Native Pollinators in Agricultural Hedgerows: An Alternative to Honeybee Colonies for Crop Pollination

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ABSTRACT

California agriculture is highly dependent on crop pollination services, provided mostly by commercial colonies of honeybees, *Apis mellifera*. However, the recent, rapid decline in these colonies is fueling interest in alternatives for agricultural pollination services. Hedgerows, or vegetation strips, planted adjacent to crop fields can provide floral resources to support native pollinators throughout the year. Over the last five summers, field assistants from the UC Berkeley Kremen Lab walked transects along hedgerows and weedy, unmanaged control sites in Yolo County, California, catching visiting pollinator species and noting the corresponding plant species. I analyzed the pollinator and plant interaction dataset by comparing control and hedgerow pollination networks. Using network-based metrics of nestedness, modularity, resilience, species generalization, and network similarity, I analyzed the potential value of hedgerows planted for crop pollination. I also examined morphological measurements of a subset of bee pollinators to explain plant species visitation. Because the study system is located in intensely cultivated fields, only abundant and generalized species can survive, so I found both hedgerow and control networks contained the same pollinator species. However, pollinators in hedgerow sites had a larger plant species selection than those at control sites and showed preference for visiting certain plant species. Planted hedgerows allow for local pollinator species to optimally forage on nutritious plant resources at times when crops are not flowering. With the continuing need for crop pollination and growing concern for honeybee availability, planted hedgerows and native pollinators could provide farmers with an alternative solution for their pollinator-dependent crops.

KEYWORDS

Pollination networks, nestedness, resilience, generalization, optimal foraging theory

INTRODUCTION

Pollination is a critical component of healthy, productive agricultural ecosystems. Roughly one third of California agriculture, which provides nearly half of the U.S.-grown fruits, nuts and vegetables, is completely dependent on insect pollinators (Klein et al. 2007, 2008, Steffan-dewenter and Westphal 2008). Farmers in California rely heavily on importing colonies of *Apis mellifera*, the European honeybee, to pollinate their crops (Forup et al. 2007, Potts et al. 2010, Carvalheiro et al. 2010). Recently, however, honeybee colonies worldwide have started to rapidly disappear. Although there is still speculation on what is causing the collapse of the colonies, this decline of honeybees threatens California's enormous agricultural industry (Forup et al. 2007, Carvalheiro et al. 2010). Scientists and farmers are seeking alternatives to honeybee pollination and have a renewed interest in native pollinators (Klein et al. 2003, Winfree and Kremen 2009). Native pollinators can contribute to crop pollination in farmed areas adjacent to native habitats, but in California most of the agricultural fields are surrounded by other industrialized agricultural fields (Kremen et al. 2004, 2007, Carvalheiro et al. 2010). As an alternative to natural habitat, planting hedgerows or strips of beneficial plants adjacent to crop fields can support local communities of beneficial pollinators (Kremen et al. 2004).

Agricultural hedgerows attract and sustain local insect species that pollinate crops during their flowering season. In a recent study, Kremen et al. (2004), found that pollinators travel from 1 to 2.5 kilometers from their natural habitat to pollinate crops. Thus, hedgerows planted at 2 to 5 kilometer intervals among agricultural fields could supply or support native pollinators for crop pollination services. In addition, hedgerows conserve native insect species by providing patches of suitable habitat throughout the year, as crops only flower for part of the season (Allen-wardell et al. 2011). Klein et al. (2007) found that the greater the pollinator diversity, the better the pollination service provided. Agricultural hedgerows may support a diverse community of pollinators, although, to date we lack a full understanding of the structure and robustness of the hedgerow pollinator communities.

Pollination networks model interactions at the community scale, connecting all pollinator species with the plant species that they pollinate in a particular study system (Olesen et al. 2006, Bascompte and Jordano 2007). A pollination network allows all community interactions to be visualized at once, revealing the important plant and pollinator species that maintain community stability (Bascompte and Jordano 2007, Martín González et al. 2010). Often, pollination networks consist of a few core generalist species interacting with a large number of specialist species**.** Generalists are often the most abundant and the most crucial species in a healthy and functioning ecosystem (Martín González et al. 2010, Kaiser-Bunbury et al. 2010) In addition to highlighting important species, pollination network characteristics can test a community's resilience to a large species extinction that may result from human disturbance or an invasive species encroachment (Memmott et al. 2004, Martín González et al. 2010).

Although many studies have examined entire pollination networks, few have looked at the relationship between particular species traits and the location of those species within a network (Stang et al. 2006, 2007). Stang et al. (2006), compared body size, dry mass, and proboscis length of pollinators to their location within a network and found a significant positive correlation between proboscis length and the number of plant species that a pollinator visited. If species morphology correlates with estimates of species-level generalization, then morphological characteristics can determine different pollinator behavior within a network and thus network topology.

Using a network-based approach, I determined the relative effectiveness of sustaining pollinator communities by comparing pollination networks of agricultural hedgerows with networks of unmanaged, weedy control sites. By analyzing hedgerow and control site pollination networks, I ascertained community topology, diversity and resilience as well as compared pollinator species traits and interaction patterns in each network. Specifically I asked the following questions: 1) Do pollination network topologies differ between hedgerow and control sites? 2) Do hedgerow and control pollination networks have different resilience to disturbance? 3) Do control and hedgerow networks contain the same species and do these species have similar interaction patterns in both networks? 4) Does proboscis length or body length predict the number of plant species a pollinator visits (generalization)? I used these questions to infer if hedgerows supply adequate resources to sustain native pollinator communities.

METHODS

Study Sites

Both the hedgerow sites and control sites studied were located in Yolo County in the California Central Valley, typically adjacent to industrialized tomato fields. Hedgerow sites were planted by farmers to attract local pollinators and varied in plant species composition. Each hedgerow was approximately 350 meters long and all hedgerows were at least five years old. Fieldwork was conduced by the Kremen Lab at U.C. Berkeley. Specimens were collected from eight mature hedgerow sites and 24 weedy control sites. Control sites consisted of unmanaged weedy plants and also spanned approximately 350 meters. All the sites were located about one kilometer away from all other sites to prevent species flow between sites.

Site Sampling

All sampling took place during summer months but sites differed in what years they were sampled, from 2006 to 2011. Hedgerow and control sites were sampled three times a summer (usually once in June, July, and August). Sampling followed a standardized protocol previously established by the Kremen Lab. One field assistant walked along the hedgerow or control site netting all pollinating insects visiting the plants and placing the insects in kill jars labeled with the corresponding plant species. Specimens were collected for a total of 90 minutes, excluding time for sample handling and notation. Jars were sent to the Kremen Lab where pollinators in the orders Lepidoptera and Hymenoptera and the family Syrphidae were identified to species.

Bee Morphology

For bee morphology trait analysis, I measured the body size and proboscis length of the 43 most abundant bee species. Body measurements were taken three times from up to 10 individuals for each bee species using a digital caliper. To maximize accuracy, the insect body was straightened and length measured from head to abdomen (±0.1mm) (Stang et al. 2006). I then measured proboscis length using a dissecting scope and digital caliper, beginning where the proboscis exited the mouth and ending at the proboscis tip (±0.1mm) (Stang et al. 2006). All of the specimens I measured were collected from the 2011 sites and presumed to represent species throughout all years and sites.

Network Analysis

I used the dataset collected and created by the Kremen Lab to generate pollination networks for the hedgerows and control sites. Because the sites varied in sampling year and number, I combined all of the data into two networks, one control and one hedgerow. The aggregated data provided an overall estimate of the pollinators' dietary breadth of plant species within each network. For all analyses, I used the two aggregate networks to compare network metrics of the two habitat types.

Nestedness

I calculated nestedness to determine species interaction patterns. Nestedness occurs when a large number of specialists interact with a few extreme generalist species; this pattern has been found in many natural systems (Bascompte and Jordano 2007, Klein et al. 2008, Blüthgen et al. 2008). Significant nestedness is characterized by extreme right skewed distribution in number of interactions or specialization asymmetry (Blüthgen et al. 2008). Nestedness was analyzed using the NODF metric (Almeida-Neto et al. 2008). All analyses were implemented in R (R Development Core Team 2011).

There are several methods to test for nestedness which vary in stringency. I assessed nestedness by running a conservative probabilistic null model. The model compared the total nestedness of the control and hedgerow networks to computer simulated networks constrained with characteristics derived from the original control and hedgerow networks. One constraint of the simulated model was that the model assigned a value between each pollinator and plant species by averaging number of interaction partners of the two species to get a probability that these plant and pollinator species would interact in the simulated model. The second constraint was that there were the same number of total interactions and the same number of interactions between different plant and pollinator species. To test for significant nestedness, the actual networks were each compared to one thousand simulated networks to determine if they were more or less nested then each of the simulated networks. By inputting the two constraints, the model was a more conservative estimate of nestedness than other published network papers without the constraints.

Modularity

Natural pollination networks also tend to be modular (Olesen et al. 2007). Modularity is the compartmentalization of specialists that interact with a few core generalists connected to the larger network. Each one of the agglomerations is considered a module and is often closely related in evolution or morphology. I calculated network modularity by breaking the community into sub-communities using edge betweenness (Newman and Girvan 2006) and calculated a modularity score (Newman and Girvan 2004).

Resilience

Network resilience is a measure of how susceptible a network is to collapse if plants or pollinators are removed from the network (Memmott et al. 2004, Kaiser-Bunbury et al. 2010). Resilience is tested with three comparable extinction functions (Memmott et al. 2004). The first, the null extinction simulation, removes either pollinators or plants at random and plots the decline of the respective species. The second extinction simulation removes the least abundant species and plots the resulting species decline, while the third simulation removes the most interconnected or generalized species before plotting decline. The areas under the curves are then used to evaluate community resilience to the extinction scenario. When the three functions are analyzed, the susceptibility of the entire community to extinction events can be determined. I used the function second.extinction in the bipartite package (Gruber et al. 2009) to simulate the extinction scenarios.

Species Specialization

To determine species specialization, I calculated *d'* values for all species within the control and hedgerow networks. The *d'* function computes weighted interaction specialization of each species, accounting for both the number of species and frequency of species–to-species interactions (Blüthgen et al. 2008). *D'* values range from zero, defined as extreme generalization, to one, defined as extreme specialization. I used a Wilcox test to compare the non-normal *d'* values averaged for pollinators and plants in each network.

Site Variation

Because of the large differential in the number of sample sites (eight hedgerows and 24 control sites), I conducted a rarefaction analysis to determine if the different pollinator generalization values could be due simply to sampling error.

Network Similarity

To examine species similarity between control and hedgerow sites, I used a permutation based MANOVA to compare the dissimilarity between sites. I examined the dissimilarity within control sites, within hedgerow sites, and between hedgerow and control sites. The dissimilarity analysis tests for difference in species composition between sites.

Body Trait Analysis

I used Spearman rank correlation to determine whether body size or proboscis length correlated to bee species generalization.

RESULTS

I used a large matrix of species interaction data in this study provided by the U.C. Berkeley Lab of Dr. Claire Kremen. Overall, 96 pollinator species were caught at hedgerow sites, which contained 69 plant species, and 106 pollinator species were caught at control sites, which contained 62 plant species.

Network Analysis

Nestedness and Modularity

Neither the hedgerow ($P = 0.99$) nor control ($P = 0.99$) networks were significantly nested. Also, neither the hedgerow network ($P = 0.70$) nor the control networks ($P = 0.26$) were significantly modular.

Resilience

The resilience of plants and pollinators appear approximately equivalent between hedgerow and control sites (Figure 1). However, plants are more susceptible to pollinator extinction than pollinators are to plant extinction in both networks.

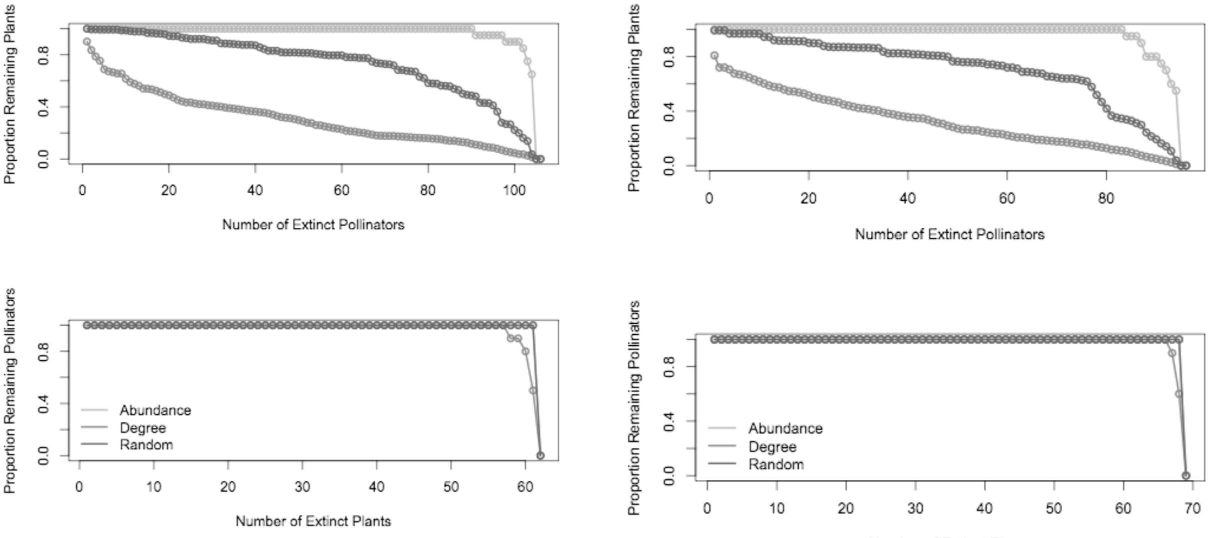

Fig. 1. Species resilience simulation. Plots of plant extinction as pollinators are removed from (A) control sites or (B) hedgerows. Plots of pollinator extinction as plants are removed from (C) control sites or (D) hedgerows.

The *d'* values for each species in the two networks suggests that the majority of both plant and pollinator species at both site types to be highly generalized (Figure 2A). Although all species on average are generalized (*d'* values less than 0.5), pollinators in the hedgerow network are significantly more specialized (0.320 +/- 0.002, mean +/- SE) than pollinators in control sites (0.199 +/- 0.001, W = 7050.5, $P < 0.001$) or plants in hedgerow sites (0.250 +/- 0.003, W = 4083, $P = 0.01$). The *d'* values of pollinators found in both control and hedgerow sites were plotted against each other to compare species behavior in each network (Figure 2B). If the species were interacting with the same number of partners with the same frequency, then the species would fall on the diagonal line. The plot shows over twice as many points lie above the line, indicating that the same pollinators are more specialized in hedgerows than in control sites.

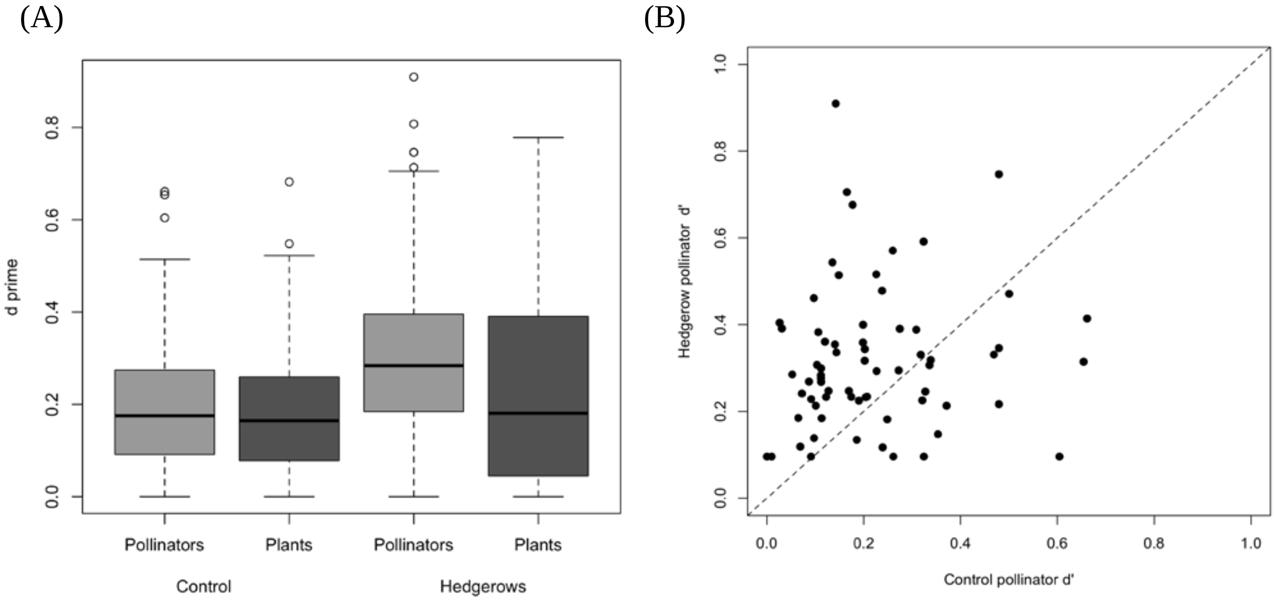

Figure 2: *D'* Specialization (A) Specialization of species in control and hedgerow sites, ranging from extremely generalized (0) to extremely specialized (1). **(B)** A comparison of pollinator *d'* values in hedgerow sites versus *d'* values of the same pollinators at control sites. ($P = 0.21$; $\rho = 0.15$)

Rarefaction

Because pollinators appeared to be significantly more specialized in hedgerows than when in control sites, I used rarefaction analysis to determine whether the generalization of control pollinators was due to larger number of sampling sites or if the species at the control sites really were more generalization in plant visitation (Figure 3). The hedgerow network *d'* value stabilized before and at a higher value than the *d'* value of the control networks.

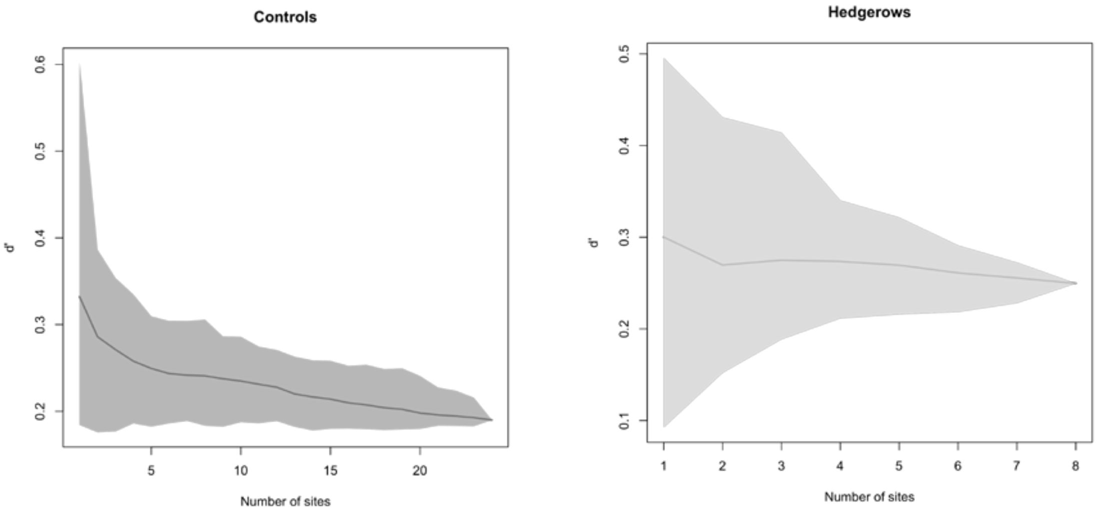

Fig. 3. Rarefaction analysis of control and hedgerow network d' values. Hedgerow and control sites stabilize atdifferent average d' values.

Species Similarity

To determine whether hedgerow sites attract different or more specialized species than control sites, I compared the dissimilarity of species within control sites and hedgerow sites, and between control and hedgerow sites (Figure 4). I found that there was no significant difference in pollinator species composition between control and hedgerow sites ($F_{1,32}$= 2.639, P = 0.109). Thus both sites are attracting the same species of pollinators.

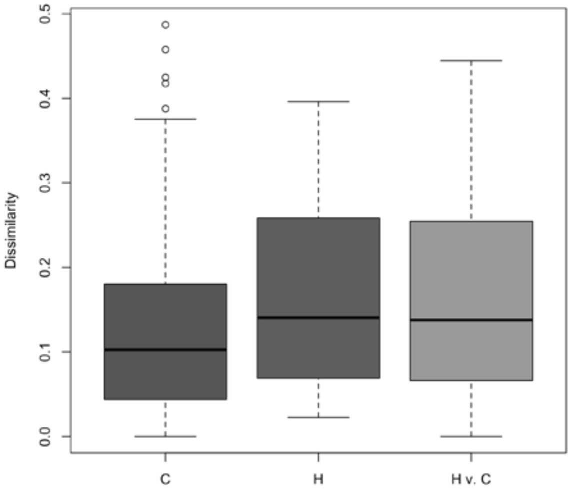

Fig. 4. Dissimilarity within control sites, within hedgerow sites and within both control and hedgerow sites. The range of species differences is no different between hedgerows and control sites (H v. C) than within hedgerow sites (H) or control sites (C).

Bee Morphology Analysis

I found no significant correlation between either body size (Hedgerow P = 0.55, ρ=0.128; Control P = 0.08, ρ=0.351) or proboscis length (Hedgerow P = 0.62, ρ = -0.106; Control P = 0.20, ρ = 0.263) and generalization value (Figure 5).

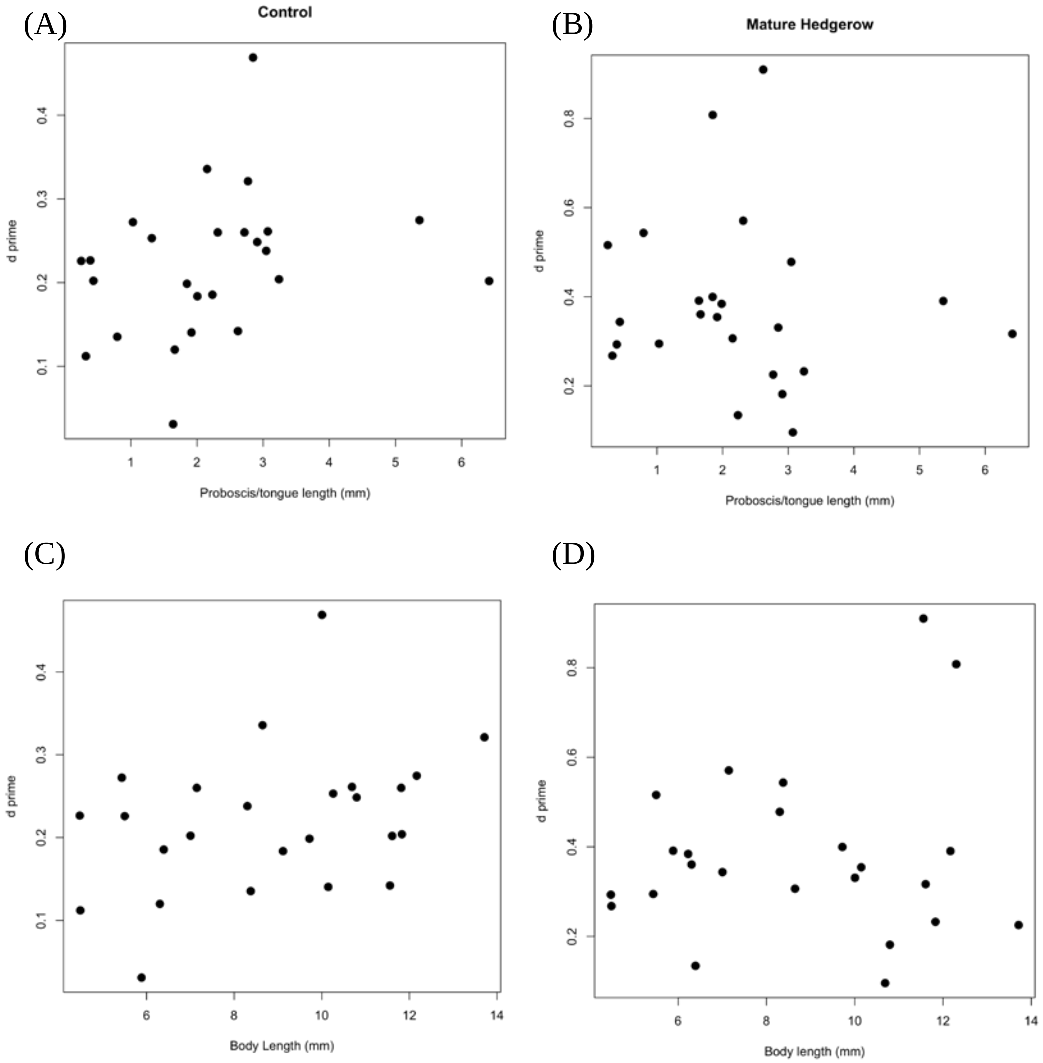

Fig. 5. Body Measurements and Generalization (*d'*) Values are not significantly correlated. *D'* values versus Proboscis lengths of bees collected from (A) control sites and (B) hedgerow sites. *D'* values versus body lengths of bees collected from (C) control sites and (D) hedgerow sites.

DISCUSSION

Native pollinators, supported in planted hedgerows adjacent to agricultural fields, may offer an alternative to overdependence on honeybees for crop pollination. To understand the behavior of pollinators and their plant resources in agricultural hedgerows, I analyzed pollinator-plant visitation data, generating pollination networks in one central California County. Using the pollination networks, I examined the overall characteristics of combined hedgerow and control networks, as well as the species interactions patterns within each network. Network analysis showed that hedgerow sites help sustain native pollinator communities which may have implications for local pollinator conservation and adjacent crop pollination.

Network Analysis

I found that neither the hedgerow nor control networks were significantly nested or modular. In both networks the majority of species were incredibly generalized and well connected, explaining the lack of specialized species interactions nested within generalist species. The high generalization also impacts modularity statistic, which tests if there are groups of specialists that interact with one or a few generalists (Bascompte and Jordano 2007, Olesen et al. 2007). Because the majority of species are generalists, there is no modularity in either pollination network. The extremely generalized pollinator communities in this agriculture system differ from pristine ecosystems, in which pollination networks have been found to be both nested and modular (Bascompte and Jordano 2007, Olesen et al. 2007, Petanidou et al. 2008, Alarcón et al. 2008). Unlike natural communities, agricultural fields do not support a broad range of specialist species commonly found in pristine environments because agriculture fields are harsh with unpredictable resource availability (Kremen et al. 2004, Klein et al. 2007). Neither hedgerow nor control sites provided enough plant resources to support a flourishing and diverse pollinator community comparable to natural systems; however, generalist pollinators were able to capitalize and benefit from these plant resources.

In both the hedgerow and control networks, the network resilience simulation showed that pollinators are not highly susceptible to plant extinction events, where as plants were more quickly affected by pollinator extinction events. The lack of pollinator vulnerability is most likely due to the generalist nature of pollinators in the network, who can continue to subsist off several other plant species if one plant species goes locally extinct. Plants are more reliant on pollinators, as they are unable to move to attract pollinators and are at the mercy of pollinator choice. Resilience is calculated as if plants require pollination to reproduce, which may not be true for the generalized agriculture system. Although the metric does not take into account plant self-fertilization, the results of pollinator robustness show that insect species are not highly dependent on any particular plant species. The results from the resilience test suggest that the pollinator populations are equally stable in control sites as well as hedgerows.

Species Level Analysis

Pollinator species generalization in both control and hedgerow networks may be important for pollinator survival in agricultural systems, which are resource deserts when the crop plants are not flowering (Kremen et al. 2004, Klein et al. 2007). For pollinator species to survive after crops have bloomed, they would have to subsist on a variety of weedy species growing within the crops or along the perimeter of the fields. It is likely that specialist pollinators could not survive in an agricultural environment. A similar argument can be made for the local plant species, which are reliant on whatever pollinator species happen to visit. Specialist plants would not survive if their complimentary pollinator species were not present. Logically, hedgerows should be planted with vegetation chosen specifically to attract a large variety of pollinators and so to be intentionally generalized.

Although both pollinators and plants at both habitat sites were generalists, the hedgerow pollinators showed significantly more specialist tendencies than the pollinators at the weedy control sites. Because there was no significant difference in the species composition between hedgerow and control sites, the appearance of specialization of the hedgerow pollinators is likely behavioral. The specialization could be attributed to pollinators' selectivity when presented with a large amount of floral resources. Pollinators in the hedgerows would likely visit the plants that provide the most nutritious or energizing pollen and nectar, optimizing their diet (Pyke 1984). If hedgerows provide more nutritious resources to local pollinators, supporting a larger abundance of pollinators than weedy control sites, then the development of these hedgerow habitats is a favorable step toward providing an alternative to imported pollinators.

I found body length and proboscis length were not correlated with species visitation behavior within the communities. In contrast, in a natural system Stang et al. (2006) found proboscis length was an adequate predictor of generalization. Due to the extreme generalization of my networks, a lack of relationship between behavior and body size or proboscis length is not surprising. Also Stang et al. (2006) determined plants are inversely generalized with the depth of their corolla tubes. The vast majority of plants in the agriculture system are naturally generalist species and therefore likely to have short corolla tubes, accessible to many pollinator species.

Limitations

The dataset used in this study was not originally captured for pollination network analysis. There were many sites with as few as one sampling year and high species turnover between sampling rounds, which limited the inferences I could make between individual control and hedgerow sites. Also, due to time constraints, I was only able to measure the most abundant bees' body sizes. Small sample size may have limited the detection of any correlation between body morphology and behavior. I measured only bee species from 2011 and assumed that these species were representative of all the other years and seasons. The network species were sampled across five years so there may be undetected variation in morphology between years.

Future Directions

To tease out the site-specific differences between control sites and hedgerows with more confidence, a few hedgerow and control sites should be selected and a larger sample size spanning more days should be collected. To determine whether local pollinators are effective in crop pollination, specimens should be collected from flowering crop fields, at varying distances from hedgerows. This would show whether the hedgerows are attracting enough beneficial pollinators to be an efficient alternative for crop pollination. Other future studies could examine which plant species are most successful at attracting beneficial pollinators and how the importance of diversity within the hedgerow ensures nectar and pollen availability throughout the summer season.

Broader Implications

Development of hedgerow habitats could provide an effective alternative to importing honeybee colonies as they both attract and sustain a large number of native pollinators which in turn could pollinate adjacent agriculture crops (Klein et al. 2007, Kremen et al. 2007). With the spread of colony collapse disorder, finding alternatives to honeybee pollination is crucial for California's fruit, nut and vegetable farmers (Allen-wardell and St 2000, Tscharntke et al. 2005). Supporting a large diversity of pollinators, hedgerows help to maintain biodiversity in areas of crop monoculture. The true contribution of many native pollinators remains unknown, making it crucial to preserve pollinator biodiversity (Kremen et al. 2002). As the global human population increases and demand for food increases, it will be wise to have many pollination service options available. The analyses of this project show that agricultural hedgerows can support stable, native pollinator populations. Optimization of such native pollinator-plant-crop networks could lead to one sustainable solution for a growing need.

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