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Wild bee species increase tomato production and respond differently to surrounding land use in Northern California

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ABSTRACT

Pollination provided by bees enhances the production of many crops. However, the contribution of wild bees remains unmeasured for many crops, and the effects of anthropogenic change on many bee species are unstudied. We experimentally investigated how pollination by wild bees affects tomato production in northern California. We found that wild bees substantially increase the production of field-grown tomato, a crop generally considered self-pollinating. Surveys of the bee community on 14 organic fields that varied in proximity to natural habitat showed that the primary bee visitors, *Anthophora urbana* Cresson and *Bombus vosnesenskii* Radoszkowski, were affected differently by land management practices. *B. vosnesenskii* was found primarily on farms proximate to natural habitats, but neither proximity to natural habitat nor tomato floral abundance, temperature, or year explained variation in the visitation rates of *A. urbana*. Natural habitat appears to increase *B. vosnesenskii* populations and should be preserved near farms. Additional research is needed to determine how to maintain *A. urbana*. Species-specific differences in dependency on natural habitats underscore the importance of considering the natural histories of individual bee species when projecting population trends of pollinators and designing management plans for pollination services. Thus, to maintain an entire bee community, multiple approaches, including maintaining natural habitat, should be implemented.

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1. Introduction

Bees may be in decline. For example, managed honey bees in the United States have declined from over 4 million colonies in the 1970s to 2.41 million colonies in 2005 (USDA National Agricultural Statistics Service, 1977, 2006), because of problems such as parasitic mites and pesticide misuse (Ellis and Munn, 2005; Matheson et al., 1996). Wild, non-*Apis* bees may also be declining because of pesticides, disease, habitat loss,

and habitat degradation (Allen-Wardell et al., 1998; Frankie et al., 1997; Ingram et al., 1996; Kevan, 1977; Kevan et al., 1993; Klein et al., 2003a,b; Kremen et al., 2004, 2003, 2002; O'Toole, 1993, 1994; Ricketts, 2004; Steffan-Dewenter and Tscharntke, 1999; Thorp and Shepherd, 2005). There are several documented examples showing that loss of bee pollinators has resulted in reduced crop yields (Kevan, 1977; Ricketts et al., 2004). With 67% of angiosperms requiring animal pollinators (Axelrod, 1960), declining bee populations

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may also disrupt natural ecosystems (reviewed in Allen-Wardell et al., 1998).

Research on how habitat loss affects pollination services has focused on how bees respond to variation across the landscape at the community level. Bee community abundance on crops declines with decreasing proximity to natural habitat (Klein et al., 2003a,b; Kremen et al., 2004, 2003, 2002; Ricketts, 2004; Steffan-Dewenter and Tscharntke, 1999). Also at the bee community level, evidence suggests that bee communities may be more species-rich and abundant on organic than on conventional farms (Kremen et al., 2004, 2002).

Species-specific responses of bees to landscape-scale anthropogenic change remain poorly understood. Because bee taxa exhibit considerable variation in life history (Michener, 2001), species may be affected differently by anthropogenic changes (Cane, 2001). For example, the composition of the stingless bee community changes with anthropogenic disturbance, and the nest-site preferences of stingless bee species may determine which species are able to persist in logged forests (Samejima et al., 2004). Degree of specialization on floral resources may also be important; bumblebees that forage primarily on Fabaceae may be rarer than those that forage on a more diverse set of plants (Goulson et al., 2005). A better understanding of species-specific bee conservation needs is vital to understanding how to maintain a species-rich bee community, which is essential for maintaining pollination services. Although some wild and crop plants can be pollinated by generalists, others require specialist pollinators (Free, 1993; Waser et al., 1996). Furthermore, a species-rich bee community may provide not only more pollination services to plants than a depauperate community (Greenleaf and Kremen, accepted; Klein et al., 2003a; Larsen et al., 2005) but also more consistent pollination services across space and time (Klein et al., 2003a; Kremen et al., 2004, 2002).

In planning our research on species-specific responses of bees to habitat variation across agricultural and wild habitats, we focused on field-grown tomato (*Solanum lycopersicum*). Tomato flowers do not produce nectar, and tomato pollen is generally accessible to bees only if they use buzz pollination, in which a specialized movement of the flight muscles sonicates the flower, thereby releasing pollen from the poricidal anthers. Honey bees, which are incapable of floral sonication, have difficulty obtaining pollen from tomato flowers (Buchmann, 1983; Free, 1993; King and Buchmann, 2003). Honey bees do not readily visit tomato flowers when other floral resources are available, and most visitors to tomato are non-*Apis* bees (Free, 1963; Higo et al., 2004).

The contribution of bee pollination to producing field-grown, fresh market tomatoes remains largely unknown despite the economic importance of these tomatoes. Even though domesticated tomato varieties are self-compatible, bee pollination dramatically increases yields of greenhouse tomatoes (summarized by Free, 1993, Delaplane and Mayer, 2000; also see Cauich et al., 2004). Bumble bees, the primary pollinator in greenhouse tomato production, are stocked at densities of 10–15 commercially produced colonies per ha (Delaplane and Mayer, 2000). Wild, native bees visit field-grown tomatoes (summarized in Free, 1993), although few were found in California (Bohart and Todd, 1961). However,

the effect of these visitors on the production of field-grown, fresh market tomatoes has not been documented.

Noting that bumble bees are important for greenhouse tomato production, we hypothesized that native bees capable of floral sonication increase field-grown tomato yields. First, we established experimentally by how much and by what mechanism wild, native bees enhance tomato production. Second, we documented which bee species visit tomato flowers and determined the proportion of visits provided by each bee species. Third, we ascertained how a major anthropogenic influence in agricultural systems – loss of natural habitat – affects bee species with differing life histories. Each of these steps is necessary both to document the contribution of wild bee species to pollination services and to develop suitable management plans to conserve the ecosystem service (Kremen, 2005).

2. Methods

We conducted research on farms in northern California. We chose the tomato variety SunGold, a common variety of hybrid cherry tomato, which is particularly likely to benefit from animal pollination because the stigma projects beyond the cone of anthers. In tomato flowers with sufficiently short styles, the stigma does not project beyond the cone of anthers, making self-pollination more likely to occur (Free, 1993). All farms were organic, and a variety of different row crops were grown near the tomatoes.

In our first experiment we determined whether wild, native bees increase tomato production, testing two mechanisms that, under natural conditions, are not mutually exclusive: (1) bees increase production by providing cross-pollination; and (2) bees increase production by increasing self-pollination through floral sonication. This research was carried out during late June–August 2001. In a row of tomatoes of uniform age, under identical management, and with a high rate of bee visitation, we randomly assigned clusters of tomato buds (no more than one per plant) to one of four groups: open pollination, artificial cross-pollination, artificial self-pollination, or control (bagged). We began the experiment with 20 clusters in the open pollination group, 15 for artificial cross-pollination, 15 for artificial self-pollination, and 20 for the control. Final sample sizes were slightly reduced by stem breakage (open pollination $n = 19$; artificial cross-pollination $n = 12$, artificial self-pollination $n = 14$, and control $n = 19$). We tagged stems well below the flower cluster to keep the tags from affecting normal bee visitation. For the three groups other than open pollination, we placed a fine mesh bag constructed from bridal veil over each cluster before the flowers opened (Kearns and Inouye, 1993), excluding all bees. After the flowers had opened, we treated the artificial self-pollination group daily, sonicating each open flower with a middle C tuning fork to mimic floral sonication provided by bees. We artificially cross-pollinated the third group by collecting pollen from flowers on other plants and then dipping the stigmas into the pollen. Pollen was collected with a tuning fork, placed in a clean plastic vial, and used immediately. The only treatment of the control group was placing exclusion bags over the clusters. The exclusion bags permitted airflow around the flowers and allowed wind to move the flower clusters. To minimize extraneous effects, we removed the bags when the

flowers senesced. When the tomatoes were at the same stage of ripeness as when they are picked by local farmers (deep orange-gold color), we counted the number of developed and aborted fruits. We then picked all developed fruits and measured the volume of each, using water displacement in a graduated cylinder. For both volume and proportion of flowers developing into fruits, we used each cluster of flowers as an independent data point. We analyzed each data set with ANOVA and Tukey HSD post hoc tests for unequal sample sizes (Sokal and Rohlf, 1997; Statistica 6.0).

We conducted a second experiment to test the effects of dipping stigmas in pollen. In the first experiment, the artificial self-pollination group and the artificial cross-pollination group varied not only in whether cross-pollination was possible but also in whether the stigma was dipped into pollen. Dipping the stigma could damage it and reduce yield; alternatively, dipping the stigma could result in more pollen grains sticking to it, thereby increasing yield. In June–August 2003, to determine which of these two differences was responsible for the observed differences in yield, we carried out a second experiment comparing two types of artificial self-pollination: (1) sonication-only; and (2) sonication + pollen-dipping. We vibrated the sonication-only flowers with a tuning fork. For the sonication + pollen-dipping group, we sonicated the flower, collected the pollen from that particular flower, and applied that pollen directly to that flower's stigma. All other methods were identical to the first experiment. We analyzed with *t*-tests both the proportion of flowers developing into fruits and the size of the resulting tomatoes (Statistica 6.0).

The sites for our abundance studies were 14 tomato fields at least 1 km apart across two watersheds in Yolo and Solano Counties, California, during 2000 (August 3–20) and 2001 (July 26–August 10). Because farmers rotate crops, it was possible to survey only 4 of the fields in both years. Combining data from all fields in both years increased power and allowed us to assess year-to-year variation. To determine if our sites were spatially independent, we used Mantel tests (999 iterations) to assess spatial autocorrelation of bee visitation rates (Sokal and Rohlf, 1997).

In each tomato field we determined the rate of bee visitation and identified bee visitors to species for the two primary visitors and to genus for infrequent visitors. We walked transects at the rate of 10 m/min, covering each row twice, once in each direction, and recording all bee visits to tomato flowers. In small fields, we walked transects along all rows. In larger fields, we surveyed up to four transects, each 80 m long. Each field was sampled between 830 and 1230 h on three different days, in the early, mid-, and late morning, respectively. We combined the data to obtain the average bee visitation rate for each field. We also recorded the temperature and assessed tomato flower density (a count of the number of flowers in a 0.5 m wide section of row; repeated at 10 m intervals down the length of the transect) in each field each time we measured bee abundance.

We used ArcView 3.2 and a ground-truthed classified satellite image of the region (see Kremen et al., 2004) to calculate the distance between each tomato field and the closest patch of natural habitat (chaparral, riparian, oak, or mixed-oak). We also calculated the proportion of natural habitat and agricultural habitat (orchard, row-crop, pasture) within a certain ra-

dius of each field. To choose the radius, we used the relationship between bee body size and foraging range (Greenleaf and Kremen, accepted) to predict the maximum foraging distance for *Bombus vosnesenskii* (2100 m) and *Anthophora urbana* (2700 m). To determine what factors affect bee visitation rates, we used multivariate regression with the following independent variables: (1) proportion of natural habitat within foraging distance of each farm; (2) log of distance to closest patch of natural habitat; (3) year (2000 or 2001); (4) mean temperature; and (5) mean tomato flower abundance (StataCorp, 2003; Sokal and Rohlf, 1997). In computing the regressions, we used the robust cluster option in Stata that is similar to boot-strapping and accounts for non-independence of data from the same farms tested in multiple years. We conducted two separate series of analyses for each of two dependent variables: *B. vosnesenskii* visitation rate and *A. urbana* visitation rate.

3. Results

In our pollination experiments, significantly more of the open pollinated and artificially cross-pollinated flowers developed into tomatoes than did the artificially self-pollinated and control (total exclusion) flowers (Fig. 1, $F_{3,60} = 34.84$, $P < 0.0001$). Tukey HSD post hoc tests for unequal sample size indicate highly significant differences between all pairs of groups ($P < 0.0001$) except between open pollinated vs. artificially cross-pollinated and the control vs. artificial self-pollination. Furthermore, the tomatoes in the open pollination group were significantly larger (Fig. 2) than tomatoes from the control group ($F_{3,39} = 3.64$, $P < 0.05$). In our second experiment, we found no significant differences between the two types of artificial self-pollination (with or without stigmas dipped in pollen), for either percent of flowers that developed into fruits ($t = -1.11$; d.f. = 19; $P = 0.28$) or volume ($t = -0.85$; d.f. = 19; $P = 0.41$).

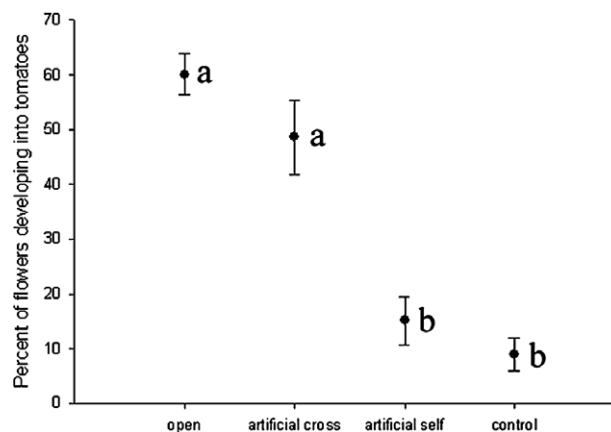


Fig. 1 – Bee pollination increases number of tomatoes produced. Means and standard error bars are shown for four experimental treatments. Open pollinated flowers were visited by bees, especially *A. urbana* and *B. vosnesenskii*; artificially pollinated flowers had insect visitors excluded and were cross- or self-pollinated by hand with the aid of a tuning fork; all visitors were excluded from control flowers.

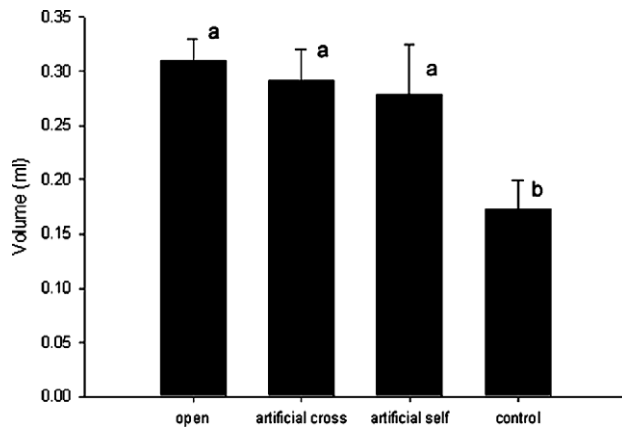


Fig. 2 – Bee pollination increases size (volume) of tomatoes produced. Means and standard error bars are shown for four experimental treatments. Open pollinated flowers were visited by bees, especially *A. urbana* and *B. vosnesenskii*; artificially pollinated flowers had insect visitors excluded and were pollinated by hand with the aid of a tuning fork; all visitors were excluded from control flowers.

In our standardized surveys of tomato fields, 34% of 2549 recorded visits were made by *B. vosnesenskii* Radoszkowski and 60% by *A. urbana* Cresson. The remaining visits were from bees in three genera: *Lasioglossum* (4%), *Halictus* (2%), and *Apis* (<1%). Similarly, *A. urbana* and *B. vosnesenskii* were common visitors in the pollination experiment.

Visitation rates of the bumble bee *B. vosnesenskii* depended on proximity to natural habitat. *B. vosnesenskii* was more abundant on fields closer to natural habitat (Fig. 3) and with more natural habitat within foraging distance (Fig. 4). The overall multiple regression with the five independent variables was highly significant and explanatory ($F_{5,13} = 17.31$; $P < 0.0001$; $R^2 = 0.82$). The only independent variables that significantly ($P < 0.05$) contributed to the model were the proportion of natural habitat within foraging distance and the log of the distance to the closest patch of natural habitat. Mantel tests showed no spatial autocorrelation in *B. vosnesenskii* visitation rates ($r = 0.04$; $P > 0.05$).

In contrast, *A. urbana* visitation rates did not depend on proximity to natural habitat (Figs. 3 and 4). The overall multiple regression with the five independent variables was not significant ($F_{5,13} = 2.01$; $P < 0.14$; $R^2 = 0.22$). This regression remained non-significant when we removed a potentially outlying data point – a site having only 11% natural habitat within foraging range but a high bee abundance ($F_{5,13} = 0.47$; $P = 0.79$; $R^2 = 0.25$). Mantel tests showed no spatial autocorrelation in *A. urbana* visitation rates ($r = -0.081$; $P > 0.05$).

4. Discussion

The majority of tomato visitors were native bees, not the introduced honey bee, which some farmers in our study had brought in for pollinating other crops. We found five native bee genera visiting tomato flowers, in sharp contrast to a much higher diversity of native bees found visiting sunflowers (16 genera; 34 species; Greenleaf and Kremen, accepted)

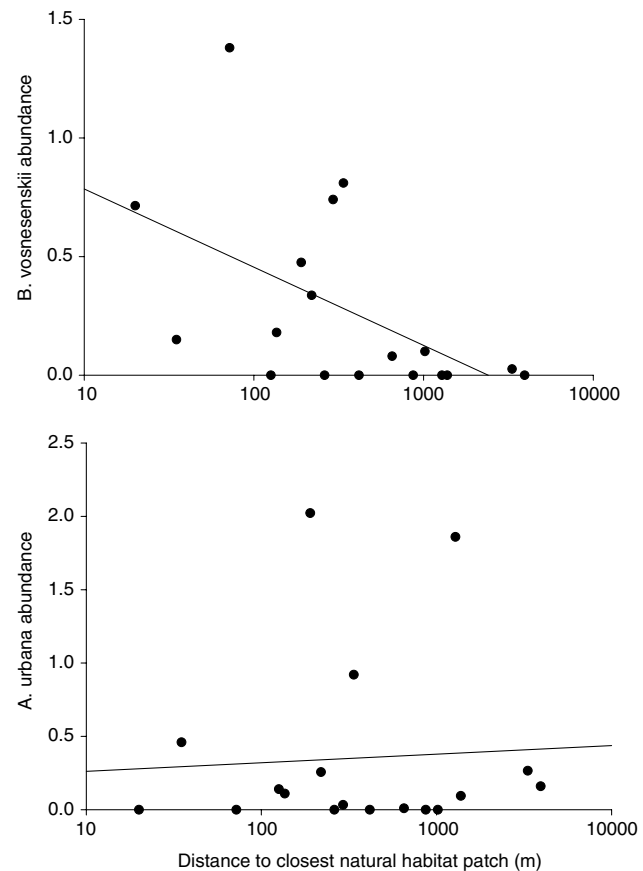


Fig. 3 – Visitation rates of *B. vosnesenskii* but not *A. urbana* are higher on fields closer to natural habitat. Each data point shows the visitation rate (mean from three days) on one field in a particular year. Distance to closest natural habitat patch (chaparral, riparian, or oak woodland) was calculated with GIS. Bee abundance was measured with standard transects on tomato fields and is reported as the number of bee visits observed along 10 m of row during 1 min.

and watermelon (39 species; Kremen et al., 2003) in the same agro-ecosystem in Yolo and Solano Counties. Like honey bees, native bee species that are unable to sonicate may not be attracted to tomato flowers because of the lack of nectar and the difficulty of extracting pollen from the poricidal anthers (Buchmann, 1983; Free, 1993; King and Buchmann, 2003).

Bee pollination substantially increased the production of field-grown SunGold tomatoes. Our experiment further suggests that cross-pollination may enhance tomato fruit set over self-pollination. The cross-pollination results are surprising because SunGold tomatoes are an F1 hybrid produced from crossing two inbred parent lines. All SunGold parents should therefore be relatively uniform genetically and cross-pollination among plants should be relatively unimportant. However, pollen-sterility, which can occur in tomatoes grown under high temperatures (Kinet and Peet, 1997; Picken, 1984), may explain the increased production in cross-pollinated flowers. Individual flowers may be differentially exposed to heat, depending on their height above ground and level of shading. Cross-pollination would increase the probability that any given flower would receive some fertile pollen. Bee-pollination

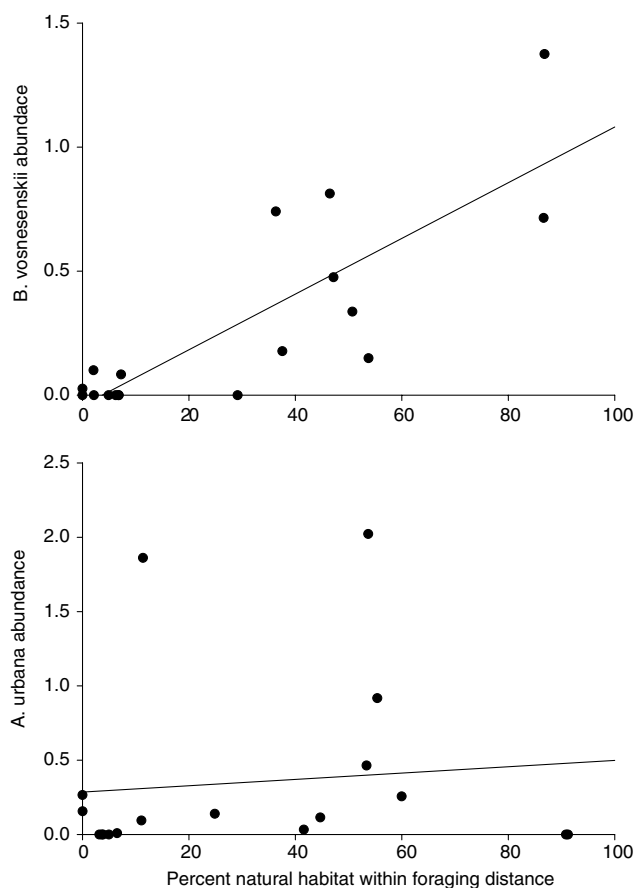


Fig. 4 – Visitation rates of *B. vosnesenskii* but not *A. urbana* are higher on fields with more natural habitat within foraging range. Natural habitat (chaparral, riparian, or oak woodland) across the landscape was measured with GIS. Bee abundance was measured with standard transects on tomato fields and is reported as the number of bee visits observed along 10 m of row during 1 min. Each data point shows the visitation rate (mean from three days) on one field in a particular year.

nated tomatoes were significantly larger than those in the total exclusion group. While artificially cross-pollinated tomatoes were larger than artificially self-pollinated tomatoes, this difference was not significant.

Our experiment showing that tomato production suffers when pollinators are excluded suggests that tomato yields across the landscape would be correlated with bee abundance. However, it is not known how SunGold tomato production is affected by sequential bee visits to the same flower; in other words, at what point do additional bee visits no longer increase production? Given that we do not know what this threshold is, it is possible that all farms in our study received sufficient pollination for maximum production.

Our finding that bee pollination has a positive effect on field-grown tomato production is most applicable to other tomato varieties that have similar flower morphology: a style that is sufficiently long to make the stigma protrude beyond the cone of anthers. Similar flower morphologies are found in many cherry tomato varieties and heirloom tomato varie-

ties (Roger Chetelat, person. commun.). Many tomato varieties grown for commercial processing, rather than consumption of fresh fruit, have probably been selected for a stigma that does not protrude beyond the cone of anthers (Free, 1993) because this morphology increases the likelihood of successful self-pollination without sonication (Rick and Dempsey, 1969). While these varieties may benefit less from bee visitation, evidence that some field-grown varieties benefit from mechanical shaking (Hanna, 1999) suggests that their production may also be enhanced by animal-mediated pollination. Regardless of how many market tomato varieties benefit from bee pollination, all tomatoes that are grown for hybrid seed production require animal-mediated or costly and time-consuming hand pollination (Free, 1993); bees providing this pollination are reported to be lacking in parts of the world including California (Bohart and Todd, 1961). Additional research is needed to determine the economic value of pollination services provided by bees to field-grown tomato.

Bee species providing services to tomato crops were affected by land management practices in different ways. The visitation rate of bumble bees pollinating tomatoes on a particular field depended on the field's proximity to natural habitat, as measured by proportion of natural habitat within foraging range and distance to closest patch of natural habitat. In contrast, none of the factors we measured explained variation in the visitation rates of *A. urbana*. These results emphasize the need to document species-specific contributions and species-specific response to land use change when studying ecosystem services (Cane, 2001; Kremen, 2005).

These differences between *B. vosnesenskii* and *A. urbana* may be explained by differences in their natural histories. *B. vosnesenskii* nests in abandoned rodent nests (Heinrich, 1979), which may be more plentiful in natural habitats than on farms, where rodents are often molested or killed. We suspect that many of the bumble bees we observed on tomatoes foraged from nests located in natural habitat. We supported our hypothesis that these bumble bees can nest in one habitat but forage in another by raising *B. vosnesenskii*, placing them in artificial nest boxes in natural habitats, marking individuals, and searching for marked bees. At two sites, we did find marked bees foraging in nearby agricultural fields (S. Greenleaf, unpublished data). Thus, the observed relationship between *B. vosnesenskii* visitation rates and natural habitat may result from the bees nesting in wild habitats and foraging on crops.

In contrast to *B. vosnesenskii*, *A. urbana* digs its own nests in the soil (Torchio and Trostle, 1986). We expect that *A. urbana* may nest in the farm fields because bees with similar ground-nesting habits, including *Halictus ligatus*, *H. tripartitus*, *Lasioglossum*, *Melissodes*, and *Svastra obliqua expurgata*, have been recorded nesting on the borders of farm fields in our study system (Kim, 2004). Furthermore, *A. urbana* has been observed nesting in three disparate locations: (1) an embankment of dry, hard-packed clay in a grazed area in the foothills of the inner Coast Range Mountains near Fresno, CA; (2) a vertical embankment of sandy clay/loam in natural habitat near Delta, UT; and (3) artificial silt/loam soil blocks in a greenhouse (Torchio and Trostle, 1986). These nesting observations suggest that *A. urbana* may nest on farms, particularly on banks along drainage ditches. Better understanding the

nesting requirements of *A. urbana* could result in the development of farm management practices to enhance natural nest sites or create artificial ones.

In addition to their different nest requirements, *A. urbana* and *B. vosnesenskii* differ in their floral resource requirements. *B. vosnesenskii* must have floral resources from the time that queens found colonies, in January in our study area, until colonies senesce, in August and September. Floral resources may not be available on many farms very early in the spring, but wild plants do begin blooming in northern California in January; thus, because of the floral resources provided in early spring, natural habitat may be essential for *B. vosnesenskii*. In contrast, the flight period of *A. urbana* is limited to summer, when many crop plants are blooming. *A. urbana* is a generalist bee; we have observed it foraging on other crops, such as sunflower, in our study area (Greenleaf and Kremen, accepted). However, some crops in northern California, such as corn, are unlikely to provide any floral resources while other crops, such as almond, do not bloom when *A. urbana* is flying. If crop rotation occurs on a sufficiently large spatial scale, then *A. urbana* populations may not persist because there may be insufficient floral resources within foraging range in some years.

If pollination services from *B. vosnesenskii* are to be maintained, habitat must be conserved at an appropriate scale. The natural habitat must be close enough to fields so that *B. vosnesenskii* can move between natural and agricultural habitats. In our study, fields that had a high *B. vosnesenskii* visitation rate were within 300 m of a patch of natural habitat and also had at least 40% natural habitat in a circle within a 2100 m radius surrounding the farm. Natural habitats at greater distances may support source populations.

Wild bee populations fluctuate widely from year-to-year, with fourfold variation documented for some euglossine bee species (Roubik, 2001). Thus, to ensure reliably adequate pollination from non-domesticated species, maintaining a community of bees, rather than just one species, is necessary (Kremen et al., 2002). Our results show how two pollinators with disparate nesting requirements are affected differently by maintenance of natural habitat. To maintain agricultural pollination services for the future, attention must be given to a variety of strategies including both native ecosystem conservation and on-farm management (e.g. providing nest sites) for wild and managed native bees (Bosch and Kemp, 2001). Furthermore, because of the wide variety of bee natural history strategies and the corresponding differences in response to anthropogenic change documented by this and other studies (Samejima et al., 2004), species-specific requirements within the greater bee community must be understood and evaluated to design conservation plans that maintain pollination function in natural habitats.

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