

Long-term surveys support declines in early season forest plants used by bumblebees

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Abstract

1. Populations of bumblebees and other pollinators have declined over the past several decades due to numerous threats, including habitat loss and degradation. However, we can rarely investigate the role of resource loss due to a lack of detailed long-term records of forage plants and habitats.
2. We used 22-year repeated surveys of more than 262 sites located in grassland, forest, and wetland habitats across Illinois, USA to explore how the abundance and richness of bumblebee food plants have changed over the period of decline of the endangered rusty patched bumblebee *Bombus affinis*.
3. We documented a decline in abundance of bumblebee forage plants in forest understories, which our phenology analysis suggests provide the primary nectar and pollen sources for foundress queens in spring, a critical life stage in bumblebee demography. By contrast, the per-unit area abundance of food plants in primarily midsummer-flowering grassland and wetland habitats had not declined. However, the total area of grasslands had declined across the region resulting in a net loss of grassland resources.
4. *Synthesis and applications.* Our results suggest a decline in spring-flowering forest understory plants is a previously unappreciated bumblebee stressor, compounding factors like agricultural intensification, novel pathogen exposure and grassland habitat loss. These findings emphasize the need for greater consideration of habitat complementarity in bumblebee conservation. We conclude that the continued loss of early season floral resources may add additional stress to critical life stages of bumblebees and limit restoration efforts if not explicitly considered in pollinator conservation.

KEYWORDS

Bombus affinis, endangered species, flowering phenology, forage plants, habitat change, habitat complementarity, pollinator conservation, wildflower declines

1 | INTRODUCTION

Declines in bumblebees and other pollinators have raised concerns over the pollination of wild plants and crops, as well as concerns

over the potential extinction of pollinator species themselves (Potts et al., 2010; Williams & Osborne, 2009). Pollinator declines are likely caused by combined factors including agricultural intensification, novel pathogen exposure, competition with non-native species

and climate change (Potts et al., 2010). Primary among these factors is the reduction of habitat quality and quantity, including the loss of key nectar and pollen sources across space and time (Baude et al., 2016; Carvell et al., 2006; Scheper et al., 2014). A reduction in habitat quality and quantity is implicated in the decline of numerous species (Mortelliti et al., 2010), and is closely tied to extinction risk (Potts et al., 2010; Wilcove et al., 1998). Few long-term surveys exist that track changes in the key pollinator plant resources found in various habitats, which leaves the roles of resource loss and habitat complementarity in pollinator declines and recovery unresolved.

Habitat loss and degradation are often tied to agricultural intensification (Foley et al., 2005). Along with the increased conversion of natural land cover to croplands, the advent of transgenic crop cultivars with engineered herbicide tolerance has increased the quantity and frequency of herbicide use in agriculture, reducing the abundance of non-target plants that may be pollinator food resources in agricultural landscapes (Zaya et al., 2017). These global trends are especially apparent within the American Midwest, where simplified agricultural landscapes dominated by corn and soya bean offer few floral resources (Meehan et al., 2011). Bee populations within this region have undergone recent declines (Burkle et al., 2013; Gixti et al., 2009), represented most acutely by substantial losses of the now-federally-listed rusty patched bumblebee, *Bombus affinis*, which has been extirpated from ~70% to 90% of its former range (USFWS, 2019). Bumblebee populations within these heavily converted landscapes rely on a mosaic of forest, grassland and wetland habitat fragments for colony growth and reproduction (Hines & Hendrix, 2005; Spiesman et al., 2017). Although the loss of habitat at broad scales is well-documented (e.g. Meehan et al., 2011), it is unknown how or if resource availability has changed within the remaining fragments and if declining habitat quality, defined here as forage plant availability, may be occurring alongside the loss of quantity.

Bumblebee populations are sensitive not only to total resource quantity, but also to the timing of resource availability (Carvell et al., 2017; Malfi et al., 2019). Bumblebees have long flight seasons, spanning the flowering phenology of several food resources and habitat types (Timberlake et al., 2019; Williams & Osborne, 2009). Colonies do not store large quantities of pollen or nectar, relying instead on a consistent supply of floral resources throughout the season to successfully grow and reproduce. As is the case for many organisms, all the resources bumblebees need may not be available within a single habitat type. Instead, mobile organisms can move between habitats that differ in timing of resource availability. These habitats are therefore complementary in time, with each habitat providing a partial share of the resources needed for sustained growth and reproduction (Mandelik et al., 2012). Because bumblebee species have relatively large foraging ranges (Mola & Williams, 2019), they may be able to access a sustained supply of resources through complementary habitat use (Mandelik et al., 2012), visiting different land cover or vegetation types through a succession of floral turnover. Therefore, the value of different habitat types to bumblebees varies between castes and throughout colony development. If floral cover is lost from any one of the habitats, there may be a disruption

to habitat complementarity in the bumblebee flight season. To understand the role of resource loss in bumblebee declines, we must consider differences in the timing of resource availability among habitats and how that may affect different demographic stages in the bumblebee life cycle.

To investigate changes in bumblebee forage resources, total habitat and temporal complementarity, we use a long-term statewide dataset from Illinois (Carroll et al., 2002; Zaya et al., 2017) to examine how floral resources in forests, grasslands and wetlands have changed over 22 years (Figure 1). We examined changes in the cover and richness of plant species with any visitation records by bumblebees in Illinois, as well as a second set of focal plants thought to be favoured by *B. affinis* and Midwestern bumblebees generally. We estimated the land cover around the focal sites to explore the hypothesis that sites with more intensive agriculture in the surrounding landscape have lower focal plant abundance. We also estimated the

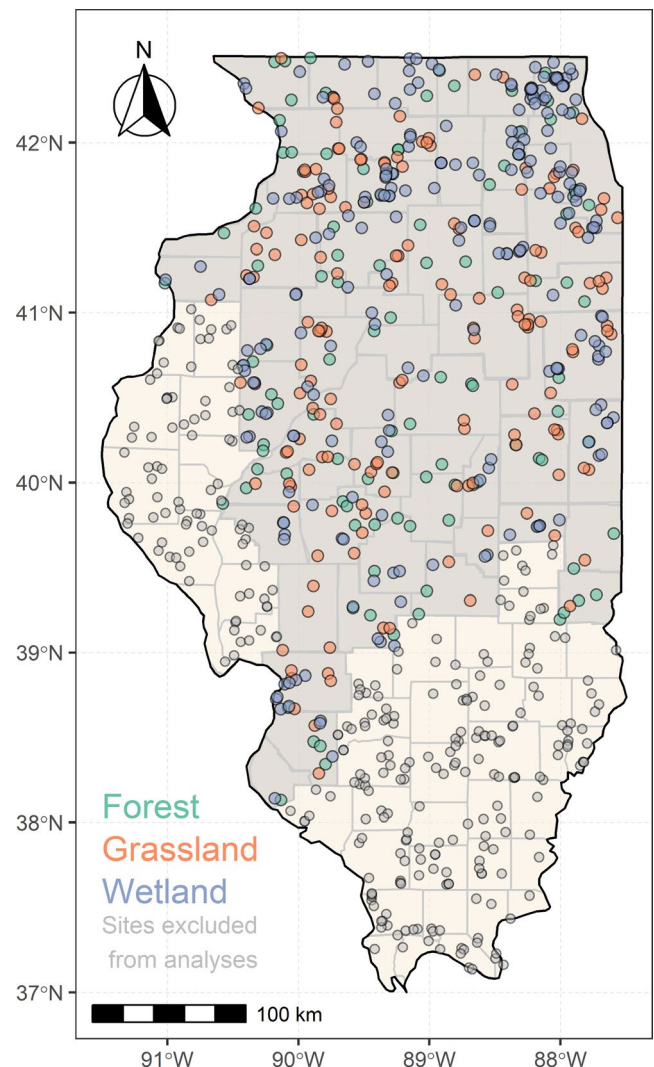


FIGURE 1 Map of Illinois (USA) showing study sites. We examined changes within forest (green), grassland (coral) and wetland (blue) sites within *Bombus affinis* historic range (shaded counties). Additional sites outside *B. affinis* range (grey circles) are not included in this study

change in total forest, grassland, and wetland cover across the entire study region. Lastly, to estimate how different habitat types vary in their seasonal importance for bumblebees, we generated habitat-level flowering curves using the records of focal plant flowering dates and overlaid the seasonal density of bumblebee museum records. We find changes in plant cover and richness over the past two decades that vary across the seasonally distinct habitats. Our results reinforce the importance of habitat complementarity for bumblebee resource continuity and highlight how resource loss may vary across different habitats.

2 | MATERIALS AND METHODS

2.1 | Data description

Survey sites come from a stratified, randomly selected set of habitat patches evenly distributed throughout Illinois with a majority of sites on private property (Critical Trends Assessment Program, 'CTAP'; Carroll et al., 2002). Sites were revisited in a 5-year rotation, so not every site is surveyed every year. As such, we binned survey events into five non-overlapping sampling periods (1997–2001, 2002–2006, 2007–2011, 2021–2016 and 2017–2019; Table S1). Plant abundance was counted as bins of groundcover within $20 \times 0.25 \text{ m}^2$ quadrats along a 41-m transect in wetland and grassland sites and 30 quadrats distributed across three 50-m transects within forest sites. Although woody plants can be key sources of early season pollen for bumblebees (e.g. Kämper et al., 2016), the ground layer vegetation surveys via quadrats excluded woody vegetation $>1 \text{ m}$ tall, as they are surveyed as separate canopies (i.e. shrub/tree counts, DBH measurements). In 1997, forest sites only contained 15 quadrats. Exclusion of this year does not change results qualitatively, so we include 1997 for consistency. Sites within each habitat type were sampled May 15–June, July and August for forest, wetlands, and grasslands respectively. Data represent plant presence and cover, not direct counts of floral abundance. We can assume a correlation between plant cover, richness and floral production for the species of interest because of the well-established positive relationships between plant size (biomass, leaf area, etc.), species richness and total flower production (e.g. Bonser & Aarssen, 2009; Ebeling et al., 2008; Samson & Werk, 1986).

2.2 | Selection of focal plant subsets

Because we are interested in how bumblebee floral resources may have changed over the survey period, we focused our investigation on plants visited by bumblebees in Illinois and the preferred plants of the endangered *B. affinis*. Given the federally endangered status of *B. affinis*, land managers must handle the weighty task of monitoring and preserving their populations, with managing floral resources being key to this strategy (USFWS, 2019). As such, to align

our analysis with these considerations, we only include sites within counties that historically contained *B. affinis* (Figure 1), although inclusion of all sites yielded qualitatively similar results.

We generated a list of floral resources used by bumblebee species within Illinois by extracting floral host records from the Bumble Bees of North America database (BBNA; Williams et al., 2014) which is updated and maintained by Dr. Leif Richardson (<https://www.leifrichardson.org/bbna.html>). This filtering yielded 159 plant species within the CTAP database used by bumblebees (Table S2). Because of the uneven distribution of records within the BBNA database, as is common with unstandardized collection records, it broadly represents floral species used by bumblebees but is not suitable for determining floral preference or the relative value of food plants (Wood et al., 2019). To focus our analysis on high-value food plants to *B. affinis* and bumblebees in general within the Midwest, we generated a second focal plant subset using the US Fish and Wildlife Service (USFWS) *B. affinis* favoured plants list (<https://www.fws.gov/midwest/endangered/insects/rpbb/plants.html>; (Table S3). The list was generated by USFWS in collaboration with regional partners and is largely congruent with other regional studies of bumblebee pollen use (Simanonok et al., 2021; Wood et al., 2019). Because the USFWS list only provided the genus for several taxa, we expanded the list to include any member of that genus within the CTAP data, resulting in 32 focal plants (Table S3). For all subsequent analyses, we filtered the plant survey data to include only the focal plant subsets, thus treating all other cover at a site as non-forage.

2.3 | Changes in plant cover and richness

To determine if focal plants changed in cover or richness over the 22-year study period, we summed the mean cover of each plant across all quadrats within a site in each time period to yield an estimate of site-level plant cover and calculated the mean richness across all quadrats. The estimates of cover are absolute (0%–100%) for each plant species, making cover values of $>100\%$ possible within quadrats with multiple overlapping species. Any sites without any focal plants or surveyed only a single time are excluded from analysis, as no change is possible. We fit linear mixed models of focal plant cover and richness as a function of sampling period and habitat type with site as a random effect to determine change over the study period. By including site as a random effect, we help account for site-level variation as well as changes in plant cover or richness that would simply be attributed to some sites being lost to development, ploughing or loss of access permissions (Carroll et al., 2002). To determine the contribution of individual plant species to plant cover, we calculated the per-species proportion of cover within each plant subset as the sum of all cover for a given species across all sites over the total cover of all species at all sites. We then calculated this proportion again for each habitat type.

2.4 | Influence of surrounding landscape on plant cover and richness

To understand possible relationships between site-level bumblebee plant cover or richness and the surrounding landscape, we estimated corn and soya bean abundance around our focal sites using land cover data obtained from NASS CDL from 1999 to 2019 (CDL data not available for 1997–1998; USDA-National Agricultural Statistics Service, 2019). Around each site we classified land cover within 1,000, 2,500, and 5,000 m and calculated the percent of soya bean and corn, the predominant agricultural crops within the region. We chose these radii to cover appropriate scales of plant community dynamics within the region (Brazner et al., 2007) and as representative of the typical foraging range of most bumblebee species (Mola & Williams, 2019). To determine if landscapes with higher amounts of intensive agriculture had lower site-level plant cover or richness, we fit linear models for each habitat with the mean site-level plant cover or richness as a function of the mean percent of corn and soya bean within the landscape across all sampling periods for each buffer radius.

2.5 | Change in habitat cover over time

We calculated the change in forest, grassland and wetland cover within our focal region (Figure 1) by comparing National Land Cover Database (NLCD; <https://www.mrlc.gov/>) estimates in 2001 and 2016, spanning as closely as possible the time period of our study. We combined NLCD cover classes (<https://www.mrlc.gov/data/legends/national-land-cover-database-2016-nlcd2016-legend>) for each habitat (forests: 41, 42, 43; grasslands: 71, 81; wetlands: 90, 91) to match classifications used within the CTAP protocol (Carroll et al., 2002).

2.6 | Complementarity and seasonality of different land covers

We generated the estimates of seasonal floral abundance for each habitat type using species-specific floral information and site-level abundance. First, we used data on first and last flowering date for each plant species (Wilhelm & Rericha, 2017) to determine the mean and standard deviation of flowering date. We assumed a normal distribution for flowering (Clark & Thompson, 2011) and generated flowering phenology curves for all plant species. Next, we calculated the estimated floral abundance of each species at every site it was present by multiplying the species flowering phenology curve by its site-level cover. We conducted this analysis separately for the all bumblebee plants subset and the *B. affinis* subset.

To compare flowering phenology to the flight season of bumblebees, we gathered all bumblebee records from Illinois within the BBNA database. To avoid bias from duplicate records and multiple collections made on a single day, we included only one record

per species per collecting event (i.e. unique combination of location, collector, species and caste) each day. For *B. affinis*, we generated a kernel density estimate of abundance across the season by caste, such that days with more unique *B. affinis* records have higher density values. For each caste, we found the maximum density value to determine the day of year likely to be associated with peak abundance. For each of these peak days, we extracted the estimated floral abundance of all sites using the results of the plant phenology estimation. We then used linear mixed models of floral abundance as a function of habitat type with site as a random effect for the peak abundance date of each caste to determine the seasonal importance of habitats to *B. affinis* across the season. For all other bumblebees, we provide only the range of day of year records for a visual comparison to plant phenology. Because we do not have reliable lists of individual species' preferred forage plants, like those available for *B. affinis*, we did not attempt a quantitative assessment (Appendix S1). Many BBNA records only indicate a specimen's sex. For *B. affinis* records with an associated photograph, we were able to determine caste since queens and workers have distinct colour patterns. For all other species, records labelled 'Worker' may include workers, queens or gynes, but exclude any specimens explicitly labelled as queens or gynes. Presumably, most of these records are workers.

2.7 | Statistical software and data availability

All data management and analysis were performed in R version 4.0.0 (R Core Team, 2020). To fit mixed-effects models, we used the package *lmer4* (Bates et al., 2007). Conditional and marginal R^2 was calculated for mixed models using the *rsquared* function from the *PIECEWISESEM* package. Tukey HSD post hoc pairwise significance tests were run using function *glht* from the *MULTCOMP* package (Hothorn et al., 2016). We conducted likelihood ratio tests of focal models against a null model with the focal effect(s) removed to obtain P-values for mixed-effects models using the *anova* function.

3 | RESULTS

3.1 | Changes in plant cover and richness

Using records from 1,033 surveys of 262 sites for bumblebee plants and 805 surveys of 201 sites for *B. affinis* plants (Table S1), we found differing degrees of change in plant cover depending on habitat type and focal plant subset (Figure 2). Forage plant cover declined in forest sites by approximately 3.7% and 2.7% for all bumblebee plants ($\beta \pm SE = -0.929 \pm 0.278$, $R_m^2 = 0.01$, $R_c^2 = 0.63$, $p < 0.001$) and *B. affinis*-preferred plants ($\beta \pm SE = -0.685 \pm 0.213$, $R_m^2 = 0.02$, $R_c^2 = 0.64$, $p = 0.001$) respectively. The response in grasslands varied between focal plant subsets with overall bumblebee floral cover remaining stable ($\beta \pm SE = -0.303 \pm 0.753$,

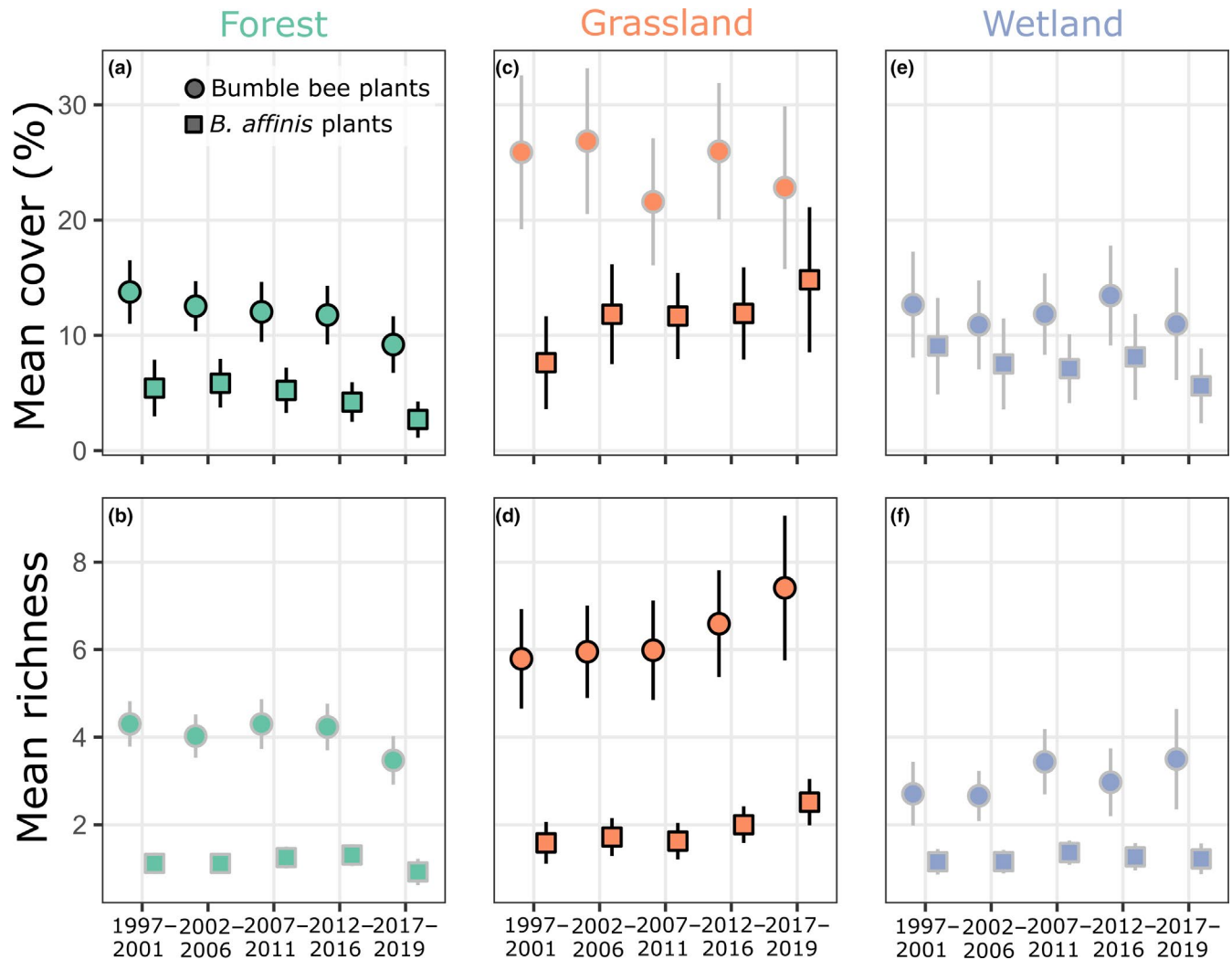


FIGURE 2 Change in mean cover (top) and mean richness (bottom) over time in forest (a and b), grassland (c and d) and wetland (e and f) sites. Focal plants in the all bumblebee plant subset are represented by circles and *Bombus affinis* focal plant subset is shown with squares. Darkened points are those with significantly increasing or decreasing coefficients ($p < 0.01$) from linear mixed models. Error bars are $\pm 95\%$ CI

$R_m^2 < 0.01$, $R_c^2 = 0.61$, $p = 0.688$) but *B. affinis* floral cover increasing by 6.96% ($\beta \pm SE = 1.740 \pm 0.509$, $R_m^2 = 0.02$, $R_c^2 = 0.63$, $p < 0.001$). There was no clear trend in wetlands for bumblebee plants ($\beta \pm SE = -0.187 \pm 0.407$, $R_m^2 < 0.01$, $R_c^2 = 0.73$, $p = 0.646$) or *B. affinis* plants ($\beta \pm SE = -0.160 \pm 0.392$, $R_m^2 < 0.01$, $R_c^2 = 0.66$, $p = 0.683$).

Trends in the species richness of plants differed by habitat type and which focal plant subset was examined (Figure 2). In forests, richness of bumblebee plants and *B. affinis*-preferred plants did not show a steady, linear decline (Bumblebee plants: $\beta \pm SE = -0.103 \pm 0.061$, $R_m^2 < 0.01$, $R_c^2 = 0.59$, $p = 0.092$; *B. affinis* plants $\beta \pm SE = -0.013 \pm 0.031$, $R_m^2 < 0.01$, $R_c^2 = 0.51$, $p = 0.684$). However, richness of floral resources in the most recent sampling period was markedly lower than in previous periods (Figure 2b). Grassland plant richness increased for both bumblebee plants ($\beta \pm SE = 0.300 \pm 0.103$, $R_m^2 < 0.01$, $R_c^2 = 0.79$, $p = 0.004$) and *B. affinis* plants ($\beta \pm SE = 0.188 \pm 0.046$, $R_m^2 = 0.02$, $R_c^2 = 0.71$, $p < 0.001$). Wetland plant richness remained unchanged for both bumblebee

plants ($\beta \pm SE = 0.117 \pm 0.066$, $R_m^2 < 0.01$, $R_c^2 = 0.77$, $p = 0.079$) and *B. affinis* plants ($\beta \pm SE = 0.045 \pm 0.038$, $R_m^2 < 0.01$, $R_c^2 = 0.51$, $p = 0.236$).

For both bumblebee plants and *B. affinis* plants, a few key species generated a large share of the total cover (Figure 3) as well as the within-habitat cover (Tables S1 and S2). *Solidago canadensis* and *Impatiens capensis* were the largest contributors to total cover, accounting for 26% of the cover in the full bumblebee plant subset and 67% of cover in the *B. affinis* subset. However, these species were rare in forests (Figure 3; Figure S1) where, for example, *Geranium maculatum* was the largest contributor to forest plant cover for both bumblebee plants (17%) and *B. affinis* plants (55%).

3.2 | Influence of surrounding landscape on site-level findings

We did not find a statistically significant relationship between site-level floral cover or richness and the amount of corn and soya bean

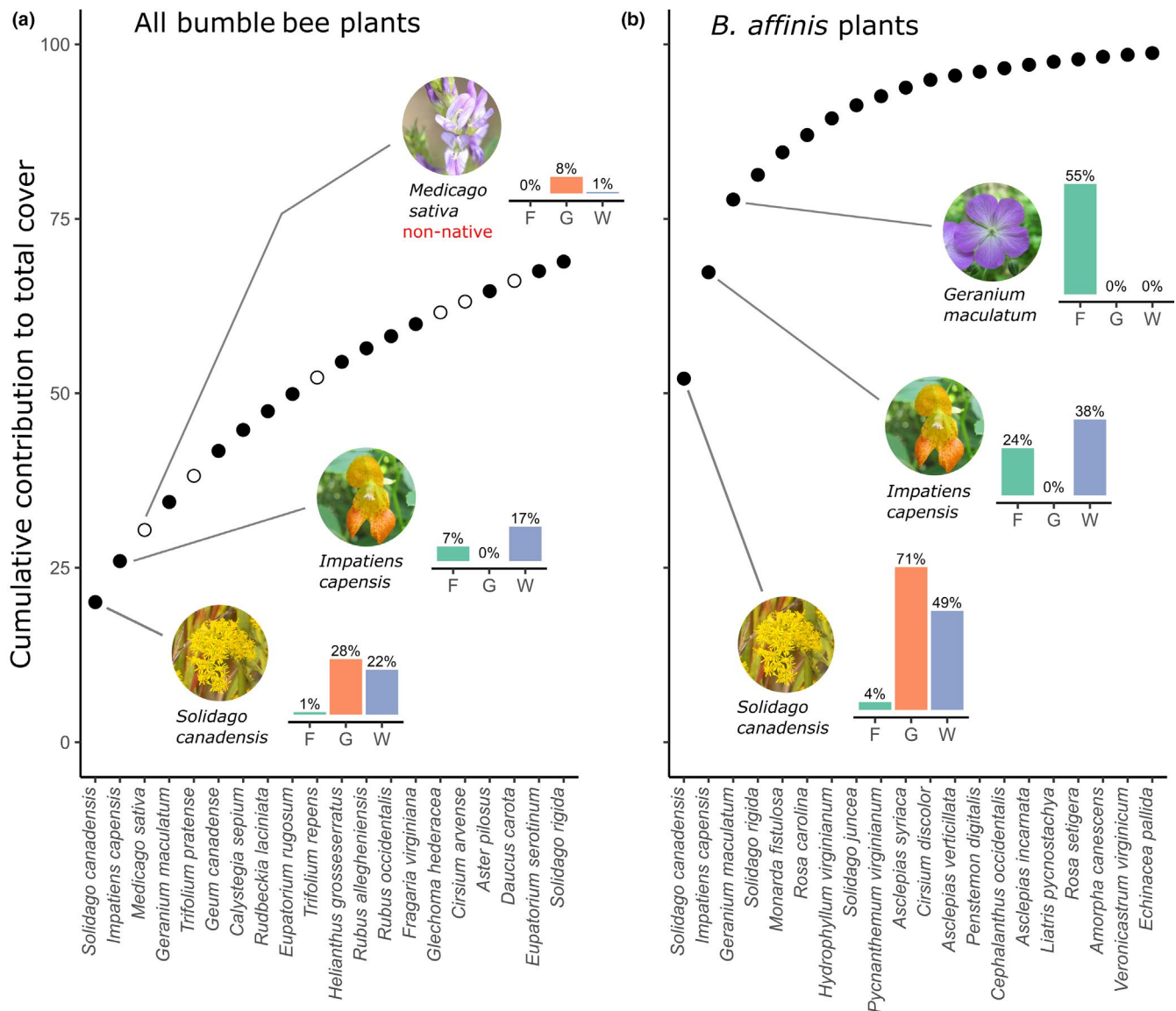


FIGURE 3 Cumulative contribution of individual plant species to the total cover of all bumblebee plants (a) and *Bombus affinis* plants (b). Insets display the top three plant species in each focal plant subset, with their relative contribution to the total cover within each habitat (F = Forest, G = Grassland, W = Wetland) displayed in the bar chart. Non-native plants are represented by open circles. For visual clarity, only the top 20 plant species in either floral subset are displayed. Photograph credits: *Medicago sativa* photograph courtesy of iNaturalist user jon_sullivan (<https://www.inaturalist.org/photos/1185717>). All other photographs are provided by Illinois Natural History Survey

in the landscape for either all bumblebee plants or *B. affinis* plants at any of the examined buffers (Table S4).

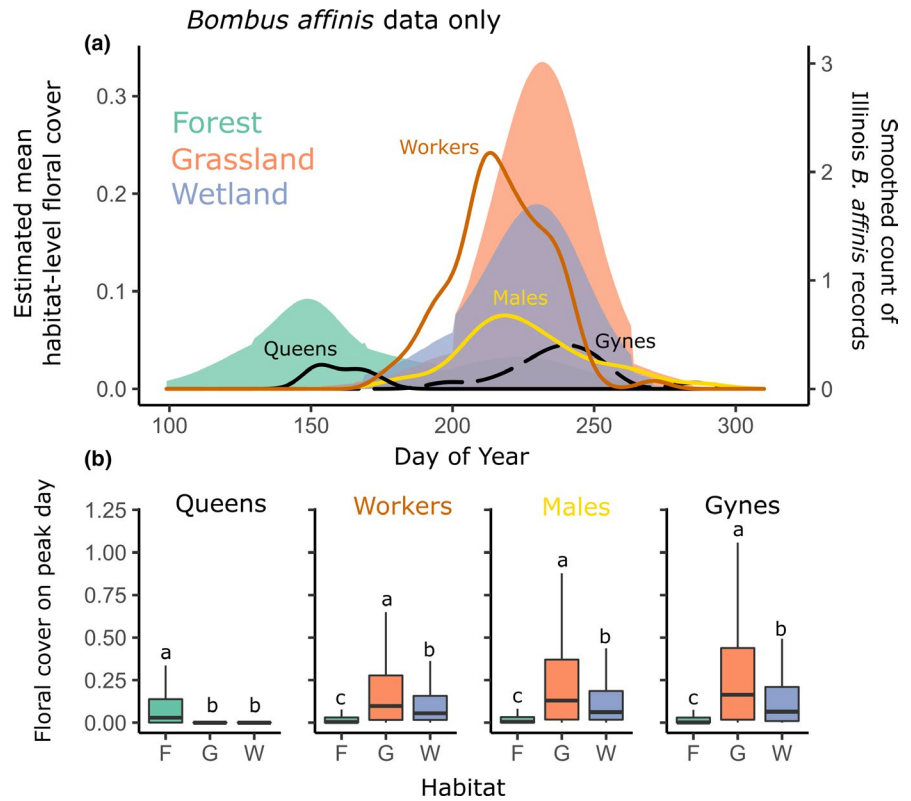
3.3 | Change in habitat cover over time

Habitat cover within the focal region changed between 2001 and 2016, largely from a 7.12% increase in developed land cover. Forests declined modestly from 9.80% to 9.68% of the area, whereas grasslands declined more substantially from 5.83% to 5.39%, or about a 7.5% loss. Wetlands remained in low abundance throughout, comprising 1.85% and 1.79% of land cover in 2001 and 2016 respectively. Cropland cover remained dominant with little change at 68.31% and 67.96% in 2001 and 2016 respectively.

3.4 | Seasonal importance of different land covers

When looking at overall plant abundance without regard to seasonality, grasslands had the highest focal plant cover and richness compared to forests or wetlands (Figure S2). However, the seasonal distribution of flowering was starkly different between habitats for *B. affinis* plants (Figure 4a), with peak forest floral abundance estimated to be May 29 (day of year 149) compared to August 20 (232) and August 18 (230) for grasslands and wetlands respectively. Accordingly, floral abundance available to different castes during their peak differed greatly. Forests had the highest floral abundance during peak spring queen activity (Figure 4b). For peak worker, male and gyne activity, grasslands had the highest floral abundance,

FIGURE 4 The abundance of *Bombus affinis* plants varies by season and habitat. (a) Estimated mean floral cover of forest (green), grassland (coral) and wetland (blue) habitats from the phenology model. *Bombus affinis* database records from Illinois (USA) are shown as smoothed kernel density estimates for spring queens (solid black), workers (rust), males (yellow) and fall gynes (dashed black). (b) Boxplots of estimated floral cover during peak abundance of each caste within forest, grassland and wetland sites. Letters show significance at $p < 0.01$ level from Tukey HSD post hoc test of linear mixed-effects model with site as a random effect. (F = Forest, G = Grassland, W = Wetland)



followed by wetlands and then forests (Figure 4b). The comparison of the flowering period of all bumblebee plants to the records of castes for the total bumblebee community similarly shows that queen activity occurs when forests contain the most flowering resources (Figure 5; Appendix S1).

4 | DISCUSSION

We found evidence for changes in resource availability for bumblebees over the survey period depending on habitat and focal plant subset. Grasslands contained the highest density of bumblebee plants and had stable or increasing cover and richness, but this within-habitat increase was more than offset by a reduction of total grassland habitat within the region. We found a decline in focal plant species within forests that may be important to critical life stages of bumblebees. This finding is striking within the context of our other results showing that forest resources overlap most strongly with the activity of spring bumblebee queens (Figures 4 and 5). Our results lend further support to the importance of complementary habitats for bumblebees and to considering temporal patterns of resource availability in species conservation (Mandelik et al., 2012; Ogilvie & Forrest, 2017).

The reduction of bumblebee resources in forests included a decline in key early season species like *Geranium maculatum* and *Hydrophyllum virginianum* (Figure 3), which declined from a combined mean of 10.2% of site cover in the first sampling period to 6.2% in the most recent sampling period (Table S5). Although our dataset precludes a formal analysis of phenology across each sampling

period, the decline in forest resources over the past couple decades appears to lead to a decrease in estimated spring resource availability (Figure S4). Due to a large variability among sites, the explanatory power of our models is somewhat limited. However, declining food plant abundance in forests is consistent with studies showing how factors like increasing deer browse (Shelton et al., 2014), invasive shrubs (Miller & Gorchoff, 2004) and disturbance from introduced earthworms (Bohlen et al., 2004) reduce spring ephemeral abundance within woodlands across the eastern United States. The declining abundance of *G. maculatum* has been documented in other studies in Illinois (Augspurger & Buck, 2017; Burkle et al., 2013) and New York (Greller et al., 1990). Notably, the understory herb flowering in central Illinois has advanced by >1 week in the last 20 years (Augspurger & Zaya, 2020), compounding the effects of resource loss by potentially increasing the asynchrony between plant flowering and pollinator emergence. Except for the most recent sampling period, the loss of resources in forests appears to be driven by a decline in plant cover (Figure 2a), not species richness (Figure 2b), consistent with evidence that species richness of plant communities lags behind trends in abundance (Price et al., 2018). If the loss of floral richness in the most recent sampling period continues, this could compound the impact on bumblebee populations as poor nutrition is associated with reduced nest founding success (Watrous et al., 2019) and persists through queen ontogeny (Woodard et al., 2019).

In contrast to the trends in forests, we found that grassland resources for bumblebees generally remained stable or increased (Figure 2c,d) with expected increases in midsummer resource availability (Figure S4), potentially due to restoration efforts and improved guidelines for conservation programs (e.g. USDA

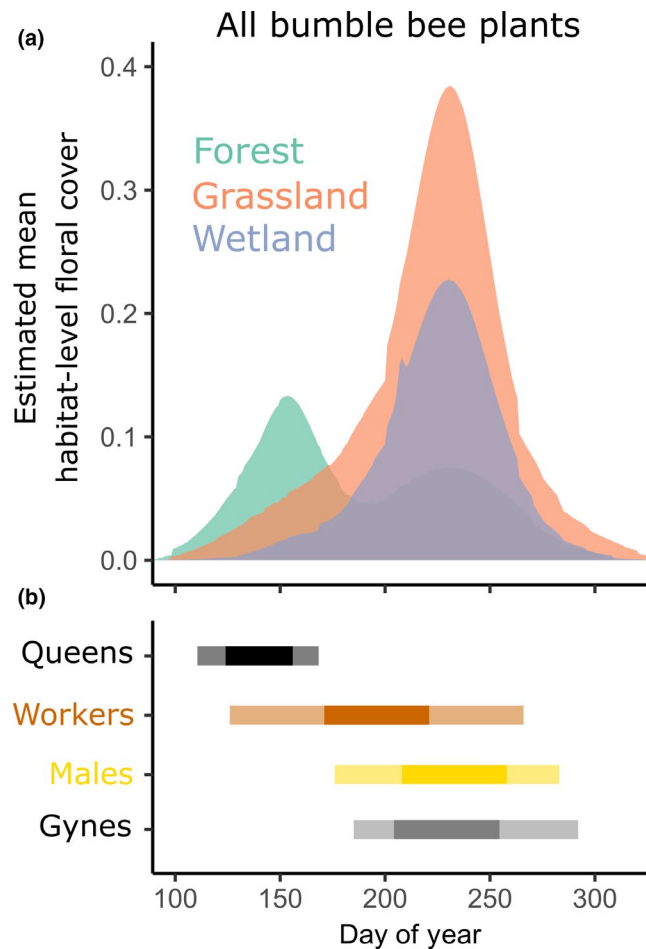


FIGURE 5 Seasonal distribution of all bumblebee plants and bumblebee specimen records. (a) Similar to the analysis for only *Bombus affinis* plants, forest (green) is the predominant resource habitat in the spring followed by grasslands (coral) and wetlands (blue) in midsummer. (b) Horizontal bars represent the inner 90th percentile range of records of bumblebee specimens (*B. affinis* excluded) in the Bumble Bees of North America database for each caste. Darkened section of the bar represents the inner 50th percentile of records

Conservation Reserve Program). However, total grassland land area declined ~7.5% within the study region, offsetting modest gains in within-habitat plant cover or richness. These recent results further the large-scale losses that have already occurred across the Midwest over the past century (Meehan et al., 2011), including the loss of nearly all native prairies (Samson & Knopf, 1994). Promisingly, we did not find evidence that sites within more agriculturally dominated landscapes have lower bumblebee plant cover or richness compared to less intensively cropped areas (Table S4), as might be expected from the increased use of herbicides applied to genetically modified herbicide-tolerant crops and simplified landscapes (e.g. a herbicide effect; Zaya et al., 2017). However, bumblebees within agriculturally dominated landscapes face numerous other challenges including insecticide and fungicide exposure and competition with managed bees (Potts et al., 2010; Williams & Osborne, 2009).

Habitats exhibited strong differences in flowering seasonality that could be an important consideration in conservation planning for *B. affinis* (Figure 4) and bumblebees generally (Figure 5). Grasslands and wetlands provide the bulk of forage for established colonies in midsummer, but these habitats lack floral resources in early spring. Forests bloom predominantly in the spring when resources within other habitats are scarce and queens are beginning to emerge. This is a critical period for bumblebee populations because floral resource availability for queens and small colonies is closely tied to population demographics (Carvell et al., 2017; Malfi et al., 2019). Because of the timing of forest surveys, our study likely underestimates the abundance of spring ephemerals and resources for bumblebees within deciduous woodlands relative to the other habitat types, suggesting resource availability within forests may be higher. However, this detection should be consistent across sampling periods and not bias estimates of trend over time. Our analysis focused on ground layer vegetation, but concurrent shrub and tree layer surveys show most forest sites contain at least one tree or shrub species used as forage by bumblebees. Comparatively, less than 25% of grassland and wetland sites had tree or shrub species used by bumblebees (Tables S6 and S7). European studies have found tree pollens to be dominant in the diets of early season *B. terrestris* (Bertrand et al., 2019; Kämper et al., 2016) and in Japan overwintered queens make use of both nectar-rich understorey ephemerals and pollen-rich canopy flowers (Inari et al., 2012). Although a comparable analysis of trends in taller woody plants was not possible with our dataset, future efforts to understand canopy resources would be worthwhile. Taken together, we conclude that consideration of habitat complementarity among forest and grassland sites could be important in creating continuous seasonal pollinator habitat and warrants targeted investigation.

A loss of resources in early spring is likely to exacerbate threats to bumblebees but is hardly the only consideration in understanding the decline and recovery. Our study focuses on *B. affinis*, a species which has undergone large declines in the past ~30 years (USFWS, 2019). However, population trajectories of North American bumblebees are not monotonic (Grixti et al., 2009; Williams & Osborne, 2009), with some species declining within the region while others remain stable or even increase in abundance. Given the general concordance between our observed trends for all bumblebee plants and *B. affinis* focal plants, it seems likely that the patterns observed here affect a range of Midwestern pollinator species. Although novel pathogen exposure is thought to be the primary cause of *B. affinis* decline and threatens other species (Cameron et al., 2016; USFWS, 2019), poor resource availability can compound the effects of pathogen exposure. For example, higher pathogen loads were found to be present in *B. impatiens* in sites with lower spring resource availability (McNeil et al., 2020), suggesting additive stress from pathogen exposure, resource availability and nutrition, which are further compounded by other threats to bee populations like pesticides or climate change (Potts et al., 2010). In total, although declining resource availability,

especially at modest levels like those observed here, is unlikely to have been the primary cause of declines for *B. affinis* and other species, substantial negative effects of declining resources are likely to be realized through interactions with several stressors.

5 | CONCLUSIONS

Habitat degradation and quality play a central role in the decline and recovery of species. In the present study, we find evidence for declines in bumblebee forage plants that vary by habitat type and therefore season. If these trends continue, they will further impede bumblebee conservation efforts if early season resources limit colony establishment or make colonies more prone to the effects of other stressors. Much of the present restoration and monitoring effort focuses on grassland restoration (Requier & Leonhardt, 2020), but our results suggest such efforts may benefit from greater emphasis on early season resources in forest habitats and increasing complementarity and connectivity between forests, grasslands, and wetlands.

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AUTHORS' CONTRIBUTIONS

J.M.M. and I.S.P. developed the initial goals of the study; G.S. and D.N.Z. provided CTAP data and expertise on Illinois plants; L.L.R. provided access to the BBNA database and guidance on its use; J.M.M. conducted analysis and wrote the initial draft of the manuscript. All the authors contributed to revisions and approved the final manuscript.

DATA AVAILABILITY STATEMENT

All raw data, intermediate output and scripts are available via the Dryad Digital Repository <https://doi.org/10.25338/B88G96> (Mola et al., 2021).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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