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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.

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 depauparate 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