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Flower handling behavior and abundance determine the relative contribution of pollinators to seed set in apple orchards

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ABSTRACT

A growing body of evidence suggests that wild bees play an important role in agricultural pollination. It is very difficult, however, to accurately quantify the contribution of wild bees relative to honeybees in most crop systems. We quantified the relative contribution of honeybees and wild bees to the pollination of an economically important, insect-pollinated crop (apple). We use an empirical dataset to identify which of three functional traits (body size, pollen load purity, and flower handling behavior) contribute significantly to seed set. We find that flower handling behavior and abundance were the only functional traits that significantly predict seed set. When we take into account flower handling behavior and abundance, wild bees contributed significantly more to seed set than honeybees in the apple orchards we surveyed. Our findings suggest that land managers may benefit from focusing on supporting communities of wild bees, rather than investing in honeybee hive rental.

1. Introduction

Pollination services provided by flower-visiting insects, especially bees, are critical to global food security (Klein et al., 2007). Moreover, a healthy human diet comprises fruits, vegetables, and oils that rely on bee pollination for their production (e.g. Eilers et al., 2011; Kant et al., 1993). While modern agriculture has traditionally used managed honeybees for pollination, global production of pollinator-dependent crops is now out-pacing world-wide production of honeybee hives (Aizen and Harder, 2009). The threat of "pollinator-deficits" is further compounded by recent honeybee declines (vanEngelsdorp and Meixner, 2010), largely due to heavy pathogen loads and exposure to pesticides (Goulson et al., 2015). Providing sustainable pollination services into the future, therefore, requires a diversification of pollination strategies, including leveraging the services provided by native and wild pollinator species.

Wild bees contribute substantially to insect-dependent crop production (Garibaldi et al., 2013; Winfree et al., 2008), particularly when wild bee communities are diverse and abundant (e.g. in strawberry (Connelly et al., 2015), watermelon (Kremen et al., 2002; Winfree et al., 2011, 2007), blueberry (Isaacs and Kirk, 2010; Javorek et al., 2002; Tuell et al., 2009), and apple (Blitzer et al., 2016; Park et al., 2015; Russo et al., 2015)). In a global study of 30 crops, wild bees provided superior pollination services (i.e. fruit set) compared to honeybees, regardless of the number of honeybees present (Garibaldi et al., 2013). Divergence in functional traits between honeybees and wild bees may explain this discrepancy in provisioned pollination service. Whereas the honeybee is a single species, wild bees comprise a diverse assemblage of species with an array of functional traits that may influence pollination services. For example, the way that bees carry pollen, their host specificity, their body size, and how they handle flowers may all play a role in pollen deposition and ultimately fruit set production and quality (Thomson and Goodell, 2001; Larsson, 2005; Martins et al., 2015; Park et al., 2015). While a positive relationship between wild bee visitation and crop pollination service is now well-described, less is known about specific functional traits of wild bee communities that afford higher quality pollination.

The relative contribution of wild bees to pollination can be estimated as the summed product of per-visit effectiveness of all species and their relative abundance (Olsen, 1996). Using this measure, Park et al. (2015) found two groups of wild pollinators to contribute less to apple pollination than honeybees due to their lower abundances. These bee groups, however, represented a small portion of the entire wild bee community. Directly comparing the pollination services of honeybees to those of the entire wild bee community is a difficult task in crop systems, like apple, which have diverse bee assemblages. Wild bees

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comprise many species, making it logistically difficult to experimentally measure the per-visit effectiveness (e.g. pollen deposition, fruit set) of every species.

Our study investigates functional traits that determine the quality of pollination services provided by wild bees for apple, *Malus domestica*. We first identify bee functional traits that predict seed set in apple orchards. We then use these functional traits as a proxy for per-visit effectiveness to estimate wild bee pollination services relative to that of honeybees at a regional scale within NY. Thus, our measure of pollinator contribution is the summed product of functional traits that predict seed set for each bee species multiplied by their relative abundance. Apple is a high-value, pollinator-dependent crop (Free, 1964; Garratt et al., 2014a) and an ideal system in which to explore the role of functional traits in crop pollination. Wild bees visiting apple blossoms are abundant and diverse (Gardner and Ascher, 2006; Sheffield et al., 2013; Russo et al., 2015; Kammerer et al., 2015), and apple fruit and seed set increase directly with wild bee abundance but not with honeybee abundance; (Martins et al., 2015; Mallinger and Gratton, 2015; Joshi et al., 2015; Blitzer et al., 2016). Indeed functional diversity is a strong predictor of pollination service (i.e. fruit and seed set) in apple orchards (Martins et al., 2015; Mallinger and Gratton, 2015; Blitzer et al., 2016). While these studies document benefits of functional diversity for apple pollination, they included a variety of traits, including some that were not likely to have a direct effect on pollination, such as sociality. Our study identifies specific functional traits that may directly affect pollinator effectiveness and have not been accounted for together in previous studies: flower handling, body size, and the composition of pollen carried by different bee species.

In this manuscript, we combine data from several studies. We identify functional traits that predict seed set, a direct correlate to fruit quality and value (Garratt et al., 2014b), and then quantify the relative pollinator contribution of bee species detected in NY apple orchards. We compare contributions of wild bees relative to managed honeybees based on the functional traits we identified as significant predictors of seed set. Our results indicate that wild bees, especially ground-nesting bees, provide the bulk of pollination services in the majority of surveyed orchards. Thus, we find that wild bees are not only a good insurance policy against honeybee declines, but also a major contributor to commercial NY apple production — both because of their abundance in NY apple orchards and their high propensity to make direct contact with a flower's anthers and stigma. Moreover, our results show that wild bees contribute significantly more to seed set relative to honeybees on average across the apple orchards we surveyed.

2. Methods

To quantitatively compare pollination services of wild bees to that of honeybees in NY apple orchards, we calculated the summed contribution to seed set of the entire wild bee community relative to that of the honeybee. There are two fundamental components to estimating the contribution of a pollinator or group of pollinators to seed set: (1) *abundance* (visitation rate) and (2) *per-visit effectiveness* (Ne'eman et al., 2010; Olsen, 1996). Abundance is relatively easy to measure even when the pollinator fauna is as diverse as that in apples. Measuring per-visit effectiveness of each species, however, poses significant challenges when pollinator diversity is high. Per-visit pollinator effectiveness is often quantified as the number of pollen grains deposited on a previously unvisited flower in a single visit (Ne'eman et al., 2010Park et al., 2015). This can be obtained by attaching a flower to a stick and "interviewing" free-foraging bees. Measures of per-visit pollen deposition have been obtained for a small fraction of the bee diversity in apple orchards. Thomson and Goodell (2001) compared bumblebees (*Bombus*) to honeybees using this method, and Park et al. (2015) compared bumblebees, honeybees, and members of the *Andrena* subgenus *Melandrena*. The interview method can only yield sufficient sample sizes for common species slow enough to place interview flowers in their foraging path.

We first identified functional traits of bees that directly influence per-visit effectiveness and could be applied to all species detected to date in New York apple orchards. Specifically, we used model selection to identify functional traits that significantly predict seed set. These significant functional traits were then used to quantify the summed pollination contribution of wild bees and honeybees. This contribution was calculated as per-visit effectiveness multiplied by abundance for each species; we used functional traits as a proxy for per-visit effectiveness and then multiplied these trait values by the abundance of the bees. Rather than correlating abundance of wild bees and honeybees to seed set (see Mallinger and Gratton 2015; Martins et al., 2015; Blitzer et al., 2016), we directly quantified their relative contribution to seed set and tested whether this contribution was significantly different.

2.1. Abundance

We used a subset of the abundance data collated by Russo et al. (2015) for the visitation rate component of the pollinator contribution equation (Ne eman et al., 2010Ne'eman et al., 2010). Bees were net collected in apple orchards during bloom at 28 orchards from 2008 to 2013 (see Russo et al., 2015 for a full description). Over 100 wild bee species were detected in these orchards, but a relatively small number of species made up the vast majority of the abundance. To compare relative pollinator contributions to seed set, we exclusively used abundance data from 2013 bee surveys of orchards (53 species, 99 15-min transects) where seed set monitoring occurred that same year (Blitzer et al., 2016). Once we identified functional traits that contributed measurably to seed set, we compared relative pollinator contribution across orchards (Figs. 1 and 2), using abundance data from 15 min standardized transects (Russo et al., 2015) surveyed in 2011–2013 (78 bee species, 363 transects) because sampling was most consistent during these years. Thus, all abundance data used in this study are from 15-min standardized net collections in NY apple orchards.

Species were assigned to functional groups based on close taxonomic relatedness and similar size and behavior patterns. These functional group classifications allowed us to include the entire wild bee community in our investigation because we could measure functional traits on a representative species from each functional group, and then assume these functional traits were similar across the group. Many bee species were represented by a small number of individuals; ignoring these rare species would have underestimated the bee community's contribution to pollination. We therefore assigned rare species to functional groups that were defined by closely related, abundant species, on which we are able to measure functional traits in a replicated fashion. When placed into functional groups, 14 species represented 99% of total functional group diversity (see Table S1 for functional group classification). Below, we describe these measurable functional traits in more detail. In the analyses reported in the main body of this paper, we use these functional group classifications. To ensure that we have not biased our findings by doing so, we repeat all of our analyses, in the supplemental materials, with a more conservative model where we only include species on which we directly measured functional traits.

2.2. Behavior

Bees that visit flowers specifically for nectar can bypass the reproductive parts of the flower (anthers and stigma) by nectar robbing (Inouye, 1983). In open flowers, such as apple and other Rosaceae, floral visitors have been observed to visit flowers in two different ways. "Side-working" bees are those that land on the petals and probe the base of the anther column without contacting the anthers or stigma (http://tinyurl.com/grvavv3), whereas "top-working" bees actively gather pollen and contact both anthers and stigma (http://tinyurl.com/