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RESEARCH ARTICLE

Limited Effects of Large-Scale Riparian Restoration on Seed Banks in Agriculture

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Abstract

I examined the effect of riparian forest restoration on plant abundance and diversity, including weed species, on agricultural lands along the Sacramento River in California (United States). Riparian forest restoration on the Sacramento River is occurring on a large-scale, with a goal of restoring approximately 80,000 ha over 160 km of the river. In multiuse habitats, such as the Sacramento River, effects of adjoining habitat types and movement of species across these habitats can have important management implications in terms of landscape-scale patterns of species distributions. Increased numbers of pest animals and weeds on agricultural lands associated with restored habitats could have negative economic impacts, and in turn affect support for restoration of natural areas. In order to determine the distribution and abundance of weeds associated with large-scale restoration, I collected seed bank soil samples on orchards between 0 and 5.6 km from adjacent restored riparian, remnant riparian, and agricultural habitats. I determined the abundance, species richness, and dispersal mode of plant species in the seed bank and analyzed these variables in terms of adjacent habitat type and age of restored habitat. I found that agricultural weed species had higher densities at the edge of restored riparian habitat and that native plants had higher densities adjacent to remnant riparian habitat. Weed seed abundance increased significantly on walnut farms adjacent to restored habitat with time since restored. I supply strong empirical evidence that large areas of natural and restored habitats do not lead to a greater penetration of weed species into agricultural areas, but rather that weed penetration is both temporally and spatially limited.

Key words: agriculture, ecosystem dis-services, restoration, riparian, seed bank, seed dispersal, transboundary, weeds.

Introduction

Restoration of riparian ecosystems is a crucial goal for reestablishing critical habitat for threatened species and supporting ecosystem services such as improved fisheries habitat and water quality. At the same time, restoration of river ecosystems is often highly contested because of the economic potential for agricultural uses within the riparian zone (Poff et al. 2003; Golet et al. 2006). Current research has highlighted the economic and ecological benefits that agriculture gains from natural habitat, ecosystem services such as pollination (Kremen et al. 2002; Ricketts 2004). However, agricultural landowners near natural habitat often focus on potential net negative impacts, or ecosystem dis-services, from natural habitat (Marshall & Moonan 1997; Golet et al. 2006; Zhang et al. 2007). Nevertheless, little is known about the ecological and agronomic effects of restored areas on land managed for food.

Habitat restoration adds an additional layer to the issue of real or perceived ecosystem services and dis-services that agriculture receives from natural habitat. Restoration that occurs in agricultural landscapes often takes agricultural land out of production. This change increases the area of natural habitat near cultivated land and can lead to a transitional early successional habitat (Blumenthal et al. 2003). Because pest species, such as small mammals or weeds, are often associated with early successional habitat, restored riparian habitat can be perceived as a source of negative economic impacts on farmers, due to farmers observing pests in the restored habitat that could move to the agricultural habitat (Buckley & Haddad 2006; Golet et al. 2007). Negative perceptions of the effects of restored habitat on agricultural lands can lead to conflict between restoration and agricultural communities (Buckley & Haddad 2006). In large-scale restoration projects, which cover hundreds of square kilometers and therefore are often adjacent to many different landowners, these conflicts can call into question the optimal extent and pattern of large-scale restoration projects and impact the chances of restoration success (Buckley & Haddad 2006; Golet et al. 2006).

In several surveys conducted within the counties associated with a large-scale restoration project along the Sacramento River, California (United States), members of the farming and larger regional community perceived the restoration of natural habitat as having mostly negative local effects

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(Wolf 2002; Singh 2004; Buckley & Haddad 2006). Seventy percent of respondents stated that increased weed infestation was a negative effect of restoration. This was due to the possibility of seeds dispersing into the cultivated land from the restored properties, increasing weed cover on farms near the restoration, leading to negative economic effects on farmers (Buckley & Haddad 2006). The goal of this study was to investigate the distribution of agricultural weed species on farms within the large-scale restoration project on the Sacramento River in order to gain a better understanding of the relationship between agricultural weed distribution and restored habitat.

Studies conducted to investigate weed movements and distributions from natural to agricultural habitats have focused on small-scale nonarable areas, such as hedgerows and field margins. These studies indicate that there is little spread of weeds from these nonarable areas into cultivated areas (Marshall 1989; Wilson & Aebischer 1995; Rew et al. 1996; Smith et al. 1999; Devlaeminck et al. 2005). For example, in a study conducted in England, Wilson and Aebischer (1995) determined that species typically found in hedges and field margins as well as characteristic arable weed species were restricted to the outer 4 m of the crop, and most were restricted to the outer 1 m. However, no studies have investigated the distribution of weeds in cultivated areas embedded within large areas of restored and remnant habitats.

In this article, I investigated the spatial distribution, abundance, and diversity of plants across a landscape mosaic of remnant riparian forest, restored riparian forest, and agricultural lands along the Sacramento River in Central California. My major objectives in this work were to determine the spatial extent and magnitude of the effects of restored riparian forest habitat on agricultural weed abundance and diversity on farms within a large-scale restoration project. My research took place on walnut orchards from 0 to 5.6 km from the edge of restored and remnant riparian forest habitats at 26 sites along 160 km of the Sacramento River.

The Sacramento River system provides an excellent area in which to investigate spatial distribution of plants due to the large-scale restoration efforts that are replicated across the landscape. The Sacramento River is a major river in the western United States and was historically surrounded up to 8 km on either side by a matrix of wetlands and riparian forest. However, since 1850, deforestation of the riparian forest, and conversion to agriculture, has led to a loss of all but approximately 4% of the original riparian habitat, which exists as small patches of remnant forest (Katibah 1984; Kelley 1989; Greco 1999). Degradation of the river has impacted fisheries and water quality in the watershed. Due to these economic and ecological impacts, in 1986 the California state legislature passed Senate Bill 1086, mandating the restoration of the Sacramento River. One of the major restoration strategies includes purchasing agricultural properties and revegetating those properties with native trees, shrubs, understory plants, and grasses (Golet et al. 2006). To date, approximately 3000 ha have been planted with riparian species along 160 km of the river.

I conducted this research on walnut farms for several reasons. The Sacramento and San Joaquin Valley account for more than 99% of the total production of walnuts for the United States. Walnuts are the ninth most significant export commodity in California and cover over 80,000 ha. This crop is often associated with riparian zones, as walnut trees are able to withstand periodic flooding (Ramos 1985). However, walnut production can be negatively affected by weed pressure, through competition for water and nutrients, and walnut pest species which might be harbored within the weeds (Ramos 1985; Garrett et al. 1996). Because walnuts are the dominant crop within the riparian zone and are sensitive to weed competition, understanding the interactions between riparian restoration, weeds, and walnut orchards is particularly important for managing this interface for the benefit of conservation, restoration, and farmers.

Materials and Methods

Site Description

Study sites were located on walnut farms along the Upper Sacramento River region in central California between Red Bluff (Tehama County) and Colusa (Colusa County) California (Fig. 1). Rainfall in this region averages 660 mm annually, with yearly total rainfall ranging between 330 and 1137 mm (UCIPM 2009). The majority of rain falls between November and April. Soils on the Sacramento River are from the Columbia series. Average mean temperatures range from 34.5°C in July to 1.3°C in January. The predominant wind direction is from the south (Zaremba & Carroll 1999). The region consists of a mosaic of remnant and restored riparian forest, wetlands, and agricultural lands that include walnuts, almonds, prunes, corn, rice, and some human settlements.

Walnut farm study sites were adjacent to remnant riparian forest, restored riparian forest (>3 years old), or non-forest habitat. Remnant riparian forest vegetation consisted of mixed riparian forest of >8 ha and included *Populus fremontii*, *Salix gooddingii*, *S. exigua*, *S. lasiolepis*, *Quercus lobata*, *Fraxinus latifolia*, *Juglans hindsii*, *Acer negundo*, and *Platanus racemosa*. Restored riparian forest sites were previously under agricultural production and during that time had been cleared of native vegetation. Sites were prepared for restoration planting by a combination of disking, burning, furrowing, leveling, and spraying with the foliar herbicide glyphosate. The earliest restored sites were planted with a combination of 6–10 woody species (including *A. negundo*, *F. latifolia*, *Platanus occidentalis*, *P. fremontii*, *Q. lobata*, *Rosa californica*, *S. exigua*, *S. gooddingii*, *S. lasiolepis*, *Sambucus mexicana,* and *Baccharis pilularis*) (Alpert et al. 1999). More recent planting of restored sites has included not only these woody species, but also understory species such as *Artemisia douglasiana*, *Carex barbarae*, and *Urtica dioica* and some grasses (Holl & Crone 2004; Gardali et al. 2006). All plant propagules in the restored sites were collected from local natural stands. Planting densities and designs were variable among sites and years. Non-native understory species were controlled by physical and chemical (1–2% glyphosate) methods during

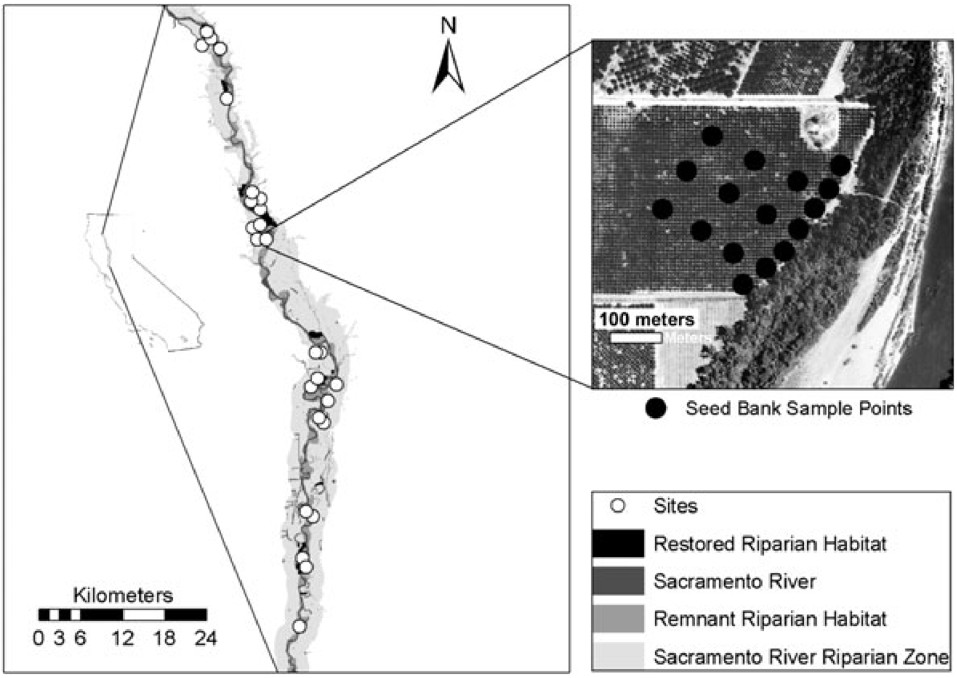

Figure 1. Orientation map for study sites along the Sacramento River, California.

the first 3 years but were largely unmanaged after that time. Non-forest habitats that were adjacent to sample orchard sites were variable and consisted of walnut orchards, almond orchards, and prune orchards.

I selected 26 walnut farms that ranged from 0 to 5.6 km from restored riparian habitat, and up to 1 km from remnant riparian forests (Fig. 1, Appendix S1). I chose farm sites by locating all walnut farms on aerial photos within the inner river zone of the Sacramento River and determining their proximity to the riparian forest habitat. From these farms, final sites were determined by (1) Willingness of owner to have research conducted on-farm; (2) Ability to establish a stratified set of farms with some sites adjacent either to older (>3 years) restored sites or to remnant forest patches, or >400 m from any riparian forest habitat. Walnut farms consisted of rows of trees spaced 8–15 m apart, depending on the size of the trees. Walnut trees ranged from approximately 10–25 m tall. Although walnut trees ranged from 5 to 50 years old, all orchards had been in agricultural production for at least 20 years. All farm sites had similar management regimes with an herbicide application (glyphosate and 2,4-dichlorophenoxyacetic acid) before the first bud break (February) and further herbicide applications using the same active ingredients approximately three times between March and September. Mowing was also conducted at these sites approximately three times during the year.

Field Methods

I sampled 26 walnut farm sites: 6 farms adjacent to sites restored between 1991 and 2001, 10 farms adjacent to remnant forest, and 10 farms from 0.4 to 1.0 km from remnant and from 0.4 to 5.6 km from restored habitat. On each farm, I sampled 16 points within a 300×300–m area, determining the first point randomly along the crop edge, and at least 50 m from any other habitats or roads. Seven sample points were on the edge, either adjacent to remnant or restored riparian forest or adjacent to a non-forest area and nine sample points were distributed within the "interior" of the walnut orchard at 50, 150, and 250 m from this edge (Fig. 1). Interior riparian forest plots were not sampled as our research was designed to capture differences among the sites in terms of adjacent land use and not specific dynamics within the adjacent habitat type. These dynamics within the restored and remnant habitats have been discussed in Holl and Crone (2004) and McClain et al. (2009). At each point, I established a 1×1–m plot at a random distance between 0 and 5 m, and a random direction from the sample point. For edge points, the random directions were only within the walnut orchards and did not place any points within the adjacent habitat. To examine the seed bank, I took a soil core (10-cm deep $\times$ 15-cm wide) within each 1×1–m plot in March 2004, prior to seed germination and after winter stratification of the seeds (Ter Heerdt et al. 1996). I analyzed the seed bank, rather than aboveground vegetation, because aboveground vegetation on the walnut farms was highly managed with several applications of herbicide and mowing regimes throughout the year. Therefore, aboveground surveys consisted of many sites with dead (herbicided) or mowed plants.

Greenhouse Methods

I used the seedling emergence technique for this study rather than seed extraction because it is not always possible to determine whether seeds are viable, and therefore seed extraction could overestimate numbers (Brown 1992). It is also easier to identify seedlings rather than seeds (Poiani & Johnson 1988). However, there are also limitations to the seedling emergence methods, including underestimating the number of viable seeds due to uneven distribution of seeds in the soil (Baskin & Baskin 1998). Nevertheless, the objective of this study was to compare the seed bank in relation to the adjacent habitat type, and as the same methods were used for all of these sites, any limitations of the seedling emergence method would be expected to be consistent across all sites.

I removed debris and root fragments from the soil samples and broke down large clumps of soil into pieces <5-mm diameter each. In order to reduce heterogeneity, I mixed each soil sample and took a 250-mL subsample to standardize the sample size. I placed each sample in a 15-cm diameter pot with 500-mL Promix HP potting soil (Premier Horticulture, Quebec, Canada) at the bottom and a 250-mL layer of the soil sample on the top. The germination layer (the top layer from the soil sample) was approximately 5-cm thick. There were a total of 419 samples in the growing room with 12-hour light and 12-hour dark and temperature that ranged between 10 and 18°C, with watering on an as needed basis.

I placed samples randomly in the greenhouse and moved them three times during the growing season in order to compensate for any gradients in growing conditions in the greenhouse. As soon as possible following germination, I identified, counted, and removed each seedling. I transplanted seedlings that could not be identified immediately into pots to allow further growth. I left all pots in the experiment for a minimum of 2 months. After 2 months, I continued watering each pot on an as needed basis and identified any seedlings until no germination had occurred for 7 days, at which point I removed the pot from the experiment.

Statistical Analyses

To address whether seed abundance and species richness varied with distance to remnant and restored habitats, I determined the effects of adjacent habitat type (restored, remnant, or agricultural) and distance from adjacent habitat type (edge, 50, 150, and 250 m from the edge) using an analysis of variance (ANOVA) and post hoc multicomparisons using Fisher's least-significant-difference test for multiple hypotheses. Each sample was treated as a replicate at the different distances. I log-transformed seed abundance when necessary to meet assumptions of normality and homoscedasticity. I used a split-plot model, with adjacent habitat type as a whole-plot effect and distance from the edge of the adjacent habitat type as the within-plot effect. The response variables included total seed abundance, non-native seed abundance, native seed abundance, invasive plants, agricultural weed seed abundance, wind dispersed seed abundance, animal dispersed seed abundance, and gravity-dispersed seed abundance. Because *Poa annua* accounted for 55% of the plants in the seed bank, I also conducted the analysis after removing *P. annua* to determine whether this was the main driver of the patterns observed. I also used the five most abundant species in the seed bank as a response variable. There were no significant differences among the three interior distances (50, 150, and 250 m) (Bonferroni correction for multiple hypotheses test, $p > 0.05$) for my response variables; therefore, I combined data from the interior distances for all reported tests. For all analyses above, I combined all ages of restored sites as one adjacent habitat type (restored). To determine how age since restoration may affect plant abundance, I separated out the sites by time since restoration and determined the average overall seed abundance, weed seed abundance, non-native seed abundance, and native seed abundance for each of these ages. These analyses were all performed with Systat version 10 (SPSS Software Inc 2000).

California invasive plant species were identified using the definitions on the invasive plant database compiled by the California Invasive Plant Council (Cal-IPC 2006). Assignment as agricultural weed species followed the University of California Integrated Pest Management data on walnut weed species (UCIPM 2007). I identified the primary seed dispersal mechanism based on the morphological features of the seed using the *Jepson Manual* (Hickman 1993) and the PLANTS database (USDA, NRCS 2007); those without a clear adaptation for wind or animal dispersal were categorized as gravity dispersed.

To determine the effects of adjacent habitat type and location on species richness, I calculated rarefied species richness for all species and native species only using EstimateS (Colwell 2005) because plant abundance and species richness were significantly correlated ($r^2 = 0.70$, $df = 415$, $p < 0.0001$). I conducted a sample-based rarefaction analysis to determine species density differences across habitat types using EstimateS (Colwell 2005). I also rescaled the x-axis in units of individuals in order to compare species richness (Gotelli & Colwell 2001).

Results

I recorded 26 (30%) native and 61 (70%) non-native species across all sampled habitats (Appendix S2). Seventy-four (85%) of these species were forbs, 11 (13%) were graminoids, and 2 (2%) were woody species. Sixty-five (75%) were annual species, 2 (2%) were annual/biennial, 4 (5%) were annual/perennial, and 16 (18%) were perennial. Sites adjacent to restored habitat had significantly higher total seed abundance ($F_{[2,364]} = 7.52$, $p < 0.001$) and edge locations had a significantly higher seed abundance for all sites ($F_{[1,364]} = 7.50$, $p = 0.01$). However, there was a significant interaction term in that the restoration edge sites had a significantly higher total abundance of seeds than other edge sites ($F_{[2,364]} = 3.61$, $p = 0.03$) (Fig. 2). *Poa annua*, a non-native, gravity-dispersed species, dominated the seed bank at all sites, with 9,711 (55%) individuals out of 17,661 total in the seed bank. When *P. annua* was removed from the analysis, there was still a significantly higher number of individuals on the edge of restored sites (location: $F_{[1,364]} = 8.75$,

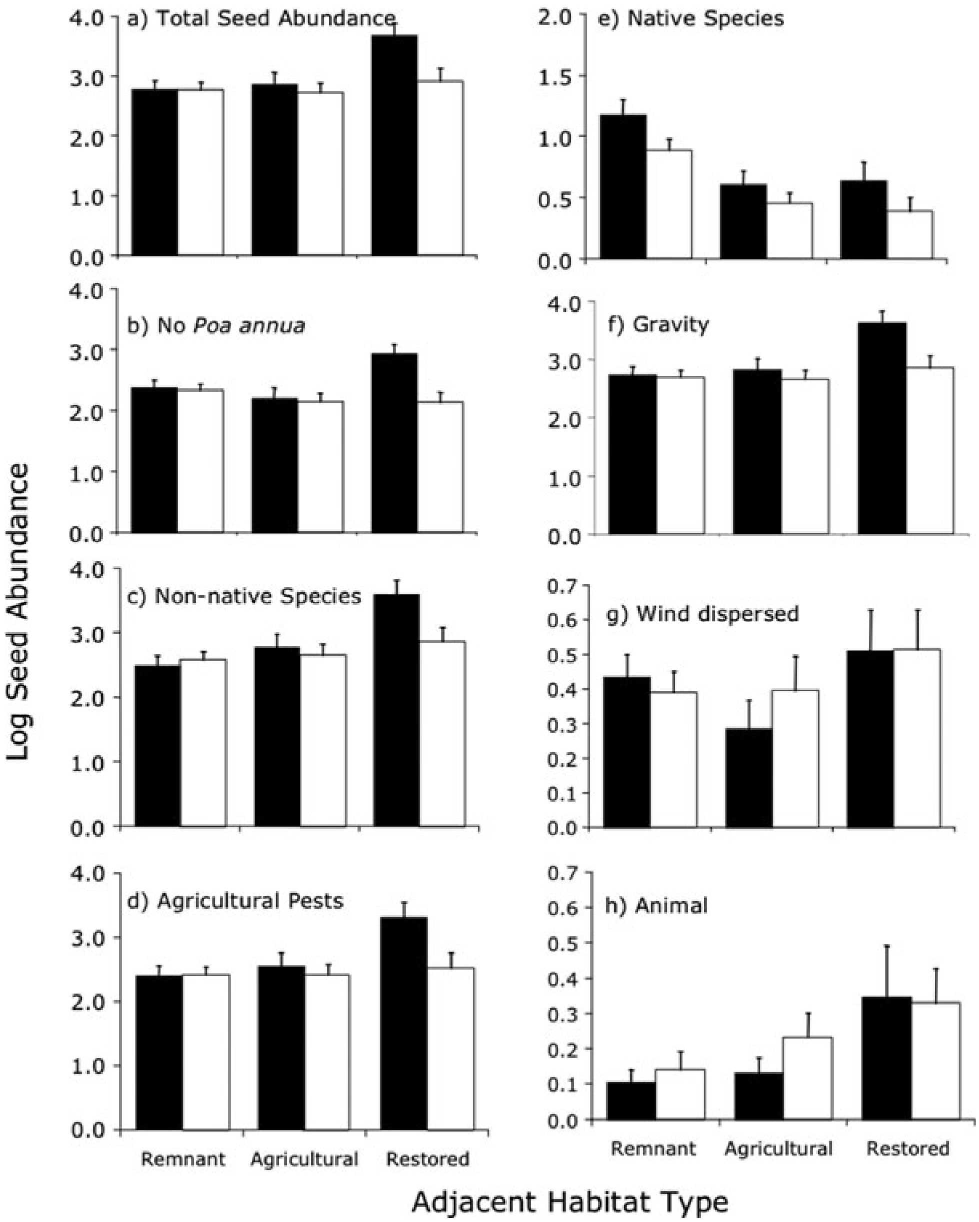

Figure 2. Log seed abundance grouped in remnant, non-forest, and restored adjacent habitat and grouped as edge (black) and interior (white). Different graphs show seed abundance of (a) total seed abundance; (b) total seed abundance without *Poa annua*; (c) non-native species; (d) agricultural pests; (e) native species; (f) gravity-dispersed species; (g) wind dispersed species; and (h) animal dispersed species. Error bars represent SE. Note different *y*-axis values.

$p < 0.001$, adjacent habitat type: $F_{[2,364]} = 3.53$, $p = 0.03$, interaction: $F_{[2,364]} = 4.78$, $p = 0.01$) (Fig. 2). Similarly, I investigated the patterns of the five most abundant species that comprised 74% of all seedlings. These species were all non-native species and included the graminoid *P. annua* and four annual forbs, *Stellaria media*, *Portulaca oleracea*, *Lamium amplexicaule*, and *Chamaesyce maculata*. For all species except *C. maculata* and *L. amplexicaule* abundance of individuals was highest on orchards adjacent to restored forest (*P. annua,* $F_{[2,364]} = 12.29$, $p < 0.001$; *S. media*, $F_{[2,364]} = 12.34$, $p < 0.001$, *P. oleracea*, $F_{[2,364]} = 9.14$, $p < 0.001$) (Fig. 3). However, the patterns differed between the three species. *Poa annua* had a significantly higher abundance on sites adjacent to restored habitat, *S. media* had a significantly lower abundance on sites adjacent to remnant habitat, and *P. oleracea* had a significantly lower abundance on sites adjacent to agricultural habitat (Fig. 3). *L. amplexicaule* had a significantly higher seed abundance adjacent to restored habitat ($F_{[2,364]} = 5.37$, $p = 0.005$), but had a significant interaction with location ($F_{[2,364]} = 6.068$, $p = 0.003$) (Fig. 3), where only samples on the edge adjacent to restored habitat had a

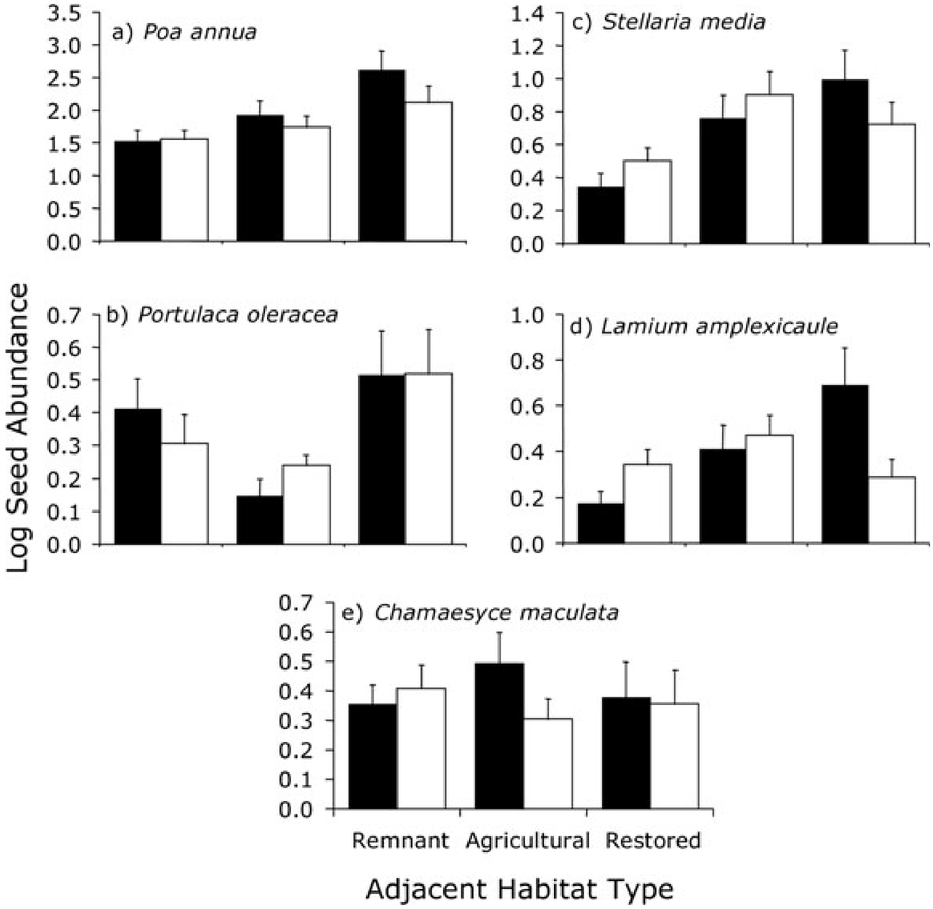

Figure 3. Log mean seed abundance for the five most abundant species in the seed bank by adjacent habitat type (remnant riparian forest, restored riparian forest, non-forest). Five species are (a) *Poa annua*; (b) *Portulaca oleracea*; (c) *Stellaria media*; (d) *Lamium amplexicaule*; and (e) *Chamaesyce maculata*. Black bars are edge samples and white bars are interior samples. Error bars represent SE. Note different *y*-axis values.

higher seed abundance. Adjacent habitat type or location had no effect on abundance of *C. maculata* (Fig. 3).

Forty-four (50%) of the species in our samples are listed as walnut farm weed species by University of California Integrated Pest Management Walnut Management Guidelines (UCIPM 2007). Three of those species are considered problem weeds (*Taraxacum officinale*, *Rumex crispus*, *Cynodon dactylon*). However, the combined abundance of these three species in the total seed bank was 0.1%. Of the agricultural weed species, 10 (23%) were native species and 34 (77%) were non-native species. Of the five most abundant species, all non-native species including the graminoid *P. annua* and four annual forbs, *Stellaria media*, *P. oleracea*, *L. amplexicaule*, and *C. maculata,* all are considered agricultural weed species except *S. media*. There was a significantly higher number of agricultural weed species on the edge of restored forest (location: $F_{[1,364]} = 6.98$, $p = 0.01$, adjacent habitat type: $F_{[2,364]} = 6.23$, $p < 0.001$, interaction: $F_{[2,364]} = 3.76$, $p = 0.03$) (Fig. 2).

Native species abundance was significantly higher in sites adjacent to remnant forest, both in the interior and on the edge ($F_{[1,364]} = 10.66$, $p < 0.001$), but there was also a significantly higher abundance of native seeds on the edge of all adjacent habitat types ($F_{[2,364]} = 22.48$, $p < 0.001$) (Fig. 2). None of the native plants in the seed bank were considered rare plant species in California (California Native Plant Society 2007). There was a significantly higher number of non-native species on the edge of restored habitat (location: $F_{[1,364]} = 4.80$, $p < 0.03$, adjacent habitat type: $F_{[2,364]} = 10.98$, $p < 0.001$, interaction: $F_{[2,364]} = 3.79$, $p < 0.02$ (Fig. 2). Seventeen species (19%) are considered invasive plants that threaten California native habitats (Cal-IPC 2006). There was no significant effect of adjacent habitat type or distance on invasive plant abundance, but there was a trend toward highest abundance on sites adjacent to restored habitat and lowest abundance on sites adjacent to remnant forest habitat ($F_{[2,364]} = 2.733$, $p = 0.066$).

The majority of species were classified as gravity dispersed (75%), while 15 (17%) were primarily wind dispersed and 6 (8%) were primarily animal dispersed. However, secondary dispersal in this landscape could include floods, agricultural equipment, and animals. There were a significantly

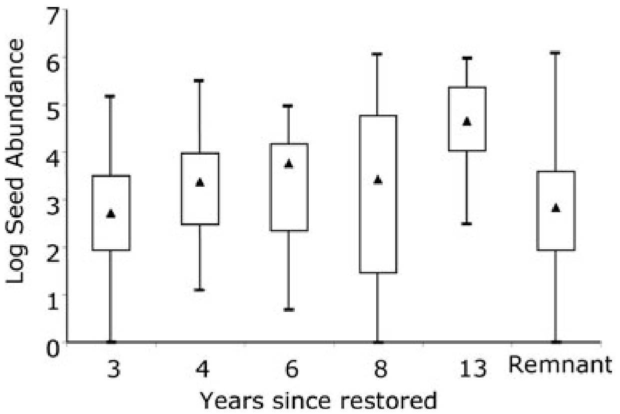

Figure 4. Log seed abundance as a function of years since restored and remnant forest. Seed abundance is displayed in box plot distributions in which each box contains the 25th to 75th percentiles and T-bars show the maximum and minimum. Solid triangles show the medians (50th percentile).

higher number of gravity-dispersed individuals on the edge of restored forest (location: $F_{[1,364]} = 9.59$, $p < 0.001$, adjacent habitat type $F_{[2,364]} = 7.43$, $p < 0.001$, interaction $F_{[2,364]} = 3.90$, $p < 0.02$) (Fig. 2). The number of animal dispersed seeds was higher on sites adjacent to restored forest, although there was no effect of distance from the edge (adjacent habitat type $F_{[2,364]} = 5.63$, $p < 0.001$) (Fig. 2). There was no significant effect of adjacent habitat type or distance from the edge of the adjacent habitat type for wind dispersed individuals (Fig. 2).

For samples taken on the edge of restored sites only and grouped by time since restored, seed abundance increased significantly for total agricultural weed seed abundance ($F_{[1,4]} = 12.11$, $r^2 = 0.75$, $p = 0.025$) with time since forest restoration (Fig. 4). There was also an increasing trend for total seed abundance ($F_{[1,4]} = 5.14$, $r^2 = 0.56$, $p = 0.086$) and non-native seed abundance ($F_{[1,4]} = 5.50$, $r^2 = 0.58$, $p = 0.079$), with time since forest restoration. There was no trend with time since forest restoration for native species. For all samples, sites adjacent to remnant forest had a much lower mean seed abundance of 28.7 (±4.4), 40% of the mean seed abundance adjacent to the oldest restored habitat of 163.4 (±31.7). In contrast, the mean seed abundance of native species in sites adjacent to remnant forest was 3.8 (±0.50), while the mean native seed abundance of the site adjacent to the oldest restored forest was 3.1 (±2.5).

For all species combined, and for just native species, remnant forest edge had the highest species richness (Fig. 5a & 5b). Remnant and restored edges had higher densities for all species combined (Fig. 5a). For native species, restored interior and edge sites had the highest species densities; however, all sites were similar (Fig. 5b).

Discussion

This research demonstrates that orchards adjacent to restored habitat can have significantly higher weed seed abundance

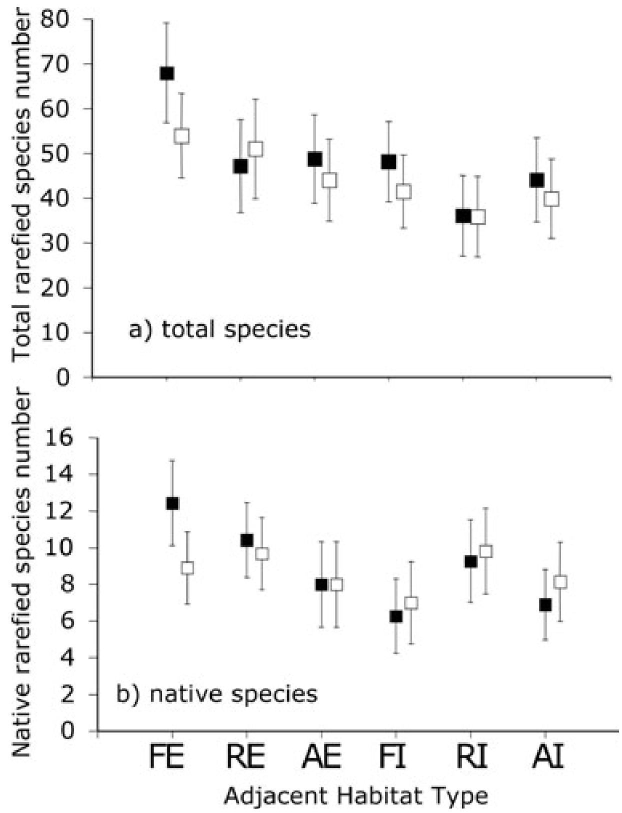

Figure 5. Individual-based and sample-based rarefied species richness for (a) total species, and (b) native species only (Colwell 2005). AE, agricultural edge; AI, agricultural edge; FE, remnant edge; FI, remnant interior; RE, restored edge; RI, restored interior. Filled in squares are individual-based rarefaction results, open squares are sample-based rarefaction results. Error bars represent confidence intervals.

than orchards adjacent to remnant riparian or agricultural habitats. However, weed seed abundance in this study was only higher immediately adjacent to restored sites. My finding that weed abundance was most affected by proximity to the habitat edge is consistent with the literature on weed invasion from small-scale field margins and hedgerows into agricultural fields (Marshall 1989; Wilson & Aebischer 1995; Smith et al. 1999; Devlaeminck et al. 2005). Experimental and modeling dispersal studies on weed species demonstrate that most seeds only disperse a few meters from the parent plant, with the greatest distances of a very few seeds up to 20 m (Wilson & Aebischer 1995; Rew et al. 1996; Rew & Cussans 1997; Blumenthal & Jordan 2001). In contrast to dispersal of weed seeds from small-scale field margins, larger areas of natural and restored habitats, such as in the Sacramento River, could lead to a greater diversity and abundance of plant species in the agricultural field and a greater probability of a long-distance dispersal event (de Blois et al. 2002; Gabriel et al. 2005). However, I found no significant differences in weed seed abundance or richness on the interior of farms.

Higher weed seed abundance on farms adjacent to restored riparian forest could be due to differences in successional dynamics, plant dispersal mechanisms, or management of the restored habitat versus the remnant or agricultural habitat. Successional dynamics in the restored sites include early successional weedy species for the first several years after restoration (Holl and Crone 2004), many of the same plants listed as weeds of concern by walnut growers (UCIPM 2007). These restored sites are managed for non-native species 3 years after the initial restoration, after that time no management occurs in the restored habitats, leading to domination of non-native early successional species (Holl & Crone 2004; McClain et al. 2009). In contrast, remnant habitat has a lower availability of resources, such as light and nutrients, that are required by many of these weedy early successional species, and therefore a reduced abundance of weedy annual species (Holl & Crone 2004; McClain et al. 2009). Agricultural habitat adjacent to the walnut farm study sites contains very little vegetation due to intensive weed management.

Research on restoration and successional dynamics has demonstrated that as restoration sites age, late-successional species can out-compete the early successional weedy species for resources (Blumenthal et al. 2003; McClain et al. 2009; Middleton et al. 2009). However, my results suggest that as the restoration sites age there is an increase in the weed seed production that disperses into the walnut farm edge, rather than a decrease in weed seed production. McClain et al. (2009) found that of 15 sites restored between 11 and 18 years earlier, 5 of the restored sites decreased in native cover (McClain et al. 2009) and restored sites, although containing some of the same species as the remnant forests, had still not reached remnant status. Similarly, Reay and Norton (1999) found that after 35 years, restored forests in New Zealand forests were somewhat dissimilar from the mature forest. It should be noted that my data on weed seed abundance adjacent to restored sites of different ages are from not more than two sites for each age class. However, even in this large-scale restoration project, it was not possible to find more restored sites that fit the study design (adjacent to walnut farms).

Plant dispersal mechanisms and orchard management could affect the penetration of seeds into agricultural areas. In terms of plant dispersal, the majority of the plants in the seed bank are gravity dispersed and therefore generally dispersed over small distances, although long-distance dispersal could occur by movement in water or by way of vertebrates that consume seeds when foraging on foliage (Willson 1993). Orchard management could affect movement of soil and secondary seed dispersal. Mowing, which occurs in these perennial crops, has been shown to disperse seeds in grassland reserves (Strykstra et al. 1997) and could influence weed dispersal. For annual crops, studies investigating the effects of secondary horizontal movement of seeds associated with combines have found that the distance of movement is greater, but for only a small percentage of individuals (Marshall & Brain 1999; Barroso et al. 2006). Rare long-distance dispersal events could influence the rate of spread of weeds, acting as foci for new patches (Barroso et al. 2006).

My results clearly show that any negative weed effects are limited in spatial extent, even a 50-m penetration into agricultural lands from current restored forest along the Sacramento River would affect less than 1% of all farmland, with these effects clustered around those farms adjacent to the restoration. However, although this is a small percentage of farmland that could be impacted by weed dispersal from restored habitats, the farms that would be impacted by increased competition for resources from a higher abundance of weeds could incur an economic impact of increased herbicide use or mowing or a decreased crop output (Garrett et al. 1996).

To address these effects on neighboring farms, management and restoration practices in the restored habitats could reduce the presence of weed species near agricultural areas. This could be accomplished either through spraying or mowing for more than the current practice of 3 years, or through planting practices, such as planting later-successional species, that could decrease the invasion of the restored site by invasive and early successional species (Blumenthal et al. 2003; McClain et al. 2009). Practices such as spraying or mowing for more than 3 years would be financially intensive and likely difficult for most restoration projects. More realistic would be a change in planting practices that encourages later-successional species; however, it is unclear which are the best planting practices to encourage later-successional species (McClain et al. 2009).

Restoration practices could also include supplying scientific information to the agricultural community on both the ecosystem services (Tscharntke et al. 2005) and dis-services (Weber et al. 1990) of having non-crop plants on the edges of the farms. For example, ecosystem services could include supplying overwintering areas for parasitoids and causing higher pest mortality on the farm (Tscharntke et al. 2005). Ecosystem dis-services could include the increasing number of pest species on crops (Weber et al. 1990). This information could be both specific to the restoration area (such as this research on the Sacramento River) and a compilation of research on a topic from different restoration sites. This type of communication is starting to occur along the Sacramento River in order to facilitate more trust between local stakeholders and conservation organizations and possibly further restoration goals (Golet et al. 2009).

Implications for Practice

- Abundance of weed species in agricultural habitat associated with restored habitat is spatially limited in that weed abundance is only higher directly adjacent to restored habitat.
- Restoration management, such as controlling weeds for longer than 3 years near agricultural land and planting practices that decrease invasion by non-native weedy species, could address the abundance of weed seeds in the agricultural system.
- Supplying information on both the ecosystem services and dis-services from research in the restoration landscape could build trust between restoration and agricultural communities.

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Supporting Information

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

Appendix S1. Site data including latitude, longitude, type of edge habitat, and if adjacent to a restored site, year site was restored.

Appendix S2. Seed bank species list. Table includes genus; species; subspecies; family; native (N) or exotic (E); annual (A), perennial (P), or biennial (B); growth type: tree (T), shrub (S), forb (F), or graminoid (G); primary seed dispersal type: wind (WI), gravity (GR), or animal (AN); listed in Cal-IPC as an invasive weed; listed in UCIPM walnut information page as an agricultural weed: not listed (N), regular weed (B), special weed problem (A); and whether the plant was detected in soil from sites adjacent to remnant, restored, or agricultural sites. Sources for information are genus, species, subspecies, family, native or exotic, annual or perennial, growth type from The Jepson Manual (Hickman 1993); primary seed dispersal mechanism based on the morphological features of the seed using the Jepson Manual (Hickman 1993) and the PLANTS database (USDA, NRCS 2007); California invasive plant species identified using the definitions on the invasive plant database compiled by the California Invasive Plant Council (Cal-IPC 2006); agricultural weed information from Pest Management Guidelines: Walnuts (UCIPM 2007).