RESEARCH ARTICLE

Restoration of Nontarget Species: Bee Communities and Pollination Function in Riparian Forests

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Abstract

Nontarget species such as pollinators may be of great importance to the restoration process and the long-term functioning of restored habitats, but little is known about how such groups respond to habitat restoration. I surveyed bee communities at five equal-aged restored sites, paired with five reference sites (riparian remnants) along the Sacramento River, California, United States. Flower availability and bee visitation patterns were also measured to examine the restoration of pollination function. Restoration of structural vegetation allowed diverse and abundant native bee communities to establish at the restoration sites; however, the composition of these important pollinator communities was distinct from that in the remnant riparian sites. Differences did not arise primarily from differences in the composition of the flowering-plant community; rather there must be other physical characteristics of the restored sites or differences in nesting site availability that led to the different pollinator communities. Because sites were spatially paired, the differences are unlikely to be driven by landscape context. Bee life-history and other biological traits may partially explain the differences between bee communities at restored and remnant sites. Patterns of visitation to native plant species suggest that pollination function is restored along with pollinator abundance and richness; however, function may be less robust in restored habitats. An examination of interaction networks between bees and plant species found at both restored and remnant riparian sites showed less redundancy of pollinators visiting some plants at restored habitats.

Key words: bees, community composition, ecological function, nonmetric multidimensional scaling, pollination webs, restoration, riparian.

Introduction

The goal of ecological restoration is to achieve a self-sustaining system that has restored function and contains a high proportion of species from the pre-degraded "natural" state (Ehrenfeld & Toth 1997; Palmer et al. 2006). Limited time and resources often compel restoration programs to focus on a limited set of elements, such as replanting structural vegetation and reintroducing specific target species. Nontarget species are left to colonize on their own as conditions become appropriate. In some cases, these species serve important functional roles in the restored ecosystem and may even enhance the restoration process. Thus, understanding the extent to which such nontarget species return and the factors that affect the composition of their communities can be useful in guiding the restoration process and for predicting long-term outcomes. Insects play diverse roles in ecosystem functioning across different systems (Didham et al. 1996; Larsen et al. 2005), but with few exceptions they are rarely part of conservation goals, let alone the targets of restoration (but see Kwilosz & Knutson 1999; McIntire et al. 2007; Talley et al. 2007).

Pollination is one critical insect-derived ecological function. The persistence of native plant communities within restored habitat relies on a pollinator community that is able to provide pollination over time (Handel 1997). Indeed, in some cases successful restoration, even during the initial seasons, requires pollination to perpetuate plant communities (Handel 1997). Restoration of pollinator communities has potential added benefit where pollinators deliver service to crops and native plants beyond the restored site (Kremen et al. 2002, 2007). From the perspective of conservation management, such trans-boundary service adds direct value to the restored habitat.

Bees are dominant pollinators of angiosperms in most terrestrial regions (Neff & Simpson 1993). In addition, their taxonomy and ecology are also relatively well characterized making them well suited for investigating response to restoration. There is also growing evidence that many species of bees may be declining globally (Biesmeijer et al. 2006; NRC-USA 2007). A meta-analysis of recent studies exploring the response of bee communities to human disturbance and land-use change at different scales shows a generally negative effect of habitat loss on abundance and species richness (Winfree et al. 2009). Given that bees and other pollinators are under substantial threat from the loss of native habitat, it is surprising that there are so few studies exploring the responses of this critical nontarget group to habitat restoration (but see Forup & Memmott 2005; Forup et al. 2008).

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Because bees provide a critical pollination service upon which plants and other organisms rely, a key question for their restoration is whether pollination is restored along with bee communities. Recent reviews of studies from a variety of ecosystems show positive correlations between biological diversity and ecological functioning (Schwartz et al. 2000; Srivastava & Vellend 2005; Balvanera et al. 2006) and studies of native pollinators in the context of landscape change have found that the level of pollination correlates with the abundance and species richness of pollinators (Kremen et al. 2002; Klein et al. 2008; Slagle & Hendrix 2009). Some researchers have suggested that the restoration of pollination may be independent of the exact pollinator species involved (Forup & Memmott 2005), but data to address this question are lacking.

To explore the response of bees and pollination to restoration, I surveyed bee and plant communities at restored riparian sites along the Sacramento River, California, United States and compared these with communities found in remnants of riparian habitat within the same region. All restored sites were at a mid-successional stage; therefore, this survey provides a picture of bee communities assembling at one point in the restoration process. I focused on three interrelated questions. How do the abundance, richness, and species composition of bee communities at restored riparian sites differ from those in remnant riparian habitats (the identified reference condition)? How important are floral communities in determining the structure of these pollinator communities? Are patterns of floral visitation at restored sites similar to those at remnant riparian sites?

The Sacramento River is the largest in California and one that has been dramatically altered by human activities. Over the past 100 years, riparian vegetation has been largely replaced by orchards and row crop agriculture leaving only 5–6% of the original riparian forest area (Greco 1999), all of it fragmented and altered by invasive plant species (Holl & Crone 2004). Following a mandate from California Senate Bill 1086 and the CALFED Bay Delta Program, The Nature Conservancy in partnership with other non-governmental organizations and government agencies launched the Sacramento River Project in an effort to provide a unified approach to restoration and management of the ecological system. The Project's strategies for restoring the Sacramento River include replanting orchards within the 2.5-year flood zone with native trees, shrubs, and understory plants (~1,457 ha thus far replanted, ~1,228 ha planned; Golet et al. 2008). Efforts have focused primarily on reestablishing structural vegetation with the hope that nontarget fauna and flora will return over time. The restoration efforts by the Sacramento River Project partners created a series of restoration sites that offer a unique system in which to study the outcome of restoration with a replicated design.

Methods

Site Information

To examine whether bee communities reestablished during the restoration of riparian habitats along the Sacramento River,

I established 1-ha sampling plots within each of five restored sites (Fig. 1). All sites were of equal age, restored from walnut or almond orchards 6 years prior to sampling, and planted with similar structural vegetation that included various perennial plant species (Table 1). At the time of sampling, the sites were mid-succession stands. I paired each restored plot with one of equal area located in neighboring remnant riparian habitat. These remnant riparian sites contained mixtures of riparian forest with *Acer* spp., *Quercus* spp. and *Salix* spp., open grass, and gravel (Alpert et al. 1999; Holl & Crone 2004). The exact stand composition varied among remnant sites; however, they were selected to represent typical mixed riparian forest habitat in the region and to have relatively consistent structure. All sites in the study fell within the 2.5-year flood zone of the river. Sampling plots were placed within sites so that they captured the variation in structural vegetation of the site. The site pairs were located along 250 km of river between the towns of Red Bluff and Chico, California, United States. Pairs were at least 5.5 km apart (most >10 km) and plots within pairs were 0.5–3.7 km apart. This provided a replicated sampling design with spatially independent sites, which is often difficult in the assessment of restoration.

Bee and Flower Sampling

I surveyed bees within the plots every 6 weeks from late February through August 2003 using net collecting and pan sampling (Roulston et al. 2007; Westphal et al. 2008). The 6-week interval may have missed a fraction of the bee fauna during the late spring when species turnover is rapid; however, because all sites were sampled during each period, it should not bias the comparison of faunas between site types. During each survey session, the restored and remnant riparian sites within a pair were always surveyed on the same day, by the same individuals. All 10 plots were surveyed within 2 days of each other. Surveys were only carried out on days with full sun, temperatures above 14°C and with wind less than 2 m/s (measured at 1.5 m above the ground). Two collectors netted bees from all flowering plants while continually walking throughout the plot for 1 hour in the morning (08:45–11:45 AM) and 1 hour in the afternoon (12:00–14:30 PM). This schedule included peak flight periods of different species. Only insects that were actively visiting flowers were netted. Collectors avoided staying at any one patch of flowers for more than 2 minutes at one time although the same patch could be sampled later in the collection period. Thus, plant species were sampled according to their proportional abundance within the plot. Insect specimens were kept separate by plant species so that floral associations for all specimens could be made.

On the same day, collectors placed 30 pan traps on the ground in an X through the center of the plot. Pans were 6 oz plastic Solo® bowls painted fluorescent yellow, fluorescent blue or plain white and filled with very weak detergent solution (http://online.sfsu.edu/~beeplot/). Traps were positioned 10 m apart with alternating colors. I avoided placing bowls under shrubs or thick grass, but otherwise they were not positioned
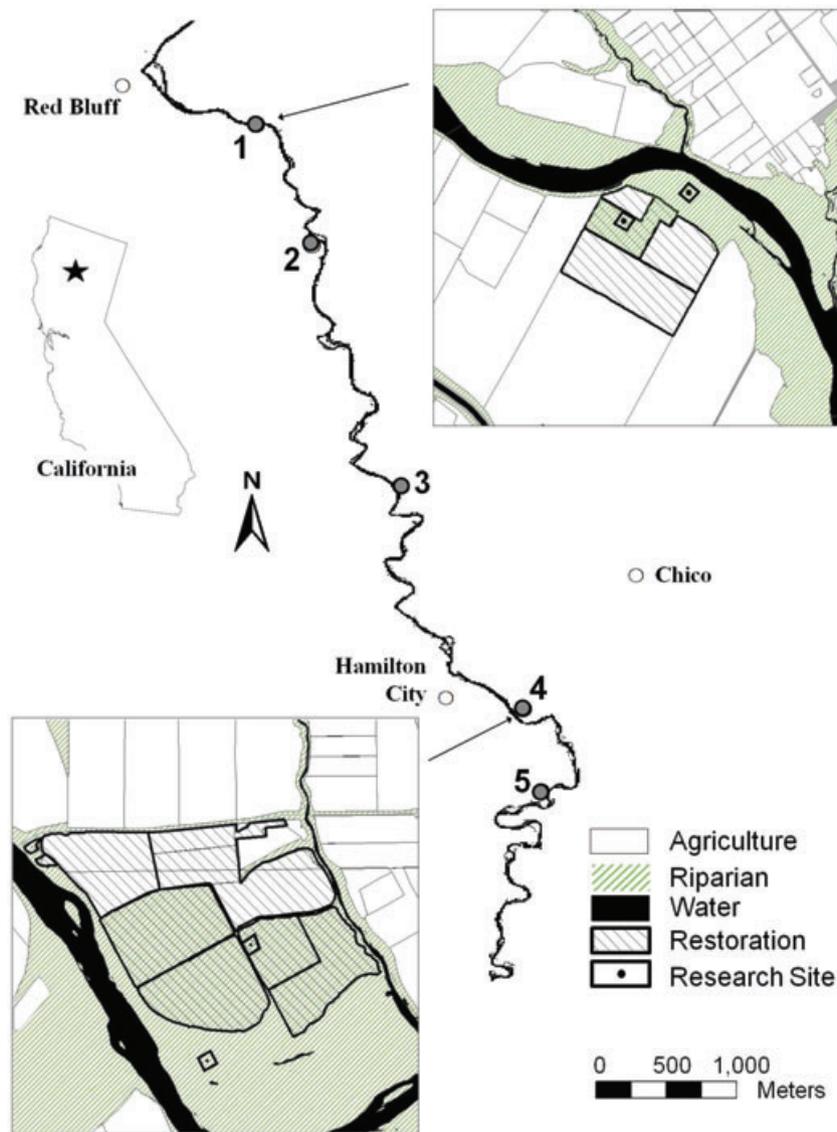
Figure 1. Map of study site locations. Numbered gray dots on the main map indicate the location of the five site pairs along the Sacramento River channel. Inset boxes show La Barranca (1) and Pine Creek (4) study sites with the locations of sampling plots within riparian remnants and restored riparian habitats. The scale bar refers to inset boxes.

Table 1. Restoration site characteristics.

Site	Target Community	Area of Restored Site (ha)	Area of Paired Remnant (ha)	% Natural 1.5 km	Prior Land Use	Plant Date	Planted Species
(1) La Barranca	Mixed riparian	14.7	75.2	19.9	Walnut	1997	1–7, 9, 10
(2) Rio Vista	Mixed riparian	55.8	55.8	30.3	Almond	1997	1–5, 7, 8
(3) Flynn	Mixed riparian	64.8	50.6	37.0	Walnut	1998	1–5
(4) Pine Creek	Mixed riparian and valley oak	20.0	51.5	47.5	Walnut/almond	1998	1–8
(5) Phelan Island	Mixed riparian and valley oak	13.9	21.2	46.3	Walnut	1998	1–6, 9

Planted species: 1, *Populus fremontii*; 2, *Platanus racemosa*; 3, *Salix* spp.; 4, *Quercus lobata*; 5, *Rosa californica*; 6, *Acer negundo*; 7, *Sambucus mexicana*; 8, *Baccharis pilularis*; 9, *Fraxinus latifolia*; 10, *Cephalanthus occidentalis*.
Site numbers correspond to those in Figure 1.

in specific microenvironments. All pan traps were set out by 8:00 AM and were retrieved by 15:00 PM.

On each survey day, collectors also assessed floral abundance within each plot using 60 0.25 × 4 m quadrats positioned in a stratified random arrangement throughout the plot (Elzinga et al. 2001). Collectors counted the number of functional flowers (inflorescences for Asteraceae and Fabaceae) within each quadrat. Functional flowers were defined as those having visible fresh anthers and/or stigmas and unwilted petals.

Analysis

I compared the abundance, evenness, and species richness of wild-bee communities between restored sites and remnant riparian sites using paired t tests. Evenness was included because different numerical responses to restoration among bee species might produce similar richness values but strong differences in species evenness between restored sites and remnant riparian sites. I tested evenness using H/H_{max}, where H is the Shannon diversity index and H_{max} is its maximum value (ln[species richness]). All response variables were first tested for and met assumptions of normality and equal variances.

The similarity among bee communities at different sites was visualized using nonmetric multidimensional scaling (NMS; Kruskal 1964; PC-ORD version 4, MjM Software, Gleneden Beach, OR, U.S.A). The ordination was based on relative Sørensen distances (McCune & Grace 2002), which are calculated from differences in the proportional abundance rather than the absolute abundance of each species. This metric allowed me to focus on differences in relative composition among sites (McCune & Grace 2002) rather than on the absolute differences in abundance of the sampled communities. Absolute abundances were already tested using paired t tests. Preliminary analysis using Sørensen index without standardization (i.e., Bray–Curtis index) yielded qualitatively similar results. The reliability of NMS ordination is based on stress and instability of the final configuration. In this study, stress measures the overall disagreement between inter-site distances in higher dimensional space and in reduced dimensionality. Instability measures how robust the reduced dimensional solution is among multiple iterations. Here, the final dimensionality was selected such that adding a dimension did not substantially reduce the stress. Data fit was tested using 50 runs with 200 iterations each with an accepted stress less than 10 and an instability less than 0.0003 (McCune & Grace 2002). After completing the ordinations, I tested the significance of the differences between bee communities at restored sites and remnant riparian sites using multi-response permutation procedures (MRPP; PC-ORD version 4, MjM Software). This procedure compares average distances among sites within a group (e.g., all restored sites) against such distances with sites randomly assigned to groups (McCune & Grace 2002). To explore whether differences of bee communities among sites were due to species identity (i.e., species unique to restored or remnant riparian habitats) or to differences in relative abundance of shared species, I repeated ordinations and MRPP testing using presence–absence data rather than relative abundances.

Similar results between the two analyses would indicate the importance of species differences between the two habitat types.

I examined the role of plant community richness and composition in determining the bee communities found at restored versus remnant riparian sites. I used Mantel tests to quantify the similarity of plant communities among sites to the similarity of bee communities among these same sites. Separate similarity matrices among all site pairs were compiled for bees and plants using relative Sørensen index values and these two were used as input for the Mantel test. NMS ordinations were used to visualize similarity of plant communities among sites. The methods and metrics for NMS were the same as those used for bee communities.

I explored whether pollination was restored using pollinator visitation patterns to plant species as a proxy for pollination. This approach ignores potential differences in quality among pollinators due to the amount or quality of pollen they transfer (Harder & Barrett 1996; Mayfield et al. 2001; Thomson 2003); however, a recent analysis suggests that it can serve as a reasonable first approximation for pollination in many instances (Vázquez et al. 2005). I first tested for differences in the connectance of wild-bee and plant communities between restored sites and remnant riparian sites and with Wilcoxon signed-rank tests. Connectance (C) measures the proportion of realized linkages (l) out of the total possible linkages between bees and plants given the number of bee (b) and plant (p) species in the sampled community, such that

$$C = \frac{l}{bp} \tag{1}$$

Thus, it provides a general measure of how many bee species are visiting the plant species. It has been used to characterize pollinator–plant interactions for a variety of different communities in different ecosystems (Jordano 1987; Jordano et al. 2003; Vázquez & Aizen 2004; Forup & Memmott 2005; Morales & Aizen 2006; Vila et al. 2009). My specific metric differs from those in most previously published studies because it adjusts for "forbidden links," which are precluded because of incongruence between pollinator and plant phenology (Jordano et al. 2003; Vázquez et al. 2009). Many studies pool visitation and plant species present at a site throughout the season; however, some plant species only flower at times beyond the flight season of certain bee species. Links between such plants and bees are precluded. Failure to remove them underestimates the functional connectance of the interaction web between plants and bees.

Although my preliminary measurement of connectance included exotic plant species, the remaining analyses focused on native plants. I tested for differences in the proportion of native plants receiving visits at restored and remnant riparian sites using Wilcoxon signed-rank tests. There were five pollinator-dependent native plant species common to restored and remnant riparian communities. For these species, I tested whether species richness and abundance of visitors to these plant species differed between restored and remnant sites using

two-way analysis of variance with site type and plant species as fixed effects. The inclusion of only plants found in both types of sites controlled for differences in bee pollinators among habitats that might result from plant species-specific differences such as floral rewards, morphology, and flowering phenology. I ran this analysis both with and without visits by *Apis mellifera* (honeybees) to consider whether persistence of these plants might depend on an exotic, managed pollinator species.

Results

Net and pan samples yielded 4,128 specimens from 124 bee species (Appendix S1). A total of 82 species were netted at flowers, some of which also occurred in pan samples. An additional 42 species were found exclusively in pan samples. A total of 90 species were found at restored sites and 91 at remnant riparian sites. Average richness, abundance, and evenness among bee species did not differ between restored and remnant riparian sites (Table 2; richness $t = 0.33$, degrees of freedom [df] = 4, $p = 0.62$; abundance $t = 1.79$, $df = 4$, $p = 0.15$; evenness $t = 0.22$, $df = 4$, $p = 0.83$).

Despite similar abundance and richness, the composition of bee communities at restored sites differed strikingly from those at remnant riparian sites (Fig. 2a; MRPP: $A = 0.12$, $p = 0.003$). When ordinated based only on presence–absence of bee species within the communities, restored sites still clustered separately from remnant riparian sites, although clustering was weaker (MMRP; $A = 0.10$, $p = 0.03$) and no clear low-dimensional solution was found using NMS ordination. On average restored sites shared only $36 \pm 3\%$ of species with their paired remnant and similarity accounting for relative species abundances equaled 0.45 ± 0.05 (relative Sørensen index). In addition, bee communities at restored sites were not strongly nested subsets of communities found at the remnant riparian sites. Over a quarter of all species (27.4%) were unique to restored sites and 28.2% of bee species were not found at any restored site. In both cases, nearly half of these were represented by only one individual. After excluding singletons, 14 of 82 (16.6%) bee species were unique to restored sites, and 15 bee species were unique to remnant riparian sites.

The average richness and abundance of flowers did not differ between habitat types (Table 2; richness, $t = 1.14$, $df = 4$, $p = 0.84$; abundance, $t = 0.73$, $df = 4$, $p = 0.51$;

Appendix S2 provides a full species list). Similar to the result for bees, the composition of floral communities at restored sites differed strikingly from those at remnant riparian sites (average similarity 0.13 ± 0.09, relative Sørensen index; Table 2). However, unlike for bees, plant communities at restored sites did not cluster separately from remnant riparian sites (Fig. 2b; MRPP: $A = 0.04$, $p = 0.41$). Thus, there was no characteristic floral community for either restored sites or riparian remnants. The first three ordination axes together explained less than 10% of variation among sites and final stress for low-dimensional solutions was not significantly lower than for randomized data. Furthermore, the similarity of bee communities between restored and remnant pairs did not correlate with the similarity of flowering resources between the same sites (Mantel $r = 0.07$, $p = 0.32$).

Functional Restoration

Pollinator visitation patterns at restored sites compared to at remnant riparian sites suggest that pollination function was restored although at a reduced level. The identities of visitors at restored sites differed from those at remnant riparian sites such that only 14.7% of the interactions were shared among the habitat types. However, connectance among bee visitors and plants did not differ between site types (mean $\pm$ standard error [SE], restored = 0.40 ± 0.07 [median = 0.38]; remnant = 0.34 ± 0.04 [median = 0.33]; Wilcoxon signed-rank, $z = 0.36$, $p = 0.72$, $df = 8$). The proportion of native plants visited was slightly higher at restored sites (mean $\pm$ SE, 0.67 ± 0.15) than at remnant riparian sites (0.48 ± 0.10), but the difference was not significant (Wilcoxon signed-rank, $z = 1.26$, $p = 0.21$, $n = 5$ site pairs). Native plants common to both remnant and restored sites were *Salix* spp., *Baccharis salicifolia*, *Lupinus* spp., *Rosa californica*, and *Acer negundo*. These species were visited by fewer individuals from fewer bee species at the restored sites than at the remnant riparian sites (mean $\pm$ SE, restored sites 0.49 ± 0.31 individuals, 0.39 ± 0.25 species collected per flower; remnant sites = 1.82 ± 1.32 individuals, 0.89 ± 0.47 species collected per flower; abundance $F_{1,14} = 11.21$, $p < 0.01$; diversity $F_{1,14} = 2.55$, $p = 0.13$). With *Apis mellifera* included, visitor abundance increased to 0.92 ± 0.42 individuals per flower for restored sites and 1.84 ± 1.31 individuals per flower for remnants but the differences remained significant

Table 2. Species richness and abundance in remnant riparian and restored sites, and similarity of bee and flowering-plant communities between these site types along the Sacramento River.

Site Pair	Bee Species Richness (Abundance)		Flower Richness (Abundance)		Similarity remnant-restored*	
	Remnant riparian	*Restored*	*Remnant riparian*	*Restored*	*Bees*	*Flowering plants*
(1) La Barranca	42 (299)	33 (311)	681 (36)	686 (42)	0.53	0.14
(2) Rio Vista	41 (225)	19 (253)	366 (21)	2458 (41)	0.47	0.05
(3) Flynn	47 (499)	41 (577)	317 (25)	401 (47)	0.41	0.04
(4) Pine Creek	42 (410)	46 (492)	1668 (21)	1478 (42)	0.45	0.15
(5) Phelan Island	37 (416)	58 (702)	1664 (25)	1300 (37)	0.40	0.28

* Similarity values = 1 − Sørensen distance.
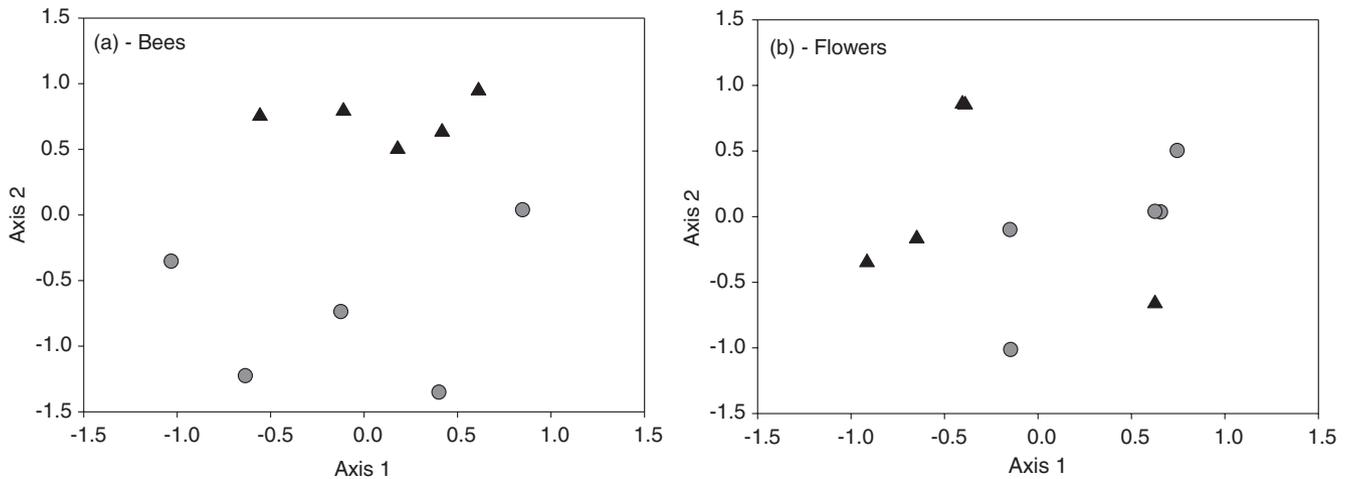Values are season-long totals.

Figure 2. Nonmetric multidimensional scaling ordination of study sites for (a) bee communities and (b) flowering-plant communities. Triangles, restored sites; circles, remnant riparian sites. Ordinations were based on Relative Sørensen distances, which emphasize proportional differences among species. Bee community ordination is a two-dimensional fit explaining 88.4% of among-site variation (73.3 and 15.1%). The flowering-plant ordination presents two dimensions of a three-dimensional fit. These two dimensions capture 1.5% of variation and the third added only 0.2%.

($F_{1,14} = 5.77$, $p = 0.03$). *Baccharis salicifolia* was very abundant at one remnant riparian site, which reduced the estimate of per flower bee diversity and the significance of the main site-type effect for diversity. The pattern of interaction involving native plant shared between remnant and restored sites also differed strikingly between site types (Fig. 3). Fewer bee species were involved overall at restored sites and two plant species, *Lupinus* spp. (Lupine) and *B. salicifolia* each relied on a single bee pollinator. *Rosa californica* in contrast was visited by over twice the number of species at restored sites as at remnant riparian sites. Similarity of interactions including visits by *A. mellifera* was low (Jaccard index = 0.13, Sørensen index = 0.17). Zero to 20% of pollinator species were shared by the native plants between restored and remnant riparian sites depending on the plant species.

Discussion

Restored riparian habitats supported communities of native bees with richness and abundance equal to that found in nearby remnants of riparian habitat. Thus, restored sites appear fully capable of supporting diverse bee communities during the process of restoration. Despite similar species richness however the compositions of the bee communities at restored sites were distinct from those at remnant riparian habitats. Thus, it is less clear that the restoration of structural vegetation and natural habitat successfully restores native bees from the reference riparian habitats. Differences in relative abundance of bee species common to both habitat types contributed to differences in composition between restored and remnant sites, but the influence was modest. In the Sacramento River system, there exists an identifiable "restored-site" bee fauna that contains a subset of species from remnants, some of which were among the numerically dominant species at these sites and others of which were not found in any remnant riparian site.

The preponderance of species unique to restored sites begs the question of where they come from. I did not sample bees from surrounding orchards, except in early spring because at other times there were no flowers from which to collect. The agricultural landscape however contains many scattered patches of weedy vegetation between fields, in temporary fallow land and in irrigation ditches. Data from neighboring regions in Northern California indicate that such patches can support diverse bee faunas including some of the species found in this study (Williams & Kremen unpublished data). Thus, a subset of the bees at restored sites may be species that persist in highly fragmented and disturbed areas. The ability of such degraded habitats to support pollinators may affect the success of restoration or habitat enhancement in agricultural habitats generally (Pywell et al. 2005).

The differences in bee communities were not driven primarily by differences in flowering-plant communities. Flower communities at restored sites and remnant riparian sites did not cluster by type. Sites with more similar floral communities also did not match those with more similar bee communities. Differences among bee communities were also not primarily the result of surrounding landscape. Paired restored and remnant sites were located close to each other and matched closely in their percentages of natural, agricultural, and developed land surrounding the sites. Differences in bee communities more likely arose from physical differences between restored sites and remnant riparian habitat. All restored sites lacked a closed canopy in any part of the plot or in the larger restoration site; the remnant riparian sites all had some areas with mature trees. Ground cover at restored sites tended to be composed of grasses interspersed with patches of bare ground and remnant riparian sites had more shrubby vegetation. Such differences in structure may influence microclimate or the availability of nesting sites for different bee species. These differences in turn translate to variation in the abundance of individuals among
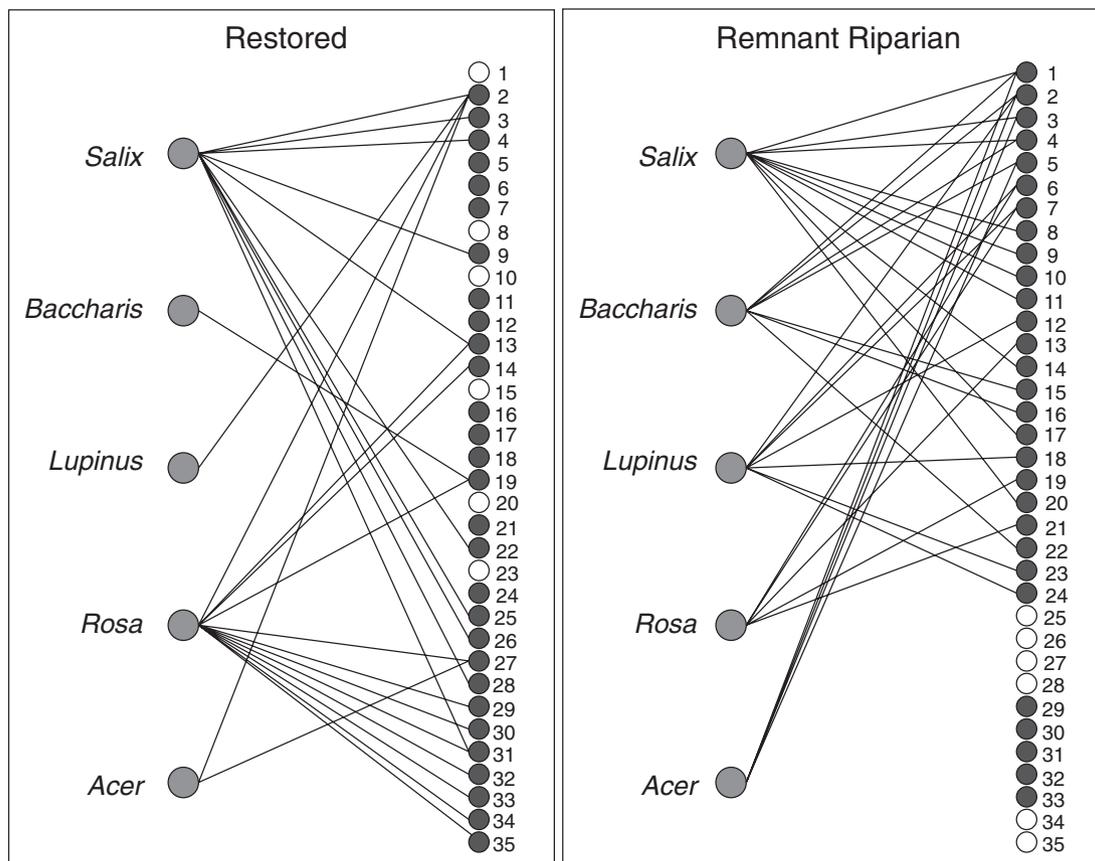
Figure 3. Plant–visitor interaction webs for the five native plant species common to both remnant riparian and restored sites. Webs are based on pooled data from all sites (*n* = 5) of given type. A total of 35 bee taxa are represented in both panels for comparison. Filled circles indicate bees found in that site type and unfilled circles indicate bee species found in the study but not in that site type. Lines connect plant species to their visitors, so that filled-unconnected circles are bee species that visit native plants not common to both habitat types and/or non-native plants. Data for *Acer* represent visitation, but not pollination because no insects were observed or collected from female flowers of this dioecious species. Bee species are listed in Appendix S1.

nesting or other guilds (Potts et al. 2005). It is perhaps not surprising that vegetation structure differed between restored sites and remnant riparian stands given that the former were mid-successional. Vegetation and also bee community results for restored sites must be interpreted in this context.

The presence of diverse bee communities at restored sites also indicates that these patches are connected with other habitat types through the movements of pollinators. Bees found at these sites must have arrived from elsewhere, because the sites were restored from almond or walnut orchards. In this study region, almond and walnut growers maintain very stringent cultivation with essentially bare ground beneath the trees, so there were no floral resources to support bees, except during early spring. If restored sites indeed support bee communities, then these sites potentially serve as sources for pollinator species that provide pollination service to crops (Kremen et al. 2007) and are important for stabilizing this service in different ecosystems (Klein 2009). Interestingly, in this study region I found little evidence for such pollination service. Almond orchards located adjacent to restored and remnant habitats had almost no native bee visitors (Ricketts et al.

2006). More recent surveys from nearby our study region suggest that riparian strips can support native bees that visit almond orchards (Klein unpublished data).

From a functional perspective, pollinator diversity is a key component of sufficient and stable pollination (Larsen et al. 2005). To date most of the studies of this issue have focused on pollination of a single plant species. Pollinator diversity will likely be even more important for sustaining pollination function (plant reproduction) across an entire plant community because of the diversity of floral morphologies (Corbet 2006; Stang et al. 2009), reproductive strategies and flowering phenology among plant species (Vázquez et al. 2009).

The degree to which interactions like pollination are restored represents a valuable metric to assess restoration success. Details of the interactions at the community level, such as the degree of redundancy of pollinators for plants or plant resources for foraging pollinators, can help us predict the sensitivity of the system to coupled extinctions that result from the loss of one mutualist partner (Morris 2003; Memmott et al. 2004). In this study, I measured visitor abundance, not pollination; however, if we accept this proxy and consider

remnant riparian habitat as a baseline from which to assess restoration within the Sacramento River system, then pollination function appears to have been restored. Connectance of bee–plant interaction networks in restored riparian habitats was similar to that in remnant riparian habitats and the proportion of native plants receiving visits by bees at restored sites did not differ from at remnant riparian sites.

Pollination function, although restored across the native plant community, may be less robust in restored habitats. Bee–plant interaction networks involving only native plants common to both site types were distinct between the site types. Species richness of visitors to these native plants was lower at restored sites and although some plant species were visited by many different bee species, others had no redundancy of pollinator species at restored sites. *Baccharais salicifolia* and *Lupinus* spp. were each visited by a single bee species at the restored sites. Lupines relied only on honey bees which, although they are a dominant component of the pollinator fauna in this region, only persist in managed populations. These comparisons involving shared native plants have inherent limitations. The data involved a limited number of plant species most of which were not present at all sites. Variability in plant abundance among sites may also have combined with natural variability in bee communities to lead to an underestimate of visitor redundancy. That said, pooling over replicated sites should have helped provide a more robust summary of interactions and of whether pollination function is restored.

Connectance values in this study were 4–10 times greater than reported in other studies of pollinator–plant networks, including those at restored habitats (Forup et al. 2008). Two factors contribute to the disparity. First, I excluded plant species widely acknowledged not to be pollinated by bees (e.g., *Aristolochia californica*, *Acer negundo*). This action removed only a small number of plants and had minor effects on overall connectance. More importantly, I excluded links that could not exist because bee and plant phenologies did not overlap at the site and excluding them dramatically increased estimates of functional connectance. Recent theoretical and empirical work highlights the importance of connectance in determining the stability of the communities in the face of species loss (Ives & Carpenter 2007). Thus, an accurate assessment of connectance is critical to predicting community dynamics especially in habitats like restored sites and riparian zones that are highly prone to physical disturbance.

Ecological restoration (Ehrenfeld & Toth 1997) adopts a comprehensive perspective that the ultimate goal should be to create a site or system with the desired mixture of species that is self-sustaining over time. Nontarget species, like pollinators, contribute ecological functions that are critical to the long-term stability of the ecosystems, but the exact identities of these species may be less important than having a diverse mixture of functional groups (Klein et al. 2008). Along the Sacramento River, bee communities differed significantly between restored and remnant habitats; however, diversity at restored sites was high and equal to at riparian remnants. Attempting to replicate preexisting pollinator communities is an unrealistic goal for

several reasons. Naturally occurring bee populations and communities vary dramatically over space and time (Williams et al. 2001) and inherent variation in edaphic characteristics, disturbance regimes and regional species pools will further affect the composition of restored communities. We should therefore not expect pollinator communities at restored sites to mirror those at any reference site including habitat remnants, nor should we set perfect congruence between remnant and restored sites as an explicit restoration goal (Ehrenfeld 2000; Forup et al. 2008). In addition, this study presents data for sites that are undergoing succession after restoration rather than mature riparian habitats and the bee and plant communities represent those at one stage in a dynamic process. Finally, it is unlikely that remnant habitats provide a perfect baseline against which to assess restoration success. The preponderance of unique bee species at restored sites supports the perspective that remnant riparian habitats may themselves be degraded and harbor subsets of the original native fauna. In the case of the Sacramento River, future assessments of pollinators must include a greater variety of reference site types including sites from the agricultural matrix. Although these are not the targets of restoration, they will likely provide a more complete understanding of the regional species pool and thus of the success of restoration at incorporating a representative fauna.

Implications for Practice

- Restoration of pollination may be possible without restoring pollinator species identical to those of reference sites. The restoration goal should be toward species rich communities to promote redundancy of pollination among plants.
- Assessment of nontarget communities following restoration requires repeated sampling at different successional stages of restoration. Persistent differences in habitat structure between restored and baseline sites may contribute to differences in native pollinator communities.
- Baseline sampling of nontarget species should include habitats other than those that are the target of restoration. Native species returning to the restored habitat may not originate from remnants of the target habitat. One also cannot rule out that reference sites (in this case remnant riparian sites) are themselves degraded.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Bee species from restored and remnant riparian sites.
Appendix S2. Plant species from restored and remnant riparian sites.

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