including honey bees and particular exotic plants with many bee visitors (Olesen et al. 2007; Albrecht et al. 2014). Although it is a distinct measure from the number of compartments, modularity in pollination networks has been connected to decreased network persistence, especially if the perturbations to the network take form in an introduced super-generalist capable of interacting across modules or compartments (Thébault and Fontaine 2010; Albrecht et al. 2014; Frost et al. 2019). Compartmentalization is more broadly reported to have stabilizing network effects because of the ability of compartments to contain effects of a perturbation within a set of interacting species, decreasing the intensity of its effects with the rest of the network (Olesen et al. 2007; Stouffer and Bascompte 2011; Tylianakis et al. 2010). Considering this in our system, diverse floral communities provided the greatest network stability by increasing the number of compartments, where a greater amount of exotic flowers and honey bees decreased network stability through fewer compartments. A higher degree of specific interactions between bee and plant species due to evolved diet restrictions naturally increase compartmentalization (Lewinsohn et al. 2006; Dupont and Olesen 2012). As such, the degree of generalism in honey bees and central exotic plant species in our system likely decreased this structural complexity, and favored a nested structure that was also evident in our study (Bascompte et al .2003).

While floral and honey bee characters in our study influenced other qualitative properties such as nestedness and compartmentalization, they minimally influenced the degree of weighted connectance. Although connectance is expected to provide a value of complexity, it is related to the degree of generalism in a network and does not consider the distribution or strength of interactions (Heleno et al. 2012). Connectance with consideration to the distribution of interactions can be interpreted as interaction evenness (Kaiser-Bunbury and Blüthgen 2015) which had a negative relationship with the amounts of native and exotic floral densities as well as honey bee abundances in our study system. These relationships may be related to the presence of dominant native and exotic plant species, as well as honey bees with central roles (Kaiser-Bunbury and Blüthgen 2015). We also saw variation in interaction diversity which may provide an enhanced perspective on the functional diversity in networks (Fontaine et al. 2006; Tylianakis et al. 2010; Blüthgen and Klein 2011). Sites with higher honey bee abundances in our study system had a lower interaction diversity, possibly due to their dominant generalist role in networks. Agreeing with another study, the higher number of floral species and flowering stems increased the interaction diversity in our study (Ebeling et al. 2011), but interaction diversity, like connectance, may be influenced by the number of species (Tylianakis et al. 2010). Still, greater interaction diversity, like biodiversity, has been associated with greater network stability and the delivery of ecosystem services such as pollination (Tylianakis et al. 2010; Ebeling et al. 2011; Devoto et al. 2012).

The implications of the changes associated with exotic plant and bee integrations into pollination networks depends of several factors, including the role of the species and whether it provides stable relationships with other species (Albrecht et al. 2014). Generalist exotic species are likely to have the greatest influence over networks but generalist introductions can facilitate interactions with other species or can rewire existing interactions by attracting pollinators away from other plants (Morales and Traveset 2009; Ferrero et al. 2013; Russo et al. 2014; Russo 2016; Goodell and Parker 2017). The key moderator of this relationship may be in the dominance of the exotic species, with species with low dominance over a network exerting less effects on other species (Hernández-Castellano et al. 2020). Regarding this in our system, honey bees and several exotic plants have central and dominant roles in North Dakota networks. Though bee generality did not seem affected, plants had fewer visiting bees when more honey bees were present at a site, potentially affecting pollination services.

Although we provide an empirical assessment of the novel pollination networks in the NGP region, understanding how exotic species change network stability requires further study. Specifically, for the NGP, future investigations involving the conspecific pollen transfer and plant reproductive success in the presence of honey bees and/or exotic plants can inform of exotic species impacts on pollination services (Larson et al. 2006). With the introduction of influential generalist species, the contemporary networks in North Dakota are largely novel. This has management implications for conserving network interactions in the NGP and in regions with dense introductions of exotic species. For example, regulating apiary density may lessen honey bee impacts on the structure and diversity of pollination networks (Cane and Tepedino 2017) as can managing the spread of dense stands of exotic floral species. It is also worth acknowledging that honey bee presence and locations in the NGP are artificially determined and subject to fluctuations associated with the economic demand for honey bee production. If honey bees are core generalists, dramatic removals in these altered systems can also have consequences for pollination services. Although exotic species' impacts greatly vary between systems, altering the structure and diversity in species interactions affects the stability of ecosystem function, making it important to investigate these relationships, especially in altered ecosystems.

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APPENDIX A

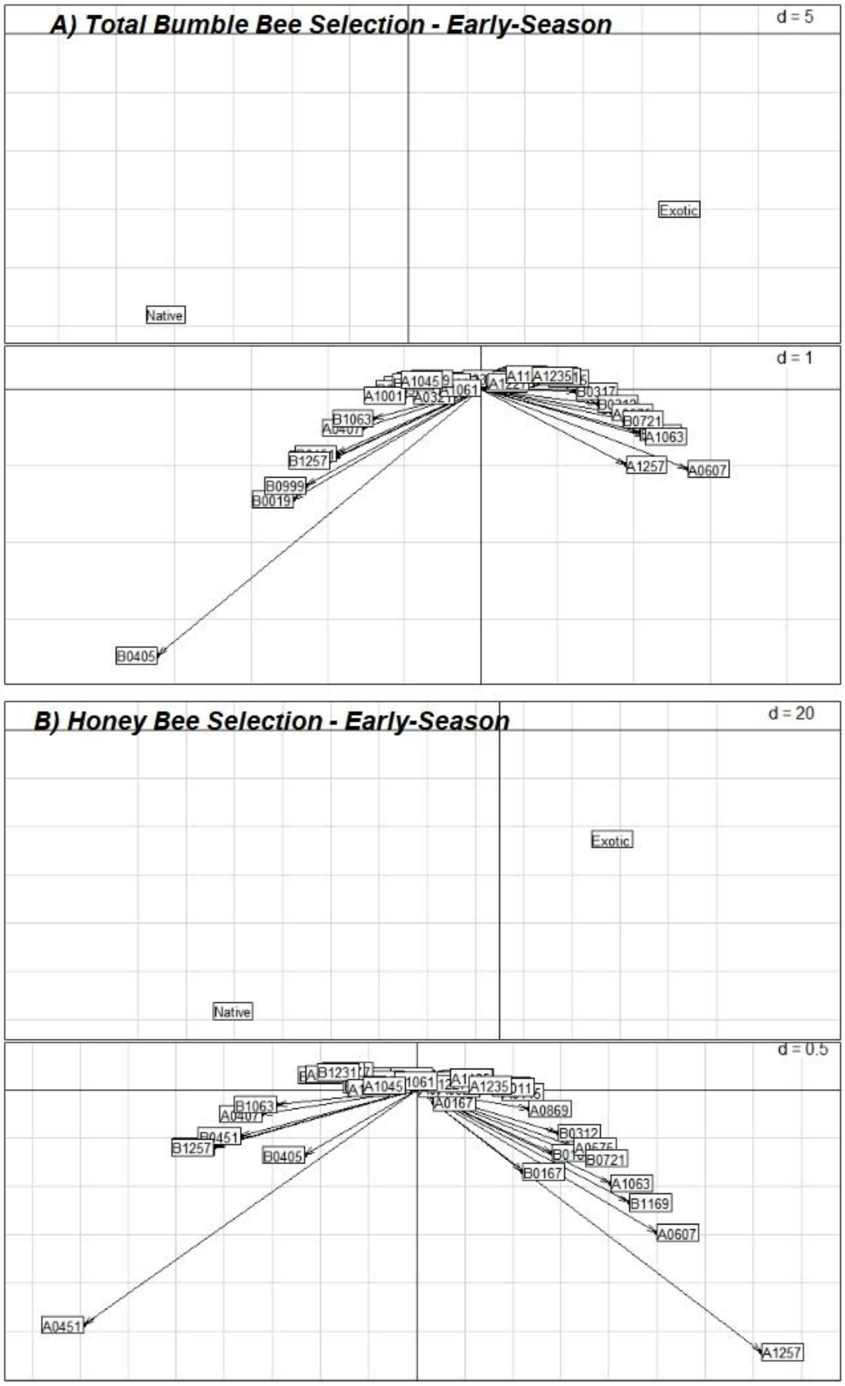


Figure A1. Eigenanalysis of selection ratio results for bumble bees (A) and honey bees (B) in 54 surveys conducted in the early seasonal periods from 2017-2020 in North Dakota. Top panels in each figure are floral resource loadings by plant species origin on the first two factorial axes and bottom panels are survey scores on the first factorial plane. (A) Axis 1 inertia: 81.85%; Axis 2 inertia: 18.15% (B) Axis 1 inertia: 77.27%; Axis 2 inertia: 22.73%.

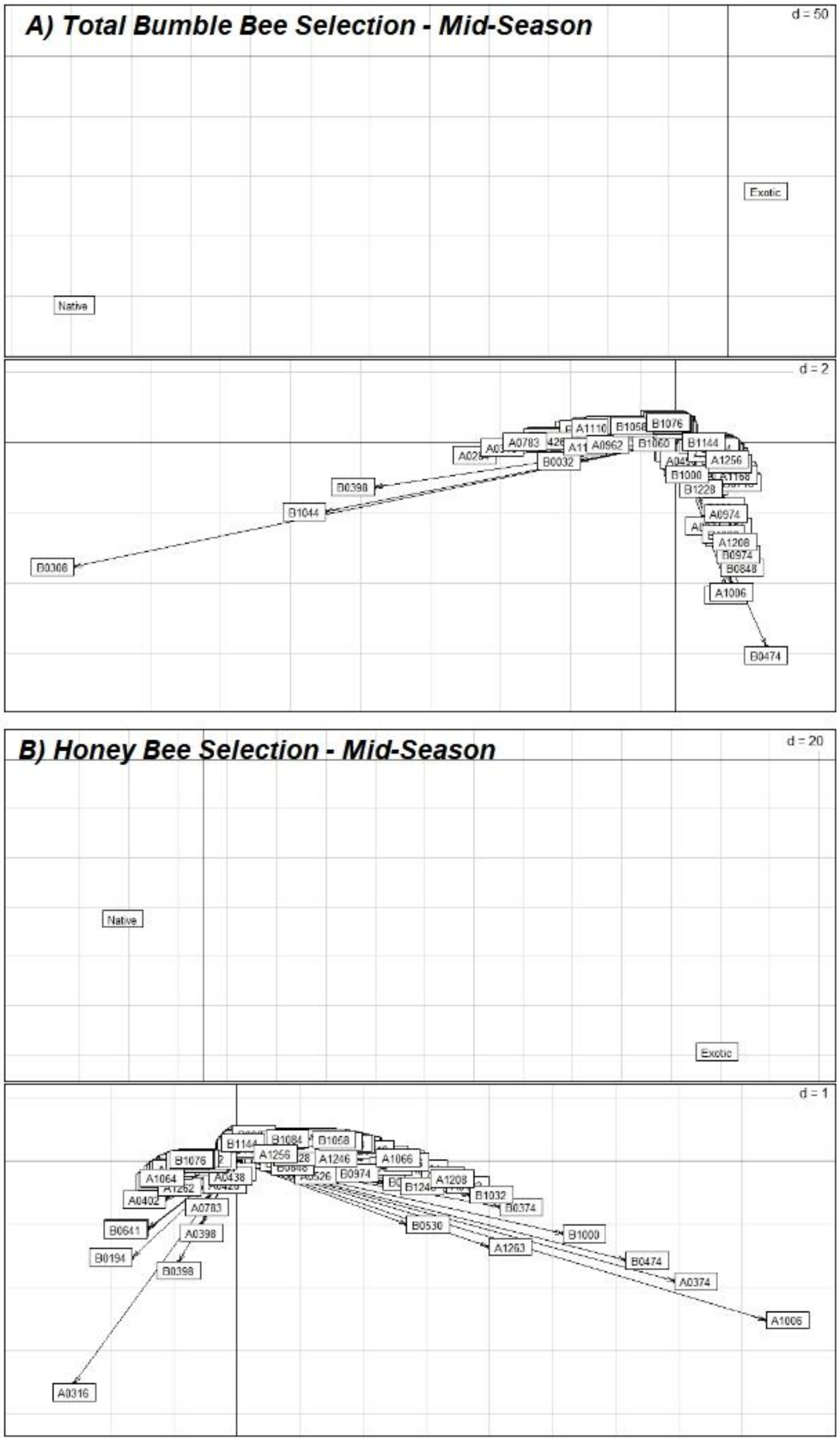


Figure A2. Eigenanalysis of selection ratio results for bumble bees (A) and honey bees (B) in 257 surveys conducted in the middle seasonal periods from 2017-2020 in North Dakota. Top panels in each figure are floral resource loadings by plant species origin on the first two factorial axes and bottom panels are survey scores on the first factorial plane. (A) Axis 1 inertia: 81.71%; Axis 2 inertia: 18.29% (B) Axis 1 inertia: 89.2%; Axis 2 inertia: 10.8%.

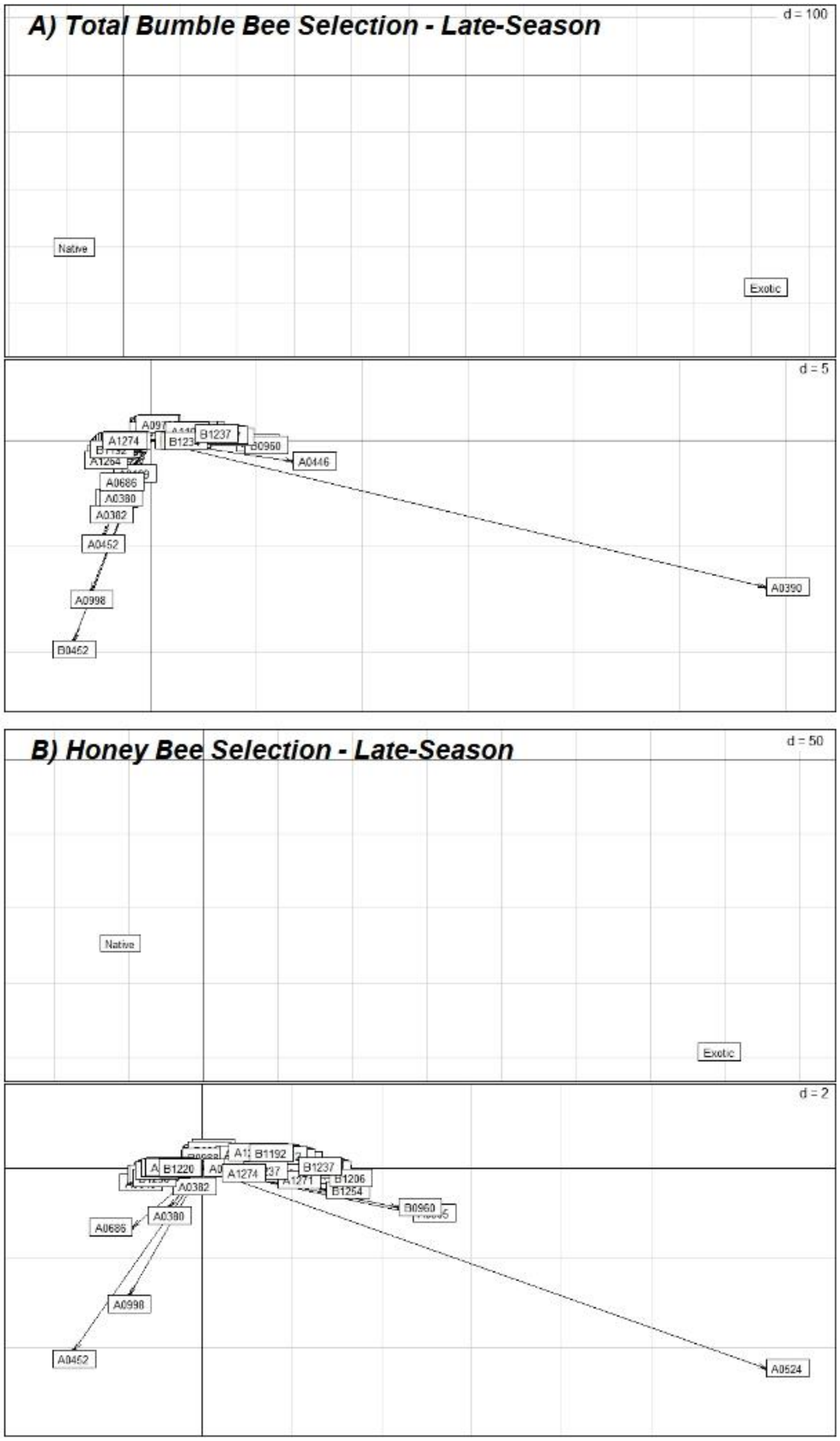


Figure A3. Eigenanalysis of selection ratio results for bumble bees (A) and honey bees (B) in 123 surveys conducted in the late seasonal periods from 2017-2020 in North Dakota. Top panels in each figure are floral resource loadings by plant species origin on the first two factorial axes and bottom panels are survey scores on the first factorial plane. (A) Axis 1 inertia: 67.93%; Axis 2 inertia: 32.07% (B) Axis 1 inertia: 77.52%; Axis 2 inertia: 22.48%.

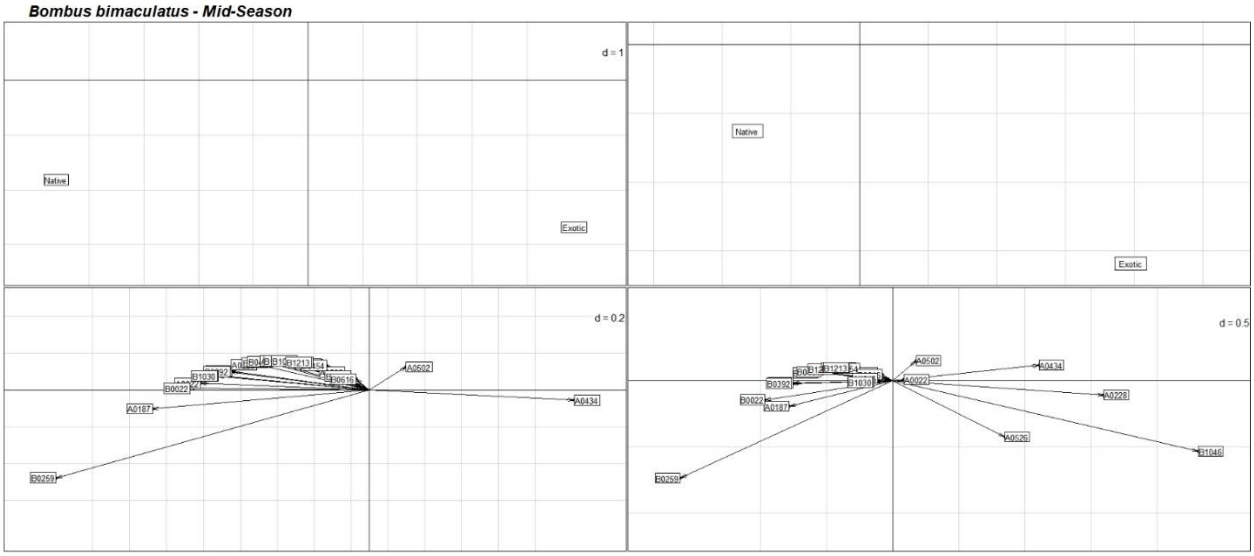
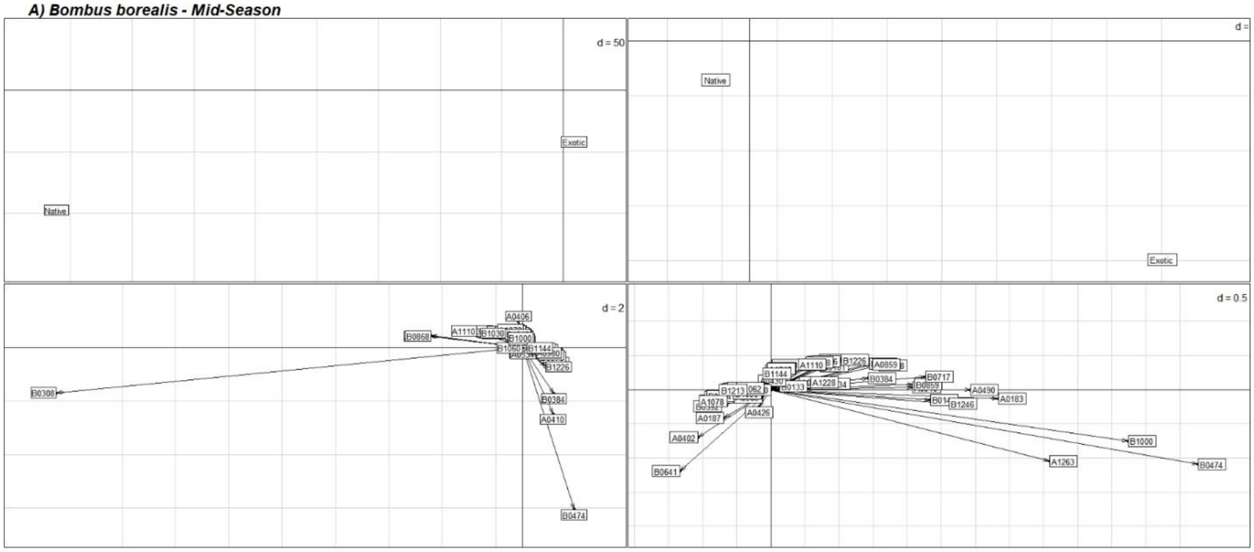


Figure A4. Eigenanalysis of selection ratio results for bumble bee Bombus bimaculatus (left; Axis 1 inertia: 96.114%; Axis 2 inertia: 3.886%) and honey bees (right; Axis 1 inertia: 91.321%; Axis 2 inertia: 8.679%) in 25 surveys conducted in the middle seasonal periods from 2017-2020 in North Dakota. Top panels in each figure are floral resource loadings by plant species origin on the first two factorial axes and bottom panels are survey scores on the first factorial plane.

A) Bombus borealis - Mid-Season



B) Bombus borealis - Late-Season

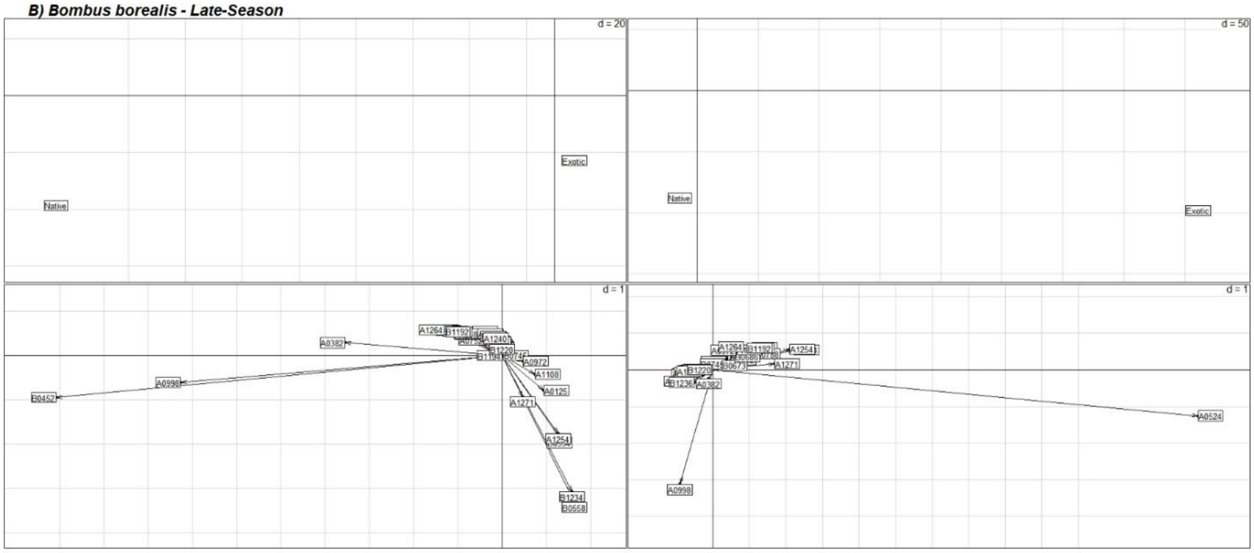


Figure A5. (A) Eigenanalysis of selection ratio results for bumble bee Bombus borealis (left; Axis 1 inertia: 87.99%; Axis 2 inertia: 12.01%) and honey bees (right; Axis 1 inertia: 93.996%; Axis 2 inertia: 6.004%) from 82 surveys in the middle season periods from 2017-2020 in North Dakota. (B) Eigenanalysis of selection ratio results for bumble bee Bombus borealis (left; Axis 1 inertia: 89.18%; Axis 2 inertia: 10.82%) and honey bees (right; Axis 1 inertia: 89.25%; Axis 2 inertia: 10.75%) from 42 surveys in late seasonal periods from 2017-2020 in North Dakota. Top panels in each figure are floral resource loadings by plant species origin on the first two factorial axes and bottom panels are survey scores on the first factorial plane.

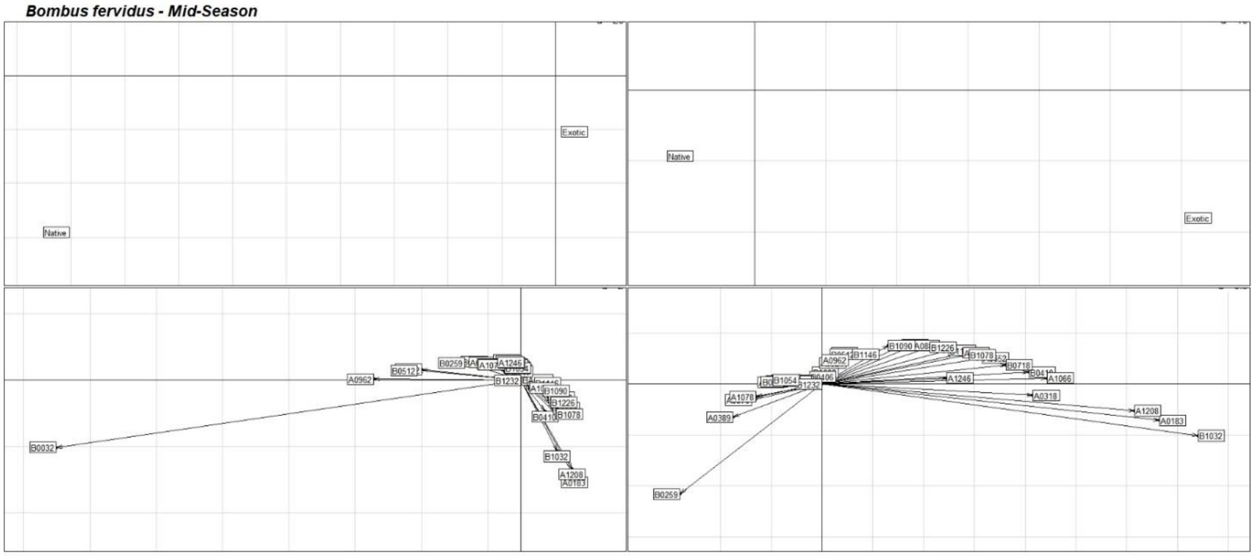


Figure A6. Eigenanalysis of selection ratio results for bumble bee Bombus fervidus (left; Axis 1 inertia: 97.15%; Axis 2 inertia: 2.85%) and honey bees (right; Axis 1 inertia: 94.882%; Axis 2 inertia: 5.118%) in 41 surveys conducted in the middle seasonal periods from 2017-2020 in North Dakota. Top panels in each figure are floral resource loadings by plant species origin on the first two factorial axes and bottom panels are survey scores on the first factorial plane.

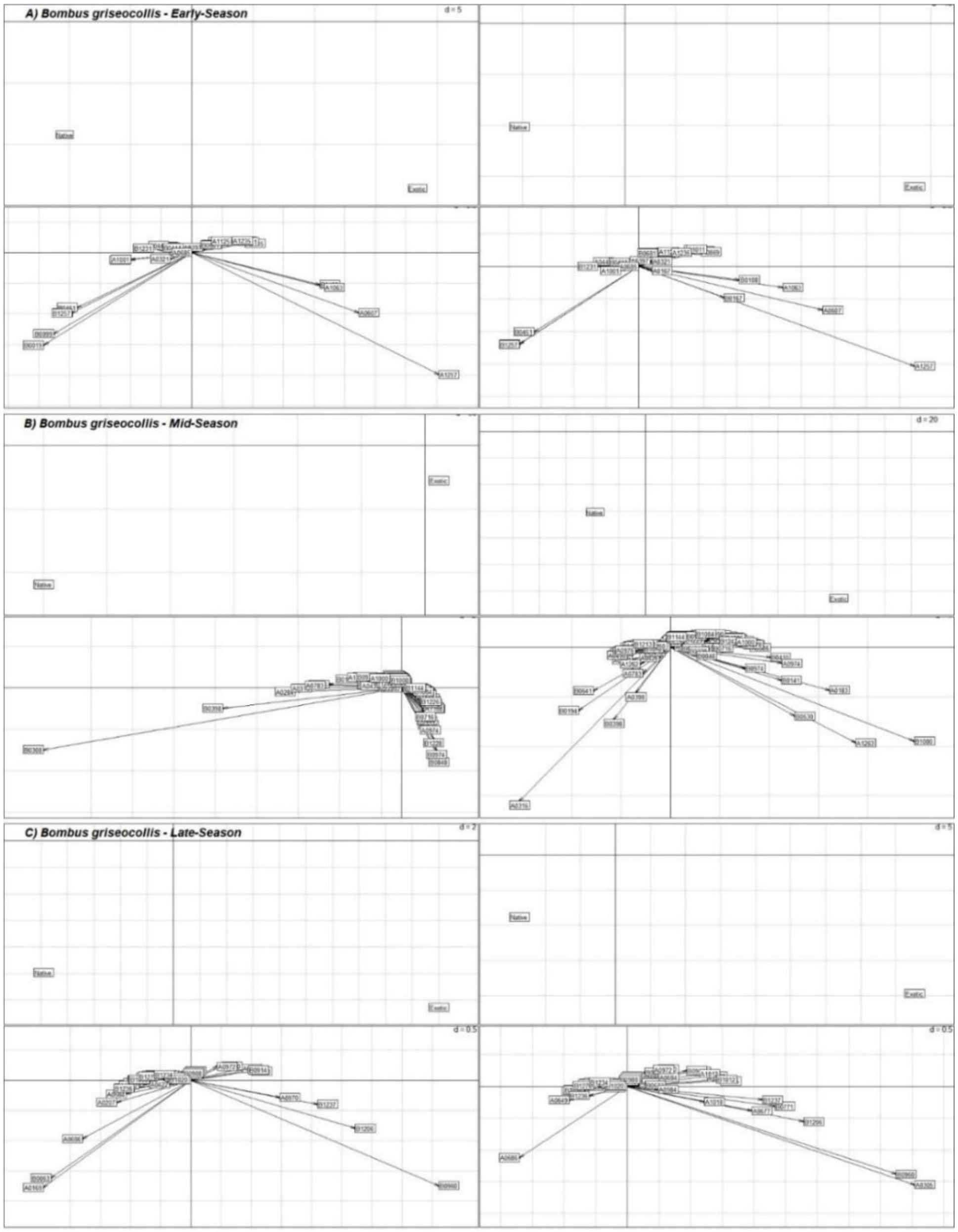


Figure A7. (A) Eigenanalysis of selection ratio results for bumble bee Bombus griseocollis (left; Axis 1 inertia: 82.9%; Axis 2 inertia: 17.1%) and honey bees (right; Axis 1 inertia: 87.07%; Axis 2 inertia: 12.93%) from 31 surveys in the early season periods from 2017-2020 in North Dakota. (B) Eigenanalysis of selection ratio results for bumble bee Bombus griseocollis (left; Axis 1 inertia: 88.08%; Axis 2 inertia: 11.92%) and honey bees (right; Axis 1 inertia: 82.13%; Axis 2 inertia: 17.87%) from 137 surveys in middle seasonal periods. (C) Eigenanalysis of selection ratio results for bumble bee Bombus griseocollis (left; Axis 1 inertia: 86.95%; Axis 2 inertia: 13.05%) and honey bees (right; Axis 1 inertia: 95.6%; Axis 2 inertia: 4.398%) from 58 surveys in late seasonal periods. Top panels in each figure are floral resource loadings by plant species origin on the first two factorial axes and bottom panels are survey scores on the first factorial plane.

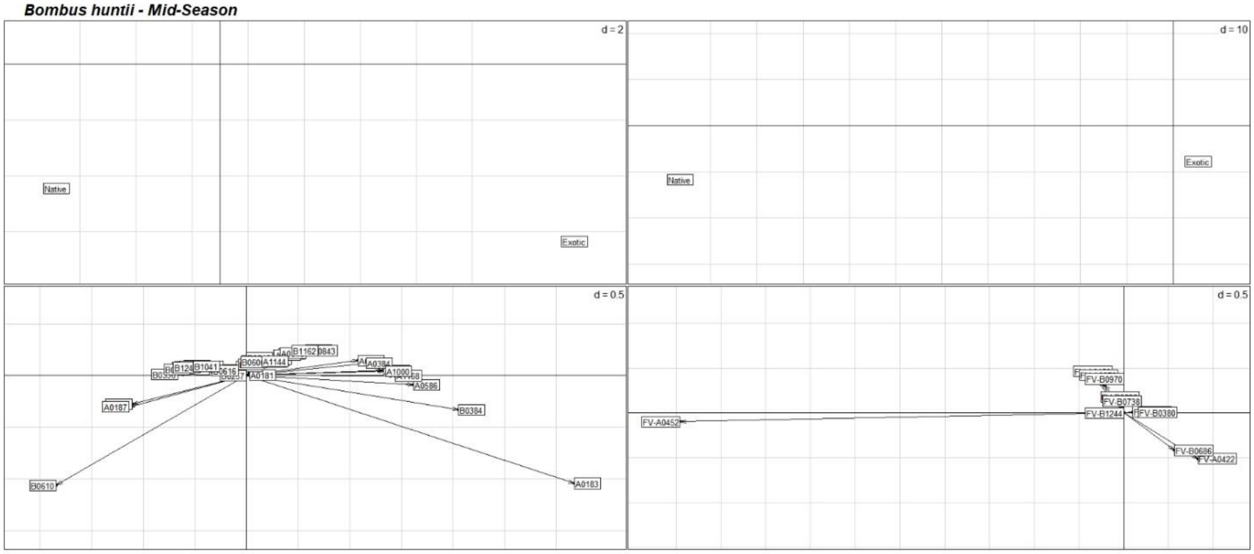
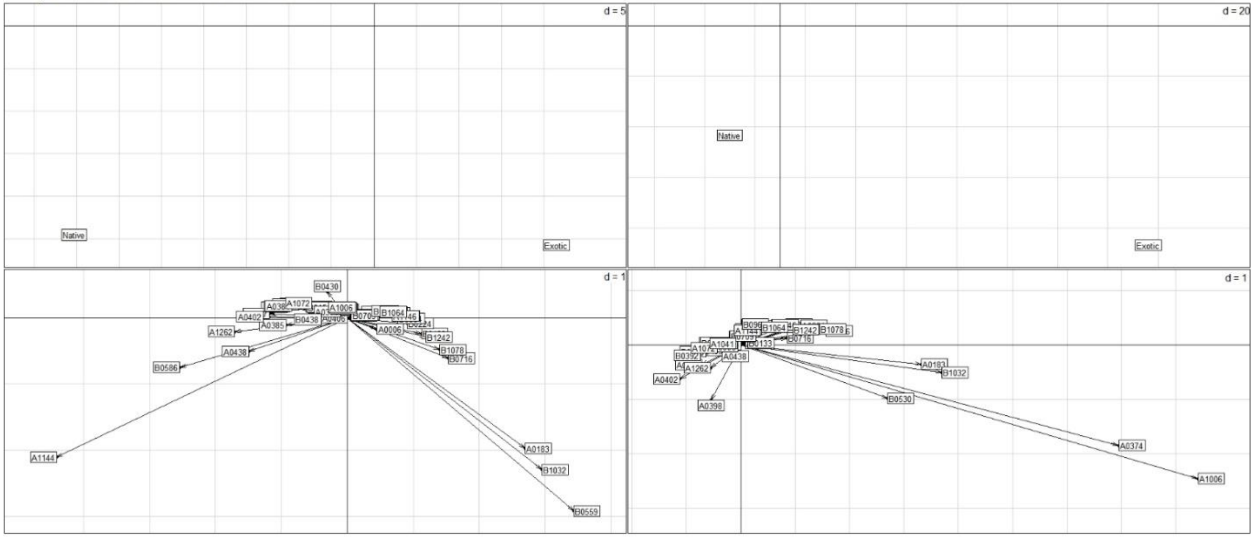


Figure A8. Eigenanalysis of selection ratio results for bumble bee Bombus huntii (left; Axis 1 inertia: 89.74%; Axis 2 inertia: 10.26%) and honey bees (right; Axis 1 inertia: 97.822%; Axis 2 inertia: 2.178%) in 46 surveys conducted in the middle seasonal periods from 2017-2020 in North Dakota. Top panels in each figure are floral resource loadings by plant species origin on the first two factorial axes and bottom panels are survey scores on the first factorial plane.

A) Bombus rufocinctus - Mid-Season



B) Bombus rufocinctus - Late-Season

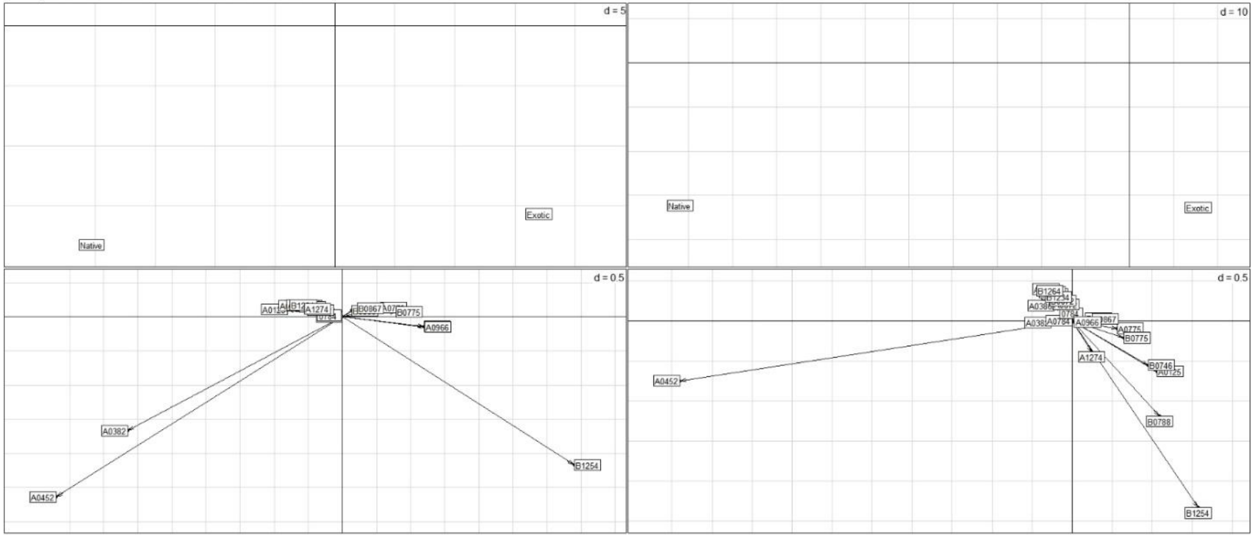
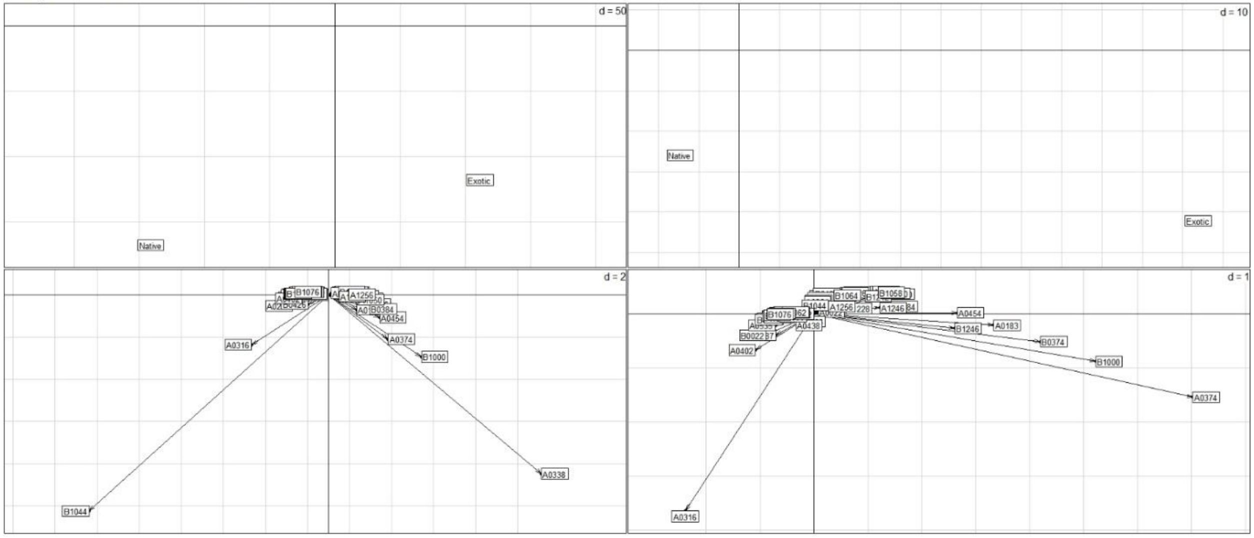


Figure A9. (A) Eigenanalysis of selection ratio results for bumble bee Bombus rufocinctus (left; Axis 1 inertia: 77.54%; Axis 2 inertia: 22.46%) and honey bees (right; Axis 1 inertia: 87.44%; Axis 2 inertia: 12.56%) from 45 surveys in the middle season periods from 2017-2020 in North Dakota. (B) Eigenanalysis of selection ratio results for bumble bee Bombus rufocinctus (left; Axis 1 inertia: 75.81%; Axis 2 inertia: 24.19%) and honey bees (right; Axis 1 inertia: 87.44%; Axis 2 inertia: 12.56%) from 22 surveys in late seasonal periods from 2017-2020 in North Dakota. Top panels in each figure are floral resource loadings by plant species origin on the first two factorial axes and bottom panels are survey scores on the first factorial plane.

A) Bombus ternarius - Mid-Season



B) Bombus ternarius - Late-Season

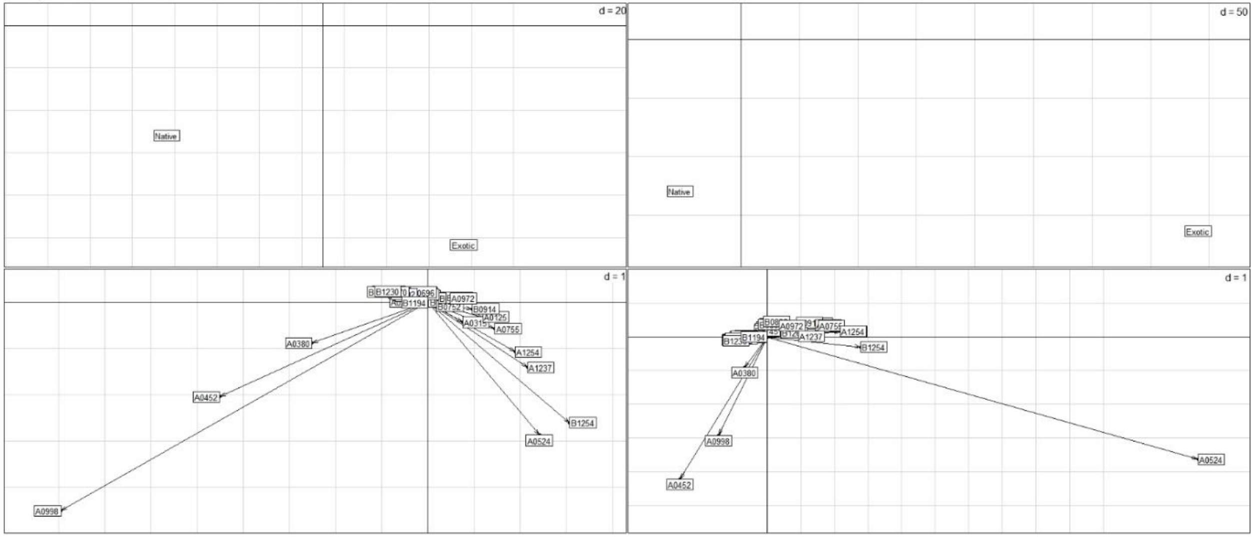


Figure A10. (A) Eigenanalysis of selection ratio results for bumble bee Bombus ternarius (left; Axis 1 inertia: 66.34%; Axis 2 inertia: 33.66%) and honey bees (right; Axis 1 inertia: 91.635%; Axis 2 inertia: 8.365%) from 74 surveys in the middle season periods from 2017-2020 in North Dakota. (B) Eigenanalysis of selection ratio results for bumble bee Bombus rufocinctus (left; Axis 1 inertia: 67.7%; Axis 2 inertia: 32.3%) and honey bees (right; Axis 1 inertia: 71.19%; Axis 2 inertia: 28.81%) from 48 surveys in late seasonal periods from 2017-2020 in North Dakota. Top panels in each figure are floral resource loadings by plant species origin on the first two factorial axes and bottom panels are survey scores on the first factorial plane.

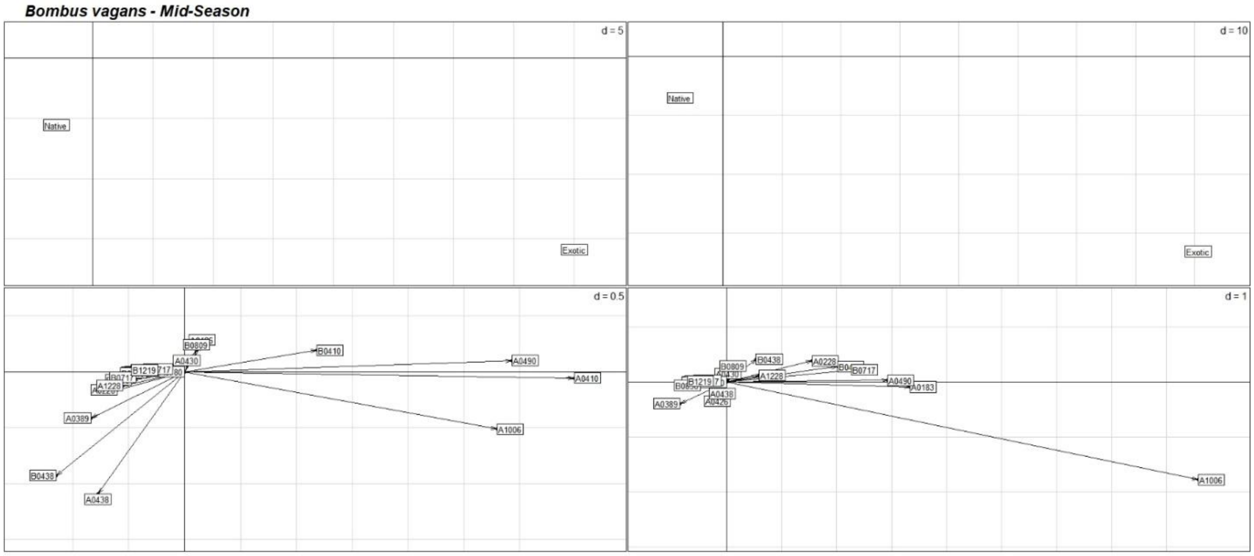


Figure A11. Eigenanalysis of selection ratio results for bumble bee Bombus vagans (left; Axis 1 inertia: 92.471%; Axis 2 inertia: 7.529%) and honey bees (right; Axis 1 inertia: 96.602%; Axis 2 inertia: 3.398%) in 24 surveys conducted in the middle seasonal periods from 2017-2020 in North Dakota. Top panels in each figure are floral resource loadings by plant species origin on the first two factorial axes and bottom panels are survey scores on the first factorial plane.

APPENDIX B

Table B1. Taxonomic revisions and reviews and other resources used for bee identification by bee genus.

Bee Genus	Identification Resources
Andrena	Laberge, W. E. (1989). A Revision of the Bees of the Genus Andrena of the Western Hemisphere. Part XIII. Subgenera Simandrena and Taeniandrena. Transactions of the American Entomological Society, 115(1), 1–56.; Laberge, W. E. (1985). A Revision of the Bees of the Genus Andrena of the Western Hemisphere. Part XI. Minor Subgenera and Subgeneric Key. American Entomological Society, 111(4), 441–567.; Laberge, W. E. (1980). A Revision of the Bees of the Genus Andrena of the Western Hemisphere. Part X. Subgenus Andrena. Transactions of the American Entomological Society, 106(4), 395–525.; LaBerge, W. E. (1969). A Revision of the Bees of the Genus Andrena of the Western Hemisphere. Part II. Plastandrena, Aporandrena, Charitandrena. American Entomological Society, 95(1), 1–47. https://doi.org/10.21900/j.inhs.v37.120; Laberge, W. E. (1973). A Revision of the Bees of the Genus Andrena of the Western Hemisphere. Part VI. Subgenus Trachandrena. Transactions of the American Entomological Society, 99(3), 235–371.; Laberge, W. E., & Ribble, D. W. (1975). A Revision of the Bees of the Genus Andrena of the Western Hemisphere. Part VII. Subgenus Euandrena. Transactions of the American Entomological Society, 101(3), 371–446.; LaBerge, W. E. (1967). A Revision of the Bees of the Genus Andrena of the Western Hemisphere. Part I. Callandrena. (Hymenoptera: Andrenidae). Bulletin of the University of Nebraska State Museum, 7, 1–318. Retrieved from https://digitalcommons.unl.edu/cgi/viewcontent.cgi?article=1090&context=museumbulletin; Donovan, B. J. 1977. A revision of North American bees of the subgenus Cnemidandrena (Hymenoptera: Andrenidae). University of California Publications in Entomology: 1-107.; Bouseman, J. K., & Laberge, W. E. (1978). A Revision of the Bees of the Genus Andrena of the Western Hemisphere. Part X. Subgenus Melandrena. Transactions of the American Entomological Society, 104(3/4), 275–389.
Calliopsis	Shinn, A. F. (1967). A Revision of the Bee Genus Calliopsis and the Biology and Ecology of C. andreniformis (Hymenoptera, Andrenidae). The University of Kansas Science Bulletin, XLVI(21), 753–936. https://doi.org/10.4324/9780203786635-2
Perdita	Timberlake, P. H. (1956). A revisional study of the bees of the genus Perdita F. Smith, with special reference to the fauna of the Pacific coast (Hymenoptera, Apoidea) Part II. University of California Publications in Entomology, 11(5), 247.; Timberlake, P. H. (1960). A revisional study of the bees of the genus Perdita F. Smith, with special reference to the fauna of the Pacific coast (Hymenoptera, Apoidea) Part IV. University of California Publications in Entomology, 17(1), 1.

Table B1. Taxonomic revisions and reviews and other resources used for bee identification by bee genus (continued).

Bee Genus	Identification Resources
Pseudopanurgus	Timberlake, P. H. (1967). New species of Pseudopanurgus from Arizona (Hymenoptera, Apoidea). American Museum Novitates. 2298.; Mitchell, T.B. (1960) Bees of the eastern United States. I. Technical bulletin (North Carolina Agricultural Experiment Station), 141, 1-538.
Anthophora	Brooks, R. W. (1983). Systematics and Bionomics of Anthophora--the Bomboides Group and Species Groups of the New World (Hymenoptera--Apoidea, Anthophoridae) (Vol. 97). Univ of California Press.; Ascher, J. S. and J. Pickering. 2020. Discover Life bee species guide and world checklist (Hymenoptera: Apoidea: Anthophila). http://www.discoverlife.org/mp/20q?guide=Apoidea_species
Apis	
Bombus	Williams, P. H., Thorp, R. W., Richardson, L. L., and Colla, S. R. 2014. Bumble Bees of North America. Princeton University Press.
Ceratina	Rehan, S. M., & Sheffield, C. S. (2011). Morphological and molecular delineation of a new species in the Ceratina dupla species-group (Hymenoptera: Apidae: Xylocopinae) of eastern North America. Zootaxa, 50(May), 35–50.
Diadasia	Adlakha, R. L. (1969). A systematic revision of the bee genus Diadasia Patton in America north of Mexico (Hymenoptera: Anthophoridae). University of California, Davis.
Eucera	Timberlake, P. H. (1969). Contribution to the systematics of North American species of Synhalonia (Hymenoptera, Apoidea).; Mitchell, T.B. (1962) Bees of the eastern United States. II. Technical bulletin (North Carolina Agricultural Experiment Station), 152, 1-557.
Melissodes	Laberge, W. E. (1956). A Revision of the Bees of the Genus Melissodes in North and Central America. Part I. (Hymenoptera, Apidae). The University of Kansas Science Bulletin, XXXVII(18).; Laberge, W. E. (1961). A Revision of the Bees of the Genus Melisscdes in North and Central America. Part III (Hymenoptera, Apidae). The University of Kansas Science Bulletin, XLIV(5).
Nomada	Cockerell, T. D. (1903). North American Bees of the Genus Nomada. Proceedings of the Academy of Natural Sciences of Philadelphia, 55, 580–614.; Mitchell, T. B. 1962. Bees of the Eastern United States, Vol. II. The North Carolina Agricultural Experiment Station, Technical Bulletin 152.; Ascher, J. S. and J. Pickering. 2020. Discover Life bee species guide and world checklist (Hymenoptera: Apoidea: Anthophila). http://www.discoverlife.org/mp/20q?guide=Apoidea_species

Table B1. Taxonomic revisions and reviews and other resources used for bee identification by bee genus (continued).

Bee Genus	Identification Resources
Svastra	Laberge, W. E. (1956). A Revision of the Bees of the Genus Melissodes in North and Central America. Part I. (Hymenoptera, Apidae). The University of Kansas Science Bulletin, XXXVII(18).
Triepeolus	Rightmyer, M. G. (2008). A review of the cleptoparasitic bee genus Triepeolus (Hymenoptera: Apidae). - Part 1. In Zootaxa.
Colletes	Stephen, W. P. (1954). A Revision of the Bee Genus Colletes in America North of Mexico. University of Kansas Science Bulletin, XXXVI(6). https://doi.org/citeulike-article-id:1327877
Hylaeus	Snelling R.R. (1966) Studies on North American Bees of the Genus Hylaeus. 1. Distribution of the Western Species of the Subgenus Prosopis with Descriptions of New Forms (Hymenoptera: Colletidae). Contributions in Science, Natural History Museum of Los Angeles County (98): 1-18.; Stephen, W. P. (1954). A Revision of the Bee Genus Colletes in America North of Mexico. University of Kansas Science Bulletin, XXXVI(6). https://doi.org/citeulike-article-id:1327877; Ascher, J. S. and J. Pickering. 2020. Discover Life bee species guide and world checklist (Hymenoptera: Apoidea: Anthophila). http://www.discoverlife.org/mp/20q?guide=Apoidea_species; Mitchell, T.B. (1960) Bees of the eastern United States. I. Technical bulletin (North Carolina Agricultural Experiment Station), 141, 1-538.
Agapostemon	Roberts, R. B. (1973). Bees of Northwestern America: Agapostemon (Hymenoptera: Halictidae).; Ascher, J. S. and J. Pickering. 2020. Discover Life bee species guide and world checklist (Hymenoptera: Apoidea: Anthophila). http://www.discoverlife.org/mp/20q?guide=Apoidea_species
Augochlorella	Coelho, B. W. T. (2004). A review of the bee genus Augochlorella (Hymenoptera: Halictidae: Augochlorini). Systematic Entomology, 29(3), 282–323. https://doi.org/10.1111/j.0307-6970.2004.00243.x
Augochloropsis	Mitchell, T.B. (1960) Bees of the eastern United States. I. Technical bulletin (North Carolina Agricultural Experiment Station), 141, 1-538.
Dufourea	Gibbs, J., Dumesh, S., & Griswold, T. L. (2014). Bees of the genera Dufourea and Dieunomia of Michigan (Hymenoptera: Apoidea: Halictidae), with a key to the Dufourea of the eastern United States. Journal of Melittology, (29), 1. https://doi.org/10.17161/jom.v0i29.4652; Dumesh, S., & Sheffield, C. S. (2012). Bees of the Genus Dufourea Lepeletier (Hymenoptera: Halictidae: Rophitinae) of Canada. Canadian Journal of Arthropod Identification, 20. https://doi.org/10.3752/cjai.2012.20

Table B1. Taxonomic revisions and reviews and other resources used for bee identification by bee genus (continued).

Bee Genus	Identification Resources
Halictus	Ascher, J. S. and J. Pickering. 2020. Discover Life bee species guide and world checklist (Hymenoptera: Apoidea: Anthophila). http://www.discoverlife.org/mp/20q?guide=Apoidea_species
Lasioglossum	Gibbs, J., Packer, L., Dumesh, S., & Danforth, B. (2013). Revision and reclassification of Lasioglossum (Evylaeus), L.(Hemihalictus) and L.(Sphecodogastra) in eastern North America (Hymenoptera: Apoidea: Halictidae). In Zootaxa (Vol. 3672). https://doi.org/10.11646/zootaxa.3672.1.1; Gibbs, J. (2011). Revision of the metallic Lasioglossum (Dialictus) of eastern North America (Hymenoptera: Halictidae: Halictini). In Zootaxa (Vol. 216). https://doi.org/10.11646/%x; Gibbs, J. (2010). Revision of the metallic species of Lasioglossum (Dialictus) in Canada (Hymenoptera, Halictidae, Halictini). In Zootaxa (Vol. 382). https://doi.org/10.11646/zootaxa.2591.1.1; McGinley, R. J. (2003). Studies of Halictinae (Apoidea: Halictidae), II: Revision of Sphecodogastra Ashmead, floral specialists of Onagraceae. Smithsonian Contributions to Zoology, 610, 1–55.; McGinley, R. J. (1986) Studies of Halictinae (Apoidea: Halictidae), I: Revision of New World Lasioglossum Curtis. Smithsonian Contributions to Zoology. 429.
Sphecodes	Mitchell, T.B. (1960) Bees of the eastern United States. I. Technical bulletin (North Carolina Agricultural Experiment Station), 141, 1-538.
Coelioxys	Baker, J. R. (1975). Taxonomy of Five Nearctic Subgenera of Coelioxys (Hymenoptera: Megachilidae). University of Kansas Science Bulletin, 50(12), 649–730.
Heriades	Michener, C. D. (1911). American Bees of the Genus Heriades. Annals of the Entomological Society of America, 31.; Mitchell, T.B. (1962) Bees of the eastern United States. II. Technical bulletin (North Carolina Agricultural Experiment Station), 152, 1-557.; Ascher, J. S. and J. Pickering. 2020. Discover Life bee species guide and world checklist (Hymenoptera: Apoidea: Anthophila). http://www.discoverlife.org/mp/20q?guide=Apoidea_species
Hoplitis	Michener, C. D. (1947). A Revision of the American Species of Hoplitis (Hymenoptera: Megachilidae) Bulletin of the American Museum of Natural History, 89(4).; Mitchell, T.B. (1962) Bees of the eastern United States. II. Technical bulletin (North Carolina Agricultural Experiment Station), 152, 1-557.; Ascher, J. S. and J. Pickering. 2020. Discover Life bee species guide and world checklist (Hymenoptera: Apoidea: Anthophila). http://www.discoverlife.org/mp/20q?guide=Apoidea_species

Table B1. Taxonomic revisions and reviews and other resources used for bee identification by bee genus (continued).

Bee Genus	Identification Resources
Megachile	Sheffield, C.S., Ratti, C., Packer, L., Griswold, T. (2011) Leafcutter and Mason Bees of the Genus Megachilidae Latreille (Hymenoptera: Megachilidae) in Canada and Alaska. Canadian Journal of Arthropod Identification No. 18, 10.3752/cjai.2011.18; Mitchell, T.B. (1962) Bees of the eastern United States. II. Technical bulletin (North Carolina Agricultural Experiment Station), 152, 1-557.
Osmia	Sandhouse, G A. (1939). The North American bees of the genus Osmia. Mem. Entomol. Soc. Wash. 1–167.; Mitchell, T.B. (1962) Bees of the eastern United States. II. Technical bulletin (North Carolina Agricultural Experiment Station), 152, 1-557.; Ascher, J. S. and J. Pickering. 2020. Discover Life bee species guide and world checklist (Hymenoptera: Apoidea: Anthophila). http://www.discoverlife.org/mp/20q?guide=Apoidea_species
Stelis	Mitchell, T.B. (1962) Bees of the eastern United States. II. Technical bulletin (North Carolina Agricultural Experiment Station), 152, 1-557.; Ascher, J. S. and J. Pickering. 2020. Discover Life bee species guide and world checklist (Hymenoptera: Apoidea: Anthophila). http://www.discoverlife.org/mp/20q?guide=Apoidea_species

Table B2. Functional trait assignments per species used in fourth-corner analysis based on diet breadth, sociality, body size, and nesting habit.

Species	Diet Breadth	Sociality	Size	Nesting
Agapostemon melliventris	Polylectic	Solitary	S	Ground
Agapostemon sericeus	Polylectic	Solitary	S	Ground
Agapostemon splendens	Polylectic	Solitary	M	Ground
Agapostemon texanus	Polylectic	Solitary	S	Ground
Agapostemon virescens	Polylectic	Communal/Semisocial	S	Ground
Andrena barbilabris	Polylectic	Solitary	S	Ground
Andrena carlini	Polylectic	Solitary	M	Ground
Andrena chromotricha	Polylectic	Solitary	S	Ground
Andrena commoda	Polylectic	Solitary	M	Ground
Andrena cressonii	Polylectic	Solitary	S	Ground
Andrena cyanophila	Polylectic	Solitary	S	Ground
Andrena forbesii	Polylectic	Solitary	S	Ground
Andrena geranii	Oligolectic	Solitary	S	Ground
Andrena haynesi	Oligolectic	Solitary	M	Ground
Andrena helianthi	Oligolectic	Solitary	M	Ground
Andrena helianthiformis	Oligolectic	Solitary	M	Ground
Andrena hirticincta	Oligolectic	Solitary	M	Ground
Andrena lupinorum	Oligolectic	Solitary	M	Ground
Andrena mariae	Oligolectic	Solitary	S	Ground
Andrena miranda	Polylectic	Solitary	S	Ground
Andrena nivalis	Oligolectic	Solitary	M	Ground
Andrena nubecula	Polylectic	Solitary	S	Ground
Andrena prunorum	Polylectic	Solitary	M	Ground
Andrena quintilis	Oligolectic	Solitary	S	Ground
Andrena runcinatae	Polylectic	Solitary	S	Ground
Andrena thaspii	Polylectic	Solitary	S	Ground
Andrena vicina	Polylectic	Solitary	M	Ground
Andrena wilkella	Polylectic	Solitary	S	Ground
Andrena ziziae	Oligolectic	Solitary	S	Ground
Anthidium clypeodentatum	Oligolectic	Solitary	M	Cavity
Anthophora affabilis	Polylectic	Solitary	L	Ground
Anthophora bomboides sodalis	Polylectic	Solitary	M	Ground

Table B2. Functional trait assignments per species used in fourth-corner analysis based on diet breadth, sociality, body size, and nesting habit (continued).

Species	Diet Breadth	Sociality	Size	Nesting
Anthophora occidentalis	Polylectic	Solitary	L	Ground
Anthophora terminalis	Polylectic	Solitary	M	Cavity
Anthophora walshii	Polylectic	Solitary	L	Ground
Apis mellifera	Polylectic	Eusocial	M	Hive
Augochlorella aurata	Polylectic	Primatively Eusocial	S	Ground
Augochloropsis sumptuosa	Polylectic	Communal/Semisocial	S	Ground
Bombus bimaculatus	Polylectic	Eusocial	M	Ground Cavity
Bombus borealis	Polylectic	Eusocial	L	Ground Cavity
Bombus centralis	Polylectic	Eusocial	L	Ground Cavity
Bombus fervidus	Polylectic	Eusocial	L	Ground Cavity
Bombus griseocollis	Polylectic	Eusocial	L	Ground Cavity
Bombus huntii	Polylectic	Eusocial	L	Ground Cavity
Bombus impatiens	Polylectic	Eusocial	L	Ground Cavity
Bombus insularis	Cleptoparasitic	Cleptoparasitic	L	Ground Cavity
Bombus nevadensis	Polylectic	Eusocial	L	Ground Cavity
Bombus pensylvanicus	Polylectic	Eusocial	L	Ground Cavity
Bombus rufocinctus	Polylectic	Eusocial	L	Ground Cavity
Bombus ternarius	Polylectic	Eusocial	L	Ground Cavity
Bombus terricola	Polylectic	Eusocial	L	Ground Cavity
Bombus vagans	Polylectic	Eusocial	M	Ground Cavity
Calliopsis andreniformis	Polylectic	Solitary	S	Ground

Table B2. Functional trait assignments per species used in fourth-corner analysis based on diet breadth, sociality, body size, and nesting habit (continued).

Species	Diet Breadth	Sociality	Size	Nesting
Ceratina mikmaqi	Polylectic	Communal/Semisocial	S	Cavity
Colletes aberrans	Polylectic	Solitary	M	Ground
Colletes americanus	Polylectic	Solitary	S	Ground
Colletes brevicornis	Polylectic	Solitary	M	Ground
Colletes hyalinus	Polylectic	Solitary	S	Ground
Colletes kincaidii	Polylectic	Solitary	S	Ground
Colletes phaceliae	Polylectic	Solitary	S	Ground
Colletes robertsonii	Polylectic	Solitary	M	Ground
Colletes simulans	Oligolectic	Solitary	M	Ground
Colletes solidaginis	Oligolectic	Solitary	S	Ground
Diadasia australis	Oligolectic	Solitary	M	Ground
Diadasia diminuta	Oligolectic	Solitary	S	Ground
Diadasia enavata	Oligolectic	Solitary	M	Ground
Dufourea marginata	Oligolectic	Solitary	S	Ground
Dufourea maura	Oligolectic	Solitary	S	Ground
Dufourea monardae	Oligolectic	Solitary	S	Ground
Eucera hamata	Polylectic	Solitary	M	Ground
Eucera kansensis	Oligolectic	Solitary	L	Ground
Eucera speciosa	Polylectic	Solitary	L	Ground
Halictus confusus	Polylectic	Eusocial	S	Ground
Halictus ligatus	Polylectic	Eusocial	S	Ground
Halictus parallelus	Polylectic	Eusocial	M	Ground
Halictus rubicundus	Polylectic	Communal/Semisocial	S	Ground
Heriades carinata	Polylectic	Solitary	S	Cavity
Heriades variolosa	Polylectic	Solitary	S	Cavity
Hesperapis carinata	Oligolectic	Solitary	S	Ground
Hoplitis pilosifrons	Polylectic	Solitary	S	Cavity
Hoplitis producta	Polylectic	Solitary	S	Cavity
Hylaeus affinis	Polylectic	Solitary	S	Cavity
Hylaeus mesillae	Polylectic	Solitary	S	Cavity
Hylaeus rudbeckiae	Polylectic	Solitary	S	Cavity
Hylaeus saniculae	Polylectic	Solitary	S	Cavity
Lasioglossum aberrans	Oligolectic	Solitary	S	Ground

Table B2. Functional trait assignments per species used in fourth-corner analysis based on diet breadth, sociality, body size, and nesting habit (continued).

Species	Diet Breadth	Sociality	Size	Nesting
Lasioglossum albipenne	Polylectic	Primatively Eusocial	S	Ground
Lasioglossum cinctipes	Polylectic	Primatively Eusocial	S	Ground
Lasioglossum coriaceum	Polylectic	Solitary	S	Ground
Lasioglossum ellisiae	Polylectic	Primatively Eusocial	S	Ground
L. heterognathum	Polylectic	Primatively Eusocial	S	Ground
L. hudsoniellum	Polylectic	Primatively Eusocial	S	Ground
Lasioglossum imitatum	Polylectic	Primatively Eusocial	S	Ground
L. incompletum	Polylectic	Primatively Eusocial	S	Ground
Lasioglossum laevissimum	Polylectic	Primatively Eusocial	S	Ground
L. leucozonium	Polylectic	Solitary	S	Ground
Lasioglossum lineatulum	Polylectic	Primatively Eusocial	S	Ground
Lasioglossum lusorium	Oligolectic	Solitary	S	Ground
L. macoupinense	Polylectic	Solitary	S	Ground
Lasioglossum novascotiae	Polylectic	Primatively Eusocial	S	Ground
Lasioglossum occidentale	Polylectic	Primatively Eusocial	S	Ground
Lasioglossum oceanicum	Polylectic	Primatively Eusocial	S	Ground
Lasioglossum packeri	Polylectic	Primatively Eusocial	S	Ground
Lasioglossum paraforbesii	Polylectic	Solitary	S	Ground
Lasioglossum pectorale	Polylectic	Solitary	S	Ground
L. perpunctatum	Polylectic	Primatively Eusocial	S	Ground
Lasioglossum pictum	Polylectic	Primatively Eusocial	S	Ground
Lasioglossum pruinosum	Polylectic	Primatively Eusocial	S	Ground
L. semicaeruleum	Polylectic	Primatively Eusocial	S	Ground
Lasioglossum sisymbrii	Polylectic	Solitary	S	Ground
L. succinipenne	Polylectic	Primatively Eusocial	S	Ground
Lasioglossum swenki	Polylectic	Solitary	S	Ground
Lasioglossum tegulare	Polylectic	Primatively Eusocial	S	Ground
Lasioglossum texanum	Oligolectic	Solitary	S	Ground
Lasioglossum trigeminum	Polylectic	Primatively Eusocial	S	Ground
Lasioglossum truncatum	Polylectic	Primatively Eusocial	S	Ground
Lasioglossum versans	Polylectic	Primatively Eusocial	S	Ground
Lasioglossum vierecki	Polylectic	Primatively Eusocial	S	Ground
Lasioglossum zephyrum	Polylectic	Primatively Eusocial	S	Ground

Table B2. Functional trait assignments per species used in fourth-corner analysis based on diet breadth, sociality, body size, and nesting habit (continued).

Species	Diet Breadth	Sociality	Size	Nesting
Lasioglossum zonulum	Polylectic	Solitary	S	Ground
Megachile brevis	Polylectic	Solitary	M	Cavity
Megachile centuncularis	Polylectic	Solitary	M	Cavity
Megachile fortis	Oligolectic	Solitary	L	Ground
Megachile frigida	Polylectic	Solitary	M	Cavity
Megachile inermis	Polylectic	Solitary	L	Cavity
Megachile latimanus	Polylectic	Solitary	M	Ground
Megachile montivaga	Polylectic	Solitary	M	Ground
Megachile pugnata	Oligolectic	Solitary	M	Cavity
Megachile relativa	Polylectic	Solitary	M	Cavity
Melissodes agilis	Oligolectic	Solitary	M	Ground
Melissodes bimaculatus	Polylectic	Solitary	M	Ground
Melissodes coloradensis	Oligolectic	Solitary	M	Ground
Melissodes communis	Polylectic	Solitary	M	Ground
Melissodes confusa	Oligolectic	Solitary	M	Ground
Melissodes coreopsis	Oligolectic	Solitary	M	Ground
Melissodes desponsa	Oligolectic	Solitary	M	Ground
Melissodes druriellus	Oligolectic	Solitary	S	Ground
Melissodes glenwoodensis	Oligolectic	Solitary	S	Ground
Melissodes illata	Oligolectic	Solitary	S	Ground
Melissodes menuachus	Oligolectic	Solitary	M	Ground
Melissodes nivea	Oligolectic	Solitary	M	Ground
Melissodes pallidisignata	Oligolectic	Solitary	M	Ground
Melissodes rivalis	Oligolectic	Solitary	M	Ground
Melissodes snowii	Oligolectic	Solitary	M	Ground
Melissodes subagilis	Oligolectic	Solitary	M	Ground
Melissodes subillata	Oligolectic	Solitary	M	Ground
Melissodes trinodis	Oligolectic	Solitary	M	Ground
Nomada articulata	Cleptoparasitic	Cleptoparasitic	S	Ground
Nomada cressonii	Cleptoparasitic	Cleptoparasitic	S	Ground
Nomada integerrima	Cleptoparasitic	Cleptoparasitic	S	Ground
Nomada modesta	Cleptoparasitic	Cleptoparasitic	S	Ground
Nomada tiftonensis	Cleptoparasitic	Cleptoparasitic	S	Ground

Table B2. Functional trait assignments per species used in fourth-corner analysis based on diet breadth, sociality, body size, and nesting habit (continued).

Species	Diet Breadth	Sociality	Size	Nesting
Nomada vincta	Cleptoparasitic	Cleptoparasitic	S	Ground
Osmia albolateralis	Polylectic	Solitary	M	Cavity
Osmia integra	Polylectic	Solitary	M	Cavity
Osmia cordata	Polylectic	Solitary	S	Cavity
Osmia distincta	Oligolectic	Solitary	S	Cavity
Osmia inurbana	Polylectic	Solitary	S	Cavity
Osmia simillima	Polylectic	Solitary	S	Cavity
Panurginus beardsleyi	Oligolectic	Solitary	S	Ground
Perdita albipennis	Oligolectic	Solitary	S	Ground
Perdita bruneri	Oligolectic	Solitary	S	Ground
Perdita ignota	Oligolectic	Solitary	S	Ground
Perdita laticincta	Oligolectic	Solitary	S	Ground
Perdita swenki	Oligolectic	Solitary	S	Ground
Pseudopanurgus albitarsis	Oligolectic	Solitary	S	Ground
P. innuptus-albitarsis	Oligolectic	Solitary	S	Ground
Pseudopanurgus labrosus	Oligolectic	Solitary	S	Ground
Pseudopanurgus parvus	Polylectic	Solitary	S	Ground
Pseudopanurgus renimaculatus	Oligolectic	Solitary	S	Ground
Sphecodes female west-small	Cleptoparasitic	Cleptoparasitic	S	Ground
Sphecodes atlantis	Cleptoparasitic	Cleptoparasitic	S	Ground
Sphecodes clematidis	Cleptoparasitic	Cleptoparasitic	S	Ground
Sphecodes coronus-form	Cleptoparasitic	Cleptoparasitic	S	Ground
Sphecodes female UNK	Cleptoparasitic	Cleptoparasitic	S	Ground
Sphecodes prosphorus	Cleptoparasitic	Cleptoparasitic	S	Ground
Sphecodes ranunculi	Cleptoparasitic	Cleptoparasitic	S	Ground
Sphecodes stygius	Cleptoparasitic	Cleptoparasitic	S	Ground
Stelis coarctatus	Cleptoparasitic	Cleptoparasitic	S	Cavity
Stelis lateralis	Cleptoparasitic	Cleptoparasitic	S	Cavity
Svastra obliqua	Oligolectic	Solitary	L	Ground
Triepeolus helianthi	Cleptoparasitic	Cleptoparasitic	M	Ground

Table B3. Plant species codes used in Figure 5 with full species name, native status, and taxonomic plant family. Plant species included are relatively common and had at least a cumulative coverage of 20% from vegetation cover surveys across North Dakota from 2017-2020. In two cases, we combined similar species that are difficult to identify apart from each other (Solidago canadensis/S. altissima and Symphyotrichum ericoides/S. falcatum). Species names and families are in accordance with those listed in the USDA PLANTS Database (USDA, NRCS. 2022. The PLANTS Database (http://plants.usda.gov). National Plant Data Team, Greensboro, NC USA.

Code	Species	Origin	Family
ACHMIL	*Achillea millefolium*	Native	Asteraceae
AMBPSI	*Ambrosia psilostachya*	Native	Asteraceae
AMOCAN	*Amorpha canescens*	Native	Fabaceae
ANECAN	*Anemone canadensis*	Native	Ranunculaceae
ANECYL	*Anemone cylindrica*	Native	Ranunculaceae
ANEPAT	*Pulsatilla patens*	Native	Ranunculaceae
ARTABS	*Artemisia absinthium*	Non-native	Asteraceae
ARTFRI	*Artemisia frigida*	Native	Asteraceae
ARTLUD	*Artemisia ludoviciana*	Native	Asteraceae
ASCSPE	*Asclepias speciosa*	Native	Apocynaceae
ASCSYR	*Asclepias syriaca*	Native	Apocynaceae
ASTAGR	*Astragalus agrestis*	Native	Fabaceae
CIRARV	*Cirsium arvense*	Non-native	Asteraceae
CIRFLO	*Cirsium flodmanii*	Native	Asteraceae
CIRUND	*Cirsium undulatum*	Native	Asteraceae
COMUMB	*Comandra umbellata*	Native	Santalaceae
CONARV	*Convolvulus arvensis*	Non-native	Convolvulaceae
DALPUR	*Dalea purpurea*	Native	Fabaceae
ECHANG	*Echinacea angustifolia*	Native	Asteraceae
EQULAE	*Equisetum laevigatum*	Native	Equisetaceae
EUPESU	*Euphorbia esula*	Non-native	Euphorbiaceae
GALBOR	*Galium boreale*	Native	Rubiaceae
GAUCOC	*Oenothera suffrutescens*	Native	Onagraceae
GLYLEP	*Glycyrrhiza lepidota*	Native	Fabaceae
HELPAU	*Helianthus pauciflorus*	Native	Asteraceae
HETVIL	*Heterotheca villosa*	Native	Asteraceae
LACTAT	*Lactuca tatarica*	Native	Asteraceae

Table B3. Plant species codes used in Figure 5 with full species name, native status, and taxonomic plant family (continued). Plant species included are relatively common and had at least a cumulative coverage of 20% from vegetation cover surveys across North Dakota from 2017-2020. In two cases, we combined similar species that are difficult to identify apart from each other (Solidago canadensis/S. altissima and Symphyotrichum ericoides/S. falcatum). Species names and families are in accordance with those listed in the USDA PLANTS Database (USDA, NRCS. 2022. The PLANTS Database (http://plants.usda.gov). National Plant Data Team, Greensboro, NC USA.

Code	Species	Origin	Family
LIAPUN	*Liatris punctata*	Native	Asteraceae
LYGJUN	*Lygodesmia juncea*	Native	Asteraceae
MEDLUP	*Medicago lupulina*	Non-native	Fabaceae
MEDSAT	*Medicago sativa*	Non-native	Fabaceae
MELALB	*Melilotus alba*	Non-native	Fabaceae
MELOFF	*Melilotus officinalis*	Non-native	Fabaceae
PEDARG	*Pediomelum argophyllum*	Native	Fabaceae
RATCOL	*Ratibida columnifera*	Native	Asteraceae
ROSARK	*Rosa arkansana*	Native	Rosaceae
SOLCAN	*Solidago canadensis/S. altissima*	Native	Asteraceae
SOLMIS	*Solidago missouriensis*	Native	Asteraceae
SOLMOL	*Solidago mollis*	Native	Asteraceae
SOLRIG	*Oligoneuron rigida*	Native	Asteraceae
SONARV	*Sonchus arvensis*	Non-native	Asteraceae
SYMERI/FAL	*Symphyotrichum ericoides/S. falcatum*	Native	Asteraceae
SYMLAN	*Symphyotrichum lanceolatum*	Native	Asteraceae
SYMOCC	*Symphoricarpos occidentalis*	Native	Caprifoliaceae
TAROFF	*Taraxacum officinale*	Non-native	Asteraceae
TRADUB	*Tragopogon dubius*	Non-native	Asteraceae

Table B4. Univariate generalized linear mixed model results explaining bee richness captured in North Dakota surveys between 2017 and 2020. Bee richness was estimated from bees captured with two bee-sampling methods.

Bee Richness	Estimate	Std.Error	Z	Pr(>|z|)
Intercept	3.0656	0.0901	34.0370	<0.0500
Forb Richness	0.00854	0.00275	3.105	0.00190*
Intercept	3.278	0.0596	55.0170	<0.0500
Kentucky bluegrass	0.001761	0.001868	0.942	0.346
Intercept	3.387	0.0575	58.936	<0.0500
Smooth brome	-0.00302	0.002316	-1.303	0.193
Intercept	3.254	0.0574	56.674	<0.0500
Other Grass	0.0044	0.00290	1.518	0.129
Intercept	3.332	0.0563	59.238	<0.0500
Litter Depth (cm)	-0.00194	0.0112	-0.173	0.863

Table B5. Univariate generalized linear mixed model results explaining forb richness captured in North Dakota surveys between 2017 and 2020. Forb richness was estimated from plant cover surveys.

Forb Richness	Estimate	Std.Error	z value	Pr(>|z|)
Intercept	3.128	0.0788	39.714	<0.0500
Other Grass	0.0145	0.00394	3.687	0.000227*
Intercept	3.501	0.0809	43.268	<0.0500
Litter Depth	-0.0343	0.0164	-2.093	0.0363*
Intercept	3.229	0.0870	37.133	<0.0500
Kentucky bluegrass	0.00500	0.00272	1.839	0.0660
Intercept	3.496	0.0841	41.570	<0.0500
Smooth brome	-0.00648	0.00339	-1.911	0.0559

APPENDIX C

Table C1. Identification resources used to identify bee species.

Bee Genus	Identification Resources
Andrena	Laberge, W. E. (1989). A Revision of the Bees of the Genus Andrena of the Western Hemisphere . Part XIII. Subgenera Simandrena and Taeniandrena. Transactions of the American Entomological Society, 115(1), 1–56.; Laberge, W. E. (1985). A Revision of the Bees of the Genus Andrena of the Western Hemisphere. Part XI. Minor Subgenera and Subgeneric Key. American Entomological Society, 111(4), 441–567.; Laberge, W. E. (1980). A Revision of the Bees of the Genus Andrena of the Western Hemisphere. Part X. Subgenus Andrena. Transactions of the American Entomological Society, 106(4), 395–525.; LaBerge, W. E. (1969). A Revision of the Bees of the Genus Andrena of the Western Hemisphere. Part II. Plastandrena, Aporandrena, Charitandrena. American Entomological Society, 95(1), 1–47. https://doi.org/10.21900/j.inhs.v37.120; Laberge, W. E. (1973). A Revision of the Bees of the Genus Andrena of the Western Hemisphere . Part VI . Subgenus Trachandrena. Transactions of the American Entomological Society, 99(3), 235–371.; Laberge, W. E., & Ribble, D. W. (1975). A Revision of the Bees of the Genus Andrena of the Western Hemisphere . Part VII. Subgenus Euandrena. Transactions of the American Entomological Society, 101(3), 371–446.; LaBerge, W. E. (1967). A Revision of the Bees of the Genus Andrena of the Western Hemisphere. Part I. Callandrena. (Hymenoptera: Andrenidae). Bulletin of the University of Nebraska State Museum, 7, 1–318. Retrieved from https://digitalcommons.unl.edu/cgi/viewcontent.cgi?article=1090&context=museumbulletin; Donovan, B. J. 1977. A revision of North American bees of the subgenus Cnemidandrena (Hymenoptera: Andrenidae). University of California Publications in Entomology: 1-107.; Bouseman, J. K., & Laberge, W. E. (1978). A Revision of the Bees of the Genus Andrena of the Western Hemisphere. Part X. Subgenus Melandrena. Transactions of the American Entomological Society, 104(3/4), 275–389.
Calliopsis	Shinn, A. F. (1967). A Revision of the Bee Genus Calliopsis and the Biology and Ecology of C. andreniformis (Hymenoptera, Andrenidae). The University of Kansas Science Bulletin, XLVI(21), 753–936. https://doi.org/10.4324/9780203786635-2

Table C1. Identification resources used to identify bee species (continued).

Bee Genus	Identification Resources
Perdita	Timberlake, P. H. (1956). A revisional study of the bees of the genus Perdita F. Smith, with special reference to the fauna of the Pacific coast (Hymenoptera, Apoidea) Part II. University of California Publications in Entomology, 11(5), 247.; Timberlake, P. H. (1960). A revisional study of the bees of the genus Perdita F. Smith, with special reference to the fauna of the Pacific coast (Hymenoptera, Apoidea) Part IV. University of California Publications in Entomology, 17(1), 1.
Pseudopanurgus	Timberlake, P. H. (1967). New species of Pseudopanurgus from Arizona (Hymenoptera, Apoidea). American Museum Novitates. 2298.; Mitchell, T.B. (1960) Bees of the eastern United States. I. Technical bulletin (North Carolina Agricultural Experiment Station), 141, 1-538.
Anthophora	Brooks, R. W. (1983). Systematics and Bionomics of Anthophora--the Bomboides Group and Species Groups of the New World (Hymenoptera--Apoidea, Anthophoridae) (Vol. 97). Univ of California Press.; Ascher, J. S. and J. Pickering. 2020. Discover Life bee species guide and world checklist (Hymenoptera: Apoidea: Anthophila). http://www.discoverlife.org/mp/20q?guide=Apoidea_species
Apis	
Bombus	Williams, P. H., Thorp, R. W., Richardson, L. L., and Colla, S. R. 2014. Bumble Bees of North America. Princeton University Press.
Ceratina	Rehan, S. M., & Sheffield, C. S. (2011). Morphological and molecular delineation of a new species in the Ceratina dupla species-group (Hymenoptera: Apidae: Xylocopinae) of eastern North America. Zootaxa, 50(May), 35–50.
Diadasia	Adlakha, R. L. (1969). A systematic revision of the bee genus Diadasia Patton in America north of Mexico (Hymenoptera: Anthophoridae). University of California, Davis.
Eucera	Timberlake, P. H. (1969). Contribution to the systematics of North American species of Synhalonia (Hymenoptera, Apoidea).; Mitchell, T.B. (1962) Bees of the eastern United States. II. Technical bulletin (North Carolina Agricultural Experiment Station), 152, 1-557.
Melissodes	Laberge, W. E. (1956). A Revision of the Bees of the Genus Melissodes in North and Central America. Part I. (Hymenoptera, Apidae). The University of Kansas Science Bulletin, XXXVII(18).; Laberge, W. E. (1961). A Revision of the Bees of the Genus Melisscdes in North and Central America. Part III (Hymenoptera, Apidae). The University of Kansas Science Bulletin, XLIV(5).

Table C1. Identification resources used to identify bee species (continued).

Bee Genus	Identification Resources
Svastra	Laberge, W. E. (1956). A Revision of the Bees of the Genus Melissodes in North and Central America. Part I. (Hymenoptera, Apidae). The University of Kansas Science Bulletin, XXXVII(18).
Colletes	Stephen, W. P. (1954). A Revision of the Bee Genus Colletes in America North of Mexico. University of Kansas Science Bulletin, XXXVI(6). https://doi.org/citeulike-article-id:1327877
Hylaeus	Snelling R.R. (1966) Studies on North American Bees of the Genus Hylaeus. 1. Distribution of the Western Species of the Subgenus Prosopis with Descriptions of New Forms (Hymenoptera: Colletidae). Contributions in Science, Natural History Museum of Los Angeles County (98): 1-18.; Stephen, W. P. (1954). A Revision of the Bee Genus Colletes in America North of Mexico. University of Kansas Science Bulletin, XXXVI(6). https://doi.org/citeulike-article-id:1327877; Ascher, J. S. and J. Pickering. 2020. Discover Life bee species guide and world checklist (Hymenoptera: Apoidea: Anthophila). http://www.discoverlife.org/mp/20q?guide=Apoidea_species; Mitchell, T.B. (1960) Bees of the eastern United States. I. Technical bulletin (North Carolina Agricultural Experiment Station), 141, 1-538.
Agapostemon	Roberts, R. B. (1973). Bees of Northwestern America: Agapostemon (Hymenoptera: Halictidae).; Ascher, J. S. and J. Pickering. 2020. Discover Life bee species guide and world checklist (Hymenoptera: Apoidea: Anthophila). http://www.discoverlife.org/mp/20q?guide=Apoidea_species
Augochlorella	Coelho, B. W. T. (2004). A review of the bee genus Augochlorella (Hymenoptera: Halictidae: Augochlorini). Systematic Entomology, 29(3), 282–323. https://doi.org/10.1111/j.0307-6970.2004.00243.x
Augochloropsis	Mitchell, T.B. (1960) Bees of the eastern United States. I. Technical bulletin (North Carolina Agricultural Experiment Station), 141, 1-538.
Dufourea	Gibbs, J., Dumesh, S., & Griswold, T. L. (2014). Bees of the genera Dufourea and Dieunomia of Michigan (Hymenoptera: Apoidea: Halictidae), with a key to the Dufourea of the eastern United States. Journal of Melittology, (29), 1. https://doi.org/10.17161/jom.v0i29.4652; Dumesh, S., & Sheffield, C. S. (2012). Bees of the Genus Dufourea Lepeletier (Hymenoptera: Halictidae: Rophitinae) of Canada. Canadian Journal of Arthropod Identification, 20. https://doi.org/10.3752/cjai.2012.20
Halictus	Ascher, J. S. and J. Pickering. 2020. Discover Life bee species guide and world checklist (Hymenoptera: Apoidea: Anthophila). http://www.discoverlife.org/mp/20q?guide=Apoidea_species

Table C1. Identification resources used to identify bee species (continued).

Bee Genus	Identification Resources
Lasioglossum	Gibbs, J., Packer, L., Dumesh, S., & Danforth, B. (2013). Revision and reclassification of Lasioglossum (Evylaeus), L. (Hemihalictus) and L.(Sphecodogastra) in eastern North America (Hymenoptera: Apoidea: Halictidae). Zootaxa (Vol. 3672).; Gibbs, J. (2011). Revision of the metallic Lasioglossum (Dialictus) of eastern North America (Hymenoptera: Halictidae: Halictini). Zootaxa (Vol. 216).; Gibbs, J. (2010). Revision of the metallic species of Lasioglossum (Dialictus) in Canada (Hymenoptera, Halictidae, Halictini). Zootaxa (Vol. 382).; McGinley, R. J. (2003). Studies of Halictinae (Apoidea: Halictidae), II: Revision of Sphecodogastra Ashmead, floral specialists of Onagraceae. Smithsonian Contributions to Zoology, 610, 1–55.; McGinley, R. J. (1986) Studies of Halictinae (Apoidea: Halictidae), I: Revision of New World Lasioglossum Curtis. Smithsonian Contributions to Zoology. 429.
Heriades	Michener, C. D. (1911). American Bees of the Genus Heriades. Annals of the Entomological Society of America, 31.; Mitchell, T.B. (1962) Bees of the eastern United States. II. Technical bulletin (North Carolina Agricultural Experiment Station), 152, 1-557.; Ascher, J. S. and J. Pickering. 2020. Discover Life bee species guide and world checklist (Hymenoptera: Apoidea: Anthophila). http://www.discoverlife.org/mp/20q?guide=Apoidea_species
Hoplitis	Michener, C. D. (1947). A Revision of the American Species of Hoplitis (Hymenoptera: Megachilidae) Bulletin of the American Museum of Natural History, 89(4).; Mitchell, T.B. (1962) Bees of the eastern United States. II. Technical bulletin (North Carolina Agricultural Experiment Station), 152, 1-557.; Ascher, J. S. and J. Pickering. 2020. Discover Life bee species guide and world checklist (Hymenoptera: Apoidea: Anthophila). http://www.discoverlife.org/mp/20q?guide=Apoidea_species
Megachile	Sheffield, C.S., Ratti, C., Packer, L., Griswold, T. (2011) Leafcutter and Mason Bees of the Genus Megachilidae Latreille (Hymenoptera: Megachilidae) in Canada and Alaska. Canadian Journal of Arthropod Identification No. 18, 10.3752/cjai.2011.18; Mitchell, T.B. (1962) Bees of the eastern United States. II. Technical bulletin (North Carolina Agricultural Experiment Station), 152, 1-557.
Osmia	Sandhouse, G A. (1939). The North American bees of the genus Osmia. Mem. Entomol. Soc. Wash. 1–167.; Mitchell, T.B. (1962) Bees of the eastern United States. II. Technical bulletin (North Carolina Agricultural Experiment Station), 152, 1-557.; Ascher, J. S. and J. Pickering. 2020. Discover Life bee species guide and world checklist (Hymenoptera: Apoidea: Anthophila). http://www.discoverlife.org/mp/20q?guide=Apoidea_species

Table C2. Candidate models used in model selection to determine the best models explaining each network property (listed in the left box) with floral density-richness, total floral density, native and exotic floral density, and honey bee abundances (“X” in candidate models to the right). Variables separated by a colon refers to an interaction.

Properties	Candidate Models
Weighted Connectance Number of Compartments Interaction Evenness H2' Network Shannon Diversity Generality Vulnerability	Property=X
	Property=X + Year
	Property=X:Year
	Property=X + Ecoregion
	Property=X:Ecoregion
	Property=X + Year + Ecoregion
	Property=X:Year:Ecoregion
	Null Model

Table C3. Plant species and their six-letter codes and origin.

Code	Species	Origin
ACHMIL	*Achillea millefolium*	Native
AGAFOE	*Agastache foeniculum*	Native
ALLSTE	*Allium stellatum*	Native
ALLTEX	*Allium textile*	Native
AMOCAN	*Amorpha canescens*	Native
AMOFRU	*Amorpha fruticosa*	Native
ANECAN	*Anemone canadensis*	Native
ANECYL	*Anemone cylindrica*	Native
ANTMIC	*Antennaria microphylla*	Native
ANTNEG	*Antennaria neglecta*	Native
ANTPAR	*Antennaria parvifolia*	Native
ASTADS	*Astragalus adsurgens*	Native
ASTAGR	*Astragalus agrestis*	Native
ASTBIS	*Astragalus bisulcatus*	Native
ASTCAN	*Astragalus canadensis*	Native
ASTCIC	*Astragalus cicer*	Non-native
ASTCRA	*Astragalus crassicarpus*	Native

Table C3. Plant species and their six-letter codes and origin (continued).

Code	Species	Origin
ASTFLE	*Astragalus flexuosus*	Native
ASTGRA	*Astragalus gracilis*	Native
ASTMIS	*Astragalus missouriensis*	Native
CALSEP	*Calystegia sepium*	Native
CALSER	*Calylophus serrulatus*	Native
CAMROT	*Campanula rotundifolia*	Native
CERARV	*Cerastium arvense*	Native
CIRARV	*Cirsium arvense*	Non-native
CIRFLO	*Cirsium flodmanii*	Native
CIRUND	*Cirsium undulatum*	Native
CIRVUL	*Cirsium vulgare*	Non-native
COMUMB	*Comandra umbellata*	Native
CONARV	*Convolvulus arvensis*	Non-native
CORVAR	*Coronilla varia*	Non-native
CRACHR	*Crataegus chrysocarpa*	Native
CYNOFF	*Cynoglossum officinale*	Non-native
DALCAN	*Dalea candida*	Native
DALPUR	*Dalea purpurea*	Native
DALVIL	*Dalea villosa*	Native
DRYARG	*Drymocallis arguta*	Native
ECHANG	*Echinacea angustifolia*	Native
ECHPUR	*Echinacea purpurea*	Native
ELACOM	*Elaeagnus commutata*	Native
ERIGLA	*Erigeron glabellus*	Native
ERIPAU	*Eriogonum pauciflorum*	Native
ERIPHI	*Erigeron philadelphicus*	Native
ERIPUM	*Erigeron pumilus*	Native
ERISTR	*Erigeron strigosus*	Native
ERYASP	*Erysimum asperum*	Native
ERYINC	*Erysimum inconspicuum*	Native
ESCVIV	*Escobaria vivipara*	Native
EUPESU	*Euphorbia esula*	Non-native
EUTGRA	*Euthamia graminifolia*	Native
GAIARI	*Gaillardia aristata*	Native

Table C3. Plant species and their six-letter codes and origin (continued).

Code	Species	Origin
GALBOR	*Galium boreale*	Native
GAUCOC	*Oenothera suffrutescens*	Native
GENAFF	*Gentiana affinis*	Native
GENPUB	*Gentiana puberulenta*	Native
GLYLEP	*Glycyrrhiza lepidota*	Native
GRISQU	*Grindelia squarrosa*	Native
GUTSAR	*Gutierrezia sarothrae*	Native
HELHEL	*Heliopsis helianthoides*	Native
HELMAX	*Helianthus maximiliani*	Native
HELNUT	*Helianthus nuttallii*	Native
HELPAU	*Helianthus pauciflorus*	Native
HELPET	*Helianthus petiolaris*	Native
HESMAT	*Hesperis matronalis*	Non-native
HETVIL	*Heterotheca villosa*	Native
HYPHIR	*Hypoxis hirsuta*	Native
LACLUD	*Lactuca ludoviciana*	Native
LACTAT	*Lactuca tatarica*	Native
LIAASP	*Liatris aspera*	Native
LIALIG	*Liatris ligulistylis*	Native
LIAPUN	*Liatris punctata*	Native
LILPHI	*Lilium philadelphicum*	Native
LINLEW	*Linum lewisii*	Native
LINSUL	*Linum sulcatum*	Native
LINVUL	*Linaria vulgaris*	Non-native
LITCAN	*Lithospermum canescens*	Native
LITINC	*Lithospermum incisum*	Native
LOTCOR	*Lotus corniculatus*	Non-native
LYGJUN	*Lygodesmia juncea*	Native
MEDLUP	*Medicago lupulina*	Non-native
MEDSAT	*Medicago sativa*	Non-native
MELALB	*Melilotus alba*	Non-native
MELOFF	*Melilotus officinalis*	Non-native
MONFIS	*Monarda fistulosa*	Native
ONOMOL	*Onosmodium molle*	Native

Table C3. Plant species and their six-letter codes and origin (continued).

Code	Species	Origin
OPUFRA	*Opuntia fragilis*	Native
OPUPOL	*Opuntia polyacantha*	Native
OXYCAM	*Oxytropis campestris*	Native
OXYLAM	*Oxytropis lambertii*	Native
OXYSPL	*Oxytropis splendens*	Native
PACCAN	*Packera cana*	Native
PACPAU	*Packera paupercula*	Native
PACPLA	*Packera plattensis*	Native
PACSPE	*Packera pseudaurea*	Native
PEDARG	*Pediomelum argophyllum*	Native
PEDESC	*Pediomelum esculentum*	Native
PENALB	*Penstemon albidus*	Native
PENGRAC	*Penstemon gracilis*	Native
PENGRAN	*Penstemon grandiflorus*	Native
PHYLUD	*Physaria ludoviciana*	Native
POTANS	*Potentilla anserina*	Native
POTHIP	*Potentilla hippiana*	Native
POTPEN	*Potentilla pensylvanica*	Native
PRUVIR	*Prunus virginiana*	Native
RATCOL	*Ratibida columnifera*	Native
ROSARK	*Rosa arkansana*	Native
Rosa spp.	*Rosa spp.*	Native
RUBIDA	*Rubus idaeus*	Native
RUDHIR	*Rudbeckia hirta*	Native
SILPER	*Silphium perfoliatum*	Native
SISMON	*Sisyrinchium montanum*	Native
SIUSUA	*Sium suave*	Native
SOLCAN	*Solidago canadensis/S. altissima*	Native
SOLGIG	*Solidago gigantea*	Native
SOLMIS	*Solidago missouriensis*	Native
SOLMOL	*Solidago mollis*	Native
SOLNEM	*Solidago nemoralis*	Native
SOLRIG	*Oligoneuron rigida*	Native
SONARV	*Sonchus arvensis*	Non-native

Table C3. Plant species and their six-letter codes and origin (continued).

Code	Species	Origin
SPHCOC	*Sphaeralcea coccinea*	Native
SPIALB	*Spiraea alba*	Native
STAPIL	*Stachys pilosa*	Native
SYMERI	*Symphyotrichum ericoides/S. falcatum*	Native
SYMLAE	*Symphyotrichum laeve*	Native
SYMLAN	*Symphyotrichum lanceolatum*	Native
SYMOCC	*Symphoricarpos occidentalis*	Native
TAROFF	*Taraxacum officinale*	Non-native
TEUCAN	*Teucrium canadense*	Native
TRIPRA	*Trifolium pratense*	Non-native
TRIREP	*Trifolium repens*	Non-native
TRADUB	*Tragopogon dubius*	Non-native
VERHAS	*Verbena hastata*	Native
VERSTR	*Verbena stricta*	Native
VICAME	*Vicia americana*	Native
VIOPED	*Viola pedata*	Native
ZIZAPT	*Zizia aptera*	Native
ZIZAUR	*Zizia aurea*	Native

Table C4. Model selection results based on Akaike's information criterion of linear models explaining weighted connectance due to native floral density observed at each study site per year in North Dakota from 2017-2020. Candidate models include native floral density with the addition of year effects and ecoregion effects as well as interactions with both year and ecoregion. Interactions are signified with a colon between variables. Models with ΔAIC ≤ 2 are considered competitive. Best model(s) are denoted with an asterisk.

Response: Weighted Connectance	K	AICc	Delta_AICc	AICcWt	Cum.Wt
~ Native Density*	3	-494.93	0.00	0.57	0.57
~ Native Floral Density + Year*	6	-493.35	1.58	0.26	0.83
~ Null Model	2	-490.18	4.75	0.05	0.88
~ Native Floral Density + Ecoregion	6	-489.73	5.19	0.04	0.92
~ Native Floral Density:Ecoregion	9	-489.63	5.3	0.04	0.96
~ Native Floral Density:Year	9	-488.06	6.87	0.02	0.98
~ Native Floral Density + Year + Ecoregion	9	-487.94	6.99	0.02	1.00
~ Native Floral Density:Year:Ecoregion	33	-465.72	29.21	0.00	1.00

Table C5. Model selection results based on Akaike's information criterion of linear models explaining the number of compartments due to floral richness observed at each study site per year in North Dakota from 2017-2020. Candidate models include floral richness with the addition of year effects and ecoregion effects as well as interactions with both year and ecoregion. Interactions are signified with a colon between variables. Models with ΔAIC ≤ 2 are considered competitive. Best model(s) are denoted with an asterisk.

Response: Number of Compartments	K	AICc	Delta_AICc	AICcWt	Cum.Wt
~ Floral Richness*	3	613.80	0.00	0.71	0.71
~ Floral Richness + Year	6	616.60	2.79	0.18	0.89
~ Floral Richness + Ecoregion	6	618.74	4.93	0.06	0.95
~ Floral Richness:Year	9	620.54	6.73	0.02	0.98
~ Floral Richness + Year + Ecoregion	9	621.77	7.96	0.01	0.99
~ Floral Richness:Ecoregion	9	622.84	9.04	0.01	1.00
~ Null Model	2	625.10	11.30	0.00	1.00
~ Floral Richness:Year:Ecoregion	33	666.93	53.13	0.00	1.00

Table C6. Model selection results based on Akaike's information criterion of linear models explaining the number of compartments due to exotic floral densities observed at each study site per year in North Dakota from 2017-2020. Candidate models include exotic floral density with the addition of year effects and ecoregion effects as well as interactions with both year and ecoregion. Interactions are signified with a colon between variables. Models with ΔAIC ≤ 2 are considered competitive. Best model(s) are denoted with an asterisk.

Response: Number of Compartments	K	AICc	Delta_AICc	AICcWt	Cum.Wt
~ Exotic Floral Density*	3	623.51	0.00	0.42	0.42
~ Exotic Floral Density + Ecoregion*	6	624.94	1.43	0.21	0.63
~ Null Model*	2	625.10	1.59	0.19	0.82
~ Exotic Floral Density + Year	6	626.19	2.68	0.11	0.93
~ Exotic Floral Density + Year + Ecoreg.	9	627.90	4.39	0.05	0.98
~ Exotic Floral Density:Ecoregion	9	630.60	7.09	0.01	0.99
~ Exotic Floral Density:Year	9	631.61	8.10	0.01	1.00
~ Exotic Floral Density:Year:Ecoregion	33	672.86	49.35	0.00	1.00

Table C7. Model selection results based on Akaike's information criterion of linear models explaining the number of compartments due to honey bee abundance (Apis) observed at each study site per year in North Dakota from 2017-2020. Candidate models include honey bee abundance with the addition of year effects and ecoregion effects as well as interactions with both year and ecoregion. Interactions are signified with a colon between variables. Models with ΔAIC ≤ 2 are considered competitive. Best model(s) are denoted with an asterisk.

Response: Number of Compartments	K	AICc	Delta_AICc	AICcWt	Cum.Wt
~ Apis Abundance*	2	628.45	0.00	0.75	0.75
~ Apis Abundance + Year	5	632.71	4.26	0.09	0.84
~ Apis Abundance + Ecoregion	5	633.03	4.58	0.08	0.91
~ Null Model	1	634.33	5.88	0.04	0.95
~ Apis Abundance:Ecoregion	8	635.1	6.66	0.03	0.98
~ Apis Abundance:Year	8	636.37	7.93	0.01	0.99
~ Apis Abundance + Year + Ecoregion	8	637.61	9.16	0.01	1.00
~ Apis Abundance:Year:Ecoregion	32	682.38	53.93	0.00	1.00

Table C8. Model selection results based on Akaike's information criterion of linear models explaining the interaction evenness due to native floral densities observed at each study site per year in North Dakota from 2017-2020. Candidate models include native floral density with the addition of year effects and ecoregion effects as well as interactions with both year and ecoregion. Interactions are signified with a colon between variables. Models with ΔAIC ≤ 2 are considered competitive. Best model(s) are denoted with an asterisk.

Response: Interaction Evenness	K	AICc	Delta_AICc	AICcWt	Cum.Wt
~ Native Floral Density:Ecoregion*	9	-350.21	0.00	0.98	0.98
~ Native Floral Density + Ecoregion	6	-341.73	8.47	0.01	1.00
~ Native Floral Density + Year + Ecoreg.	9	-336.19	14.01	0.00	1.00
~ Native Floral Density	3	-330.44	19.77	0.00	1.00
~ Null Model	2	-330.33	19.88	0.00	1.00
~ Native Floral Density + Year	6	-325.66	24.54	0.00	1.00
~ Native Floral Density:Year	9	-319.65	30.56	0.00	1.00
~ Native Floral Density:Year:Ecoregion	33	-305.67	44.53	0.00	1.00

Table C9. Model selection results based on Akaike's information criterion of linear models explaining the interaction evenness due to honey bee (Apis) abundance observed at each study site per year in North Dakota from 2017-2020. Candidate models include honey bee abundance with the addition of year effects and ecoregion effects as well as interactions with both year and ecoregion. Interactions are signified with a colon between variables. Models with ΔAIC ≤ 2 are considered competitive. Best model(s) are denoted with an asterisk.

Response: Interaction Evenness	K	AICc	Delta_AICc	AICcWt	Cum.Wt
~ Apis Abundance*	3	-401.76	0.00	0.41	0.41
~ Apis Abundance:Ecoregion*	9	-400.59	1.17	0.23	0.63
~ Apis Abundance + Ecoregion*	6	-399.85	1.91	0.16	0.79
~ Apis Abundance + Year	6	-399.04	2.72	0.1	0.89
~ Apis Abundance:Year	9	-398.41	3.35	0.08	0.97
~ Apis Abundance + Year + Ecoregion	9	-396.47	5.29	0.03	1.00
~ Apis Abundance:Year:Ecoregion	33	-360.96	40.8	0.00	1.00
~ Null Model	2	-330.33	71.43	0.00	1.00

Table C10. Model selection results based on Akaike's information criterion of linear models explaining the interaction Shannon diversity due to floral richness observed at each study site per year in North Dakota from 2017-2020. Candidate models include floral richness with the addition of year effects and ecoregion effects as well as interactions with both year and ecoregion. Interactions are signified with a colon between variables. Models with ΔAIC ≤ 2 are considered competitive. Best model(s) are denoted with an asterisk.

Response: Interaction Shannon Diversity	K	AICc	Delta_AICc	AICcWt	Cum.Wt
~ Floral Richness + Year + Ecoregion*	9	296.75	0.00	0.74	0.74
~ Floral Richness + Year	6	299.82	3.07	0.16	0.9
~ Floral Richness:Year	9	300.97	4.22	0.09	0.99
~ Floral Richness + Ecoregion	6	306.47	9.71	0.01	1.00
~ Floral Richness	3	307.98	11.23	0.00	1.00
~ Floral Richness:Ecoregion	9	311.74	14.99	0.00	1.00
~ Null Model	2	324.88	28.13	0.00	1.00
~ Floral Richness:Year:Ecoregion	33	330.37	33.62	0.00	1.00

Table C11. Model selection results based on Akaike's information criterion of linear models explaining the interaction Shannon diversity due to honey bee (Apis) abundance observed at each study site per year in North Dakota from 2017-2020. Candidate models include honey bee abundance with the addition of year effects and ecoregion effects as well as interactions with both year and ecoregion. Interactions are signified with a colon between variables. Models with ΔAIC ≤ 2 are considered competitive. Best model(s) are denoted with an asterisk.

Response: Interaction Shannon Diversity	K	AICc	Delta_AICc	AICcWt	Cum.Wt
~ Apis Abundance + Year + Ecoregion*	9	286.15	0.00	0.85	0.85
~ Apis Abundance + Year	6	289.81	3.66	0.14	0.99
~ Apis Abundance:Year	9	294.57	8.41	0.01	1.00
~ Apis Abundance + Ecoregion	6	302.64	16.49	0.00	1.00
~ Apis Abundance:Ecoregion	9	303.2	17.05	0.00	1.00
~ Apis Abundance	3	304.76	18.61	0.00	1.00
~ Apis Abundance:Year:Ecoregion	33	318.28	32.12	0.00	1.00
~ Null Model	2	324.88	38.73	0.00	1.00

Table C12. Model selection results based on Akaike's information criterion of linear models explaining the generality of bee partners due to native floral densities observed at each study site per year in North Dakota from 2017-2020. Candidate models include native floral density with the addition of year effects and ecoregion effects as well as interactions with both year and ecoregion. Interactions are signified with a colon between variables. Models with ΔAIC ≤ 2 are considered competitive. Best model(s) are denoted with an asterisk.

Response: Generality	K	AICc	Delta_AICc	AICcWt	Cum.Wt
~ Native Floral Density:Year*	9	153.92	0.00	0.39	0.39
~ Native Floral Density*	3	155.02	1.11	0.23	0.62
~ Native Floral Density + Year	6	155.94	2.03	0.14	0.76
~ Native Floral Density + Ecoregion	6	156.52	2.61	0.11	0.87
~ Native Floral Density + Year + Ecoreg.	9	157.39	3.48	0.07	0.94
~ Null Model	2	157.92	4.00	0.05	0.99
~ Native Floral Density:Ecoregion	9	162.3	8.38	0.01	1.00
~ Native Floral Density:Year:Ecoregion	33	190.09	36.18	0.00	1.00

Table C13. Model selection results based on Akaike's information criterion of linear models explaining the generality of bee partners due to total floral densities observed at each study site per year in North Dakota from 2017-2020. Candidate models include total floral density with the addition of year effects and ecoregion effects as well as interactions with both year and ecoregion. Interactions are signified with a colon between variables. Models with ΔAIC ≤ 2 are considered competitive. Best model(s) are denoted with an asterisk.

Response: Generality	K	AICc	Delta_AICc	AICcWt	Cum.Wt
~ Floral Density*	3	152.53	0.00	0.41	0.41
~ Floral Density + Year*	6	153.08	0.56	0.31	0.72
~ Floral Density:Year	9	154.84	2.31	0.13	0.85
~ Floral Density + Ecoregion	6	156.08	3.55	0.07	0.91
~ Floral Density + Year + Ecoregion	9	156.7	4.17	0.05	0.97
~ Null Model	2	157.92	5.39	0.03	0.99
~ Floral Density:Ecoregion	9	160.73	8.21	0.01	1.00
~ Floral Density:Year:Ecoregion	33	192.27	39.74	0.00	1.00

Table C14. Model selection results based on Akaike's information criterion of linear models explaining the vulnerability (generality of plant partners) due to honey bee (Apis) abundances observed at each study site per year in North Dakota from 2017-2020. Candidate models include honey bee abundance with the addition of year effects and ecoregion effects as well as interactions with both year and ecoregion. Interactions are signified with a colon between variables. Models with ΔAIC ≤ 2 are considered competitive. Best model(s) are denoted with an asterisk.

Response: Vulnerability	K	AICc	Delta_AICc	AICcWt	Cum.Wt
~ Apis Abundance + Year*	6	506.29	0.00	0.83	0.83
~ Apis Abundance + Year + Ecoregion	9	510.69	4.39	0.09	0.92
~ Apis Abundance:Year	9	511.57	5.28	0.06	0.98
~ Apis Abundance	3	514.05	7.75	0.02	1.00
~ Apis Abundance + Ecoregion	6	518.74	12.45	0.00	1.00
~ Apis Abundance:Ecoregion	9	523.93	17.63	0.00	1.00
~ Null Model	2	526.09	19.8	0.00	1.00
~ Apis Abundance:Year:Ecoregion	33	559.43	53.14	0.00	1.00