# THE ROLE OF NATIVE BEES ON ORGANIC FARMS IN HUMBOLDT COUNTY, CALIFORNIA.

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# ABSTRACT

## THE ROLE OF NATIVE BEES ON ORGANIC FARMS IN HUMBOLDT COUNTY, CALIFORNIA.

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A growing body of literature supports the position that both natural habitat surrounding farms and high flowering crop diversity helps insure farms against pollination shortfalls and an overreliance on European honeybees. I assessed the importance of native pollinators for the ostensibly bee-rich farm habitat of Humboldt County, California (USA). I also evaluated the management potential of an indigenous bee, *Osmia lignaria*, for orchard crop pollination. I found native bees were less diverse and abundant than expected based on predictions from surveys in other regions on similar crops. The importance of native bees compared to honeybees was especially low on spring crops, and became a little more balanced on summer crops. However, the only two crops where native bees were the main pollinators, squash and tomato, were visited almost exclusively by a single species of bee, and therefore still exhibited an extremely low diversity of pollinators. Studies of *O. lignaria* showed promising management potential on coastal farms, where their flight season overlapped strongly with orchard bloom and females regularly collected apple pollen. Overall, my study demonstrates that crop pollination may still depend disproportionately on the non-native honeybee, even in areas with high semi-natural habitat in close proximity to farms. Furthermore, the variable importance of native bees across crops and time of season demonstrates that full-season multi-crop studies should be conducted when assessing the role of native bee communities within a region. To safeguard against potential declines in honeybee populations, nesting structures should be deployed on farms to manage local populations of native bee species.

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# INTRODUCTION

Estimates show that approximately 90% of flowering plants depend on an animal vector for pollination (Kearns et al. 1998), with up to 35% of agricultural production relying on the pollination services of bees (Hymenoptera: Anthophila) for successful crop harvests (Klein et al. 2007). Within agricultural areas, these services are largely provided by managed colonies of the European honeybee (*Apis mellifera*; Berenbaum et al. 2007). This disproportionate reliance on a single species of pollinator poses a risk to crop yield as honeybee colonies continue to decline due to colony collapse disorder (Stokstad 2007), varroa mite infestation (Watanabe 1994) and other species-specific threats (Berenbaum et al. 2007). These threats to honeybees and concerns about a global decline in other pollinators (Buchmann and Nabhan 1997, Kearns et al. 1998, Biesmeijer et al. 2006) have sparked renewed interest in the role native bees play in agricultural settings. Many recent studies focus on understanding the population and community dynamics of native bees relative to landscape context characteristics such as proximity to natural habitat (Williams and Kremen 2007, Kennedy et al. 2013), determining the current contributions of native bees to pollination services (Winfree et al. 2007b, Garibaldi et al. 2013), and assessing the potential management possibilities of native pollinators (Torchio 1985, Artz et al. 2013).

There are over 16,000 described bee species(Michener 2000), many of which contribute to the pollination of agricultural crops (Klein et al. 2007). Wild bees are known to be significant pollinators of many important crops such as pumpkin (Esther Julier and Roulston 2009), watermelon (Kremen et al. 2002, 2004), sunflower (Greenleaf and Kremen 2006a), and apples (Torchio 1985, Bosch and Kemp 2002). Oftentimes, these native pollinators are more effective pollinators than honeybees (e.g., Vicens & Bosch 2000, Winfree *et al.* 2007a), transferring and depositing more pollen per visit and/or foraging over a wider range of weather conditions. Wild bees have been shown to provide the majority of flower visits in some systems (Winfree et al. 2007c) and afford sufficient crop pollination (Kremen et al. 2002, Winfree et al. 2007b). However, our knowledge of bee communities and management options is mostly limited to a few landscape types and crop cultivars; to date, many studies on native bee pollination services have been conducted in agriculture-dominated landscapes such as California’s central valley (e.g. Kremen et al. 2004, Winfree and Kremen 2009, Williams et al. 2011), or focus on a single crop within a region and are further limited by sampling during only one portion of the season. While relevant for ecological research and local farmers, studies that target a single crop within a single region are of little practical import for small-scale farmers who may be growing many crops across the season or growing in areas far from the major agricultural hubs. Many small farms are seemingly high quality bee habitat with high on-farm crop diversity and a high proportion of natural vegetation in the surrounding landscape, factors shown to be correlated with bee abundance and diversity (Ricketts 2004, Kennedy et al. 2013). Farmers running small farms may be unable to improve native pollinator habitat through the use of hedgerows or other on-farm improvements, rendering many of the management recommendations and conclusions of the primary literature impractical (Winfree 2010). While the habitat quality of these farms suggests they are well insured against pollination shortfalls, many small-scale farmers still rent honeybee colonies and are interested in improving pollinator habitat. As such, studies should be conducted across a wide range of crops, seasons, and regions in order to improve the information available to small-scale farmers.

Therefore, I set out to determine the role native bees play in local agriculture on the diverse small farms of Humboldt County, CA (see *Study Region*, below). Given the abundance of natural habitat surrounding Humboldt County farms, the diversity of crops grown on the farms, and the abundance of weedy flowering plants adjacent to crops, I expected to find correspondingly high bee abundance and diversity on crops. By determining the importance of native bees to pollination on a variety of crops across the growing season and evaluating the local management feasibility of an indigenous pollinator, *Osmia lignaria*, I tested the assumption that a diverse set of native bees pollinate Humboldt County crops and move towards a greater understanding of the role of pollinators in agricultural settings where natural habitat is abundant and crop diversity is high. This research is a necessary first step to inform local Humboldt County growers on the status of native pollination services, and can serve as a step in amassing crop pollination studies across a wide range of farm scales, seasons, and regions.

Currently, one of the most promising alternative pollinators to honeybees is the blue orchard bee, *Osmia lignaria* (Torchio 1985, Vicens and Bosch 2000, Bosch and Kemp

2002). *Osmia lignaria* can be a more efficient pollinator of certain crops, is active at colder temperatures, works synergistically with honeybees, and can be effectively managed in artificial nesting structures (Bosch and Kemp 2002, Brittain et al. 2013). The species can be managed by providing wooden blocks with drilled holes to simulate natural nesting substrate. The use of these blocks can bolster local populations and enhance pollination of orchard crops (Bosch and Kemp 2002). While there have been many studies of *O. lignaria* on orchards in Utah (e.g. (Torchio 1985, Sgolastra et al. 2011) and nascent investigations on *O. lignaria* in California almond orchards (Bosch et al. 2000, Artz et al. 2013), little is known of the feasibility of *O. lignaria* management in other locations. In particular, it is unknown if Humboldt County's populations of *O. lignaria* have an overlapping phenology with the timing of local orchard bloom and frequently visit orchard flowers versus non-crop flowers. To track phenological overlap and pollen preferences, studies have utilized the linear nesting habit of *O. lignaria* to collect its pollen provisions throughout the nesting season. The relative proportions of pollen species in provisions can serve as a proxy measure of *O. lignaria's* fidelity for orchard flowers and therefore the species' ability to successfully pollinate orchard crops (Kraemer and Favi 2005, Williams and Kremen 2007). Overlapping phenology between *O. lignaria* and orchard flowers, colonization of nesting blocks, and collection of crop pollen would suggest promising management potential. While this species is a seemingly advantageous native pollinator, landowners may be hesitant to rear *O. lignaria* until research demonstrates favorable management potential in their region.

To document the current status of native pollination services on Humboldt County farms I (i) estimated the importance of local bee species by determining their visit rates and abundance on crop flowers and (ii) determined if *O. lignaria* is a feasible management option for local growers by investigating phenological overlap, nest colonization rates, and pollen preferences.  These measures will set the ground work for identifying key knowledge gaps in the understanding of local crop pollination for future study, and allow growers to begin to make informed decisions regarding the management of local pollination services.

# METHODS

## Study Region

The landscape of the study region, Northern Humboldt County, can be broadly characterized as a mix of closed canopy forest and agricultural land. Most of the agricultural land is devoted to grazing, but a large number of polycultural fruit and vegetable farms are also present. The typical Humboldt County crop farm is less than 4 hectares, grows 10+ crops, sells to the local farmer's markets, is situated in a river valley, and is located adjacent to US Forest Service land. Stroll's Locavore Index[1], which rates states based on number of farmer's markets, Community Supported Agriculture programs, and local food distribution hubs per capita, ranks Humboldt County far above California as a whole (7.67 versus 1.40, respectively), and second to only Vermont (16.94, all other state values <7.00). The characteristics measured in the Stroll's Locavore Index place the study region in stark contrast with larger commercial agriculture regions, such as California's Central Valley, where large, intensively managed, monocultural farms typically sell produce to wholesale distributors, rather than local markets.

## Spring Site & Crop Selection

I conducted point-count surveys to estimate the relative abundance of bee species on orchard crops, giving me a proxy measure of their local importance to crop pollination. Six farms were chosen for point-count surveys of spring orchard crops (Table 1). Orchard sizes ranges from small (0.2-2 hectare) to medium (2-4 hectare) orchards. Orchard species diversity varies from farms growing a few cultivars of a single species, to farms growing several cultivars of several species. The main crops include apples, pears, pluots and peaches, with several farms having trees of other fruits including cherry, plum, and nuts. All farms have at least 0.2 hectares of orchard, are certified organic, and are buffered from the next nearest site by at least 1.0 km. Farm locations fall into two geographic groups, coastal and inland. Coastal farms (n=3) are located within 15 km of the coast near Blue Lake and Arcata, CA, and inland farms (n=3) are located 40-50 km from the coast along California Highway 96 in Willow Creek, Hoopa, and Orleans, CA. On coastal farms, I observed apple (*Malus domestica*) crops and on inland farms, the focal crop was pear (*Pyrus communis*). Hereafter, pear and apple are referred to as inland and coastal crops, respectively.

Pear and apple were chosen since they are economically important for local farms, are good pollen sources for *O. lignaria* (Bosch and Kemp 2002), and have a generalist floral morphology which likely attracts a large range of early-season pollinators (Free 1993). The morphological similarity of pear and apple flowers allowed me to confidently attribute any differences in floral visitors to farm location rather than morphological differences between crop flowers. However, most of the apple cultivars in my study have

1. http://www.strollingoftheheifers.com/wp-content/uploads/2013/04/Locavore-Index-2013-data.pdf

erect stamens in comparison to the more spreading stamens of pear cultivars, which can cause differences of bee foraging behavior (Free 1993, Thomson and Goodell 2001).

## Spring Pollinator Abundance

Pollinator abundance surveys occurred on each farm every 3-7 days between 0900 and 1700 throughout the orchard flowering season, weather permitting. The order in which farms were visited was randomized each survey day to minimize effects of time of day on visit rate across farms. Twelve branches used for the point-count observations were haphazardly selected. I selected branches where the whole branch was visible, that were located approximately halfway up the tree, and had recently opened blooms. Observers spent 5 minutes recording all visitors foraging on flowers within a view area of approximately $1m^2$ on each branch, for a total survey duration of 60 minutes per farm per day. The number of flowers within the viewshed was also counted, allowing me to calculate per flower visit rate. Pollinators were identified as *Apis mellifera*, *Bombus* sp., *Andrena* sp., *Osmia lignaria*, flies, other bees, and “other” (including wasps, lepidopterans, beetles, etc). Foraging behavior (pollen, nectar, mixed, or side foraging) was recorded where applicable, since differences in behavior can reflect differences in pollination efficiency (Thomson and Goodell 2001). When a visitor was collecting a single resource, either pollen or nectar, it was classified accordingly. If a pollinator collected both pollen and nectar, it was classified as a mixed visit. Lastly, if a visitor collected nectar but failed to make contact with either the anthers or pistils, the visit was classified as a side visit.

## *O. lignaria* Management – Phenology & Nesting

On the same days as pollinator abundance surveys, I estimated crop floral abundance and tracked crop bloom. Twelve pear and apple trees were tagged on each farm for monitoring flowering phenology. Trees were selected to be proportional to the number of crop cultivars available on site, when possible. Approximately 0.125 to 0.25 of the flowers on each tree were counted and then a total per tree flower count was estimated from that fraction (e.g., 100 flowers on 0.125 of the tree totals ~800 flowers). This method is susceptible to observer bias, but several initial tests where observers counted the same tree and compared results showed little variation in counts.

I placed three nest blocks on each farm to monitor *O. lignaria* nesting activity. Nest blocks consisted of 105 holes drilled into wooden blocks, 30.48×13.97×13.97 cm, and lined with removable paper straws (Appendix A; Aardvark Paper Drinking Straws[1]). Blocks were mounted on fences, poles, or trees, approximately 1.5 m above the ground on the edges of the orchard, on the North, East, and West ends, each block facing Southeast. Nest blocks were installed in late February, prior to the crop flowering season, and the expected *O. lignaria* flight season.  Blocks were monitored every 5-7 days throughout the flight season by shining a penlight into each nesting hole. Nesting straws

1. http://www.aardvarkstraws.com/

were recorded as ‘initiated’ if a mud plug or a pollen mass was observed in the tube and ‘completed’ if the tube had an exterior plug closing off the straw. All intermediate stages were classified as ‘partial’. For analysis, tubes were given a score of 3, 2, or 1, for complete, partial, or initiated, respectively. Adding up the number of completed, initiated, or partial tubes calculated a single-day cumulative score and then the score up to that day was subtracted off, yielding a score of activity since the previous census. Total full-season score was calculated for both inland and coastal sites and used to calculate proportion of activity for a given interval. This approach allowed me to track nest provisioning during the season, rather than simply counting completed tubes or counting cocoons at the end of the season.

### *O. lignaria* Management – Pollen Samples

One to two small samples of pollen were collected throughout the nesting season from completed tubes to determine pollen proportions in provisions. I made a small incision in the nesting tube to remove a pollen sample (Williams and Kremen 2007). Pollen samples were homogenized by “double dipping” in the pollen mass to make the sample representative of the whole provision. The incision was re-sealed, and the tube returned to the nesting block to mature. This method is non-deleterious to bee larvae (Neal Williams, personal communication).

Pollen samples were acetolyzed to aid in pollen identification (Erdtman 1969, Neal Williams, unpublished protocol). One hundred grains of pollen were counted from each slide by moving in horizontal transects and counting the first 100 grains viewed. To minimize bias, all pollen grains within the field of view were counted, resulting in some counts over 100 grains. Pollen was identified to the lowest taxonomic level possible utilizing a reference collection of pollen obtained directly from flowers. For each sample, proportions of the identified pollen taxa were calculated. Since I collected pollen only from completed tubes, the collection date assigned to a pollen sample is later than the date the pollen was provisioned. This results in a time-lag of 1-7 days from when the pollen was provisioned by nesting females to the date used in analysis.

## Summer Site & Crop Selection

Summer bee abundance was studied at seven farms on several crop types, though not all crops were available at all sites (Table 1). Some sites were the same as for spring crops, others were far removed. All farms are certified organic, and grow some member of Cucurbitaceae, along with several other crop species. Pollinator abundance was measured on four farms with mixed Cucurbitaceae crops (hereafter, cucurbit), four farms with *Cucurbita* (sampled separately from other Cucurbitaceae due to morphological dissimilarity; hereafter, squash), and three sites with *Solanum lycopersicum* (hereafter, tomato; Table 1). Surveys were conducted in July 2013.

Focal crops were chosen in order to broadly characterize the local bee community on farms by choosing a range of floral morphologies. I observed several mixed fields of cucurbits (muskmelons, watermelons, and cucumber), tomato, and squash (winter and summer varieties). Cucurbit flowers are open, generalist-type flowers attracting a wide range of bee species. Squash and tomato flowers are both more specialized. Squash flowers open early in the day and are only open for a few hours. The oligolectic ‘squash bees’ of the genera *Peponapis* and *Xenoglossa*, which forage early in the morning, are considered some of the most important pollinators for the crop (Tepedino 1981, Cane et al. 2011). Tomato flowers produce no nectar, and have poricidal anthers that require disturbance to release pollen. While *Apis* can drum the anther cone to remove pollen, the process is inefficient and studies document low abundances of *Apis* on tomato blossoms (Greenleaf and Kremen 2006b). *Bombus* species that sonicate the anther cone are most effective at collecting pollen, making them some of the dominant tomato pollinators (Free 1993). Most tomato varieties are self-fertile and have low insect pollination requirements, though typically fruit quality is improved with bee visitation. Two of the three tomato crops I studied were the SunGold cultivar, which is known to have marked improvements in fruit set with bee visitation (Greenleaf and Kremen 2006b).

## Cucurbit and Tomato Surveys

I conducted point-count surveys for visitors to crops on three farms for tomato and four farms for cucurbit (Table 1). On a survey day, observers walked a row of the crop at a slow pace, tallying all visitors to crop flowers encountered within line of sight approximately 1m from observer. Surveys were conducted for 5 minutes every half hour between 1000 and 1300, for a total of 30 minutes of observation time per site per day. For tomato, each site was visited once, and for cucurbits, each site was visited twice.

## Squash Surveys

The dominant pollinators of local squash crops were determined using the protocol of the Squash Pollinators of the Americas Survey (SPAS; Jim Cane, personal communication). Surveys were conducted on two coastal and two inland farms (Table 1), starting at sunrise inland and at ~1100 on the coast due to the colder temperatures. A survey consisted of counting the bees in 50 flowers at the moment of observation. The deep corolla of squash flowers necessitates this type of observation, as the interior of several flowers cannot be easily seen at once.

# RESULTS

## Spring Pollinator Abundance

I conducted 122 and 108 five-minute pollinator observations on coastal and inland farms, respectively, for a total of 1,150 minutes of observation. *Apis* was the dominant visitor at both inland and coastal sites, with *Apis* in both locations having a mean visit rate greater than all other species combined (Figure 1, Table 2). *Apis* was present 72 and 65 of the coastal and inland observation periods, respectively (Table 2). *Bombus, Andrena, O. lignaria,* other bees, flies, and other visitors combined were present in 57 coastal and 111 inland observation periods. Most species exhibited nectar or mixed foraging behavior during visits, rarely side visiting (Table 2).

## *O. lignaria* Management – Phenology & Nesting

*Osmia lignaria* was observed on all farms but colonized nest blocks at only one inland farm and two coastal farms. Inland, nesting activity lasted 41 days, from late March to mid May, with 19 completed nests being provisioned and 8 partial nests remaining incomplete at the end of the season, all within a single block (Table 3). On the coast, the period of nesting activity was shorter, lasting only 18 days from mid April until early May across 3 colonized blocks at 2 farms. A total of 4 completed nests were provisioned, with an additional 5 partial and 6 initiated nests remaining at the end of the season (Table 3). While the nesting period inland was longer and more nests were established, it did not overlap with the flowering period of pears, occurring later in the season. Coastal nesting length, despite being shorter than inland nesting period, overlapped strongly with the flowering period of apple (Figure 2). Additionally, nesting blocks on all farms were colonized by non-*Osmia* species including *Megachile* sp. and wasps (Appendix B).

### *O. lignaria* Management – Pollen Samples

A total of 37 pollen samples, 24 inland and 13 coastal, were collected from nests throughout the season. Six pollen taxa were identified from the samples, though several non-crop pollen species could not be identified (Table 4). *Malus* was the most important pollen source at coastal farms, which is consistent with the strong synchrony between nesting activity and coastal flowering. On coastal farms, *Malus* made up an increasing proportion of the pollen samples as the nesting season continued (Figure 2, Figure 3). Pears accounted for less than 2% of the pollen grains from inland samples, due to a lack of phenological synchrony between nesting activity and crop flowering (Figure 2). In sum, crop pollen accounted for 71.8% and less than 2% of coastal and inland pollen collected by *O. lignaria*, respectively. Inland, *Brassica* was a main pollen source, but almost all of the *Brassica* pollen was collected late in the nesting season (Figure 3). Even though there were no managed apple trees at inland farms, unmanaged apple trees flowered in synchrony with inland nesting and made up a large portion of collected pollen for most of the season (Figure 3).

## Cucurbit and Tomato Surveys

A total of 1,010 visits were recorded to cucurbit flowers during 3 hours of observation. *Apis* accounted for 63.8% of the total visits across all farms (Figure 4). *Bombus* was observed on cucurbits at all farms, but only at Luna Farm was it the most abundant visitor (56.5% of visits; Figure 5). A total of 109 visits were observed during 1.5 hours of tomato surveys. *Bombus* made all but three of the visits, with two visits by *Apis* and a single hoverfly.

## Squash Surveys

*Peponapis* was abundant on inland squash flowers, but largely absent on coastal squash, where *Apis* was a more important visitor (Figure 4). However, the total number of bees observed at inland versus coastal sites differed markedly. Inland, I observed 130 visitors to squash flowers, with *Peponapis* representing nearly 75% of the visits. On the coast, I observed only 31 visitors (despite observing the same number of blossoms), 67.7% and 25.8% of which were *Apis* and *Bombus vosnesenskii*, respectively. Only one visit by *Peponapis* was observed on the coast.

# DISCUSSION

## The Role of Native Pollinators

Despite the well-documented relationship between proximity to natural habitat and native bee abundance and diversity (Kremen et al. 2002, Ricketts et al. 2008, Holzschuh et al. 2012, Kennedy et al. 2013), I found the native bee community visiting crops in Humboldt County to generally be low in abundance and diversity compared with previous studies (Winfree et al. 2007b, 2007d, Park et al. 2010, Watson et al. 2011). Given that the farms in this region are surrounded by large tracts of uninterrupted natural habitat, have high on-farm crop diversity, and have weedy flowering edges, I expected a diverse community of native bees would account for a higher proportion of crop visits. The lack of diversity in the native bee community was especially noticeable early in the season, when the European honeybee, *Apis mellifera*, dominated the visitor community on pear and apple crops. The relative proportion of visits by *Apis* compared to native species became more balanced during the summer crop season, but the diversity and abundance of native bees still fell well short of other studies of those same crops (Winfree et al. 2007b, 2007d). While a dominance of *Apis* is not unusual even in studies documenting a strong relationship between habitat quality and native bee abundance (Kremen et al. 2002), my study stands in contrast by having a clear dominance of *Apis* and a comparatively poor native bee community. Despite the close proximity to natural habitat, the relatively poor local bee community is likely explained by the quality of that habitat. Similar to a few previous studies documenting a decrease in bee diversity and abundance with increases in closed-canopy forests, the mixed conifer forests surrounding farms in my study system probably are not beneficial for bee populations since they offer few floral resources (Winfree et al. 2007a, Romey et al. 2007).

It's also probable that a phenological mismatch between native pollinators and non-native crop species is partly responsible for the poor bee community. Native bee diversity and abundance was comparatively low for the entirety of the growing season when compared to other studies of similar crops (e.g., Kremen et al. 2002, Park et al. 2010), however the importance of native bees early in the season was especially low. Two lines of evidence indicate that phenology likely plays a role in explaining the low native bee diversity on the orchard crops in my study. First, pear and apple bloomed before most native plants in the area. If native bee flight periods are strongly linked to the bloom period of local native flowering plants, then the low diversity of bees on orchard crops may at least in part be explained by dormant species being unavailable at that time of year. Second, the next most abundant pollinators after honeybees on orchard crops, *Andrena* sp. and various flies, are known early season pollinators active before most other species (Free 1993). The relative abundance of these early-season species suggests the local pollinator community was still emerging and that most bee species were not yet active, rather than foraging elsewhere.

While inland squash and tomato crops in my study were dominated by native bee visitation, they should be viewed as an exception to the general trend of honeybee dominance on Humboldt County crops, likely due to their specialized floral morphology. Even though the visitors of these crops were mostly native species, two species of bee were largely responsible for this result, belying any suggestion that a diverse assemblage of bees pollinate these crops. Furthermore, the main visitor to squash, *Peponapis pruinosa*, nests directly under the vines of squash plants (Free 1993, Julier and Roulston 2009) and therefore is not affected by the landscape characteristics that likely drive the pollinator assemblages observed on other crops. Overall, crop yields in Humboldt County should not be viewed as well insured against honeybee declines by native pollinators despite their proximity to natural habitat for all of the farms in my study system.

## Management of *Osmia lignaria*

Colonization of the nest blocks by native populations of *O. lignaria* was low, with only 3 farms and 4 of 18 blocks being occupied. However, this finding is consistent with surveys from other locations (Neal Williams, personal communication), which suggests that when unmanaged, natural populations of *O. lignaria* tend to be small in most localities. Of the blocks that were colonized, several females utilized the cavities creating multiple nests, suggesting that once a block is found, numerous individuals will colonize that block. However, other blocks go completely uncolonized, implying initial detection of blocks limits colonization rate. A study employing multiple nest designs of varying sizes and densities may more effectively assess local *O. lignaria* abundance and reveal more efficient management practices. Additionally, success rate in subsequent years after initial management attempts tends to be higher as *O. lignaria* often return to their maternal nesting site (Bosch and Kemp 2002).

I found that while more nests were provisioned at inland farms (Table 3), the timing and pollen selection of coastal nesters was better (Figure 2), suggesting that local management may only be successful at coastal farms. However, it is possible to induce earlier emergence of *O. lignaria* for pollination (Bosch and Kemp 2002), so this phenological gap could be overcome with active management efforts. The results of my study suggest that *O. lignaria* has promising management potential at coastal farms with little time investment, and further work could demonstrate successful management at inland farms with incubation and release timed for pear bloom. Despite the apparently small natural population sizes, efforts to manage *O. lignaria*, at least on coastal farms, may be well rewarded with increases in population sizes and orchard pollination.

## Conclusions

At present, many studies focusing on the ability of on- and off-farm habitat to support bee populations study a single crop species within an area (e.g., Park et al. 2010). While a recent analysis of studies from across the globe demonstrated large contributions to pollination by native bees even in honeybee dominated systems (Garibaldi et al. 2013), rarely are multiple crops studied within the same area to assess the importance of native bees to local pollination services across the growing season. The varying importance of native bees across crop and season in Humboldt County highlights the need for multi-crop surveys of flower visitors on farms to accurately determine the importance of native bees within a study region. For example, if I had sampled only on spring crops, it would seem that honeybees were essentially the lone important pollinators despite promising habitat quality. While honeybees remained the dominant pollinator throughout the season, including other crops across the season revealed instances where native bees were more important visitors.

While the primary focus of my study, and of many recent studies on agricultural pollination, is on native bees, the target crops are usually non-native (e.g., Greenleaf and Kremen 2006b, Park et al. 2010, Brittain et al. 2013). As a result, it’s often assumed the pollination requirements of non-native crops will be fulfilled by native bee species. Recognizing this phenological assumption becomes especially pertinent when recommendations for enhancing pollination services include efforts to increase native vegetation and habitat (e.g., Kremen et al. 2004), without considering whether those efforts will be rewarded due to possible phenological mismatches between indigenous pollinators and exotic crops. Incorporating this perspective will allow pollination biologists and farmers to develop strategies for ensuring crop pollination across the full-spectrum of the growing season.

While the low abundance of native bees in the spring is likely explained by some combination of crop-pollinator phenology and the low quality of the surrounding forest, the mechanism that explains the poor native bee community in the summer is less evident. Further research on summer crop flowers in the area could determine if landscape quality or on-farm floral resources have a larger influence on the local bee community. Despite the close proximity to native habitat for Humboldt County farms, the habitat may be of low value for bees since much of the area is covered with closed-canopy forests. Alternatively, it may be that native pollinator abundance is high, but poorly represented on crop flowers. This poor representation could occur if non-crop flowers are abundant and attractive enough to native pollinators to draw them away from crop flowers without bolstering populations enough to serve as a source.

At present, it is clear that Humboldt County farms rely heavily on the European honeybee, especially early in the season. In the few instances where crop flowers are visited mostly by native bee species, the diversity of the bees providing that service is restricted to a single species (i.e. *Bombus vosnesenskii* on tomato, and *Peponapis pruinosa* on squash). Therefore, even though tomato and squash are native pollinator dominant, these crops are at risk of a pollination shortfall if their single species' population declines. Given the high level of habitat connectivity and robust on-farm floral resources characteristic of local agriculture, management of landscape or farm characteristics to promote native bee populations is unlikely to provide insurance against local collapses of honeybees. Direct efforts to manage native bee species, such as *O. lignaria*, especially for early season orchard crops, should be implemented to ensure continued crop pollination and reduce the local reliance on European honeybees.

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# TABLES

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Table 1: Location and size of study farms. X’s indicate participation in a portion of the study.

| Farm Name | Location | Orchard size (hectares) | Farm size (hectares) | *Osmia* Management | Orchard | Squash | Cucurbit | Tomato |
|---|---|---|---|---|---|---|---|---|
| **Inland Farms** | | | | | | | | |
| Neukom - 1 | Willow Creek | 1.6 | 2.2 | x | x | | | |
| Neukom - 2 | Willow Creek | - | 2.0 | | | x | x | x |
| Green Fire - 1 | Hoopa | 0.4 | 2.8 | x | x | | x | x |
| Green Fire - 2 | Hoopa | - | 0.2 | | | | x | |
| Fruitwood | Orleans | 1.0 | 3.4 | x | x | | | |
| Pierce Family | Orleans | - | 8.0 | | | x | | |
| Luna | Willow Creek | - | 0.8 | | | | x | x |
| **Coastal Farms** | | | | | | | | |
| Honey Apple | Blue Lake | 0.6 | 0.8 | x | x | | | |
| Feral Family | Blue Lake | 0.2 | 0.4 | x | x | | | |
| Swallowdale | Bayside | 0.6 | 0.6 | x | x | | | |
| Warren Creek - 1 | Blue Lake | - | 8.0 | | | x | | |
| Warren Creek - 2 | Arcata | - | 2.8 | | | x | | |

Table 2: Visit rates and behaviors of pollinators of pear and apple crops. Count is the number of 5-minute observation periods where a taxon was observed. Mean visit rate is the number of visits by a taxon over the number of flowers in that observation period. n is the total number of flowers visited by a given taxon across all observation periods. Visit behaviors by taxa were classified and proportions are presented below. Side visits are distinguished from nectar visits by a lack of contact with reproductive whorls. Mixed visits are characterized by collection of pollen and nectar.

| | | **Visit Rates** | | | | **Behavior Proportions** | | | |
|---|---|---|---|---|---|---|---|---|---|
| **Taxon** | **Location** | **Count** | **Mean** | **SD** | **n** | **Nectar** | **Side** | **Pollen** | **Mixed** |
| *Apis* | Inland | 65 | 0.1354 | 0.1971 | 747 | 0.13 | 0.00 | 0.24 | 0.63 |
| *Andrena* | Inland | 39 | 0.0183 | 0.0334 | 94 | 0.16 | 0.03 | 0.23 | 0.57 |
| Fly | Inland | 42 | 0.0143 | 0.0244 | 94 | NA | | | |
| Bee | Inland | 13 | 0.0038 | 0.0124 | 25 | 0.24 | 0.00 | 0.16 | 0.60 |
| *Osmia* | Inland | 7 | 0.0029 | 0.0180 | 21 | 0.33 | 0.00 | 0.00 | 0.67 |
| *Bombus* | Inland | 4 | 0.0017 | 0.0095 | 8 | 1.00 | 0.00 | 0.00 | 0.00 |
| Other | Inland | 6 | 0.0014 | 0.0068 | 5 | NA | | | |
| *Apis* | Coastal | 72 | 0.1067 | 0.1360 | 447 | 0.37 | 0.05 | 0.34 | 0.24 |
| *Bombus* | Coastal | 21 | 0.0207 | 0.0746 | 79 | 0.73 | 0.00 | 0.06 | 0.20 |
| Fly | Coastal | 27 | 0.0160 | 0.0453 | 70 | NA | | | |
| Bee | Coastal | 7 | 0.0036 | 0.0169 | 20 | 0.40 | 0.15 | 0.45 | 0.00 |
| Other | Coastal | 1 | 0.0016 | 0.0173 | 1 | NA | | | |
| *Osmia* | Coastal | 1 | 0.0004 | 0.0048 | 2 | 0.00 | 0.00 | 0.00 | 1.00 |

Table 3: Dates of phenological events observed in orchard studies. While costal crop flowering and *Osmia* nesting overlaps more strongly, the total amount of nesting activity on inland farms was greater and lasted longer. Initiated/Halfway/Completed indicates the number of tubes remaining in those respective states at the end of the nesting season. See *Methods* for calculation of total nest score.

| | **Date** | |
|---|---|---|
| **Event** | **Inland** | **Coastal** |
| First Flower | 24-March | 5-April |
| Last Flower | 13-April | 14-May |
| Peak Flower | 2-April | 25-April |
| Duration (days) | 20 | 39 |
| First Nest | 31-March | 21-April |
| Last Nest | 11-May | 9-May |
| Peak Nest | 4-May | 25-April |
| Duration (days) | 41 | 18 |
| Initiated/Partial/Completed | 3/8/19 | 6/5/4 |
| Total Nest Score | 76 | 28 |

Table 4: Mean and standard deviation of the relative proportion of pollen grains of plant taxa sampled from *O. lignaria* nests. While *Brassica* pollens are the largest proportion of Inland pollens, for most of the nesting season *Malus* is the dominant pollen source (Figure 3).

| **Taxon** | **Location** | **Mean (SD)** |
|---|---|---|
| *Brassica* | Inland | 0.372 (0.427) |
| *Malus* | Inland | 0.308 (0.327) |
| Unknown | Inland | 0.168 (0.250) |
| *Rubus* | Inland | 0.099 (0.143) |
| *Fragaria* | Inland | 0.019 (0.031) |
| *Pyrus* | Inland | 0.017 (0.042) |
| *Cercis* | Inland | 0.017 (0.042) |
| *Malus* | Coastal | 0.719 (0.169) |
| *Rubus* | Coastal | 0.188 (0.128) |
| Unknown | Coastal | 0.066 (0.082) |
| *Brassica* | Coastal | 0.015 (0.052) |
| *Fragaria* | Coastal | 0.012 (0.013) |
| *Pyrus* | Coastal | 0.001 (0.003) |
| *Cercis* | Coastal | - |

# FIGURES

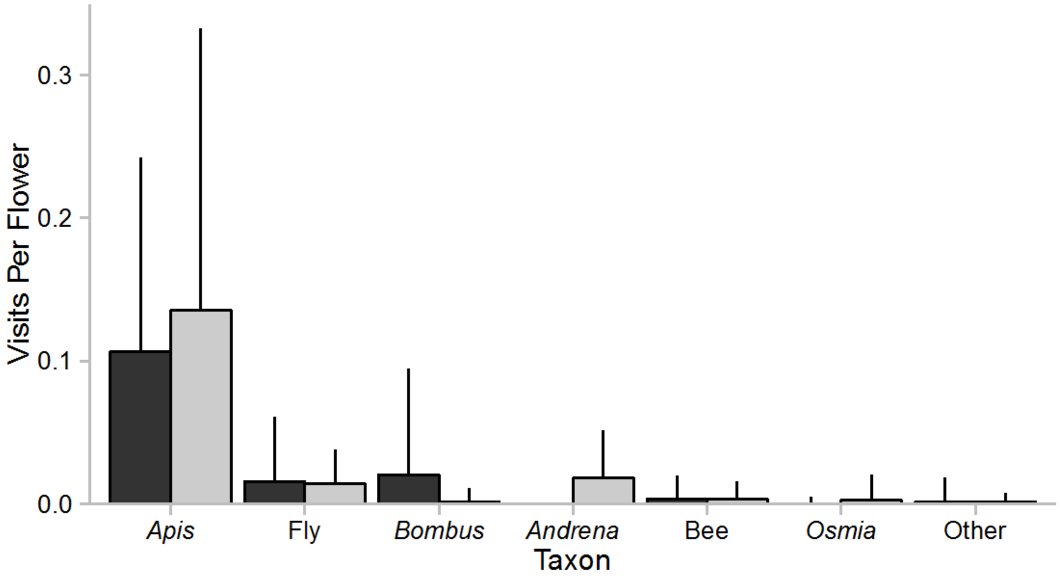

Figure 1: Visit rates of pollinator taxa observed on orchard crops. Black bars are coastal (apple) visitors; grey bars are inland (pear) visitors. Taxa are sorted by global (inland and coastal) means. Black lines indicate 1.0 standard deviation.

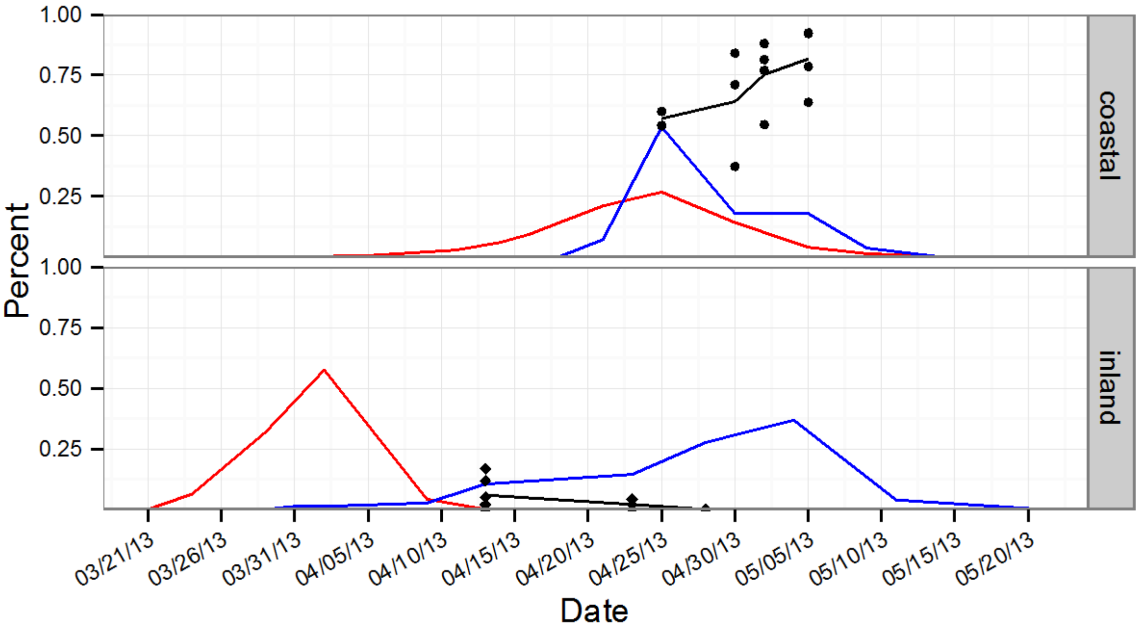

Figure 2: Proportion of flowering and nesting activity observed on a given day. *Osmia lignaria* nesting (blue) and target crop flowering (apple on coast, pears inland; red). Points represent proportions of crop pollen in nesting provisions when crop pollen was present; the black line is the mean. Cells may have been provisioned before the collection date, resulting in a time lag between when pollen was likely provisioned and when it is plotted relative to crop flowering.

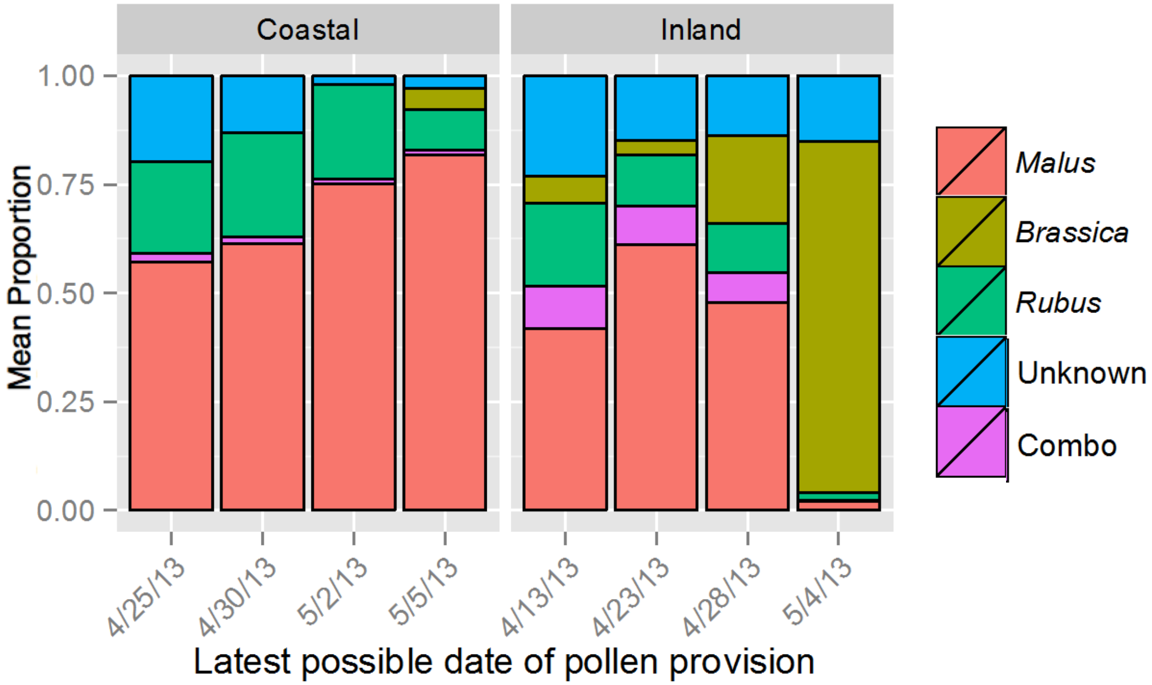

Figure 3: Pollen collection proportions of 24 inland and 13 coastal provisions, sorted by date. For simplicity, *Fragaria*, *Pyrus*, and *Cercis* pollens were lumped and are shown as ‘Combo’.

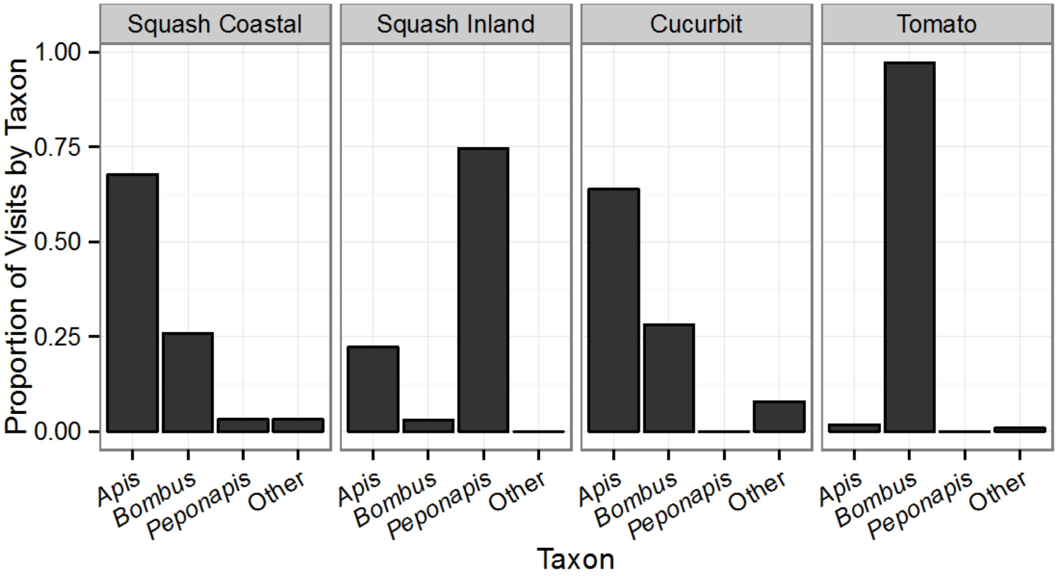

Figure 4: Mean proportion of visitors to summer crops. *Apis* is the clear dominant pollinator on cucurbit and coastal squash crops. Inland squash and tomato were visited primarily by native bee species, *Peponapis* and *Bombus*, respectively.

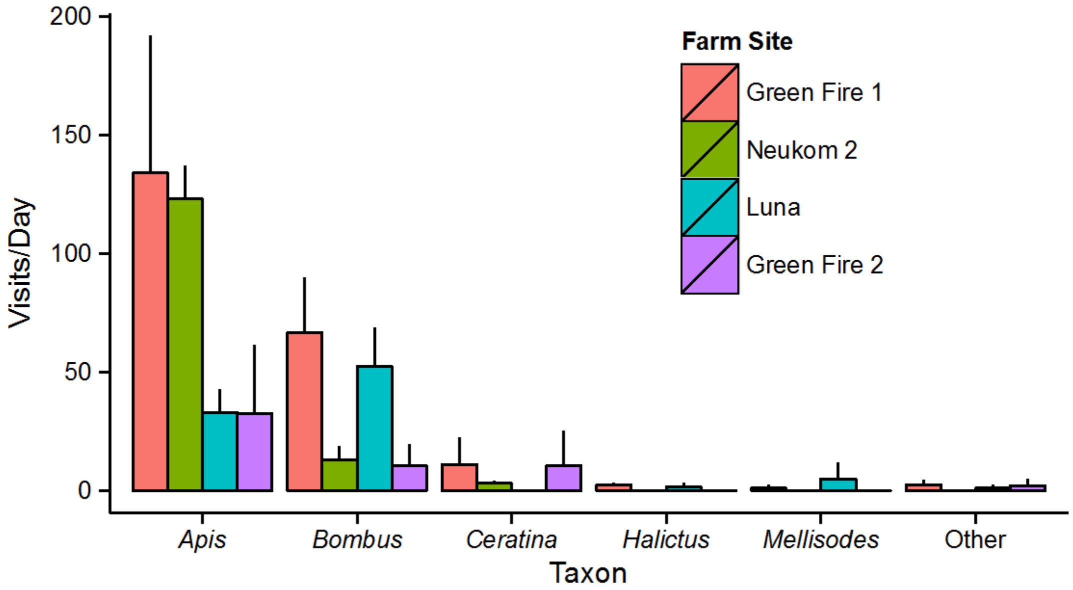

Figure 5: Mean (+1.0 SD) visits per day to cucurbit crops at inland farms across 3 sampling days.

# APPENDICES

Appendix A – Photo showing nest block design (left) and an active *O. lignaria* female at nest entrance (right).

Appendix B - Table nest occupants. Where a taxonomic distinction wasn’t possible, habit is described in parentheses. Only presence/absence is reported, abundance was not estimated. Parasites of *Megachile* sp. are indicated with an asterisk (*). Reference specimens and nesting materials of all taxa are kept at Humboldt State University’s Bee Lab for later identification.

| Taxon | Green Fire | Neukom Family | Fruitwood | Honey Apple | Feral Family | Swallowdale |
|---|---|---|---|---|---|---|
| *Osmia lignaria* | x | | | x | x | |
| *Osmia sp.* #2 | x | x | | | x | |
| *Megachile* sp. (full cell) | | x | x | x | x | x |
| *Megachile* sp. (cell caps) | x | x | x | | | |
| *Megachile* sp. (masticated cell caps) | x | | | | | |
| *Callanthidium* sp. | x | | | | | |
| Wasp (clavicle antennae) | x | x | x | x | x | x |
| Flower beetle* | | x | | | | |
| Carpet beetle* | | x | | | | |
| Parasitic fly* | | | x | | | |