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ARTICLE

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# Landscape-scale floral resource discontinuity decreases bumble bee occurrence and alters community composition

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**Abstract**

Agricultural practices and intensification during the past two centuries have dramatically altered the abundance and temporal continuity of floral resources that support pollinating insects such as bumble bees. Long-term trends among bumble bees within agricultural regions suggest that intensive agricultural conditions have created inhospitable conditions for some species, while other species have maintained their relative abundances despite landscape-level changes in flower availability. Bumble bee responses to spatiotemporal resource heterogeneity have been explored at the colony and behavioral level, but we have yet to understand whether these conditions drive community structure and ultimately explain the diverging patterns in long-term species trends. To explore the relationship between landscape-level floral resource continuity and the likelihood of bumble bee occurrence, we mapped the relative spatial and temporal availability of floral resources within an intensive agricultural region in the US Upper Midwest and related this resource availability with bumble bee species relative abundance. Across the bee community, we found that relative bumble bee occurrence increases in landscapes containing more abundant and more temporally continuous floral resources. Declining species, such as *Bombus terricola*, exhibited the strongest, positive responses to resource abundance and continuity whereas common, stable species, such as *Bombus impatiens*, showed no statistical relationship to either. Together with existing experimental evidence, this work suggests that efforts to increase spatiotemporal flower availability, along with overall flower abundance at landscape scales may have positive effects on bumble bee communities in the US Upper Midwest.

**KEYWORDS**

bumble bee, floral resources, resource continuity, resource dynamics, wild bee conservation

## INTRODUCTION

Biodiversity studies in the Anthropocene have highlighted a pattern of species that are "winners" and "losers" in relation to ongoing anthropogenic disturbance to ecosystems (Dornelas et al., 2019; McKinney & Lockwood, 1999). Factors such as urbanization, agricultural intensification, climate change, and changes in habitat and resource availability have favored species that tolerate novel, swiftly changing environmental conditions. Many of the species that are filtered out of ecological communities provide critical ecosystem services including provisioning, cultural, and supporting services (e.g., coral reefs, Stuart-Smith et al., 2021) and regulating services (e.g., pollination, Grab et al., 2019; Hemberger et al., 2021).

Bumble bees, an important group of insects that pollinate a wide range of wild and economically important plants, are a taxon that fits this trend. In North America, several studies have identified species, such as *Bombus terricola* and *Bombus pensylvanicus*, that have exhibited major declines in range and local occurrence (Colla et al., 2012; Colla & Packer, 2008) as a result of anthropogenic disturbances including agriculture (Duchenne et al., 2020; Hemberger et al., 2021), climate change (Jackson et al., 2022; Kerr et al., 2015), and increasing disease pressure (Cameron et al., 2011; Colla & Packer, 2008; Szabo et al., 2012). Other species such as *Bombus impatiens*, however, continue to be abundant under the same conditions and landscapes (Hemberger et al., 2021; Looney et al., 2019).

One of the factors known to influence the bumble bee population and occurrence trends over time is the availability of resources, that is, flowers, in the surrounding landscape. Previous work has demonstrated strong links between floral resource availability and bumble bee behavior (Hemberger & Gratton, 2018; Vaudo et al., 2016; Westphal et al., 2009), colony growth and reproduction (Hemberger et al., 2020; Samuelson et al., 2018), and long-term population trends (Kleijn & Raemakers, 2008; Scheper et al., 2014). Moreover, resource availability (i.e., limitation) can interact with other stressors such as pesticide exposure (Stuligross & Williams, 2020) and disease (Schmid-Hempel & Schmid-Hempel, 1998). For bumble bee communities in agricultural regions, more than a century of intensified practices including the loss of leguminous cover crops (Rasmont & Iserbyt, 2013), increased control of flowering weeds (Hicks et al., 2016), and a transition to yield-focused monocultures leading to highly simplified landscapes (Brown & Schulte, 2011) has had a profound impact on resource availability for pollinators (Carvell et al., 2006; Timberlake et al., 2019).

Changes in land cover have also influenced a pronounced shift in the temporal dynamics of resource availability that influences bee communities (Königslöw et al., 2022; Schellhorn et al., 2015). Agricultural and other land use practices, such as the cultivation of extensive monocultures of cereal grains and grasses, can decrease resource continuity through time, a factor critical to the success of bumble bee colonies that are active from late spring to early fall. However, due to the logistic challenges associated with measuring floral resources over large spatiotemporal extents, resource continuity is typically not accounted for when evaluating resource availability in landscapes (Malfi et al., 2022; Timberlake et al., 2019, 2021; but see N. M. Williams et al., 2012). Studies that have examined the effects of resource abundance and continuity show that bumble bee behavior (Hemberger & Gratton, 2018) and colony growth and reproduction (Hemberger et al., 2020, 2022) are highest when resources are abundant and continuous. However, whether the interaction of abundance and temporal availability can explain bumble bee occurrence and community composition in natural communities is largely unknown (but see Nicholson et al., 2021).

Resource abundance and temporal continuity independently and in combination can influence consumers. Conceptually, we can envision hypothetical scenarios with discontinuous resources at low (Figure 1A) and high (Figure 1B) resource abundance, along with temporally continuous resources at low (Figure 1C) and high (Figure 1D) abundance. Such a conceptualization suggests several hypotheses that can be tested given empirical data on resource availability throughout the course of a season. We predict that increasing floral resource abundance would increase the likelihood of bumble bee occurrence across species (Hemberger et al., 2020, 2022, Figure 1B,D), but that the benefits of more abundant floral resources would be greatest when they are temporally continuous at the landscape scale (Königslöw et al., 2022, Figure 1D; Schellhorn et al., 2015). That is, there would be an interaction between resource abundance and temporal continuity of resources (Figure 1E).

Moreover, this relationship may be species specific. We expected the positive effects of temporal continuity would be stronger for species that have declined in areas of intensive agriculture (Figure 1E, Hemberger et al., 2021). In contrast, we expected stable species (Figure 1F) to be less sensitive to temporal continuity, in line with recent laboratory and field experimentation that has shown these species to be tolerant to variable resource conditions (Hemberger et al., 2022; Hemberger & Gratton, 2018; Schmid-Hempel & Schmid-Hempel, 1998). Moreover, common species have other traits that are likely to enhance adaptability to resource heterogeneity including a highly plastic body size (Austin & Dunlap, 2019) that is more resistant to starvation (Couvillon et al., 2010) and a wider diet breadth (Wood et al., 2019) than declining species.

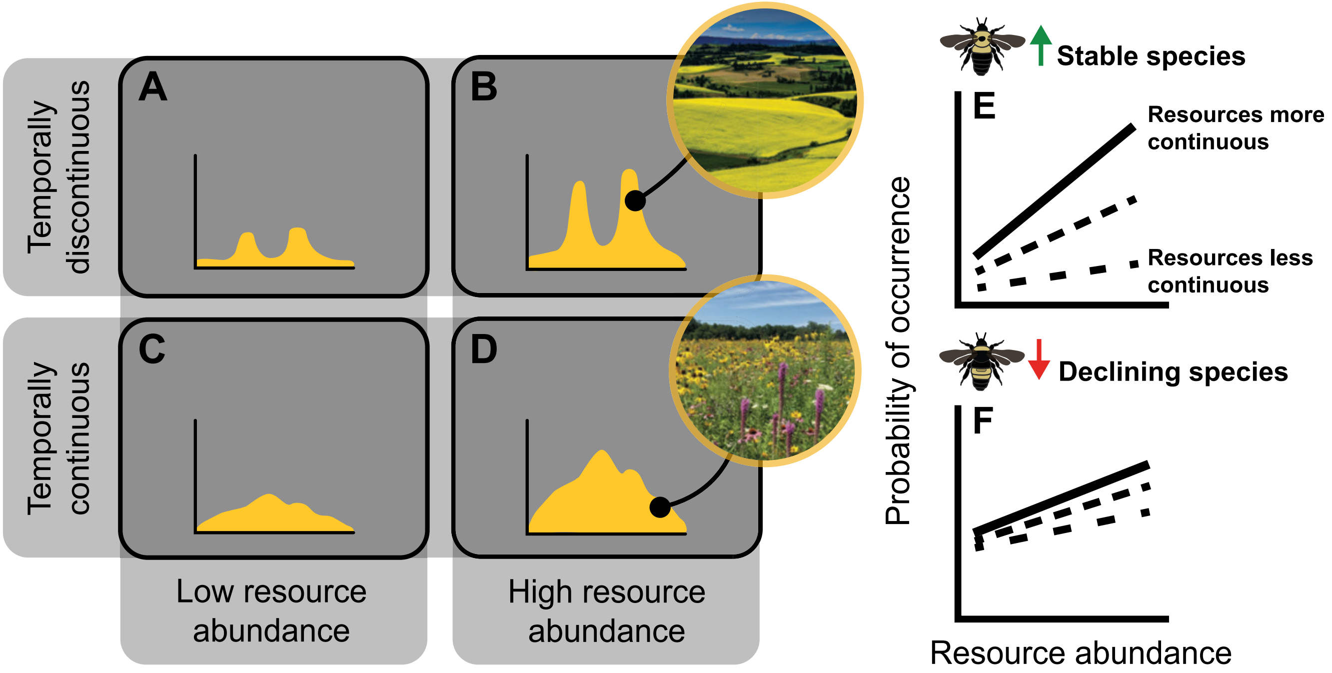

**FIGURE 1** Conceptual representation of landscape-scale floral resource availability in terms of total abundance and temporal continuity. Four scenarios are depicted, describing temporally discontinuous resources at low (A) and high (B) abundance, and temporally continuous resources at low (C) and high (D) abundance. Given diverging long-term trends in bumble bee occurrence, we hypothesized that species with declining populations (e.g., *Bombus terricola*, E) would be more sensitive to both resource abundance and temporal continuity, whereas stable species (e.g., *Bombus impatiens*, F) would respond mostly to resource abundance given their continued dominance in landscapes dominated by agriculture that exhibit low resource continuity. Photographs obtained from Unsplash (https://unsplash.com/).

We designed a study to test whether floral resource abundance, temporal continuity, and their interaction predicted bumble bee occurrence and community composition. We combined several years of extensive, spatiotemporally detailed floral resource measurements and bumble bee occurrence surveys across a gradient of agricultural intensity in Central Wisconsin (USA). Testing the hypotheses outlined above is critical given ongoing efforts to restore floral resources and manage threatened bumble bee species within agriculturally dominated landscapes. A more thorough understanding of the interplay of resource quantity and continuity would be instrumental in the design and implementation of conservation programs that support these efforts.

# METHODS

We conducted all data cleaning, analysis, and visualization in R version 4.2.1 (R Core Team, 2017) using the following packages: *glmmTMB* (Brooks et al., 2017), *emmeans* (Lenth, 2022), *performance* (Lüdecke et al., 2021), *sjPlot* (Lüdecke, 2021), *janitor* (Firke, 2021), and *tidyverse* (Wickham et al., 2019).

## Study region and site selection

We focused this study on the Central Sands region of Wisconsin, USA (Monroe, Jackson, Wood, Juneau, and Adams counties); an agriculturally important region that contains the state's principal vegetable and fruit production. We located our study areas in and around cranberry (*Vaccinium macrocarpon* [Hill] A. Gray) agroecosystems and the surrounding natural habitat. Cranberries bloom *en masse* from mid-June to early July, saturating the landscape with an abundance of flowers (Hemberger & Gratton, 2018). The presence of landscapes containing resource pulses from cranberries allowed us to select sites that would span a gradient of both total floral resource abundance, and temporal resource continuity throughout the growing season.

## Estimating floral resource landscapes

Central to this work was developing an estimate of the amount and temporal continuity of floral resources across an area. We collected and calculated our estimates to be relative measures of resource abundance and continuity and did not intend our estimates to represent the “true” value of resource availability within a landscape. To accomplish this, we conducted spatiotemporally extensive surveys of all flowering plants within the major land cover categories (described below) across the study region. We initially used resource estimates from a previous study in the region (Hemberger & Gratton, 2018) to haphazardly select locations for floral surveys within representative land covers (grassland, shrubland, woodland, cranberry, and two land cover categories defined by our survey teams, field/woodland edge, road edge; $n = 44$ replicate sites, 1–5 land cover types per site). For land covers present within a site, we made efforts to survey at every time point (six in 2017, four in 2018), but were not able to for every site/land cover due to accessibility (e.g., during management operations such as pesticide spraying). Sites were selected such that they spanned the two resource gradients of interest (high to low resource abundance, high to low resource continuity), as well as across the North–South and East–West bounds of our study region.

In 2017 and 2018, we conducted transect/quadrat surveys of four different land cover categories delineated by the USDA Cropland Data Layer (grassland, shrubland, woodland, cranberry) and two land cover categories defined by our survey teams (field/woodland edge, road edge) at six time points in 2017, and four time points in 2018, from May to August (Appendix S1: Figure S1). The periods covered by our surveys represent a critical period of growth for colonies to build up sufficient worker forces to maximize resource acquisition and produce reproductive individuals (i.e., gynes, drones). Colonies without access to sufficient resources in this period will probably fail to produce sufficient reproductive individuals (Crone & Williams, 2016). Shrubland was a rare land cover, occupying less than 1% of the total land area in our study area. We also found that patches classified as shrubland were typically like herbaceous grasslands, and as such, we used floral estimates from grasslands for pixels classified as shrubland in our analyses. We did not sample in two major land cover types: crop fields and wetlands. The primary crops cultivated in this region outside of cranberries are corn and soybean. Both crops use standard chemical control of flowering weeds and the crops themselves are not highly utilized floral resources for foraging bees (Danner et al., 2014). As such, we assumed that crop fields contained few if any floral resources and instead focused on field and road edges where flowering weeds and wildflowers were more abundant. Woodlands (~51.2% of the study region) were also not extensively surveyed after 2017 as results from this and a previous study (Hemberger & Gratton, 2018) found almost no understory floral resources during the summer when floral surveys were conducted. Wetlands (~11.3% of the study region) were also not sampled as accessing and conducting surveys within these areas was prevented by irrigation canals and areas of standing water. However, wetlands were evenly dispersed across the sampling sites so any resources present should also be evenly distributed and have minimal effect on our estimates of resource abundance and continuity.

At each site, we randomly chose two 50 m transects per land cover category to survey. We placed a 1 × 1 m quadrat, divided into four 0.5 × 0.5 m subquadrats, on alternate sides of the line transect every meter (50 total placements, 200 total subquadrats per transect). In 2017, each transect had 800 total subquadrats as we surveyed an area twice as wide along each transect. This protocol was modified in 2018 to increase the efficiency of surveys. The survey estimates varied little between these methods. For each placement, we measured the number of subquadrats that had flowering plants, yielding a proportion of quadrats occupied for each blooming flower species. Plant species were identified with the aid of the University of Wisconsin Virtual Herbarium (https://wisflora.herbarium.wisc.edu/index.php). For our analysis, we filtered to only include six families of bumble bees that are known to regularly visit, including Ericaceae, Asteraceae, Fabaceae, Rosaceae, Brassicaceae, and Lamiaceae.

We averaged proportional coverage across all species, transects, and sites to generate a single estimate of the proportion of quadrats with flowers for a given land cover at a given time point, which we used as our approximate measure of floral abundance. We estimated floral coverage for a total of six time points, using the estimates from six survey time points in 2017 and four in 2018, matching the dates from each time point/year as closely as possible. For time points that were common in both 2017 and 2018, we averaged the estimates of each land cover/time point combination and did not consider interannual variability in our analyses. The values we used to determine landscape-scale resource abundance and continuity were based on the average of our survey estimates. Flower abundance is inherently variable, but we felt that our procedures were sufficient to quantify uncertainty at the landscape scale despite variation in flower abundance within certain land cover types, particularly road, field, and woodland edges (Appendix S1: Table S1).

To estimate floral abundance and temporal continuity at the landscape scale at which bumble bees forage (defined here as a 2000 m radius around a sampling point, e.g., N. M. Williams et al., 2012), we assigned proportional floral coverage values to each respective land cover type to a land cover raster (30 m resolution, reclassified from USDA Cropland Data Layer [CDL], hereafter, floral raster). Because of the CDL’s low accuracy in cranberry classification, we manually burned in rasterized polygons outlining all cranberry marshes in the study region. We grouped several similar land cover categories into our five surveyed categories to increase the spatial coverage of our floral resource estimates (e.g., combined mixed, deciduous, and evergreen forests into one class, Appendix S1: Table S2). To include road and field edges (which are not included in the current CDL classification) into our estimates, we buffered all crop fields and roads (using the CDL and TIGRIS [Topologically Integrated Geographic Encoding and Referencing System for use with Geographic Information Systems] road data layers, respectively) using a 30-m pixel buffer. Because road and field edges are rarely this width, we included a scaling factor (×0.166) to reduce the floral resource estimate of these pixels to ~5-m edges for all fields and roads. We then used these data to create a floral raster for each time point ($n = 6$) by assigning the pixel values to the land cover floral resource estimate (average proportion of quadrats containing a flower from the focal plant families), and then extracted a distance-weighted sum of floral resource abundance within 2000 m of trap locations (summing floral proportion for all pixels in the landscape after multiplying by a distance weighting matrix). We followed N. M. Williams et al. (2012), using a negative exponential distance weighting function to reduce the influence of areas farther from sampling points:

$$w = \mathrm{e}^{-D/\alpha}, \tag{1}$$

where the weighting factor $w$ is calculated from $D$, the distance of a given pixel from the trap location, and α, the approximate foraging distance of a bumble bee. We used 800 m as an estimate of foraging distance (α). Bumble bees are known to fly farther than this (e.g., Rao & Strange, 2012), however this value reflects the average maximum foraging distance currently described in the literature (Kendall et al., 2022; Osborne et al., 2008; Redhead et al., 2016).

To assess floral resource abundance and temporal continuity at a given site, we extracted the sum of pixel values from each time point distance-weighted floral raster. For ease of interpretation, we scaled total resource abundance by the site with maximum resources across all sites/years, creating a floral resource index that ranges from 0 to 1. We estimated the temporal continuity of floral resources by calculating the percent coefficient of variation (%CV) across the six time point estimates of total floral resource abundance. For the remainder of the manuscript, we use CV as our measure of temporal resource continuity, with high values indicating highly variable floral resources over time with peaks and valleys suggesting low resource continuity (i.e., discontinuity), while low values of CV indicate stable and more continually available resources over time. We used these values of floral resources (relative abundance and resource continuity) as the index of flowers available in all years of the analyses (see following paragraphs), assuming that while interannual variability in floral abundance may occur, the relative rankings of the floral resources and their temporal variability across land cover types would be similar between years.

We used the site-level floral resource estimates calculated from the floral raster to determine the resource conditions at each site for all bumble bee sampling years given that the change in land cover classifications for the CDL for these years was almost nonexistent (Lark et al., 2017, http://www.ag-atlas.org/). Moreover, the plant species observed in our surveys have existed within the landscapes of our study region for well over a century (e.g., clover, USDA Plants Database). To visualize resource patterns across the spatial extent of the study, we generated a 5-km hexagonal grid across the study region and calculated a total flower abundance index (from 0 to 1) and %CV for each grid cell.

## Bumble bee occurrence, relative abundance, and community composition

We collected data on bumble bee occurrence and relative abundance from two different sources. First, we deployed blue vane traps (SpringStar LLC, Woodinville, WA, USA) throughout our study region in a mixture of agricultural (cranberry), natural areas, and roadsides. Twenty-five traps were deployed in 2017 and 39 were deployed in 2018 for ~72 h in mid-July (between the 11 July and the 16 July in both years) on warm, sunny days. Eighteen trap sites were identical between 2017 and 2018. A single blue vane trap was deployed at each site. Sites were trapped along with floral survey locations of a given land cover type (i.e., cranberry, grassland, road edge). Within a given year, sites were between 1.4 and 95.1 km apart, with an average distance of 33.2 ± 19.3 km (Appendix S1: Figure S2).

We suspended traps on fiberglass poles ~1 m from the ground. All traps were placed near field and road edges to standardize the structural surroundings of each trap. Second, we combined our trap data with bumble bee collections from a previous study in this region by Gaines-Day (2013) from 2008 to 2011 that used bee bowls to survey wild bee abundance and diversity within cranberry farms. Although bee bowls may not be as attractive to bumble bees relative to blue vane traps (M. Hall, 2018), the duration of trapping and capture rates in that study were similar to the blue vane traps deployed in 2017 and 2018. In addition, because counts are eventually relativized to total abundance per site, the relative frequencies of individual species can be compared. Both bee bowls and vane traps are known to be biased in their sample rates, but they provided a logistic solution to simultaneously sample relative abundance/species occurrence at a large spatial scale and are found to be effective relative to other sampling techniques (Prendergast et al., 2020). We sampled bumble bees at 77 unique sites across all years, with 18 of the 77 sites sampled either 2 or 3 times in different years (Appendix S1: Table S3) meaning that, in total, we had 95 unique site/year combinations. Bumble bees were removed from traps, washed, dried, and pinned for enumeration and identification using P. H. Williams et al. (2014).

Because samples from bowl and vane traps do not measure true abundance, we instead calculated measures of species' relative abundance at each site. By using the relative abundance of species at a site and sampling carried out for multiple years, the effects of any systematic bias within the sampling of a given year (e.g., weather) are accounted for as measures are relative within a site and year. To be included in the dataset for calculating relative abundance across species in the sampling landscape, a series of steps were used to ensure enough data was available for accurate estimates. First, a trap at a given site needed to collect a minimum of two bumble bees over the course of the sampling period in a year. We did not include traps where no bumble bees were caught, which means that relative abundances are calculated at sites where some bee activity was observed. This approach therefore does not estimate occupancy, rather it is a measure of the relative abundance (i.e., likelihood of occurrence within a community) of species given that bumble bees were present at a site. Because several species were rare (combined <1.5% of all captures), we further limited our analysis to the eight species whose relative abundance could be calculated in at least 15 of the 95 site/year combinations. These species included: *B. bimaculatus* Cresson, *B. borealis* Kirby, *B. fervidus* Fabricius, *B. griseocollis* De Geer, *B. impatiens* Cresson, *B. ternarius* Say, *B. terricola* Kirby, and *B. vagans* Smith. Species excluded from the analyses due to rarity included: *B. auricomus* Robertson, *B. fernaldae* Franklin, *B. pensylvanicus* De Geer, *B. rufocinctus* Cresson, and *B. sandersoni* Franklin. Each of these species is known to occur within our study region, and our analysis sought to determine whether species were more or less likely to occur given flower availability in space and time.

## Statistical analyses

$$\begin{aligned}\text{Model: relative abundance of bumble bees}\\ \sim \text{floral abundance} \times \text{floral CV} + \text{species} + \text{year}\\ + (1\,|\,\text{site}) + (1\,|\,\text{observation}).\end{aligned}$$

We fitted a generalized linear mixed model (GLMM) to evaluate the interactive effect of resource abundance and temporal continuity on the likelihood of bumble bee species occurrence (i.e., relative abundance). Given this data structure, we fitted a GLMM with a binomial error structure, weighting each relative abundance value by the total number of bumble bees collected at a given site and year. This model structure allows us to predict the relative likelihood of bumble bee species occurrence at a site given floral resource conditions. Zero relative abundances (i.e., species absences from traps) were not included in the model. We included fixed effects of the collection year and species identity to account for differences in capture rates between years and varying trends among species. Site was added as a random intercept to account for repeated measures, in addition to an observation-level random effect to account for overdispersion. We tested model terms for multicollinearity (variance inflation factors) using the performance package. Given the spatial structure of our data collection, we tested model residuals for evidence of spatial autocorrelation in simulated residuals using the *DHARMa* package (Hartig, 2022). To explicitly test if the relationship between species occurrence and floral abundance and continuity varied according to long-term bumble bee population trends, we also compared two separate models for stable species (*B. bimaculatus* Cresson, *B. griseocollis* De Geer, *B. impatiens*, *B. ternarius*, *B. vagans* Smith) and declining species (*B. borealis* Kirby, *B. fervidus* Fabricius, *B. terricola*). We then used the fitted model including all species to predict the probability of occurrence for each species using calculated values of floral abundance and 1/CV, along with the mean study year across the spatial extent of our study region.

# RESULTS

## Floral resource abundance and temporal continuity vary widely

In June to August of 2017 and 2018, we conducted 171 floral resources surveys across five land cover types in Central Wisconsin, yielding 17,551 occurrence records of 54 flower species (Appendix S1: Table S4). Most common were nonnative weedy species, such as white clover (*Trifolium repens* L.) and spotted knapweed (*Centaurea* spp.). The most common native species included common yarrow (*Achillea millefolium* L.) and common cinquefoil (*Potentilla simplex* Michx.). Cultivated cranberry (*Vaccinium macrocarpon*) was the only flowering crop observed flowering throughout our surveys as it was the only extensive crop attractive to pollinators in the study region (and thus the only crop surveyed).

Floral resource abundance varied across the season, peaking in mid to late June and early July; during that time the mean floral index (range 0–1) of surveyed sites was 0.11 ± 0.18 (mean ± SD, Figure 2). In these landscapes, it is evident that cranberry bloom represented a massive pulse of flower availability between the third week of June and the first week of July, accounting for on average 82% of flower availability in the landscape (Figure 2A). In contrast, sites without cranberries peaked at similar times, but altogether had a much lower abundance of floral resources (mean floral index = 0.03 ± 0.02, Figure 2B). Aside from cranberry, field edge habitats contributed the most to total resource abundance, followed by road edges and grasslands (Figure 2B). Overall, there was substantial variation in resource abundance across the region (Figure 3A).

The continuity of floral resources varied widely, with seasonal %CV across survey time points ranging from 30.8% to 149.0% with a mean of 128.9% ± 26.2% (mean ± SD). Sites with low floral resource continuity (i.e., high CV) were largely near cranberry marshes given the massive bloom of cranberry crop flowers in June and July (Figure 3B).

## Bumble bees are more likely to occur in landscapes with abundant and continuous floral resources

In total, 1377 bumble bees were caught in traps in 2008, 2010, 2011, 2017, and 2018, representing 13 species—more than half of the bumble bee diversity known to historically occur in Wisconsin (Appendix S1: Table S5). The likelihood of bumble bee occurrence was related to both the abundance of floral resources in the surrounding landscape (Figure 4A, Wald $\chi 1 = 3.82$, $p = 0.05$) and the temporal continuity (%CV) of resources during the season (Figure 4B, Wald $\chi 1 = 5.39$, $p = 0.02$). These two effects did not interact (Wald $\chi 1 = 1.71$, $p = 0.19$). Of these two, the temporal continuity of resources had a stronger association with bumble bee occurrence. Given an average abundance of floral resources across all sites, bumble bees in landscapes with the highest continuity of floral resources were 50% more likely to occur compared with landscapes with the lowest continuity. This is compared with landscapes with an average amount of resource continuity, where bumble bees in landscapes with the highest floral resource index had only a 25% increase in occurrence relative to landscapes with the lowest floral resource index. The relative likelihood of bumble bee occurrence varied by species (i.e., species effect; Figure 4A,B; Wald $\chi 7 = 53.98$, $p < 0.001$), relative occurrence across all species decreased during the course of the study years (i.e., year effect; Wald $\chi 1 = 4.07$, $p = 0.04$).

When species relative abundances were analyzed by grouping species by long-term population trends (i.e., stable vs. declining species), we found that the relationships between floral abundance and temporal continuity were driven mostly by species that were declining (*B. borealis*, *B. fervidus*, *B. terricola*), with a strong interaction found between floral resource abundance and temporal continuity (Figure 5; Wald $\chi 1 = 16.51$, $p < 0.001$). The results for stable species, while qualitatively similar to both the global and declining species models, had no statistical support for either the interactive or independent effects of resource abundance or temporal continuity (Appendix S1: Table S6).

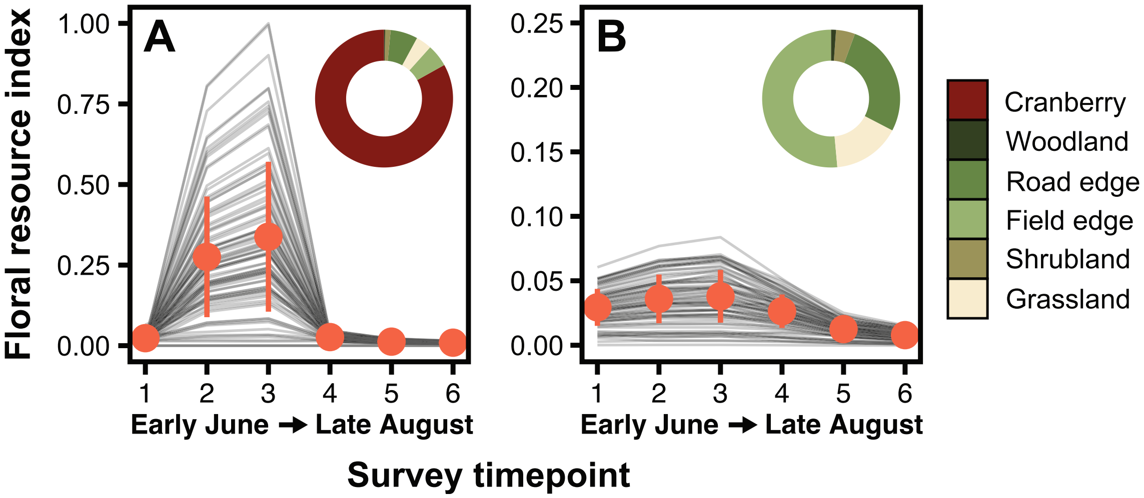

**FIGURE 2** Season-long (31 May to 18 August) phenology of floral resources surrounding sites combined from 2017 and 2018 surveys with (A) and without (B) cranberry farms in the landscape. Black lines represent individual sites, while red points represent the average floral resource index at each time point (±SD). Survey time points are ~2 weeks apart. Inset donut charts are the average proportion of floral abundance (across all sites, time points) from each land cover category surveyed to depict which land covers contribute most to resource abundance throughout the season. Note that the *y*-axis scale in panel (B) (0–0.25) is different from panel (A) (0–1).

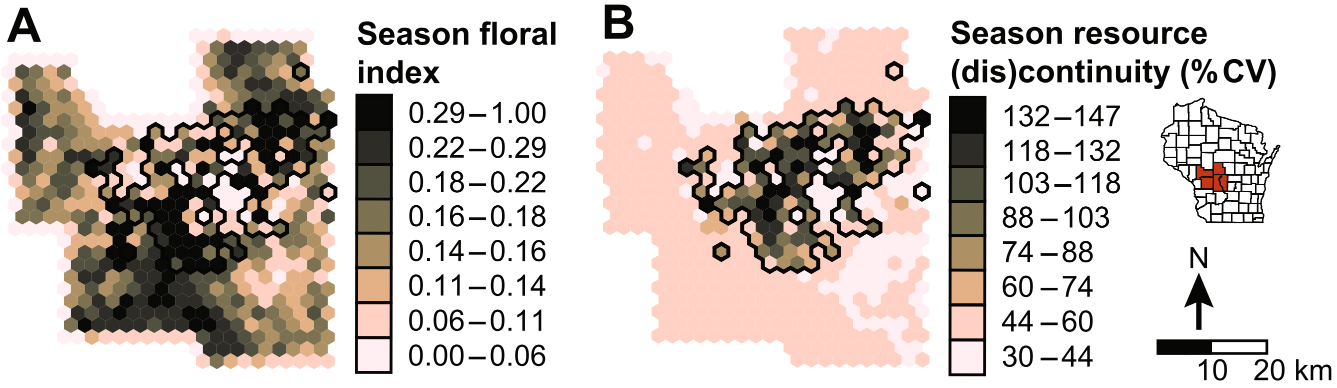

**FIGURE 3** Spatial depiction of seasonal flower availability index (A: with 1 being the most flowers) and continuity (B: measured as coefficient of variation, larger numbers indicate greater resource discontinuity). Grid cells outlined in black contain at least one intensive cranberry farm. Each grid cell is 5 km wide. Inset map indicates the focal study counties of the study region within Wisconsin.

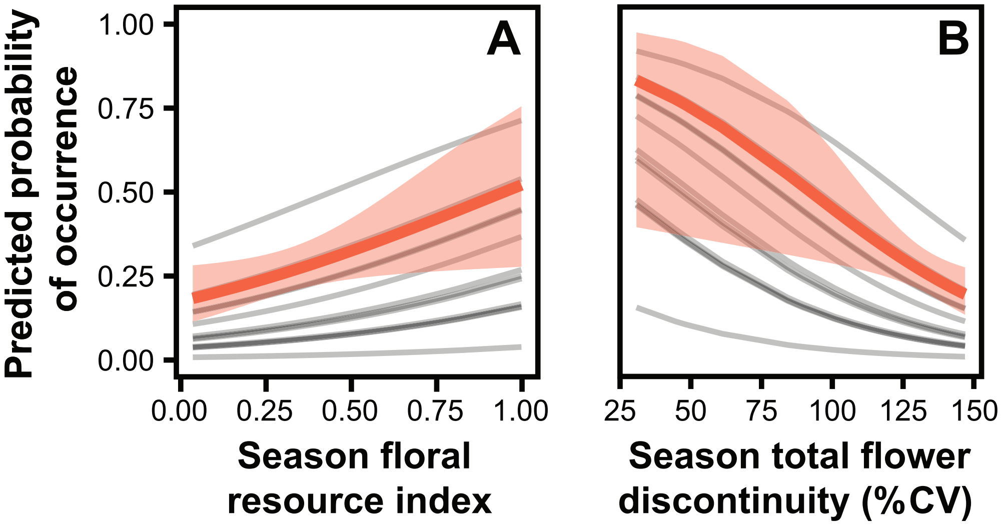

**FIGURE 4** Marginal effects of seasonal floral resource index (A) and seasonal flower continuity (measured as percent coefficient of variation, high values indicate less continuous resources, B) on the predicted probability of bumble bee occurrence from a model including all study species. Bold, red lines are mean global predictions (with 95% confidence interval [CI]), while gray lines (some overlap) are marginal predictions for each bumble bee species included in the analysis.

When model predictions were mapped back onto the study area, the patterns of higher bumble bee occurrence probability correspond well to regions of resource continuity (e.g., Figure 3B) for both stable (Figure 6A) and declining (Figure 6B) species. Declining species are far less likely to occur in areas of low resource continuity even though resource abundance is near its peak (due to intensive cranberry production, cells outlined in black).

## DISCUSSION

Using a novel approach for evaluating spatial and temporal floral resource patterns at a landscape scale, we found that the temporal continuity of flowering resources in diverse agricultural landscapes was a strong driver of the likelihood of bumble bee occurrence. That is, when landscapes surrounding our sampling sites had more consistent amounts of floral resources over time, bumble bees were more likely to occur relative to landscapes where floral resources were highly variable over time, such as those dominated by mass-flowering cranberries. We also found that an increase in flower abundance in the surrounding landscape also led to a greater probability of bumble bee occurrence, supporting many existing studies (Goulson et al., 2015; Hyjazie & Sargent, 2022; Roulston & Goodell, 2011). However, the effect of resource abundance was slightly weaker than that of resource continuity.

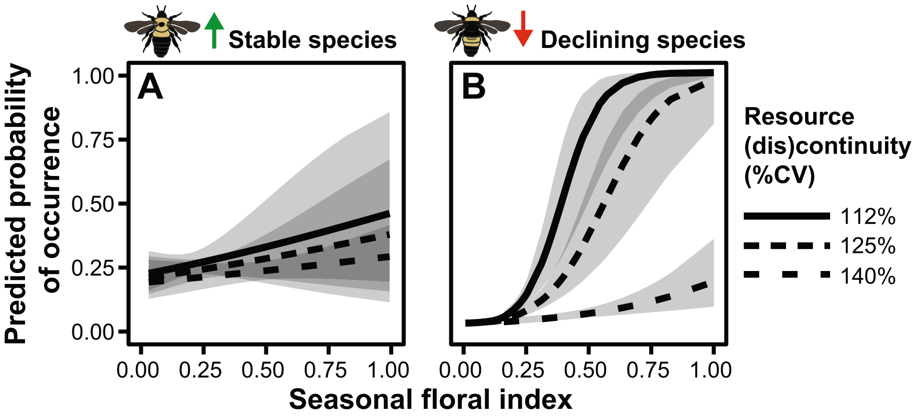

**FIGURE 5** Interactive effect of floral resource abundance (*x*-axis) and (dis)continuity (line type) for species whose long-term occurrence trends are stable (A) and declining (B) with 95% CI. Discontinuity (%CV) values selected are the mean ±1 SD within the dataset. Each interaction plot is from a separate model.

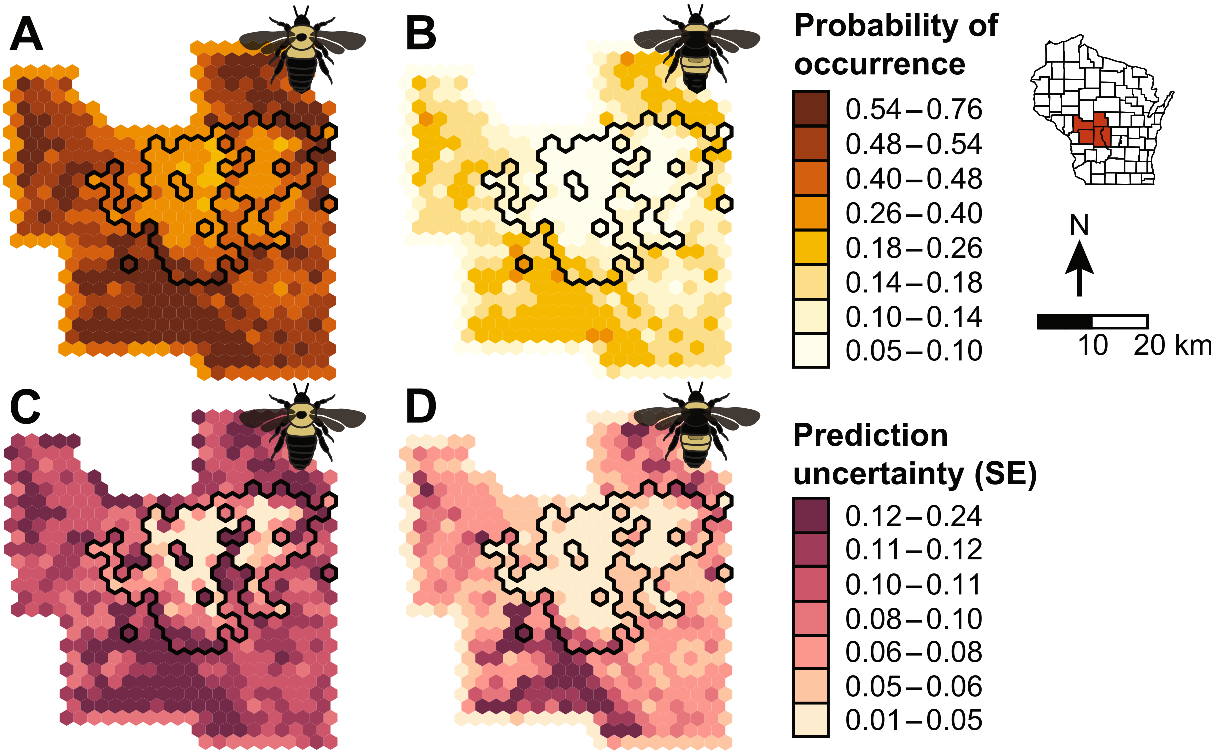

**FIGURE 6** Model predictions of the probability of bumble bee occurrence along with prediction uncertainty for a stable species (A, C: *Bombus impatiens*) and declining species (B, D: *Bombus terricola*) given the conditions of floral abundance and percent coefficient of variation in each grid cell, location, and controlling for species identity and the year of sampling (other species are mapped in Appendix S1: Figure S3). Grid cells outlined in black indicate that the grid cell contains at least one intensive cranberry farm. Each grid cell is 5 km wide.

In line with our predictions, the strength of species' response to resource abundance and continuity was partitioned by long-term population trends and conservation agency listings (Cameron et al., 2011; Hemberger et al., 2021, Wisconsin DNR). Declining species in this region, such as *B. terricola* and *B. fervidus*, had a strong, interactive response to resource conditions, with the likelihood of occurrence increasing rapidly when landscapes contained abundant and more continuous resources. In contrast, stable species, such as *B. impatiens* and *B. bimaculatus*, were not significantly influenced by either temporal resource continuity or total resource abundance.

The dichotomy of species' responses to landscape floral resource conditions and their alignment with long-term population trends suggests a putative mechanism.

The fact that common species have a high likelihood of occurrence despite low resource abundance and continuity suggests these species have the capacity to adapt to resource scarcity that declining species lack. Experiments with *B. impatiens* support this explanation: colonies can still grow and reproduce adequately even with highly variable resource availability in both laboratory (Hemberger et al., 2020) and field settings (Hemberger et al., 2022). Moreover, bumble bee species intolerant to discontinuous resource conditions in the landscape have limited diet breadths (Wood et al., 2019) and reduced plasticity in worker size (Austin & Dunlap, 2019), a trait related to starvation tolerance (Couvillon & Dornhaus, 2010). However, manipulative experiments that specifically test these relationships within declining bumble bee species are largely absent. Our analyses also excluded several rare species for which we did not have sufficient data to build models. Several of these are also declining regionally (e.g., *B. pensylvanicus*, *B. fernalde*, *B. sandersoni*) and may be expected to respond similarly to the declining species included in our analyses, however additional research on declining species, while challenging, is needed to further confirm the proposed mechanisms.

The temporal dynamics of resources has long been considered important for insects' persistence (Root, 1973; Schellhorn et al., 2015) but is not often considered in landscape-scale research studies. Our study, while observational, provides some of the first evidence at the community level that enhancing landscape-level resource continuity is associated with an increase in the occurrence of beneficial insects. Such an association is to be expected given the bumble bee life history. Most species' colonies persist for months and require a consistent supply of nectar and pollen throughout this period from the surrounding landscape, accessed by their ability to disperse widely from a central foraging location in search of resources (Roulston & Goodell, 2011).

As this study relies on existing resource gradients, it is possible that resource abundance and continuity may also co-vary with other drivers of bumble bee occurrence including aspects of agricultural intensity (e.g., insecticide use, proximity to managed honey bees) potentially confounding the interpretation of resource-driven patterns of bumble bee relative abundance. We found that bumble bee occurrence decreased with increasing resource variability, which occurred in areas with a high abundance of cranberry agriculture. Yet, we also observed a positive relationship between bumble bee occurrence and resource abundance, which in part was common in areas of high cranberry production. As such, we would expect that any negative effect of intensive cranberry production on bee occurrence would manifest through a negative relationship with increasing resource abundance, a trend opposite of what we found. Thus, it is unlikely that the negative effects of cranberry management were the primary determinant of bumble bee occurrence, rather floral resource continuity per se is the primary contributor to bumble bee occurrence patterns. In addition, given that our blue vane trapping partially overlapped with cranberry bloom, potentially limiting the attractiveness of the traps relative to a superabundant resource pool. Our collection rates across locations with and without cranberries in the surrounding landscape were largely similar, however we cannot rule out a potential impact of co-blooming cranberries on bumble bee abundance and species diversity collected in our blue vane traps.

Our results indicate that programs aimed at bolstering both floral resource abundance and temporal continuity in agroecosystems are likely to have beneficial outcomes for bumble bees. For example, managing landscapes such that blooming flowers from crop and noncrop sources are available in abundance throughout the season. In addition, the diversity of floral resources may be an important driver of bumble bee occurrence and populations (Sutter et al., 2017), but addressing this was beyond the scope of our study. Of the two variables considered, we found that increasing floral resource continuity had on average a greater positive impact on bumble bee occurrence. Although this suggests a focus on planting floral resources that increase resource continuity, such a strategy may be more logistically challenging than simply adding flowers to the landscape, requiring specific knowledge of what, and more importantly, when existing resources are available. Possible ways to side-step this challenge include ensuring that flower planting schemes include blooming periods that span the growing season in hopes that any interruptions or bottlenecks in resource continuity are at least partially filled (Stowe et al., 2022).

Another challenge in actualizing the enhancement of floral resources is finding suitable locations in working landscapes. Our surveys found that the most abundant noncrop floral resources are constrained to interstitial/marginal habitats, such as road and field edges, that are not traditionally quantified when correlating land use to a given pollinator response. These landscape areas could be further enhanced without taking land from production or other uses and are found extensively across most agricultural landscapes. Indeed, landscape edge features are often the target of flower plantings that have been shown to benefit pollinator abundance and pollination services (Albrecht et al., 2020; Blaauw & Isaacs, 2014). Such areas are critical for foraging bumble bees, and recent work has documented the importance of interstitial, seminatural habitats in providing season-long pollen across mosaic agricultural landscapes (Hemberger & Williams, in review).

In addition to improving interstitial habitat, other strategies include increasing flowering crop diversity (Hemberger et al., 2021), implementing cover crops (Mallinger et al., 2019), or in-field solutions such as prairie strips (Schulte et al., 2017). Although these strategies are not compatible with cranberry production, they are increasingly common across more common agroecosystems. Mass-flowering crops can be highly attractive to foraging bumble bees and beneficial for colony growth (Westphal et al., 2009). However, in certain contexts, mass-flowering crops are largely unused (Hemberger & Williams, in review), suggesting their use as a conservation resource or bridging gaps in floral resource phenology may be insufficient to promote bumble bee persistence. Mass-flowering crops may, however, support additional taxa (Holzschuh et al., 2013; Jauker et al., 2012). Regardless, efforts to diversify agricultural landscapes broadly are essential and can support other taxa, including other pollinator species (Albrecht et al., 2020; Hopwood, 2008; Lowe et al., 2021), natural enemies (Haan et al., 2021; Iuliano & Gratton, 2020; Spiesman et al., 2020), farmland birds (M. A. Hall et al., 2022; Hardman et al., 2016) and, in many cases, the ecosystem services these taxa provide.

Our measures of resource abundance and continuity, while a much higher spatiotemporal resolution than many landscape-scale studies, are still relatively coarse and a best-effort approximation. Because we were unable to survey several land covers, locations, and a greater range of times within a year means that our estimates may underestimate the true resource conditions available to bumble bees. Moreover, we were not able to estimate interannual variability that could be important to consider. Several methodological advances are rapidly improving our ability to estimate floral resource availability, including remote and drone-based surveillance (e.g., Cruzan et al., 2016; Habel et al., 2016). Although aligned with our research questions, our measurements of resources may not allow us to easily calculate the scale of augmentation needed to increase resource abundance and continuity in a landscape. As a result, although an increase in resource abundance or continuity is statistically associated with an increase in bumble bee occurrence on average, creating meaningful increases of resources (this itself a contentious topic, Dicks et al., 2015) for certain species may require augmentation either beyond the scope of many conservation actions or allowable given the context of the landscape or competing land uses. Additional research is needed to create robust connections between measurements of resource abundance and continuity and the actions that can be taken to improve both.

## CONCLUSIONS

Floral resources are a key factor in understanding where, when, and which pollinator species will occur in agricultural landscapes. Here, we confirm previous work highlighting the importance of floral resource abundance for a widespread group of insect pollinators but improve upon it by showing that the continuity of floral resources over time is an even stronger determinant of bumble bee species occurrence and community composition. Critically, we find that landscapes with temporally continuous floral resources are the most suitable, with bumble bees on average 50% more likely to occur compared with landscapes with temporally discontinuous resources. The response of individual species is well matched to long-term population trends and suggests an adaptive capacity for several species while others struggle under modern resource conditions. Our results suggest several solutions to increase resource continuity in agroecosystems including restoring marginal habitat, adding flowering cover crops, and diversifying the number of flowering crops in the landscape. If addressed, these solutions could improve the suitability of landscapes for bumble bees, pollinators, and wildlife, supporting ecosystem services and the long-term sustainability of our agroecosystems.

## AUTHOR CONTRIBUTIONS

Jeremy Hemberger and Claudio Gratton conceived the study design. Jeremy Hemberger and Olivia M. Bernauer carried out fieldwork and laboratory identification. Hannah R. Gaines-Day contributed data from previous work. Jeremy Hemberger analyzed the data. Jeremy Hemberger wrote the first draft of the manuscript. Jeremy Hemberger, Olivia M. Bernauer, Hannah R. Gaines-Day and Claudio Gratton contributed to manuscript revisions.

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## CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

## DATA AVAILABILITY STATEMENT

Code (Hemberger, 2023a) is available in Figshare at https://doi.org/10.6084/m9.figshare.21507906.v1. Data (Hemberger, 2023b) are available in Figshare at https://doi.org/10.6084/m9.figshare.21507900.v1.

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## SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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