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Pollination services for apple are dependent on diverse wild bee communities

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ABSTRACT

Understanding the importance of biodiversity in applied settings is a central theme for ecologists. Pollination is an essential ecosystem service, which may rely on biodiversity for effectiveness and stability. Empirical examples which link functional outcomes of increased biodiversity to pollination services are rare. To investigate the importance of wild and managed pollinator communities to apple production, we assessed the effect of wild and managed bee abundance and diversity on pollen limitation and seed set on commercial farms in New York State. Seed set increased and pollen limitation decreased with increasing wild bee species richness, functional group diversity (based on nesting, sociality, and size traits), and abundance, but not with honey bee abundance. Functional group diversity explained more variation in apple seed set than species richness. Our findings demonstrate the important role of functional complementarity of wild bees, defined here as functional group diversity, to crop pollination even in the presence of large populations of managed honey bees. Therefore, our results suggest that management of diverse pollinator communities may decrease reliance on managed honey bees for pollination services and enhance crop yields.

1. Introduction

The importance of pollinators to global agricultural stability is well documented (Klein et al., 2007; Garibaldi et al., 2013). Worldwide an estimated 35% of crop production, including many of our most nutritious foods, benefit from insect pollination (Klein et al., 2007; Aizen et al., 2008). For many crops, the most widely used pollinator is the European honey bee (*Apis mellifera* L.). However, honey bee colonies in North America have suffered sharp declines in recent decades (Holden, 2006; Potts et al., 2009, 2010). The necessity of relying so heavily on one species of managed pollinators is now being questioned (Garibaldi et al., 2013). Wild pollinator species can, especially in heterogeneous landscapes, provide much of the pollination service needed for crop production and may enhance fruit quality regardless of honey bee visitation (Garibaldi et al., 2011, 2013).

Apple (*Malus domestica* Borkh.) is an economically important crop in the United States, with New York State being the second largest production region in the country (USDA NASS 2011). Typically apple cultivars are self-incompatible and successful apple pollination requires cross-pollination from a "pollinizer" variety (McGregor, 1976; Free, 1993; Garratt et al., 2014a). Although honey bees are generally viewed as essential pollinators in apple orchards, apple blossoms are also visited by a diverse community of wild pollinators (Sheffield et al., 2013; Garratt et al., 2014b; Park et al., 2015; Russo et al., 2015). Because honey bees are supplemented at increasing cost and effort to apple growers (http://www.ars.usda.gov), apple provides an important test case for the efficacy of wild bee pollination for sustainable crop production. Other studies have linked pollen deficits to decreases in apple fruit and seed set (Garratt et al., 2014b), and calculate that pollinators in UK apple orchards contribute £36.7 million per annum to apple production (Garratt et al., 2014a). Recent studies in apple orchards found that wild pollinators alone were able to achieve comparable fruit set levels to orchards with managed honey bees (Mallinger and Gratton, 2014) and that functional diversity can improve pollination services in Canadian orchards (Martins et al., 2015). However, more evidence linking wild pollinator biodiversity and abundance to harvest level production data (i.e., seed set) in apple orchards, with direct consequences for fruit quality and market value (Garratt et al., 2014b), is essential.

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There is a growing consensus that biodiversity enhances ecosystem function in general (Hooper et al., 2005) and the delivery of the ecosystem service of pollination in particular (Kremen et al., 2002; Klein et al., 2003; Hoehn et al., 2008). Three main hypotheses have been proposed to explain this positive diversity-pollination services relationship: (1) selection effects, where diverse communities are more likely to include highly effective species (Loreau and Hector, 2001); (2) functional facilitation, under which some community members may enhance effectiveness of other members (Cardinale et al., 2002); and (3) functional complementarity where, through niche partitioning in space and time, diverse pollinator communities provide more pollination services. Niche complementarity (Loreau and Hector, 2001) is the most commonly invoked mechanism for the increase of pollination services in species rich communities (Fontaine et al., 2006; Hoehn et al., 2008; Tylianakis et al., 2008). However, studies which quantify the relationship between crop production and pollinator species richness and functional group diversity are still quite rare (Hoehn et al., 2008; Mallinger and Gratton, 2014; Martins et al., 2015).

In this study we investigate the effects of pollinator abundance and diversity on apple production at 17 farms in New York State. On each farm we quantified wild and managed bee visitors to apple blossoms along with apple seed set. At a subset of 12 farms we experimentally tested for pollination limitation. We asked the following questions: (1) How do wild bee species richness and abundance impact apple pollination? (2) How does honey bee abundance impact production? (3) Does niche complementarity, as measured by functional group diversity, increase pollination in apple?

2. Materials and methods

2.1. Study area and site selection

This study was conducted on 17 apple orchards in three counties (Wayne, Tompkins, and Seneca) in western New York State. We focused our study on two of the most common apple varieties for this region: McIntosh and Golden Delicious. On the few farms which did not grow Golden Delicious apples, we substituted with the Golden Delicious cross varieties Jonagold or Crispin. New York State is the second largest apple producing state in the country, with Wayne County being New York's top producing county. Our study farms included orchards which vary widely in size (from 0.05 to 182 ha), management intensity (integrated fruit management to heavy use of synthetic pesticides), and proportion of surrounding natural area in a 2 km radius (from 19% semi-natural habitat to 66% semi-natural habitat). In this study, we broadly defined 'natural' habitat as land that was minimally managed and not cultivated for arable crops. Specifically, natural habitat included forests, wooded and herbaceous wetlands, shrublands and grasslands. These farms represent the variety of apple orchards typically found in New York State.

2.2. Wild and managed bee abundance and diversity

Collections of all bee visitors to apple blossoms were made during the apple bloom period (May 6–17, 2013) at all 17 farms. Bees were net collected visiting apple blossoms throughout the orchard along two 15-min, standardized, 100 m transects per farm, placed within 150 m of edge in rows of full bloom. Collections were made on sunny days between 10:00 and 15:30, when temperatures exceeded 15 °C. Each farm was surveyed twice during the bloom. Apple bloom was assessed at the farm level by categorizing bloom as early, peak, or past, as well as at the individual transect level by counting the number of open blossoms per cluster on three trees per transect. To ensure independence among farms, the minimum distance between sites was 1.9 km, which is greater than the typical foraging distance of most bees (Zurbuchen et al., 2010). All bees were identified to the species level using published keys and comparison to voucher material in the Cornell University Insect Collection (http://cuic.entomology.cornell.edu/). All voucher material is deposited in the Cornell University Insect Collection.

2.3. Pollen limitation and seed set experiments

To study the impact of wild and managed bee communities on apple yield we used two methods: pollen supplementation experiments and seed set measurements. Pollen supplementation experiments test for pollen limitation by comparing the fruit or seed set of plants given supplemental pollen to the fruit/seed set of control plants which receive ambient pollen loads (Knight et al., 2006). Comparing pollen limitation values allows for a measure of pollination services which control for variation within and between sites. On a subset of 12 of our 17 study orchards we set up a pollen supplementation experiment. At each farm we selected twelve experimental trees, six each of McIntosh and Golden Delicious varieties. Before the apple bloom period (early May 2013), we chose two branches of approximately equal diameter and location within the tree to reduce any potential horticultural effects on seed set. We returned to each farm during peak apple bloom (May 13–23, 2013) and first removed all nonviable (damaged, unopened, or past receptivity) blossoms. Branches were then randomly assigned to either an "open" or "hand" pollination treatment. The open-pollination treatment received natural pollination from managed and wild bees. The hand-pollination treatment also received natural pollination, but all blossoms were hand-supplemented with additional Red Delicious pollen (Firman Pollen Company, Yakima, Washington, USA) applied directly to the stigma.

To expand our apple yield experiments to include all 17 farms surveyed for bees we also set up a more simple measurement of apple pollination without pollen supplementation controls. We selected a set of six Golden Delicious or closely related (Jonagold or Crispin varieties) trees per farm. At peak apple bloom we chose one branch of similar diameter and location per tree and counted all blossoms along a 1 m segment of each branch.

For both experiments we recorded data on early season (pre thinning) fruit set when apple fruitlets were 5–10 mm and on mature fruit from experimental branches prior to fall harvest. For all mature fruit we counted all developed seeds per fruit. In our final analysis we used number of seeds per fruit as our measure of apple pollination. Seeds per fruit is correlated with apple weight, and is a more direct measure of pollination efficacy (Hoehn et al., 2008).

2.4. Pollinator behavior functional grouping

To understand the mechanisms driving potential effects of bee species richness we assigned all wild bee species collected from apple into functional guilds, based on differences in nesting substrate, sociality and body size. We chose nesting and sociality traits as a way to investigate the functional outcome (pollination services) of niche partitioning and complementarity (i.e., Ground nesting bees are solitary and often more host-plant specific than cavity nesters such as bumblebees.). Nest classes were assigned categorically as ground, cavity/hive, or wood/stem. Species were classified as solitary, communal, cleptoparasitic, or eusocial. Nest and sociality classes were based on relevant literature (reviewed in (Michener, 2000) and extrapolations based on phylogenetic relationships (Danforth et al., 2003; Gibbs et al., 2012). Body size was used as a proxy for foraging range, and classifications of small,