

## RESEARCH ARTICLE

# Early spring orchard pollinators spill over from resource-rich adjacent forest patches

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**Funding information**

National Science Foundation, Grant/Award Number: 1650441; Northeast SARE, Grant/Award Number: GNE 18-188

**Handling Editor:** Lori Lach

**Abstract**

1. Pollinator communities are more abundant and diverse in agricultural matrices with more natural habitat, although the reasons for these correlations remain unclear. It is possible that forest fragments and edges provide resources for pollinators in important early weeks of spring, after which time those insects can then 'spill over' into crops such as apple orchards during bloom.
2. To explore how forest edges may feed and therefore promote flower visitor communities in adjacent agricultural habitats, we sampled springtime pollinators in nine orchards and their adjacent forest edge canopies and understories. We identified pollen consumed by pan-trapped bees and flower flies to assess if pollinators ate pollen where they were caught, and if their diets similarly 'spill over' from forest to orchard. We further explored sex differences in habitat usage.
3. Our spatially replicated sampling found that bee and flower fly abundance peaks first in the forest understory, then in the forest canopy and finally in the orchard.
4. Analysis of digestive tracts showed significant usage of forest canopy pollen throughout the spring, especially before apple bloom. Pollinators had often eaten pollen from a different habitat than the one in which they were caught, suggesting frequent movement between habitats. Digestive tract pollen is an underused but powerful avenue for ecological insight.
5. In *Andrena*, which are important orchard pollinators and one of the most abundant wild bee taxa in this study, male bees were primarily found in the woods but not the orchards where conspecific females were later active.
6. *Synthesis and applications:* Forested areas, especially forest canopy trees, provide large amounts of early spring resources that facilitate build-up and spillover of wild pollinator populations into apple orchards during bloom. Forests also provide critical habitat for male bees, which were rarely found in orchards. Despite their importance for bee reproduction, the needs of male bees are usually not considered in conservation planning. Overall, our data indicate that ensuring there is adequate forest habitat adjacent to orchards can improve the long-term sustainability of pollinator populations that provide essential crop pollination services.

## KEYWORDS

Andrenidae, apple orchards, habitat spillover, native bees, pollination, Syrphidae, temperate forests, woodlands

## 1 | INTRODUCTION

There is extensive correlative evidence connecting natural and forested habitats in agroecosystems with higher wild pollinator abundance and diversity in crops (Bailey et al., 2014; Kammerer et al., 2016; Park et al., 2015; Pfeiffer et al., 2019; Ricketts et al., 2008; Watson et al., 2011), buffered pesticide exposure (McArt et al., 2017; Park et al., 2015), lower pathogen loads (McNeil et al., 2020) and even higher yields and pollination success (Castle et al., 2019; De Marco & Coelho, 2004; Földesi et al., 2016; Gemmill-Herren & Ochieng', 2008; Halinski et al., 2020; Proesmans, Bonte, et al., 2019). In both tropical and temperate systems, diverse habitat matrices which include forests have higher bee abundance and diversity (Ganuza et al., 2022; Mandelik et al., 2012; Montagnana et al., 2021; Rahimi et al., 2022). Temperate deciduous forest edges host high abundance and richness of wild bees in forest edges in early spring (Bailey et al., 2014; Urban-Mead et al., 2021), although the importance of forests varies greatly over space and time (Mola, Hemberger, et al., 2021; Proesmans, Smaghe, et al., 2019) and forest pollinator abundance and richness generally declines across the summer (Harrison et al., 2018). Early spring forest resources may result in a healthier bumble bee community across the season (Malfi et al., 2019; Woodard et al., 2019), and saproxylic flower flies are reliant on nutrient-rich forest habitats for larval microhabitats (Sommaggio, 1999). Forests may thus complement the cropland where these insects later forage (Eeraerts et al., 2021; Mandelik et al., 2012; Moquet et al., 2018); this complementarity and spillover may have important implications for pollinator biodiversity and pollination (Blitzer et al., 2012).

Habitat complementarity can result from multiple processes which operate at different scales. First, at the community level, changing resource availability may require the community of pollinators to use different habitats at different times (sensu Mandelik et al., 2012). Second, within a community, where different life stages or sexes of the same species may use different habitats. Third, at the individual level, where observation of an insect's flight or diet may directly demonstrate complementary habitat use by individuals. At the community level, if the same species of pollinators can be found first in one and then later a second habitat, then this can be considered spillover, with implications for ecosystem services (Blitzer et al., 2012; emphasizes that spillover can be from natural habitats to crops and from crops to natural habitats). In contrast, if a forest habitat hosts an entirely different suite of species than are later active in crop fields, this would instead be considered community-level turnover (e.g. Samnegård et al., 2015; Winfree et al., 2018). This is an important consideration particularly in forest habitats, as one-third of the northeastern bee fauna have been identified as 'forest associated', while other species use forests for at least part of their

life (Smith et al., 2021), so may or may not move out of the woods. Yet, different species thrive in landscapes with different amounts of forest, and even forest-dependent species may need resources from across habitats across time or different life stages (sensu Mola, Hemberger, et al., 2021). Thus, we might hypothesize that at the edge interface of orchard-adjacent forested habitats, there will be strong patterns of spillover (e.g. many shared species) between forests and crops.

Complementarity of habitat use by different sexes or life stages within a species may be easily overlooked in species with cryptic sexes, developmental stages and castes, yet may be key to successful conservation for threatened bees and flower flies. This may especially be true for animals that nest in different habitats than where people usually observe them foraging, such as many pollinators. Indeed, flower flies have strikingly different habitat needs as larvae and adults, requiring complementary habitats within flight range (Moquet et al., 2018; Sommaggio, 1999). And, male bees are known to have different foraging patterns (Roswell et al., 2019), pollination efficiency (Ogilvie & Forrest, 2017; Ostevik et al., 2010) and pollen consumption rates (Urban-Mead et al., 2022) than their conspecific females. However, little work has explored differential landscape-level habitat use by sex within a bee species. In this paper, we evaluate differences in foraging and pollen consumption in male versus female *Andrena* because it is the only genus within our dataset where significant numbers of conspecific males and females were active in early spring.

Habitat networks are useful descriptive tools for visualizing how pollinator species may move across habitats and between diets (Marini et al., 2019). Such networks differ from traditional plant-pollinator networks in that they use the habitat itself as the network 'node', instead of a host plant (Marini et al., 2019), and so can depict the habitats used across an organism's life cycle. Here, we additionally integrate different sexes and individual insect pollen diets within habitat networks. That is, in some analyses, the nodes represent sexes within a species connected to either the habitat of capture or the habitat from which a pollen source originated. By building networks whose nodes are built from diet source versus capture location, we can compare which habitats are occupied and/or used for forage by different pollinators over time (e.g. Mandelik et al., 2012). To our knowledge, no previous studies have examined habitat networks from the perspective of both capture and diet.

Understanding pollen sources used by spring-flying pollinators with short activity windows can facilitate conservation planning (Ogilvie & Forrest, 2017). Because organisms may use habitats for different reasons, their observed presence/absence or capture in a passive trap (e.g. pan trap, malaise, vane) may not indicate their foraging patterns. For example, if a bee visits a particular habitat primarily for mating purposes (e.g. male *Andrena* scent-marking or

exhibiting 'hill-topping' behaviour in nonblooming trees (Eickwort & Ginsberg, 1980)), then we may have high capture rates but low dietary association. Similarly, bees such as shiny blue and green sweat bees who nest in rotting logs in the forest may prefer to forage elsewhere (Stockhammer, 1966, 1967; Ulyshen et al., 2010). Capture and diet data thus provide complementary but not redundant ecological information.

In this paper, we combine pollinator sampling from pan traps, sex-based habitat networks and pollen diet characterization to explore temporal shifts in habitat occupancy, resource use and spillover of pollinators from forest edges into adjacent orchards. *Question 1: Are bee and hover fly communities found in complementary habitats over time?* We predict that the habitat with highest captured abundance of bees and flower flies—forest understorey, canopy or adjacent orchard—will change over the course of the spring growing season. *Question 2: Do male and female *Andrena* use complementary habitats?* Based on prior work finding sex-based differences in habitat association (Urban-Mead et al., 2021), we predict that *Andrena* males will primarily be caught in understorey habitat, while females will be found primarily in the orchard. *Question 3: Do the pollen diets of bees and flower flies track their movement among habitats?* We further ask if the habitat associations revealed by pan trap captures differ from those revealed by pollen diet analysis. We predict that we will find evidence of individual-level habitat complementarity and spillover (sensu Blitzer et al., 2012), in that both the bee community and the diet of those bees will move between the forest to the orchard, with some bees actively foraging across habitats.

## 2 | MATERIALS AND METHODS

Our study did not require special permits for fieldwork or for animal ethics.

### 2.1 | Field and laboratory methods

#### 2.1.1 | Bee and flower fly collection

This study was completed in the Finger Lakes region of New York, in the northeastern United States. Bees and flower flies (Syrphidae), two major groups of agricultural pollinators (Rader et al., 2016) were collected in nine second-growth deciduous forest patches that were selected for their adjacency to orchards. The most abundant tree species across sites were *Acer saccharum*, *Acer rubrum*, *Quercus rubra*, *Fagus sylvatica* and *Betula* spp. Several sites also had *Tilia americana*, *Populus deltoides*, *Juglans nigra*, *Carya ovata* or *Carya cordiformis* (see per cent basal area at each site in Supplemental Figure S1). For simplicity, we will refer to bees and flower flies as 'pollinators' hereafter. For full forest sampling methods, see Urban-Mead et al. (2021). Briefly, five paired canopy and understorey pan traps in sets of vertically randomized blue, yellow and white were

deployed in canopy-dominant trees in second-growth forests and woodlots beginning in mid-March of 2018–2019. A BigShot® sling-shot was used to set a line of paracord with which to rig up the canopy traps at 20–25 m above-ground; canopy traps were not visible from the forest floor; paired understorey traps were ~1 m above-ground.

In addition to our canopy and understorey sampling, we placed identical sets of traps in the branches of five randomly selected apple trees haphazardly spaced across an orchard block <300 m from the forest edge. Management varied between orchards, whose selection was constrained by forest adjacency. These pan traps were emptied and reset once every 7–10 days, on the same schedule as parallel forest sampling, until after apple orchards stopped blooming (corresponding roughly to the first week of June in both years). Pollinators were transferred directly into Whirlpak bags (Nasco Whirlpak, Fort Atkinson, WI) with 95% ethanol in the field. Specimens were identified to species with a variety of taxonomic keys (Bouseman & LaBerge, 1978; Gibbs, 2011; Gibbs et al., 2013; LaBerge, 1971, 1973, 1980, 1985). Difficult taxa were supported by expert knowledge (Jason Gibbs assisted with *Lasioglossum* (*Dialictus*), and Kaitlin Deutsch and Andrew D. Young with family Syrphidae, and DNA barcoding (for full methods, see (Urban-Mead et al., 2021)). All specimens have been accessioned to the Cornell University Insect Collection.

For clarity and consistency, we will use the term 'farm' or 'site' to refer to a given orchard and its adjacent forest location, while 'habitat' refers to the unique sampling location within each replicate site: the canopy, understorey and orchard. The five trees per habitat (canopy, understorey or orchard) were 100–200 feet apart, so are summed or averaged for most analyses due to their small spatial scale relative to pollinator flight distances (Greenleaf et al., 2007).

#### 2.1.2 | Digestive tract dissection and pollen slide preparation

Each insect was dissected directly upon removal from the Whirlpak bags while still pliable and soft from ethanol storage. Under a dissecting scope, each bee's sternal segments were peeled backwards towards the thorax with fine forceps, allowing for a second pair of forceps to extract the full digestive tract (crop, ileum, midgut and rectum) without damage to external characters, as these were required for later species identification (Urban-Mead et al., 2021). The gut contents were placed on a microscope slide and macerated with forceps to release internal pollen and homogenized until evenly distributed across the slide. We removed large tissue fragments and broke up pollen clumps using forceps. Several drops of Calberla's solution were added until pollen grains turned distinctly pink; a constant volume was not possible due to different pollen volumes. Each slide was covered with a 22 × 50 mm coverslip.

Pollen identified from an individual adult bee is usually collected from its scopal loads following net collection, and represents the current foraging bout's collection for brood provisioning. However, for

bees caught in pan traps or other liquid traps, this scopal pollen can wash off or become contaminated, making it difficult to assign external pollen confidently to a given specimen. In these cases, identification and characterization of digestive tract pollen can provide insight into adult consumption (e.g. Cane et al., 2017; Dobson & Peng, 1997; Kapyla, 1978; Taniguchi, 1956; Urban-Mead et al., 2022). Pollen eaten by an adult bee may differ from that collected for brood provisioning, so gut pollen should only be interpreted in the context of adult bee diet unless both are simultaneously recorded. We suggest that this method has the benefit of likely representing multiple visited flowers over several hours rather than simply the most recent foraging bout; many bees are constant within a single foraging bout but not between bouts or days (Brosi, 2016). Although poorly studied, healthy bumble bees can take over 13 h to defecate after a meal (Giacomini et al., 2022), so digestive tract pollen likely represents foraging bouts of at least a day.

### 2.1.3 | Pollen identification

In both years, we collected pollen from blooming plants to create a reference library and maintained detailed phenological records at each site. Only the site name and date were revealed to allow for phenologically informed identification; all other metadata was hidden to avoid bias. We used a compound Olympus BX41 microscope at 400x magnification (40x with 10x ocular). We began each sample at a randomly generated point along the slide's short edge and moved along the length of the slide categorizing all pollen in the field of view. We categorized up to 300 grains or up to 10 unique transects per slide; slides were marked as 'no pollen' if there were fewer than 30 grains of pollen (Harmon-Threatt & Kremen, 2015).

Each grain was identified and then sorted into one of three pollen categories: canopy, Rosaceae and other. Pollen types in the category 'canopy' included: *Acer*, *Populus*, Betulaceae, *Carya*, *Fagus*, *Juglans*, Pine-type, *Quercus* and *Fraxinus*. The 'Rosaceous' category, due to similar morphology, broadly included all apple, peach, apricot and other related orchard trees. It may also include *Rubus* and wild strawberry, known to be favoured hosts of many Syrphid species, and *Amelanchier*, all of which were often found within the orchard or along edges. Black Cherry (*Prunus serotina*) is also rosaceous but was not a dominant tree in our woods, so we do not believe meaningfully impacts our inferences (mean per cent of total basal area  $3.3\% \pm 1.9$  SD). Not all understory or other species could be identified with confidence; these were combined into a macro-category 'Understorey, Other and Unknown Pollen'.

We took multiple voucher images for each slide; see Supplemental Table S1 for detailed pollen categories and vouchers.

## 2.2 | Data analyses

All data analyses were conducted in R version 4.0.1, 'See Here Now'.

### 2.2.1 | Question 1: Are bee and hover fly communities found in complementary habitats over time?

To ask if female pollinator abundance peaked at different times by habitat, we built a linear and quadratic model each for understory, canopy and orchard (R package LME4, function glmer). In each model, the response variable was the abundance of bees caught in that habitat per site per day. Day of Year (days since 1 January) was a fixed effect, site was a random effect, and we assumed a Poisson distribution with a log link due to using count data. In AIC comparisons, the quadratic (squared Day of Year) model performed better than the linear model for each habitat (delta AIC canopy: 88.15, delta AIC understory: 92.86, delta AIC orchard: 5.23). As a result, we used the squared term for the remainder of the analyses (with syntax `poly(DayofYear,2)`). We calculated the day with the peak abundance per habitat for each model (model results plotted with R package JTOOLS, function `effect_plot` and peak abundance date were calculated in R package STATS, function `fnpredict`). Finally, we ran the same models except this time included the interaction of site and squared Day of Year as a fixed effect; this allowed us to predict the day of peak abundance for each site, as site was the replicate in this study. Using this site-replicated data, we asked if there was a difference in peak date among habitats using a type I ANOVA (R package STATS).

### 2.2.2 | Question 2: Do male and female *Andrena* use complementary habitats?

For *Andrena*, the only genus active in early spring with multiple conspecific individuals of both sexes, we visualized a complete habitat network for the 10 most abundant species caught in all habitats (R package BIPARTITE, Dormann et al., 2009). We used *Andrena* sex as one set of nodes and the habitat of capture as the other. Using the pollen data from gut dissections, we visualized another network that represented only *Andrena* who had eaten pollen. To quantify these patterns, we constructed GLMMs for the following response variables: number of individual pollinators per sex and site caught in each habitat, or who had eaten pollen per habitat. In each model we set the interaction of sex and habitat as a fixed effect and kept site as a random effect, and again asked if there were differences using a type III ANOVA (R package CAR; letters for figures generated by function `multcomp`). We created habitat networks of capture for each of the 10 most abundant *Andrena* species included in the combined figure, to see if the pattern was consistent across species (Figure 4).

### 2.2.3 | Question 3: Do the pollen diets of bees and flower flies track their movement among habitats?

We summarized the pollen diets for bees caught each day of the year in each habitat and visualized them as stacked bar plots. We similarly graphed the diets of male and female *Andrena* with filled bar plots.

To visualize the diet-based habitat network for *Andrena* male and females, we again used *bipartite*, but instead of the habitat where a pollinator was captured, we used the habitat source of pollen a pollinator had eaten as the nodes in the bipartite graph (Supplemental Figure S4).

### 3 | RESULTS

We collected 2885 bees and flower flies. We caught 1251 pollinators in 2018, of which 20.8% were males, and 1634 pollinators in 2019, of which 28.7% were male. Syrphidae, the flower fly family, comprised only 93 individuals (3.2%). By habitat, 1033 (35.8%) pollinators were caught in the understorey, 996 (34.5%) in the canopy and 856 (29.7%) in the orchard; see Supplemental Figure S2 for annual abundance and diversity by habitat. The most common genera were *Lasioglossum* ( $n = 1166$ ; 40.4%) and *Andrena* ( $n = 931$ ; 32.2%), followed by *Augochlora* ( $n = 186$ ; 6.4%) and *Augochlorella* ( $n = 108$ ; 3.7%), *Ceratina* ( $n = 144$ , 5%), *Osmia* ( $n = 127$ , 4.4%), *Nomada* ( $n = 70$ ; 2.4%), *Bombus* ( $n = 24$ ; 0.8%) and *Halictus* ( $n = 21$ ; 0.7%). See Supplemental Table S4 for full species lists by habitat; see Supplemental Table S3 for more summary tables of flower fly data.

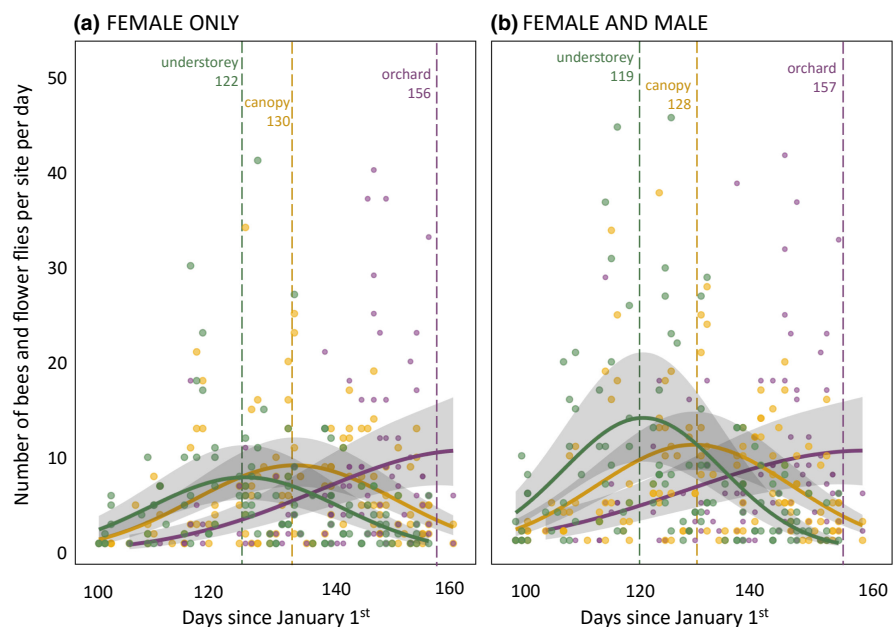
#### 3.1 | Question 1: Are bee and hover fly communities found in complementary habitats over time?

In the overall model for female abundance over time, we found that bee abundance peaked in the understorey on Day of Year 122, in the canopy on day 130, and in the orchard on day 157 (Figure 1a); for males and females together, bee abundance peaked in the understorey on Day of Year 119, in the canopy on day 128, and in the orchard on day 156 (Figure 1b). Similarly, in the model with the

site\*day interaction term, the day of peak female abundance calculated per site per habitat for the canopy was  $130.4 \pm 1.0$ , with the understorey abundance peak  $9.67 \pm 1.47$  days earlier and the orchard  $20.11 \pm 1.47$  days later (error is standard error; Supplemental Figure S3 with full model output, effect sizes and confidence intervals). Female pollinators were subset from the full community in order to explore the role of pollinator sex in phenological abundance patterns (Figure 1).

#### 3.2 | Question 2: Do male and female *Andrena* use complementary habitats?

There was a significant interaction between sex and habitat, both in the model of *Andrena* bee abundance ( $\chi^2 = 154.18$ ,  $p < 0.001$ ) and abundance of *Andrena* who ate pollen ( $\chi^2 = 85.59$ ,  $p < 0.001$ ) (see Supplemental Table S2 for full output). Male *Andrena* were  $6.9 \pm 0.02$  times more likely to be caught in the understorey than the orchard, and  $2.45 \pm 0.04$  times as likely to be caught in the understorey than the canopy. Female *Andrena* were  $2.12 \pm 0.33$  times as likely to be caught in the orchard than the understorey, and  $2.25 \pm 0.35$  times as likely to be caught in the canopy than the understorey. For visual representation of this pattern across the 10 most abundant *Andrena* species, which together represented 82% of all captured *Andrena*, see Figure 4. Of those that had eaten pollen, we found that there were  $5.7 \pm 0.05$  times as many *Andrena* males who had eaten pollen caught in the understorey than the orchard, and  $1.78 \pm 0.09$  than the canopy. There was no difference in the number of females who had eaten pollen caught in the canopy than the orchard (emmeans ratio  $1.04 \pm 0.12$ ), but there were  $2.7 \pm 0.49$  times as many females who had eaten pollen caught in the orchard than the understorey and  $2.81 \pm 0.5$  times caught in the canopy than the understorey (Figure 2; all odds ratios and standard errors calculated in *emmeans*).



**FIGURE 1** Peak bee and hover fly abundance shifted from forest to canopy to orchard in the early spring months. (a) Female pollinators only. (b) All pollinators. Curves and 95% confidence intervals of the Poisson models; Y axis is abundance of pollinators per site per habitat per day. The numbers under the habitat labels indicate the day of the year with peak abundance (peak of the curve) identified by the quadratic model. Orchard bloom peaked between days 135 and 145 across all nine orchards.

### 3.3 | Question 3: Do the pollen diets of bees and flower flies track their movement among habitats?

We dissected all 2885 bees and flower flies, of which 1310 (45.4%) had at least 30 grains of pollen and were included in pollen analyses. A higher proportion of female bees had pollen than males (49.9% relative to 31.9%). There was pollen in the digestive tracts of 59.1% flower flies ( $n = 93$ ); 50% of males (18 of 36) had eaten pollen. Although pollen diets largely tracked the location of capture (Figure 3), large amounts of pollen eaten by insects caught in the understorey came from canopy trees (Figure 3A1,B1), and insects had often eaten pollen from a different habitat in which they were caught (see Figure 3 for diets summarized by day of year and habitat of capture; also see Supplemental Figure S5 for individual bee diets for 17 of the most commonly caught species and genera; see Supplemental Table S3 for flower fly diets by day and habitat of capture).

## 4 | DISCUSSION

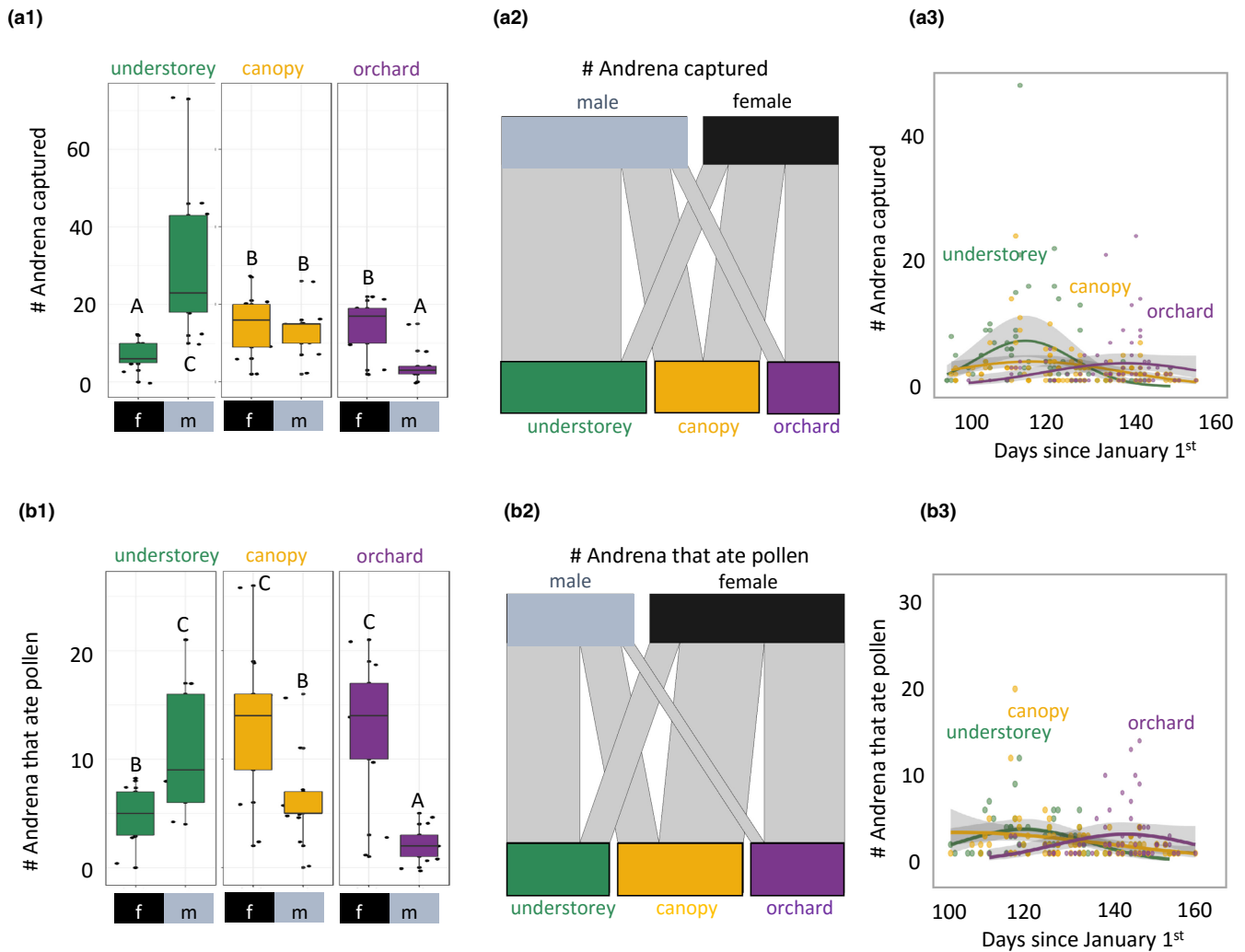
We here present several lines of evidence from adult bee and flower fly pollen diets and captures throughout the spring season in temperate deciduous forest understoreys, canopies and adjacent orchards, finding results consistent with habitat complementarity between forest patches and pollination-dependent orchards. The diets of pollinators active in all three habitats include large proportions of canopy-tree pollen. Pollen diets revealed active movement of many pollinator species back and forth across the forest–orchard interface, which coupled with temporal trends indicates wild pollinator spillover between the habitats (sensu Blitzer et al., 2012). These results have clear ecosystem services implications. Apples, peaches, cherries and other fruit crops are all dependent on pollinators across the world (Blitzer et al., 2016; Burns & Stanley, 2022; Garratt et al., 2016; Klein et al., 2007; Vicens & Bosch, 2000). With more and more growers choosing to rely on native pollinators for pollination (Park et al., 2020), our results provide insights into how land managers can actively promote habitats surrounding orchards to provide early season resources, including often ignored canopy pollen. Not only do these important pollinators visit and occupy forest edges in advance of orchard bloom, but also the males of *Andrena*, an important orchard-pollinating genus, relied heavily on forest habitat. As pollinator abundance in crop fields reliably declines with distance from edge (e.g. Aljuwayd, 2017; Bailey et al., 2014; Chacoff & Aizen, 2006; MacInnis et al., 2020), complex landscapes with diverse matrices of forests and natural habitat are essential to maintain pollination services and food security.

An early spring peak in forest pollinator abundance is consistent with prior research, and we now demonstrate an additional peak in pollinator abundance in the forest canopy between the early understorey and later orchard. As the literature increasingly highlights the importance of forests for bees and beneficial insects (e.g. Eeraerts et al., 2021; Fowler, 2016; González et al., 2016; Mola, Hemberger,

et al., 2021; Mola, Richardson, et al., 2021; Proesmans, Bonte, et al., 2019; Smith et al., 2021; Splitt et al., 2021; Wood et al., 2021; Wood & Roberts, 2017, 2018), we additionally emphasize the importance of including the canopy's resources in these studies (also see Allen & Davies, 2022). Previous work found a strongly vertically stratified flower fly community composition: they found higher species richness and abundance in the understorey but with some species only found in the canopy, and a strong association of male flower flies with the canopy strata (Birtele & Hardersen, 2012). In work on bees in the southeastern United States, overall richness abundance was also highest in spring and diversity highest in the canopy, although *Augochlora pura* then dominated canopy catches all summer (Ulyshen et al., 2010). A comprehensive study using season-long ground-level sampling similarly found high spring forest bee abundance which declined over summer as bee abundance increased in agricultural and urban sites (Harrison et al., 2018). In our study, the striking pattern of abundance shifting across habitats in all nine replicate sites is consistent with complementary temporal habitat usage. Although many if not most species were found in all habitats and thus 'spilled over', there were some taxa that primarily stayed in the woods or others that were mostly found in the orchard (Supplemental Table S4). It will be exciting for future research to explore these patterns in light of different nesting biology, diet breadths, importance for conservation or forest association (sensu Smith et al., 2021).

We used digestive tract pollen to help us disentangle capture data from diet choices, that is, avoid the conflation of capture with habitat use (sensu Portman et al., 2020). Digestive tract pollen is an unusual and powerful methodological approach that we believe provides many potential ecological insights (Cane et al., 2017, p. 20; Urban-Mead et al., 2022, etc). Indeed, many pollinators caught in the forest had eaten pollen from plants known to grow in a different habitat than the one in which they had caught. For example, we might have inferred from capture data that male *Andrena* were restricted to understoreys, but their diets included substantial canopy pollen (Figure 3b; also see Supplemental Figure S5). Similarly, as spring progressed, canopy-caught pollinators transitioned from canopy-tree diets to include significant Rosaceous pollen. That is, even as population-level abundance shifted to the orchard (Figure 1a), individual insects still flew across habitat boundaries and foraged in both the canopy and orchard (Figure 3a, Supplemental Figures S4 and S5). Although flower flies (Syrphidae) were not very abundant in our dataset, males were more abundant in the forest (81% of males), and flies caught in the orchard had also eaten canopy and other pollens. Both types of information were necessary for these conclusions. We note that our sampling was intentionally conducted within 200m of orchard edges, as forest fragments are common in northeastern agroecosystems, and speculate that diets might demonstrate less overlap deeper in the forest (e.g. McLaughlin et al., 2022) or in large orchard blocks (e.g. MacInnis et al., 2020).

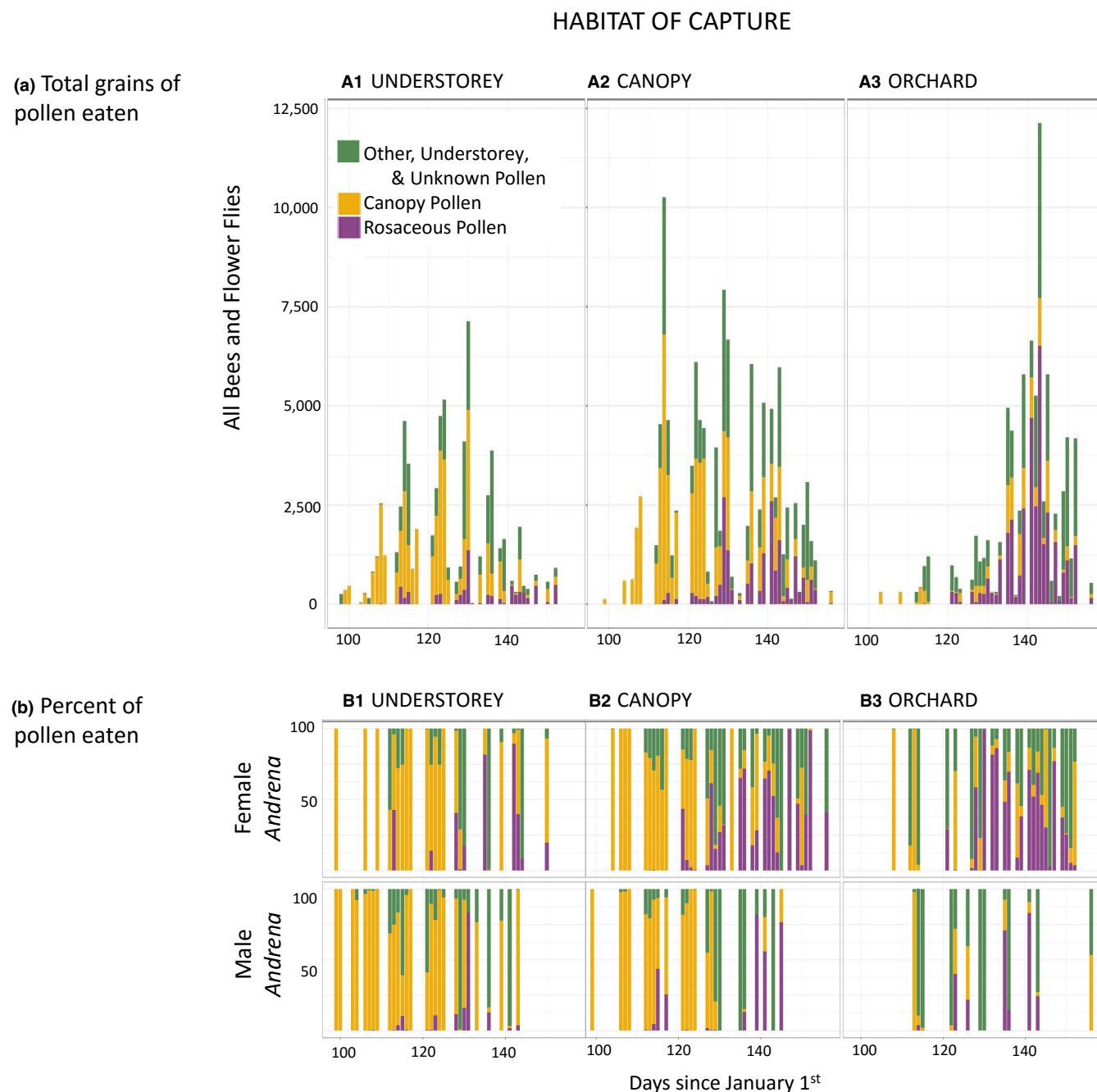
Male and female *Andrena* ate contrasting diets (Figure 3b), and males were primarily in the understorey, while females were primarily in the canopy and orchard. Prior research in crop fields also finds more



**FIGURE 2** *Andrena* males and females use different habitats on the orchard-forest interface. (a) Males and females were both caught frequently in the canopy, while males were more often captured in the understory and females in the orchard. (b) More female bees who ate pollen were caught in the canopy and orchard, while more male bees who ate pollen were caught in the understory. Each point represents *Andrena* per sex per habitat per site (boxplots, left) or *Andrena* per habitat per site per day (curves generated by Poisson models with 95% confidence interval, right). Orchard bloom peaked between days 135 and 145 across all nine orchards.

males near forest edges (e.g. Bailey et al., 2014; Calabuig, 2000). This pattern held for all of our most abundant *Andrena* species, so was not driven by species-level turnover (Figure 4). It is instead likely a result of within-species phenology, life cycle priorities and energetic requirements. Exploring habitat complementarity at the scale of sexes within a species requires incorporating natural history knowledge, and provides clear pathways for conservation action. Ground-nesting males emerge first and seek mates, while females emerge later and collect pollen for brood provisioning. Female *Andrena* also had more often eaten pollen from across habitats, reflecting their need to seek out large volumes of high-quality pollen and return to ground nests, some of which are in the forest (e.g. Schrader & LaBerge, 1978). In studies of solitary bees, we highlight that phenology and sex are almost inevitably going to be confounded—or at least complicating—and encourage future research to take into account or disentangle these thoroughly. Future conservation research should more explicitly consider such habitat partitioning among life stages.

There are several sources of uncertainty that complicate our ability to draw higher-resolution inference from our analyses. First, because gut passage time is poorly known, it is hard to know the time frame represented by pollen (although see Giacomini et al., 2022). Similarly, when a bee was caught in our traps, we have no way to know how old they are, what time of day they were caught, whether they were beginning or ending a foraging trip or if they were engaged in another behaviour such as mate seeking. Due to this imprecision, large sample sizes were required to allow us to compare between sexes or genera. Future research could choose focal taxa and collect individuals at known and repeated time intervals in order to characterize changes in consumption over the course of a day or week (sensu Isenberg et al., 1997). Furthermore, we did not sample in other nearby habitats and emphasize that other habitats are also important resources for orchard-pollinating bees, such as old fields, ditches and wetlands (Centrella et al., 2020; Eeraerts et al., 2021; Mandelik et al., 2012; Moquet et al., 2018). Finally, due



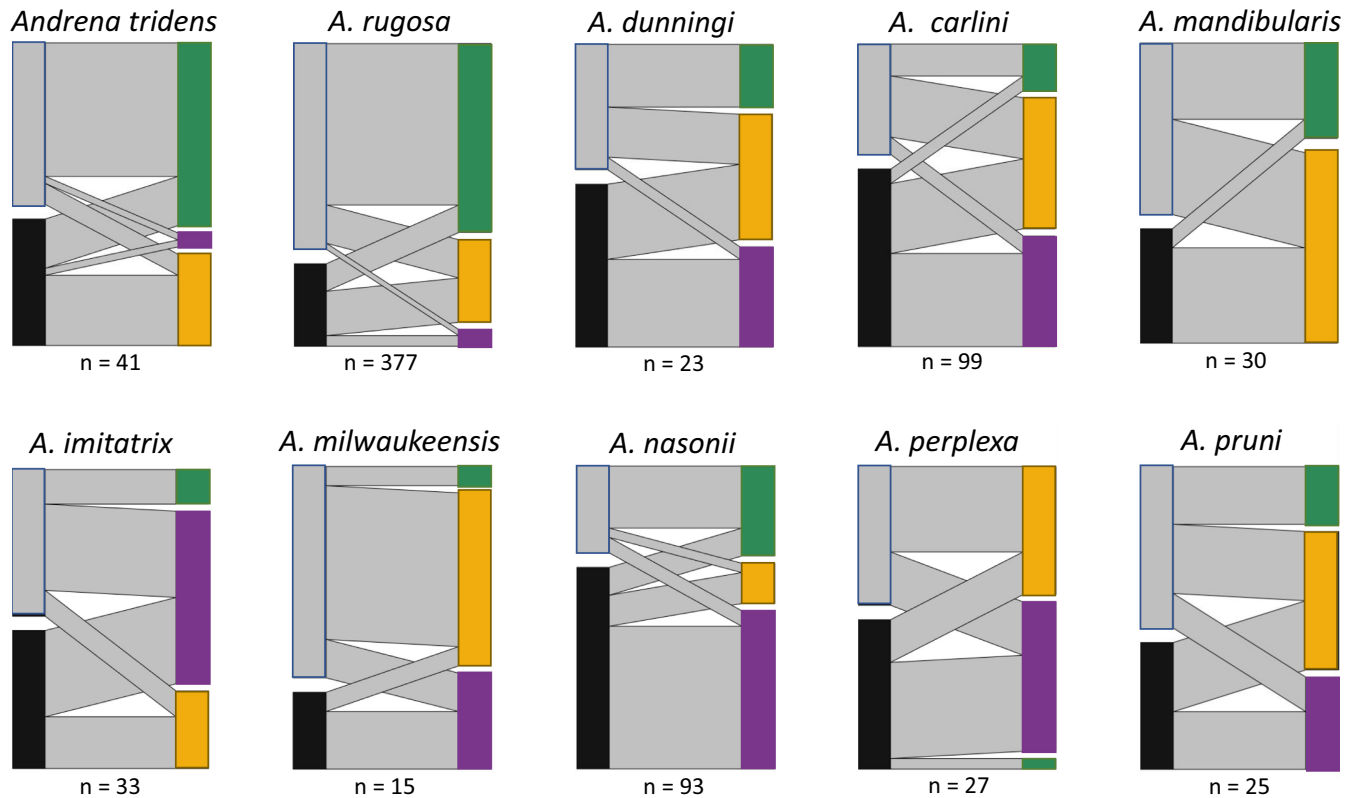
**FIGURE 3** Pollen eaten by bees and flower flies across the spring, by habitat of capture. A1–A3 (top): All pollinator diets in total pollen grains per day. B1–B3 (bottom): *Andrena*-only diets, showing diet proportion per day. Top row = females, bottom row = males. Number of pollinators represented each day varied based on catch.

to the difficulty in pollen analyses, our ‘orchard’ category could have included Rosaceous plants from outside the orchard, and the ‘Understorey or Other’ category certainly also included plants on the edge of the orchard, weeds and possible other plants from outside the two major habitats.

Our study emphasizes two specific habitat elements that are often overlooked in pollinator conservation. Many other studies have emphasized landscape-scale diversity for pollinator conservation (Burns & Stanley, 2022; Garratt et al., 2016; Kammerer et al., 2016; Ricketts et al., 2008; Vicens & Bosch, 2000; Watson et al., 2011),

yet the importance of movement between the forest canopy and orchards has not yet been reported, likely because canopy sampling is difficult and rarely attempted (Ulyshen, 2011; Urban-Mead et al., 2021). Although conservation planning often includes consideration for forage material, nest sites and even specialized needs such as mud for mason bees, flowers and leaves for leaf-cutters, or resin or oil-producing plants (Requier & Leonhardt, 2020), canopy resources should be more actively considered. Second, we additionally suggest that different bee sexes should be more explicitly included in conservation plans. Indeed, if male bees are not supported,





**FIGURE 4** Individual *Andrena* species-level networks and species richness per habitat. Bipartite habitat networks for each of the 10 most abundant *Andrena* species, ordered left to right by phenology (earliest day caught). Female bees (black) are more connected to orchard (purple) and canopy (gold) habitat nodes, while male bees (grey) are more connected to canopy and understory (green) habitats.

mating success and genetic diversity may be compromised in subsequent generations.

Growers and land managers are increasingly choosing to support and rely on free-living wild pollinators (Blitzer et al., 2016; Park et al., 2020). Here, we find evidence of complementary habitat use at the community level, between sexes, and at the individual insect level, and provide important new evidence exploring the forage and habitat benefits of forests for healthy pollinator communities. This is important as forest patches are globally important for their role as buffers to pesticide and pathogen risks in agroecosystems (e.g. McNeil et al., 2020; Obregon et al., 2021; Park et al., 2020) and that there is higher bee abundance, visitation, pollination success and even yield in crops and rows near woods (Bailey et al., 2014; Castle et al., 2019; Chacoff & Aizen, 2006; Ganuza et al., 2022; Gemmill-Herren & Ochieng', 2008; MacInnis et al., 2020; Proesmans, Bonte, et al., 2019; Rahimi et al., 2022; Watson, 2013). Actively managing forests for health, diversity and climate resilience is thus an important conservation action for supporting vibrant pollinator communities in orchard agroecosystems.

#### AUTHOR CONTRIBUTIONS

Katherine R. Urban-Mead, Bryan N. Danforth and Scott H. McArt conceived the ideas and designed the methodology; Katherine R. Urban-Mead collected the data; Katherine R. Urban-Mead, Maria van Dyke, Paige Muñiz and Andrew D. Young identified specimens;

Katherine R. Urban-Mead analysed the data and led the writing of the manuscript; all authors provided edits and gave final approval for publication.

#### ACKNOWLEDGEMENTS

This work was funded by SARE Graduate Student Grant GNE18-188 and NSF Graduate Research Fellowship Grant No. 1650441, both awarded to Katherine R. Urban-Mead. We thank Wee Hao Ng and Erika Mudrak for statistical help, Heather Grab, Julie Davis, John Mola, and the Danforth and McArt labs for comments on an earlier version of this manuscript. We thank Todd Ugine for first suggesting we look at digestive tract pollen at a Plant-Insect Group Meeting. We thank Kaitlin Deutsch, Rachel Fordyce, Rin Krichilsky and Anna Espinoza for taxonomic help, and Xavier Carroll and Andrea Jaruffe for help in the laboratory. We are grateful to the orchardists and growers who so generously welcomed us in their woods and orchards.

#### CONFLICT OF INTEREST

We declare that no authors have conflict of interest.

#### DATA AVAILABILITY STATEMENT

Data available via the Dryad Digital Repository <https://doi.org/10.5061/dryad.xd2547dmn> (Urban-Mead et al., 2022).

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## REFERENCES

- Aljuwayd, M. (2017). *Examining forest edge effects on the distribution of bees (Hymenoptera: Apoidea), hover flies (Diptera: Syrphidae) and vespid wasps (Hymenoptera: Vespidae), in Pennsylvania apple orchards*. M.S., Long Island University, The Brooklyn Center. <https://search.proquest.com/docview/1972622521/abstract/E8E59AEE841B4759PQ/1>
- Allen, G., & Davies, R. G. (2022). Canopy sampling reveals hidden potential value of woodland trees for wild bee assemblages. *Insect Conservation and Diversity*, 1–14. <https://doi.org/10.1111/icad.12606>
- Bailey, S., Requier, F., Nusillard, B., Roberts, S. P. M., Potts, S. G., & Bouget, C. (2014). Distance from forest edge affects bee pollinators in oilseed rape fields. *Ecology and Evolution*, 4(4), 370–380. <https://doi.org/10.1002/ece3.924>
- Birte, D., & Hardersen, S. (2012). Analysis of vertical stratification of Syrphidae (Diptera) in an oak-hornbeam forest in northern Italy. *Ecological Research*, 27(4), 755–763. <https://doi.org/10.1007/s11284-012-0948-2>
- Blitzer, E. J., Dormann, C. F., Holzschuh, A., Klein, A.-M., Rand, T. A., & Tscharntke, T. (2012). Spillover of functionally important organisms between managed and natural habitats. *Agriculture, Ecosystems & Environment*, 146(1), 34–43. <https://doi.org/10.1016/j.agee.2011.09.005>
- Blitzer, E. J., Gibbs, J., Park, M. G., & Danforth, B. N. (2016). Pollination services for apple are dependent on diverse wild bee communities. *Agriculture, Ecosystems & Environment*, 221, 1–7. <https://doi.org/10.1016/j.agee.2016.01.004>
- Bouseman, J. K., & LaBerge, W. E. (1978). A revision of the bees of the genus *Andrena* of the Western hemisphere. Part IX. Subgenus *Melandrena*. *Transactions of the American Entomological Society* (1890–), 104(3/4), 275–389 JSTOR.
- Brosi, B. J. (2016). Pollinator specialization: From the individual to the community. *New Phytologist*, 210(4), 1190–1194. <https://doi.org/10.1111/nph.13951>
- Burns, K. L. W., & Stanley, D. A. (2022). The importance and value of insect pollination to apples: A regional case study of key cultivars. *Agriculture, Ecosystems & Environment*, 331, 107911. <https://doi.org/10.1016/j.agee.2022.107911>
- Calabuig, I. (2000). *Solitary bees and bumblebees in a Danish agricultural landscape* (PhD thesis). University of Copenhagen (p. 103).
- Cane, J. H., Dobson, H. E. M., & Boyer, B. (2017). Timing and size of daily pollen meals eaten by adult females of a solitary bee (*Nomia melanderi*) (Apiformes: Halictidae). *Apidologie*, 48(1), 17–30. <https://doi.org/10.1007/s13592-016-0444-8>
- Castle, D., Grass, I., & Westphal, C. (2019). Fruit quantity and quality of strawberries benefit from enhanced pollinator abundance at hedgerows in agricultural landscapes. *Agriculture, Ecosystems & Environment*, 275, 14–22. <https://doi.org/10.1016/j.agee.2019.01.003>
- Centrella, M., Russo, L., Moreno Ramírez, N., Eitzer, B., van Dyke, M., Danforth, B., & Poveda, K. (2020). Diet diversity and pesticide risk mediate the negative effects of land use change on solitary bee offspring production. *Journal of Applied Ecology*, 57(6), 1031–1042. <https://doi.org/10.1111/1365-2664.13600>
- Chacoff, N. P., & Aizen, M. A. (2006). Edge effects on flower-visiting insects in grapefruit plantations bordering premontane subtropical forest. *Journal of Applied Ecology*, 43(1), 18–27. <https://doi.org/10.1111/j.1365-2664.2005.01116.x>
- De Marco, P., & Coelho, F. M. (2004). Services performed by the ecosystem: Forest remnants influence agricultural cultures' pollination and production. *Biodiversity and Conservation*, 13(7), 1245–1255. <https://doi.org/10.1023/B:BIOC.0000019402.51193.e8>
- Dobson, H. E., & Peng, Y.-S. (1997). Digestion of pollen components by larvae of the flower-specialist bee *Chelostoma florissome* (Hymenoptera: Megachilidae). *Journal of Insect Physiology*, 43(1), 89–100.
- Dormann, C. F., Fründ, J., Blüthgen, N., & Gruber, B. (2009). Indices, graphs and null models: Analyzing bipartite ecological networks. <http://www.goedoc.uni-goettingen.de/goescholar/handle/1/5837>
- Eeraerts, M., Van Den Berge, S., Proesmans, W., Verheyen, K., Smagghe, G., & Meeus, I. (2021). Fruit orchards and woody semi-natural habitat provide complementary resources for pollinators in agricultural landscapes. *Landscape Ecology*, 36, 1377–1390. <https://doi.org/10.1007/s10980-021-01220-y>
- Eickwort, G. C., & Ginsberg, H. S. (1980). Foraging and mating behavior in Apoidea. *Annual Review of Entomology*, 25(1), 421–446. <https://doi.org/10.1146/annurev.en.25.010180.002225>
- Földesi, R., Kovács-Hostyánszki, A., Kőrösi, Á., Somay, L., Elek, Z., Markó, V., Sárosspataki, M., Bakos, R., Varga, Á., Nyisztor, K., & Báldi, A. (2016). Relationships between wild bees, hoverflies and pollination success in apple orchards with different landscape contexts. *Agricultural and Forest Entomology*, 18(1), 68–75. <https://doi.org/10.1111/afe.12135>
- Fowler, J. (2016). Specialist bees of the northeast: Host plants and habitat conservation. *Northeastern Naturalist*, 23(2), 305–320. <https://doi.org/10.1656/045.023.0210>
- Ganuz, C., Redlich, S., Uhler, J., Tobisch, C., Rojas-Botero, S., Peters, M. K., Zhang, J., Benjamin, C. S., Englmeier, J., Ewald, J., Fricke, U., Haensel, M., Kollmann, J., Riebl, R., Uphus, L., Müller, J., & Steffan-Dewenter, I. (2022). Interactive effects of climate and land use on pollinator diversity differ among taxa and scales. *Science Advances*, 8(18), eabm9359. <https://doi.org/10.1126/sciadv.abm9359>
- Garratt, M. P. D., Breeze, T. D., Boreux, V., Fountain, M. T., Mc Kerchar, M., Webber, S. M., Coston, D. J., Jenner, N., Dean, R., Westbury, D. B., Biesmeijer, J. C., & Potts, S. G. (2016). Apple pollination: Demand depends on variety and supply depends on pollinator identity. *PLoS ONE*, 11(5), e0153889. <https://doi.org/10.1371/journal.pone.0153889>
- Gemmill-Herren, B., & Ochieng', A. O. (2008). Role of native bees and natural habitats in eggplant (*Solanum melongena*) pollination in Kenya. *Agriculture, Ecosystems & Environment*, 127(1), 31–36. <https://doi.org/10.1016/j.agee.2008.02.002>
- Giacomini, J. J., Moore, N., Adler, L. S., & Irwin, R. E. (2022). Sunflower pollen induces rapid excretion in bumble bees: Implications for host-pathogen interactions. *Journal of Insect Physiology*, 137, 104356. <https://doi.org/10.1016/j.jinsphys.2022.104356>
- Gibbs, J. (2011). Revision of the metallic *Lasioglossum* (*Dialictus*) of eastern North America (Hymenoptera: Halictidae: Halictini). *Zootaxa*, 3073(1), 1. <https://doi.org/10.11646/zootaxa.3073.1.1>
- Gibbs, J., Packer, L., Dumesh, S., & Danforth, B. N. (2013). Revision and reclassification of *Lasioglossum* (*Evylaeus*), L. (*Hemihalictus*) and L. (*Sphecodogastra*) in eastern North America (Hymenoptera: Apoidea: Halictidae). *Zootaxa*, 3672(1), 1–117. <https://doi.org/10.11646/zootaxa.3672.1.1>
- González, E., Salvo, A., Defagó, M. T., & Valladares, G. (2016). A moveable feast: Insects moving at the forest-crop interface are affected by crop phenology and the amount of forest in the landscape. *PLoS ONE*, 11(7), e0158836. <https://doi.org/10.1371/journal.pone.0158836>
- Greenleaf, S. S., Williams, N. M., Winfree, R., & Kremen, C. (2007). Bee foraging ranges and their relationship to body size. *Oecologia*, 153(3), 589–596. <https://doi.org/10.1007/s00442-007-0752-9>

- Halinski, R., Garibaldi, L. A., dos Santos, C. F., Acosta, A. L., Guidi, D. D., & Blochtein, B. (2020). Forest fragments and natural vegetation patches within crop fields contribute to higher oilseed rape yields in Brazil. *Agricultural Systems*, 180, 102768. <https://doi.org/10.1016/j.agry.2019.102768>
- Harmon-Threatt, A. N., & Kremen, C. (2015). Bumble bees selectively use native and exotic species to maintain nutritional intake across highly variable and invaded local floral resource pools. *Ecological Entomology*, 40(4), 471–478. <https://doi.org/10.1111/een.12211>
- Harrison, T., Gibbs, J., & Winfree, R. (2018). Forest bees are replaced in agricultural and urban landscapes by native species with different phenologies and life-history traits. *Global Change Biology*, 24(1), 287–296. <https://doi.org/10.1111/gcb.13921>
- Isenberg, S. B., Cameron, S. A., & Whitfield, J. B. (1997). Crop storage of pollen and its functional significance in the solitary bee, *Melissodes rustica* (Hymenoptera: Apidae). *Journal of the Kansas Entomological Society*, 70(4), 353–358.
- Kammerer, M. A., Biddinger, D. J., Rajotte, E. G., & Mortensen, D. A. (2016). Local plant diversity across multiple habitats supports a diverse wild bee community in Pennsylvania Apple Orchards. *Environmental Entomology*, 45(1), 32–38. <https://doi.org/10.1093/ee/nvv147>
- Käpylä, M. (1978). Bionomics of five wood-nesting solitary species of bees (Hym., Megachilidae), with emphasis on flower relationships. *Biological Research Reports of the University of Jyväskylä*, 5, 3–89.
- Klein, A.-M., Vaissiere, B. E., Cane, J. H., Steffan-Dewenter, I., Cunningham, S. A., Kremen, C., & Tscharntke, T. (2007). Importance of pollinators in changing landscapes for world crops. *Proceedings of the Royal Society B: Biological Sciences*, 274(1608), 303–313. <https://doi.org/10.1098/rspb.2006.3721>
- LaBerge, W. E. (1971). A revision of the bees of the genus *Andrena* of the Western Hemisphere. Part IV. *Scapteropsis*, *Xiphandrena* and *Rhaphandrena*. *Transactions of the American Entomological Society* (1890-), 97(3), 441–520 JSTOR.
- LaBerge, W. E. (1973). A revision of the bees of the genus *Andrena* of the Western Hemisphere. Part VI. Subgenus *Trachandrena*. *Transactions of the American Entomological Society* (1890-), 99(3), 235–371 JSTOR.
- LaBerge, W. E. (1980). A revision of the bees of the genus *Andrena* of the Western Hemisphere. Part X. subgenus *Andrena*. *Transactions of the American Entomological Society* (1890-), 106(4), 395–525 JSTOR.
- LaBerge, W. E. (1985). A revision of the bees of the genus *Andrena* of the Western Hemisphere. Part XI. Minor subgenera and subgeneric key. *Transactions of the American Entomological Society* (1890-), 111(4), 441–567 JSTOR.
- MacInnis, G., Buddle, C. M., & Forrest, J. R. K. (2020). Small wild bee abundance declines with distance into strawberry crops regardless of field margin habitat. *Basic and Applied Ecology*, 44, 14–23. <https://doi.org/10.1016/j.baae.2020.02.007>
- Malfi, R. L., Crone, E., & Williams, N. (2019). Demographic benefits of early season resources for bumble bee (*B. vosnesenskii*) colonies. *Oecologia*, 191(2), 377–388. <https://doi.org/10.1007/s00442-019-04472-3>
- Mandelik, Y., Winfree, R., Neeson, T., & Kremen, C. (2012). Complementary habitat use by wild bees in agro-natural landscapes. *Ecological Applications*, 22(5), 1535–1546. <https://doi.org/10.1890/11-1299.1>
- Marini, L., Bartomeus, I., Rader, R., & Lami, F. (2019). Species–habitat networks: A tool to improve landscape management for conservation. *Journal of Applied Ecology*, 56(4), 923–928. <https://doi.org/10.1111/1365-2664.13337>
- McArt, S. H., Urbanowicz, C., McCoshum, S., Irwin, R. E., & Adler, L. S. (2017). Landscape predictors of pathogen prevalence and range contractions in US bumblebees. *Proceedings of the Royal Society B: Biological Sciences*, 284(1867), 20172181. <https://doi.org/10.1098/rspb.2017.2181>
- McLaughlin, R., Keller, J., Wagner, E., Biddinger, D., Grozinger, C., & Hoover, K. (2022). Insect visitors of black cherry (*Prunus serotina*) (Rosales: Rosaceae) and factors affecting viable seed production. *Environmental Entomology*, 51, nvab141. <https://doi.org/10.1093/ee/nvab141>
- McNeil, D. J., McCormick, E., Heimann, A. C., Kammerer, M., Douglas, M. R., Goslee, S. C., Grozinger, C. M., & Hines, H. M. (2020). Bumble bees in landscapes with abundant floral resources have lower pathogen loads. *Scientific Reports*, 10(1), Article 1. <https://doi.org/10.1038/s41598-020-78119-2>
- Mola, J. M., Hemberger, J., Kochanski, J., Richardson, L. L., & Pearse, I. S. (2021). The importance of forests in bumble bee biology and conservation. *Bioscience*, 71(12), 1234–1248. <https://doi.org/10.1093/biosci/biab121>
- Mola, J. M., Richardson, L. L., Spyreas, G., Zaya, D. N., & Pearse, I. S. (2021). Long-term surveys support declines in early season forest plants used by bumblebees. *Journal of Applied Ecology*, 58(7), 1431–1441. <https://doi.org/10.1111/1365-2664.13886>
- Montagnana, P. C., Alves, R. S. C., Garófalo, C. A., & Ribeiro, M. C. (2021). Landscape heterogeneity and forest cover shape cavity-nesting hymenopteran communities in a multi-scale perspective. *Basic and Applied Ecology*, 56, 239–249. <https://doi.org/10.1016/j.baae.2021.08.004>
- Moquet, L., Laurent, E., Bacchetta, R., & Jacquemart, A.-L. (2018). Conservation of hoverflies (Diptera, Syrphidae) requires complementary resources at the landscape and local scales. *Insect Conservation and Diversity*, 11(1), 72–87. <https://doi.org/10.1111/icad.12245>
- Obregon, D., Guerrero, O. R., Stashenko, E., & Poveda, K. (2021). Natural habitat partially mitigates negative pesticide effects on tropical pollinator communities. *Global Ecology and Conservation*, 28, e01668. <https://doi.org/10.1016/j.gecco.2021.e01668>
- Ogilvie, J. E., & Forrest, J. R. (2017). Interactions between bee foraging and floral resource phenology shape bee populations and communities. *Current Opinion in Insect Science*, 21, 75–82. <https://doi.org/10.1016/j.cois.2017.05.015>
- Ostevik, K. L., Manson, J. S., & Thomson, J. D. (2010). Pollination potential of male bumble bees (*Bombus impatiens*): Movement patterns and pollen-transfer efficiency. *Journal of Pollination Ecology*, 2(4), 21–26.
- Park, M. G., Blitzer, E. J., Gibbs, J., Losey, J. E., & Danforth, B. N. (2015). Negative effects of pesticides on wild bee communities can be buffered by landscape context. *Proceedings of the Royal Society B: Biological Sciences*, 282(1809), 20150299. <https://doi.org/10.1098/rspb.2015.0299>
- Park, M. G., Joshi, N. K., Rajotte, E. G., Biddinger, D. J., Losey, J. E., & Danforth, B. N. (2020). Apple grower pollination practices and perceptions of alternative pollinators in New York and Pennsylvania. *Renewable Agriculture and Food Systems*, 35(1), 1–14.
- Pfeiffer, V., Silbernagel, J., Guédot, C., & Zalapa, J. (2019). Woodland and floral richness boost bumble bee density in cranberry resource pulse landscapes. *Landscape Ecology*, 34(5), 979–996. <https://doi.org/10.1007/s10980-019-00810-1>
- Portman, Z. M., Bruninga-Socular, B., & Cariveau, D. P. (2020). The state of bee monitoring in the United States: A call to refocus away from bowl traps and towards more effective methods. *Annals of the Entomological Society of America*, 113, 337–342. <https://doi.org/10.1093/aesa/saaa010>
- Proesmans, W., Bonte, D., Smaghe, G., Meeus, I., Decocq, G., Spicher, F., Kolb, A., Lemke, I., Diekmann, M., Bruun, H. H., Wulf, M., Van Den Berge, S., & Verheyen, K. (2019). Small forest patches as pollinator habitat: Oases in an agricultural desert? *Landscape Ecology*, 34(3), 487–501. <https://doi.org/10.1007/s10980-019-00782-2>
- Proesmans, W., Smaghe, G., Meeus, I., Bonte, D., & Verheyen, K. (2019). The effect of mass-flowering orchards and semi-natural

- habitat on bumblebee colony performance. *Landscape Ecology*, 34(5), 1033–1044. <https://doi.org/10.1007/s10980-019-00836-5>
- Rader, R., Bartomeus, I., Garibaldi, L. A., Garratt, M. P. D., Howlett, B. G., Winfree, R., Cunningham, S. A., Mayfield, M. M., Arthur, A. D., Andersson, G. K. S., Bommarco, R., Brittain, C., Carvalheiro, L. G., Chacoff, N. P., Entling, M. H., Foully, B., Freitas, B. M., Gemmill-Herren, B., Ghazoul, J., ... Woyciechowski, M. (2016). Non-bee insects are important contributors to global crop pollination. *Proceedings of the National Academy of Sciences of the United States of America*, 113(1), 146–151. <https://doi.org/10.1073/pnas.1517092112>
- Rahimi, E., Barghjelveh, S., & Dong, P. (2022). Amount, distance-dependent and structural effects of forest patches on bees in agricultural landscapes. *Agriculture & Food Security*, 11(1), 10. <https://doi.org/10.1186/s40066-022-00360-x>
- Requier, F., & Leonhardt, S. D. (2020). Beyond flowers: Including non-floral resources in bee conservation schemes. *Journal of Insect Conservation*, 24, 5–16. <https://doi.org/10.1007/s10841-019-00206-1>
- Ricketts, T. H., Regetz, J., Steffan-Dewenter, I., Cunningham, S. A., Kremen, C., Bogdanski, A., Gemmill-Herren, B., Greenleaf, S. S., Klein, A. M., Mayfield, M. M., Morandin, L. A., Ochieng', A., & Viana, B. F. (2008). Landscape effects on crop pollination services: Are there general patterns? *Ecology Letters*, 11(5), 499–515. <https://doi.org/10.1111/j.1461-0248.2008.01157.x>
- Roswell, M., Dushoff, J., & Winfree, R. (2019). Male and female bees show large differences in floral preference. *PLoS ONE*, 14(4), e0214909. <https://doi.org/10.1371/journal.pone.0214909>
- Samnegård, U., Hambäck, P. A., Eardley, C., Nemomissa, S., & Hylander, K. (2015). Turnover in bee species composition and functional trait distributions between seasons in a tropical agricultural landscape. *Agriculture, Ecosystems & Environment*, 211, 185–194. <https://doi.org/10.1016/j.agee.2015.06.010>
- Schrader, M. N., & LaBerge, W. E. (1978). The nest biology of the bees *Andrena* (*Melandrena*) *regularis* Malloch and *Andrena* (*Melandrena*) *carlini* Cockererell (Hymenoptera: Andrenidae). *Biological Notes* No. 108. Illinois Natural History Survey (p. 24).
- Smith, C., Harrison, T., Gardner, J., & Winfree, R. (2021). Forest-associated bee species persist amid forest loss and regrowth in eastern North America. *Biological Conservation*, 260, 109202. <https://doi.org/10.1016/j.biocon.2021.109202>
- Sommaggio, D. (1999). Syrphidae: Can they be used as environmental bioindicators? *Agriculture, Ecosystems & Environment*, 74(1), 343–356. [https://doi.org/10.1016/S0167-8809\(99\)00042-0](https://doi.org/10.1016/S0167-8809(99)00042-0)
- Splitt, A., Skórka, P., Strachecka, A., Borański, M., & Teper, D. (2021). Keep trees for bees: Pollen collection by *Osmia bicornis* along the urbanization gradient. *Urban Forestry & Urban Greening*, 64, 127250.
- Stockhammer, K. A. (1966). Nesting habits and life cycle of a sweat bee, *Augochlora pura* (hymenoptera: Halictidae). *Journal of the Kansas Entomological Society*, 39(2), 157–192 JSTOR.
- Stockhammer, K. A. (1967). Some notes on the biology of the blue sweat bee, *Lasioglossum coeruleum* (Apoidea: Halictidae). *Journal of the Kansas Entomological Society*, 40(2), 177–189.
- Taniguchi, S. (1956). Biological studies on the Japanese bees (III): Request in flower-visiting of infrasocial bees. *Science Reports of the Hyogo University of Agriculture Series Agricultural Biology*, 2, 37–51.
- Ulyshen, M. D. (2011). Arthropod vertical stratification in temperate deciduous forests: Implications for conservation-oriented management. *Forest Ecology and Management*, 261(9), 1479–1489. <https://doi.org/10.1016/j.foreco.2011.01.033>
- Ulyshen, M. D., Soon, V., & Hanula, J. L. (2010). On the vertical distribution of bees in a temperate deciduous forest. *Insect Conservation and Diversity*, 3(3), 222–228. <https://doi.org/10.1111/j.1752-4598.2010.00092.x>
- Urban-Mead, K. R., van Dyke, M., Muñoz, P., Danforth, B. N., & McArt, S. H. (2022). Data from: Early spring orchard pollinators spill over from resource-rich adjacent forest patches. *Dryad Digital Repository*. <https://doi.org/10.5061/dryad.xd2547dmn>
- Urban-Mead, K. R., Muñoz, P., Gillung, J., Espinoza, A., Fordyce, R., van Dyke, M., McArt, S. H., & Danforth, B. N. (2021). Bees in the trees: Diverse spring fauna in temperate forest edge canopies. *Forest Ecology and Management*, 482, 118903. <https://doi.org/10.1016/j.foreco.2020.118903>
- Urban-Mead, K. R., Walter, E., Mcart, S. H., & Danforth, B. N. (2022). Nearly half of spring-flying male *Andrena* bees consume pollen, but less than female conspecifics. *Apidologie*, 53(4), 49. <https://doi.org/10.1007/s13592-022-00951-4>
- Vicens, N., & Bosch, J. (2000). Pollinating efficacy of *Osmia cornuta* and *Apis mellifera* (Hymenoptera: Megachilidae, Apidae) on 'Red Delicious' apple. *Environmental Entomology*, 29(2), 235–240. <https://doi.org/10.1093/ee/29.2.235>
- Watson, D. M. (2013). The relative contribution of specialists and generalists to mistletoe dispersal: Insights from a neotropical rain forest. *Biotropica*, 45(2), 195–202. <https://doi.org/10.1111/j.1744-7429.2012.00905.x>
- Watson, J. C., Wolf, A. T., & Ascher, J. S. (2011). Forested landscapes promote richness and abundance of native bees (Hymenoptera: Apoidea: Anthophila) in Wisconsin Apple Orchards. *Environmental Entomology*, 40(3), 621–632. <https://doi.org/10.1603/EN10231>
- Winfree, R., Reilly, J. R., Bartomeus, I., Cariveau, D. P., Williams, N. M., & Gibbs, J. (2018). Species turnover promotes the importance of bee diversity for crop pollination at regional scales. *Science*, 359(6377), 791–793. <https://doi.org/10.1126/science.aao2117>
- Wood, T. J., & Roberts, S. P. M. (2017). An assessment of historical and contemporary diet breadth in polylectic *Andrena* bee species. *Biological Conservation*, 215(Supplement C), 72–80. <https://doi.org/10.1016/j.biocon.2017.09.009>
- Wood, T. J., & Roberts, S. P. M. (2018). Constrained patterns of pollen use in Nearctic *Andrena* (Hymenoptera: Andrenidae) compared with their Palaearctic counterparts. *Biological Journal of the Linnean Society*, 124(4), 732–746. <https://doi.org/10.1093/biolinnean/bly080>
- Wood, T. J., Vanderplanck, M., Vastrade, M., Vaudo, A. D., & Michez, D. (2021). Trees for bees: Could woody plant pollen be used as a consistent resource in bee-focused Agri-environment schemes? *Entomologia Generalis*, 42, 361–374. <https://doi.org/10.1127/entomologia/2021/1241>
- Woodard, S. H., Duennes, M. A., Watrous, K. M., & Jha, S. (2019). Diet and nutritional status during early adult life have immediate and persistent effects on queen bumble bees. *Conservation Physiology*, 7(1), coz048. <https://doi.org/10.1093/conphys/coz048>

## SUPPORTING INFORMATION

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

**How to cite this article:** Urban-Mead, K. R., Van Dyke, M., Muñoz, P., Young, A. D., Danforth, B. N., & McArt, S. H. (2023). Early spring orchard pollinators spill over from resource-rich adjacent forest patches. *Journal of Applied Ecology*, 00, 1–12. <https://doi.org/10.1111/1365-2664.14350>