Restoration Ecology
THE JOURNAL OF THE SOCIETY FOR ECOLOGICAL RESTORATION INTERNATIONAL

RESEARCH ARTICLE

Bee Preference for Native versus Exotic Plants in Restored Agricultural Hedgerows

Lora A. Morandin[1,2] and Claire Kremen[1]

Abstract

Habitat restoration to promote wild pollinator populations is becoming increasingly common in agricultural lands. Yet, little is known about how wild bees, globally the most important wild pollinators, use resources in restored habitats. We compared bee use of native and exotic plants in two types of restored native plant hedgerows: mature hedgerows (>10 years from establishment) designed for natural enemy enhancement and new hedgerows (≤2 years from establishment) designed to enhance bee populations. Bees were collected from flowers using timed aerial netting and flowering plant cover was estimated by species using cover classes. At mature hedgerow sites, wild bee abundance, richness, and diversity were greater on native plants than exotic plants. At new sites, where native plants were small and had limited floral display, abundance of bees was greater on native plants than exotic plants; but, controlling for floral cover, there was no difference in bee diversity and richness between the two plant types. At both mature and new hedgerows, wild bees preferred to forage from native plants than exotic plants. Honey bees, which were from managed colonies, also preferred native plants at mature hedgerow sites but exhibited no preference at new sites. Our study shows that wild bees, and managed bees in some cases, prefer to forage on native plants in hedgerows over co-occurring weedy, exotic plants. Semi-quantitative ranking identified which native plants were most preferred. Hedgerow restoration with native plants may help enhance wild bee abundance and diversity, and maintain honey bee health, in agricultural areas.

Key words: agriculture, Apoidea, ecosystem services, pollinators.

Introduction

Seventy-five percent of the leading food crops and 35% of global food production is dependent on pollinators (Klein et al. 2007). Bees are the primary crop pollinators, with managed honey bees being the most important pollinator globally (Watanabe 1994). However, recent problems with honey bee colony health (Neumann & Carreck 2010) and a greater than 300% increase in area devoted to pollinator-dependent crops in the last 50 years, has made reliance on managed honey bees a risky proposition (Aizen & Harder 2009). Native pollinators supply a significant amount of pollination to many agricultural crops. In areas with large amounts of natural or semi-natural land, native bees can fully meet pollination requirements of a crop without the need for managed honey bees (Kremen et al. 2004; Morandin & Winston 2006; Winfree et al. 2007). However, intensive agricultural systems often are lacking in native pollinators (Winfree et al. 2009) and hence native pollination services to crops (Kremen et al. 2002; Klein et al. 2003; Morandin & Winston 2006; Ricketts et al. 2008).

[1] Department of Environmental Science, Policy & Management, University of California, Berkeley, 130 Mulford Hall, Berkeley, CA 94720, U.S.A.
[2] Address correspondence to L. A. Morandin, email lora_morandin@berkeley.edu

doi: 10.1111/j.1526-100X.2012.00876.x

While growers have little or no control over amounts of natural habitat in their region, they are able to implement farm-scale habitat enhancements. Restoration of weedy field edges with native shrubs and forbs is a feasible, and increasingly popular, method for increasing semi-natural land and thus native pollinator diversity, abundance, and possibly pollination services in working farmlands (Pywell et al. 2005; Hopwood 2008; Hannon & Sisk 2009). While restoration initiatives to enhance native pollinators in agricultural lands increasingly are being promoted through incentive or outreach programs, very little is known about resource use by pollinators within such restored areas (Winfree 2010).

Habitat enhancements for wild pollinators generally aim to enhance the abundance and diversity of floral resources in order to provide a consistent supply over the flight season (Vaughan et al. 2007; Menz et al. 2011). Often, non-native annual plants are recommended for pest-control enhancement on farm sites, despite the fact that native plants are more suitable for conservation efforts that intend to also preserve native plants and the beneficial insects associated with them (see Tuell et al. 2008 and references therein). Most studies on bee use of native and exotic plants in disturbed habitats have found that exotic plants receive more visits than native plants by native bees because of greater attraction and rewards (Brown et al. 2002). In a meta-analysis of 40 studies that examined effect of exotic plants on native plant pollination and reproductive success, Morales and Traveset (2009) showed a negative impact on native pollination and reproductive success in the presence of exotic plants. Vila et al. (2009) examined plant–pollinator interactions in invaded (presence of exotic species) and un-invaded networks and found that pollinators interacted more with exotic species than they did with native species in invaded areas, but found no clear effect on whether the greater visits to exotic plants negatively impacted visits to native plants. Williams et al. (2011), working in disturbed agricultural plots in California, found that wild bees did not exhibit a preference for either native or exotic plants, but utilized both in proportion to their availability. These studies beg the question as to whether native plantings provide important resources for wild bees and honey bees in agricultural settings, where exotics often are numerically dominant; yet, there is little information on whether pollinators preferentially choose to forage from native plant restoration plantings rather than co-occurring exotic species. Despite increasing funds and effort to restore agricultural areas with native plants, we know of no studies that examine pollinator use of native versus exotic plants in agricultural restorations.

We quantitatively assessed native bee preference for exotic and native plants in new and mature native plant hedgerows in an agriculturally intense area of Northern California. We asked the questions, (1) Do abundance, richness, and diversity of bee species foraging on exotic versus native plant species differ? (2) Do native bees preferentially forage on native as opposed to exotic plants in agricultural hedgerow restoration sites? (3) Is bee utilization of exotic and native plants different in mature hedgerows, where native plants dominate, versus newly planted hedgerows, where exotic plants still dominate? and, (4) Within the native plant species, are there species that are preferred or avoided relative to other native plants? We expected that native and exotic plants would be used in proportion to their availability in new and mature hedgerow sites, and would only be an important resource if availability was high.

Methods

Hedgerow Sites and Plantings

Newly established hedgerow sites were planted between 2007 and 2008 for the purpose of enhancing native bee populations. They were approximately 350 m long, located adjacent to natural or man-made sloughs, and contained a mix of native shrubs and forbs.

Mature hedgerow sites were established in 1996 and were comprised of a row of perennial shrubs, 305–550 m long, bordered by a stand of perennial grasses. While mature hedgerows were planted to promote natural enemy and reduce pest insect abundances (Bugg et al. 1998), the majority of the native flowering plant species also are part of the native planting palette that was used for the new hedgerow sites in this study.

Composition varied among sites in native plants due to differences in service focus (pollination enhancement at new hedgerows, pest control at mature hedgerows), differences in species choices made by the land owner, and differential survival among sites. All new and mature hedgerows contained varying ratios of *Ceanothus griseus* (California lilac), *Eriogonum fasciculatum* (California buckwheat), *Rosa californica* (California wild rose), *Rhamnus californica* (California coffeeberry), *Baccharis pilularis* (coyote brush), *Sambucus mexicana* (Mexican elderberry), and *Heteromeles arbutifolia* (toyon). Most, but not all sites contained *Salvia* spp. (sage), *Eschscholzia californica* (California poppy), *Grindelia camporum* (gumplant), *Achillea millefolium* (yarrow), and *Atriplex lentiformis* (quail bush).

The primary herbaceous exotic weeds found in both new and mature hedgerows were *Brassica* spp. (mustard), *Convolvulus arvensis* (field bindweed), *Malva parviflora* and *neglecta* (mallow), and *Picris echioides* (bristly oxtongue). Hedgerows were planted adjacent to rotational field crops of approximately 32 ha, that included primarily wheat, processing tomatoes, and alfalfa, which is typical of crop production in this region.

Study Design

We examined four mature hedgerows and four new hedgerow sites in Yolo County, CA, in 2009. There was a minimum of 1.5 km distance among hedgerows to ensure spatial independence.

New hedgerow sites were sampled three times over the course of the season, from late April until early August, with approximately 1.5 months between sample rounds. Mature hedgerow sites were sampled four times during the growing season, from early May until late July, with approximately 1 month between sample rounds. At each sample round, flowering vegetation was quantified using fifty 1 m^2 quadrats evenly spaced along the hedgerow. Within the quadrats, all plants with mature flowers were identified to species and flower cover of each species was estimated using a Braun-Blaunquet cover scale. Cover estimates were made by envisioning all flowers of a species within the vertical plane of the quadrat as a two-dimensional flat surface. To standardize estimates among collectors, all observers used an example “score-sheet” and were trained collectively to standardize and score in a consistent manner.

Bee communities were quantified using timed aerial netting. At mature hedgerow sites, bees were collected off of flowers for 30 minutes and at new hedgerows for 1 hour. The shorter amount of time at mature hedgerows was due to additional sampling protocols not reported here. As the collector slowly walked along the hedgerow, they checked every flower for the presence of a bee. If a bee was observed touching the reproductive parts of a flower it was netted and put into a labeled vial specific to that plant species. The timer was stopped after the bee was captured in the net, until the collector was ready to recommence flower observations, so that total observation time was standardized among collections. Because the observer examined every flower along the path for the presence of bees, time viewing each plant species was in proportion to its floral cover. Collected bees were pinned for later species identification, which was conducted by Prof. E. R. W. Thorp

(U. C. Davis, Henry B. Laidlaw Bee Biology Center). The non-native, but naturalized solitary bee species, *Megachile apicalis* and *Ceratina dallatoreana* were included in our native bee dataset; the combined total of these two naturalized bee species made up less than 2% of the total non-*Apis* bees in our samples.

In our study region, honey bees (*Apis mellifera*) primarily come from managed colonies. Because high recent colony losses of honey bees (Neumann & Carreck 2010) may partially be due to nutritional deficiencies that make bees more susceptible to disease (vanEngelsdorp et al. 2009), enhancing quality, abundance, diversity, and continuity of foraging resources may aid managed honey bee colony health. Therefore, we also examined honey bee use and preference of exotic and native plants in hedgerows. Because honey bees could reliably be identified to species in the field, honey bees were captured, recorded, and then released.

Data Analyses

Each dataset (mature sites and new hedgerow sites) was analyzed separately due to the slightly different methodologies employed. Floral cover from each quadrat, at each sample round, was summed to get a total cover score for that plant type (exotic or native) at that site for that sample round. Therefore for new hedgerow sites, there were four sites and three sample rounds, resulting in 12 records for native plants and 12 for exotic plants and at mature hedgerow sites there were four sites and four sample rounds, resulting in 16 records each for native and exotic plants. Mean floral cover of native and exotic plants was compared using a mixed model analysis of variance with a poisson distribution and log link function (GLIMMIX procedure, SAS 1999). Sample round nested within site was included as a repeated factor and site as a random factor.

We compared the response variables native bee abundance, richness, and diversity (Shannon index) on native and exotic plants (fixed factor) using a mixed model analysis of covariance with a log link function and poisson or negative binomial distribution (the poisson distribution was tried first and if the over-dispersion was not corrected than the negative binomial distribution was used) for bee abundance and richness data, and a normal distribution for diversity data. We included sample round nested within site as a repeated factor, site as a random factor, and floral cover as the covariate. We first included the interaction between cover and plant type to test the assumption of homogeneity of regression slopes. If the interaction was non-significant, we removed the interaction term from the analyses and report on the test of fixed effects for plant type. If the interaction was significant, we kept the interaction term and report least squares mean difference and the region(s) of significance between native and exotic plants along values of the covariate, flower cover (Johnson & Neyman 1936; Milliken & Johnson 2002). Including flower cover as a covariate acts to standardize for effort as flowers were observed in proportion to their cover. For bee abundance on native and exotic plants, standardizing for floral cover of natives and exotics additionally gives a measure of "preference" (Johnson 1980). That is, controlling for floral cover of plant type, preference is established if bees are more abundant on one plant type than the other (Alldredge & Ratti 1992). For preference analyses, we excluded sites that had less than 10 bees collected at that site and sample round, because sites with less than 10 bees collected would not have enough replication on exotic or native plants to give meaningful information on preference. Therefore, there are different results from "abundance" analyses controlling for cover (where all sites are included) and "preference" analyses where only a subset of sites are included.

We additionally utilized the reduced dataset to examine preference by native bees among native plant species semi-quantitatively at mature hedgerow sites (where there was enough cover of mature plants to permit meaningful analyses among species). The data were not amenable to statistical analyses such as Chi-square because of a large number of samples under five for each plant species. Therefore, we used a ranking system at each site calculated by number of bees found on each plant species at a site and sample round divided by the flower cover of that plant species. We ranked species according to this ratio, with higher numbers getting higher ranks (i.e. relatively more attractive).

Results

Floral Cover

At new hedgerow sites, cover of exotic flowers was greater than native flowers ($F_{[1,19]} = 11.81$, $p = 0.005$) with mean total cover score (SE) of 35.5 (6.8) and 10.1 (6.8), respectively. At mature hedgerow sites, there was no difference in floral cover between exotic and native plants ($F_{[1,26]} = 0.34$, $p = 0.57$) with mean total cover score (SE) of 19.1 (7.3) and 25.8 (7.1), respectively.

Bee Abundance, Richness, and Diversity

Of the 23 species of native bees netted on flowers at the new hedgerow sites, 7 species were observed only on exotic plants and 7 species were observed only on native plants. Of the 30 species of native bees netted on flowers at mature hedgerow sites, 23 bee species were observed only on native plant species and only 1 bee species was found only on exotic plant species.

There was an interaction between floral cover and native bee abundance at new hedgerow sites ($F_{[1,17]} = 8.08$, $p = 0.01$). We found significantly more native bees on native plants than exotic plants ($t_{[17]} = -3.32$, $p = 0.004$; Fig. 1) and $p < 0.05$ for all floral cover values greater than 15. At new hedgerow sites, there was no difference in native bee species richness and diversity between native and exotic plants (richness: $F_{[1,18]} = 0.83$, $p = 0.37$, diversity: $F_{[1,18]} = 0.17$, $p = 0.68$; Fig. 2).

At mature hedgerow sites, there was greater abundance (Fig. 1), richness, and diversity (Fig. 2) of native bees on native plants than exotic plants (abundance: $F_{[1,25]} = 19.22$, $p = 0.0002$, richness: $F_{[1,25]} = 13.07$, $p = 0.001$, diversity: $F_{[1,25]} = 10.00$, $p = 0.004$). Honey bee abundance was the same on native and exotic plants at new hedgerow sites

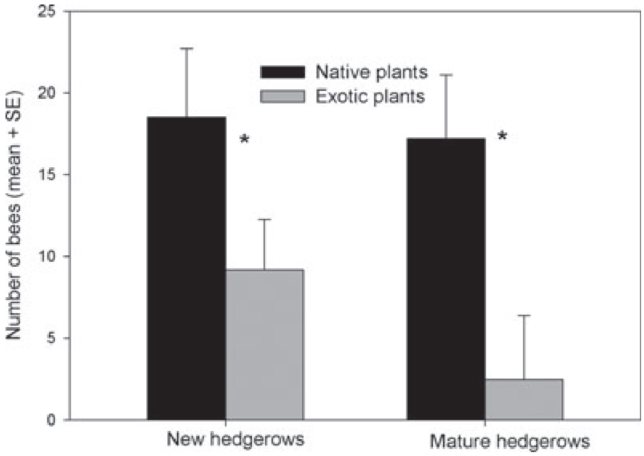

Figure 1. Mean number of native bees on exotic versus native plants from each site at each sample round. *Above bars indicates the response variable is different between native and exotic plants at $p < 0.05$.

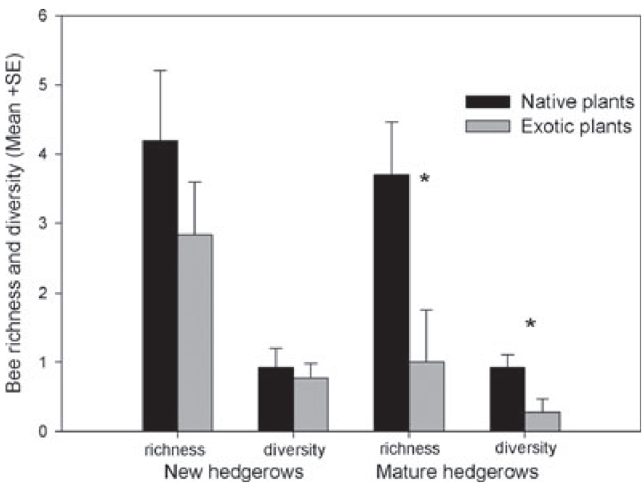

Figure 2. Mean native bee species richness and diversity (Shannon's diversity index) from each site and sample round at new hedgerow sites and mature hedgerow sites. * Above bars indicates the response variable is different between native and exotic plants at $p < 0.05$.

($F_{[1,17]} = 0.38$, $p = 0.55$). At mature sites, there was an interaction between floral cover and plant type on honey bee abundance ($F_{[1,24]} = 105.2$, $p < 0.0001$). Closer inspection of the region of significance revealed that honey bee abundance was greater on native plants at all cover levels and that the magnitude of difference between honey bee abundance on native versus exotic plants increased with increasing cover score.

Preference

At new hedgerow sites, regression slopes were significantly different for native bee abundance on native versus exotic plants (floral cover by plant type interaction: $F_{[1,11]} = 10.64$, $p = 0.008$). Mean bee abundance on native plants was greater than abundance on exotic plants ($t_{[11]} = -5.44$, $p = 0.0002$). At floral cover scores greater than 10, native bees showed a preference for native plants. As floral cover score increased, the difference between bee abundance on native and exotic plants increased (Fig. 3). Native bees preferred native plants over exotic plants at mature hedgerow sites at all cover amounts ($F_{[1,13]} = 39.08$, $p < 0.0001$) (Fig. 3).

Honey bees exhibited no preference for exotic or native plants in new hedgerow sites ($F_{[1,16]} = 0.01$, $p = 0.93$). In mature hedgerow sites, however, honey bees preferentially selected native plant species ($F_{[1,12]} = 102.81$, $p < 0.0001$) (Fig. 4).

Native Species Ranking

Semi-quantitative ranking of preference among native plant species showed that when present, *Eriogonum fasciculatum* and *Salvia* spp. were the most preferred native plant species (Table 1). Other species within the top preferred native plants for bee forage were *Eschscholzia californica*, *Rhamnus californica*, and *Grindelia camporum*. *Heteromeles arbutifolia*, *Achillea millefolium*, and *Atriplex lentiformis* had mixed results in terms of preference. *Sambucus mexicana* and *Rosa californica* were consistently less preferred by native bees when other native species were available. However, large numbers of syrphid flies (Family Syrphidae), which also can be important native pollinators of agricultural crops (Jauker & Wolters 2008), were caught on elderberry (L. Morandin & C. Kremen, unpublished data). Of the native bee species that were represented by greater than two individuals (17 species), four bee species were found on only one species of native plant in this subset of samples.

Discussion

These data indicate that native bees prefer to forage on native plants in both new and mature hedgerow sites. In addition, we found that bee abundance was greater on native plants in both new and mature hedgerows and bee richness and diversity were greater on native plants than exotic plants in mature hedgerows. Strikingly, 77% of bee species at mature hedgerows were only found on native plant species. These results indicate that in intense agricultural landscapes native plants are important for sustaining both abundance and diversity of native bee species.

Our finding of greater preference by native bees for native plants is contrary to some bee preference studies in natural or semi-natural areas that found greater or equal preference for exotic plants (Vila et al. 2009; Williams et al. 2011). At our new hedgerow sites, native shrubs were less than 3 years, and cover of exotic plants was greater at most sites; yet, we found that native bees preferentially chose native plants even when relative abundance of native plants was low.

Despite preference for native plants, at new hedgerow sites where native plants were sparse, substantial proportions of native bee (45%) and honey bee (66%) collections were on exotic plants. In contrast, at mature hedgerow sites, where native flowers were as abundant as exotic flowers, exotic plants

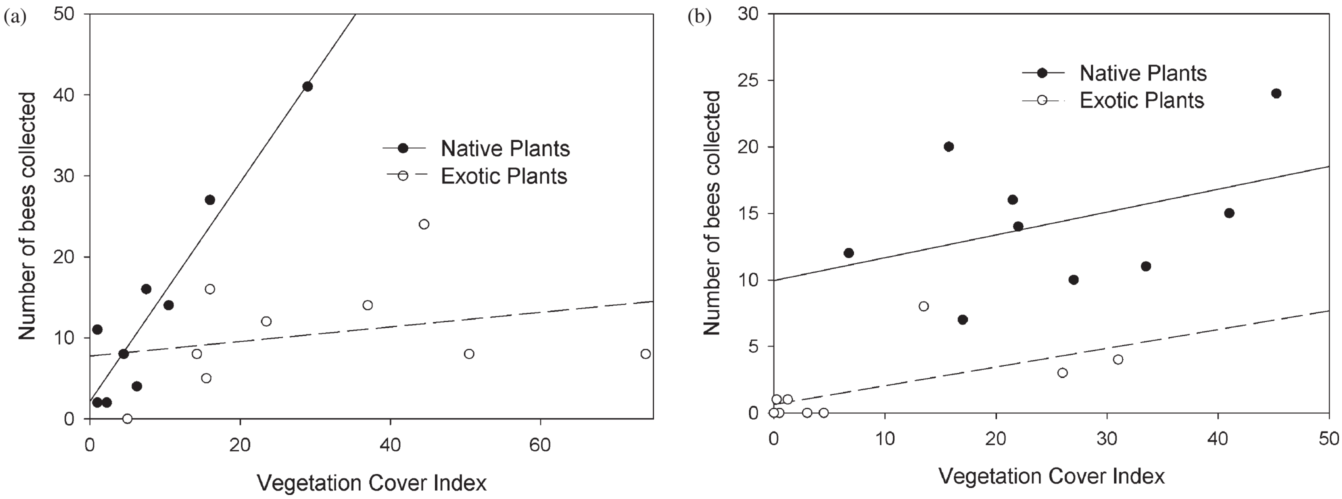

Figure 3. Native bee abundance on exotic and native plants at (a) new hedgerow sites and (b) mature hedgerow sites. Cover of exotic and native plants at each site, sample round combination was included as a covariate in the model in order to assess bee preference.

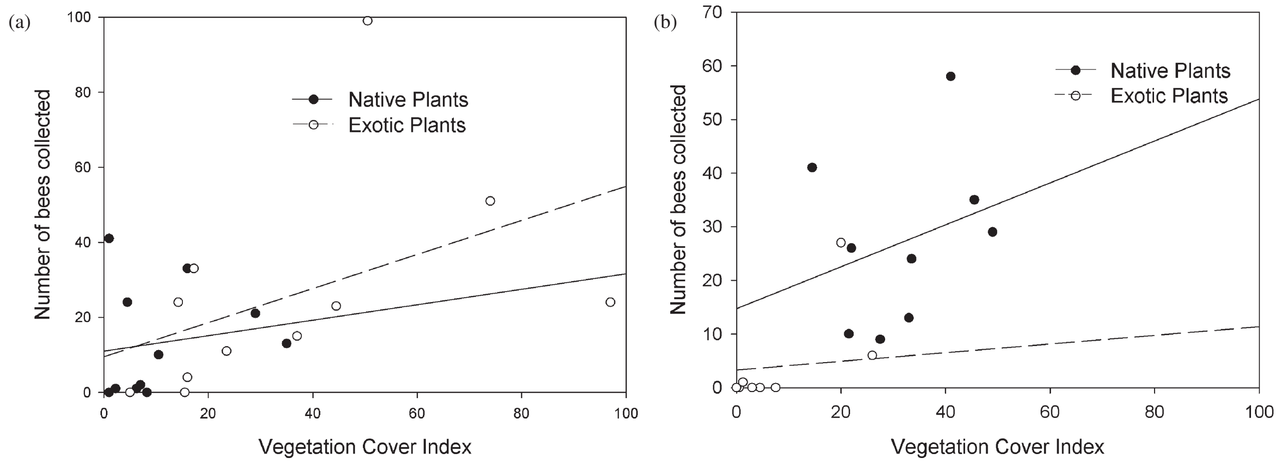

Figure 4. Honey bee abundance on exotic and native plants at (a) new hedgerow sites and (b) mature hedgerow sites. Cover of exotic and native plants at each site, sample round combination was included as a covariate in the model in order to assess bee preference.

were a less important resource for native or honey bees (12 and 16% of collections, respectively). This suggests that in regions where exotic plants dominate, they can be an important resource for native and managed bees. Williams et al. (2011) proposed that the greater reliance of native bees on alien species found in their study was driven by a subset of "super-generalist" plants that form links with a large proportion of native bees. Some of the alien species that were highly abundant and visited in the Williams et al. (2011) study were also found in relatively high density in our new and mature hedgerow sites (e.g. *Brassica nigra* and *Convolvulus arvensis*); yet we did not find these species to be preferred over co-occurring native plants.

Honey bees in new hedgerow sites did not prefer native plants but rather used native and exotic plants in proportion to their abundance. Honey bees are eusocial and recruit foragers to rewarding patches (Winston 1987). Returning honey bee foragers communicate information regarding location and floral odor of rewarding patches to the hive (Arenas et al. 2007). As native plants generally had low amounts of floral display at new hedgerow sites, there likely would be little recruitment to these plant species. Interestingly, at mature hedgerow sites where native floral cover was similar to the exotic floral cover, honey bees were found to prefer native plants. This suggests that given roughly equal floral display, honey bees were recruiting more bees to native plants in the mature hedgerow sites. In light of the recent serious declines of honey bees and suspected role of poor nutrition in agricultural settings (vanEngelsdorp et al. 2009), creation of native plant hedgerows in intense agricultural areas may benefit honey bee colony health.

At mature hedgerow sites bee species richness and diversity on native plants were greater than richness and diversity of native bees on exotic plant species. Recent studies suggest that habitats with greater bee diversity can result in greater or more stabilized crop production (Klein et al. 2007; Klein

Table 1. Semi-quantitative ranking of bee preference for native plant species in four hedgerow restoration sites in 2009.

Site	SR	1	2	3	4	Co-occurring native plants with no bee visits during our sample
1	1	ERFA2	SALVI	ACMI2		CEGR2
1	2	SALVI				HEAR5, ACMI2,S
1	3	SALVI	ACMI2	ERFA2		HEAR5,EPCA4
1	4	ERFA2	SALVI	EPCA4		ACMI2
2	3	ERFA2	ASFA			HEAR5
2	4	HEAR5	RHCA	SAME5	ERFA2	
3	2	ERFA2	GRCA	HEAR5		SAME5
3	3	ASFA				SAME5, ATLE
4	1	ESCA2	PHCA			
4	2	ESCA2	GRCA			ROCA2, HEAR5, FRCA6,S
4	3	GRCA	RHCA	ATLE		ROCA2,SAME5

ACMI2, *Achillea millefolium*; ASFA, *Asclepias fascicularis*; ATLE, *Atriplex lentiformis*; CEGR2, *Ceanothus griseus*; EPCA4, *Epilobium californicum*; ERFA2, *Eriogonum fasciculatum*; ESCA2, *Eschscholzia californica*; FRCA6, *Fremontodendron californicum*; GRCA, *Grindelia camporum*; HEAR5, *Heteromeles arbutifolia*; PHCA, *Phacelia californica*; RHCA, *Rhamnus californica*; ROCA2, *Rosa californica*; SALVI, *Salvia* spp.; SAME5, *Sambucus mexicana*.
Preference rank (1–4) was assigned by calculating the number of bees collected off of each flower type (at a site and sample round [SR]) divided by the cover proportion of flowers of each plant species. Plants with the highest value relative to other plants at each site and sample round were ranked as "1," the next highest value was ranked as "2," etc.

et al. 2009; Garibaldi et al. 2011). While few studies have examined mechanisms underlying the relationship between bee diversity and stability of pollination services, there is evidence that functional complementarity among bee groups may be an important factor leading to greater crop production (Hoehn et al. 2008; Winfree & Kremen 2009). Thus, native plant hedgerows, by enhancing bee diversity over exotic weedy edges, may help to stabilize or enhance crop production.

Recommendations for hedgerow plantings to promote pollinators often stress the use of a range of plant species in order to provide diverse and continuous resources throughout the season (Menz et al. 2011). Yet, in a review of restoration for bees, Winfree (2010) found that most studies showed that only a few plant species provided the majority of resources for bees, suggesting that restoration could be made more cost effective by focusing on the highly attractive subset of plant species. However, most of the reviewed studies were conducted in the EU on *Bombus* species. In contrast, we found wild bees on all native plant species in bloom in our hedgerows, except *Rosa californica* on which we have observed and netted native bees in other studies. Native plants with the highest visitation rates per unit of cover (preference score) changed among sample rounds within sites. This changing preference likely reflects differences in availability of flower species throughout the season as well as temporal turnover in bee community composition. Because a quarter of native bee species that had greater than two individuals collected at these sites were found on only one native plant species, and each on a different native plant species, our data suggest that a diversity of native plants is essential to maintaining native bee diversity. Our data support planting a wide range of native plants that are attractive to bees in order to provide spatially and temporally diverse resources.

Our study focuses on habitat enhancement using native perennial plants, whereas most studies on agricultural habitat enhancement in agroecosystems have examined non-native annual plants (Fiedler et al. 2008). Enhancement with native perennial plants can create long-term bee habitat that requires little input from the landowner after the first few years of maintenance (Long & Anderson 2010), and can provide other benefits such as conservation of native plants and associated fauna (Fiedler et al. 2008). Although the mature hedgerows were designed for natural enemy enhancement and pest control, the native plants were an important resource for bees. Previous research in the mature hedgerows examined in this study showed that natural enemy to pest ratios were greater in hedgerows relative to weedy areas (Morandin et al. 2011). Similar to our findings, Tuell et al. (2008) observed overlap in use of native plant species by pollinator and natural enemy insects suggesting that they may provide multiple ecosystem services (Fiedler et al. 2008).

The combination of low-maintenance and enhancement of multiple guilds of beneficial insects may provide incentives for growers to adopt hedgerow restoration with native plants. Our study provides promising first evidence that native bees preferentially choose native plants as forage resources in hedgerows. In addition, these data indicate that hedgerows of mature native plants will attract or promote a more species rich and diverse community of native bees than field edges where exotic plants dominate, possibly aiding stability of pollination function.

Implications for Practice

- In intense agricultural landscapes hedgerow restoration using native shrubs and forbs provide valuable resources for native bees.
- Native plants within these small, linear habitat elements are the most important resource for enhancing native bee abundance and diversity in degraded landscapes.
- Native and honey bee preference for native plants over co-occurring exotic plants supports the use of native plants in hedgerow restoration for pollination.
- A diversity of native plants is required to enhance native bee diversity.

Acknowledgments

We thank the growers and land owners in Yolo County, CA, that allowed us to work on their property. C. Locke, H. Wallis, S. Ambercrombie, C. Valiente, and G. Panlasigui, and J. Brennan assisted with the data collection. The research was funded by an NSERC Postdoctoral Fellowship to L.A.M., a Conservation Innovation Grant, a National Science Foundation grant, and a National Geographic Society Research and

Exploration grant. Members of the Kremen Laboratory, UC Berkeley, provided valuable comments on manuscript drafts.

LITERATURE CITED

Aizen, M. A., and L. D. Harder. 2009. The global stock of domesticated honey bees is growing slower than agricultural demand for pollination. Current Biology **19:**915–918.

Alldredge, J. R., and J. T. Ratti. 1992. Further comparison of some statistical techniques for analysis of resource selection. Journal of Wildlife Management **56:**1–9.

Arenas, A., V. M. Fernandez, and W. M. Farina. 2007. Floral odor learning within the hive affects honeybees' foraging decisions. Naturwissenschaften **94:**218–222.

Brown, B. J., R. J. Mitchell, and S. A. Graham. 2002. Competition for pollination between an invasive species (purple loosestrife) and a native congener. Ecology **83:**2328–2336.

Bugg, R. L., J. H. Anderson, C. D. Thomsen, and J. Chandler. 1998. Farmscaping in California: hedgerows, roadside plantings and wild plants for biointensive pest management. In C. H. Pickett and R. L. Bugg, editors. Enhancing biological control: habitat management to promote natural enemies of agricultural pests. University of California Press, Berkeley.

Fiedler, A. K., D. A. Landis, and S. D. Wratten. 2008. Maximizing ecosystem services from conservation biological control: the role of habitat management. Biological Control **45:**254–271.

Garibaldi, L. A., I. Steffan-Dewenter, C. Kremen, J. M. Morales, R. Bommarco, S. A. Cunningham, L. G. Carvalheiro, N. P. Chacoff, J. H. Dudenhoffer, S. S. Greenleaf, et al. 2011. Stability of pollination services decreases with isolation from natural areas despite honey bee visits. Ecology Letters **14:**1062–1072.

Hannon, L. E., and T. D. Sisk. 2009. Hedgerows in an agri-natural landscape: potential habitat value for native bees. Biological Conservation **142:**2140–2154.

Hoehn, P., T. Tscharntke, J. M. Tylianakis, and I. Steffan-Dewenter. 2008. Functional group diversity of bee pollinators increases crop yield. Proceedings of the Royal Society B: Biological Sciences **275:**2283–2291.

Hopwood, J. L. 2008. The contribution of roadside grassland restorations to native bee conservation. Biological Conservation **141:**2632–2640.

Jauker, F., and V. Wolters. 2008. Hover flies are efficient pollinators of oilseed rape. Oecologia **156:**819–823.

Johnson, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. Ecology **61:**65–71.

Johnson, P. O., and J. Neyman. 1936. Tests of certain linear hypotheses and their application to some educational problems. Statistical Research Memoirs **1:**57–93.

Klein, A. M., C. M. Mueller, P. Hoehn, and C. Kremen. 2009. Understanding the role of species richness for pollination services. Pages 195–208 in A. H. D. Bunker, M. Loreau, C. Perrings, and S. Naeem, editors. Biodiversity, ecosystem functioning, and human wellbeing: an ecological and economic perspective. Oxford University Press, Oxford, United Kingdom.

Klein, A. M., I. Steffan-Dewenter, and T. Tscharntke. 2003. Pollination of *Coffea canephora* in relation to local and regional agroforestry management. Journal of Applied Ecology **40:**837–845.

Klein, A. M., B. E. Vaissiere, J. H. Cane, I. Steffan-Dewenter, S. A. Cunningham, C. Kremen, and T. Tscharntke. 2007. Importance of pollinators in changing landscapes for world crops. Proceedings of the Royal Society B: Biological Sciences **274:**303–313.

Kremen, C., N. M. Williams, R. L. Bugg, J. P. Fay, and R. W. Thorp. 2004. The area requirements of an ecosystem service: crop pollination by native bee communities in California. Ecology Letters **7:**1109–1119.

Kremen, C., N. M. Williams, and R. W. Thorp. 2002. Crop pollination from native bees at risk from agricultural intensification. Proceedings of the National Academy of Sciences of the United States of America **99:**16812–16816.

Long, R. F., and J. Anderson. 2010. Establishing hedgerows on farms in California. Agriculture and Natural Resources Publication 8390 (available from http://ucanr.org/freepubs/docs/8390.pdf).

Menz, M. H. M., R. D. Phillips, R. Winfree, C. Kremen, M. A. Aizen, S. D. Johnson, and K. W. Dixon. 2011. Reconnecting plants and pollinators: challenges in the restoration of pollination mutualisms. Trends in Plant Science **16**:4–12.

Milliken, G. A., and D. E. Johnson. 2002. Analysis of messy data. Volume III: analysis of covariance. Chapman and Hall/CRC, Boca Raton, Florida.

Morales, C. L., and A. Traveset. 2009. A meta-analysis of impacts of alien vs. native plants on pollinator visitation and reproductive success of co-flowering native plants. Ecology Letters **12:**716–728.

Morandin, L. A., and M. L. Winston. 2006. Pollinators provide economic incentive to preserve natural land in agroecosystems. Agriculture Ecosystems & Environment **116:**289–292.

Morandin, L. M., R. F. Long, C. Pease, and C. Kremen. 2011. Hedgerows enhance beneficial insects on farms in California's Central Valley. California Agriculture **65:**197–201.

Neumann, P., and N. L. Carreck. 2010. Honey bee colony losses. Journal of Apicultural Research **49:**1–6.

Pywell, R. F., E. A. Warman, C. Carvell, T. H. Sparks, L. V. Dicks, D. Bennett, A. Wright, C. N. R. Critchley, and A. Sherwood. 2005. Providing foraging resources for bumblebees in intensively farmed landscapes. Biological Conservation **121:**479–494.

Ricketts, T. H., J. Regetz, I. Steffan-Dewenter, S. A. Cunningham, C. Kremen, A. Bogdanski, B. Gemmill-Herren, S. S. Greenleaf, A. M. Klein, M. M. Mayfield, et al. 2008. Landscape effects on crop pollination services: are there general patterns? Ecology Letters **11:**499–515.

SAS. 1999. SAS system for Windows. SAS Institute Inc., Cary, North Carolina.

Tuell, J. K., A. K. Fiedler, D. Landis, and R. Isaacs. 2008. Visitation by wild and managed bees (Hymenoptera: Apoidea) to eastern US native plants for use in conservation programs. Environmental Entomology **37:**707–718.

vanEngelsdorp, D., J. D. Evans, C. Saegerman, C. Mullin, E. Haubruge, B. K. Nguyen, M. Frazier, J. Frazier, D. Cox-Foster, Y. P. Chen, et al. 2009. Colony collapse disorder: a descriptive study. Plos One **4:**e6481.

Vaughan, M., M. Shepherd, C. Kremen, and S. H. Black. 2007. Farming for bees. The Xerces Society for Invertebrate Conservation, Portland, Oregon.

Vila, M., I. Bartomeus, A. C. Dietzsch, T. Petanidou, I. Steffan-Dewenter, J. C. Stout, and T. Tscheulin. 2009. Invasive plant integration into native plant-pollinator networks across Europe. Proceedings of the Royal Society B-Biological Sciences **276:**3887–3893.

Watanabe, M. E. 1994. Pollination worries rise as honey bees decline. Science **265:**1170.

Williams, N. M., D. Cariveau, R. Winfree, and C. Kremen. 2011. Bees in disturbed habitats use, but do not prefer, alien plants. Basic and Applied Ecology **12:**332–341.

Winfree, R. 2010. The conservation and restoration of wild bees. Annals of the New York Academy of Sciences **1195:**169–197.

Winfree, R., R. Aguilar, D. P. Vazquez, G. Lebuhn, and M. A. Aizen. 2009. A meta-analysis of bees' responses to anthropogenic disturbance. Ecology **90:**2068–2076.

Winfree, R., T. Griswold, and C. Kremen. 2007. Effect of human disturbance on bee communities in a forested ecosystem. Conservation Biology **21:**213–223.

Winfree, R., and C. Kremen. 2009. Are ecosystem services stabilized by differences among species? A test using crop pollination. Proceedings of the Royal Society B: Biological Sciences **276:**229–237.

Winston, L. 1987. The biology of the honey bee. Harvard University Press, Cambridge, Massachusetts.