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Predicting landscape-scale native bumble bee habitat use over space, time, and forage availability

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Abstract

The distribution and abundance of foraging resources are key determinants of animal habitat use and persistence. Decades of agricultural expansion and intensification, along with the introduction of exotic species, have dramatically altered resource distributions in space and time. The nature of contemporary landscapes requires new approaches to understand how mobile organisms utilize the resulting highly fragmented, heterogeneous resources. We used colonies of the native bumble bee (*Bombus vosnesenskii*) deployed among habitat types and a land use gradient to characterize how resource availability and use change as a function of landscape composition throughout the season in a diverse agricultural region of Northern California. We employ a novel probabilistic framework to identify the spatiotemporal patterns of bumble bee resource use in different habitats. Bumble bee resource preference (i.e., pollen foraging) and availability (i.e., flowering plant abundance) are driven by the composition of the surrounding landscape and the time of year. Bumble bees strongly preferred pollen from native plants, which was overrepresented in samples across the season relative to its estimated availability. Our probabilistic model framework also revealed a strong reliance on seminatural habitat in the landscape (e.g., oak savannahs, chapparal, and riparian corridors)—features that are increasingly rare in anthropogenically dominated landscapes. In fact, pollen resource use by colonies even in the most intensive landscapes was largely limited to interstitial habitat (e.g., field and road edges) despite available mass-flowering crops. Our results highlight the importance of mosaic landscapes (i.e., landscape heterogeneity) in allowing bumble bees to link resources through the season. The framework we develop also serves to enhance predictions of insect resource use within fragmented landscapes.

KEYWORDS
agroecosystem, bumble bee, insect foraging, resource use

INTRODUCTION

For mobile organisms that forage widely in the landscape, the structure and composition of habitat patches ultimately determines resource availability (Haan et al., 2021; Magioli et al., 2019; Silveira et al., 2016; Tremblay et al., 2005). Over the past half-century, anthropogenic climate change (Descamps et al., 2021), altered patterns of land use (Carvell et al., 2006; Williams et al., 2012), and chemical inputs (Egan et al., 2014) have reduced the amount of resource-rich habitat in many regions, fundamentally altering resource distributions in both space and time. For example, declines of bees and other flower-foraging insects have been linked to a loss of floral resources due in large part to human modifications to the landscape (Roulston & Goodell, 2011). Within these altered landscapes, the persistence of insect and other animal species depends on the continued availability and temporal continuity of resources, as well as on a species' capacity to access them (Schellhorn et al., 2015).

In anthropogenically dominated landscapes, mobile organisms like bees must access temporally discontinuous floral resources from sources such as mass-flowering crops along with those from ruderal and native plant species in field borders and road edges (Gardner et al., 2021; Schellhorn et al., 2015; Vasseur et al., 2013). In contrast, bees in landscapes dominated by undisturbed habitat such as natural or seminatural areas may have access to a variety of floral resources from diverse habitat patches and may more easily integrate these over the season (Mallinger et al., 2016; Schellhorn et al., 2015). In both cases, the identity of the floral resources used by bees and the habitats from which they are collected change over space and time (Danner et al., 2016). Bees also are central place foragers that are anchored to specific nesting locations (Cresswell et al., 2000). As a result, sufficient resources must exist within the foraging range of individuals relative to the location of their nests. Moreover, access to different habitats and the forage resources within them, as well as bees use of these resources, is expected to change across gradients of anthropogenic land use due to habitat fragmentation and turnover of the plants within these areas (Danner et al., 2016; Williams et al., 2012).

Several studies explore temporal resource use for bumble bees in the lab (Hemberger et al., 2020; Schmid-Hempel & Schmid-Hempel, 1998); however, the exploration of spatiotemporal resource use in the field is more limited. Studies that do consider free foraging bees often focus on their use of floral landscape enhancements (e.g., flower strips) rather than determining their reliance of different flowers within natural and seminatural habitat within the landscape (Carvell et al., 2015; Rundlöf et al., 2022; Hemberger et al., 2022; but see Williams & Kremen, 2007). Although landscape context, floral resource identity, and resource continuity have been linked to the survival and reproductive success of bumble bees (Crone & Williams, 2016; Jachuła et al., 2022; Williams et al., 2012), previous studies stop short of connecting specific resource and habitat use and their availability to understand how bees are using different landscape elements (e.g., flowering crops, fallows, seminatural remnants) through the season. Recent use of dance decoding for honey bees has allowed researchers to accurately document reliance on different habitat types and even pinpoint specific locations used by colonies at different types throughout the season (Bänsch et al., 2020; Danner et al., 2016). For non-*Apis* bees, making such a link requires documenting pollen and/or nectar collection from plants associated with various landscape elements and assessing how reliance on these plants might change in different landscape contexts and over time (Harmon-Threatt & Kremen, 2015; Jha & Kremen, 2013; Williams & Kremen, 2007). Here, we provide a new framework to create this linkage that will (1) identify critical habitat features supporting bumble bee populations; (2) help improve existing modeling frameworks for bee resource use in the landscape (e.g., Lonsdorf et al., 2009); and (3) aid in the development of enhanced assessments of risk to bumble bees in habitats where anthropogenic stressors are abundant (e.g., agrichemical use and microclimatic shifts associated with climate change).

A direct assessment of which plant species bumble bee colonies rely on for pollen through the season provides critical information on the interaction of resource use and landscape context needed to understand the landscape and habitat features critical to supporting bumble bee populations. Some researchers have argued that seminatural habitats provide resources critical to support bee populations (Requier et al., 2015; Roulston & Goodell, 2011). Within agricultural landscapes, others highlight the role that mass-flowering crops themselves may play in providing continuity of floral resources to support pollinators (Rundlöf et al., 2014; Westphal et al., 2009), suggesting cropped habitat configuration and composition are important elements of designing and maintaining agricultural landscapes for bumble bees and other flower-visiting insects. Most landscapes contain a mixture of seminatural and agricultural habitats, but the relative proportions of each that are necessary to support insect populations is a topic of debate (Eeraerts, 2023; Tscharntke et al., 2005).

In addition to changes in landscape composition, the availability of different types of plants varies across agricultural to seminatural land use gradients. The prevalence of flowering crops tends to increase with the extent of cultivated versus natural habitat. Additionally, in most agricultural landscapes, native flowering plants are replaced by exotic weeds with increasing intensification and extent of cultivation (Balfour & Ratnieks, 2022; Williams et al., 2011). As a result, the importance of these different types of plants and habitat types in supporting flower-visiting insects will potentially change across different landscape contexts (Danner et al., 2016; Rutschmann et al., 2023). Identifying the relative use of different flowering plants and the habitat features in which they occur would allow for an improved understanding of the spatiotemporal dynamics of insect foraging and habitat use in anthropogenic landscapes (see Requier et al., 2015 for temporal shifts in resources). Such work could highlight areas where conservation schemes (e.g., floral enhancements and habitat restoration) could be used to bolster insect populations (Iuliano & Gratton, 2020).

In this study, we use a native bumble bee (*Bombus vosnesenskii* Radoszkowski) as a model species to characterize resource use across the growing season in a diverse, agricultural region of Northern California. To do so, we combined colony-level pollen collection patterns with highly resolved, landscape-scale floral resource surveys for replicated sites. Because tracking nectar collection among plant species at the colony level is experimentally infeasible for most bees (but see Requier et al., 2015 for honey bees), we focus here on the collection of pollen. By selecting sites across an agricultural-seminatural habitat gradient, we test two predictions regarding spatiotemporal floral resource use by bumble bees in relation to availability throughout the landscape: (1) The pollen that bumble bee colonies collect will reflect plant availability and, therefore, be largely correlated with the proportion of seminatural habitat in the landscape throughout the season; and (2) bumble bee habitat use will depend on the landscape context. Pollen foraging will reflect the floral availability in the surrounding landscape, with bees in habitats containing low seminatural habitat using primarily flowering crops and interstices (which includes crop field borders, small patches of uncultivated land, as well as tree lines and hedgerows), while bees in landscapes with greater seminatural habitat availability will forage primarily on plants within seminatural features (Figure 1).

METHODS

Given the complexity and range of methods utilized throughout, many additional details are included in Appendix S1. The following methods are an abbreviated summary of the data collection, processing, and analyses.

Site selection and colony monitoring

The study was carried out in a 50 × 50 km area in Yolo and Solano counties in Northern California (Appendix S1: Figure S1). The region has a gradient of land cover dominated by orchard and row crop agriculture to the east and seminatural habitats of mixed oak grassland and chaparral to the west. Remnants of seminatural oak woodland and grassland remain along riparian corridors in the agricultural areas. We established 39 study landscapes within the region spaced along the gradient of seminatural to agricultural land. Each landscape was a 2-km circle surrounding a central location where we placed pairs of bumble bee colonies (*B. vosnesenskii*) reared from wild-caught queens (Appendix S1: Section S1). All landscapes were at least 2.5 km apart (average 10 km) measured from center to provide spatial independence of foraging bees. These same colonies were the subject of a separate study investigating

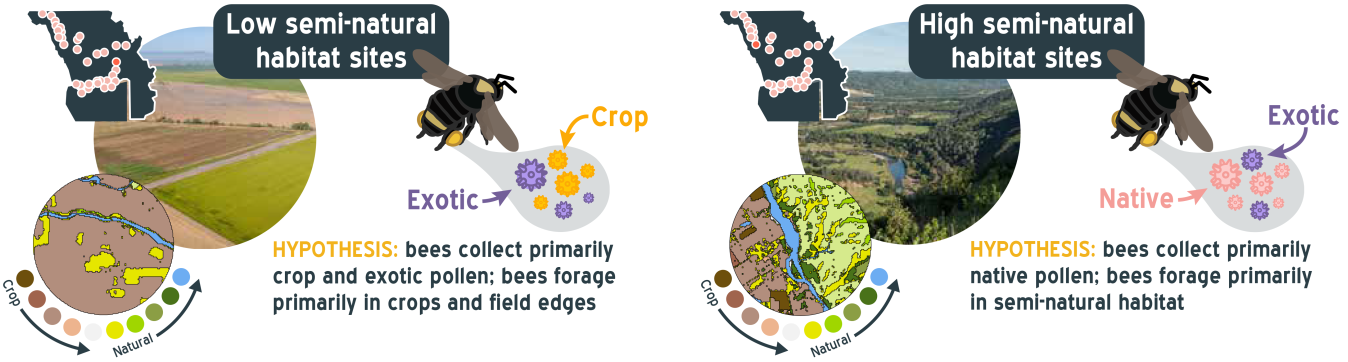

FIGURE 1 Expectations of bumble bee pollen foraging preferences across a gradient of seminatural habitat. In landscapes containing low seminatural habitat, we expected workers of *Bombus vosnesenskii* to collect primarily exotic and crop pollen from marginal habitat/field edges and crop fields, respectively. In landscapes containing high seminatural habitat, we expected workers to collect primarily native pollen from within seminatural habitat features. Inset photos by and illustrations by Jeremy Hemberger.

the impact of spatiotemporal floral resource abundance on bumble bee colony performance (Williams et al., 2012). Local habitat types included 12 conventional farm, 13 organic farm, and 14 riparian sites.

Pollen collection and identification

At monthly intervals from March to June, 2003 we randomly selected a colony from each site from which to collect pollen of returning workers. Field researchers collected 10 returning foragers into specially designed collection tubes and removed pollen loads before releasing them into the colony. During the final sample the team sampled from only 15 sites because many colonies were beginning to decline or had senesced for the season. Pollen loads were returned to the lab individually prepared with acetolysis (Appendix S1: Sections S3 and S4). Acetolyzed pollen samples were mounted onto microscope slides and identified to the lowest taxonomic level possible (mostly species) with the aid of a pollen reference collection. Herbarium specimens of plants are deposited at the University of California–Davis herbarium, and pollen specimens and digitized photos are maintained as a reference collection in the Williams Lab at UC Davis.

Mapping floral resource landscapes

To empirically estimate the spatiotemporal availability of flowers in the landscape, we used the survey and GIS approach used by Williams et al. (2012) (Appendix S1: Section S5). Briefly, we conducted quadrat-based floral resource surveys across all land cover categories represented in the landscapes surrounding bumble bee colonies to estimate average floral resource density at a species level. Because our landscapes follow a larger, regional gradient from those dominated by seminatural habitat to those dominated by orchard and row crop agriculture, we expected the proportions of native plants, exotic weeds, and crop species to vary strongly among study landscapes, even if individual species abundances might be idiosyncratic within the landscapes. We therefore categorized all surveyed flowering plants species as either crop, exotic, or native. All analyses henceforth are based on this categorization. For each of these three plant categories, we projected floral density estimates for all surveyed flower species onto a land cover raster, assigning density estimates to each land cover class from which they were surveyed. From these rasters, we created maps of the estimated abundance of floral resources for each plant type as well as for total floral density within a 1500-m radius landscape surrounding each site and calculated a landscape-scale floral availability estimate from a 1500-m buffer area surrounding the colony locations. For this landscape calculation, we applied a negative exponential function to down-weight distant resources given the energetic expense of long-distance foraging on bumble bees (Williams et al., 2012) and then summed the total weighted values within each landscape. This decision essentially reduces the expected probability of resource use as a function of their distance from the colony.

Statistical analyses

We used separate statistical models to evaluate whether bumble bee pollen collection (model 1) and plant availability (model 2) varied as a function of landscape composition, time, and plant type. Together, these models enabled us to link relative pollen use by bumble bee colonies with the relative availability of landscape-scale floral resources across the flight season. In doing so, we could assess whether bumble bee pollen returns mirrored relative availability in the landscape, or whether colonies targeted specific plant types in excess of their relative occurrence in the landscape (Harmon-Threatt & Kremen, 2015). All analyses and visualizations were conducted in R version 4.0.3 (R Core Team, 2017).

Model 1: Bumble bee pollen collection—Proportion pollen ~ seminatural habitat × month × plant type + (1|site)

We modeled the collected pollen as a function of the plant type, seminatural habitat, the month, and their interactions. First, we rescaled pollen grain counts from specific plant types (crop, exotic, and native) into the relative abundance of each plant type and then fit a binomial generalized linear mixed model, with each observation weighted by the total number of counted pollen grains for that sample. We opted to relativize pollen counts to avoid overinterpreting pollen grain counts as an absolute estimate and instead discuss our results in terms of the relative collection of various pollen types in the landscape. In doing this, our models allowed us to predict the probability of a colony collecting pollen of a given plant type over the different months and landscape contexts. This can also be thought of as the proportion of pollen from a given plant type. We fit each plant type pollen model using “site” as a random grouping factor. In addition to accounting for repeated measures over time, the site-level random effect also allowed us to estimate how consistent responses were among bumble bee colonies. We also modeled each plant type separately to strictly meet the model assumption of outcome independence. The results were identical but did not allow us to explicitly test for a three-way interaction between seminatural habitat, month, and plant type.

Model 2: Flower availability in the landscape—Proportion plant type ~ seminatural habitat × month × plant type + (1|site)

To model the availability of flowers in the landscape as a function of plant type, seminatural habitat, and the month, we first rescaled the weighted sum of flower density estimates into a measure of relative abundance of each plant type in the landscape. To do this, we divided the total weighted sum of flower densities across all three plant types within sites and periods by the total weighted sum of a given plant type. For example, to calculate the relative abundance of exotic plant flowers for a given site in May, we divided the weighted sum of exotic flower density within the landscape at that site in May by the total weighted sums of exotic, native, and crop flower densities for that site in May. We also filtered the dataset to include only flower species known to be visited by *Bombus* spp. from observations in previous studies and personal observation of the research team in the field. Then, we fit a binomial generalized linear mixed model predicting the relative abundance as a function of the proportion of seminatural habitat in the surrounding 1500-m landscape, month, plant type, and their interactions with "site" as a random grouping factor. Using this approach, we were able to generate predictions of the probability of a given plant type occurring (i.e., relative abundance) in the landscape given the month and amount of seminatural habitat and whether the effect of seminatural habitat, if any, depended on the month or type of plant. This approach aligned the floral data and model format to that of the bumble bee pollen collection, easing the comparison of model predictions. Similarly, we modeled each plant type separately to strictly meet the model assumption of outcome independence. The results were identical but did not allow us to explicitly test for a three-way interaction between seminatural habitat, month, and plant type.

Under/overrepresentation in pollen foraging

To assess whether bumble bees exhibited a preference for specific plant pollen types or whether preferences shifted over the study months and landscape context, we plotted the difference between the proportion of pollen collection and the proportion of flowering plant occurrence in the landscape for each plant type and month. The resultant values provide a qualitative assessment of favored or over-/underrepresented plant type pollen collected across the gradient of seminatural habitat over the study duration. For this analysis, values above 0 indicate that the proportion of a given plant type in the pollen samples is greater than in the floral surveys, whereas values below zero indicate the proportion of a given plant type in the pollen samples is less than in the floral surveys. We constructed a 95% tolerance (prediction) interval around these values to evaluate where values were above/below equal proportion (i.e., plant availability and pollen collection proportions equal; no preference).

Predicting foraging in the landscape

To visualize bumble bee's dynamic, spatiotemporal use of pollen, we combined maps of flower availability along with predictions of pollen use from the bumble bee pollen collection model to produce spatially explicit predictions of the probability of bees foraging in different landscape elements at each study site. First, we normalized our distance-weighted maps of flower availability (see *Mapping floral resource landscapes* section above) based on the highest observed floral density estimate observed for each study month and plant type creating rasters with values ranging from 0 to 1, with 0 being the lowest likelihood of the plant occurring and 1 being the highest likelihood. Then, we multiplied the normalized raster values by the probability of pollen collection given the month, plant type, and amount of seminatural habitat based on model 1. This step yielded, for each site, a 3 × 3 matrix of rasters with values representing the probability of bumble bees foraging in each pixel for the three plant pollen types (native, exotic, and crop pollen) over the three study months (May, June, and July). To aggregate these predictions, we added these probability rasters for each plant type together yielding three rasters representing the probability of bumble bees from a colony foraging for any plant type pollen on any given landscape feature within a site across the three study months. For brevity, we visualize this for three example landscapes spanning the seminatural habitat gradient in our study region.

Model visualization

We used the interactions package to visualize marginal model effects for each model (Long, 2019). For all figures, crop, exotic, and native plant types are represented by gold, purple, and rose colors, respectively.

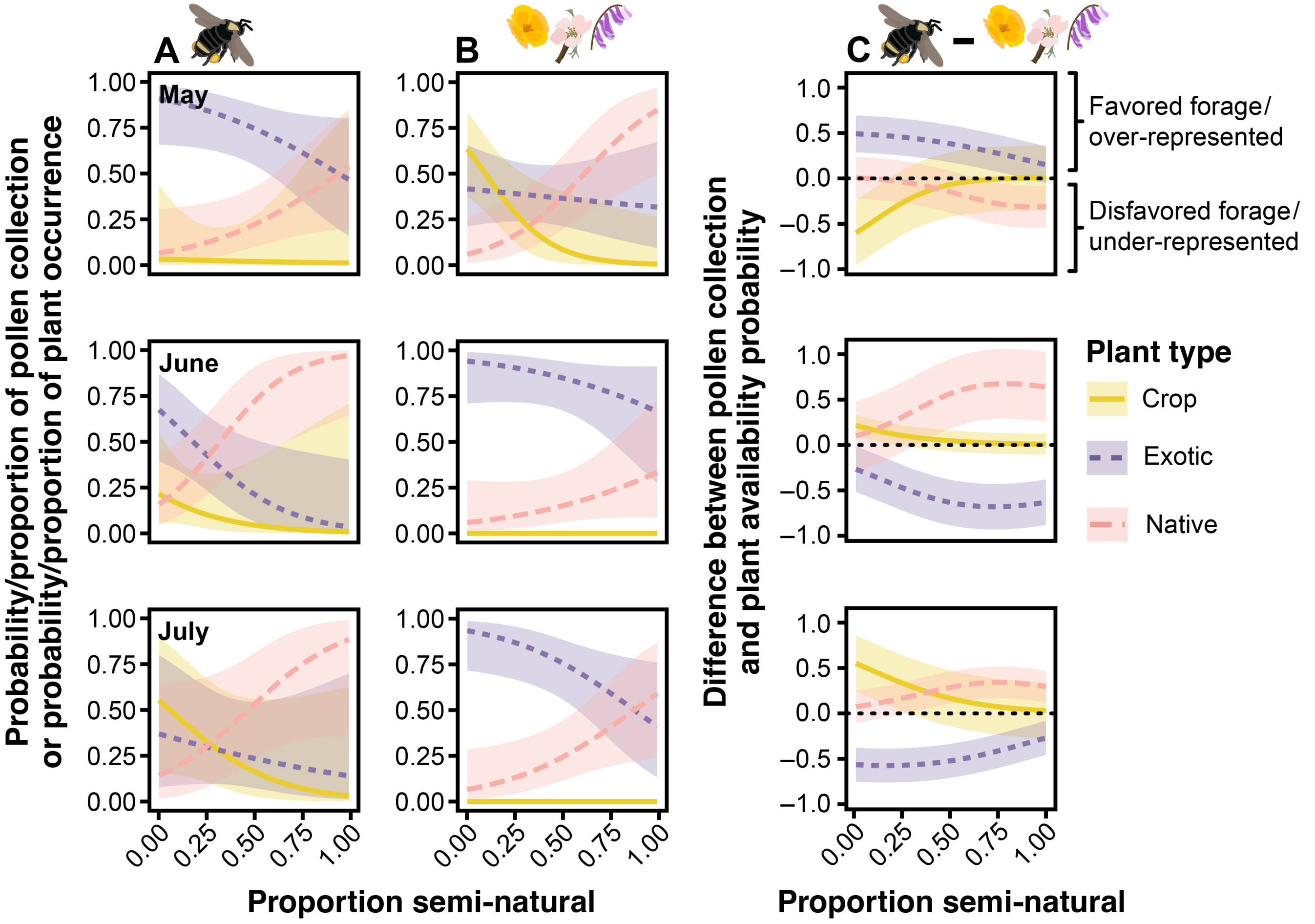

FIGURE 2 Interaction figures showing the model-predicted probability of bumble bee colonies pollen collection (A) of flower availability (B) for crop (gold), exotic (purple), and native (rose) plant pollen as a function of the proportion of seminatural habitat in the landscape, the period, and their interaction (with 95% CIs). Subtracting the fitted values from each plant type in (A) from those in (B) yields a proximate estimate of favored/disfavored plant types within bumble bee pollen collection across the gradient of seminatural habitat over the three study months with ±1 SD intervals (C). Values above zero indicate a pollen preference or that a specific plant type was overrepresented in collected pollen relative to its predicted occurrence in the landscape, whereas values below zero indicate a disfavored pollen or that a specific plant type was underrepresented in collected pollen relative to its predicted occurrence in the landscape. Flower icons do not correspond to any pollen or plant type prediction. Illustrations by Jeremy Hemberger.

RESULTS

Pollen collection and landscape composition

General patterns of pollen collection

We identified and counted 127,548 pollen grains from 4058 bee pollen loads across 39 sites from May 11 to July 11, 2003. Colonies collected pollen from a total of at least 55 plant species including 7 crop, 22 exotic, and 25 native species. Tomato (*Solanum lycopersicum*) dominated collected crop pollen (especially in July, Appendix S1: Table S1). Hairy vetch (*Vicia villosa*) was the dominant exotic pollen, and deerweed (*Lotus scoparius*) the dominant native pollen collected (Appendix S1: Table S1).

Pollens collected related to seminatural habitat but varied by month and plant type

The relative likelihood of a pollen type occurring in corbicular samples was driven by a significant interaction between the month and plant type (Wald $\chi_{24} = 9.66$, $p = 0.046$), and between seminatural habitat in the surrounding landscape and plant type (Wald $\chi_{22} = 7.33$, $p = 0.026$). The relative likelihood of exotic pollen collection decreased as seminatural habitat increased and decreased through the season from May to July (Figure 2A). Native pollen collection increased rapidly with increasing seminatural habitat. Native pollen collection also increased from spring to summer, peaking in June (Figure 2A). Bees collected crop pollen only in landscapes with relatively low seminatural habitat (<50%; Figure 2A).

Plant availability and landscape composition

General patterns of flower availability

We recorded 181 flowering plant species across surveys of 561 transects at 98 sites from May 1 to July 30, 2003. Of the species surveyed, 13 were crops, 66 were exotic, and 102 were native. The most abundant flowering crops in surveys included Apiaceae seed crops (e.g., parsley/cilantro), tomato (*S. lycopersicum*), and melons (*Cucumis* spp.; Appendix S1: Table S2). For exotic plants, black mustard (*Brassica nigra*), pepperweed (*Lepidium latifolium*), and yellow star-thistle (*Centaurea solstitialis*) were the most common, and for native plants, deerweed (*Lotus scoparius*) dominated. Overall, raw flower abundance in the landscape irrespective of landscape composition was relatively consistent across the three study months for both exotic and native plants. Crop plants, however, exhibited a distinctive pulse in June corresponding to the bloom of tomato and sunflower, most notably at agricultural sites with little seminatural habitat in the surrounding landscape (Appendix S1: Figure S2). Overall crop flowers dominated the landscape, particularly in May and June at sites with low-seminatural habitat in the landscape.

Flower availability depended on seminatural habitat, season, and plant type

The relative likelihood of plant occurrence in the landscape depended on the amount of seminatural habitat in the landscape and the type of plant (Wald $\chi_{24} = 14.67$, $p = 0.001$). For crop plants, the relative likelihood of flower occurrence decreased rapidly as the amount of seminatural habitat in the landscape increased and was essentially absent after May (Figure 2B). At sites with more than 50% seminatural habitat in the landscape, the probability of crop flowers occurring was less than 5%. For exotic plants, the relative likelihood of flower occurrence decreased marginally with the proportion of seminatural habitat in the landscape and was highest in June. Unsurprisingly, the relative likelihood of native flower occurrence increased as the proportion of seminatural habitat in the landscape increased and was highest in May.

Pollen preferences

Native pollen is overrepresented relative to supply in the landscape

By subtracting the model estimated probability of flower occurrence in the landscape from the probability of pollen collection for each plant type, we reveal that bumble bees tended to prefer collecting pollen from native plants from June onward; however, the amount of seminatural habitat in the landscape strongly mediated this response (Figure 2C). Preference for native pollen increased as seminatural habitat increased and was overrepresented across most of the landscape gradient in both June and July; however, in May native pollen was under used in areas dominated by seminatural habitat, probably because native flowers were so abundant there. Exotic pollen was a critical early-summer resource, with sentinel colonies collecting more exotic pollen than would be expected in May across the seminatural habitat gradient despite the lowest occurrence of exotic flowers at this time (Figure 2B). Finally, crop pollen was consistently underrepresented in pollen samples except at sites very low in seminatural habitat (i.e., intensive agricultural sites) mid to late in the season.

Foraging in the landscape

Maps of floral availability combined with pollen model predictions yielded maps describing the probability of *B. vosnesenskii* foraging within any given habitat or location (Figure 3, Appendix S1: Figure S3). From this, we observed distinct patterns of foraging probability given the month and amount of seminatural habitat in the surrounding landscape. At sites with low seminatural habitat, bumble bees were likely to forage consistently in agricultural interstices and crop fields throughout the study. At sites with high seminatural habitat, foraging in May was concentrated along agricultural interstices; however, this shifted to seminatural habitats during June and July. A clear preference for foraging within such margins and seminatural habitats is evident, with little foraging in crop fields except within sites low in seminatural habitat in the landscape (Appendix S1: Figure S3).

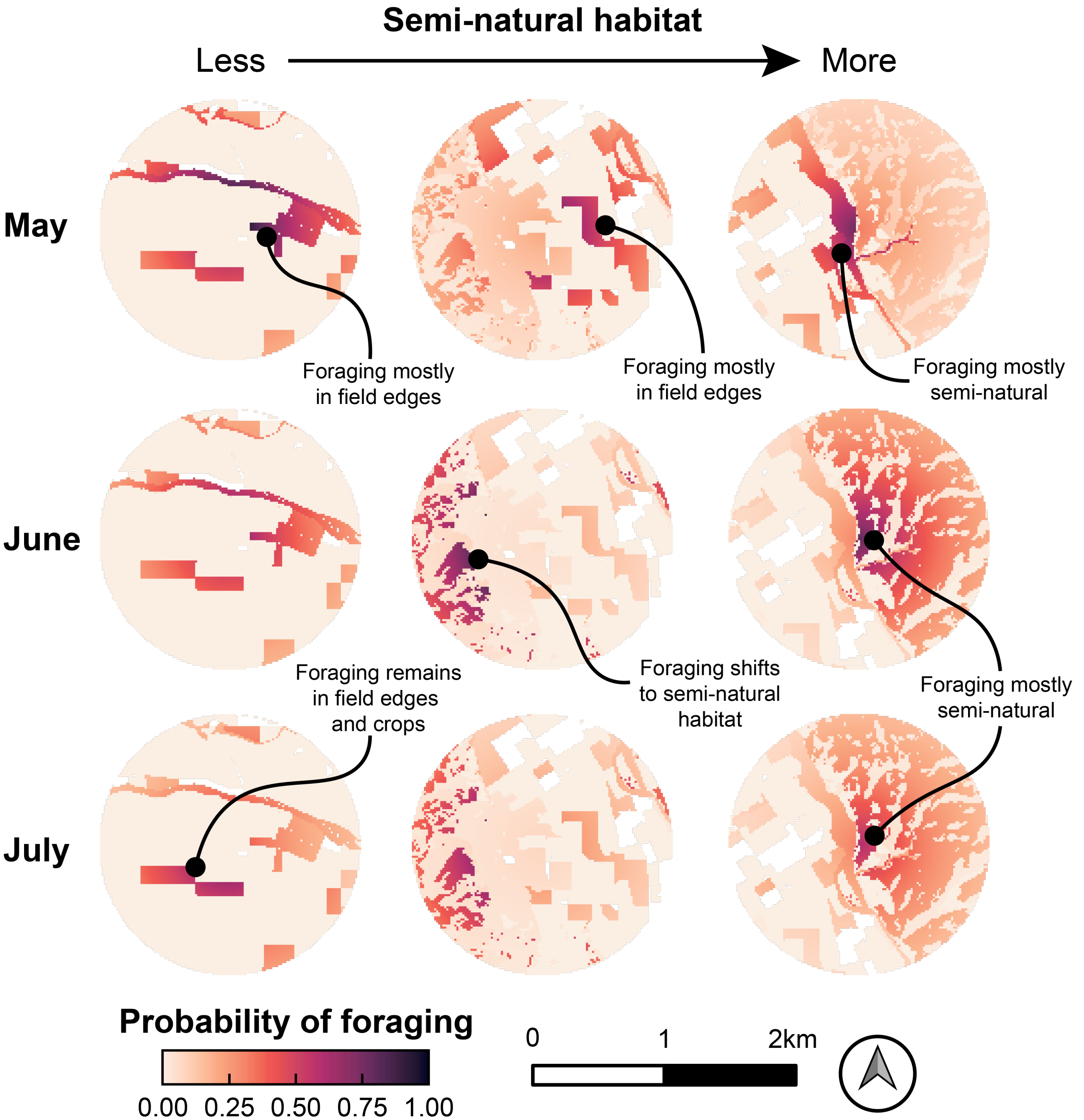

FIGURE 3 Combining spatial information on distance-weighted flower abundance from surveys along with model-predicted foraging probability given seminatural habitat amount reveals the probability of bumble bees foraging on different landscape elements at three representative sites across the gradient of seminatural habitat (columns) and study months (rows). Darker colors indicate a higher probability of *Bombus vosnesenskii* foraging in each pixel.

DISCUSSION

Because of the difficulty in tracking pollinators in real time, the spatiotemporal use of resources by wild pollinators is considerably understudied. Nonetheless such information is vital to conservation planning. Especially when used with knowledge of pollinator performance at different locations (e.g., Williams et al., 2012), it provides a mechanistic link to identify key habitats and resources for supporting pollinator populations. Thus far, the literature has largely used collections of individual bees on flowers to determine foraging preferences. Although these approaches are informative, they miss colony-level pollen use and whether use reflects plant availability in the surrounding landscape (Harmon-Threatt & Kremen, 2015; Jha et al., 2013). These gaps limit our capacity to understand colony persistence and deploy conservation actions. By surveying pollen collected by bumble bee colonies across many study landscapes and nearly the entire flight season, we show that landscape context, specifically the proportion of different broad habitat types, strongly influenced the types of pollens used (and preferred) by bumble bee colonies. The detailed pollen data and general association of specific plants with different habitat elements also revealed the importance certain habitats for supporting bumblebees throughout the season (Bänsch et al., 2020). When present in the landscape, non-crop areas such as seminatural habitat (e.g., riparian areas and chaparral), as well as field and road margins, support floral resources that together provide the majority pollen used by bumble bee colonies in our study region. These results confirm the important role these habitat interstices between extensive crop fields play in supporting pollinator populations by providing abundant and temporally continuous resources over time.

Landscape composition and the time of the season largely explained the probability of colonies collecting pollen from each focal plant type. Colonies in landscapes containing relatively large amounts of seminatural habitat foraged primarily on pollen from native flowering plants throughout the season. Even colonies in landscapes with moderate amounts of seminatural habitat still used pollen from native plants despite their relative scarcity in the landscape. For these colonies, native pollen use increased over the season. Colonies in landscapes dominated by cropped area switched between reliance on exotic plants from non-crop areas to reliance on pollen from crops depending on the time of year. Use of exotic pollen declined strongly from sites in crop-dominated landscapes to those with more seminatural habitat and declined as the season progressed. Crop pollen was used by colonies essentially only in landscapes containing little seminatural habitat and mostly later in the season, some in June and more in July. This period corresponds to largely after the peak bloom of dominant mass-flowering crop (e.g., tomato; Williams et al., 2012). These patterns were remarkably consistent between colonies, with relatively little additional variance explained by site-level (where colony identity varied) random intercepts.

Interestingly, and for all plant types and across the landscape gradient, the probability of pollen use from a given plant type was opposite to the temporal occurrence of its flowering in the landscape. For example, bumble bees collected almost exclusively native flower pollen in July even though native flower occurrence was lowest during this period, and exotic flowers were dominant across the landscape gradient. Exotic pollen collection followed a similar pattern, but in the opposite temporal direction. Our results suggest that bumble bees move across the landscape in search of preferred food plants, adjusting their foraging behaviors across both the landscape gradient and time to gather pollen. Such patterns match well other bumble bee studies that investigate temporal (Hemberger & Gratton, 2018) and spatial (Jha & Kremen, 2013) resource use, in addition to nutrition preferences that drive foraging behavior (Vaudo et al., 2016).

The patterns of pollen collection we observed provide clear support for the importance of non-crop floral resources within interstitial habitat and seminatural areas in supporting bumble bee colonies. Even in agriculturally dominated landscapes (<5% seminatural habitat), bumble bees collected pollen from what little seminatural habitat existed or on field and road edges where most native flowers and many exotics grow. Surprisingly, pollen collection from mass-flowering tomato and sunflower was relatively modest, occurring only in July in landscapes containing almost exclusively agriculture and where exotic and native plant availability were lowest. Like exotic and native pollen collection, the highest probability of crop pollen collection occurred when the probability of crop flowers occurring in the landscape was near its lowest. Other studies have found that cultivated mass-flowering crops (e.g., canola) can boost colony growth (Westphal et al., 2009) and reproduction (Rundlöf et al., 2014); however, our results suggest that mass-flowering crops may not be an adequate resource for *B. vosnesenskii*, especially given that our samples showed almost no crop pollen collection when crop flowers were highly abundant in May. Although crop flowers dominated our estimates of total flower availability in our study landscapes, the presence of crop flowers at a given location was highly variable and most landscapes did not contain any flowering crop fields. This may ultimately explain the difference between total flower availability and model-predicted flower occurrence of crops. Alternatively, the dominate flowering crops may not be a preferred bumble bee source of forage, or we may have missed periods of reliance due to the weekly interval of pollen sampling at any location over the season. High densities of managed honey bees within these landscapes also may have limited bumble bee foraging on some crops (e.g., sunflower) given increased interspecific competition and resource depletion (Cane & Tepedino, 2017; Mallinger et al., 2017). As such, intensive agricultural landscapes in which floral resources are mostly mass-flowering crops are likely substandard landscapes for wild bees (Proesmans et al., 2019). The use of mass-flowering crops as a conservation resource or to bridge gaps in floral resource phenology may be insufficient to promote bumble bee colony persistence in some regions, although they may support additional taxa beyond the scope of this study (Holzschuh et al., 2013; Jauker et al., 2012). Instead, the promotion of non-crop flowering habitat appears to be critical to ensure that foraging bumble bees have access to adequate pollen resources for successful colony growth and reproduction (Crone & Williams, 2016).

In line with our predictions, the proportion of seminatural habitat was a strong driver of flower occurrence, particularly for native and crop plants. The clear dichotomy in landscape composition across our study region explains this: landscapes low in seminatural habitat (<30%) are composed almost entirely of large, monocultural fields of annual and perennial crops with non-crop plants occurring primarily along field margins and roadsides. In contrast, landscapes with greater amounts of seminatural habitat (>30%) include large, contiguous patches of chaparral and mixed oak woodland, as well as larger riparian corridors associated with native flower occurrence. Exotic plants generally increased across the gradient of increasing cropped land, but the relationships were less pronounced. In addition, the occurrence of exotic flowers increased from May to July. This more consistent occurrence across the landscape fits given that exotic flowers were most often surveyed in field margins and roadsides: features common across the landscape gradient regardless of seminatural habitat amount.

Unlike other studies which found no distinct preference for native or non-native plant pollen (Harmon-Threatt & Kremen, 2015; Jha et al., 2013; Williams et al., 2011), native pollen was overrepresented in pollen collections by *B. vosnesenskii* colonies relative to native flower occurrence across most of the seminatural habitat gradient and throughout study months. Lupine (*Lupinus* spp.), deerweed (*Lotus scoparius*), toyon (*Heteromeles arbutifolia*), and poppies (*Eschscholzia californica*) were among the native plant pollen most collected. Bumble bee preference for specific plant pollen may be driven by availability in the landscape, nutritional/dietary preference, or a combination of the two (Harmon-Threatt et al., 2017). Our results are consistent with the idea that *B. vosnesenskii* may selectively use specific plant pollens according to a dietary need/preference even when their availability in the landscape is low (e.g., May exotic pollen use at low seminatural study landscapes, July native pollen use across the seminatural gradient). This targeted use may enhance the reproductive performance of bumble bee colonies, like was seen for the solitary species *Osmia lignaria* within these same study landscapes (Williams & Kremen, 2007). Some species of bumble bees are sensitive to the quality of pollen, selecting for specific nutritional ratios to meet dietary needs (Vaudo et al., 2016). Moreover, the rate of nutritional intake, including constituent pollen components of lipids and protein, is strongly related to colony growth and reproductive output (Vaudo et al., 2018). Indeed, in a separate study with the same bumble bee colonies and same locations, we found that bumble bee colonies in landscapes rich in native plants gained the most mass and produced more workers and males than those at sites dominated by agriculture suggesting a direct link between selective pollen foraging and colony success (see Williams et al., 2012 for data).

Bumble bee pollen foraging has been increasingly a focus of research, given its importance for understanding foraging behavior (Harmon-Threatt & Kremen, 2015; Hemberger & Gratton, 2018), colony development (Hass et al., 2019; Hemberger et al., 2020; Moerman et al., 2017), population and community structure Wood et al. (2019), and conservation planning (Hall et al., 2022; Rundlöf et al., 2022). Here, we show that examining landscape-scale plant availability and pollen collection patterns provides a robust understanding of how *B. vosnesenskii* colonies use pollen resources through space and time. While our pollen collections represent a subset of foraged pollen, they are a more representative example of the foraging patterns than other studies which examine pollen foraging on an individual basis and over reduced spatiotemporal scales (Harmon-Threatt & Kremen, 2015; Jha et al., 2013; Jha & Kremen, 2013). Nectar is also a critical target of foraging that supports bumble bee worker nutritional demands. Here, we did not examine nectar foraging as it is not logistically feasible or possible to easily identify the species of plant from which nectar is being collected. Including nectar could change the observed outcomes, specifically regarding bumble bee use of crop fields that may be used exclusively as a nectar source. Despite this limitation and by censusing pollen intake at the colony level, we were able to explicitly tie landscape-level resource abundance to bumble bee foraging, enhancing our understanding of where and when bumble bees forage for pollen within mosaic landscapes and further confirming the importance of interstitial habitats.

Given the generality of bumble bee foraging and heterogeneity of plant types across our study landscapes, we cannot be certain at a landscape scale where bumble bees (or other species) are foraging. Indeed, it is only in rare cases where the floral resource used by bees occur in unique locations or habitats that we can track location explicitly (Osborne et al., 2008; Williams & Kremen, 2007). Moreover, other methods to explore foraging location are far more resource intensive and logistically difficult (e.g., radio telemetry). Our probability models, while imperfect, offer a simple solution that provides clearer insight into where colonies are likely gathering resources throughout the season. These predictions can be used with additional information (i.e., crop identity and phenology) to reduce threats to foraging bees in these habitats, for example, from pesticide applications, that may help to sustain pollinator population in working lands (Rundlöf et al., 2022).

CONCLUSIONS

Understanding the spatiotemporal resource use among beneficial insects within fragmented landscapes is key to understanding how changes in habitat due to large-scale patterns of land use are likely to impact insect populations. Here, we describe how the pollen intake of an important, common pollinator in Californian agroecosystems, changes in accordance to an interaction of landscape, time, and preference. Critically, our study highlights the importance of mosaic landscapes and landscape heterogeneity in allowing foraging bumble bees to link resources through time, ultimately leading to the reproductive success of the colony. Despite the time since the collection of these data, the results from this work are robust and still relevant for the region of study, and the analysis framework relevant and applicable to additional study systems. This study can serve as a framework to develop enhanced spatiotemporal predictions of insect resource use within mosaic landscapes, adding another tool to direct conservation and landscape restoration efforts. As we continue to shape the landscapes of tomorrow, it is imperative that we understand how mobile animals and the resources they depend on respond so that we can ensure that biodiversity not only persists but thrives.

AUTHOR CONTRIBUTIONS

Jeremy Hemberger performed analyses, constructed data visualizations, wrote the first draft manuscript, and contributed to revisions. Neal Williams conceived of the experiment, conducted all field work and pollen identifications, and contributed to writing and revisions.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data and R code (Hemberger, 2024) are available in Fighare at https://doi.org/10.6084/m9.figshare.23527995.

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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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