

# Applicability of landscape and island biogeography theory to restoration of riparian understorey plants

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## Summary

1. Ecosystem recovery is influenced by processes at different spatial scales, yet land managers lack specific predictions on the relative importance of such processes that might guide management decisions. We tested whether ideas from landscape ecology (local vs. landscape scales) and island biogeography theory (patch size and isolation) predict restoration success for understorey plant communities in a highly fragmented riparian landscape, in an effort to provide guidance on how to allocate scarce restoration resources.

2. We sampled naturally colonizing riparian forest understorey plant communities in 15 riparian forests restored by planting native woody species along a 150-km stretch of the Sacramento River in central California. We analysed native and exotic understorey species richness and cover as a function of biotic and abiotic local and landscape variables.

3. Cover and species richness of exotic understorey plants decreased strongly with increasing overstorey cover, and were lower in quadrats closer to river base flow.

4. Native understorey species richness and cover were negatively related to exotic cover and positively related to connectivity with remnant forest. Cover of native wind-dispersed species was best explained by higher percentage forest cover surrounding a site within a 1000-m buffer, whereas cover of native water-dispersed species was higher closer to the river.

5. Neither patch size nor time since restoration explained a significant amount of native or exotic species richness or cover.

6. *Synthesis and applications.* Local factors explained more of the variance in understorey plant communities, but much of the variance remained unexplained. Our results provide weak support for the predictions of island biogeography theory and the importance of landscape-scale variables. These theories did not have strong predictive power in this applied restoration context at this temporal scale. Given limited resources, efforts to restore understorey plant communities in this highly fragmented system should focus on local-scale restoration methodologies, such as increasing cover of native overstorey species and reducing cover of exotic plants.

*Key-words:* herbaceous, large-scale, Sacramento River, succession, vegetation

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## Introduction

More than a decade ago Bradshaw (1987) suggested that restoration could serve as an ‘acid test’ for our understanding of ecological processes. Although small-

scale experiments are increasingly used to elucidate factors influencing forest recovery (Cabin *et al.* 2002; Hooper, Condit & Legendre 2002; Sweeney, Czapka & Yerkes 2002), multiple restoration sites can be valuable as experiments to evaluate factors that influence forest restoration or to test the applicability of general predictions of ecological theory to management questions. These opportunities have rarely been realized (Holl, Crone & Schultz 2003).

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Although landscape patterns (the spatial relationship of ecosystems) and processes (the flow of genes, individuals, materials and energy across large areas) are important to ecosystem recovery (Forman & Godron 1986; Bell, Fonseca & Motten 1997; Holl, Crone & Schultz 2003), the relative importance of local- vs. landscape-level patterns and processes on ecosystem restoration has rarely been measured in the field (Holl, Crone & Schultz 2003). Where similar restoration techniques have been repeated at multiple sites that differ with respect to local biotic and abiotic conditions, as well as surrounding land use, community composition of these sites can be used to assess the importance of local vs. landscape factors for ecosystem recovery. In previous work in a range of managed landscapes, some studies have highlighted the importance of landscape patterns for community composition (Saab 1999; Mitchell, Lancia & Gerwin 2001; Luck & Daily 2003). A few have suggested that local parameters are more important than the surrounding landscape (Brose 2001; Clergeau, Jokimaki & Savard 2001; Graham & Blake 2001) and most have shown that patterns and processes at multiple scales affect community composition (Mörtberg 2001; Verheyen & Hermy 2001; Fisher, Suarez & Case 2002; Fletcher & Koford 2002; Lee *et al.* 2002).

For plants, the relative importance of local vs. landscape patterns for community composition is likely to vary with dispersal ability (Brose 2001; Verheyen & Hermy 2001; Campbell, Rochefort & Lavoie 2003). For example, in abandoned agricultural lands forest recovery is often limited by proximity to seed sources (a landscape factor). Restoration efforts that increase local woody vegetation cover are likely to enhance seed dispersal of animal- but not wind- or gravity-dispersed species (Robinson & Handel 2000; Harvey 2000; Holl 2002), thereby lowering the relative importance of landscape patterns for certain dispersal guilds.

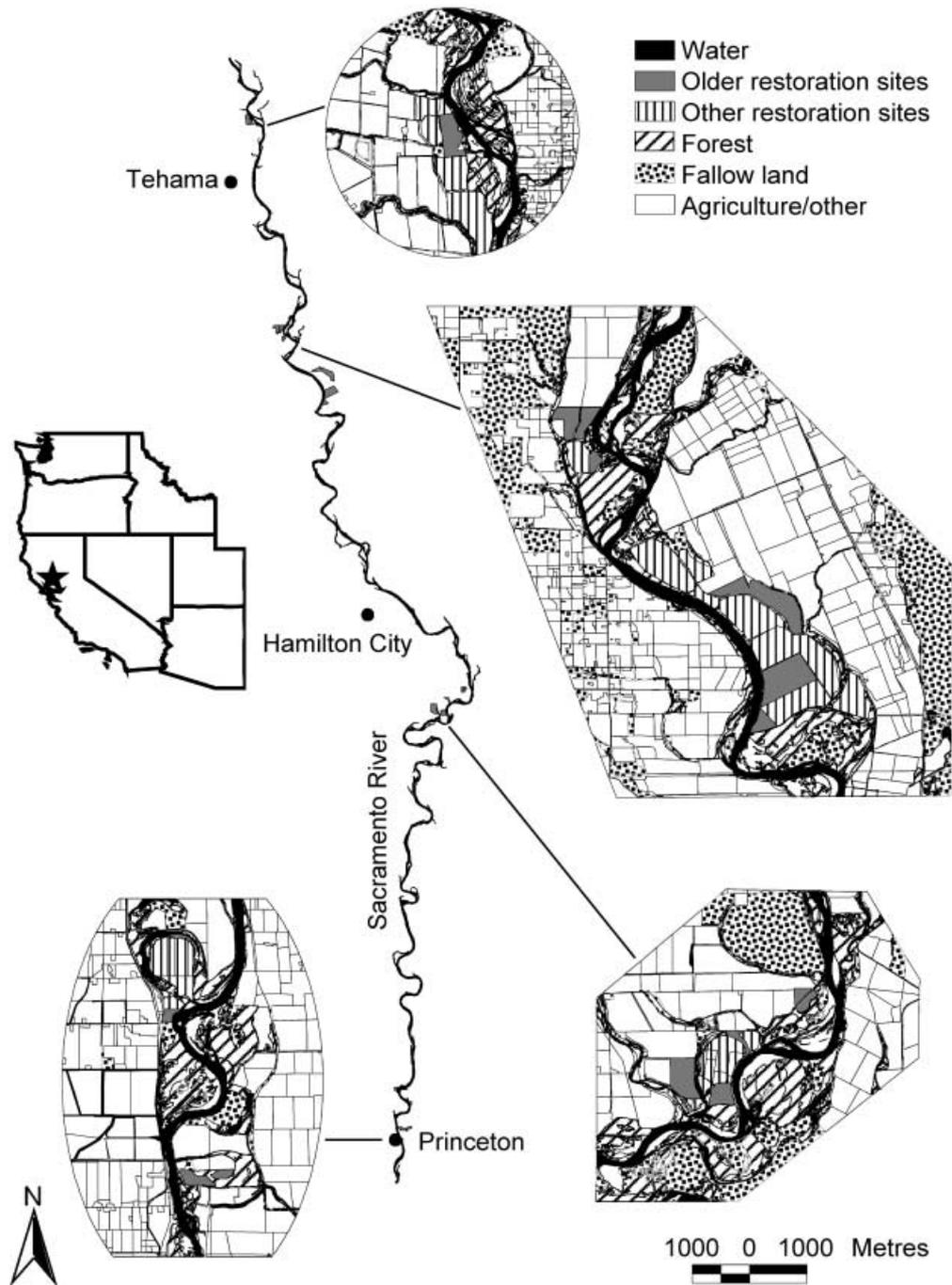
Restored sites that differ in size and isolation from natural vegetation could also serve as a test of specific predictions from island biogeography theory (MacArthur & Wilson 1967) for restoration planning. In most restoration projects a few species are planted, with the expectation that others will colonize naturally once suitable site conditions (e.g. light and nutrient levels, safe sites for germination, mutualistic species) are available. If extinction-colonization dynamics are important for natural colonization of restored sites, island biogeography theory predicts that few species would be found in smaller and/or more isolated restoration sites. However, most restoration efforts, including our study system, differ from controlled manipulation of patch size and isolation (Cairns *et al.* 1969; Simberloff & Wilson 1969; Molles 1978; Dickerson & Robinson 1985) in several important ways. First, restored sites are seldom, if ever, true experimental replicates, identical in all ways except size and isolation. In restoration sites the effects of patch size and isolation may be small, relative to heterogeneity

in abiotic and biotic conditions within sites and the vegetation matrix separating them (Lomolino & Perault 2001; Ricketts 2001; Fleishman *et al.* 2002). Thus, the community composition of restored sites suggests whether patch size and isolation are important variables for land managers to consider relative to other sources of variation, not whether size and isolation would be important, all else being equal. Secondly, if restoration 'success' is evaluated, it typically occurs within 5–10 years of implementation (Holl & Cairns 2002), whereas species richness may take decades to reach equilibrium. Thus, colonization patterns of restored sites tell us whether patch size and isolation matter over typical restoration and management time frames, not whether they determine equilibrium patterns.

We analysed large-scale riparian forest restoration at multiple sites along the upper Sacramento River (California, USA). This river, the largest in California, has been dammed and leveed for flood control and irrigation since the late 1800s. The Sacramento River riparian ecosystem was heavily deforested for fuelwood in the second half of the 19th century, with additional clearing in the 1950s and 1960s for conversion to orchards and row crops (California Resources Agency 2000). By the late 1970s only 5.5% of the original riparian forest cover remained (Greco 1999). The remaining forest is highly fragmented and impacted by altered hydrology and invasion by exotic species.

Several private and public agencies are working together to acquire lands and alter flow regimes to maintain and restore both hydrological processes and riparian habitat, under the mandate of California Senate Bill 1086 and the CALFED Bay Delta Program (CALFED Bay-Delta Program; California Resources Agency 2000). Thus far, most restoration efforts along the Sacramento River have focused on replanting orchards with native trees and shrubs, although geomorphological and hydrological processes are an increasing focus of restoration efforts. The Nature Conservancy (TNC) and other organizations aim to purchase properties within the 2.5-year floodplain along the 160 km of river between Red Bluff and Colusa (Griggs 1993). To date these organizations have planted approximately 2000 ha of riparian land with native tree species, with the hope that over time additional native flora and fauna will colonize the sites. Although there have been no previous systematic surveys or mechanistic studies of the understorey flora, observations suggest that restored sites are often dominated by aggressive exotic species, such as *Centaurea solstitialis*, *Lolium perenne* and *Sorghum halepense* (TNC, unpublished restoration reports). These observations further suggest that the assumption that native understorey communities will naturally recover has not yet been met, and that establishment is limited by factors at the local and/or landscape scale.

Our goal was to assess the relative importance of several local- and landscape-level variables on natural establishment of understorey vegetation at 15 sites



**Fig. 1.** Map of study sites and the surrounding landscape. Older restoration sites include the 15 sites sampled. Other restoration sites include more recently restored sites and older sites that were not sampled. Agriculture/other land includes orchard and row crops and other land cover, such as gravel and developed land.

planted with trees to restore forests in four sections of the upper Sacramento River (Fig. 1). Based on predictions of island biogeography theory and field observations, we hypothesized that (i) native species richness and cover would be higher in sites that were larger, were closer to forest and had lower exotic cover; and (ii) species richness and cover of exotic species would be higher in sites surrounded by a high proportion of fallow lands, where herbicides are not used to control exotic species of agricultural concern. To quantify different scales at which the surrounding landscape might

affect restoration success, we summed the amount of surrounding forest and fallow lands over different distances. In addition, we compared the proportion of within- and among-site variance in native and exotic species richness and cover explained by landscape effects, relative to probable sources of biotic and abiotic heterogeneity. Specifically, we included elevation and distance to the river (as indicators of flood interval and moisture availability), soil texture and past land use as abiotic factors that are typically considered important in restoration planning.

## Materials and methods

### SITE DESCRIPTION

The upper Sacramento River region receives an average of 662 mm of rainfall annually, with high interannual variability (range 330–1137 mm between 1989 and 2001) and the majority falling between November and April. Average mean temperatures range from a maximum of 34.5 °C in July to a minimum of 1.3 °C in January. Soils at all study sites were from the Columbia series, usually sandy loams. All sites surveyed were within the 2.5-year floodplain except one, River Vista 1996, which was within the 10-year floodplain. Groundwater depth was variable within sites, ranging from 2 to 5 m. Restored sites were planted at a density of 520–1300 trees ha<sup>-1</sup>, with 6–10 native riparian tree and shrub species, most commonly *Acer negundo*, *Baccharis pilularis*, *Fraxinus latifolia*, *Platanus occidentalis*, *Populus fremontii*, *Quercus lobata*, *Rosa californica*, *Salix exigua*, *Salix goodingii*, *Salix lasiolepis* and *Sambucus mexicana* (nomenclature follows Hickman 1993). Plants ranged from 30 to 90 cm tall at outplanting and were usually irrigated for 3 years using either sprinkler, drip or furrow irrigation. Exotic understorey species were generally removed by physical removal and herbicide (1–2% glyphosate) during the first growing season, and by mowing and/or herbicide for the second and third years (TNC, unpublished restoration reports). After 3 years no further management actions were taken. Survival and growth of planted tree and shrub species varied greatly by site (Alpert, Griggs & Peterson 1999). No effort was made to plant understorey species. All sites flooded in 1997 (United States Army Corps of Engineers 1999), which probably facilitated colonization by understorey species. Throughout this paper, native species richness and cover refer to native understorey species that were not planted as part of restoration efforts. We use the term forest 'restoration' to refer to the planting of native tree species, consistent with the Society for Ecological Restoration definition of ecological restoration 'the process of assisting the recovery of an ecosystem that has been degraded, damaged, or destroyed' (Society of Ecological Restoration Science and Policy Working Group 2002).

### UNDERSTOREY VEGETATION SURVEYS

In spring 2001, we surveyed the understorey vegetation in 15 sites that were restored between 1989 and 1996 (older restored sites), five reference forest sites, and three sites restored in 2000 (newly restored sites). Site characteristics are detailed in Appendix S1 (see Supplementary material). A few of the older restored sites we sampled were adjacent to each other; we defined sites as separate if they were planted with different overstorey species mixes at separate times, and if more than half of their perimeters bordered differing adjacent land uses. All restored sites had been used for

row crops and/or orchards for at least 30 years; a few sites that had been previously used for row crops or orchards had been left fallow with no herbicides or other management for 1–3 years prior to restoration.

We measured the understorey vegetation in all sites in late April/early May 2001. We sampled the understorey vegetation in 18–69 1 × 1-m quadrats per plot, with the number adjusted for total site size. We walked a systematic grid of points separated by 40–80 m. We chose the minimum distance to avoid spatial autocorrelation of data in small sites, and the maximum distance to distribute observations evenly across and ensure that spatial heterogeneity was adequately sampled in the largest sites. Upon reaching the predetermined location, we walked a random distance, ranging from 0 to 5 m to the left or the right perpendicular to the transect line, to locate the sampling quadrat. Because the data from newly restored areas and reference sites were collected only to assess the degree to which planting efforts reduced exotic species and restored native species, rather than to test theoretical predictions, we sampled only part of these sites. We sampled 20 quadrats separated by 50 m (total area sampled 5 ha) in newly restored sites, and 25–40 quadrats separated by 50 m (total area sampled 6.25–10 ha) in reference forest sites.

At each quadrat we estimated total live cover, total litter cover and bare ground to the nearest 5%, and estimated the cover of individual species using a slightly modified Braun Blanquet ranking scale: 0–1%, 1–5%, 5–25%, 25–50%, 50–75%, 75–100% (Mueller-Dombois & Ellenberg 1974). We used the mid-points of these ranges for cover analyses. We took four measurements of overstorey cover using a spherical densiometer. At the outset, each recorder made independent estimates of overstorey and understorey cover in the same plots to ensure consistency in our cover estimates. The origin of species (native or exotic) was determined from *The Jepson Manual* (Hickman 1993). A few plants were only identifiable to genus or family, so it was not possible to determine origin.

Surface soil texture was determined by a single person (to ensure consistency) using the texture-by-feel method (Thien 1979). For each soil type three to five samples were analysed for particle size (Gee & Bauder 1982) at the University of California, Davis Division of Agriculture and Natural Resources Analytical Laboratory (Davis, CA). We used the mean percentages of sand, silt and clay for these samples for each of the soil types in subsequent analyses. Locations of quadrats were recorded using a global positioning system (GPS; Pathfinder Pro XRS with TSC1 Data Collector, Trimble Navigation, Sunnyvale, CA) for global information system (GIS) analyses.

### GIS ANALYSIS

We combined GIS coverages of riparian vegetation and agricultural and urban land uses, which were constructed by the GIS laboratories at California State

University Chico (CA) and the California Department of Water Resources (Sacramento, CA) based on aerial photography and field data collected in 1998–99. We calculated the percentages of surrounding land in riparian forest, the most probable source of native species, and grassland/fallow land, the most probable source of exotic species (hereafter simply fallow land), within 50-, 100-, 500- and 1000-m radius circles around each quadrat and each site for quadrat- and site-level analyses, respectively. We calculated the distance from each quadrat to the main river channel and to forest patches of at least 0.25 and 1 ha. As the distances to forest patches of these sizes were highly correlated ( $R^2 = 0.85$ ) and results were identical using both patch sizes, we reported results for 0.25 ha only. We did not consider forest patches < 0.25 ha because patches smaller than this size are likely to be a few remnant trees that do not represent forest microclimate or vegetation conditions; they may also include spurious patches that result from 'slivers' due to overlaying multiple GIS layers.

For an area including 11 of our 15 older restored sites, a spatial model of surface topography relative to dry-season base flow was developed by S. Greco (University of California, Davis, CA) using a digital elevation model (DEM) from the US Army Corps of Engineers (Sacramento, CA) and an idealized dry-season flow model based on mean summer flows calculated from historical gauge station records (1 June–30 September from 1945 to 1997); this model did not include four of our sites due to the lack of a DEM for this area. Where possible, we overlaid our quadrat locations with Greco's model results (S. Greco, unpublished data) to estimate elevation above river base flow (hereafter elevation).

#### VEGETATION ANALYSIS

Before analysis, we calculated rarefied species richness for each site in a number of ways, first-order jack-knife, bootstrap and abundance-base coverage estimator, using EstimateS (Colwell 2001). Estimates of species richness in restored forest were only slightly higher than observed species richness, and the results of regressions using these estimates were identical to results with observed species richness as the dependent variable, so we only report the results of observed species richness here. Rarefied estimates of species richness suggested that we slightly underestimated species richness in reference sites, where sampling was much less extensive than in restored sites.

We log-transformed species richness and cover when necessary to meet assumptions of normality and homoscedasticity. For soil texture, we conducted a principal components analysis (PCA) of the percentages of sand, silt and clay. The first principal component (PC) explained 95% of the variation and was highly correlated with all soil particle sizes ( $R^2 > 0.92$  in all cases). Therefore, sample location along the first component axis was used in the regression. Finally, distances to river and forest were log + 1-transformed.

To address our primary questions, we tested effects of patch size and isolation, general scales of landscape influences, and a suite of abiotic and biotic variables on understory plant communities in older restored sites. Because some variables were highly heterogeneous within sites (e.g. overstorey cover, elevation) and others were completely homogeneous within sites (e.g. patch size, previous land use), we conducted two separate analyses. In both, we used stepwise regression to identify variables that best explained exotic and native species richness and cover, with forward addition of parameters. We reported all variables that entered the model at the  $P < 0.05$  level, and identified those that were significant after approximate Bonferroni correction for multiple hypothesis tests ( $P < 0.002$  for sample analysis,  $P < 0.004$  for site analysis; for a critical review of Bonferroni corrections see Stewart-Oaten 1995).

First, we analysed the full data set of 538 quadrats for variables that were heterogeneous within sites. Specifically, we tested the hypotheses that: (i) exotic understory cover and species richness depend on percentage fallow land within 50, 100, 500 and 1000 m of each quadrat, distance from each quadrat to the river, overstorey cover, soil texture, percentage bare ground and elevation; and (ii) native understory cover and species richness depend on distance from each quadrat to the nearest forest larger than 0.25 ha, percentage forest within 50, 100, 500 and 1000 m of each quadrat, distance to the river, soil texture, overstorey cover, exotic understory cover, percentage bare ground and elevation. Elevation data were available for only 394 of 538 quadrats (11 of 15 sites); we repeated analyses with and without elevation included. In each analysis, we accounted for fixed differences among sites by forcing all regression models to include dummy variables for site means. In other words, we tested the relationship between among-quadrat residuals from site means and potential explanatory variables. This procedure ameliorates the worst potential problem of pseudoreplication, fixed among-site differences due to variables other than those manipulated or measured by researchers (Hurlbert 1984). Because native species richness was either 0, 1 or 2 in 97% of the quadrats, we analysed native species richness and percentage cover using ordinal logistic regressions of the number of native species and ranked cover categories (0 = 0% cover, 1 = 0–5% cover, 2 = 5–25% cover, 3 = 25–50% cover, 4 = 50–75% cover, 5 = 75–100% cover).

Secondly, we analysed differences among the 15 site means for variables that were homogeneous within sites and for average values of some heterogeneous variables. We tested if native and exotic species richness and average cover depended on site age, site area, past land use, average distance to forest (native species only), average distance to river, percentage fallow (exotic species only) or forest (native species only) land at 50, 100, 500 and 1000 m, average overstorey cover, average exotic cover (native species only) and average percentage bare ground. In addition to analysing the aggregate native

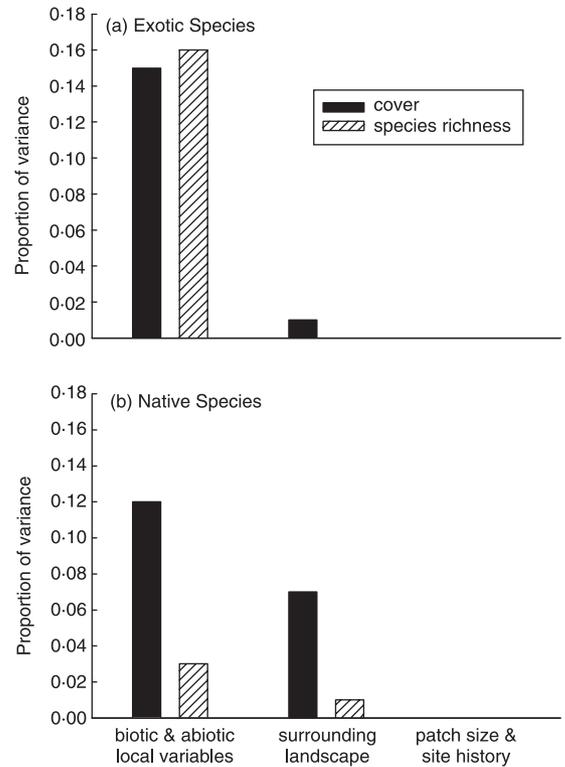
plant community, we repeated the analysis of cover separately for species grouped by dispersal mechanism. We categorized species that had clear adaptations for animal- or wind-dispersal, and included the remaining species in gravity- or water-dispersed, although many animal- and wind-dispersed species can be secondarily dispersed by flooding (Johansson, Nilsson & Nilsson 1996).

## Results

We recorded 40 native and 58 exotic species, in addition to 11 plant genera or families for which we could not identify the origin. All of the common overstorey species, such as *Acer negundo*, *Populus fremontii*, *Quercus lobata* and *Salix* spp., were native and were planted in restored sites. As expected, average overstorey cover was higher in reference sites, although two of the older restored sites had > 50% overstorey cover, approaching the 74–90% range of remnant forests (Table 1).

Native understorey cover in older restored sites was intermediate between reference forests and newly restored sites (Table 1). Native understorey species richness was much higher in reference forests compared with older restored sites, despite the fact that in many cases larger areas were surveyed in older restored sites (Table 1). Understorey exotic cover and species richness were not significantly different in reference and restored sites. Variance in native and exotic cover and species richness was high among sites, particularly the older restored sites (Table 1). The exotic grasses *Bromus* spp., *Cynodon dactylon*, *Lolium multiflorum*, *Sorghum halepense* and *Vulpia* spp., as well as *Brassica* spp., dominated understorey cover in older restored sites (Appendix S2 in Supplementary material). In these sites, only two native understorey species, *Artemisia douglasiana* and *Galium aparine*, were common. A number of other native species common in the remnant forest understorey, such as *Aristolochia californica*, *Carex barbarae*, *Rubus ursinus* and *Vitis californica*, were much less common in or absent from restored sites (Appendix S2 in Supplementary material). Thus, restored riparian forests appeared to be recruiting some native plant species, but the composition of older restored sites still differed substantially from remnant forest.

In general, biotic and abiotic variables, rather than the amount of surrounding fallow land, explained substantially more of the variance in both exotic species richness and cover at older restored sites (Fig. 2). When data were analysed by quadrat, exotic species richness and cover differed strongly among sites (Table 2). Both were higher with lower overstorey cover and higher elevation (Table 2). Exotic species richness was significantly higher near the river, although only 1–2% of the variance was explained (Table 2); surprisingly, distance to the river was weakly negatively correlated with



**Fig. 2.** Proportion of variance explained by biotic and abiotic local variables (overstorey cover, exotic cover, bare ground, elevation, soil texture), surrounding landscape (distance to forest, distance to Sacramento River, percentage surrounding forest or fallow land) and patch size and site history (age, past land use) for (a) exotic and (b) native species. Quadrat- and site-level results were combined by multiplying the site-level coefficients by the proportion of variance explained by site in the quadrat analysis, and summing these with quadrat results.

**Table 1.** Vegetation species richness and cover in newly restored (1 year old,  $n = 3$ ), older restored (5–12 years old,  $n = 15$ ) and reference sites ( $n = 5$ ). Values are means per site (minimum–maximum). Means with the same letter are not significantly different ( $P < 0.05$ ) across habitat type based on Tukey's LSD

	Newly restored	Older restored	Reference
Overstorey cover	0 <sup>a</sup>	29.2 (3.7–54.4) <sup>b</sup>	82.0 (73.5–90.0) <sup>c</sup>
Understorey native richness*	3.3 (2–5) <sup>a</sup>	5.1 (2–8) <sup>a</sup>	11.8 (11–13) <sup>b</sup>
Understorey native cover*	1.5 (0.3–3.3) <sup>a</sup>	9.7 (1.3–35.7) <sup>a</sup>	50.7 (30.8–66.7) <sup>b</sup>
Understorey exotic richness	17.3 (14–20) <sup>a</sup>	15.4 (8–30) <sup>a</sup>	10.2 (4–14) <sup>a</sup>
Understorey exotic cover	42.0 (35.2–46.2) <sup>a</sup>	40.0 (10.2–66.6) <sup>a</sup>	21.3 (4.0–44.7) <sup>a</sup>
Understorey total cover	40.3 (35.0–45.8) <sup>a</sup>	50.1 (30.7–78.8) <sup>a</sup>	73.3 (64.2–79.8) <sup>b</sup>

\*Includes only species that were not planted in restored sites.

**Table 2.** Stepwise forward regression of abiotic, biotic and landscape variables on native and exotic understorey cover and species richness at quadrats (1 × 1 m)

Dependent	Independent	d.f.	Standardized coefficient	R <sup>2</sup>	F/χ <sup>2</sup>	P	Regression
Exotic species richness, <i>n</i> = 538 (all quadrats)							
	Sites	14		0.22	10.5	< 0.0001*	Linear
	Overstorey cover	1	-0.316	0.09	63.9	< 0.0001*	
	Distance to river	1	-0.207	0.02	11.8	0.0006*	
	Bare ground	1	0.006	0.01	5.7	0.0172	
Exotic species richness, <i>n</i> = 394 (subset of quadrats with elevation data)							
	Sites	10		0.14	6.3	< 0.0001*	Linear
	Overstorey cover	1	-0.317	0.09	42.4	< 0.0001*	
	Elevation	1	0.300	0.04	18.5	< 0.0001*	
	Distance to river	1	-0.191	0.01	7.2	0.0071	
	Bare ground	1	0.128	0.01	5.4	0.0201	
Exotic species cover, <i>n</i> = 538 (all quadrats)							
	Sites	14		0.17	7.6	< 0.0001*	Linear
	Overstorey cover	1	-0.367	0.11	76.9	< 0.0001*	
	Bare ground	1	-0.121	0.01	8.9	0.0030	
	Fallow land at 50 m	1	0.093	0.01	5.2	0.0231	
Exotic species cover, <i>n</i> = 394 (subset of quadrats with elevation data)							
	Sites	10		0.10	4.3	< 0.0001*	Linear
	Overstorey cover	1	-0.43	0.13	67.4	< 0.0001*	
	Elevation	1	0.41	0.03	15.2	< 0.0001*	
	Bare ground	1	-0.10	0.01	4.5	0.0350	
Native species richness, <i>n</i> = 538							
	Sites	14		0.21	109.4	< 0.0001*	Logistic
	Exotic cover	1	-0.18	0.03	16.7	< 0.0001*	
	Distance to forest	1	-0.23	0.01	7.5	0.0063	
Native species cover, <i>n</i> = 538							
	Sites	14		0.21	118.4	< 0.0001*	Logistic
	Exotic cover	1	-0.18	0.07	37.8	< 0.0001*	
	Distance to forest	1	-0.48	0.02	14.6	< 0.0001*	

R<sup>2</sup> values for logistic regression are based on estimated maximum scaled R<sup>2</sup>.

Results of analysis using the subset of data with elevations are presented where elevation effects were statistically significant.

\*Statistically significant after Bonferroni correction.

**Table 3.** Stepwise forward regression of local and landscape variables on native and exotic cover and species richness at the site level

Dependent	Independent	Standardized coefficient	d.f.	R <sup>2</sup>	F	P
Exotic species richness						
Exotic cover						
Native species richness						
Native cover	Forest at 1000 m	0.63	1	0.31	5.9	0.0306
	Exotic cover	-0.50	1	0.24	6.6	0.0246
Native wind-dispersed	Forest at 1000 m	0.70	1	0.49	12.4	0.0037*
Native externally dispersed	Past land-use fallow	-0.70	1	0.49	12.5	0.0037*
Native gravity- or water-dispersed	Distance to river	-0.73	1	0.54	15.2	0.0018*

\*Statistically significant after Bonferroni correction.

elevation ( $R = -0.16$ ,  $P = 0.0012$ ). The small amounts (*c.* 1%) of the variance in exotic species richness (bare ground only) and cover explained by bare ground and percentage fallow land at 50 m were not significant after Bonferroni correction (Table 2). At the site level, none of the 11 variables tested was significantly related to exotic species cover or richness, even before Bonferroni correction (Table 3).

Native species composition at older restored sites was explained by biotic interactions, in concert with

connectedness with forest (Fig. 2). Like exotic species, at the quadrat level native species richness and cover differed strongly among sites (Table 2). In addition, native species richness and cover decreased somewhat (3–7% of the total variance) with increasing exotic cover (Table 2). We found more native species in quadrats closer to forest, although this difference was small relative to the total variation and significant only for cover after Bonferroni correction (Table 2). Including elevation in native species cover and richness models

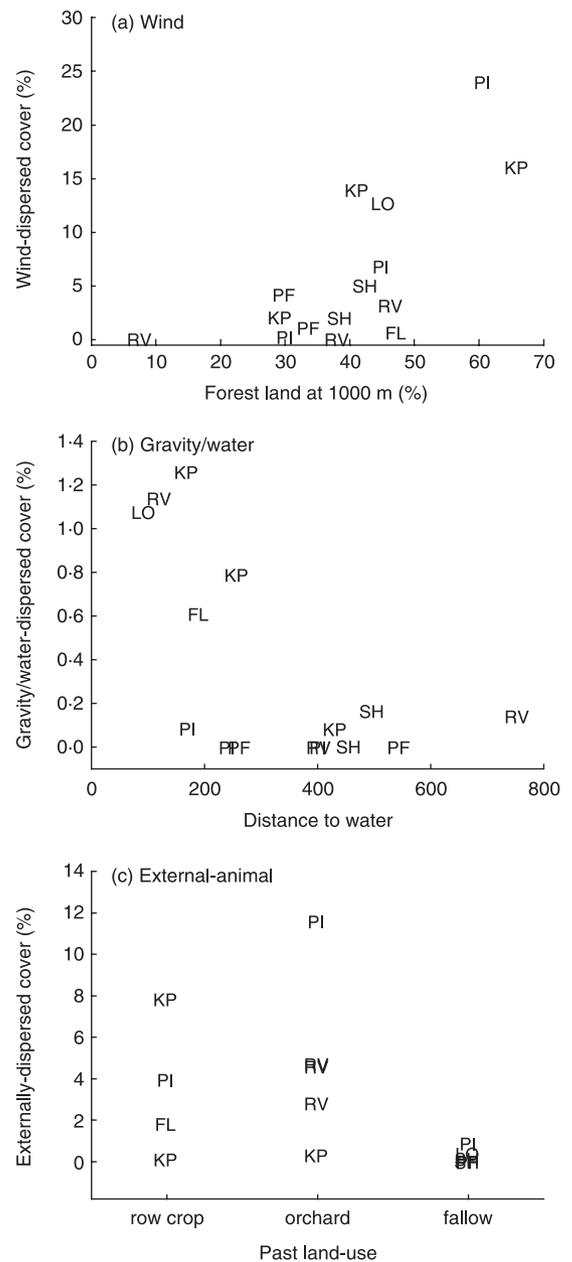
did not explain additional variance. At the site level, average native cover was positively related to percentage forest at 1000 m surrounding the site, and negatively related to average exotic cover; although these relationships explained a substantial amount of variance in native cover (31% and 24% of the variance, respectively), they were not significant after Bonferroni correction given the low number of sites (Table 3). Contrary to our expectations, none of the independent variables in the site-level model, including site area and time since restoration, explained a significant amount of variation in native species richness.

Separating native species by dispersal strategy, we found higher than average cover of wind-dispersed species, the most common of which was *Artemisia douglasiana*, in regions with high forest cover (Table 3 and Fig. 3a). Not surprisingly, gravity- or water-dispersed species (e.g. *Carex barbarae* and *Urtica dioica*) were more likely to be found nearer the river (Table 3 and Fig. 3b). Cover of native externally animal-dispersed species (primarily *Galium aparine*) was always low at sites that had been left fallow for a few years prior to restoration, whereas in sites that were utilized for orchard or row crops immediately prior to restoration, cover was variable but on average higher (Table 3 and Fig. 3c). The presence of internally animal-dispersed species was sufficiently low that it was not possible to draw conclusions about distribution patterns. Interestingly, sites that were located in close proximity to one another (indicated by the same two-letter symbol on Fig. 3) varied substantially in native species composition, exotic species composition (data not shown) and most landscape and local variables.

## Discussion

The colonization of restored sites by native species appeared to be limited by the presence of exotic understorey species and lack of connectivity with remnant forest, whereas cover of exotic species was primarily associated with low percentage overstorey cover and, to a lesser degree, high floodplain position (Tables 2 and 3). Dispersal limitation may be important for particular exotic species during the invasion process. We suspect, however, that the exotic species that establish in an area at high abundance are likely to have a nearly ubiquitous seed distribution in landscapes dominated by disturbed lands. Therefore, native species, which primarily occur in habitat remnants, are more likely to be dispersal limited. None the less, in our system, native species distributions were more negatively related to presence of exotic species than to isolation.

Based on our results, the best way to ensure successful establishment of native understorey species in this system may be first to choose sites with low elevation relative to river base flow and near remnant forests, and then tend planted overstorey species so that the canopy closes quickly and exotic understorey species are shaded out. Seeding or planting species after establish-



**Fig. 3.** Significant explanatory variables of native plant cover at the site level by dispersal strategy (a) Wind-dispersed; (b) gravity- or water-dispersed; (c) externally animal-dispersed. Site locations are indicated by two letter acronyms (see Appendix S1 for full names). Note differences in y-axis scales.

ing an overstorey cover would almost certainly increase establishment rates, but would cost a great deal and would require a longer term commitment than is currently typical (3 year) for these projects.

Species' distributions in restored sites support the importance of both local- and landscape-scale factors, both within and among sites, although local abiotic and biotic factors explained a larger proportion of the total variance (Fig. 2). Exotic species cover was most affected by overstorey cover of planted native species, which is probably determined by local conditions, but also by landscape position relative to the floodplain

(Alpert, Griggs & Peterson 1999). Native understorey species' distributions were negatively related to cover of exotic understorey species. Although statistically significant, landscape position effects were smaller than has been found in other studies of vegetation distribution in floodplains (Rot, Naiman & Bilby 2000; van Coller, Rogers & Heritage 2000; Drezner, Fall & Stromberg 2001). This may be because TNC primarily conducts horticultural restoration in the 2.5-year floodplain, so sites are relatively uniform in elevation and proximity to the river. It also may be because many studies of riparian communities focus on overstorey, rather than understorey, plant species (Scott, Friedman & Auble 1996; Shafroth, Stromberg & Patten 2000; van Coller, Rogers & Heritage 2000).

Native species with different dispersal mechanisms were affected differentially by local and landscape factors. Wind-dispersed species were most abundant when the surrounding landscape within 1 km was more than 20% remnant forest (Fig. 3). Externally animal-dispersed species were best explained by past land use, a site feature, whereas gravity- and water-dispersed species were most abundant within 250 m of the Sacramento River main channel (Fig. 3).

As a test of the relevance of island biogeography theory to restoration, native species distribution in restored forests provides weak support for effects of isolation. Native species richness and cover were significantly higher near remnant forests, but these effects explained only about 7% of the total variation in native cover and about 1% of the total variation in species richness (Table 1). In part, this relationship might be weakened by analysis at the community level. For wind-dispersed species cover, percentage forest in the surrounding landscape explained about 50% of the among-site variance in cover, which would be approximately 10–12% of the total variance.

Our sites violate a number of assumptions of island biogeography theory. Some native species are present in areas other than remnant forests, and not all remnant forests contain all native species. Our predictive power would almost certainly increase if we could map all potential source populations of all native species, and relate species-specific colonization probabilities to isolation (Bastin & Thomas 1999). In addition, while we assume that few seeds of native species were present in the seed bank due to > 30 years of intense agricultural use, including regular herbicide treatments of herbaceous species, past studies in long-used agricultural lands in the temperate zone (Hutchings & Booth 1996; Bekker *et al.* 1997; Middleton 2003) suggest that some seeds of some native understorey plants may persist under such conditions. However, these violations of the assumptions of island biogeography theory are common, if not universal, to restored sites in complex landscape mosaics. Therefore, they do not undermine our ability to test whether effects of patch size and proximity to remnant habitat, drawn from island biogeography theory and commonly recommended as considerations

in restoration planning (e.g. Sauer 1998; Hobbs 2002), are important predictors of restoration success.

Our results provide no support for effects of patch size on species richness. Although species–area relationships are widely documented in natural habitat remnants (Diamond 1972; Freemark & Merriam 1986; Laurance *et al.* 2002), they may not be applicable to restored systems approximately a decade after establishment, because they refer to long-term equilibria. Plant communities in the restored forests we surveyed were intermediate between newly planted restoration sites and reference forests (Table 1), suggesting ongoing succession. Furthermore, a number of recent studies point to the importance and potential confounding effects of among-site variation in patch quality (Brose 2001; Foster 2001; Verheyen & Hermy 2001; Fleishman *et al.* 2002). In our sites, among-site variation in biotic and abiotic factors was high, which is typical for restored sites.

A few unexpected trends resulting from our analyses bear further discussion. First, we were surprised that site age (i.e. time since restoration) did not explain a significant amount of variance in native or exotic species cover or richness. A common assumption in restoration is that restored sites will follow a successional trajectory towards a reference system (Bradshaw 1984; MacMahon 1987). The probable explanation for this result is that restoration methodologies have improved over time, resulting in more rapid establishment of overstorey cover in more recently restored sites. Over time, species have increasingly been selected for sites and locations within sites based on improved knowledge of adaptations to soil type and depth to groundwater. In addition, irrigation and control of exotic species of agricultural concern, through a combination of herbicides and mowing, have become more systematic. Alternatively, the 1997 flood could have generated a single, overriding colonization pulse.

Secondly, the negative correlation between elevation relative to river base flow and distance to river seems counterintuitive. It is important to note, however, that all these sites have been levelled for agriculture and many have levees at the river edge, which has altered their natural topography. As a result, a number of the sites slope slightly upwards in the direction of the river. The significant effect of elevation above river base flow highlights the important effect of even small difference in depth to the water table for plant communities in these arid systems (Hupp & Osterkamp 1996; Goodwin, Hawkins & Kershner 1997; Shafroth, Stromberg & Patten 2000).

Thirdly, although soil texture has often been demonstrated to strongly influence riparian plant communities (Hosner & Minkler 1963; Johnson, Burgess & Keammerer 1976; Alpert, Griggs & Peterson 1999), we did not find significant soil texture effects. This lack of significance might be due to the fact that we only surveyed the soil texture at the surface, which may not be a good indicator of soil texture at greater depths (Alpert, Griggs &

Peterson 1999). Alpert, Griggs & Peterson (1999), working on a subset of these sites, reported higher growth of tree species on soils that were deeper and finer grained in the top 1.5 m. Augering to obtain detailed soil profiles was not feasible given the large number of quadrats we sampled.

In closing, we revisit the applicability of ideas from landscape ecology and island biogeography theory to restoration planning. As in many landscape studies, both local and landscape factors appeared to influence plant communities, supporting the general idea that community dynamics operate across multiple scales. Patch size and isolation, the key factors in island biogeography theory, explained only a small amount of variance in species richness and cover. Our data also demonstrate strong heterogeneity among sites and ongoing change in plant communities, *c.* 10 years after planting. Thus, from a theoretical perspective, restoration at multiple sites appears to be a poor test of island biogeography theory because the sites do not meet theoretical assumptions. From the restorationists' perspective, however, we can conclude that patch size and, to a lesser extent, isolation are relatively unimportant predictors of understorey plant species richness and cover in this system, after a time period greater than that used to evaluate the success of most restoration projects. Therefore, in order to restore native understorey plant communities in this highly fragmented landscape mosaic, managers should focus on local-scale restoration methodologies, such as efforts to increase native overstorey cover and reduce exotic plant cover, and place less emphasis on choosing sites near remnant forest.

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### Supplementary material

The following material is available from <http://www.blackwellpublishing.com/products/journals/suppmat/JPE/JPE949/JPE949sm.htm>

**Appendix S1.** Site descriptions.

**Appendix S2.** Common exotic and naturally colonizing native understorey species averaged across all quadrats.

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