Bumble Bee (*Bombus*) Species Distribution, Phenology, and Diet in North Dakota

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Abstract - A growing number of bumble bee species are under review and proposal for federal protection in North America. However, many regions are underrepresented in population assessments. We address the deficiency of bumble bee information in North Dakota, USA using a novel sampling effort across all counties in the state to provide essential information on species distributions, relative abundances, phenology, and diet associations. We detected 16 bumble bee species during 2017–2020, including species of high conservation concern. We share the distribution of bumble bee richness in North Dakota and provide species-specific density maps. We also provide phenology timelines of each species and identify distinct groups of bumble bees based on floral associations through cluster analysis to further inform conservation efforts.

Introduction

The risks to the security and persistence of bee populations (Hymenoptera: Apoidea) and their associated ecological services are globally concerning. Most cultivated crops are dependent on insect pollination, a service valued annually at over $180.5 billion (Gallai et al. 2009). Though humans recognize commercial pollinators such as the honey bee (Apidae: *Apis mellifera* Linnaeus) for crop pollination services, the equivalent role of wild bee pollination services to humans and the importance of functionally diverse pollinator communities is increasingly acknowledged (Blitzer et al. 2016, Garibaldi et al. 2013, Garibaldi et al. 2014). The attention to wild bees may be largely attributed to declines in honey bee colonies (Stokstad 2007) and emergent evidence of declines in other bee species (Potts et al. 2010). However, declines in wild bee populations are difficult to assess, emphasizing the need for increased monitoring efforts in order to create the most informed conservation strategies (Woodard et al. 2020).

The most reliably documented declines in wild bee populations are in the bumble bee (*Bombus* Latreille) species of Europe and North America (Cameron and Sadd 2020, Colla et al. 2012, Kosior et al. 2007). The sources of bumble bee decline are largely anthropogenic, chiefly among these being the loss of foraging and nesting resources due to land conversion to homogenous agricultural expanses and other human development (Carvell et al. 2006, Goulson et al. 2008a, Goulson et al. 2015, Roulston and Goodell 2011, Williams and Osborne 2009). Additionally, intensive pesticide use in agricultural settings, pathogens, climate change, extreme climatic events, and competition are all documented stressors (Crall et al. 2018, Graystock et al. 2013, Kerr et al. 2015, Rasmont and Iserbyt 2012, Thomson 2016). These factors, along with unidentified sources of decline, are not independent of each other and interact, making the primary causes for declines difficult to identify for bumble bee species of concern (Szabo et al. 2012).

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Based on phylogeny and life history traits, particular groups of bumble bees are more at risk of population decline and warrant focused conservation intervention. Furthermore, these species of concern vary between regions; those in subgenera *Thoracobombus* and *Cullumanobombus* are estimated to be most threatened globally (Arbetman et al. 2017), while populations within the subgenera *Bombus senso stricto* (which includes *Bombus affinis* Cresson, the first continental bee species listed under the US Endangered Species Act) and *Psithyrus* have had the most drastic recent declines in North America (Cameron et al. 2011, Colla et al. 2012). Aside from similar phylogenetic relatedness, bumble bee species with restricted ranges, limited diet preferences, smaller colony sizes, and increased levels of competition are at the most risk of rapid decline (Goulson and Darvill 2004, Kleijn and Raemakers 2008, Williams et al. 2009, Williams and Osborne 2009).

A deficiency in available data makes it difficult to identify which bumble bee populations are undergoing declines and connect these species with the environmental factors driving them. Even worse, the data researchers depend on contain regional biases (Cameron and Sadd 2020, Pyke and Ehrlich 2010). For example, in the United States, the highest concentration of records is located toward coastal regions or areas with higher human populations and established research facilities (Cameron et al. 2011, Colla et al. 2012). Therefore, increased data collection in regions with sparser records is necessary to best inform current population statuses of bumble bee species of concern and subsequent conservation management strategies. Without sufficient data from a species' full distribution, we may not detect important distributional changes and will have a limited view of the resources required by species.

The Northern Great Plains region in North America is expected to host substantial bumble bee diversity (Williams et al. 2014) but is underrepresented in continent-wide databases. Data in this region are critical considering its mid-continental location serves as a transition from species with eastern distributions to those with western distributions. North Dakota, in particular, has sparse records of native bee species, making it difficult to assess the statuses of species of concern historically found in the state, such as *Bombus terricola* Kirby, *B. occidentalis* Greene, *B. pensylvanicus* De Greer, *B. insularis* Smith, and *B. affinis* Cresson. Gaining information on the relative abundances and diversity of bumble bee species and their associated resources in North Dakota is also pertinent because of its agricultural landscape and consequent reduction of native floral resources. High levels of invasive grasses and forbs have additionally transformed the composition of grassland communities in North Dakota, impacting species that depend on the native plant community (Raffery 2017). In addition, North Dakota is the largest honey bee producer in the United States (US Department of Agriculture 2020). Native bumble bees are the most similar group of bees to European honey bees in morphology and life history and are most likely to be impacted by dense introductions of a competing species that may alter bumble bee production and behavior (Goulson and Sparrow 2009, Thomson 2004).

The overarching goal of this paper is to provide current information on bumble bee species in North Dakota. We address the data gaps in the state using data from a statewide sampling effort of bee and associated plant species. Here, our objectives are to 1) present current bumble bee species' distributions from our survey data and 2) provide species-specific phenology that displays the abundance of bumble bee queens, workers, and males detected over the growing season. We will also 3) illustrate comparative and species-specific bumble bee-plant associations through the proportional floral visitations we observed of each bumble bee species in order to identify important floral resources.

Study Area

The presence or absence of historic glacial activity created a gradient of ecoregions in North Dakota. Tallgrass prairie characterizes grasslands along state's border in the Lake Agassiz Plain ecoregion and changes to a mixed-grass system in the central majority of the state in the Northern and Northwestern Glaciated Plains ecoregions (Whitman and Wali 1975). Mixed-grass and short-grass systems represent the southwestern unglaciated portion characterized as the Northwestern Great Plains. However, extensive invasions of grass species *Poa pratensis* Linnaeus (Kentucky Bluegrass) and *Bromus inermis* Leyssera (Smooth Brome) and introductions of exotic forb species such as *Cirsium arvense* Linnaeus (Canada Thistle), *Euphorbia esula* Linnaeus (Leafy Spurge), *Medicago sativa* Linnaeus (Alfalfa), and *Melilotus* spp. (Sweet Clovers) have altered historical grassland communities. Various land uses fragment the remaining grasslands throughout much of North Dakota, with more continuous tracts in the southwestern quarter of the state (Niemuth et al. 2021).

We selected sites with at least 50 acres (~20 hectares) of contiguous grassland area based on available public lands managed by North Dakota Department of Trust Lands (n = 115), US Fish and Wildlife Service (n=131), North Dakota Game and Fish Department (n = 72), US Forest Service (n = 28), other agencies (n = 7), and volunteered private lands (n = 124). Grassland tracts managed by public agencies were under various land management strategies including those for livestock grazing, haying, and wildlife conservation. Private lands included these, as well as idle grasslands and those enrolled in state programs to enhance wildlife and national conservation programs such as the Conservation Reserve Program, Conservation Reserve Enhancement Program, and Wetlands Reserve Program.

Methods

Surveys

Five teams of observers sampled bee communities at 477 sites throughout North Dakota grasslands each summer growing season between 2017 and 2020. We surveyed at 3 sites in each of the 53 North Dakota counties per study year, keeping 1 site the same in each county for all 4 years (n = 53) and establishing 2 new sites every year (n = 424) in order to maximize the spatial span of this study. We arbitrarily defined 2 study plots at each site, placed at least 328.08 ft (100 m) apart, using aerial mapping to ensure plots did not include large amounts of water (Fig. 1). Where possible, we situated plots at least 164.04 ft (50 m) from the edge of the grassland tract to reduce edge effects. We performed netting surveys for bee species at each of the 159 sites per year 2 times during the summer between the end of May and mid-September. We established a first round of surveys at each site to take place in the first half of the growing season before 15 July and in the last half of the growing season after 15 July to account for some phenological changes. Two observers performed independent netting surveys at each site visit, bringing the total number of netting surveys to 2,544. Additionally, we used passive bee-bowl sampling at 69 sites in 52 counties to complement our netting methods.

Netting surveys took place between 9:00–18:00 hours under temperatures between 69.8–96.8 F° (21–36 C°), 50% and below cloud cover, and sustained winds below 15.53 mph (25 km/h). Netting surveys consisted of 2 collectors separately surveying for bee species in a 164.04 ft^2 (50 m^2) plot for 30 minutes (Fig. 1). The plot surveys comprised a systematic search restricted to 3, 164.04 ft (50-m) long transects within the plot for 15 minutes, while collectors used the remaining 15 minutes to freely search within the plot (Fig. 1). Collectors recorded plant species on which bees were captured and did not include

specimen handling in survey time. Collectors then stored bees in 95% alcohol-filled vials until they could be processed and identified.

We randomly selected a subset of sites each year to perform passive bee-bowl sampling surveys. We chose a subset of sites due to logistical constraints associated with the deployment and next-day retrieval of this method while concurrently visiting a high number of sites. At selected sites, we situated an approximately 246.06 ft (75 m)-transects of 15 colored (light blue, white, and yellow) plastic 16-oz stadium cups (height: 4.44 in; base diameter: 2.56 in; rim diameter: 3.5 in; DiscountMugs, Miami, FL, USA) filled with soapy water along a side of each 164.04 ft^2 (50m^2) plot for a total of 30 bee-bowls per survey instance (Fig. 1; Droege et al. 2010, Shapiro et al. 2014). We positioned cups on individual stakes (0.5 in diameter; approximately 15.75–19.69 inches in length) supported by adjustable steel pipe-hanging strap rings (Sioux Chief Manufacturing Company, Kansas City, MO, USA) that we lowered level to surrounding vegetation to simulate a natural flowering height and left on-site for 24 hours to passively collect bees. Upon retrieval, collectors separated bees from non-bee arthropods and stored specimens in alcohol-filled vials until processing and identification. Bee-bowl sampling took place 2 times over the sampling season at each site selected for bee-bowl surveys.

Data Processing and Analysis

We treated bumble bee abundance data at the site level, combining individual plot surveys across both visits per site. For the distributional and floral resource information, we used data from the netting surveys only because we cannot obtain floral associations
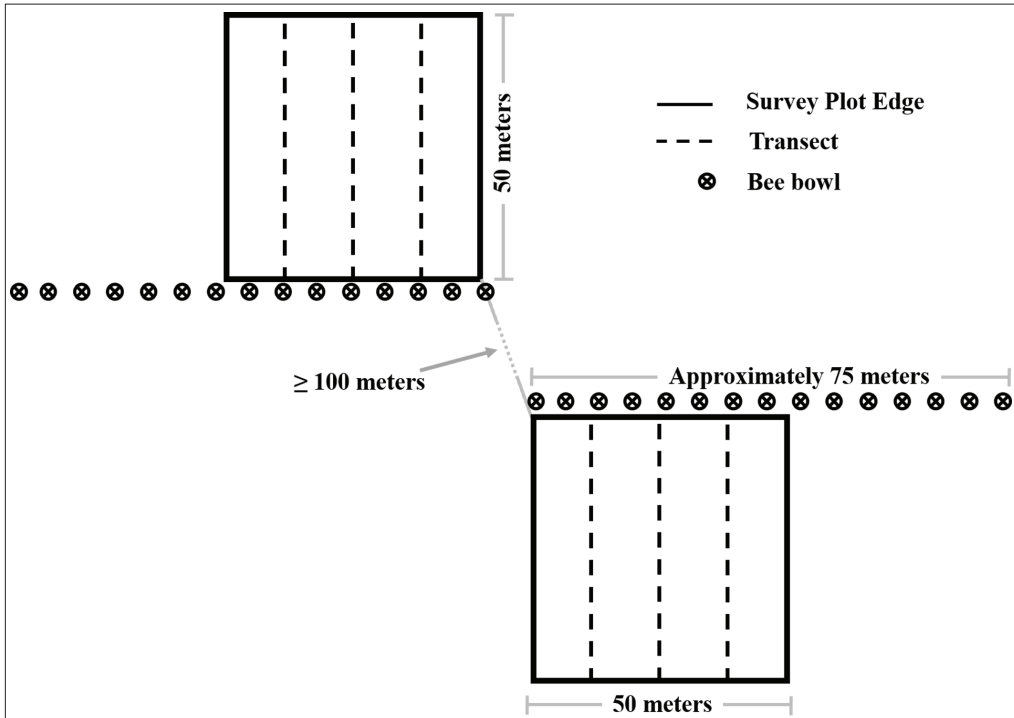

Figure 1. Survey plot setup at each grassland site showing 2, 50x50-m plots separated by at least 100 meters. Two collectors in their respective plots performed netting surveys separately. Collectors surveyed bees for 5 minutes on each of the 3 transects within the plot, indicated by the vertically oriented dashed lines for a total of 15 minutes, then surveyed freely within the plot for an additional 15 minutes. At randomly selected sites, bee-bowl transects of 15 bee-bowls were set up along an edge of each plot.

from the bee-bowl data. Additionally, bee-bowl data would disrupt relatable bumble bee species densities because we performed bee-bowl surveys at a subset of sites. We used both netting and bee-bowl survey data for creating species phenology graphs as this is not sensitive to the type of survey and use of both survey types increases the available phenological data.

Distribution. We averaged the abundance between years for the 53 sites we visited each year to avoid over-representing abundance at those recurring sites. We calculated kernel density estimates of abundance for each species and mapped results using geographic information system software ArcMap 10.3 (ESRI, Redlands, CA) to display species distributions in the state and densities. Here, kernel density mapping calculates a composite density created from our observed samples of bumble bee abundance (Bolstad 2012). Individual sample density points are calculated using observed bumble bee abundance in relation to a bandwidth calculated from mean abundance across sites, each observation distance from the mean, the weighted median from these distances, along with standard deviations (ESRI 2014).

Phenology. We categorized specimens in each species as a "queen" (including gynes, which are future queens produced at the end of the colony cycles), "worker", or "male" based on measurements from species descriptions (Mitchell 1962, Williams et al. 2014). We classified it as "undetermined" if we could not categorize a female bumble bee based on size or color pattern. We used bumble bee abundances summed for each species captured from both netting and bee-bowl surveys over all survey years to obtain the phenology of queens, workers, and males in each species. We visualized the phenology of queens, workers, and males based on the smoothed abundances captured at each date proportional to the abundance captured per bumble bee grouping using streamgraphs built in R statistical environment (*ggstream* package: Sjoberg 2021).

Floral associations. We investigated floral visitation per bumble bee species and determined which species could be grouped based on similar compositions of visited flowering plant species. Bees mainly collect pollen to provision larvae and use nectar primarily as an energy source for adults. Diet specialization in bees refers to the pollen resources important to particular bees. As such, we wish to increase the meaningfulness of floral associations by using worker data from netting surveys only. We included species with at least 10 worker observations (Goulson et al. 2008b) to include as many bumble bee species possible but with enough observations for comparisons. We also excluded associations with plant species in the milkweed family Apocynaceae due to the pollinium form of pollen grains that bees do not collect for larval provisioning and use the nectar as a carbohydrate source (Michener 2007, Morse 1981). We acknowledge that our bee surveys do not differentiate whether a bee used a floral resource for pollen or nectar, but filtering out queen and male floral interactions and known plants that do not provide pollen increases the importance of the bee-floral associations used in our comparisons. We converted raw abundance of interactions between bumble bees and plants summed over all years to proportional values in order to compare the composition of floral associations over species. We then performed a cluster analysis to determine if logical clusters of bumble bees based on similar floral associations existed. We determined the most appropriate number of clusters based on the highest Caliński-Harabasz criterion (Caliński and Harabasz 1974) using the vegan package in R (v.2.5-7; Oksanen et al. 2015). We used non-metric multidimensional scaling (NMDS) to show relationships between identified bumble bee species clusters and the floral species on which they were captured (Wood et al. 2019) with respect to plant species origin and plotted those results (*vegan* package; Oksanen et al. 2015).

Results

We captured 4,027 bumble bee specimens of 16 species during 2017–2020 (Table 1). Yearly capture totals fluctuated with 834 bumble bees captured in 2017, 1,389 in 2018, 756 in 2019, and 1,048 in 2020. Of 2,544 total netting surveys, 41.9% of surveys and 78.4% of sites we visited contained bumble bees. Across netting surveys from all years, bumble bee richness was highest in the east-central parts of the state, but there was also substantial bumble bee richness in the western badlands region (Fig. 2).

Distribution. The observed distributions of *Bombus bimaculatus* Cresson, *B. borealis* Kirby, *B. fervidus* Fabricius, *B. griseocollis* De Greer, *B. huntii* Greene, and *B. rufocinctus* Cresson were relatively statewide but with areas of highest abundance dependent on species (Fig. 3). We captured *B. ternarius* Say, *B. terricola*, and *B. vagans* Smith primarily in the northern and eastern portion of the state while *B. pensylvanicus* De Geer and cuckoo bee species *B. insularis* distributions were without any observable spatial pattern throughout the state. We found B. *impatiens* Cresson, an eastern North American species, only in the 5 southeasternmost counties. Our surveys detected ≤7 occurrences of *Bombus centralis* Cresson and *B. perplexus* Cresson in discrete areas and *B. fraternus* Smith with 1 occurrence, indicating these species are rare in the state.

Phenology. Species with greater detections exhibited phenology patterns that followed expected colony cycles with peak abundances of queens captured in the beginning and end of the growing season and worker and male abundances highest in later season (Fig. 4; Table 1).

Table 1. Total bumble bee species count collected in North Dakota between 2017 and 2020 by bumblebee class (Undetm. = undetermined female specimens that could not be assigned to a class). Abundances from bee-bowl surveys are indicated within brackets while those from netting surveys are outside brackets.

Bumble Bee Species Count

Subgenus	Species	Queen	Worker	Male	Undetm.	Total
Bombias	*Bombus nevadensis* Cresson	33 [3]	44	15 [2]	13	110
Bombus	*Bombus terricola* Kirby	4 [2]	21 [1]	8		36
Cullumano-bombus	*Bombus fraternus* Smith		1			1
	Bombus griseocollis De Geer	143 [13]	710 [38]	359 [9]	22 [1]	1,295
	Bombus rufocinctus Cresson	58 [38]	173 [27]	65 [5]	5 [1]	372
Psithyrus	*Bombus insularis* Smith	8 [1]	1	10		20
Pyrobombus	*Bombus bimaculatus* Cresson	15 [1]	78 [3]	24		121
	Bombus centralis Cresson		4 [2]	1		7
	Bombus huntii Greene	49 [7]	176 [10]	27	2 [1]	272
	Bombus impatiens Cresson	3	51	1	1	56
	Bombus perplexus Cresson		1	1		2
	Bombus ternarius Say	47 [34]	433 [14]	43 [1]	7 [2]	581
	Bombus vagans Smith	26 [9]	88 [8]	9	7	147
Subterraneo-bombus	*Bombus borealis* Kirby	77 [31]	374 [37]	103 [9]	10 [2]	643
Thoracobombus	*Bombus fervidus* Fabricius	18 [29]	151 [79]	57 [3]	2 [3]	342
	Bombus pensylvanicus De Geer	1 [2]	9 [8]	[2]		22

We observed *B. huntii* (n = 56), *B. fervidus* (n = 47), and *B. ternarius* (n = 81) queens having earlier first peak abundances of queens while first peaks of *B. borealis* (n = 108) and *B. griseocollis* (n = 156) queens occurred later. Our surveys did not observe definitive first peaks of *B. nevadensis* Cresson (n = 36) and *B. rufocinctus* (n = 96) queens as abundances remained relatively stable throughout the early season. Of species with considerably high observed abundances, *B. bimaculatus* (n = 121), *B. nevadensis* (n = 110), and *B. vagans* (n = 147) did not extend much past the end of August.

Floral associations. We excluded 4 species from our floral association comparisons due to the small number of observations. However, we included *B. pensylvanicus,* which had 9 worker observations because of its relevance as a species of conservation concern (Table 1). Cluster analysis identified 4 distinct groups of bumble bees based on proportional floral associations of workers (Fig. 5). Bumble bee species within a cluster visited a more similar proportion and composition of plant species than species found in other clusters. The group containing *B. griseocollis*, *B. huntii*, *B. rufocinctus*, *B. ternarius*, and *B. terricola* generally interacted with more plant species, with larger proportions of visitations to *Melilotus officinalis*, *Dalea purpurea*, *Cirsium* spp., and *Solidago* spp. (Fig. 6A; Appendix [available online at https://eaglehill.us/prnaonline/suppl-files/prna-010b-pei-s1.pdf]). *Bombus bimaculatus*, *B. borealis*, *B. nevadensis*, and *B. vagans* had a large proportion of interactions with *Monarda fistulosa*, which ranged from 15.8% to 34.2% of visitations per species and *Cirsium flodmanii*, ranging from 7.9% to 8.6% of visitations per species (Fig. 6B; Appendix). We observed the
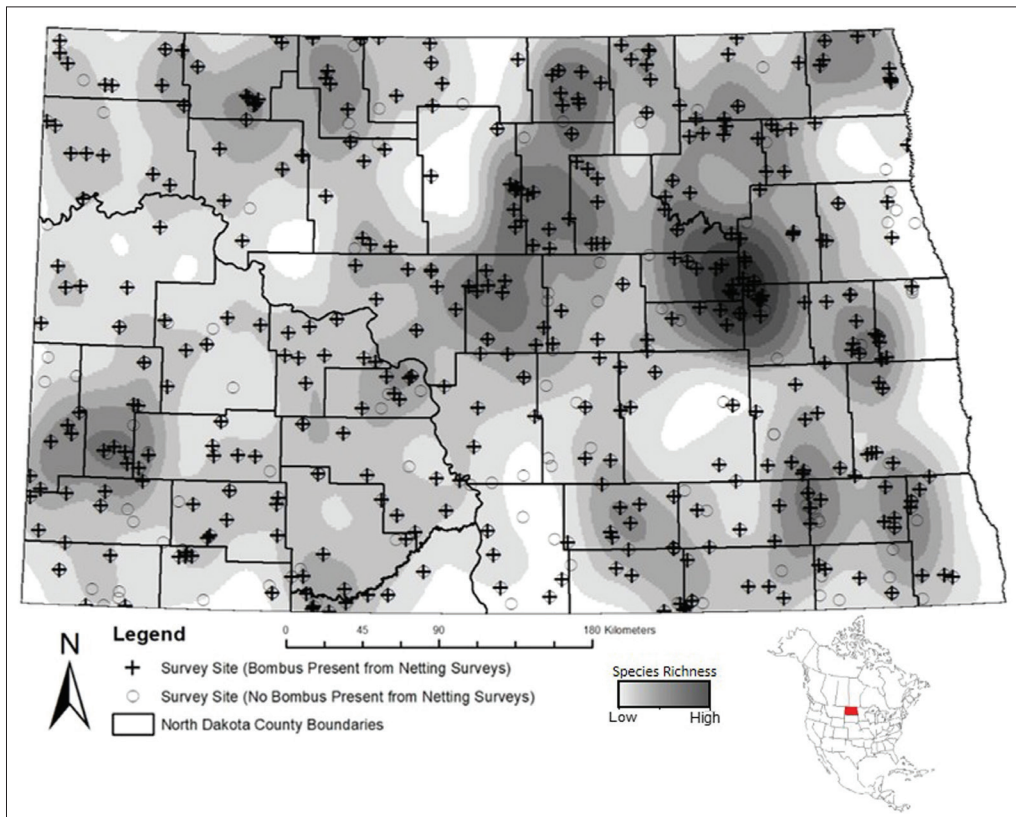

Figure 2. Kernel density map of bumble bee richness detected in netting surveys in North Dakota between 2017 and 2020. Estimated richness values are represented in the grayscale shading with darker areas conveying a higher species richness. Survey sites are indicated with empty circles and an overlaid cross symbol if bumble bees were present.

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group comprised of *B. fervidus* and *B. pensylvanicus* having most interactions with *Cirsium flodmanii*, *Dalea purpurea*, *Melilotus officinalis*, and *Liatris punctata* (Fig. 6C; Appendix). Our observed floral associations of *B. impatiens* were distinct from other groups and comprised largely of *Solidago* spp. (Fig. 6D; Appendix). Plotted NMDS ordination results display relationships between proportional associations between bumble bees and plants but also emphasize the relationships between bumble bee species and exotic and native plants. *B.*
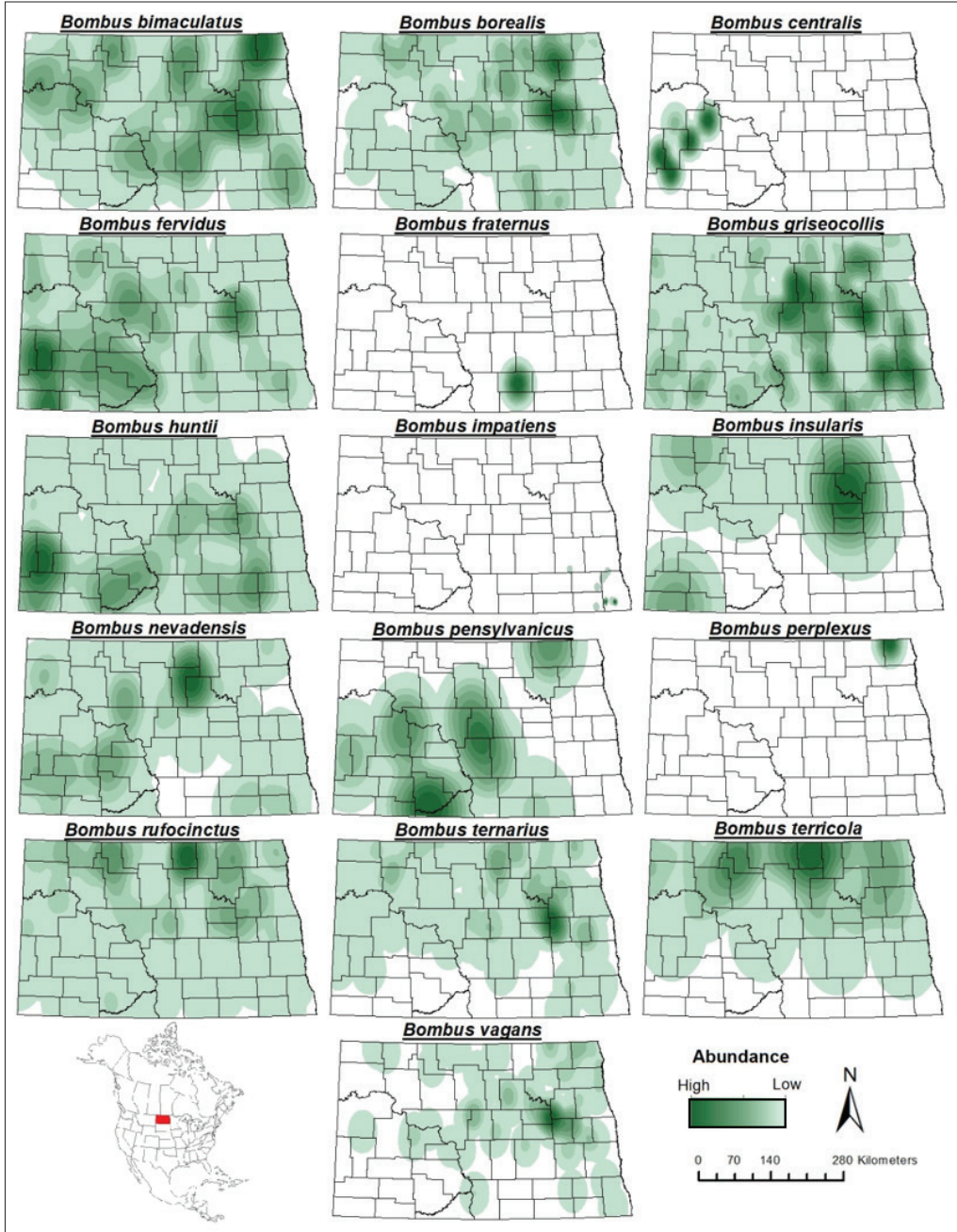
Figure 3. Kernel density maps of estimated abundance per bumble bee species captured in North Dakota between 2017 and 2020. Darker shading conveys higher observed abundance.

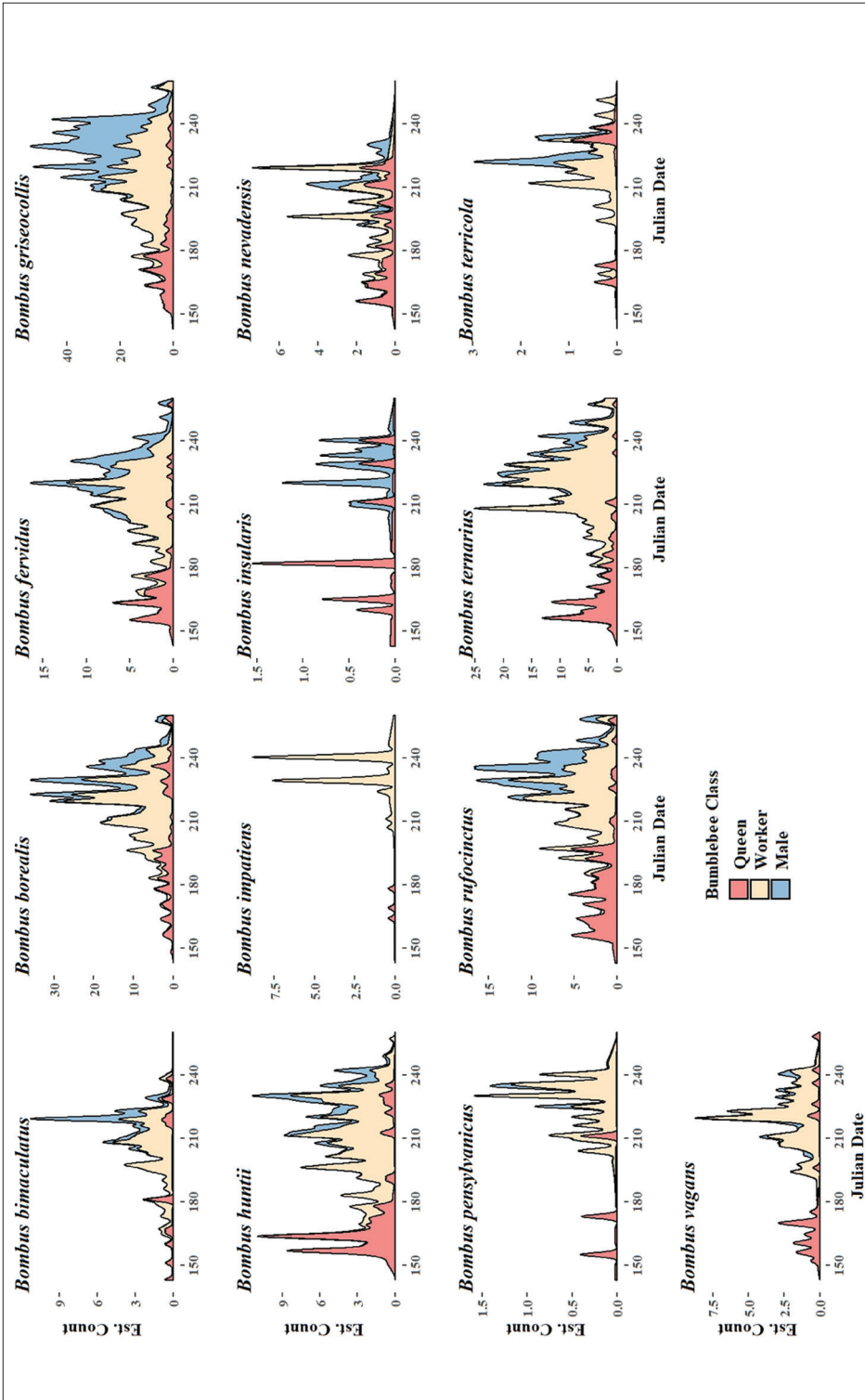C.K. Pei, T.J. Hovick, R.F. Limb, J.P. Harmon, and B.A. Geaumont

Figure 4. Estimated abundance (y-axes) of each bumble bee class (Queen, red; Worker, tan; Male, blue) over time per species captured in North Dakota between 2017 and 2020. Time is measured on the x-axis as Julian date. We omitted 3 species due to low detections.

griseocollis, *B. huntii*, *B. rufocinctus*, *B. ternarius*, and *B. terricola* interacted with a greater proportion of exotic plants than other bumble bee clusters while *B. bimaculatus*, *B. borealis*, *B. nevadensis*, and *B. vagans* largely interacted with a greater proportion of native plant species (Fig. 7).

Discussion

This extensive effort to perform a statewide bumble bee survey delivers distributional patterns of bumble bee species richness and individual species. In addition, this dataset provides phenological and floral resource information necessary to characterize bumble bee species specific to North Dakota, a state previously lacking native bee information. The data were collected with documented methodology and can be used as a baseline in future bumble bee population assessments by conservation managers and in conservation policy formation. It is essential that conservation strategies are data-driven with data that represents areas throughout species ranges rather than primarily based on historical occurrence records that are sparse in particular regions (Pyke and Ehrlich 2010). In addition , our surveys help address a deficiency of bumble bee data in North Dakota grasslands which have undergone compositional landscape and plant community transformations pertinent to the availability of bumble bee resources.

Range size impacts a threatened species' viability, making it important to obtain current distributional data (Williams et al. 2009). Results from our surveys inform current distribu-
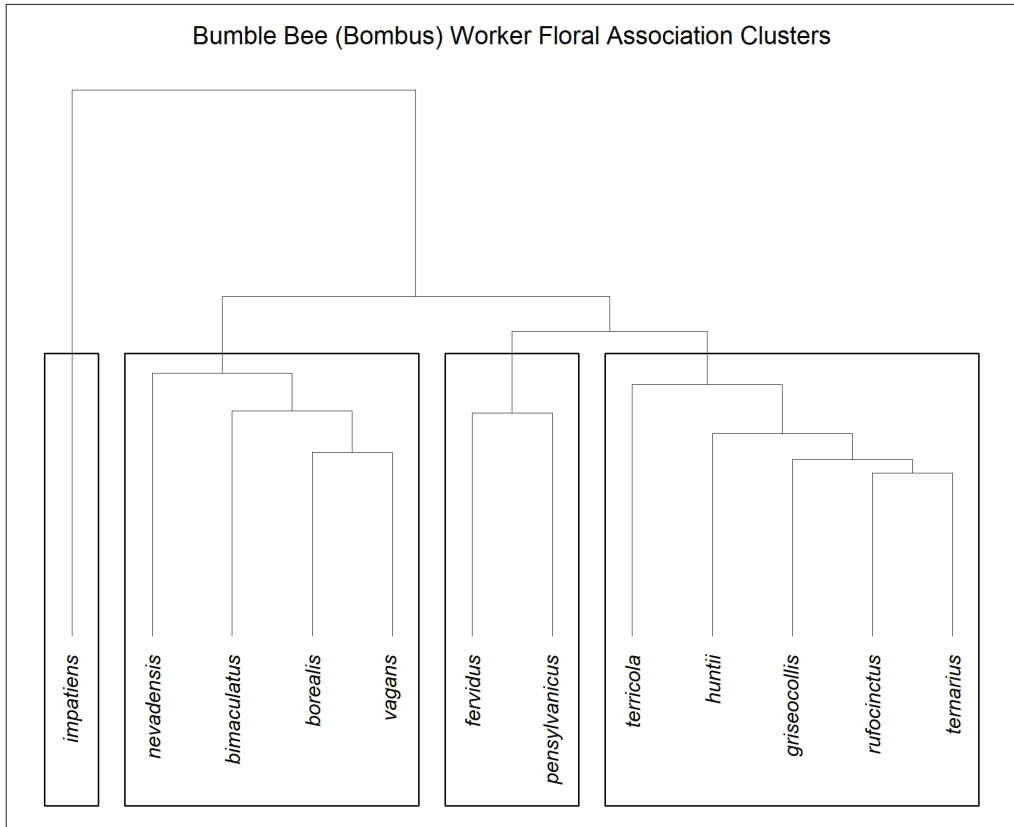

Figure 5. Cluster analysis results of bumble bee species based on similar proportional floral visitations from North Dakota between 2017and 2020. Rectangular boxes identify clusters.

tions and relative abundances of North American species of federal concern. We did not detect the endangered Rusty-patched Bumble Bee *B. affinis*, which was historically found in eastern North Dakota (US Fish and Wildlife Service 2017), nor did we observe *Bombus occidentalis*, a species whose status is currently under review by the US Fish and Wildlife Service (US Fish and Wildlife Service 2016). Our surveys are subject to discrete survey instances in time and space, but our high number of surveys and site visits may indicate that management for these species in North Dakota may not be practical. However, we detected modest occurrences of *B. terricola*, a species documented to be rare in other areas of the US Midwestern region (Grixti et al. 2009, Novotny et al. 2021). The conservation status of *Bombus terricola* warranted review
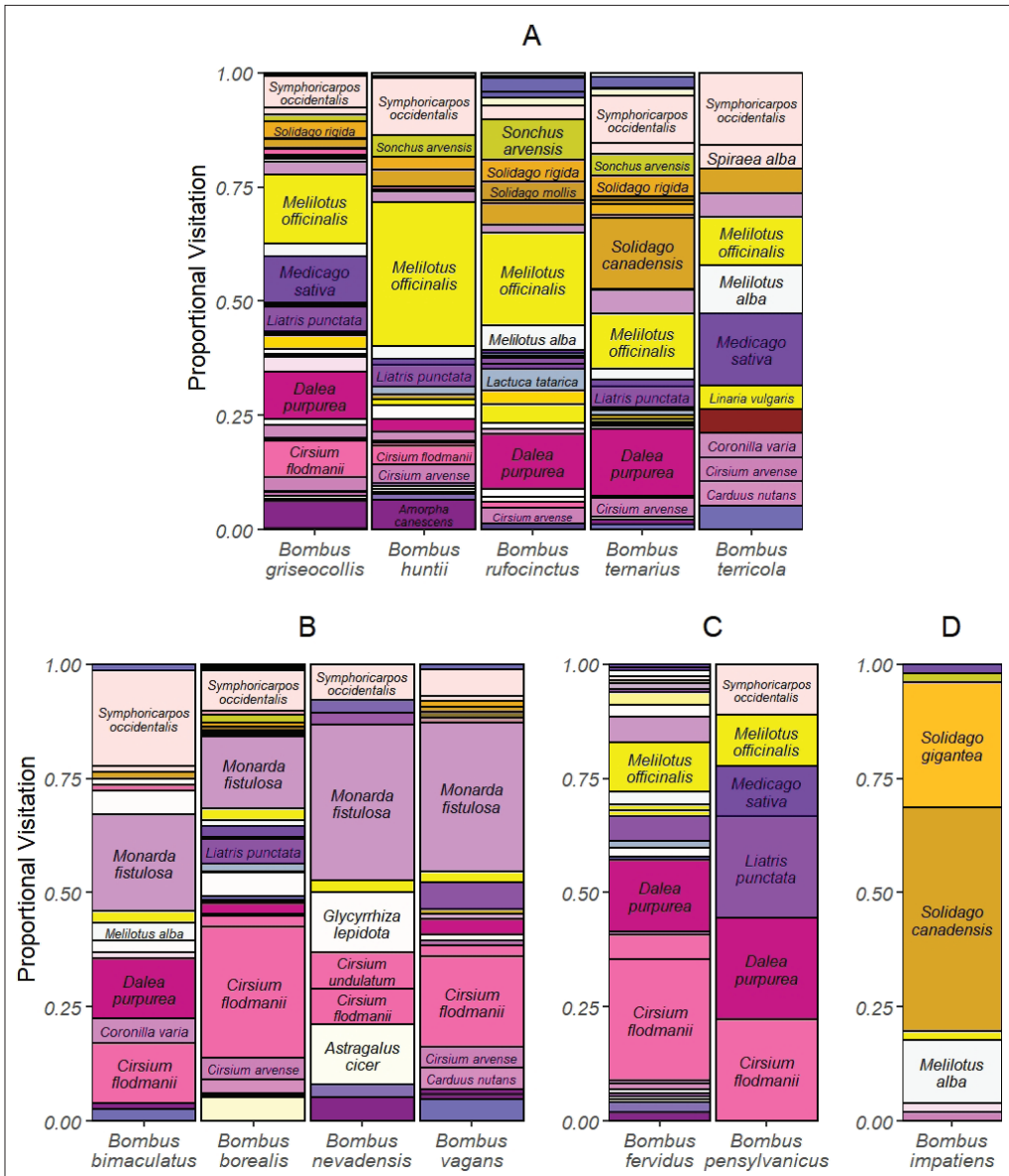

Figure 6. Proportional floral visitation by bumble bee species observed in North Dakota between 2017 and 2020. Bumble bee species are grouped based on cluster analysis results. Colors are consistent between all groups. Top 40% of plant species with which bees interacted are labeled.

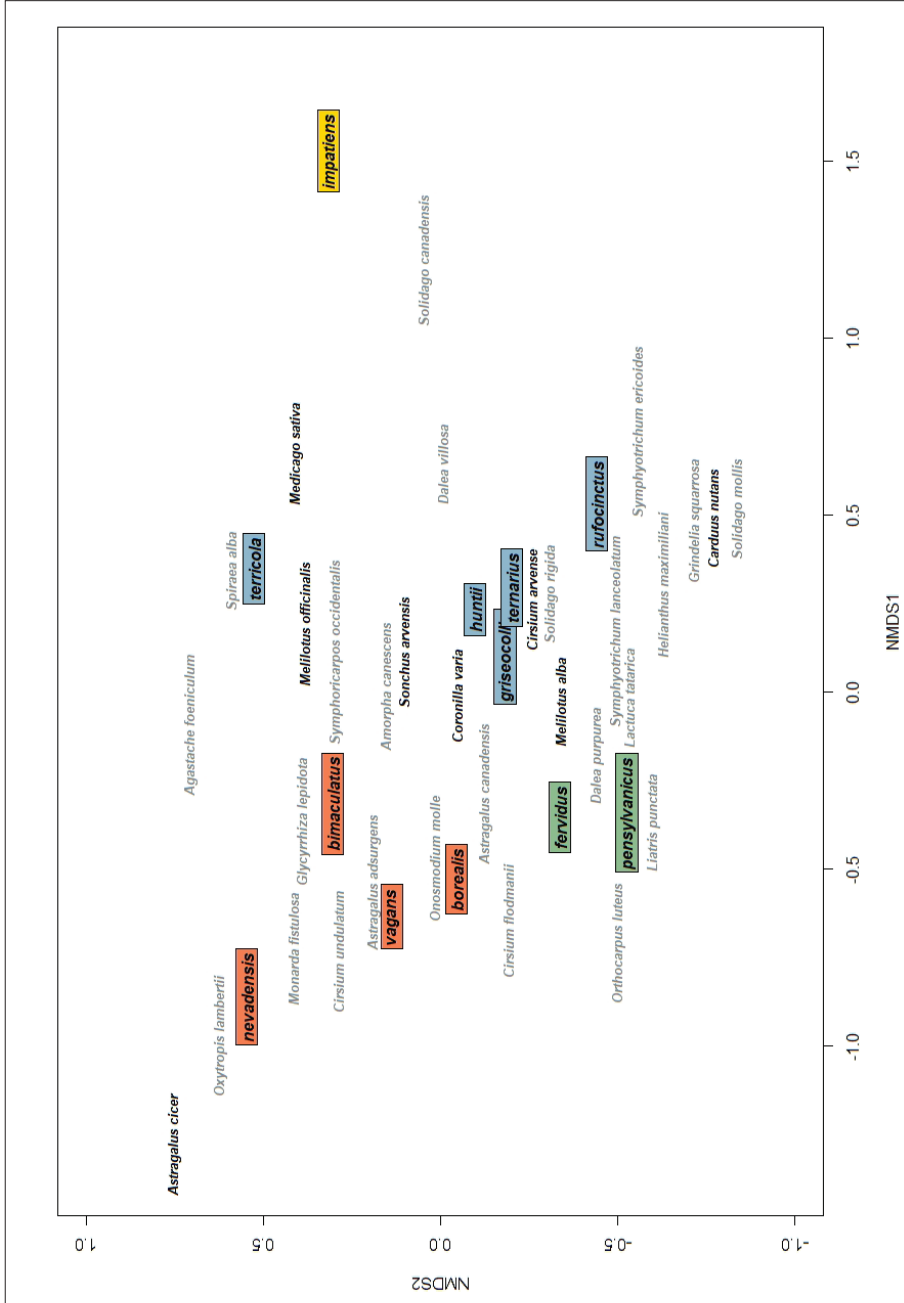C.K. Pei, T.J. Hovick, R.F. Limb, J.P. Harmon, and B.A. Geaumont

Figure 7. Non-metric multidimensional scaling ordination results displaying relationships between bumble bee species and proportional floral associations. Bumble bee species are labeled as their specific epithet and are colored to represent groupings based on cluster analysis on similar composition of floral visitations. Plant species names in grey are native while those in black are exotic plant species. Only the top 40% of plant species with which bees interacted are displayed for clarity.

by the US Fish and Wildlife Service, but the species was ultimately not listed for federal protection (US Fish and Wildlife Service 2016, 2019). Its northern distribution in the state delineates a region for targeted conservation strategies of this species.

Other species found in our study have been documented to have declining populations within their ranges. *Bombus fervidus* had relatively high abundances across North Dakota, but its status across North America may vary by region and appears to be declining in some areas, based on comparisons of museum and present-day records in Michigan, Vermont, New Hampshire, and Ontario, Canada (Colla et al. 2012, Colla and Packer 2008, Jacobson et al. 2018, Richardson et al. 2019, Wood et al. 2019), but its population is stable in Ohio (Novotny et al. 2021). Our observed distribution of *B. pensylvanicus* was sparse, with low relative abundance throughout North Dakota. This may be expected because North Dakota lies on the northern edge of its larger species distribution in the continent (Ascher and Pickering 2020, Williams et al. 2014). Cuckoo bumble bees (*Psithyrus* spp.) are suspected to be vulnerable to increased pressures due to the fact they are dependent on the presence of host bumble bee species in addition to other documented sources of decline (Colla and Packer 2008), but they may be more difficult to detect due to their life history. We only observed 1 *Psithyrus* species, *Bombus insularis*, of the 3 *Psithyrus* species previously recorded in the state (Colla et al. 2012, Williams et al. 2014).

In addition to distributional data, phenology breadths and periods can inform conservation efforts. Species that occur in narrower time frames may be more vulnerable because of increased dependence on floral resource availability during those specific time periods (Bartomeus et al. 2013, Goulson and Darvill 2004). However, the timing of peak abundances is likely important (Williams et al. 2009), as species with greatest population declines tend to have late peak abundances (Williams et al. 2009, Wood et al. 2019). Bumble bees with high abundances in the early season and late seasons in North Dakota may be more at risk of early or late cold events common in the Northern Great Plains (Kukal and Irmak 2018, Vasiliev and Greenwood 2021). Adverse risks of these events are greater when preceded by warm temperatures or when they occur multiple times (Bale and Hayward 2010, Roitberg and Mangel 2016). Additionally, early-season growth of invasive cool-season Kentucky Bluegrass decreases native forb diversity (DeKeyser et al. 2015, Gasch et al. 2020), adding another obstacle for bumble bees dependent on early-season floral resources.

Suitable floral availability is likely the most influential factor to bumble bee species (Cameron and Sadd 2020, Carvell et al. 2006, Edwards and Williams 2004, Williams and Osborne 2009), making it essential to accompany species data with floral associations. Bumble bees are generalists and exhibit high plasticity in pollen choices (Maebe et al. 2021), but they are known to be selective in their preferences, placing more value with some plant species than others (Carvell et al. 2006, Kleijn and Raemakers 2008, Wood et al. 2019). The groups (clusters) of bumble bees we identified convey this with 1 group comprised of *B. griseocollis*, *B. huntii*, *B. rufocinctus*, *B. ternarius*, and *B. terricola* having a wider diet breadth with a relatively higher perceived value placed on non-native plant species such as Sweet Clovers and Alfalfa, but another group having greater visitations with native species such as Wild Bergamot (*Monarda fistulos* Linnaeus) and native thistles (*Cirsium* spp.). *Bombus fervidus* and *B. pensylvanicus* seemed to visit a suite of flowers intermediary between the 2 groups above. Though visitation records do not necessarily represent preference (Carvell et al. 2006), these tendencies across a high number of sites and surveys may imply the relative value a plant species has for each bee species. These differences in associated plant species found between North Dakota bumble bees are important to conservation as they emphasize that floral resources for some species

may not serve others. This is especially pertinent in North Dakota, where high densities of Alfalfa and Sweet Clover are used in hayfields and other land management (Sanderson 2016). Though these species are valuable to honey bees (Niemuth et al. 2021, Otto et al. 2020, Smart et al. 2016) and may have some value to particular bumble bee species, they may be of little benefit to other bumble bees that prefer native plant resources (Otto et al. 2017). These differences in relative floral use convey the importance of the diverse availability of flowering plant species in supporting bumble bee diversity.

Future research on the ecology of bumble bees in the state should consider the potential anthropogenic pressures most relevant in North Dakota (Winfree et al. 2009). Grasslands and accompanying floral resources are subject to frequent conversion to cropland (Wimberly et al. 2017). Landscape studies can give insight into how patchy resources impact bumble bee species typically have greater mobility than other native bees (Hines and Hendrix 2005). In addition to reducing floral resources, the high levels of non-native plant species in the state warrant greater understanding of how changing resource availability affects bumble bee forage selection (Harmon-Threatt and Kremen 2015, Williams et al. 2011). For this, specific investigations into non-native nectar or pollen use are necessary for evaluating exotic plants' potential as resources for bumble bee species (Stout and Tiedeken 2017, Tepedino et al. 2008). Moreover, the density of honey bees is distinctive in North Dakota, prompting studies that include the relative importance of broad-scale resources to both honey bee and native bees (Evans et al. 2018, Simanonok et al. 2021). However, we find no evidence of investigations into direct honey bee relationships with native bees in the greater Northern Great Plains region. Evidence of competitive effects and transmission of parasites and pathogens from honey bees to wild bees warrants increased understanding of these relationships, particularly in this region of elevated honey bee colony density (Goulson 2003, Goulson and Sparrow 2009, Herbertsson et al. 2016, Thomson 2004).

Management Implications

Data in North Dakota are underrepresented in larger efforts to determine population trends of North American bumble bee species. It is necessary to include data from areas with knowledge gaps to avoid mischaracterizing populations and to support conservationists in creating the most informed management strategies. We provide important aspects of bumble bee ecology necessary to inform management for this group of increasing conservation interest. Distributional data provides spatial targets for conservation. While we provide species-specific distributions, we identified areas of the state with the greatest bumble bee richness, highlighting the importance of maintaining adequate floral resources in these state regions to support bumble bee diversity (Crone and Williams 2016). Phenological trends help understand species vulnerabilities, especially climatic variability and the timing of floral availability (Bartomeus et al. 2013, William et al. 2009). Our survey data highlight the floral resources most visited by each species in the state and provide evidence that managers should evaluate important floral resources on a bumble bee species-specific basis. Native bee species' diverse resource requirements necessitate land management practices that promote diverse floral resource availability.

Acknowledgements

Literature Cited

Arbetman, M.P., G. Gleiser, C.L. Morales, P. Williams, and M.A. Aizen. 2017. Global decline of bumblebees is phylogenetically structured and inversely related to species range size and pathogen incidence. Proceedings of the Royal Society B: Biological Sciences 284(1859):1–8. https://doi.org/10.1098/rspb.2017.0204

Ascher, J.S., and J. Pickering. 2020. Discover Life bee species guide and world checklist (Hymenoptera: Apoidea: Anthophila). Available online at http://www.discoverlife.org/mp/20q?guide=Apoidea_species. Accessed July 2021.

Bale, J.S., and S.A.L. Hayward. 2010. Insect overwintering in a changing climate. Journal of Experimental Biology 213:980–994. https://doi.org/10.1242/jeb.037911

Bartomeus, I., J.S. Ascher, J. Gibbs, B.N. Danforth, D.L. Wagner, S.M. Hedtke, and R. Winfree. 2013. Historical changes in northeastern U.S. bee pollinators related to shared ecological traits. Proceedings of the National Academy of Sciences of the United States of America 110(12):4656–4660. https://doi.org/10.1073/pnas.1218503110

Blitzer, E.J., J. Gibbs, M.G. Park, and B.N. Danforth. 2016. Pollination services for apple are dependent on diverse wild bee communities. Agriculture, Ecosystems and Environment 221:1–7. https://doi.org/10.1016/j.agee.2016.01.004

Bolstad, P. 2012. GIS Fundamentals: A First Text on Geographic Information Systems. 4th Edition. XanEdu. Ann Arbor, MI, USA. 688 pp.

Caliński, T., and J. Harabasz. 1974. A dendrite method for cluster analysis. Communications in Statistics 3:1–27. https://doi.org/10.1080/03610927408827101

Cameron, S.A., and B.M. Sadd. 2020. Global trends in bumble bee health. Annual Review of Entomology 65:209–232. https://doi.org/10.1146/annurev-ento-011118-111847

Cameron, S.A., J.D. Lozier, J.P. Strange, J.B. Koch, N. Cordes, L.F. Solter, and T.L. Griswold. 2011. Patterns of widespread decline in North American bumble bees. Proceedings of the National Academy of Sciences of the United States of America, 108:662–667. https://doi.org/10.1073/pnas.1014743108

Carvell, C., D.B. Roy, S.M. Smart, R.F. Pywell, C.D. Preston, and D. Goulson. 2006. Declines in forage availability for bumblebees at a national scale. Biological Conservation 132:481–489. https://doi.org/10.1016/j.biocon.2006.05.008

Colla, S.R., and L. Packer. 2008. Evidence for decline in eastern North American bumblebees (Hymenoptera: Apidae), with special focus on *Bombus affinis* Cresson. Biodiversity and Conservation 17:1379–1391. https://doi.org/10.1007/s10531-008-9340-5

Colla, S.R., F. Gadallah, L. Richardson, D. Wagner, and L. Gall. 2012. Assessing declines of North American bumble bees (*Bombus* spp.) using museum specimens. Biodiversity and Conservation 21:3585–3595. https://doi.org/10.1007/s10531-012-0383-2

Crall, J.D., C.M. Switzer, R.L. Oppenheimer, A.N. Ford Versypt, B. Dey, A. Brown, M. Eyster, C. Guérin, N. E. Pierce, S.A. Combes, and B.L. de Bivort. 2018. Neonicotinoid exposure disrupts bumblebee nest behavior, social networks, and thermoregulation. Science 362:683–686. https://doi.org/10.1126/science.aat1598

Crone, E.E., and N.M. Williams. 2016. Bumble bee colony dynamics: Quantifying the importance of land use and floral resources for colony growth and queen production. Ecology Letters 19:460–468. https://doi.org/10.1111/ele.12581

DeKeyser, E.S., L.A. Dennhardt, and J. Hendrickson. 2015. Kentucky bluegrass (*Poa pratensis*) Invasion in the Northern Great Plains: a story of rapid dominance in an endangered ecosystem. Invasive Plant Science and Management 8:255–261. https://doi.org/10.1614/IPSM-D-14-00069.1

Droege, S., V.J. Tepedino, G. Lebuhn, W. Link, R.L. Minckley, Q. Chen, and C. Conrad. 2010. Spatial patterns of bee captures in North American bowl trapping surveys. Insect Conservation and Diversity 37:15–23. https://doi.org/10.1111/j.1752-4598.2009.00074.x

Edwards, M., and P. Williams. 2004. Where have all the bumblebees gone, and could they ever return? British Wildlife 15:305–312.

Environmental Systems Research Institute (ESRI). 2014. ArcGIS Desktop Help 10.3 Spatial Analyst.

Evans, E., M. Smart, D. Cariveau, and M. Spivak. 2018. Wild, native bees and managed honey bees benefit from similar agricultural land uses. Agriculture, Ecosystems and Environment 268:162–170. https://doi.org/10.1016/j.agee.2018.09.014

Gallai, N., J.M. Salles, J. Settele, and B.E. Vaissière. 2009. Economic valuation of the vulnerability of world agriculture confronted with pollinator decline. Ecological Economics 68:810–821. https://doi.org/10.1016/j.ecolecon.2008.06.014

Garibaldi, L.A., L.G. Carvalheiro, S.D. Leonhardt, M.A. Aizen, B.R. Blaauw, R. Isaacs, M. Kuhlmann, D. Kleijn, A.M. Klein, C. Kremen, L. Morandin, J. Scheper, R. Winfree. 2014. From research to action: Enhancing crop yield through wild pollinators. Frontiers in Ecology and the Environment 12:439–447. https://doi.org/10.1890/130330

Garibaldi, L.A., I. Steffan-Dewenter, R. Winfree, M.A. Aizen, R. Bommarco, S.A. Cunningham, C. Kremen, L.G. Carvalheiro, L.D. Harder, O. Afik, I. Bartomeus, F. Benjamin, V. Boreux, D. Cariveau, N.P. Chacoff, J.H. Dudenhoffer, B.M. Freitas, J. Ghazoul, S. Greenleaf, J. Hipolito, A. Holzschuh, B. Howlett, R. Isaacs, S.K. Javorek, C.M. Kennedy, K.M. Krewenka, S. Krishnan, Y. Mandelik, M.M. Mayfield, I. Motzke, T. Munyuli, B.A. Nault, M. Otieno, J. Petersen, G. Pisanty, S.G. Potts, R. Rader, T.H. Ricketts, M. Rundlof, C.L. Seymour, C. Schuepp, H. Szentgyorgyi, H. Taki, T. Tscharntke, C.H. Vergara, B.F. Viana, T.C. Wanger, C. Westphal, N. Williams, and A.M. Klein. 2013. Wild pollinators enhance fruit set of crops regardless of honey bee abundance. Science 339:1608–1611. https://doi.org/10.1126/science.1230200

Gasch, C. K., D. Toledo, K. Kral-O'Brien, C. Baldwin, C. Bendel, W. Fick, L. Gerhard, J. Harmon, J. Hendrickson, T. Hovick, M. Lakey, D. McGranahan, S.K. Nouwakpo, and K. Sedivec. 2020. Kentucky bluegrass invaded rangeland: Ecosystem implications and adaptive management approaches. Rangelands 42:106–116. https://doi.org/10.1016/j.rala.2020.05.001

Goulson, D. 2003. Effects of introduced bees on native ecosystems. Annual Review of Ecology, Evolution, and Systematics 34:1–26.

Goulson, D., and B. Darvill. 2004. Niche overlap and diet breadth in bumblebees; are rare species more specialized in their choice of flowers? Apidologie 35:55–63. https://doi.org/10.1051/apido

Goulson, D., and K.R. Sparrow. 2009. Evidence for competition between honeybees and bumblebees; effects on bumblebee worker size. Journal of Insect Conservation 13:177–181. https://doi.org/10.1007/s10841-008-9140-y

Goulson, D., G.C. Lye, and B. Darvill. 2008a. Decline and Conservation of Bumble Bees. Annual Review of Entomology 53:191–208. https://doi.org/10.1146/annurev.ento.53.103106.093454

Goulson, D., G.C. Lye, and B. Darvill. 2008b. Diet breadth, coexistence and rarity in bumblebees. Biodiversity and Conservation 17:3269–3288. https://doi.org/10.1007/s10531-008-9428-y

Goulson, D., E. Nicholls, C. Botías, and E.L. Rotheray. 2015. Bee declines driven by combined stress from parasites, pesticides, and lack of flowers. Science 347:1255957 https://doi.org/10.1126/science.1255957

Graystock, P., K. Yates, S.E.F. Evison, B. Darvill, D. Goulson, and W.O.H. Hughes. 2013. The Trojan hives: Pollinator pathogens, imported and distributed in bumblebee colonies. Journal of Applied Ecology 50:1207–1215. https://doi.org/10.1111/1365-2664.12134

Grixti, J.C., L.T. Wong, S.A. Cameron, and C. Favret. 2009. Decline of bumble bees (*Bombus*) in the North American Midwest. Biological Conservation 142:75–84. https://doi.org/10.1016/j.biocon.2008.09.027

Harmon-Threatt, A.N., and C. Kremen. 2015. Bumble bees selectively use native and exotic species to maintain nutritional intake across highly variable and invaded local floral resource pools. Ecological Entomology 40(4):471–478. https://doi.org/10.1111/een.12211

Herbertsson, L., S.A.M. Lindstrom, M. Rundlof, R. Bommarco, and H.G. Smith. 2016. Competition between managed honeybees and wild bumblebees depends on landscape context. Basic and Applied Ecology 17:609–616. https://doi.org/10.1016/j.baae.2016.05.001

Hines, H.M., and S.D. Hendrix. 2005. Bumble bee (Hymenoptera : Apidae) diversity and abundance in tallgrass prairie patches: Effects of local and landscape floral resources. Environmental Entomology 34:1477–1484. https://doi.org/10.1603/0046-225X-34.6.1477

Jacobson, M.M., E.M. Tucker, M.E. Mathiasson, and S.M. Rehan. 2018. Decline of bumble bees in northeastern North America, with special focus on *Bombus terricola*. Biological Conservation 217:437–445. https://doi.org/10.1016/j.biocon.2017.11.026

Kerr, J.T., A. Pindar, P. Galpern, L. Packer, S.G. Potts, S.M. Roberts, P. Rasmont, O. Schweiger, S.R. Colla, L.L. Richardson, D.L. Wagner, L.F. Gall. D.S. Sikes, and A. Pantoja. 2015. Climate change impacts on bumblebees converge across continents. Science 349:177–180. https://doi.org/10.1126/science.aaa7031

Kleijn, D., and I. Raemakers. 2008. A retrospective analysis of pollen host plant use by stable and declining bumble bee species. Ecology 89:1811–1823. https://doi.org/10.1890/07-1275.1

Kosior, A., W. Celary, P. Olejniczak, J. Fijał, W. Król, W. Solarz, and P. Płonka. 2007. The decline of the bumble bees and cuckoo bees (Hymenoptera: Apidae: Bombini) of Western and Central Europe. Oryx 41:79–88. https://doi.org/10.1017/S0030605307001597

Kukal, M.S., and S. Irmak. 2018. US agro-climate in 20th century: Growing degree days, first and last frost, growing season length, and impacts on crop yields. Scientific Reports 8:1–14. https://doi.org/10.1038/s41598-018-25212-2

Maebe, K., A.F. Hart, L. Marshall, P. Vandamme, N.J. Vereecken, D. Michez, and G. Smagghe. 2021. Bumblebee resilience to climate change, through plastic and adaptive responses. Global Change Biology April:1–15. https://doi.org/10.1111/gcb.15751

Michener, C. 2007. The Bees of the World (2nd Edition). Johns Hopkins University Press, Baltimore, MD, USA. 992 pp.

Mitchell, T.B. 1962. Bees of the Eastern United States, Vol. II. The North Carolina Agricultural Experiment Station, Technical Bulletin 152.

Morse, D.H. 1981. Modification of bumblebee foraging: The effect of milkweed pollinia. Ecology 62:89–97.

Niemuth, N.D., B. Wangler, J.J. Lebrun, D. Dewald, S. Larson, T. Schwagler, C.W. Bradbury, R.D. Pritchert, and R. Iovanna. 2021. Conservation planning for pollinators in the U.S. Great Plains: considerations of context, treatments, and scale. Ecosphere 12:1–22. https://doi.org/10.1002/ecs2.3556

Novotny, J.L., P. Reeher, M. Varvaro, A. Lybbert, J. Smith, R.J. Mitchell, and K. Goodell. 2021. Bumble bee species distributions and habitat associations in the Midwestern USA, a region of declining diversity. Biodiversity and Conservation 30:865–887. https://doi.org/10.1007/s10531-021-02121-x

Oksanen, J., F.G. Blanchet, R. Kindt, P. Legendre, P. Minchin, R. O'Hara, G.L. Simson, P. Solymos, M.H.H. Stevens, and H. Wagner. 2015. Vegan: Community Ecology Package. R Package Version 2.3-0. Retrieved from http://cran.r-project.org/package=vegan%0A. Accessed July 2021

Otto, C.R., S. O'Dell, R.B. Bryant, N.H. Euliss, R.M. Bush, and M.D. Smart. 2017. Using publicly available data to quantify plant-pollinator interactions and evaluate conservation seeding mixes in the northern Great Plains. Environmental Entomology 46:565–578. https://doi.org/10.1093/ee/nvx070

Otto, C.R., A. Smart, R.S. Cornman, M. Simanonok, and D.D. Iwanowicz. 2020. Forage and habitat for pollinators in the Northern Great Plains—implications for US Department of Agriculture conservation programs. US Geological Survey Open-File Report 1037:1–63.

Potts, S.G., J.C. Biesmeijer, C. Kremen, P. Neumann, O. Schweiger, and W.E. Kunin. 2010. Global pollinator declines: Trends, impacts and drivers. Trends in Ecology and Evolution, 25:345–353. https://doi.org/10.1016/j.tree.2010.01.007

Pyke, G.H., and P.R. Ehrlich. 2010. Biological collections and ecological/environmental research: A review, some observations and a look to the future. Biological Reviews 85:247–266. https://doi.org/10.1111/j.1469-185X.2009.00098.x

Rafferty, N.E. 2017. Effects of global change on insect pollinators: multiple drivers lead to novel communities. Current Opinion in Insect Science 23:22–27. https://doi.org/10.1016/j.cois.2017.06.009

Rasmont, P., and S. Iserbyt. 2012. The Bumblebees Scarcity Syndrome: Are heat waves leading to local extinctions of bumblebees (Hymenoptera: Apidae: *Bombus*)? Annales de La Société Entomologique de France 48:275–280. https://doi.org/10.1080/00379271.2012.10697776

Richardson, L.L., K.P. McFarland, S. Zahendra, and S. Hardy. 2019. Bumble bee (*Bombus*) distribution and diversity in Vermont, USA: A century of change. Journal of Insect Conservation 23:45–62. https://doi.org/10.1007/s10841-018-0113-5

Roitberg, B.D., and M. Mangel. 2016. Cold snaps, heatwaves, and arthropod growth. Ecological Entomology 41:653–659. https://doi.org/10.1111/een.12324

Roulston, T.H., and K. Goodell. 2011. The role of resources and risks in regulating wild bee populations. Annual Review of Entomology 56(1):293–312. https://doi.org/10.1146/annurev-ento-120709-144802

Sanderson, M.A. 2016. Forage and grasslands as pollinator habitat in North Dakota. Crop, Forage and Turfgrass Management 2:1–6. https://doi.org/10.2134/cftm2016.08.0061

Shapiro, L.H., V.J. Tepedino, and R.L. Minckley. 2014. Bowling for bees: optimal sample number for "bee bowl" sampling transects. Journal of Insect Conservation 18:1105–1113. https://doi.org/10.1007/s10841-014-9720-y

Simanonok, S.C., C.R.V. Otto, and D.A. Buhl. 2021. Floral resource selection by wild bees and honey bees in the Midwest U.S.A: Implications for designing pollinator habitat. Restoration Ecology 1–11. https://doi.org/10.1111/rec.13456

Sjoberg, D. 2021. ggstream: Create Streamplots in 'ggplot2'. R package version 0.1.0.

Smart, M.D., J.S. Pettis, N. Euliss, and M.S. Spivak. 2016. Land use in the Northern Great Plains region of the US influences the survival and productivity of honey bee colonies. Agriculture, Ecosystems and Environment 230:139–149. https://doi.org/10.1016/j.agee.2016.05.030

Stokstad, E. 2007. The case of the empty hives. Science 316(5827):970–972. https://doi.org/10.1126/science.316.5827.970

Stout, J. C., and E.J. Tiedeken 2017. Direct interactions between invasive plants and native pollinators: Evidence, impacts and approaches. Functional Ecology 31(1):38–46.

Szabo, N.D., S.R. Colla, D.L. Wagner, L.F. Gall, and J.T. Kerr. 2012. Do pathogen spillover, pesticide use, or habitat loss explain recent North American bumblebee declines? Conservation Letters 5(3):232–239. https://doi.org/10.1111/j.1755-263X.2012.00234.x

Tepedino, V.J., B.A. Bradley, and T.L. Griswold. 2008. Might flowers of invasive plants increase native bee carrying capacity? Intimations from Capitol Reef National Park, Utah. Natural Areas Journal 28:44–50. https://doi.org/10.3375/0885-8608(2008)28[44:MFOIPI]2.0.CO;2

Thomson, D. 2004. Competitive interactions between the invasive European honey bee and native bumble bees. Ecology 85:458–470. https://doi.org/10.1890/02-0626

Thomson, D.M. 2016. Local bumble bee decline linked to recovery of honey bees, drought effects on floral resources. Ecology Letters 19(10):1247–1255. https://doi.org/10.1111/ele.12659

US Department of Agriculture National Agricultural Statistics Service. 2020. North Dakota Agricultural Statistics 2020. www.nass.usda.gov (Accessed July 2021).

US Fish and Wildlife Service. 2016. Endangered and threatened wildlife and plants; 90-Day Findings on 29 Petitions. Federal Register 81:14058–14072.

US Fish and Wildlife Service. 2017. Endangered and threatened wildlife and plants; Endangered species status for rusty patched bumble bee. Federal Register 82:3186–3208.

US Fish and Wildlife Service. 2019. Endangered and Threatened Wildlife and Plants; 12-Month Findings on Petitions to List Eight Species as Endangered or Threatened Species. Federal Registrar 84:41694–41699.

Vasiliev, D., and S. Greenwood. 2021. The role of climate change in pollinator decline across the Northern Hemisphere is underestimated. Science of the Total Environment 775:145788. https://doi. org/10.1016/j.scito tenv.2021.145788

Whitman, W.C. and M.K. Wali. 1975. Grasslands of North Dakota. Prairie: A Multiple View. University of North Dakota Press. Grand Forks, ND, USA. 433 pp.

Williams, N.M., D. Cariveau, R. Winfree, and C. Kremen. 2011. Bees in disturbed habitats use, but do not prefer, alien plants. Basic and Applied Ecology 12:332–341. https://doi.org/10.1016/j.baae.2010.11.008

Williams, P., S. Colla, and Z. Xie. 2009. Bumblebee vulnerability: Common correlates of winners and losers across three continents. Conservation Biology 23:931–940. https://doi.org/10.1111/j.1523-1739.2009.01176.x

Williams, P.H., and J.L. Osborne. 2009. Bumblebee vulnerability and conservation worldwide. Apidologie 40(3):367–387. https://doi.org/10.1051/apido/2009025

Williams, P.H., R.W. Thorp, L.L. Richardson, and S.R. Colla. 2014. Bumble Bees of North America. Princeton University Press, Princeton, NJ, USA. 208 pp.

Williams, P., S. Colla, and Z. Xie. 2009. Bumblebee vulnerability: Common correlates of winners and losers across three continents. Conservation Biology 23:931–940. https://doi.org/10.1111/j.1523-1739.2009.01176.x

Wimberly, M.C., L.L. Janssen, D.A. Hennessy, M. Luri, N.M. Chowdhury, and H. Feng. 2017. Cropland expansion and grassland loss in the eastern Dakotas: New insights from a farm-level survey. Land Use Policy 63:160–173. https://doi.org/10.1016/j.landusepol.2017.01.026

Winfree, R., R. Aguilar, D.P. Vazquez, G. Lebuhn, and M. Aizen. 2009. A meta-analysis of bees' responses to anthropogenic disturbance. Ecology 90:2068–2076.

Woodard, S.H., S. Federman, R.R. James, B.N. Danforth, T.L. Griswold, D. Inouye, L. Morandin, D.L. Paul, E. Sellers, J.P. Strange, M. Vaughan, N.M. Williams, M.G. Branstetter, C.T. Burns, J. Cane, A.B. Cariveau, D.P. Cariveau, A. Childers, C. Childers, D.L. Cox-Foster, E.C. Evans, K.K. Graham, K. Hackett, K.T. Huntzinger, R.E. Irwin, S. Jha, S. Lawson, C. Liang, M.M. López-Uribe, A. Melathopoulos, H.M.C. Moylett, C.R.V. Otto, L.C. Ponisio, L.L. Richardson, R. Rose, R.W. Singh, and W. Wehling. 2020. Towards a U.S. national program for monitoring native bees. Biological Conservation 252:108821. https://doi.org/10.1016/j.biocon.2020.108821

Wood, T. J., J. Gibbs, K.K. Graham, and R. Isaacs. 2019. Narrow pollen diets are associated with declining Midwestern bumble bee species. Ecology 100(6):1–15. https://doi.org/10.1002/ecy.2697