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Climate Change

Can Native Plants Mitigate Climate-related Forage Dearth for Honey Bees (Hymenoptera: Apidae)?

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Abstract

Extreme weather events, like high temperatures and droughts, are predicted to become common with climate change, and may negatively impact plant growth. How honey bees (*Apis mellifera* L. [Hymenoptera: Apidae]) will respond to this challenge is unclear, especially when collecting pollen, their primary source of protein, lipids, and micro-nutrients. We explored this response with a data set from multiple research projects that measured pollen collected by honey bees during 2015–2017 in which above-average temperatures and a drought occurred in 2017. We summarized the abundance and diversity of pollen collected from July to September in replicated apiaries kept at commercial soybean and corn farms in Iowa, in the Midwestern USA. The most commonly collected pollen was from clover (*Trifolium* spp. [Fabales: Fabaceae]), which dramatically declined in absolute and relative abundance in July 2017 during a period of high temperatures and drought. Due to an apparent lack of clover, honey bees switched to the more drought-tolerant native species (e.g., C*hamaecrista fasciculata* [Michx.] Greene [Fabales: Fabaceae], *Dalea purpurea* Vent. [Fabales: Fabaceae], *Solidago* spp. [Asterales: Asteraceae]), and several species of Asteraceae. This was especially noticeable in August 2017 when C. *fasciculata* dominated (87%) and clover disappeared from bee-collected pollen. We discuss the potential implications of climate-induced forage dearth on honey bee nutritional health. We also compare these results to a growing body of literature on the use of native, perennial flowering plants found in Midwestern prairies for the conservation of beneficial insects. We discuss the potential for drought resistant-native plants to potentially promote resilience to climate change for the non-native, managed honey bee colonies in the United States.

Key words: rainfall, temperature, native plant, *Apis mellifera*, climate change

Shortage in forage caused by loss of natural and semi-natural habitat contributes to high colony losses of honey bees (*Apis mellifera* L. [Hymenoptera: Apidae]) in both the United States and Europe (Naug 2009, Neumann and Carreck 2010, Potts et al. 2010, vanEngelsdorp and Meixner 2010, Goulson et al. 2015, Paudel et al. 2015, Steinhauer et al. 2018). In addition to this loss of habitat, climate change is expected to exacerbate honey bee health issues by further limiting forage (Le Conte and Navajas 2008, vanEngelsdorp and Meixner 2010, Reddy et al. 2012, Goulson et al. 2015). Even in the absence of extreme weather events, precipitation and temperatures appear to have a strong impact on honey bee health (Calovi et al. 2021). An increase in summer temperatures and reduced rainfall are associated with the changing climate and are anticipated to reduce plant diversity (Moran et al. 2014, Scheper et al. 2014, Harrison et al. 2015). Honey bees reduce the amount of nectar and pollen foraging trips when high temperatures occur to avoid overheating during flight (Woods et al. 2005). Drought can reduce the availability of nectar and pollen from plants (Waser and Price 2016, Phillips et al. 2018) which could further exacerbate the impact of climate change on forage availability for honey bees (vanEngelsdorp and Meixner 2010). Pollen is an extremely important component of the honey bee diet, providing the majority of their protein/amino acids, lipids, and

micro-nutrients (Black 2006, Vaudo et al. 2015, Wright et al. 2018). Anticipating the effect of climate change on honey bees' ability to collect pollen can help develop measures to ensure forage availability for honey bees and other pollinators.

Since honey bees are extreme generalists, capable of foraging on a wide range of plants, it is unclear how extreme weather events will affect pollen collection (e.g., its abundance and taxon richness). Honey bees may be buffered from climate-induced shifts in forage availability due to their polylectic feeding habits, especially in landscapes with diverse floral resources. Honey bees may be able to shift from using plants affected by certain forms of climate-change induced stress (e.g., drought-sensitive) to others (e.g., drought-tolerant). However, if floral resources are already limited in an agricultural landscape, the additional constraint of severe weather may make honey bees more susceptible to the negative impacts of forage dearth. Efforts to restore or reconstruct habitat for pollinator conservation without considering the consistency of the plant community over time will limit the value of these efforts for conserving honey bees and other pollinators. Studying forage use by honey bees across multiple years with fluctuating weather patterns that include extreme temperatures and drought can reveal how pollinators respond to these events.

The Midwestern United States is an example of where forage loss due to agricultural intensification has had a negative impact on honey bee health (Wright and Wimberly 2013, Otto et al. 2018, Dolezal et al. 2019). The climate in this region is predicted to become warmer, with more frequent droughts into the rest of the 21st century (Wuebbles et al. 2017). Studying the potential impact of climate change on honey bee health is challenging given the large foraging range of honey bees throughout the entire growing season. We took advantage of multi-year and multi-month investigations of honey bee health and foraging behavior in central Iowa to determine if extreme high temperatures (above historical average and surpassing the temperatures for optimal growth of plants) and drought during these experiments explained variation in honey bee foraging behavior. These weather data were compared to a data set of honey bee-collected pollen from multiple years of deploying sentinel apiaries at or in fields of corn or soybean. We aimed to find potential correlations in the amount and diversity of bee-collected pollen with inter-year climatic variation, and inform ways to modify the landscape such that honey bees could be more resilient to climate change.

Table 1. Summary of information about research sites, colonies, and sampling frequency

Year	Number of sites (apiary)	Pollen traps per site (apiary)	Frequency of pollen sampling/ colony inspection		
			Jul.	Aug.	Sep.
2015	10	1	5/2	3/2	2/1
2016	10	1	4/2	3/2	1/1
2017[a]	7 (4)[b]	2	2/1	2/2	3/2
	7 (3)	2	5/2	4/3	3/2

[a]In 2017, the two subsets of sites (four vs three) has different sampling frequency, and we use average pollen per date to account for the variation in sampling frequency. Pollen abundance data from all the seven sites were used for analysis.

[b]Taxon richness of plants as pollen source from the subset of four sites were used for analysis.

Materials and Methods

Sites and Honey Bee Colonies

Data were collected from a total of 27 sites (10 in both 2015 and 2016, and 7 in 2017) distributed across three counties (Boone, Marshall, and Story) in central Iowa, USA (Table 1). These sites were used for previous experiments exploring the impact of agriculture on honey bee health and productivity (Dolezal et al. 2019, Zhang 2020, Zhang et al. 2020). These experiments included the location of placing an apiary next to 26 soybean fields and one cornfield (used in 2017 only). Previous analysis of data in this region indicated that amount of honey bee-collected pollen did not vary significantly between apiaries located at corn and soybean fields (Zhang 2020). The locations varied among years but were in the same three-county region. Agriculture is common in central Iowa's landscape, with approximately 64% of this three county area used for soybean and corn production (USDA-NASS 2019). In each year, the dominant features surrounding the apiaries in a 1.6 km radius were soybean and corn fields (64% in 2015, 59% in 2016 [data cited from Dolezal et al. 2019] and 66% in 2017). Neither reconstructed nor remnant prairies were adjacent to any apiaries in 2015 and 2016. In 2017, two of our seven sites had access to small patches of prairie inside an adjacent crop field (Zhang 2020).

Each site with an apiary was an experimental unit in this analysis. The number of colonies (Table 1) and the position of an apiary varied by year. Colonies were equalized at the beginning of each year to a consistent size and then randomly assigned to each location. All the colonies predominantly derived from stocks of Italian honey bees (*Apis mellifera ligustica*) and housed in conventional Langstroth hives. No supplemental food (sugar solution or pollen patty) was provided to colonies in any year after they were moved to soybean or corn fields. Colonies were treated with thymol (Apilife Var, Chemicals Laif SPA, Vigonza, Italy) to control Varroa mite infestations in the end of August or the beginning of September to control infestations. In 2015 and 2016, apiaries were comprised of four colonies and were located at a margin of a soybean field at 10 sites. In 2017, we had four sites (three soybean fields and one corn field) with apiaries of two colonies located at field margins, and three sites with apiaries of 16 colonies located in the center of a soybean field. Although the number of colonies in an apiary varied, we did not observe a significant difference in the mean amount of pollen collected by a colony when kept in apiaries of two versus 16 colonies (Supp Fig. 1 [online only]).

Pollen Collection and Identification

One colony was randomly selected at each site for an entrance pollen trap (Brushy Mountain Bee Supply, Wilsonville) in 2015–2016. In 2017, sites with two colonies had a pollen trap on each colony; while, the sites with 16 colonies had two randomly selected colonies used for pollen collection (Table 1). Pollen was collected during a 24-h period, selected based on weather forecasts considered favorable for honey bee foraging (e.g., no precipitation). In 2015 and 2016, the weight of pollen collected within a trap in each apiary was recorded. When two traps at an apiary were used in 2017, the weight of pollen sample from each trap was measured separately and the average weight was calculated. The average weight was used in our analysis, as each location was considered the experimental unit. We estimated the correlation of a weather pattern within a month period with the amount of pollen collected in that month across years. The frequency of pollen collected varied between years in each month, therefore, we calculated the pollen weight per colony per date (24 h collection period) to account

for the variation in sampling frequency. We summed the pollen weight per colony per date across collection days within a month and divided by number of days in which pollen was collected. We also monitored colony weight in 2015–2017 and these data indicated that abundance of pollen (i.e., pollen weight per colony per date) collected by honey bees was positively associated with colony weight (Supp Fig. 2 [online only]).

To account for the variation in pollen abundance due to variation in colony size (i.e., weight) among years, the average pollen weight per date at each apiary was normalized by the average colony weight during the same month at the corresponding apiary. Colonies with pollen traps were weighed with a digital scale during regular colony inspections (Table 1). The colony weight was calculated by estimating the difference between the whole colony weight (including both hive equipment and bee biological matters, e.g., bees, food stores, and wax comb) and hive equipment weight (including hive box, lid, bottom board, frames without wax comb, and pollen trap). In 2015 and 2016, the weight of the single colony with a pollen trap in each apiary was measured during each apiary inspection and average weight across a month was used for normalizing pollen. In 2017, the weight of two colonies with pollen traps at an apiary was averaged for each inspection date and then the monthly average weight was calculated across all the inspection dates. Pollen samples were stored at −20°C until the abundance and richness of plant taxa could be estimated.

To assess the richness of plant taxa used by honey bees for pollen, 2 g of pollen was randomly extracted from homogenously mixed pollen. This sub-sample was taken from each pollen trap at every apiary on all sampling dates in 2015 and 2016. When a site had two pollen traps in 2017, pollen from the two traps were mixed and a 2 g subsample was randomly extracted. Because pollen collected from three sites with 16 colonies per site was used in other experiments, taxon richness was only estimated among the rest four sites in July 2017. Each pollen pellet within the subsample was sorted by color and pellets of the same color were combined and weighed (Almeida-Muradian et al. 2005, Bilisik et al. 2008, Girard et al. 2012). Pollen pellets of the same color were dissolved in Calberla's fluid, and then mounted onto separate glass slides. The pollen on a slide was assigned to a plant species after examining the morphological features of 100 random pollen grains under a light microscope at 200-magnification. In our study, the majority of pollen pellets of the same color mounted to slides were from single plant. If pollen from a second plant was observed but accounted for less than 15% of the grains, the pellet was assigned to the species representing the remaining 85%. In cases when pollen was more evenly distributed among two to three plant species, we calculated the proportion of each pollen considering both their number and size within the 100 grains. The percentage of each plant represented in the pollen was calculated by dividing the weight of pollen pellets of the same color from the 2 g subsample. Number of plants represented in pollen samples per apiary per date were used to compare taxa richness across each year.

To describe the general foraging pattern for pollen by honey bees, we summarized the most common plants that were collected by honey bees that represented > 5% of the weight for each sample at all sites. These pollens were identified to reference images of pollen collected from plants found within 100 m radius of bee hives at the research sites during this study to confirm the source of pollen. Those pollen grains that represented <5% were combined into a separate category (i.e., 'other pollen').

Estimation of Extreme Weather Events

We estimated if extreme high temperatures and droughts occurred from July to September across a 3-yr period (2015–2017) by comparing summer temperatures and rainfall with optimal temperatures for plant growth and average historical rainfall. Instead of using raw temperature data, we used growing degree days (GDD, which better reflects the impact of temperature on plant growth and development) (Kadioğlu and Şaylan 2001, Thuiller et al. 2005). After converting temperatures to GDD, we compared the actual GDD occurring during 2015–2017 with optimum GDD for flowering plants in each month.

The following formula was used for calculating actual daily GDD: 1/2 (maximum temperature + minimum temperature) − base temperature. The monthly GDD was a sum of daily GDD within a month. Maximum and minimum temperatures for a location were determined from local weather stations. Temperature data were collected from three weather stations (USC00130200 in Boone County, USW00094988 in Marshall County, and USW00094989 in Story County) which were within 21.2 Km of each apiary. These data were downloaded from the National Centers for Environmental Information website (National Oceanic and Atmospheric Administration, Asheville).

We lack information regarding the base and optimum temperatures for the many wild flowering plants growing in Iowa that are used by honey bees for pollen. We selected white clover (*Trifolium repens* L. [Fabales: Fabaceae]) as a representative plant to calculate an optimum GDD for all flowering plants. We selected clover because it is commonly used for pollen by honey bees in Iowa (Zhang et al. 2020), and its response to temperature has been well studied. We used 10°C as the base temperature for white clover (Baxter et al. 2019) to initiate growth in the GDD equation. White clover (*T. repens*) is also considered to be sensitive to a limited water supply (Woodfield et al. 1996), and optimum growth can decrease from 30°C to 24°C when water is restricted (Mitchell and Lucanus 1962, Ostrowski 1972). Selecting white clover to represent the response of all plants to heat and drought stress results in several assumptions regarding how all of the plants used by honey bees would respond to weather. For example, some clover species (*T.* spp.) have been introduced to North America and grown deliberately through domestication and cultivation within pastures. These varieties may have been selected for agronomic features and not necessarily to match the ecology of this region. We anticipate that a subset of plants native to this region are more drought and heat tolerant, and thus less responsive to variation in both temperature and water availability, resulting in greater resilience. Therefore, we note that this overall estimate of plant response to extreme weather is a conservative estimate. The optimum GDD for clover was calculated with the following equation: 1/2 (optimum temperature + minimum temperature) − base temperature. The monthly optimum GDD was calculated as a sum of daily optimum GDD across all days within each month. To confirm if high temperatures occurred in the periods when we estimated GDD, we also counted the number of days with temperature above 30°C in July to September in 2015–2017.

Rainfall was monitored for the past 20 yr across all of these weather stations adjacent to our research sites, and an average historical monthly rainfall was calculated within this 20-yr period (1998–2017). We defined drought (classified as a meteorological drought defined at https://www.weather.gov/safety/drought-types) as a period time when precipitation was below the 20-yr average. Duration of meteorological droughts can vary from weeks to decades, and in our study, we explored if drought occurred by comparing rainfall totals accrued per month (July to September) during

the 3 yr of this study (2015–2017) to 20-yr averages for each corresponding month. Rainfall data were extracted from the three weather stations described above.

Statistical Analysis

We used ANOVA to determine if there was significant variation in the total pollen collected between years, including one year in which extreme occurred (see Results). A Wilcoxon test was used to determine if plant richness of bee-collected pollen varied significantly between years in each month (July–September) (JMP Pro 15.2, SAS, Cary, NC). Pollen abundance data were transformed with natural logarithm to increase normality. A Wilcoxon test was used to compare the abundance of pollen from drought tolerant species among years.

Results

Occurrence of Extreme Weather Events

We first determined if extreme weather events (i.e., high temperatures and droughts) occurred during the period when we monitored pollen foraging by honey bees. The lowest monthly rainfall for the month of July occurred in 2017 (71.6 mm) which was 26% lower than the 20-yr average (96.7 mm) (Supp Table 1 [online only]). We considered this month to have experienced meteorological drought. Monthly optimum GDD for clover would be 430°C when water supply is sufficient (Supp Table 2 [online only]). This optimum GDD for clover can be as low as 337°C (Supp Table 3 [online only]) when considering the impact of drought in this month. Because the actual monthly GDD (437°C) for July in 2017 (Fig. 1) was higher than optimum monthly GDD for clover (430°C and 337°C with and without sufficient water supply), we considered that high temperatures occurred in July of 2017. We counted number of days with temperatures above 30°C in each month of July to September across the 3 yr to confirm the accuracy of the above estimation using GDD. There were 16 d above 30°C during July 2017 and only 6.3 d in 2015 and 9.5 d in 2016 (Supp Table 4 [online only]). Neither extreme high temperatures nor meteorological drought occurred in July of 2015 and 2016, but temperature and rainfall in July of 2016 was intermediate between 2015 and 2017.

Drought also occurred in August of 2017, as the monthly rainfall was 103.3 mm, or 13.59% lower than the 20-yr average (119.54 mm) (Fig. 1, Supp Table 2 [online only]). The monthly GDD (313.5°C) did not exceed the optimum monthly GDD (366.90°C) in August across these 3 yr, and we used this as evidence that these times did not experience unusual high temperatures (Fig. 1, Supp Table 2 [online only]). The drought during August 2017 likely reduced the optimum temperature from 30°C to 24°C, resulting in monthly GDD (313.5°C) exceeding the optimum monthly GDD (288.85°C).

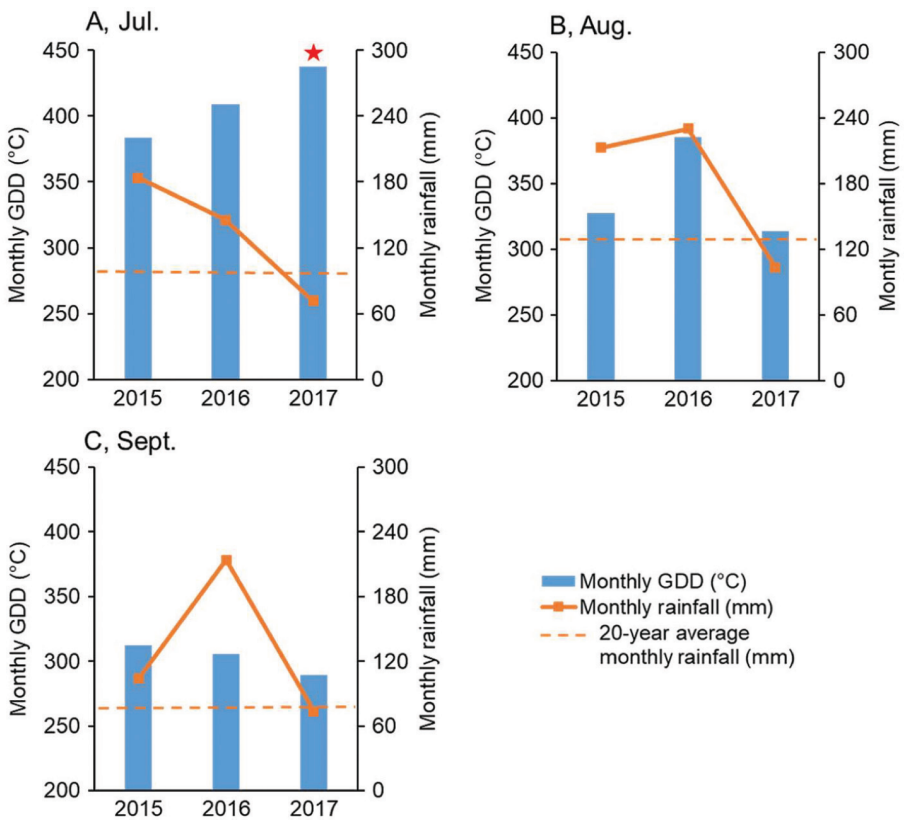

Fig. 1. Monthly growing degree days (GDD) and monthly rainfall in the study area across 3 yr (2015–2017). The monthly rainfall of July in 2017 was below the 20-yr average monthly rainfall (labeled with orange dash line), indicating a drought. In the same month, the actual monthly GDD was above optimum GDD no matter if the impact of drought is considered or not, indicating the extreme high temperatures (labeled with a red star). July 2017 had 16 d with temperatures above 30°C; while, 6.3 d in July 2015 and 9.5 d in 2016, in accordance with the estimation of GDD. In August 2017, a drought occurred based on the below average monthly rainfall. The actual monthly GDD did not exceed optimum monthly GDD (this value calculated with optimum temperature at 30°C) when the impact of drought was not considered. However, if the potential of drought on plant was considered (a drop in optimum temperature from 30 to 24°C), the actual GDD would exceed optimum GDD, suggesting a potential high temperature. In September 2017, a slight drought was monitored, but the temperature was not considered extreme.

The monthly rainfall in September of 2017 (73.7 mm) was 5.3% lower than the 20-yr average (77.81 mm), indicating a slight drought occurred. Temperatures cooled down in September of 2017 following the hot and drought July and August. Neither high temperatures nor drought occurred in September of 2015 and 2016.

Variation in Pollen Collection

The amount of pollen collected in July 2017 was significantly lower than that collected in 2015 (F = 3.695; df = 2, 26; P = 0.0399; multiple comparison by HSD; Fig. 2A); and the 2016 pollen amount was numerically intermediate, and not statistically different from either between 2015 or 2017. The amount of pollen did not significantly differ among years for August (F = 1.925; df = 2, 26; P = 0.168; Fig. 2B) and September (F = 0.998; df = 2, 25; P = 0.384; Fig. 2C).

In July, the richness of pollen collected in 2017 was significantly higher than that of 2015; while the richness in 2016 was intermediate between 2015 and 2017 (χ^2 = 8.15; df = 2; P = 0.017; multiple comparison by Wilcoxon; Fig. 3A). The richness represented in bee-collected pollen did not significantly differ among years for August (χ^2 = 0.73; df = 2; P = 0.694; Fig. 3B) and September (χ^2 =5.23; df = 2; P = 0.073; Fig. 3C).

The five most common sources of pollen (i.e., > 5% and collected at more than two sites on any sampling date) were clover (*Trifolium* spp. [Fabales: Fabaceae]), partridge pea (*Chamaecrista fasciculata* [Michx.] Greene [Fabales: Fabaceae]), purple prairie clover (*Dalea purpurea* Vent. [Fabales: Fabaceae]), sunflowers (*Helianthus, Heliopsis & Silphium* spp. [Asterales: Asteraceae]), and goldenrod (*Solidago* spp. [Asterales: Asteraceae]). Across the 3 yr, clover was the most common non-native pollen source in every month except for August 2017, and partridge pea (Houck and Row 2019) was the most common native pollen source from July to August (Fig. 4). Sunflower and goldenrod were common native pollen sources for honey bees in July and September 2017.

We explored the relationship between the contributions of clover versus the contribution of native, more drought-tolerant plants to the pollen collected by honey bees in July. The percent of clover pollen was statically lower in July 2017 than 2015 (χ^2 = 5.99; df = 2; P = 0.05; nonparametric comparisons using Wilcoxon method; Supp Tables 5 and 6 [online only]; Fig. 4), and clover pollen from July 2016 was intermediate. The absolute abundance of clover in bee-collected pollen in July 2017 was statistically lower than both 2015 and 2016, while 2016 was intermediate (Supp Table 7 [online only]). When summing pollen collected from the three most common taxa (sunflowers, goldenrod, purple prairie clover) that are drought tolerant, we found they were significantly higher in both absolute abundance (χ^2 = 10.37; df = 2; P = 0.0056) and relative abundance (in percentage, χ^2 = 10.47; df = 2; P = 0.0053; Fig. 4) in July 2017. The presence of pollen from these native plants was not limited to the two sites that had access to small patches of reconstructed prairie in 2017. All three of these taxa were found in at least 50% of all sites and at least two taxa were found at all sites in July 2017. In contrast, honey bees collected these species at < 50% sites in July of 2015 and 2016 and the percentage of these species was < 1.1%. This switch to drought tolerant species for pollen across multiple sites was likely not due to the two sites having access to small patches of prairie. Rather, these results suggest that a change occurred in the honey bee foraging behavior during July in this 3-yr period across all sites.

Discussion

There is increasing concern for the impact of climate change on forage availability in the context of bee health (Kammerer et al. 2021). Extreme weather events (e.g., high temperatures and droughts) are predicted to be more common in the future, while honey bee health and nutritional issues continue to deteriorate. Understanding how bees utilize different sources of forage under extreme weather conditions can provide insight into how this could be mitigated. We were fortunate to have the resources to study the foraging behavior of honey bees with standardized apiaries deployed in several on-farm settings across central Iowa. We were even more fortunate to conduct these experiments during a 3-yr period in which extreme weather occurred in at least 1 yr for several weeks. We recognize that this is a limited data set and that the approach we used to explore the impact of extreme weather is not ideal, as it explores data collected in different apiary locations and similar though separate experiments (Dolezal et al. 2019, Zhang 2020, Zhang et al. 2020). Despite this potential source of variation, we do not think it is responsible for observed trends in pollen foraging. The specific experiments from which these data were designed to explore the impact of

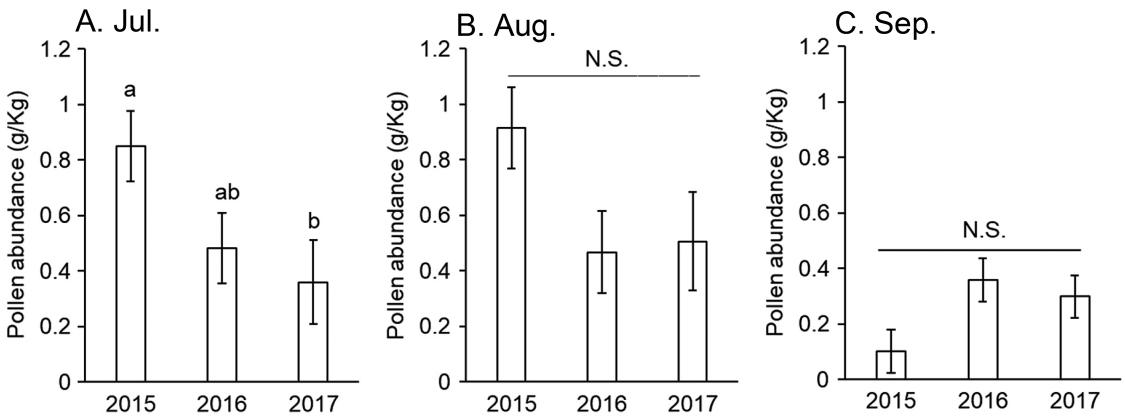

Fig. 2. Abundance of honey bee-collected pollen (mean g/Kg + SE per colony per day) in 3 mo across 2015–2017.The weight of pollen was divided by the weight of the colony to adjust for variation in colony size between years, resulting in a unit of g/kg for the measurement of abundance. Abundance data collected from ten sites in both 2015 and 2016 and from seven sites in 2017 were used for this analysis. (A) Different letters on each column indicate differences (F = 3.695; df = 2, 26; P = 0.0399). In July, pollen abundance from 2017 was significant lower than 2015; abundance from 2016 was intermediate between 2015 and 2017. In both August (B) and September (C), pollen abundance did not differ significantly (N.S.) between years (August: F = 1.925; df = 2, 26; P = 0.168; September: F = 0.998: df = 2, 25; P = 0.384).

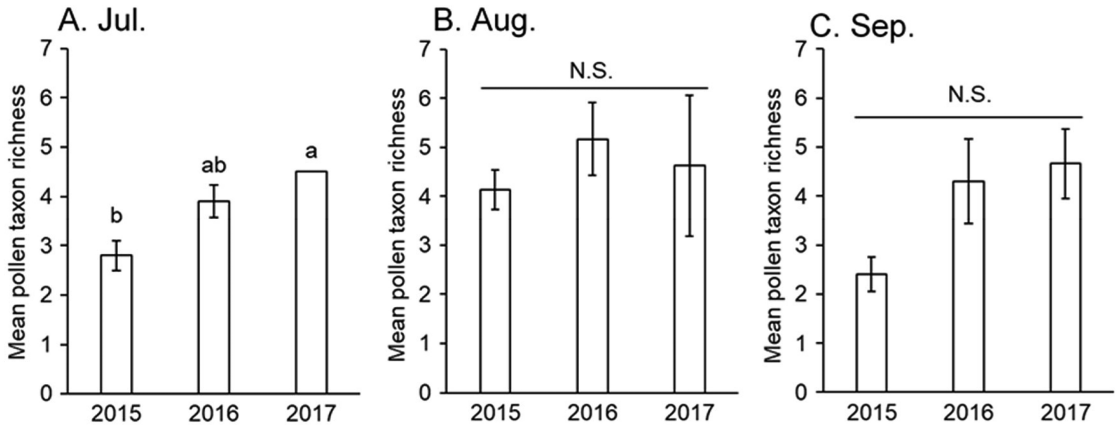

Fig. 3. Taxon richness (+ SE) of honey bee-collected pollen per apiary per date in 3 mo across 2015–2017. Data collected from 10 sites from both 2015 and 2016 and from 4 sites from 2017 were used for this analysis. (A) Different letters on each column indicate differences ($\chi^2 = 8.15$; df = 2; $P = 0.017$). In July, taxon richness from 2017 was significantly higher than 2015; 2016 was intermediate between 2015 and 2016. Although there were fewer samples of pollen collected in July of 2017, we observed higher taxa richness in this month indicating the difference in sampling frequency was not responsible for the difference in taxon richness among years in July. The taxa richness in July 2017 had zero variance with an average of 4.5 taxa observed per location; while in July 2015, eight of ten sites had < 3 taxa found. The pattern suggests the unequal amount of site replications was not responsible for the difference in taxon richness. In both August (B) and September (C), pollen taxon richness was not significant (N.S.) different between years (August: $\chi^2 = 0.73$; df = 2; $P = 0.694$; September: $\chi^2 = 5.23$; df = 2; $P = 0.073$).

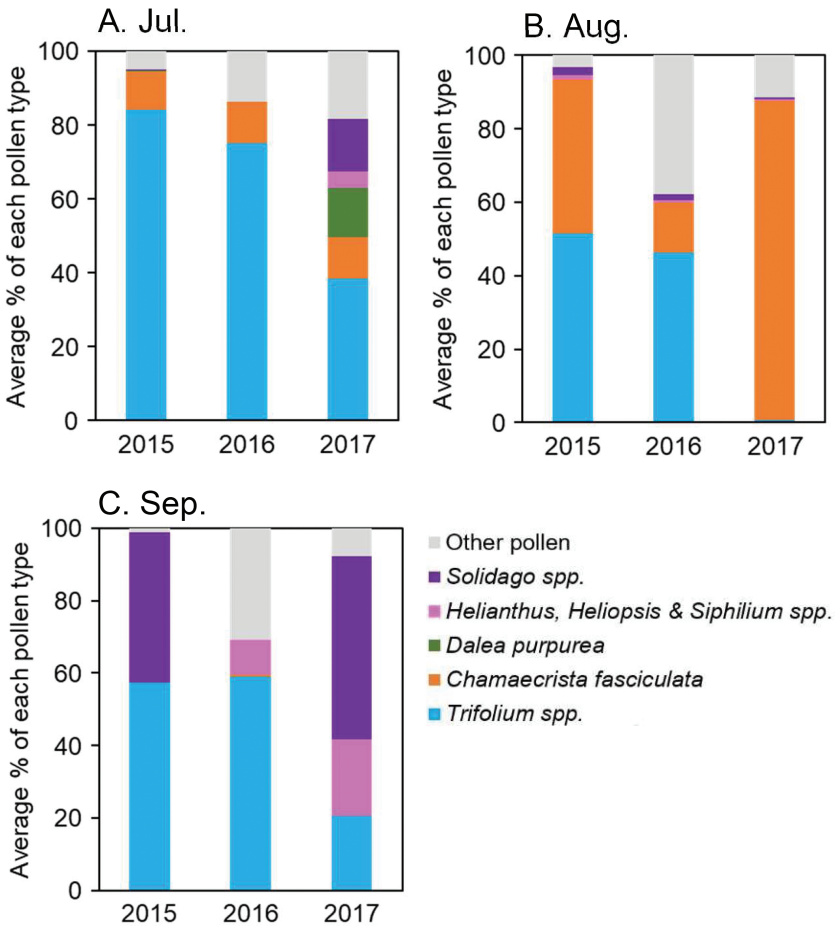

Fig. 4. Composition of honey bee-collected pollen by taxa in each apiary for each of 3 mo across 2017–2019. Data collected from 10 sites from both 2015 and 2016 and from 4 sites from 2017 were used for this analysis. The percentage of each pollen type was calculated by dividing total amount of a pollen type collected per apiary in a month by total amount of pollen collected at that apiary. Average % of each pollen type was calculated across all apiaries.

the immediate crop or surrounding landscape on honey bee foraging behavior. To ensure that honey bees had access to a specific crop, in most cases soybean, we had to change the location of our apiaries to account for the corn-soybean rotation practiced in Iowa. Despite this change in the specific location of any given site across the 3 yr of this study, the central Iowa landscape was consistently used

for corn and soybean production. Analysis of the impact of landuse surrounding these apiaries revealed that honey bees colonies were able to both grow their populations and produce honey within this homogenous, simplified landscape (Dolezal et al. 2019, Zhang et al. 2020). The dominance of corn and soybean within the Iowa landscape did not prevent honey bees from finding clover, the most commonly used plant for pollen (Zhang et al. 2020). The percentage and amount of clover pollen collected was consistent during 2015 and 2016 in July to September, indicating the ubiquitous occurrence of this forage in this landscape, at least in absence of the extreme weather events of 2017.

Of the 3 yr in which we measured temperature and rainfall, 2017 was the hottest and driest, with the most extreme conditions occurring in July. Based on historical records, a meteorological drought occurred during July of 2017, but not during 2015 and 2016. During the July 2017 drought, clover accounted for less than 40% of the bee-collected pollen, in contrast, clover was a higher percentage (>75%) in July of 2015 and 2016. Not only did the percentage of clover pollen decrease (Fig. 4; Supp Table 5 [online only]) in July 2017, but also the absolute abundance of clover (Supp Table 7 [online only]). In the same month (July 2017), honey bees appear to have resorted to several native plants to supplement their pollen needs during this drought. As the drought prolonged from July to August 2017, the presence of clover also disappeared in bee-collected pollen (Fig. 4 and Supp. Table 5 [online only]), indicating a further collapse of clover as a source of pollen. During August of 2017, honey bees relied heavily on a native species, partridge pea, which accounted for > 80% of the collected pollen. When extreme weather dissipated in September of 2017, clover (20%) did not recover to a level matching the same month in previous years, i.e., 2015 (57%) and 2016 (59%).

We estimated pollen abundance at 10 sites in both 2015 and 2016 and seven sites at 2017, but could only estimate plant diversity (taxon richness) in bee-collected pollen from four sites in 2017. Goldenrod, sunflower and purple prairie clover were found in pollen at all sites with the highest abundance in July 2017. In contrast, goldenrod, sunflower and purple prairie clover were found in two, two and three of ten sites in 2015, and four, one and no sites in 2016, respectively. Pollen from those three taxa were also in low abundance (<1.1%) in 2015 and 2016. This trend suggests the change of foraging behavior of honey bees observed in July 2017 was a result of extreme weather and not from a reduction in the amount of site replication. The greater diversity of plants represented in the bee-collected pollen during July 2017 further suggests that honey bees expanded their foraging range to collect enough pollen to satisfy their nutritional needs.

Two sites used in 2017 had access to small patches of prairies established through the prairie-strip conservation reserve program (i.e., CP 43, USDA 2019). There are several lines of evidence to suggest that these two sites are not responsible for the trends we observed across the 3 yr. First, when removing those two sites with access to prairie strips from our analysis, the observed trend of higher taxon richness did not change (Supp Fig. 3 [online only]). Second, colonies at sites without access to small (<2.2 ha) patches of prairie collected pollen from the same number of taxa as sites with access to prairies in July 2017, indicating extreme weather event potentially makes honey bees collect pollen from more species of plants.

Another limitation of this study is the introduction of variation in 2017 regarding the number of colonies used within the apiaries. In only this year, apiaries varied between either two or 16 colonies. Despite the lack of a statistical difference, we did observe a numerical difference, with the amount of pollen collected by a colony in an apiary of 2 colonies was nearly twice that collected by a colony in an apiary comprised of 16 colonies (Supp Fig. 1 [online only]). To confirm that the density of colonies in an apiary was not responsible for the year-to-year trend in pollen abundance collected in July, we conducted a post-hoc analysis. Removing data collected from sites with 16 colonies, we still observe less pollen collected in July of 2017 than 2015 and 2016 (ANOVA, $F = 5.58$; df = 2, 23 $P = 0.0113$).

Despite limitations that introduced variation to our data set, there are several components that make this a useful data set for studying the dynamic response of honey bee foraging to abiotic factors. Colonies were maintained in a consistent manner with limited genetic variation, similar starting population sizes, and consistent year-to-year management practices. Because we cannot control for the occurrence of often stochastic weather events or recreate a same scale of experiment on free-flight colonies in lab, these data sets can provide useful insights. These data provide an example of the interplay between climate and pollen forage in the context of the Midwestern United States agro-ecosystem, an area that has been recognized as a critical area for pollinator conservation (Grixti et al. 2009, Otto et al. 2016).

Our data on plants represented in bee-collected pollen suggest bees shifted their foraging choices to more drought tolerant plants in 2017. This included a higher percentage of pollen from three native, drought tolerant plants, including purple prairie clover, goldenrod, and sunflowers (*Helianthus*, *Heliopsis & Siphilium* spp.), all of which were uncommon in bee-collected pollen during July of any other year but 2017. Combined, these results suggest honey bees utilize drought-tolerant native plants as a supplement to non-native plants (such as *T. repens*) to which they may have a co-evolved relationship derived in Europe. Although honey bees collected these plants actively in a drought, we do not know where these plants were located in the surrounding landscape. These plants were originally found in prairies before European settlers arrived and brought honey bees into Iowa. Remnant and reconstructed prairies exist in small patches throughout Iowa, and such patches were present at two sites used in 2017. These patches were established through CP-43, a new conservation practice added to the Conservation Reserve program (CRP) of the USDA in the 2018 Farm Bill (USDA 2019). These are not the only possible patches of perennial habitat that native plants could be found in Iowa, which actively cultivates them along roadsides managed by the state (Wright and Wimberly 2013).

In central Iowa, honey bees rely on non-native plants as a significant source of nectar (i.e., soybean [*Glycine max*] and white clover [*T. repens*]) and pollen (i.e., white clover) until August when a dearth results in a decline in colony honey stores (Dolezal et al. 2019, Zhang et al. 2020). When honey bee colonies are given access to prairie during this period of dearth, honey stores are replenished (Dolezal et al. 2019). As non-native plants cease blooming, native plants become the most common source of honey bee-collected pollen (Zhang et al. 2021). These native plants that flower after non-natives and are resistant to unfavorable weather may serve as a 'nutritional reservoir' for honey bees, allowing them to meet colony nutritional needs. In this study, we used two sites with access to small patches of prairie, which likely increased their access to these native plants. However, apiaries without these immediate patches of native plants were able to collect pollen from these plants. For these native plants to be of the greatest value to honey bees, the distance to these patches from an apiary may help optimize their value as a nutritional reservoir. By keeping honey bees within or near the patches of native plants established by CP-43 or other CRP programs, the

proximity may reduce the foraging energy cost, especially under high temperature, suggesting a valuable resource of these native plants for honey bees during the extreme weather conditions of the future.

Increasing temperatures in the United States and many other parts of the world are well documented, beginning in the 20th century (Wuebbles et al. 2017). The Midwestern United States (including Iowa) is predicted to experience warmer temperature (Wuebbles et al. 2017). The amount of rainfall that the Midwest receives may not decrease, but more rainfall will occur in intensive events in a shorter period, and at the same time, days without rainfall will increase, indicating potential drier weather and more droughts. A warming and drying climate is predicted to reduce regional or global plant diversity (Harrison et al. 2015). This decline in plant diversity may pose a challenge for honey bees to find forage beyond cultivated plants. In the Midwest, two federal programs, CP-42 (Eagan et al. 2019) and CP-43 (UDSA 2019), can support landowners to incorporate perennial, native flowering plants back into lands committed to agriculture. The instructions for these programs allow for the incorporation of a wide-range of native plants suitable for the location. Despite the small size, these reconstructions increase the abundance and diversity of native pollinators (Schulte et al. 2017, Kordbacheh et al. 2020) and can improve honey bee health and productivity (Zhang 2020). To address the anticipated hardships that will come with continued changes to the environment, due to climate change, we suggest a more deliberate incorporation of drought-tolerant plants in these habitats. A subset of native plants that are drought tolerant were observed to be attractive to wild and managed pollinators in Michigan (Rowe et al. 2018). By comparing plant taxa used by honey bees in Michigan with our results in Iowa, we found three native, drought tolerant taxa (purple prairie clover, sunflower, and goldenrod) were used in both regions. Partridge pea was not included in the Michigan study (Rowe et al. 2018), but it could be an additional choice of forage enhancement for honey bees outside Iowa as this plant is adapted to a wide range of climates (Houck and Row 2019). A challenge for beekeepers and those interested in conservation will be in providing an adequate amount of these plants such that they meet the needs of both apiculture and wild pollinators during extreme weather events.

Conclusions

In conclusion, we observed an extreme weather event, specifically, a combination of high temperatures and drought, was associated with a decrease in the amount of pollen collected, but also an increase in the diversity of plants used as a source of pollen. Because of limitations of our post-hoc analysis to these data sets, a well-designed study with multiple extreme weather events would help determine if these trends are consistent and occur across multiple environments. When considering restoring or reconstructing native habitat to enhance the floral resources for honey bees and wild pollinators, we recommend considering a plant community with species both attractive to bees and also tolerant to extreme weather. Partridge pea, purple prairie clover, goldenrod, and sunflowers are examples of native plants that appear to be both attractive to honey bees and have the capability to flourish during adverse weather. Such plants could be an optimal choice for meeting broader conservation goals and supporting managed honey bee health.

Supplementary Data

Supplementary data are available at *Journal of Economic Entomology* online.

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