

## A Century of Change for Prairie Bees and Their Floral Associations

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**Abstract** - To examine changes in bee communities and bee–flower relations in the Prairie Pothole Region of the Northern Great Plains, we compared bee specimens and their floral associations collected in eastern North Dakota during 2010–2012 to bee specimens and their floral associations collected from the same region during 1910–1920 by pioneering naturalist Orin Alva Stevens. We also examined citizen science photographic records from 2012–2021. Using rarefaction, we found similar estimated bee species richness between the 1910s ( $135.98 \pm 9.82$ ) and the 2010s ( $125.42 \pm 8.14$ ). Bumble bees were less frequently present in collecting events in the 2010s, with one bumble bee species, *Bombus terricola*, declining from 7% presence in collecting events in the 1910s to 0.4% in the 2010s. *Hylaeus annulatus*, *Andrena miranda*, and *Hesperapis carinata* were each in the top 25% of species most frequently present in collecting events in the 1910s but were absent in the 2010s. Citizen science images documented range expansions for *Bombus impatiens* and the non-native *Anthidium manicatum*. Based on the floral association data, we recommend that pollinator plantings include (1) flowers that were formerly common in bee association records but that had decreased presence or were absent from modern collections and (2) flowers visited by possibly declining bee species, as indicated by historic flower associations for bee species that were absent or less frequently present in modern collecting events. The persistence of many bee species, including those of conservation concern, in agriculturally dominated landscapes points to the importance of restoring key floral resources to wide-ranging habitats.

### Introduction

Pollinator conservation is a priority for many land managers (Black et al. 2011, Otto et al. 2018, Wojcik et al. 2018). Actions to preserve or restore pollinator populations are often generalized because detailed information on both past and current pollinator communities is lacking (Dicks et al. 2016, Woodard et al. 2020). Comparing historic bee specimen records and their floral associations to present-day data can help land managers identify shifts in bee and flower communities and target resources likely to benefit bee species that have become rare or may be in danger of extirpation.

While comparisons with historic datasets can provide insights into bee species persistence and changes in plant–pollinator interactions (Bartomeus et al. 2013, Bommarco et al. 2012, Burkle et al. 2013, Cameron et al. 2011, CaraDonna et al. 2021, Colla et al. 2012, Dupont et al. 2011, Gardner and Spivak 2014, Grixti et al. 2009), it is difficult to determine the reliability of observed changes because of lack of information on original goals and protocols, such as collection methods (Goldstein and Scott 2015). Typically, modern collections focus on capturing species irrespective of their identity and abundance to get an unbiased estimate of the bee community. Historic collections often lack detailed explanations of methods, and some may have focused on documenting a wide range of interactions rather than quantifying frequency or abundance.

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A previous study of ours explored how land use affected the diversity and abundance of native bees (Evans et al. 2018). The specimen records from that study include bee–flower associations from 2010 to 2012 in an area in eastern North Dakota in the Prairie Pothole Region of the Northern Great Plains. Records from digitized museum specimens collected by Orin Alva Stevens in the 1910s (e.g., Stevens 1917, 1919, 1920a, 1921, 1948a, 1948b, 1949, 1950a, 1951) were available for the same area. Stevens’ work can be considered an extension of the research programs established by Robertson and Graenicher, which assembled the first detailed information on North American bee–flower associations (Graenicher 1935; Hurd 1979; Robertson 1929; Stevens 1920b, 1923). The breadth and detail of Stevens’ collections provide a unique and important dataset for understanding historic ecological interactions in the Northern Great Plains. Although details of Stevens’ collection methods are not available, specimen records provide evidence of a broad scope for both geography and habitat, likely including prairie remnants to an unknown degree, with floral association records including native plants as well as non-native plants that are typical of disturbed habitats.

Our objectives were to (1) compare historic and modern bee species richness and community composition, including functional traits, (2) compare historic and modern bee–flower associations, and (3) use this information to evaluate plants suitable for supporting bees in ecological restorations. To reduce the impact of differences in collection and curation methods and spatial extent, we compared frequencies of presence in collecting events and focused on differences for the most frequently present genera and species (Bartomeus et al. 2013). We also examined image records validated by us from web-based public biodiversity portals from 2012 to 2021 to provide additional presence information for readily identifiable taxa. We used observations of broad-scale changes in the bee community and bee–flower associations to make historically informed recommendations for pollinator plantings.

### Study Area

The Prairie Pothole Region of the Northern Great Plains once formed the largest grassland–wetland ecosystem on Earth (Gascoigne et al. 2013). Prior to European colonization, this region was composed of tallgrass prairie, riparian areas, and shrub thickets. In the 1880s, 30 to 40 years prior to Stevens’ collections, over 90% of this region was converted to agricultural land use (Severson and Sieg 2006). Between 1959 and 2007, an additional million acres in the Prairie Pothole Region were converted to cropland (Gascoigne et al. 2013). Further, beginning in the mid-20<sup>th</sup> century, agricultural land use intensified, reducing availability and quality of bee habitat through increased chemical inputs and loss of many field margins (Benton et al. 2003, Holzschuh et al. 2010, Le Féon et al. 2010).

Modern collection locations were in eastern North Dakota in an area encompassed by latitude 46°57’13” N to 47°16’48” N and longitude 98°1’49” W to 98°56’3” W in Griggs, Stutsman, and Barnes counties. All collections were within 75 km of a central point (Fig. 1). We limited historic digitized museum specimen vouchers and image records from public biodiversity portals to within 200 km of the central point of the 2010–2012 collections, which was an area encompassed by latitude 45°47’29” N to 48°28’45” N and longitude 96°31’20” W to 100°27’52” W (Fig. 1).

### Methods

The methods for our collections in 2010–2012 were designed to examine the impact of land use on the diversity of native bee communities. We collected data with the primary goal of characterizing the bee community (Evans et al. 2018). This data collection overlapped spatially

with bee–flower association records from Stevens’ collections in the 1910s, providing an opportunity to compare them. Digitized museum specimens from the 1910s were filtered to include only those collected by Stevens and matching collecting dates for the 2010–2012 specimens. All of Stevens’ specimens were noted as being collected using netting. We created two datasets from these digitized museum specimens from the 1910s. The first dataset was used to examine changes in bee community composition. We filtered specimen records to those within 100 km of the central point of the 2010–2012 collections so that both record sets covered a similar spatial extent (Fig. 1, Table 1). Since many western and eastern bee species have their range edges in eastern North Dakota (LaBerge 1986, Stevens 1920b), a larger extent would increase the likelihood of changes in presence being caused by differences in range. The second dataset was used to examine flower associations and bee species presence. We filtered records from Stevens’ bee specimen data to include records within 200 km of the central point of the 2010–2012 collections. We chose the extent of 200 km to compare a similar number of specimens with flower associations from the 1910s and 2010–2012. We also used the extent of 200 km to compare species presence between Steven’s bee specimen data and the subset of bee species documented by public biodiversity portals (Fig. 1, Table 1). While the plant communities across the 200-km extent are similar, the greater spatial extent may include some plants that are at the edge of their range and that were not covered by the smaller spatial extent of the 2010–2012 collections (Stevens 1950b). We use qualitative comparisons of common flower associations to minimize the risk of observed differences being due to changes in plant ranges. We considered unique date and location combinations to be collecting events. We examined the numbers of collecting events for the digitized specimen records from the 1910s and the 2010s as well as the numbers of species collected during collecting events to assess collecting effort (Table 1).

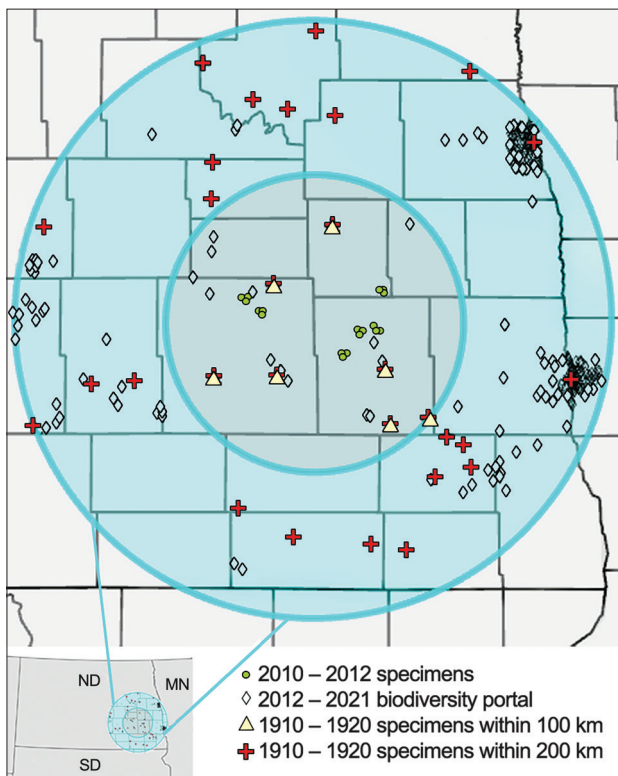


Figure 1. Locations of historic (1910s) and modern (2010–2021) bee collections in the Prairie Pothole Region of North Dakota. Historic bee specimen records were filtered into two datasets, one within 100 km of the center of 2010–2012 collecting locations (the gray-shaded circle) and another filtered to within 200 km (the blue-shaded circle). We also examined image records from web-based public monitoring efforts within 200 km of the center of 2010–2012 collecting locations. County and state lines are indicated by gray

E. Evans, J. Ascher, D. P. Cariveau, and M. Spivak

Table 1. Spatial extent, collecting events, bee species numbers, and estimated richness measures for specimen records from the 1910s and the 2010s in North Dakota. We used rarefaction to the fewest number of collections (43) to estimate the expected number of species in a pooled sample for the 1910s (100-km spatial extent) and the 2010s datasets. We used a first-order jack-knife richness estimator with 100 runs to estimate species richness for all datasets. We note which datasets we used to compare bee community composition, floral associations, and bee species richness.

Years	1910s			2010s		
	100 km	200 km	2010–2012	75 km	2012–2021	200 km
Collection, rarefied, or public biodiversity portal	Collection <sup>a</sup>	Collection <sup>c</sup>	Collection <sup>a,c</sup>	Rarefied <sup>b</sup>	Rarefied <sup>b</sup>	Public
Collecting events	43	262	237	43	43	
No. locations	12	28	97			
No. specimens	420	2742	14,954		2704	371
No. bee species	83	170	162	90.66 ± 4.48	90.36 ± 5.81	39
$\bar{x}$ species no. per collecting event ± SD	4.1 ± 4.5	4.9 ± 4.7	10.8 ± 7.0			
Min., max. species no. per collecting event	1, 18	1, 25	1, 31			
Estimated species richness ± SD	126.95 ± 8.38	206.86 ± 6.75	213.78 ± 9.39	125.42 ± 8.14		

<sup>a</sup>Used to compare bee community composition; <sup>b</sup>Used to compare bee species richness; <sup>c</sup>Used to compare floral associations

### Digitized Museum Specimens from 1910–1920

The American Museum of Natural History (AMNH) provided digitized specimen records for the bees of North Dakota, available as part of a web-based collaborative databasing project (Schuh et al. 2010). Records are shared publicly through the Discover Life global mapper ([www.discoverlife.org](http://www.discoverlife.org)) and via iDigBio as a Darwin Core Archive (Ascher 2016). We (JA) made efforts to locate, identify, and digitize all North Dakota and vicinity bee specimens in the AMNH, identifying previously unidentified material, rechecking existing identified material, and consulting with experts where appropriate to ensure proper identification (notably J. Gibbs, University of Manitoba, Winnipeg, Manitoba, Canada). Specimen documentation is near complete for material residing in the AMNH. Gaps would likely pertain to material sent on loan and not accessible to digitization or to vouchers that were otherwise dispersed (e.g., through specimen exchanges, mostly involving duplicates).

Stevens may have focused his collection efforts on groups of bees for which there was a higher likelihood of discovering undescribed species, as evidenced by his collecting primary type specimens for 18 valid species (15 from North Dakota, of which Stevens himself described 3; most others were described by Myron Harmon Swenk), three taxa now in synonymy (*Hylaeus stevensi* was thought for decades to be a native species but is now known to be synonymous with the non-native *Hylaeus leptocephalus*), and one valid subspecies (Table S1 in Supplemental File 1, available online at <https://eaglehill.us/prnaonline/suppl-files/prna-010f-evans-s1.pdf>). Eleven of the valid species and one subspecies belong to the genus *Nomada*. We do not know what portion of bees originally collected by Stevens are represented in the portion of the collection that is housed at the AMNH, but we can say that faunal coverage is very extensive, as no major bee groups are lacking among the specimen records.

### Bee Specimens from Ecological Surveys from 2010–2012

We collected bee specimens by netting, bowl traps, and trap nests. Locations for collecting bees by netting were chosen based on the presence of floral resources. Most collecting events were at locations in roadside ditches (59%), but we also collected bees within a National Wildlife Refuge (15%), Conservation Reserve Program lands (10%), ephemeral wetlands (7%), pastures (4%), shelterbelts (3%), flowering crops (1%), and riparian areas (1%). All specimens were lethally collected except for readily identifiable netted bees, primarily bumble bees, which were identified to species, counted, and released when collectors had expertise in identification (EE and J. Gardner, University of Manitoba, Winnipeg, Manitoba, Canada). Collectors repeatedly sampled by netting and bowl traps at 18 locations every 3 to 4 weeks between mid-May and mid-September in 2010, 2011, and 2012. During each sampling period, we collected bees by netting at the 18 repeatedly sampled locations twice (10 minutes between 1000 h and 1300 h DST and another 10 minutes between 1300 h and 1800 h DST). Collectors netted all flowers along transects, pausing timers to place bees in vials and attach notation on their floral associations. Transect paths varied to cover blooming plants in the area at the time of collecting. We visually scanned the area before starting the transect to determine its path based on the presence of blooming flowers. We trained to walk at a consistent pace so that we covered ~100 m<sup>2</sup> within 10 minutes. We set out bowl traps for 24 hours at the same 18 locations used for netting transects during the same sampling periods. Bowl traps consisted of sets of thirty-six 200-ml plastic cups painted either fluorescent blue, fluorescent yellow, or white (Guerra Paint and Pigment, New York, NY); filled with a 2% soap solution (Dawn dish soap, Procter & Gamble, Cincinnati, OH); and attached to bamboo stakes, elevating the traps slightly above vegetation height to ensure visibility. To increase the species richness of our bee sampling, we supplemented netting along transects and bowl traps with additional netting outside of transects and trap nests (Grundel et

al. 2011, Westphal et al. 2008). Following the same schedule as the repeatedly visited transects, during each sampling period in 2011 and 2012, we chose 12 areas outside of transect locations but within the spatial limits of the study area with an abundance of flowering resources thought to be attractive to bees based on experience observing bees in the area. We delineated a 25-m<sup>2</sup> area based on high floral density and netted all bees in that area within 5 minutes, noting floral associations. Trap nests (6 in 2010 and 2011, 18 in 2012) were set up near wooded areas near transect locations in early April and remained out until mid-September. Wooden observation nest blocks were made and housed in shelters based on the design of Hallett (2001), with sets of blocks having 150-mm-long bores that were five widths between 3.2 and 9.5 mm for a total of 90 holes per block. In addition, bundles of 50 to 60 bamboo sticks 12 to 22 cm in length were held in plastic pipe segments attached to the top of each shelter box. We removed nest blocks and stick bundles from their field locations in mid-September and stored them in an incubator at 4 °C. Over the winter, we removed cocoons and prepupae from nest blocks and stick bundles and put them in individually labeled gelatin capsules. We photographed nests before removing bees to accurately track a specimen's original position, which aided in identification. We returned the cocoons and prepupae to storage at 4 °C until spring, at which time they were kept at outdoor temperatures until emergence as adults. We lethally collected adult bees when they emerged for later identification.

We identified bees to species whenever possible using keys and comparisons with previously identified materials (Gibbs 2010, 2011; LaBerge 1969; Laverty and Harder 1988; Mitchell 1960, 1962; Rehan and Sheffield 2011; online keys at [www.discoverlife.org](http://www.discoverlife.org)). Subsets of bees (5%) were sent to taxonomic experts (J. Gardner, J. Gibbs, M. Arduser [Missouri Department of Conservation, St. Charles, MO], S. Droege [Eastern Ecological Science Center, Laurel, MD], K. Wright [Texas A&M University, College Station, TX]) for creation of a synoptic set, confirmation of identifications, and identification of groups for which there were no available keys. Species-level identification was not possible in all cases. Ten bee morphospecies were identified to species groups (1% of specimens). In some cases (13%), a likely identification was noted but with a qualifier (cf.) indicating uncertainty due to unresolved issues with the taxonomy or resemblance to a valid named species that could not be confirmed. Most of the species labeled as cf. are in the subgenus *Dialictus* of the genus *Lasioglossum*, a difficult group despite recent revisions and sharing of our materials with experts (Gibbs 2010, 2011). Specimens are held at the University of Minnesota Insect Collection and the University of Minnesota Bee Lab.

### Citizen Science Records from 2012–2021

We also examined records of bees compiled from the web-based biodiversity portals iNaturalist and Bumble Bee Watch. We limited records to those within 200 km of the center of the collection locations for the records from the 2010s (Fig. 1, Table 1). The earliest records were from 2012. We included records through the 2021 season. All species-level data were confirmed by authors (JA for iNaturalist, EE for Bumble Bee Watch). We were only able to include bee species that were identifiable by photographs. Because of this, we only used these records to provide additional presence information for readily identifiable taxa. We have no data on habitat associations or observational methods for these records.

### Floral Association

Floral association records were available for most bee specimens collected by netting in collecting efforts from the 1910s (91%) and 2010s (83%). Stevens collected plants extensively throughout North Dakota from 1909 through the 1960s, depositing vouchers in the herbarium at North Dakota State University, where his contributions form a key asset (Stevens 1950b, 1966).

The portion of Stevens' records used for this study has 77 floral associations identified to species and 11 to genus. For the modern survey, we identified 64 floral associations to species and four to tribe. We collected voucher plant specimens that are housed at the University of Minnesota Bee Lab.

### Data Analysis

To determine the sufficiency of sampling effort, we used EstimateS software (version 9.1.0) to generate sample-based rarefaction curves for bee species richness (Colwell 2013). To compare diversity, we used first-order jack-knife estimates of species richness and expected number of species based on rarefaction of all collections to the minimum sample size of 43 collecting events (unique location and date combination) and using 100 iterations of random samples from the datasets.

Although we lack detailed records of Stevens' collecting methods, the broad faunal coverage and his record of publishing exhaustive reviews of bee taxa suggest that Stevens attempted to document all bees and bee-flower interactions possible, albeit not necessarily in proportion to absolute or even relative abundance. To compare the impact of collecting methods on observed species richness, we summarized the specimen records from the 1910s and the 2010s as the mean, minimum, and maximum number of bee species found at each unique collecting event. We reduced the impact of possible variation in collecting goals by examining relative frequency of presence in a collecting event, rather than relative abundance. We view this approach as being more conservative than using measures of relative abundance in the overall collections, which are often used for comparisons with museum records (Gotelli et al. 2021). If Stevens collected many specimens of one species during a particular collecting event, as is sometimes done for taxonomic purposes, we reduced the impact of those records by only considering presence in that collecting event. We summarized the bee specimen records from the 1910s and 2010–2012 as the presence of each species in a collecting event. We then determined the frequency of each species' presence across all collecting events in each time period. We used these data to examine changes in the frequency of a species or genus in collecting events, determined as the number of collections containing a particular species or genus divided by the total number of collections in that specimen record set. We used 2-tailed Z-tests of equal proportions (following Colla and Packer 2008) to determine differences in relative frequency of presence in a collection between the 1910s and the 2010s. The null hypothesis was no change.

We examined the functional traits of bee species whose frequency increased or decreased between the 1910s and the 2010s. We included nesting habit, season of active foraging, length of active season, and pollen specialization (Table 2). These traits are important descriptors of bee ecology and can be predictors of bee community stability (De Palma et al. 2015, Grundel et al. 2010, Hopfenmüller et al. 2014, Michener 2000, Moretti et al. 2009, Weiner et al. 2014).

To compare flower use by bees between the 1910s and the 2010s, we summarized bee-flower association data as relative visitor abundance (the total abundance of bee visitors to a flower divided by the total abundance of bees in that time period) and bee-flower interaction richness (the number of bee species collected from a flower divided by the total number of bee species in that bee specimen record set). We compared the frequency of associated flowers at the genus level between bee specimen datasets from the 1910s and 2010s using 2-tailed Z-tests of equal proportions to determine whether visitor abundance and bee-flower interaction richness for plant genera differed between the 2 time periods. We compared seasonal patterns of bee-flower associations across the century, excluding plants that were associated with less than 1% of records in each time period. We grouped associated flower records into six ~20-day periods that generally coincided with the bloom time of flowers that were commonly associated with

bees. For bee species associated with flowers that had large decreases in visitor abundance from the 1910s to the 2010s, we examined the bees’ modern floral associations. We also examined the floral associations of bee species that changed in frequency of collection from the 1910s to the 2010s.

**Results**

**Bee Specimens from 1910–1920**

The digitized museum specimens from the 1910s filtered to include records within 200 km of the center of the 2010–2012 collections included 2,742 bee specimens from 262 collecting events representing 170 bee species, whereas the dataset filtered to include records within 100 km included 420 bee specimens from 43 collecting events representing 83 species (Table 1, Table S2 in Supplemental File 1). A rarefaction curve extrapolated to three times the number of collections showed that the reference sample for the dataset within 200 km accounted for 83% of the expected species number, indicating that sampling was sufficient to characterize the bee community (Fig. 2). The dataset within 100 km only accounted for 65% of the expected species number, indicating that this subset is less likely to accurately characterize the bee community.

**Bee Specimens from 2010–2012**

We collected 14,954 bee specimens from netting, bowl traps, and trap nests representing 162 species or morphospecies (several species-level taxa in addition to identifiable valid species that experts were not able to distinguish from one another) from 237 collecting events during surveys from 2010–2012 (Table 1, Table S2 in Supplemental File 1). A rarefaction curve with extrapolation to three times the number of collecting events showed that our specimens accounted for 76% of expected species numbers (Fig. 2).

**Citizen Science Records from 2012–2021**

Records from the public biodiversity portals iNaturalist and Bumble Bee Watch were compiled from the area within 200 km of the central point of the 2010–2012 collections. Species-level identifications were available for 371 photographic records representing 39 species, with bumble bees accounting for 73% of records (Table 1, Table S2 in Supplemental File 1).

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Table 2. Traits used to examine changes in bee communities in North Dakota. Nesting habit, categorized as below ground or above ground, was derived from literature. Short active-season-length bees were active 1 to 2 months, medium active-season-length bees were active 3 to 4 months, and long active-season-length bees were active 5 to 6 months. Early season bees were active before June, mid-season bees were active in June and July, late season bees were active after July. Pollen specialization was categorized as polylectic, visiting a wide variety of floral hosts, or oligolectic, visiting a limited range of floral hosts.

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Functional trait	Categories	Source of data
Nesting habit	Below ground, above ground	Hobbs 1966, 1967, 1968; Michener 2000; Sheffield et al. 2008
Active season length	Short, medium, long	Historic and modern collections
Active season	Early, mid, late	Historic and modern collections
Pollen specialization	Polylectic, oligolectic	Fowler 2016, Hurd et al. 1980, Robertson 1926, Wolf and Ascher 2008

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**Comparison of Bee Specimens from the 1910s and the 2010s**

Collections from the 2010s had a higher and more variable mean number of species per collecting event and a higher maximum number of species per collecting event compared to records from the 1910s within 100 km, the 1910s spatial extent used for all bee community comparisons (Table 1). With rarefaction to the smallest number of collections, the estimated numbers of bee species and estimated species richness measures were similar between the 1910s and the 2010s (Table 1). Nearly all bee genera were shared between specimen datasets (Table S2 in Supplemental File 1).

Observed differences in frequency of presence in collecting events from the 1910s and the 2010s suggest changes in bee community composition. At the genus level, *Bombus*, which was the most frequently present genus in collecting events in the 1910s, decreased from being present in 59% of collecting events in the 1910s to 41% of collecting events in the 2010s (Fig. 3). Within *Bombus*, *B. terricola* was less frequently present in collecting events in the 2010s, whereas *B. griseocollis* was more frequently present (Table 3). Three species of conservation concern that were frequently collected in the 1910s were found in low abundances in the public biodiversity portal records: *Bombus terricola*, *Bombus fervidus*, and *Bombus pensylvanicus* (Table S2 in Supplemental File 1). *Bombus ashtoni* (sometimes considered to be conspecific with *Bombus bohemicus* of the Old World), another species of conservation concern that was present in the 1910s, was absent from biodiversity portal records and recent specimen records, including ours. *Lasioglossum*, the most frequently present genus in collecting events in the 2010s, increased in frequency of presence in collecting events from 34% in the 1910s to 86% in the 2010s (Fig. 3). Five of the nine species that increased in frequency of presence in collecting events in the 2010s belonged to the genus *Lasioglossum* (Table 3).

There were 25 species or species groups that were present in the specimen records from the 1910s but absent from the specimen records from the 2010s (Table S2 in Supplemental File 1). Species absent from the specimen records from the 2010s included species that are typically rare in collections, such as the oil-collecting bee *Macropis nuda*; floral specialists, including *Colletes robertsonii*, and *Andrena nigrae*; and cleptoparasites, including *Coelioxys rufitarsis* and *Holcopasites pulchellus* (Gibbs et al. 2017, Hofmann et al. 2019, Sheffield et al. 2013). There

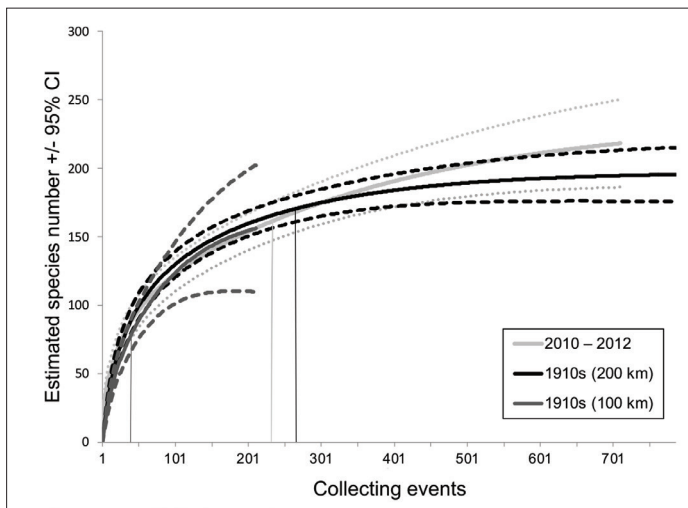


Figure 2. Sample-based rarefaction curve of bee species richness of specimens collected from 1910–1920 and 2010–2012 in North Dakota. Data points beyond the vertical lines (reference samples) were extrapolated to 3 times the reference sample using non-parametric methods (Colwell et al. 2013). Solid curved lines represent the estimated species number, and dashed lines represent the 95% confidence interval. The reference samples accounted for 76% (2010–2012), 83% (1910s within 200 km of the center of 2010–2012 collecting sites), and 65% (1910s within 100 km of the center of 2010–2012 collecting sites) of the extrapolated species richness.

were also several species that were absent from specimen records from the 2010s but were common in the records from the 1910s (in the top 25% most frequently collected species), including *Hylaeus annulatus*, *Andrena miranda*, and *Hesperapis carinata* (Table S2 in Supplemental File 1). The 101 species or species groups absent in the 1910s but present in the 2010s included five non-native species (*H. leptocephalus*, *Andrena wilkella*, *Lasioglossum leucozonium*, *Lasioglossum zonulum*, and *Megachile rotundata*) as well as 33 species represented by only one specimen (including *Hylaeus nelumbonis*, *Andrena macoupinense*, *Dufourea maura*, *Agapostemon femoratus*, *Lasioglossum texanum*, *Pseudopanurgus dakotensis*, *Svastra obliqua*, and *Eucera hamata*) (Table S2 in Supplemental File 1).

Of the nine bee species that decreased in relative frequency of presence in collecting events from the 1910s to the 2010s, all were active late in the season, two nested above ground, and six were pollen specialists. Of the six pollen specialists, four were only active late in the season and specialized on flowers in the family Asteraceae. Of the nine bee species that increased in relative frequency of presence in collecting events from the 1910s to the 2010s, one was a pollen specialist, all nested in the ground, and all had a long season of activity.

**Comparison of Flower Visitation Between the 1910s and 2010s**

We compared visitor abundance and bee–flower interaction richness for 31 plant genera from which bees were collected during both the 1910s and the 2010s (Table 4, Table S3 in Supplemental File 1). Specimen records from the 1910s included only those within the spatial extent of 200 km. The plant genera *Centaurea*, *Ratibida*, *Zizia*, and *Amorpha* each had an over 80% decrease in visitor abundance and bee–flower interaction richness in the 2010s compared to the 1910s. For example, there were 261 bees belonging to 35 species collected from *Zizia* in

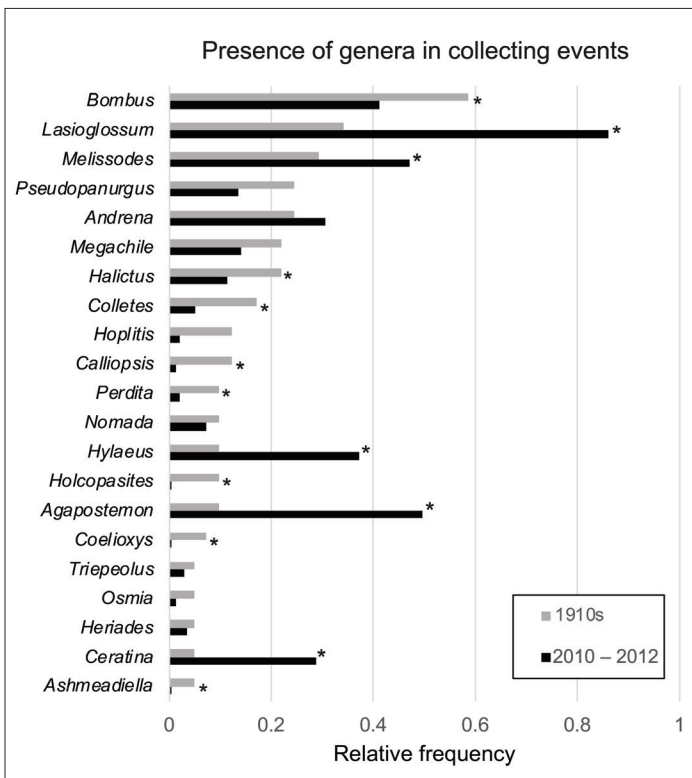


Figure 3. Changes in frequency of presence of bee genera in collecting events from the 1910s and the 2010s in North Dakota. The relative frequency represents the number of collecting events a genus was found in divided by the total number of collections for that record set. Records from 1910–1920 were filtered to those within 100 km of the center of 2010–2012 collecting sites. \* represents significant difference at  $P < 0.05$  based on Z-tests of equal

the 1910s and 17 bees belonging to four species collected from *Zizia* in the 2010s (Table S3 in Supplemental File 1). The plant genera *Solidago*, *Sinapis*, and *Heterotheca* each had an over 80% decrease in visitor abundance but not bee–flower interaction richness in the 2010s compared to the 1910s. The plant genus *Sonchus* had an over 80% increase in visitor abundance and bee–flower interaction richness in the 2010s, while native *Heliopsis* and non-native *Brassica* and *Thlaspi* each had an over 80% increase in visitor abundance but not bee–flower interaction richness from the 1910s to 2010s.

To view changes in seasonal patterns of flower use, we compiled bee visitation for all plants associated with more than 1% of the total bee abundance separately for specimen records from the 1910s and the 2010s (Fig. 4). Historically, *Zizia aurea* and *Hydrophyllum virginianum* were associated with a high diversity and abundance of bees in late spring, and *Lactuca pulchella* and *Cirsium undulatum* were associated with a high diversity and abundance of bees during mid-summer, but these flowers were either infrequently visited or not detected in the collecting efforts of the 2010s. Bee visitation from late spring to mid-summer in the 2010s was predominantly to non-native *Melilotus officinalis*, *Brassica nigra*, and *Sonchus arvensis* (Fig. 4). Late summer showed less dramatic shifts in bee visitation from the 1910s to 2010s, with consistently high use of native composites, such as *Grindelia squarrosa*, *Solidago canadensis*, and *Helian-*

Table 3. Bee species that increased or decreased in relative frequency of presence in collecting events in North Dakota in the 2010s compared to the 1910s. Z-scores and P-values are from comparison of the frequency of species presence in collecting events. A negative Z-score indicates a decrease from the 1910s to the 2010s. The null hypothesis was that the relative frequency of presence for each species was equal in both periods. Selected species were present in both specimen record sets. Specimens from the 1910s were filtered to include only those within 100 km of the center of 2010–2012 specimen locations.

Family	Species	Relative presence in collecting events		Z	P
		1910s	2010–2012		
Less frequent in modern record set					
Colletidae	<i>Colletes rufocinctus</i>	0.07	0.004	-3.33	<0.01
Andrenidae	<i>Calliopsis coloradensis</i>	0.07	0.004	-3.33	<0.01
	<i>Pseudopanurgus aestivalis</i>	0.09	0.008	-3.43	<0.01
	<i>Pseudopanurgus piercei</i>	0.07	0.004	-3.34	<0.001
Megachilidae	<i>Megachile latimanus</i>	0.12	0.042	-2.07	<0.05
Apidae	<i>Bombus terricola</i>	0.07	0.004	-3.33	<0.01
	<i>Melissodes coreopsis</i>	0.07	0.008	-2.79	<0.01
	<i>Melissodes menuachus</i>	0.047	0.004	-2.48	<0.05
More frequent in modern record set					
Halictidae	<i>Agapostemon texanus</i>	0.047	0.371	4.20	<0.001
	<i>Agapostemon virescens</i>	0.047	0.342	3.90	<0.001
	<i>Lasioglossum admirandum</i>	0.047	0.312	3.60	<0.01
	<i>Lasioglossum albipenne</i>	0.09	0.595	6.10	<0.001
	<i>Lasioglossum paraforbesii</i>	0.07	0.418	4.36	<0.001
	<i>Lasioglossum pruinosum</i>	0.023	0.506	5.88	<0.00
	<i>Lasioglossum semicaeruleum</i>	0.19	0.553	4.38	<0.001
	Apidae	<i>Bombus griseocollis</i>	0.07	0.228	2.37
<i>Melissodes agilis</i>		0.023	0.333	4.14	<0.001

*thus maximiliani*, across time periods (Fig. 4). We also summarized all associated flower use across the entire season as the abundance and species richness of bee visitors per plant species (Table S3 in Supplemental File 1). Overall, associated flower diversity decreased from 92 species in the 1910s to 69 species in the 2010s. Non-native plants composed 27% of associated flowers in the 1910s and 59% in the 2010s.

To see how persisting bees adapted to potential changes in the plant community, we examined changes in bee–flower interactions for bee species present in specimen records from both the 1910s and the 2010s. We selected plants that had high relative visitor abundance and bee–flower interaction richness in the 1910s and had reduced presence or were absent from the

Table 4. Change in relative bee–flower interaction richness and visitor abundance for plant genera in North Dakota from 1910–1920 to 2010–2012. Z-tests of equal proportions were run for bee–flower interaction richness and visitor abundance for flowers present in both bee specimen sets. A negative Z-score indicates a decrease from the 1910s to the 2010s. The null hypothesis was that the bee–flower interaction richness and visitor abundance were equal in both time periods. Specimens from the 1910s were filtered to include only those within 200 km of the center of 2010–2012 specimen locations.

Associated plants		Bee–flower interaction richness		Visitor abundance	
Plant family	Plant genus	Z	P	Z	P
Apiaceae	<i>Zizia</i>	-13.47	<0.001	-4.20	<0.001
Apocynaceae	<i>Apocynum</i>	-0.88	0.38	1.07	0.29
	<i>Asclepias</i>	-0.19	0.85	-1.18	0.24
Asteraceae	<i>Argentina</i>	-0.34	0.73	-0.40	0.69
	<i>Centaurea</i>	-5.61	<0.001	-3.84	<0.001
	<i>Cirsium</i>	4.16	<0.001	4.55	<0.001
	<i>Erigeron</i>	-3.39	<0.001	-0.59	0.56
	<i>Grindelia</i>	-8.57	<0.001	-0.64	0.52
	<i>Helianthus</i>	-2.30	<0.001	0.77	0.44
	<i>Heliopsis</i>	4.47	<0.001	1.51	0.13
	<i>Heterotheca</i>	-5.49	<0.001	-0.43	0.66
	<i>Oligoneuron</i>	3.43	<0.05	3.17	<0.05
	<i>Ratibida</i>	-5.23	<0.001	-2.36	0.02
	<i>Solidago</i>	-13.99	<0.001	1.18	0.24
	<i>Sonchus</i>	10.35	<0.001	7.55	<0.001
	<i>Symphyotrichum</i>	-5.49	<0.001	-2.70	<0.05
Brassicaceae	<i>Taraxacum</i>	3.28	<0.001	0.51	0.61
	<i>Brassica</i>	5.29	<0.001	1.28	0.20
	<i>Sinapis</i>	-2.25	<0.05	-1.47	0.14
	<i>Sisymbrium</i>	-0.89	0.37	-0.40	0.69
Caprifoliaceae	<i>Thlaspi</i>	2.20	<0.05	1.64	0.10
	<i>Symphoricarpos</i>	-3.43	<0.001	-0.66	0.51
Fabaceae	<i>Amorpha</i>	-4.72	<0.001	-2.40	<0.05
	<i>Medicago</i>	0.21	0.83	1.38	0.17
	<i>Melilotus</i>	14.38	<0.001	3.45	<0.001
	<i>Trifolium</i>	-4.21	<0.001	-0.94	0.35
Lamiaceae	<i>Stachys</i>	-0.74	0.46	0.57	0.57
Onagraceae	<i>Oenothera</i>	-1.14	0.26	-0.98	0.33
Ranunculaceae	<i>Anemone</i>	2.18	<0.05	2.15	<0.05
Rosaceae	<i>Rosa</i>	-2.68	<0.05	-1.53	0.13
Salicaceae	<i>Salix</i>	-4.86	<0.001	0.31	0.76

E. Evans, J. Ascher, D. P. Cariveau, and M. Spivak

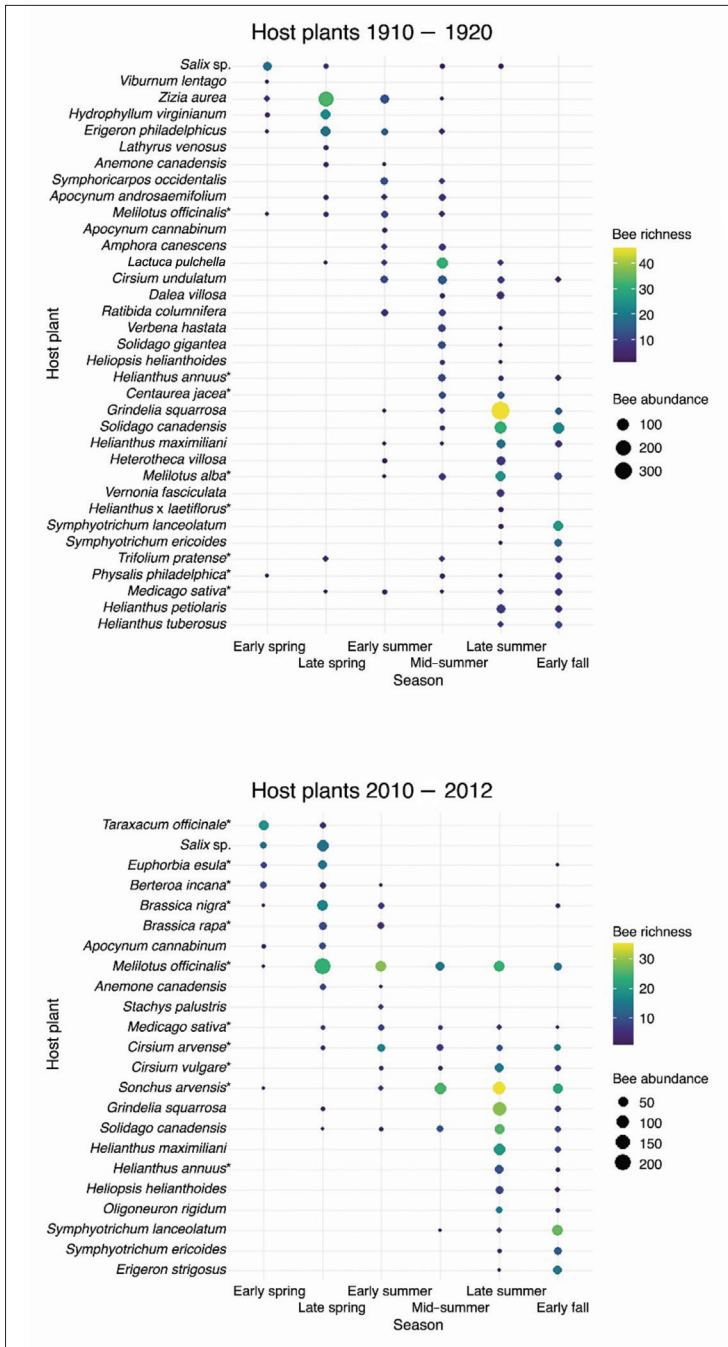


Figure 4. Seasonal floral associations for bee specimen records in 1910–1920 and 2010–2012 in North Dakota. We limited bee specimen records from 1910–1920 to those within 200 km of the center of 2010–2012 collecting sites. We excluded plant species with bee visitors composing less than 1% of total abundance within each record set. We grouped records into six ~20-day time periods. Early spring = 10 May to 30 May, Late spring = 31 May to 21 June, Early summer = 22 June to 14 July, Mid-summer = 15 July to 6 August, Late summer = 7 August to 28 August, Early fall = 29 August to 18 September. \* indicates non-native plants.

E. Evans, J. Ascher, D. P. Cariveau, and M. Spivak

Table 5. Changes in floral associations for bee species associated with plants that had reduced presence in bee specimen records in North Dakota in the 2010s. Selected plants had high relative visitor abundance and bee-flower interaction richness in the 1910s and had reduced presence or were absent from the 2010–2012 bee specimen record set. Selected bee species were present in both periods. Numbers in parentheses are the abundances of the bee species associated with the flower.

Season	Bee species	Associated plant 1910s	Associated plants 2010–2012
Late spring 31 May to 21 June	<i>Hylaeus leptcephalus</i> <sup>a</sup> <i>Bombus ternarius</i> <i>Lasiglossum zephyrus</i>	<i>Zizia aurea</i> (25) <i>Hydrophyllum virginianum</i> (7) <i>H. virginianum</i> (4)	<i>Melilotus officinalis</i> <sup>b</sup> (3), <i>Euphorbia esula</i> <sup>b</sup> (2), <i>Salix</i> sp. (1) <i>Sonchus arvensis</i> <sup>b</sup> (7) <i>Salix</i> sp. (3)
Early summer 22 June to 14 July	<i>Andrena lupinatorum</i> <i>Megachile brevis</i>	<i>Symphoricarpos occidentalis</i> (4) <i>Amorpha canescens</i> (5)	<i>M. officinalis</i> <sup>b</sup> (3), <i>Medicago sativa</i> <sup>b</sup> (1), <i>Salix</i> sp. (1), <i>Rosa arkansana</i> (1) <i>Cirsium arvense</i> <sup>b</sup> (1)
Mid-summer 15 July to 6 August	<i>Halictus ligatus</i> <i>Calliopsis nebraskensis</i> <sup>a</sup>	<i>Lactuca pulchella</i> (8) <i>Verbena hastata</i> (13)	<i>S. arvensis</i> <sup>b</sup> (2), <i>Grindelia squarrosa</i> (1) <i>Solidago canadensis</i> (1)
Late summer 7 August to 28	<i>Calliopsis coloradensis</i> <sup>a</sup>	<i>Heterotheca villosa</i> (7)	<i>G. squarrosa</i> (2)
Early fall 29 August to 18 September	<i>Megachile relativa</i>	<i>Physalis philadelphica</i> (3)	<i>Helianthus</i> sp. (1)

<sup>a</sup>Floral specialist, <sup>b</sup>Non-native plant

E. Evans, J. Ascher, D. P. Cariveau, and M. Spivak

Table 6. Primary floral associate changes between the 1910s and 2010s for bee species with changes in frequency of collection. Selected bee species were absent from the 2010–2012 record set or showed changes in frequency of presence in collecting events between the 1910s and 2010–2012. NA denotes associations that were not present in the 2010–2012 specimen records or that lacked floral association records because of collection from bowl traps.

Change	Bee species	Primary floral association 1910s	Primary floral association 2010–2012
Absent from 2010–2012 record set	<i>Perdita perpallida</i> <sup>a</sup>	<i>Dalea villosa</i>	NA
	<i>Hylaeus annulatus</i> <sup>a</sup>	<i>Zizia aurea</i>	NA
	<i>Andrena miranda</i>	<i>Z. aurea</i>	NA
	<i>Andrena nigrae</i> <sup>a</sup>	<i>Salix sp.</i>	NA
	<i>Lasioglossum swenki</i>	<i>D. villosa</i>	NA
	<i>Melissodes denticulatus</i> <sup>a</sup>	<i>Vernonia fasciculata</i>	NA
	<i>Hesperapis carinata</i> <sup>a</sup>	<i>Helianthus petiolaris</i>	NA
	<i>Bombus pensylvanicus</i>	<i>Cirsium undulatum, Centaurea jacea</i> <sup>b</sup>	NA
	Less frequent in 2010–2012 record set	<i>Calliopsis coloradensis</i> <sup>a</sup>	<i>Grindelia squarrosa, Heterotheca villosa,</i>
<i>Bombus terricola</i>		<i>Solidago canadensis, Physalis philadelphica</i>	1 collected from Poacea species <sup>b</sup>
<i>Pseudopanurgus aestivalis</i> <sup>a</sup>		<i>G. squarrosa</i>	<i>Helianthus maximiliani</i>
<i>Bombus griseocollis</i>		<i>Helianthus annuus</i> <sup>b</sup> , <i>Medicago sativa</i> <sup>b</sup>	<i>Cirsium arvense</i> <sup>b</sup> , <i>Sonchus arvensis</i> <sup>b</sup> , <i>Melilotus officinalis</i> <sup>b</sup>
More frequent in 2010–2012 record set	<i>Lasioglossum semicaeruleum</i>	<i>G. squarrosa, Ratibida columnifera</i>	<i>Brassica rapa</i> <sup>b</sup> , <i>M. officinalis</i> <sup>b</sup>
	<i>Melissodes agilis</i> <sup>a</sup>	<i>H. annuus</i> <sup>b</sup> , <i>H. maximiliani</i>	<i>Cirsium vulgare</i> <sup>b</sup> , <i>H. maximiliani, S. arvensis</i> <sup>b</sup>
	<i>Colletes brevicornis</i> <sup>a</sup>	<i>Campanula rotundifolia</i>	NA
Only collected from bowl traps in 2010–2012	<i>Andrena robervalensis</i>	<i>Lactuca pulchella, C. undulatum</i>	NA
	<i>Pseudopanurgus piercei</i> <sup>a</sup>	<i>H. maximiliani</i>	NA

<sup>a</sup>Floral specialist, <sup>b</sup>Non-native plant

2010–2012 record set (Table 5). Many bee species that were associated with native flowers in the 1910s were associated with non-native flowers in the 2010s. Several floral specialists were found associated with different plant species in the same family.

To see how plant community changes affected bees with reduced modern presence, we examined the primary floral associations for selected bee species that had reduced frequency of presence in collecting events from the 2010s compared to the 1910s (Table 6). Several of the bee species associated with the native plants *Z. aurea*, *Dalea villosa*, and *C. undulatum* in the 1910s were absent from specimen records from the 2010s. Some bee species were only collected from bowl traps or from non-flowering plants in the specimen records from the 2010s, despite netting from flowers at the same locations as the bowl traps (Table 6). Examined bee species that were more frequent in the modern record set were associated with plants that did not decrease in frequency of visitation.

### Discussion

We compared bee community and floral association data recorded between 2010 and 2021 with digitized museum specimens from between 1910 and 1920 to examine possible changes in the bee community and bee–flower associations. We found a similar number of bee species in both record sets but changes in community composition. We found an overall decrease in frequency of bumble bee presence per collecting event from the 1910s to the 2010s. Several bee species that decreased in frequency of presence per collecting event from the 1910s to the 2010s had been associated with native plants in the 1910s but were associated with non-native plants in the 2010s. Several bee species absent from the specimen record sets from the 2010s were found in the 1910s predominantly on flowers that had decreased frequency in the specimen records from the 2010s. These findings indicate that pollinator plantings in the Northern Great Plains could better support the bee species that have persisted and those that are facing possible extirpation by including native flora that were formerly associated with diverse and abundant bees and were associated with bees in probable decline.

### Comparing Specimen Records from the 1910s and the 2010s

Caution is needed when interpreting changes between bee specimen record sets that possibly had different original goals or survey methods (Goldstein and Scott 2015). As Stevens' collections were not part of an ecological study with explicit goals, we can only infer his intentions from his body of scientific work and available data. The collections from the 2010s had a higher average number of species per collecting event, as would be expected from our use of multiple collection methods. The 2010–2012 collections also had higher variability. We intentionally sampled a variety of habitats, whereas Stevens may have focused his collecting efforts on habitats known to attract a high abundance or diversity of bees, like other collectors of that time period. The similar estimated species numbers for the 1910s and the 2010s collections indicate similarity in overall species number between collections, but caution is still needed when examining changes for individual species. Bee surveys in eastern North America often have many species only represented by one specimen, and these singletons are a well-known problem when comparing bee faunas (Cusser et al. 2015, Giles and Ascher 2006, Grundel et al. 2011, Williams et al. 2001). Because of Stevens' intimate knowledge of the best collecting locations for bees and plants from his decades of experience observing bee–flower interactions within North Dakota, we are not confident inferring local extirpations based on absences from our collection. While the estimated species number for the records from the 1910s that were used for bee–flower association comparisons accounted for 83% of the expected species number, the records used for bee faunal comparisons were limited to those within 100 km and only accounted



for 65% of the expected species number. While we cannot rule out different collecting or curation methods causing some of the observed changes, we focused on changes to bee species that were likely to have been abundant historically, based on the frequency of their presence in Stevens' collecting events.

Observed changes in bee–flower associations could also be affected by the smaller spatial extent of the collections during 2010–2012 or the habitats we were able to access. While plant communities are similar across the spatial extent of this study, our collecting efforts in 2010–2012 may have missed some plants because we covered a smaller area over fewer years (Stevens 1950b). Many of our surveys were in roadsides, which are often dominated by non-native plants, potentially biasing the bee–flower association records from the 2010–2012 specimen records toward non-native plants. While roadsides are known to provide important bee habitat (Hopwood 2008, Phillips 2020), they may not be suitable for the full range of native plants found on prairie remnants by Stevens (Smart et al. 2021). Our study could have been improved by identifying and including additional collection locations with a higher presence of native plants.

### Changes in the Bee Community

Species richness was similar between the specimen record sets from the 1910s and 2010s, but our observations suggest changes in species composition, with possible losses and gains of species and decreases and increases in the frequency of presence in collecting events at the genus and species level between time periods. Many species that were present in only one record set were pollen specialists or cleptoparasites, groups that are often underrepresented in collections (Gibbs et al. 2017, Hofmann et al. 2019, Sheffield et al. 2013). The absence of a specialist or cleptoparasitic species in either period could indicate a regional species loss or gain, but the absence could also be due to low detection probabilities for these rare species or the spatial limits of collecting efforts.

While it is difficult to know if the absence of rare species is due to their actual absence or a lack of detection, the absence of species in the specimen records from 2010s that were common in the digitized museum specimens from the 1910s suggests possible loss of species and their floral interactions, especially when larger-scale regional or national specimen and image databases show similar patterns. Species that were frequently collected in the 1910s but absent from the specimen records from the 2010s (*Hylaeus annulatus*, *A. miranda*, and *Hesperapis carinata*) may be in decline. These probable declines may be related to changes in preferred plants, as the predominant flowers associated with these three species declined in frequency or richness of bee visitors between the 1910s and the 2010s (*Zizia* for *H. annulatus* and *A. miranda*; *Helianthus* for *H. carinata*). In addition, the probable decline of *H. annulatus* may be related to lack of nesting sites, as populations have been shown to be dependent on the amount of standing dead wood in an area, a habitat that has been negatively affected by agricultural expansion in eastern North Dakota (Severson and Sieg 2006, Westerfelt et al. 2018). Additional caution is needed to interpret decline for *H. carinata*, as its prevalence in Stevens' collections may be due to his special interest (initial description of the species) and knowledge of its habitat (Table S1 in Supplemental File 1) (Stevens 1919).

While still present, other bee taxa decreased in frequency from the 1910s to the 2010s. The decreased frequency of *Bombus* presence in collecting events in the records from the 2010s may be due to decreased presence of a subset of bumble bee species in the study area. As expected, based on patterns across North America (Hatfield et al. 2015), not all bumble bee species decreased in frequency of collection. Frequency of presence in collecting events decreased for *B. pensylvanicus* as well as for *B. terricola*, and their respective parasites, *B. variabilis* and *B. ashtoni*, were not detected at all. *Bombus ashtoni* was noted by Stevens as the most common

cuckoo bumble bee in North Dakota (Stevens 1948b). In contrast, *Bombus griseocollis* increased in frequency of presence in collecting events, and others, such as *Bombus ternarius* and *B. fervidus*, showed no change. Although we documented a dramatic decline in frequency of presence in collecting events for *B. terricola* within the spatial extent of our 2010–2012 collections (a decline from 7% in the 1910s to 0.4% in the 2010s), we did document their presence with recent public biodiversity portal records within 200 km of our 2010–2012 collection locations. *Bombus terricola* may be sporadically distributed in North Dakota or could have experienced a range shift. Public biodiversity portals, such as iNaturalist and Bumble Bee Watch, are important tools for the detection of sporadically distributed species and documentation of range shifts.

Decreases in frequency of presence in collecting events at the genus level for *Colletes*, *Holcopasites*, and *Ashmeadiella* are difficult to interpret. Stevens addressed these genera in detail in his works on the bees of North Dakota and provided type specimens for species (Stevens 1950a, 1951). Their higher frequency of presence in the specimen records from Stevens' collection may be due to his interest in these groups, especially after he discovered new species described by leading taxonomists of his era (Table S1 in Supplemental File 1).

The traits of bee species that declined between the 1910s and the 2010s can inform habitat needs to support diverse bee communities. Bee species present in both record sets that declined in frequency of presence in collecting events in the 2010s were mostly active late in the season, including many pollen specialists as well as several stem-nesting species. This finding suggests that bee species that remain present in highly altered landscapes can be supported by providing diverse floral resources, particularly late in the season and including plants in the family Asteraaceae. Retaining and creating stem-nesting habitat will also be important to supporting persisting bees (Graham et al. 2021, Sheffield et al. 2014). The species that were present in both record sets that increased in frequency of presence in collecting events in the modern record set were mostly bees with long active seasons and ground-nesting species. It is possible that changes in climate over the last 100 years could favor bees with a longer active season. As climate becomes more variable, bees that are active for shorter periods of time may have more challenges due to extreme weather and lengthening or shortening of seasons (Slominski and Burkle 2019). Although we saw increased frequency of presence in collecting events for ground-nesting bees, it is challenging to provide management recommendations for these taxa because their habitat needs are highly variable with very little documentation of specific needs for most species (Cane 1991, Harmon-Threatt 2020, Sardinas and Kremen 2014). As we learn more about the habitat needs of different species of ground-nesting bees, more refined habitat management recommendations should become available.

Examining species that were absent from the 1910s but present in the 2010s, we observed several potential range expansions. We documented 6 non-native species in the 2010s. Only one non-native bee species, *H. leptocephalus* (described by Stevens as a new native species, *H. stevensi*, and only recognized as non-native in the 1970s [Hurd 1979]), was present in the digitized museum specimens from the 1910s. The impact of these non-native species on the native bee community is unknown (Cane 2003, Russo 2016). In addition to non-native expansions, public biodiversity portal records documented 11 *Bombus impatiens*, a species native to eastern North America, in areas beyond the northwestern edge of its known range, demonstrating a range expansion.

Several bees increased in frequency of presence in collecting events from the 1910s to the 2010s. The causes of increased frequency of *Lasioglossum* from the 1910s to the 2010s are unknown but may be due to historical avoidance of collection of *Lasioglossum*. *Lasioglossum* specimens present taxonomic and curatorial challenges due to their abundance, diversity, small size, and difficult identification and are captured by bowl traps very effectively, whereas they

are relatively inconspicuous to net collectors (Gibbs 2010, Portman et al. 2020). At the time of Stevens' collecting effort, there were no taxonomic experts working on *Lasioglossum* in North America. An alternative explanation is that the increase in relative frequency of presence of *Lasioglossum* in collecting events, as well as *Halictus* and *Agapostemon*, may indicate an ability of these bees to utilize non-native plants, nest in disturbed soils, and better adapt to human disturbance than other bee genera. Many *Lasioglossum* species, particularly ground-nesting species of the subgenus *Dialictus*, appear to have resilience to agricultural land-use conversion (Grab et al. 2019).

Bee and pollinator conservation measures can only be effective in preserving biodiversity if a sufficient species pool still exists in a region. Despite loss of most native habitat and potential changes in the composition of the bee community over the last century, the specimen records from 2010–2012 and public biodiversity portal records from 2012–2021 included habitat and diet specialists and species of conservation concern. To prevent further declines in abundance and diversity of these important bee pollinators, habitat improvements should be made to enhance their floral resources and nesting habitats.

### Changes in Bee–flower Associations

Shifts in bee–flower associations from the specimen records of the 1910s to the 2010s can indicate important plant species to include in pollinator plantings. Most of the plants with large decreases in bee visitor abundance between historic and modern record sets were native in origin: *Hydrophyllum*, *Amorpha*, *Zizia*, and *Ratibida*. In the modern record set, few bees were collected from these genera. Most of the plants with large increases in visitor abundance in the modern record set were non-native, except for *Heliopsis*, *Salix*, and *Anemone*.

Non-native plants have been common in the Prairie Pothole region for over 120 years, while native plants have decreased in abundance (Severson and Sieg 2006, Stevens 1920b, Upham 1892). Changes in the plant community are reflected in changes we observed in bee–flower associations between the specimen records from the 1910s and 2010s. The native plants *Z. aurea*, *H. virginianum*, *D. villosa*, *Amorpha canescens*, *Heterotheca villosa*, and *L. pulchella* were all much less frequently visited or had no documented visitation in the 2010–2012 record set. Many bee species that were associated with these flowers in the 1910s were found on non-native flowers, such as *S. arvensis*, *M. officinalis*, and *Euphorbia esula*, in the 2010s. Examining the floral associations of bees that decreased in frequency or were absent in the specimen records from the 2010s compared to the specimen records from the 1910s, many had used *Dalea*, *Zizia*, *Vernonia*, and other natives as their primary floral associations. Although we cannot know if a bee species is absent or declining because of changes in availability of preferred floral hosts or because of other pressures, such as pesticides and climate change, including these native plants in pollinator plantings may support possibly declining bee populations. The association of some of these plants, such as *Zizia* and *Hydrophyllum*, with woodland edges (Stevens 1950b) indicates that restoration of both wooded areas and prairies is warranted.

Since land use changed significantly in the decades before the historic collecting efforts, looking further back in time can provide an indication of the earlier flowering plant community. Plants collected by Charles A. Geyer along the James River in 1839 indicate possible floral hosts from earlier than the 1910s record set (Upham 1892). The following are some of the forbs commonly found during that collection that are known to be utilized by bees and were not commonly found in the collection from the 1910s: *Hypericum ellipticum*, *Astragalus crassicaarpus*, *Desmodium canadense*, *Eutrochium purpureum*, *Campanula rotundifolia*, *Monarda fistulosa*, and *Agastache foeniculum* (Upham 1892). These are additional plant species that could benefit the persisting members of the native bee community.

In the modern record set, the high abundance of visitors to *M. officinalis*, *S. arvensis*, and *G. squarrosa* is likely due to the high abundance of these plants that we noted in our separate ecological study (Evans 2016). It is well known that floral choice by bees is not driven by floral abundance alone, as other characteristics, including reward quality, also are influential on floral choice (Essenberg 2012). For example, *Oligoneuron rigidum*, which was also visited by many bee species in the 2010s, was found at a low frequency in the study area. This observation is supported by a study that found a high rate of selection of this plant by wild bees (Simanonok et al. 2021).

### Management Implications

Prairie restoration is an important and effective tool for pollinator conservation in the Northern Great Plains (Harmon-Threatt and Hendrix 2015, Tonietto et al. 2017, Tonietto and Larkin 2018). Inclusion of the native plants *Z. aurea*, *H. virginianum*, *Dalea candida*, *Dalea purpurea*, *D. villosa*, *A. canescens*, *H. villosa*, *O. rigidum*, *L. pulchella*, and *Vernonia fasciculata* in restoration efforts in the Northern Great Plains could help to restore native bee–flower interactions that were more frequent in the 1910s. It is likely that the bee community that was seen in the 1910s was shaped by a plant community that had itself been significantly altered in the previous 40 years. While we do not have bee records from these earlier times, knowledge of pre-colonial grassland, wetland, and riparian vegetation can help recreate functional landscapes. While prairies and grasslands dominate the native vegetation of the Great Plains, several potentially important plants are associated with wooded edges, presumably associated with riparian wooded areas, indicating the importance of including woodland restorations in plans for pollinator plantings (Mola et al. 2021, Requier and Leonhardt 2020). In both historic and modern record sets, many bee specimens and bee species were collected from *M. officinalis* and *S. arvensis*. Despite their non-native status, their ubiquitous presence in the agricultural landscape in this region has provided important resources for supporting diverse native bee communities over 100 years. If these plants are eliminated, it is important to provide alternative sources of pollen and nectar (Vray et al. 2017).

Potential declines in abundances of historically common bee species point to the urgency of enacting bee conservation measures. Our findings indicate that stem-nesting bees, pollen specialists, and bees active late in the season are at a greater risk of decline. Public biodiversity portals can provide useful presence information for many bee species, including bumble bees, and can supplement specimen data in documenting range extensions and retractions. These records can also identify locations for recovery efforts. The persistence of bee species in agriculturally dominated landscapes points to the importance of including agricultural areas in pollinator habitat restoration efforts. Historically informed pollinator plantings can provide habitat to conserve and restore the bee and plant communities of the Northern Great Plains.

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