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RESEARCH ARTICLE

Floral resource discontinuity contributes to spatial mismatch between pollinator supply and pollination demand in a pollinator-dependent agricultural landscapes

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Abstract
Context Wild insects provide essential ecosystem services, including pollination, in both wild and managed landscapes. Over the past century, agricultural intensification and habitat loss have affected the amount and temporal availability of floral resources in the landscape—resources that all pollinating insects depend on. A reduction in the abundance and temporal continuity (i.e., gaps/bottlenecks in resources) of resources, for example, is associated with decreased occurrence of several bumble bee species within agricultural landscapes in Wisconsin. This has the potential to decrease the supply of pollination services to a variety of economically important crops.
Objective We inventoried the supply and demand of pollinators and pollinator dependent crops in a major fruit and vegetable production area in Wisconsin.
Method We applied a model to predict the occurrence of wild bumble bees as a function of landscape-scale resource abundance and continuity as an index of pollinator "supply" and combined this with spatially-explicit data on pollinator-dependent crop production to identify areas of high pollination "demand".
Results In an important fruit producing area of central Wisconsin, we found a clear spatial mismatch between pollinator supply and pollination demand, with nearly 70% of landscapes with 15 or more hectares of pollinator dependent crops (e.g., cranberries, squash) exhibiting a lower bumble bee supply index relative to the intensity of crop demand. We found the source of this mismatch was largely due inadequate floral resource conditions for bumble bees, particularly due to high levels of resource discontinuity observed in the most agriculturally intensive landscapes (which also had the greatest pollination demands).
Conclusions Our results suggest that measures to increase crop diversity, reduce the size of fields, and focus on conserving and improving semi-natural habitat in the landscapes surrounding crop fields may support improved floral resource conditions. Such changes could ultimately bolster bumble bee populations, help stabilize the supply of pollination services, and improve the sustainability and economic stability of Wisconsin's agricultural landscapes.

Keywords Resource continuity · Floral resources · Pollination services · Agroecosystem · Ecosystem services

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s10980-023-01707-w.

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Introduction

Wild insects provide essential ecosystem services in agricultural landscapes, including the control of pests (Losey and Vaughan 2006) and pollination of crops (Klein et al. 2006). In the case of pollination, wild bees are often the primary contributors to crop pollination even in the presence of managed honey bees (Klein et al. 2006; Garibaldi et al. 2013; Winfree et al. 2007). Over the past 20 years, a growing body of work has found that the composition and structure of the landscape is a strong determinant of wild bee behavior (Westphal et al. 2006; Goulson and Nicholls 2022), populations (Kennedy et al. 2013), community structure (Kennedy et al. 2013; Martínez-Núñez et al. 2022), and crop visitation (Ricketts et al. 2008) within agroecosystems. As such, managing landscapes to support wild pollinators is critical and a focus of many agri-environmental schemes across the world in order to ensure the stability of pollination services (Carvell et al. 2015; Marja et al. 2018).

Key landscape factors associated with wild bees include the presence of natural and semi-natural habitat surrounding crop fields which act as a source of wild bees. These habitats provide nesting habitat and floral (food) resources (Roulston and Goodell 2011; Liczner and Colla 2019). Semi-natural habitats are believed to provide a more temporally stable source of floral resources allowing foraging bees to find flowers when there are gaps in the availability of flowers from crops over the course of the growing season (e.g., Fig. 1A, B vs. Fig. 1C, D; Williams and Kremen 2007; Williams et al. 2012; Schellhorn et al. 2015; Hemberger and Williams, *unpublished data*). In many agroecosystems, simple quantifications of semi-natural habitat availability in the landscape [e.g., the amount of edge habitat; (Tscharntke et al. 2021), distance from natural habitat (Ricketts et al. 2008)] can be strong indicators of wild bee abundance and crop visitation, effectively serving as a proxy for more specific factors like the availability of flowering resources in a landscape (which are difficult to measure at the landscape scale; Cusser et al. 2016). Despite their importance, the rapid intensification of agricultural practices over the last century has significantly reduced semi-natural habitat in agricultural landscapes (Brown and Schulte 2011), in turn reducing floral resources and fragmenting their continuity over time. Among other factors, the loss of these habitats has led to substantial declines in insect abundance and diversity (Goulson et al. 2015; Habel et al. 2019; Sánchez-Bayo and Wyckhuys 2019; Hemberger et al. 2021) and threatens to destabilize the supply of pollination services (Pérez-Méndez et al. 2020), potentially leading to mismatches between the supply and demand of pollination services.

The importance of maintaining wild pollinator supply within agroecosystems has prompted modeling efforts that translate landscape features (e.g., food and nesting resources) into measures of pollinator abundance (i.e., supply; Lonsdorf et al. 2009). A recent inventory of pollinator supply

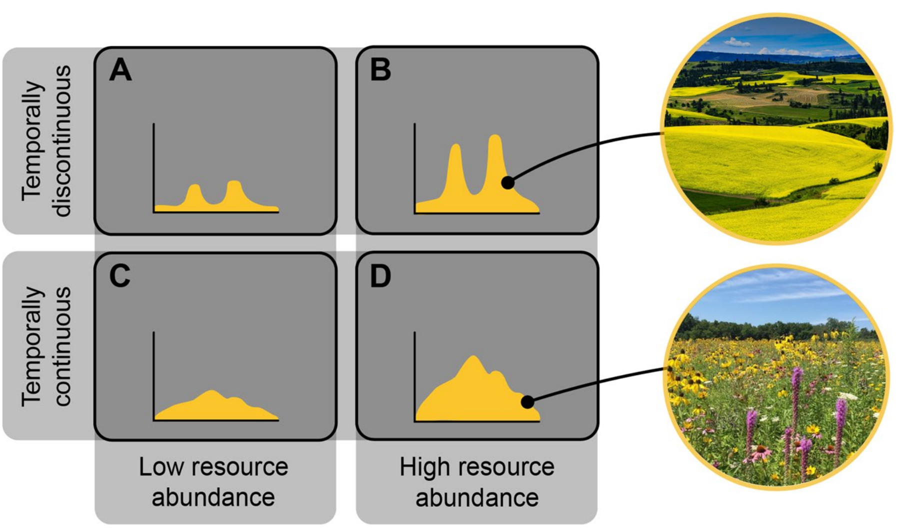

Fig. 1 Conceptual representation of landscape-scale resource abundance and temporal continuity. Four scenarios are depicted, describing temporally discontinuous resources at low (**A**) and high (**B**) abundance, and temporally continuous resources at low (**C**) and high (**D**) abundance

across the United States found that as much as 39% of the pollinator-dependent crop area suffers from a mismatch of supply and demand, with crops most dependent on pollinators found in areas where pollinators are expected to be least abundant, i.e., showing mismatches (Koh et al. 2016). Though useful as a starting point to explore scenarios and identify areas of uncertainty to focus additional research, current approaches operate at coarse scales (e.g., counties) and are unable to predict pollinator abundance in landscapes that lack strong contrasts between crop and semi-natural landscape features (Lonsdorf et al. 2009). Moreover, models applied at large scales often depend on expert opinion to estimate floral resources and, as a result, largely do not account for the temporal continuity of resources over time at a resolution that may matter for crop pollination. Accounting for the temporal dynamics of resources is critical for long-lived wild bee species (e.g., bumble bees Schellhorn et al. 2015; Hemberger et al. 2022) and bee communities, generally (Königslöw et al. 2022).

In this study, we applied a model that predicts the occurrence of wild bumble bees, a critical pollinator of a variety of crops, as a function of fine-scale information of landscape-scale resource (flower) abundance and continuity (Hemberger et al., in review). These predictions were used to map the relative supply of bumble bees in a fruit and vegetable production region in central Wisconsin. This study region accounts for ~63% of the United States' production of cranberries and grows a variety of cucurbit crops (e.g., pickling cucumbers, melons, pumpkins). We compared predictions of bumble bee occurrence, our estimate of pollination "supply", to spatial information on occurrence of pollinator-dependent crops as a measure of pollination "demand". In line with a previous, national assessment (Koh et al. 2016), we predicted that the areas highly dependent on pollination services would have the lowest supply of bumble bees due to the simplification and intensification of agricultural regions. We expected that the gap between pollination supply and demand would in part be attributed to the floral resource conditions within the landscape. That is, landscapes with more abundant and more continuously available floral resources would have a higher ratio of pollinator supply:demand, whereas landscapes with fewer and more discontinuous floral resources would have a lower ratio of pollinator supply:demand. Testing these predictions could be relevant for identifying specific landscape attributes that could be improved to increase the supply of wild bumble bees and pollination services.

Methods

Study region

We focused our analysis on the primary fruit and vegetable production region of Wisconsin, the Central Sands area, which includes Monroe, Jackson, Clark, Marathon, Wood, Juneau, Adams, Portage, Waushara, Marquette, and Waupaca counties. The region has a gradient of land use cover, ranging from intensive monocultures of row crops, such as corn and soybean, to areas of extensive natural habitat (forest and wetlands). A variety of pollinator-dependent crops are grown here, including cranberries (~8,704 ha), cucurbits (~1,074 ha), dry beans (~14,457 ha), peas (~2,689 ha) and sunflower (~51 ha). Other crops that benefit but are not dependent on pollinators include soybeans (~139,080 ha) and alfalfa (~168,134 ha).

Predicting pollinator (bumble bee) supply

We used an existing model to predict a relative index of supply of 8 bumble bee species native to this region (Hemberger et al. in review). This included common species (*Bombus bimaculatus* Cresson, *B. griseocollis* De Geer, *B. impatiens*, *B. ternarius*, *B. vagans* Smith) and rare species (*B. borealis* Kirby, *B. fervidus* Fabricius, *B. terricola*). Bumble bees are a critical wild pollinator of crops in this region, particularly cranberry for which bumble bees are the most effective (Cane and Schiffhauer 2003). Moreover, bumble bees are broadly generalists in their resource use, aligning them well to other important pollinator taxa such as honey bees and several groups of solitary bees. We used a relative index of bumble bee abundance to predict pollinator supply given that the original bumble bee abundances were determined from passive traps which are not suited to measure true abundance.

The model was initially developed for a subset of the study counties centered around cranberry agroecosystems and trained using spatiotemporally extensive surveys of all flowering plants within the major land cover categories across the study region along with 5 years of bumble bee occurrence data collected using passive trapping (Hemberger et al. *in review*). In short, the abundance and temporal continuity of floral resources was estimated from 171 floral resource surveys in 2017 and 2018 across 6 major land cover types: grasslands, shrubland, woodland, cranberry, field/woodland edges, and road edges. Flowers were surveyed 6 times per year during the growing season (May-August), yielding 17,551 flower occurrence records for 54 flower species commonly visited by bumble bees. We used flower presence data to estimate the total proportion of each land cover containing floral resources, and then created spatial rasters using these values applied to each land cover type for each of the 6 different time points. These rasters were extended beyond the original extent of the floral surveys conducted by Hemberger et al. (*in review*); however, the landscape contexts and floral communities of this region are largely similar to those in the original study, and the majority of the study region covered in the following analyses directly overlaps the study region from the original model (for full details see Appendix 1).

To assess the abundance and temporal continuity of floral resources across our study region, we applied a 3-km hexagonal grid (i.e., ~ 7.7 sq km) across the extent of the region and then extracted the sum of pixel values from each time point floral raster. From hereafter, we refer to a single grid cell as a "landscape". To relativize these values and avoid direct interpretation of the floral resource estimates, we scaled total resource abundance relative to the landscape with the maximum resource estimate across all landscapes, creating a season-long floral resource index that ranges from 0 to 1, comparable to the pollinator index of Lonsdorf et al. (2009) and Koh et al. (2016).

We estimated the temporal discontinuity of floral resources within each landscape 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 discontinuity, with high values indicating highly variable floral resources over time with peaks and valleys suggesting high resource discontinuity, while low values of CV indicate stable and more continually available resources over time (i.e., low discontinuity).

We used a generalized linear mixed model (GLMM) with the floral resource index and % CV along with species identity and geographic location to predict the probability of a bumble bee species occurring in a given landscape along with the prediction uncertainty (standard error of the estimate). For this, we used the model fitted and trained using data from Hemberger et al. in review. In each landscape, we averaged the probability of occurrence across all eight species as an aggregate index of bumble bee supply, weighting each species estimate by its relative abundance in the dataset used to train the model. We interpreted this measure as a relative index of bumble bee supply, ranging from 0 to 1.

Assessing crop pollination demand

We determined demand for pollination services by crop using the USDA Cropland Data Layer (USDA, 2022). First, we extracted the land use composition by summing the total number of pixels of each crop type within each landscape. Second, we converted the number of 30 × 30 m pixels to total area in hectares and then weighted the area estimates by the crop's approximate dependence on pollination (Klein et al. 2006). The weighting factors range from 0 to 1, with 0 indicating a wind-pollinated crop (no dependence on animal pollination) and 1 indicating obligate outcrossing crop (complete dependence on animal pollination). To better match our approximate measure of bumble bee supply, we scaled the total weighted area of pollinator dependent crops relative to the landscape (3-km grid cell) in our study region with the maximum area of pollinator-dependent crops, creating a demand index ranging from 0 to 1.

Statistical analyses

We assessed the spatial overlap in predicted bumble bee supply and crop pollination demand by creating a bivariate choropleth map (OLSON 1981). We binned each variable into three quantiles (0–33%, 33–66%, 66–100%) and plotted them against each other. The map provides a qualitative assessment and visualization of where pollination supply and and pollination demand are spatially matched or mismatched.

In addition, the match/mismatch in supply and demand was calculated as the ratio of supply:demand indices, and modeled as a function of the abundance and temporal continuity of floral resources in each replicate landscape. We focused this analysis on the areas of our study region that had a moderate amount of pollination demand by filtering to include landscapes with 5 or more hectares of pollinator dependent crops. A ratio of 1:1 signifies equivalent indices of supply and demand which we use as a point of an approximate reference for over/undersupply of pollination services. We describe landscapes where supply is less than demand as those experiencing “mismatches” of pollinator supply relative to pollinator demand (i.e., ratio of supply:demand < 1).

Model 1: Supply:demand ~ Floral resource index × Floral resource continuity × Crop area + smooth (Latitude, Longitude)

We fitted a generalized additive model (GAM, Model 1) to predict the ratio of supply to demand (with higher values indicating a greater supply relative to demand) as a function of the floral resource abundance index, temporal continuity (% CV), and area of pollinator dependent crops, and their interactions. We included crop area to determine whether the strength of landscape resource conditions would change depending on the area of crops, as a proxy of agricultural intensity. Together, these variables also allowed us to determine if there was a threshold of crop area and landscape resource conditions beyond which a mismatch of pollination supply and demand occurred.

Our initial model revealed significant residual spatial autocorrelation, so we fitted a spatial GAM to account for the spatial dependencies of our observations. To account for the spatial structure of our observations, we included a two-dimensional smooth of the location of each landscape (latitude and longitude of the centroid of the 3 km landscape). Two-dimensional smooths account for the spatial structure of the data, i.e., the similarity of nearby locations. We tested simulated residual spatial autocorrelation using the DHARMa package (Hartig 2022) to confirm that we had successfully accounted for spatial dependencies along with inspecting residual plots for model fit (Moran’s I test, $\boldsymbol{p} = 0.291$). We also checked the fitted GAM smooths basis dimensionality using the `gam.check()` function. To aid in mode interpretation, we used the sjPlot package to visualize the marginal, interactive effects of resource abundance, temporal continuity, and crop area.

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 2023), mgcv (Wood 2017), janitor (Firke 2023), raster (Hijmans 2023), sf (Pebesma 2018), paletteer (Hvitfeldt 2021), extactextractr (Daniel Baston 2022), and tidyverse (Wickham et al. 2019).

Results

Floral resource abundance and temporal continuity in central WI agricultural landscapes

Floral resource abundance across the region was generally low, with ~86% of landscapes having a seasonal floral index less than 0.10 (range 0–0.995; Fig. 2A). The floral index peaked in late July with a regional average of 0.07 ± 0.08 (mean ± SD). Landscapes with relatively low floral abundance were also those with low levels of temporal resource discontinuity, with ~90% of landscapes % CV below 100% (Fig. 2B). Landscape resource discontinuity varied between 29 and 245%, with an average of 54.9 ± 25.5%. Resource discontinuity was largely a function of single, large peaks in floral resource abundance preceded and/or followed by extremely low resource abundance (Fig. 2C, D). This pattern was mostly a result of intensive cranberry operations that flower en masse in late June and Early July. Average resource abundance and low resource discontinuity in the landscape was primarily a function of field/road edges and grassland area (Hemberger et al. *in review*).

Pollinator supply

The weighted probability of occurrence for all bee species (i.e., supply) was highly variable across the region (Fig. 3A). The supply index ranged from 0.05 to 0.62, with a landscape average of 0.25 ± 0.04 (mean ± SD). Stable species, such as *B. impatiens*, were highly likely to occur across

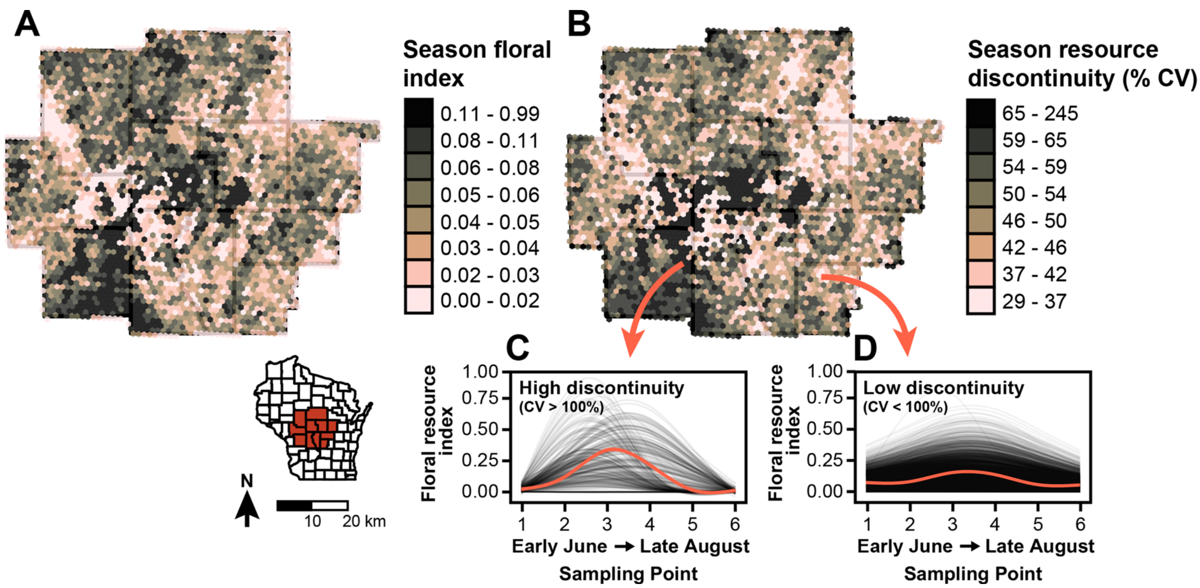

Fig. 2 **A** Spatial depiction of seasonal flower availability index (with 1 being the mostflowers) and **B** continuity (measured as coefficient of variation, largernumbers indicate greater resource discontinuity). Inset graphs are alongitudinal depiction of resource abundance over time for landscapes with **C** high (% CV is greater than 100) and **D** low (% CV is less than 100)discontinuity. Each landscape is a ~3 km hexagon

the region, but less likely in areas of scarce, discontinuous resources. Declining species, such as *B. terricola*, however, were substantially less likely to occur across most of the region, particularly where resource discontinuity was high. Other species in the analysis roughly followed these same patterns (Fig. S1).

Crop pollination demand

The area of pollinator dependent crops was largely concentrated to one sub-region, with cranberry dominating the overall demand (Fig. 3B). Other pollinator dependent crops were present, but they largely occurred in smaller patches across the region. Landscapes contained between 0 and 461 ha of pollinator dependent crops, with an average of 55.53 ± 54.34 ha. After weighting by a pollinator dependence index, the range of weighted area was 0-127 ha, with an average of 4.58 ± 10.29 ha of pollinator-dependent crops. The relativized crop demand index used for our spatially-explicit model ranged from 0 to 1, with an average of 0.04 ± 0.08.

Comparison of pollinator supply and pollination demand

The probability of bumble bee occurrence (our index of pollinator supply) was lowest in areas with the highest pollination demand (Fig. 3C). Approximately 36% of landscapes had relatively high pollinator demands (i.e., the set of 3 upper left cells in 3×3 choropleth matrix) but where pollinator supply was less than that of demand (Fig. 3D). However, almost 70% of high demand landscapes (area of pollinator dependent crops $>= 15$ ha, top row of 3×3 supply-demand choropleth matrix, had fewer than half of the relative supply of bees (Fig. 3E).

Relationship between resource amount, discontinuity, and pollinator supply and pollination demand

In agreement with our qualitative comparison, we found a significant impact of the amount of pollinator dependent crop in the landscape on the ratio of pollinator supply to pollination demand, but the effect depended on the amount and discontinuity of resources (Fig. 4; $F_{1,\ 659} = 50.95$, $p < 0.001$). As the area of crops (i.e., demand) increased, the

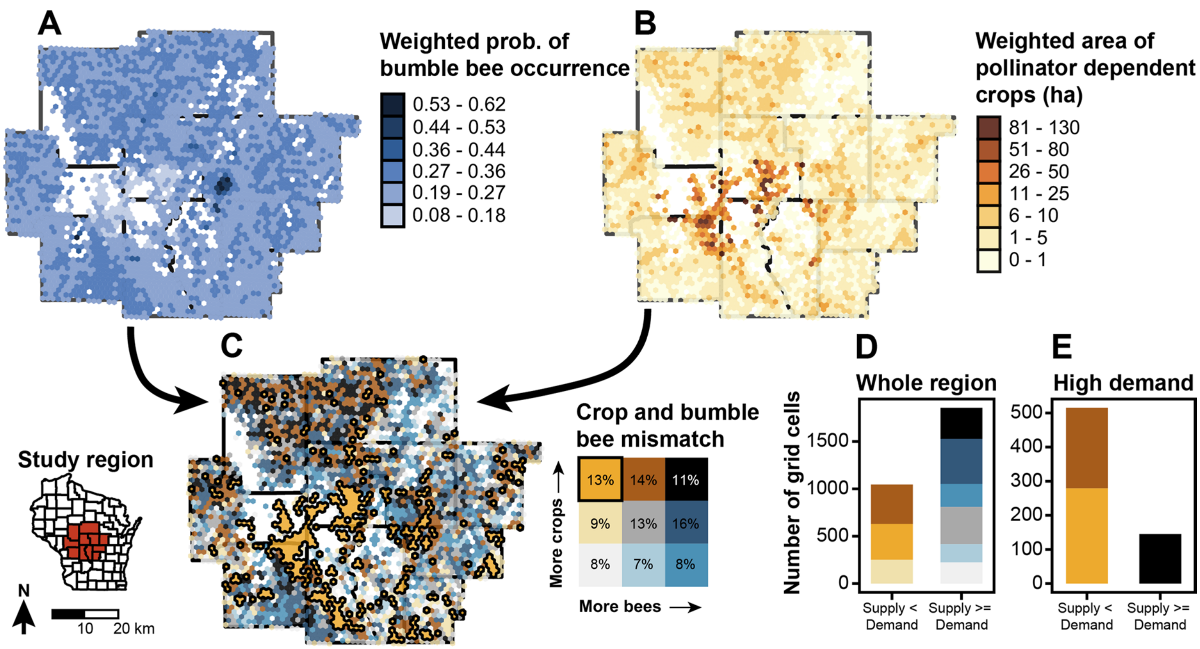

Fig. 3 **A** The total probability of occurrence for 8 bumble bee species (combined), eachweighted by their relative abundance in the dataset (i.e., an index ofpollination supply), and **B** total area of pollinator dependent crops, weightedby their estimated dependence on pollination services (i.e., an index ofpollination demand). **C** Overlaying these two metrics yields a map of thematch/mismatch of landscapes regarding pollination demand and supply.Landscapes in white and outlined in black represent landscapes with thegreatest demand for pollination services but the lowest supply (i.e., predictedoccurrence) of bumble bees (top left cell in 3 × 3 choropleth matrix). **D** Thetotal number of landscapes (grid cells) where supply is either less thandemand, or greater than or equal to demand for the entire region and **E** forhigh demand landscapes (top row in 3 × 3 matrix) where the total area ofpollinator dependent crops is 15 ha or more

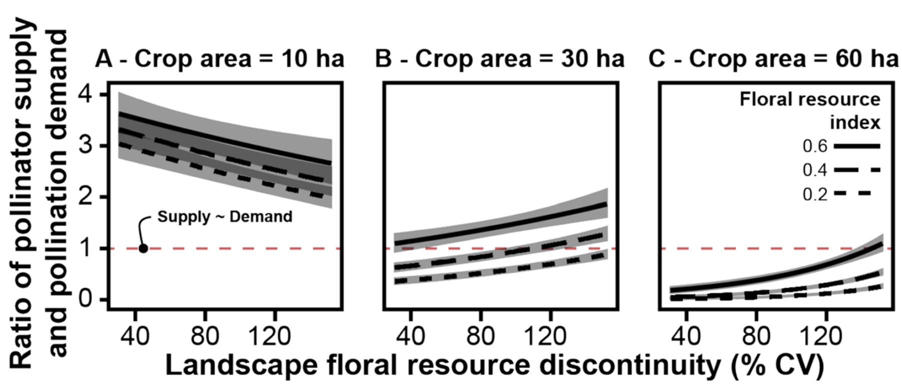

Fig. 4 Theinteractive effect of temporal resource discontinuity (x-axis), resourceabundance (line type), and crop areas (panel) on the ratio between pollinatordependent crop area and bumble bee occurrence indices (y-axis). The model ispredicted for **A** 10, **B** 30, and **C** 60 ha of pollinator dependent crops.Higher values on the y-axis indicate greater pollinator supply relative topollination demand. The red dashed line indicates where indices of supply anddemand are approximately equivalent. Estimated values and 95% confidenceintervals are predicted from a spatial generalized additive model

supply:demand ratio decreased (e.g., Fig. 4A vs. Figure 4C). For landscapes with the most pollinator dependent crops (area > = 60 ha), the ratio of supply to demand was below 1 for nearly all landscapes, regardless of the resource conditions (Fig. 4C).

In addition, and in line with our predictions, the ratio of supply and demand decreased significantly as resource discontinuity increased, and the magnitude depended on the amount of resources in the landscape (Fig. 4; $F_{1,\,659}$ = 50.95, $p < 0.001$). This effect was consistent across the range of resource discontinuity (Fig. 4A, differences between line types). The impact of resource abundance was greater than we expected, providing a stabilizing effect on supply:demand, with landscapes containing high amounts of resources (resource index > = 0.6) exhibiting a consistent, or in some cases increasing ratio of supply and demand across the gradient of resource discontinuity. Despite this statistical pattern, it is relevant to note that only 2.3% of landscapes have a resource index > = 0.6, conversely, 75% of landscapes had a resource index of less than 0.35, meaning that the overwhelming majority of landscapes would experience a mismatch in the ratio of supply and demand as resource discontinuity increased.

Discussion

By combining a regional model of bumble bee occurrence based on floral resource availability over space and time that establishes an index of pollinator supply along with the area of pollinator dependent crops as a measure of pollination demand, we found a clear spatial mismatch between the two in Wisconsin's primary fruit and vegetable production region. Nearly 70% of landscapes with 15 or more hectares of pollinator dependent crops had a lower bumble bee supply index relative to demand. Low-demand landscapes, however, had significantly higher ratios of bumble bee supply relative to demand, suggesting these areas are less likely to experience pollination shortfalls.

We found that the source of this mismatch is influenced by substandard floral resource conditions within agriculturally intensive landscapes (i.e., those with a high amount of pollinator dependent crops). Specifically, high resource discontinuity and low resource abundance within the landscape led to a lower bumble bee supply index and therefore a lower ratio of supply relative to demand. Despite a stabilizing effect of increased floral resource abundance on bumble bee occurrence, the highly variable floral resource conditions within intensive agriculture in our study region resulted in a significantly lower index of bumble bee occurrence. Such areas are expected to support a smaller, less diverse community of bumble bees—a critical group of pollinators to crops within the region. Our results support previous work describing how changes in land-use and agricultural conditions drive pollinator communities (Cusser et al. 2018; Hemberger et al. 2021), but also animals more broadly (Perzanowski et al. 2019).

The approach we present provides a more nuanced understanding of the drivers of the delivery of ecosystem services such as pollination. Previous work suggested that a mismatch between pollinator supply and crop pollination demand could be explained by crop expansion that ultimately decreases total habitat quality (i.e., flower abundance) needed for bees (Koh et al. 2016). Using this more temporally and spatially resolved model of bee abundance, based on locally-derived empirical data, we were able to expand on Koh et al. (2016) findings to show that the temporal dynamics of resources is an important determinant of supply and demand patterns.

In this area, the primary sources of continuous floral resources are natural and semi-natural habitats. Specifically, interstitial habitat such as road and field edges provide the greatest diversity and most consistent supply of flowers through the season, supporting findings from the US and EU (Hemberger and Williams, *unpublished data*; Requier et al. 2020, respectively). These smaller landscape features are often overlooked in many discussions of natural or semi-natural habitat that favor large, continuous areas, but are essential to support higher wild bee abundance (Hass et al. 2018) and bolster pest control (Redlich et al. 2018). Supporting larger areas of natural habitat is also critical; however, focusing on improving the conditions within the agricultural matrix is also a critical need to support biodiversity (Tscharntke et al. 2021). The landscapes in our region contained a diversity of landscape contexts, including intensive agricultural operations surrounded by high amounts of natural habitat (e.g., cranberry), and a range of more traditional agricultural practices including commodity row crops, pasture, and extensive vegetable production. Relative to other intensive agricultural regions, our region of study had above-average amount of semi-natural habitat but is generally representative of agriculture across Wisconsin and other portions of the North Central Midwest.

Though Koh et al. (2016) accounted for aspects of temporal variation in flower resources, the use of expert opinion-based approaches to estimate floral conditions within land cover types showed remarkably invariant patterns over the three time points estimated (early, middle, late in growing season). Using empirical estimates of flowers, we found floral resources much more variable over time, with empirically measured % CV being on average 6–7 times larger than expert opinion % CV (Hemberger 2020). This greater variability shows more differences among habitats than previously possible, thus enabling a test of the effects of flower availability over time on pollinator communities.

In addition to preserving and improving natural and semi-natural areas, increasing crop diversity within the agricultural matrix can also improve conditions for service-providing biodiversity (Sirami et al. 2019; Hemberger et al. 2021; Tscharntke et al. 2021). Mass-flowering crops (MFC) can be particularly attractive to social bees like Bombus spp. – improving the growth of bumble bee colonies (Westphal et al. 2009) and increasing bee densities in the landscape (Westphal et al. 2003). However, MFC tend to benefit only a few common, stable species capable of readily adapting to shifts in floral resource abundance and continuity (Knapp et al. 2019; Hemberger et al. 2021, 2022). The restricted temporal nature of one or many temporally overlapping MFC can also leave bees with extended periods of low resource abundance, unable to support continued reproduction (Schellhorn et al. 2015). For example, extensively cultivated, early-season MFC can act as ecological traps, luring foundress bumble bee queens with an abundance of floral resources but failing to support developing colonies with alternate floral resources for the remainder of the season leading to colony failure (Galpern et al. 2017). An over-abundance of MFC may also lead to a dilution of pollinators (Holzschuh et al. 2016) and negatively impact the pollination of crops (Shaw et al. 2020) and wild plants in the surrounding landscape (Holzschuh et al. 2011). Despite this, some systems may be robust to these dilution effects (Magrach et al. 2018). Together, current evidence suggests that we must work to reverse the trend of collapsing crop diversity (e.g., Crossley et al. 2021) by renewing efforts to diversify agricultural landscapes through increased crop diversity, reducing field size, and conserving and improving semi-natural habitat. Such efforts have substantial benefits on biodiversity without significantly reducing farmland productivity (Tscharntke et al. 2021).

In addition to changes that largely affect the composition of our agricultural landscapes, it is likely important to consider habitat and landscape configuration. In fact, the benefits of configuration often interact strongly with landscape composition to yield benefits across ecosystem services (Martin et al. 2019).

In the context of our study system, a variety of challenges stand in the way of implementing strategies that improve the resource conditions for pollinators. A primary challenge is the mismatch in scale between the actions needed (i.e., increase in natural and semi-natural habitat area, crop diversity) and the current scales of control growers and land-managers possess (i.e., on-farm practices). A need for programs that incentivize cooperative or collective action to address conservation and support of ecosystem services at landscape scales that bridge land ownership boundaries (e.g., agglomeration bonuses; Krämer et al. 2018) may offer a path forward in this regard. Second, top-down political (e.g., US Farm Bill) and economic (e.g., market availability) forces largely dictate what crops growers produce. Such forces constrain growers' capacity to diversify the crops they grow and ultimately push agroecosystems to more intensive production systems that are at odds with biodiversity conservation (Hendrickson and James, 2005). Although individual grower actions (e.g., pollinator gardens, cover crops, etc.) can have a beneficial effect, incentivizing collective action at the landscape-scale can increase the benefits of conservation actions. In the case of our work, this suggests enacting changes at scales sufficient to make a measurable impact on the mismatch between where crops are grown and where the ecosystem services that support those crops occur.

Our results point to a clear spatial mismatch in pollinator demand and supply; however, it is important to consider the limitations of our approach. First, our model includes only a small subset of the total pollinator diversity known to occur in this region

(Lowenstein et al. 2012; Gaines Day 2013). Solitary and small-bodied pollinators could respond differently to the resource conditions in the landscape; however, several parallel studies suggest that, while the scale of responses may vary, the general trends are likely to be similar (Williams and Kremen 2007; Williams et al. 2012). Second, the relative indices of supply and demand used here should be viewed as qualitative comparisons of relative patterns. Whether high or low pollinator supplies translate to actual differences crop pollination will require more detailed studies that link bumble bee abundance to pollination services, as well as a specific focus on the movement of pollen mediated by bumble bees and the ultimate efficiency of pollination services delivered by this taxa. Despite this, having relatively few bees compared to crops is a sign that landscapes could be at an enhanced risk of pollination deficits (see Koh et al. 2016), especially if other pollinator taxa are similarly impacted by resource conditions in the landscape. Third, resource conditions likely co-vary with other, unmeasured drivers, such as insecticide exposure, the crops that dominate the landscape, or disease risk from managed honey bees, which may confound the interpretation of resources driving patterns of bumble bee occurrence. However, intensive agricultural land use is highly correlated with insecticide use (Meehan et al. 2011; Meehan and Gratton 2015), and managed pollinator use is ubiquitous across pollinator-dependent crops in this region, making it difficult to statistically parse these effects from those of resources. Finally, our empirical estimates of floral abundance and continuity, while a clear improvement from expert opinion, likely still underestimate both resource abundance and discontinuity. For example, other than cranberry, floral measurements do not include other flowering, pollinator dependent crops in the region. Such an omission may alter our estimates of resource abundance but are less likely to impact our estimates of temporal discontinuity as the phenology of crop bloom in our region is largely similar.

Conclusions

Improving our understanding of which factors drive biodiversity and its associated ecosystem services is a key challenge for ecologists today. Linking specific attributes of the resource landscape, namely abundance and temporal continuity, to the supply of an important group of insect pollinators within a major agricultural region in the North Central US is an improvement in our understanding of drivers of ecosystem services. Our results suggest that the discontinuity in floral resources associated with intensive agricultural land-use leads to a lower occurrence of beneficial organisms (see also Schellhorn et al. 2015; Iuliano and Gratton 2020; Königslöw et al. 2022). Although several bumble bee species in our study are less affected by changes in the floral landscape, the loss of just a single major species can have dramatic effects on crop production (Pérez-Méndez et al. 2020). To protect bumble bee biodiversity and address potential pollination shortfalls, resource continuity can be improved in various ways including increasing crop diversity, expanding the phenology of flowering crops, reducing field size, and conserving and improving semi-natural habitat in the landscapes surrounding crop fields. These solutions can not only enhance landscapes for a variety of pollinators, but also bolster related ecosystem services such as pest control and soil and water quality. Such efforts would mark an essential shift in the intensive agricultural paradigm, supporting the long-term sustainability of agroecosystems.

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Data availability All data and R code for analyses are available on FigShare via https://figshare.com/s/e379f588a89e41333316 (data) and https://figshare.com/s/1c72e2d937cbd9efc8fa (code) and will be made public upon publication of this manuscript.

Declarations

Competing interests The authors declare no competing interests.

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