

# Maximizing Benefits from Riparian Revegetation Efforts: Local- and Landscape-Level Determinants of Avian Response

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**Abstract** With limited financial resources available for habitat restoration, information that ensures and/or accelerates success is needed to economize effort and maximize benefit. In the Central Valley of California USA, riparian habitat has been lost or degraded, contributing to the decline of riparian-associated birds and other wildlife. Active restoration of riparian plant communities in this region has been demonstrated to increase local population sizes and species diversity of landbirds. To evaluate factors related to variation in the rate at which bird abundance increased after restoration, we examined bird abundance as a function of local (restoration design elements) and landscape (proportion of riparian vegetation in the landscape and riparian patch density) metrics at 17 restoration projects within five project areas along the Sacramento River. We developed *a priori* model sets for seven species of birds and used an information theoretic approach to identify factors associated with the rate at which bird abundance increased after restoration. For six of seven species investigated, the model with the most support contained a variable for the amount of riparian forest in the surrounding landscape. Three of seven bird species were positively correlated with the number of tree species planted and three of seven were positively correlated with the planting densities of particular tree species. Our results indicate that restoration success can be enhanced by selecting sites near existing riparian habitat and planting multiple tree species. Hence, given limited resources, efforts to restore riparian habitat for birds should focus on

landscape-scale site selection in areas with high proportions of existing riparian vegetation.

**Keywords** Birds · California · Landscape-scale · Local-scale · Restoration · Riparian · Sacramento River

## Introduction

The science and practice of ecological restoration have made great advances over the past several decades. Still, our knowledge of how best to accomplish restoration remains incomplete (Herrick and others 2006; Hobbs and Cramer 2008), especially in the context of changing environments of the future (Choi and others 2008), and the need to make decisions about how best to allocate limited financial resources (Thomson and others 2009).

The factors that influence ecosystem recovery through restoration operate at multiple spatial and temporal scales and the influence of scale varies among organisms and processes. Most restoration studies have necessarily been small-scale, reflecting both the amount of area restored and the economic constraints of conducting large-scale, long-term investigations. Large-scale studies composed of multiple restoration sites have the potential to bridge the gap between ecological theory and on-the-ground management actions (Holl and Crone 2004). One example of ecological theory that contributes to restoration is our body of knowledge of landscape ecology. While site-level considerations, such as soils and disturbance history (Alpert and others 1999), have often been the focus of restoration design, considering the landscape in which projects are embedded may also be critically important (Fahrig 2003; Holl and others 2003; Lindenmayer and others 2010).

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While it is well known that birds and other organisms respond at multiple scales (e.g., Saab 1999; Miller and others 2004; Koh 2008), the relative importance of local-versus landscape-scale process that influence the success of restoration efforts has rarely been studied, yet knowledge of these factors can have direct application for restoration practitioners (Holl and Crone 2004; Lindenmayer and others 2010). With limited financial resources available for ecological restoration, information that ensures and/or accelerates success is needed to economize effort and maximize benefit.

Along California's largest river, the Sacramento River, over 95% of the riparian habitat has been lost to fuelwood harvest, flood control, and conversion to agriculture and urban development (Katibah 1984). As a result, riparian dependent wildlife populations have declined or been extirpated. Considering just birds for example, Least Bell's Vireo (*Vireo belli pusillus*) and Willow Flycatcher (*Empidonax traillii*) have been extirpated and the Bank Swallow (*Riparia riparia*) is currently listed as State Threatened and the Western Yellow-billed Cuckoo (*Coccyzus americanus occidentalis*) as State Endangered (RHJV 2004).

Large-scale restoration projects have been ongoing since 1989; to date 2,337 ha have been revegetated, another ~1,000 are currently underway or planned (Golet and others 2008, Golet pers. comm.), and the goal is to add 4,500 additional ha (Central Valley Joint Venture 2006). Strategies for restoring the Sacramento River include: (1) conserving flood-prone lands, giving priority to those that contain and/or border remnant riparian habitats; (2) revegetating land with native trees, shrubs and understory species; and (3) restoring natural river processes (Golet and others 2003, 2008).

Our study of birds in restored and remnant forests along the Sacramento River since 1993 have shown that revegetation has increased the abundance and diversity of bird communities (Gardali and others 2006; Golet and others 2008). Gardali and others (2006) measured broad-scale response to restoration, yet individual restoration projects varied considerably in terms of planting design and landscape context. Presumably, these factors influence ecological responses to restoration in the same ways that plant and animal communities are influenced by patterns and processes at multiple spatial scales (e.g., Verheyen and Hermly 2001; Götmark and others 2008).

Our objective in this study is to identify specific restoration practices that maximize increases in the number and diversity of birds. We focus on restoration design considerations that can most easily be controlled by the practitioner—the location of a restoration project based on landscape context and once a location is determined, how

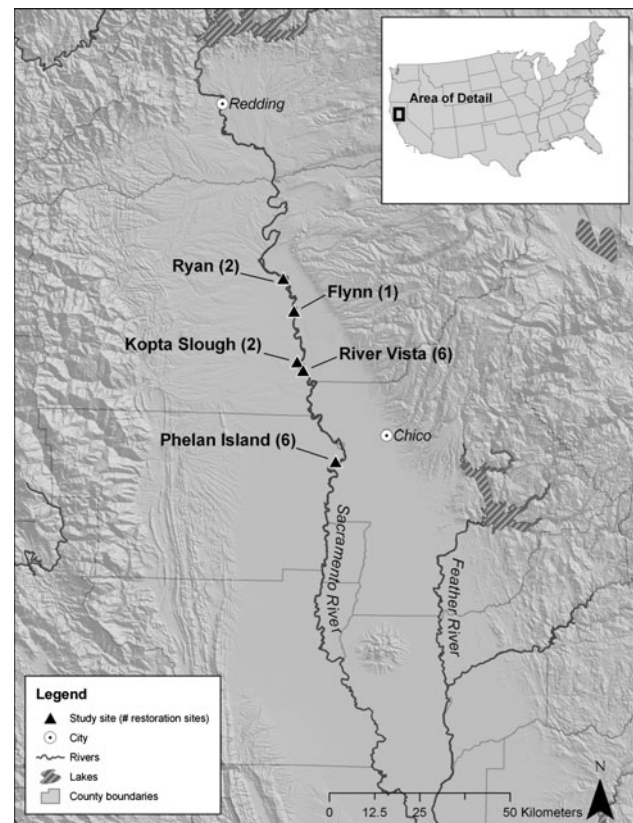
many and of what species to plant. The results can thus be used to inform future acquisitions and restoration activities.

## Methods

### Study Sites

We surveyed birds at 17 restoration projects distributed among 5 project areas along the Sacramento River between Red Bluff, Tehama County, and Colusa, Colusa County, California, USA (Fig. 1, Table 1). Restoration projects varied by planting year, landscape context, and planting designs ranging in size from approximately 4 to 74 ha, with a mean size of 28 ha. In total, approximately 475 ha of revegetated lands were used in this analysis.

Details of restoration techniques are described in Alpert and others (1999) and Holl and Crone (2004). In general, restoration projects had recently been under agricultural production, had been cleared of all native vegetation, and were adjacent to remnant riparian forest. The projects were prepared for restoration plantings by a combination of disking, burning, furrowing, leveling, and/or spraying with



**Fig. 1** Location of project areas (restoration sites) along the Sacramento River, California, USA

**Table 1** Site name, planting size, year planted, number of point count stations established within planting, and years in which surveys took place in the Sacramento Valley, CA, USA

Site	Project	Hectares	Year planted	Number of stations	Years surveyed
Flynn	1	64.75	1998	4	1998–2001, 2003
	Kopta Slough	2	7.28	1989	1
River Vista	3	16.59	1990	3	1996–2003
	4	9.31	2000	2	2000–2003
	5	16.59	1995	3	1995–2003
	6	74.46	1999	2	1999–2003
	7	53.42	1998	1	1998–2003
	8	44.52	1994	2	1994–2003
	9	55.85	1997	4	1997–2003
Ryan	10	14.57	1997	2	1998–2003
	11	33.99	2001	2	2001–2003
Phelan Island	12	23.07	1999	5	1999–2003
	13	8.90	2001	2	2001–2003
	14	4.05	2001	1	2001–2003
	15	4.45	2001	2	2001–2003
	16	13.76	1991	4	1994–2003
	17	29.14	1992	5	1994–2003

herbicides. The native riparian tree and shrub species planted were most commonly box elder *Acer negundo*, coyote brush *Baccharis pilularis*, Oregon ash *Fraxinus latifolia*, sycamore *Platanus racemosa*, cottonwood *Populus fremontii*, Valley oak *Quercus lobata*, California rose *Rosa californica*, willows *Salix exigua*, *Salix goodingii*, and *Salix lasiolepis*, and elderberry *Sambucus mexicana*.

Deciduous fruit and nut orchards dominated the landscape around our study sites, with smaller areas of remnant riparian forest, field crops, pasture, rice fields, and urban/residential development.

#### Model Variables

The landscape level riparian habitat data include information from several sources derived from aerial photos and satellite imagery and were manipulated using ArcGIS 9 (ESRI 2006). These sources included the Department of Water Resources (metadata: <http://www.water.ca.gov/landwateruse/lusrvymain.cfm>), the California Department of Fish and Game (metadata: <http://gis.ca.gov/catalog/BrowseRecord.epl?id=31366>), and the United States Fish and Wildlife Service's National Wetland Inventory (metadata: [http://www.fws.gov/nwi/downloads/metadata/nwi\\_meta.txt](http://www.fws.gov/nwi/downloads/metadata/nwi_meta.txt)). For analysis, layers were converted into 30 x 30 m grids from the original vector formats to match the California Department of Fish and Game grid layer. Patch density was derived using FRAGSTATS moving window metrics and is defined as the number of patches of the corresponding patch type divided by total landscape area (McGarigal and Marks 1995).

Data on planting design (species and densities) were obtained from unpublished reports which were an accurate

account of the as-built species composition and planting densities (Golet personal communication). Projects were planted with 0–4 species of shrubs (mean = 2.5) and 1–7 species of trees (mean = 5.0). Planting densities were highly variable, both within and across species. For example, cottonwoods were used at 14 of the 17 sites and ranged in planting density from 20 to 430 per ha. Willows were also used at 14 of the 17 sites and ranged in planting densities from 27 to 320 per ha, whereas coyote bush was only used at 8 of the 17 sites, ranging in planting density from 8 to 46 per ha. In total, over 312,000 rooted plants or propagules were used across the restoration projects that we examined.

#### Field Methods

We estimated the relative abundance of seven species of riparian birds using point-counts (Ralph and others 1993, 1995). We established 45 point-count survey stations approximately 200 m apart and within the boundaries of projects. The number of stations within a project varied from 1 to 5 (Table 1). Each point-count station was surveyed two times per year for 3–10 years during the breeding season (Table 1). Each count lasted 5 min, during which all birds seen or heard within 50 m of the observer were recorded. We assumed that detection probabilities were similar within this distance among study areas and years. Counts began at dawn and continued for up to 4 h past sunrise.

#### Statistical Analyses

We estimated riparian bird species richness as the number of species (from a list of 20 species previously identified as

focal species for conservation work in this region; Gardali and others 2006) detected within 50 m of the observer for each year at each survey point. We estimated abundance indices for a subset of seven of these species that included Western Wood-Pewee, Nuttall's Woodpecker, Bewick's Wren, Ash-throated Flycatcher, Spotted Towhee, Common Yellowthroat, and Black-headed Grosbeak (scientific names for bird species are given in Table 3). These species were selected for analysis because there was sufficient rates of occurrence to allow model fitting and because they represent the full complement of nesting guilds present at these sites including an open cup ground/low nester (Spotted Towhee), shrub nester (Common Yellowthroat), and canopy nesters (Western Wood-Pewee and Black-headed Grosbeak), as well as high and low cavity nesters (Ash-throated Flycatcher and Bewick's Wren). In addition, they include long-distance Neotropical migrants (Western Wood-Pewee, Ash-throated Flycatcher, Black-headed Grosbeak), a short-distance migrant (Common Yellowthroat), and year-round residents (Nuttall's Woodpecker, Bewick's Wren, and Spotted Towhee).

We were unable to explicitly model detection probabilities, and therefore only included detections within 50 m of observers. At this cut-off we assume probability of detection is similar among observers, sites, and years and further presume that our fixed radius index provides a useful measure of abundance (Johnson 2008). If detection probability did indeed change as a function of restoration age we suspect it would decline as a function of increasing vegetation density limiting our ability to detect birds. It is worth noting that most species exhibit increasing abundance as a function of restoration age and corresponding vegetation development (Gardali and others 2006). We have no empirical reason to believe that detection probability declined through time, but if it did the effect sizes for positive trends could be biased low.

We used negative binomial regression to examine the effects of restoration design on abundance and bird species richness indices. The negative binomial distribution often provides a good fit for counts of biological populations where zeros are commonplace (Anscombe 1949, Bliss and Fisher 1953). This distribution has proved useful for bird-count data in part because it provides for a highly skewed distribution but does not assume that the mean equals the variance, as is the case with the Poisson distribution (White and Bennetts 1996). Models were parameterized with dispersion as a function of the expected mean for the  $i$ th observation ( $\text{dispersion} = 1 + \alpha \cdot \exp(x_i \cdot b)$ ). Thus,  $\alpha = 0$  corresponds to  $\text{dispersion} = 1$  and is therefore not different from a Poisson model. For ease of model interpretation we present model coefficients as Incidence Rate Ratios (IRR). Regression coefficients reflect differences between the logs of expected counts and since the

difference of two logs is equal to the log of their quotient, the regression parameter estimate is the log of the ratio of expected counts. IRRs are simply the exponentiated form of the coefficients. Thus, if an explanatory variable has an IRR of 1.05, a one-unit change in the explanatory variable corresponds to an increase in the response variable by a factor of 1.05.

Because restoration projects were clustered within the five project areas, we employed a robust variance estimator for cluster-correlated data (Williams 2000; Stata Corporation 2003). This estimator accounts for the lack of independence of survey points within a project or adjacent sets of projects. Thus, the unit of analysis is individual survey points within a given year, but variance is adjusted to account for covariation based on clusters of points. This approach has been shown to perform just as well as a mixed model approach with a random effect (Williams 2000) and was preferred over averaging points within projects for several reasons. Fine scale variation among clustered points in the landscape metrics contributed to the models and variation in local planting metrics for smaller plantings that were adjacent and therefore not fully independent also contributed to the models, while lack of independence is accounted for in variance estimates. In addition, this approach allowed us to preserve the count-based data (rather than a non-integer average for each cluster) which allowed us to use the appropriate negative binomial distribution in regression models.

For each dependent variable, we evaluated a set of 18 candidate models in an information-theoretic framework (Table 2). Because previous work including these and other sites demonstrated an increase in abundance associated with restoration age (Gardali and others 2006), the variable "years since planting" was included in all models. Our null model was the relationship between either a particular bird species' abundance or bird species richness and restoration age. Our *a priori* model set (Table 2) included two landscape variables that were derived from remotely-sensed data at scales of 500 m and 2 km and were attributed to points using a Geographic Information System (GIS). These were the percent of the surrounding landscape that was classified as riparian forest and riparian patch density which is a measure of the number of remnant riparian forest patches per unit area (McGarigal and others 2002). We included these landscape variables because it is widely recognized that the success of individual restoration projects depends upon the matrix in which they are embedded (Holl and others 2003; Lindenmayer and others 2010). The amount of surrounding riparian vegetation was likely to be important as the most probable source of bird species and hence their ability to disperse into the restoration sites. Patch density was calculated because it measures spatial heterogeneity which may be important for

**Table 2** Model set estimated for each species, and for bird species richness

Model #	Variable 1	Variable 2	Variable 3
1	Years since planting	–	–
2	Years since planting	Patch density (500 m)	–
3	Years since planting	Patch density (2 km)	–
4	Years since planting	Percent riparian (500 m)	–
5	Years since planting	Percent riparian (2 km)	–
6	Years since planting	Shrub species richness	–
7	Years since planting	Tree species richness	–
8	Years since planting	Valley oak planting density	–
9	Years since planting	Blue elderberry planting density	–
10	Years since planting	Cottonwood planting density	–
11	Years since planting	Willow planting density	–
12	Years since planting	Percent riparian (500 m or 2 km) <sup>a</sup>	shrub species richness
13	Years since planting	Percent riparian (500 m or 2 km) <sup>a</sup>	tree species richness
14	Years since planting	Percent riparian (500 m or 2 km) <sup>a</sup>	blue elderberry planting density
15	Years since planting	Percent riparian (500 m or 2 km) <sup>a</sup>	Cottonwood planting density
16	Years since planting	Percent riparian (500 m or 2 km) <sup>a</sup>	Valley oak planting density
17	Years since planting	Percent riparian (500 m or 2 km) <sup>a</sup>	Willow planting density
18	Years since planting	Tree species richness	Shrub species richness

<sup>a</sup> The geographic scale (500 m or 2 km) for percent of the landscape currently in riparian habitat with the lower AIC for a given species (model #3 vs. model #4), was used in this model

some species. Several GIS data sources were combined to produce a single representation of Sacramento Valley riparian habitat (PRBO unpublished data, Central Valley Joint Venture 2006). Some models also included one or more of six local planting design variables based on data associated with individual restoration plantings (The Nature Conservancy, unpublished data). Planting variables included the number of tree species planted, the number of shrub species planted, and planting densities of blue elderberry, willows, Valley Oak, and cottonwood trees. These were the most commonly planted species (occurred at >50% of point count surveys and projects) for which complete data was available. Other species were planted at fewer than half of the survey points (Oregon ash, coyote brush), or data on planting density was not available for all sites which precluded their use (sycamore, box elder, and California rose).

For each model, we calculated Akaike's Information Criterion (AIC) and the difference in AIC between each candidate model and the model with the lowest AIC value ( $\Delta$ AIC) to rank and select the best models (Burnham and Anderson 2002). We considered candidate models with  $\Delta$ AIC < 2 to have substantial support but did not employ model averaging due to uncertainty in its ability to reduce bias (Richards 2005). Instead, we present all models that obtained substantial support. We did not employ AIC<sub>c</sub> in model selection because it shows no clear improvement over AIC (Richards 2005).

## Results

All species we examined showed an increasing trend in abundance with restoration age (Table 3; Fig. 2). Rates of increase varied from a low of 15% per year for Ash-throated Flycatcher to an astonishing 51% per year for Bewick's Wren.

The importance of a landscape-level variable was apparent in every species-specific model set, either in the best model or in a competing model with substantial support (Table 3). Each of Western Wood-Pewee, Ash-throated Flycatcher, Spotted Towhee and Common Yellowthroat had only one model, while Nuttall's Woodpecker and Bewick's Wren had two and three models, respectively, with  $\Delta$ AIC < 2. Bird species richness had two models that had  $\Delta$ AIC < 2.

The amount of remnant riparian habitat in the landscape was included in top models for 6 of the 7 species. The scale at which this relationship had more support was 500 m for Western Wood-Pewee, Nuttall's Woodpecker, and Ash-throated Flycatcher. Spotted Towhee, Bewick's Wren, and Black-headed Grosbeak had more support for a relationship with percent of riparian in the landscape at the 2 km scale. For Common Yellowthroat, the only model with support was for riparian patch density at 2 km. This variable reflects having more, usually smaller, discrete patches of riparian forest that may provide the moist edge habitat—comprised of herbaceous vegetation—that this species uses

**Table 3** Incidence rate ratios (IRR) with robust confidence intervals and dispersion parameter (alpha) for top models ( $\Delta AIC \leq 2$ ) in each model set

Response	$\Delta AIC$	Alpha <sup>a</sup>	Pseudo R <sup>2b</sup>	Predictor	IRR	Robust 95% CI	
						low	high
Western Wood-Pewee <i>Contopus sordidulus</i>	0	0.0825	0.30	Years since planting	1.2454	1.1277	1.3753
				Percent riparian 500 m	1.0308	0.9922	1.0708
				Willow spp. density (100's/ha)	1.8755	1.5708	2.2394
Nuttall's Woodpecker <i>Picoides nuttallii</i>	0	<0.0001	0.29	Years since planting	1.3343	1.2459	1.4290
				Percent riparian 500 m	1.0556	1.0478	1.0634
				Tree species richness	1.3105	1.2289	1.3976
Bewick's Wren <i>Thryomanes bewickii</i>	2.013	<0.0001	0.22	Years since planting	1.3247	1.2399	1.4153
				Percent riparian 500 m	1.0496	1.0374	1.0619
				Valley oak density (100's/ha)	1.5130	1.4207	1.6114
Ash-throated Flycatcher <i>Myiarchus cinerascens</i>	0	0.0301	0.10	Years since planting	1.5130	1.4207	1.6114
				Percent riparian 2 k	1.0416	1.0126	1.0714
				Valley oak density (100's/ha)	1.0404	1.0264	1.0546
Spotted Towhee <i>Pipilo maculatus</i>	1.463	<0.0001	0.31	Years since planting	1.5464	1.4555	1.6430
				Percent riparian 2 k	1.0529	1.0405	1.0655
				Cottonwood density (100's/ha)	0.8358	0.8120	0.8603
Common Yellowthroat <i>Geothlypis trichas</i>	1.835	0.0507	0.31	Years since planting	1.5328	1.4065	1.6704
				Valley oak density (100's/ha)	1.0486	1.0185	1.0795
				Years since planting	1.1509	1.0863	1.2192
Black-headed Grosbeak <i>Pheucticus melanocephalus</i>	0	0.3296	0.15	Percent riparian 500 m	1.0205	0.9970	1.0446
				Tree species richness	1.1421	1.0770	1.2113
				Years since planting	1.3561	1.2766	1.4407
Bird species richness	0	<0.0001	0.14	Percent riparian 2 k	1.0462	1.0000	1.0945
				Valley oak density (100's/ha)	1.0382	1.0180	1.0589
				Years since planting	1.2607	1.1380	1.3967
Bird species richness	0	0.7600	0.20	Patch density 2 k	7.7370	3.0446	19.6612
				Years since planting	1.2131	1.1597	1.2689
				Percent riparian 2 k	1.0460	1.0293	1.0630
Bird species richness	0	0.3296	0.15	Tree species richness	1.1547	1.0275	1.2976
				Years since planting	1.1313	1.1068	1.1564
				Tree species richness	1.0451	0.9816	1.1128
Bird species richness	1.244	0.0035	0.13	Shrub species richness	0.9378	0.8507	1.0339
				Years since planting	1.1409	1.1353	1.1467
				Tree species richness	1.0524	0.9874	1.1218

<sup>a</sup> This is the estimate of the dispersion parameter. If the dispersion parameter equals zero, the model reduces to the simpler poisson model;

<sup>b</sup> McFaddens Pseudo R<sup>2</sup>, calculated as  $1 - \log \text{likelihood}(\text{model}) / \log \text{likelihood}(\text{null})$

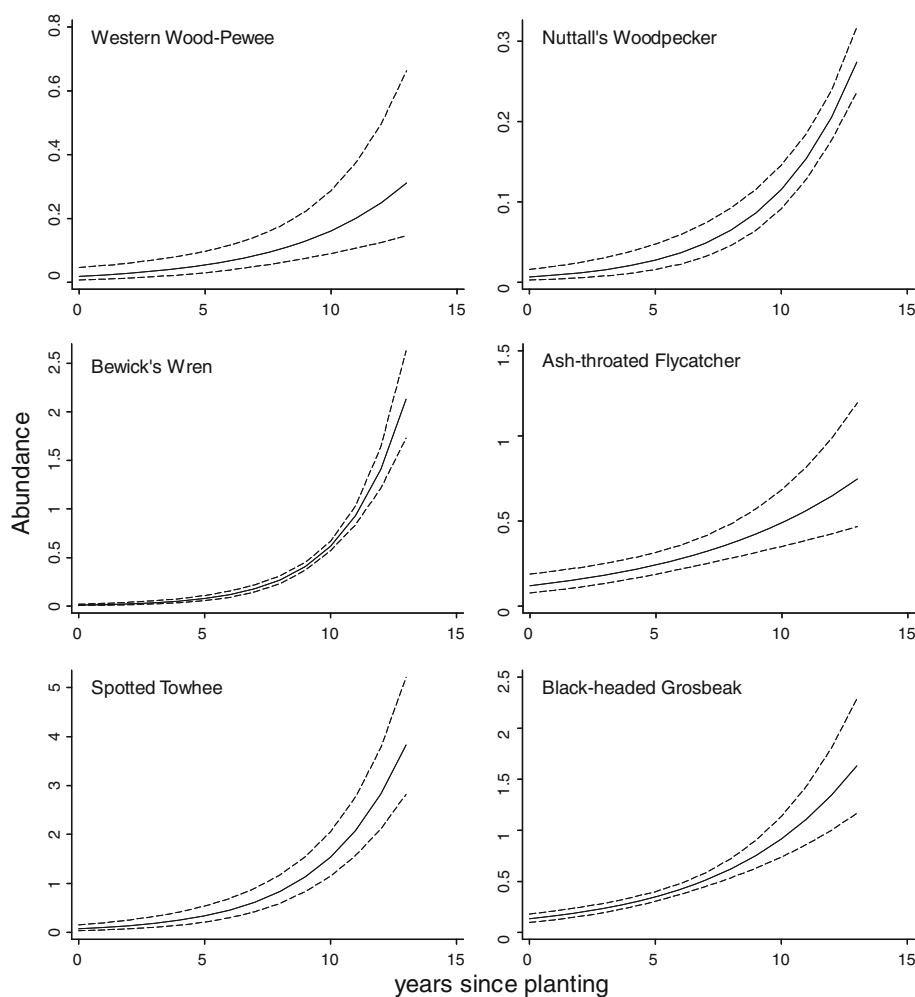
for nesting. The relationship between these landscape variables and the bird metrics was positive in every case; incidence rate ratios >1 (Table 3; Fig. 3) but the 95% confidence interval for the incidence rate ratios contained 1 for Western Wood-Pewee and Ash-throated Flycatcher (Table 3). No landscape variable was an important predictor of bird species richness (Table 3).

In addition to the landscape variables, some local planting design characteristics were also important. Of these, the number of tree species planted occurred in the model with the most support for Nuttall's Woodpecker, Ash-throated Flycatcher, and Black-headed Grosbeak

(Table 3), suggesting that for each additional tree species planted, abundance increased by a factor of 1.14–1.31 depending on the species. For Nuttall's Woodpecker this equates to approximately a four-fold increase in abundance at 10 years post planting for sites with seven species of trees versus those with only a single tree species (Fig. 3).

The relationship between tree species richness and bird species richness was also positive, but questionable as its lower limit of the 95% confidence interval was below 1 (Table 3). The number of shrub species planted was a component of the top model for bird species richness. The model suggests a slight negative effect on bird species

**Fig. 2** Abundance of Western Wood-Pewee, Nuttall's Woodpecker, Bewick's Wren, Ash-throated Flycatcher, Spotted Towhee, and Black-headed Grosbeak in relation to age of revegetation (years since planting). *Solid lines* show values predicted from negative binomial regression with *dash lines* showing the  $\pm 95\%$  confidence intervals. Other variables in models (Table 2) were held at their mean values with the exception of Valley oak planting density which was held at the median value



richness, but its upper limit of 95% confidence interval exceeds 1 (Table 3).

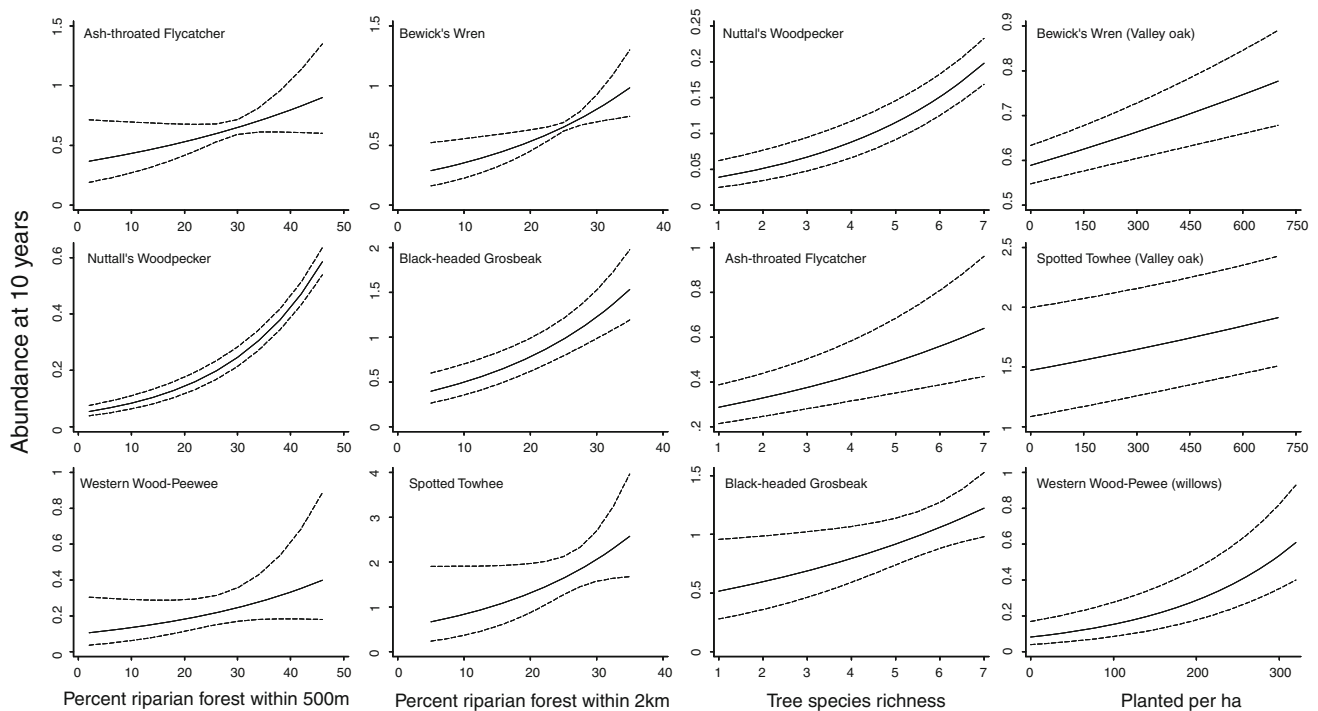
For three bird species, the planting densities of particular tree species (or groups of species in the case of willows) were important (Table 3). For Western Wood-Pewee the top model suggests that for each additional 100 willows planted per ha abundance increases by a factor of 1.9 (Fig. 3). For both Bewick's Wren and Spotted Towhee, an increase of 100 Valley oak trees per ha resulted in an increase in abundance by a factor of about 1.04. A competing model for Bewick's Wren, however, suggested a negative correlation with cottonwood density—each increase of 100 trees per ha resulted in a decrease by a factor of 0.84 (Table 3).

The most frequent pattern was one in which the amount of remnant riparian habitat in the landscape was paired with a local-level restoration design feature. This was the case for six of the seven bird species. The exception was Common Yellowthroat, for which only patch density at the 2 km scale was supported as a predictor of abundance. There were no landscape-level variables in the top models for bird species richness.

## Discussion

Our results illustrate that the amount of remnant riparian forest in the landscape, together with attributes of planting design such as the number of tree species planted, can greatly influence the response of birds to revegetation projects. Our results support those of Lindenmayer and others (2010) who concluded that content and context of restoration plantings were important to bird species richness and presence of individual species on restoration projects in Australia. That restoration design should incorporate planning at both the local- and landscape-scale for birds is consistent with what is known more generally about the parameters that affect bird species richness and abundance (e.g., Saab 1999; Miller and others 2004; Koh 2008).

The Sacramento River restoration strategy intentionally located revegetation plots near existing remnant riparian forests (Golet and others 2003). Locating revegetation plots near extant forest is a strategy presumably based on habitat fragmentation theory that posits that larger more connected patches are preferable to smaller highly disconnected



**Fig. 3** Predicted bird abundance at 10 years post planting in relation to landscape and local restoration parameters. *Solid lines* show values predicted from negative binomial regression with *dash lines* showing

the  $\pm 95\%$  confidence intervals. Local or landscape planting variables included in top models (Table 2) were held at their mean values except Valley oak planting density which was held at its median value

patches (Andr n 1994). Our results confirm the utility of this practice. Although the amount of riparian habitat in the landscape was important in most models, the scale at which response was the strongest varied among species: Western Wood-Pewee, Nuttall’s Woodpecker, and Ash-throated Flycatchers responded most strongly to landscape context within 500 m. These are all species that rely on larger trees for nesting—so their use of restoration projects may be primarily for foraging and be dependent upon suitable nesting substrate (mature trees) nearby. Trees large enough to support cavities for the latter two species are unlikely to exist in plantings for the first 10 or 15 years. In contrast, species that readily use shrubby earlier successional habitats (Bewick’s Wren, Spotted Towhee, and Black-headed Grosbeak) responded most strongly to landscape context within 2 km. The scale at which species respond most strongly may also reflect their dispersal performance or their mobility (Doak and others 1992). It appears for the species we examined, that the proximity of revegetation plots to extant forest was suitable for facilitating dispersal. Additionally, intentionally positioning revegetation sites near remnant forest minimizes the hazards that exist during transit between fragments (e.g., Errington 1946; Dawson and others 1987).

Landscapes with more extant riparian forests may increase the rate at which birds respond to restoration in several related ways. Relative to many other organisms,

birds have a greater ability to disperse simply because of their ability to fly. However, even if direct dispersal is not limited, it may be functionally limited by dispersal behavior, which, is still not well understood. Some species may explore or “prospect” potential sites post-breeding (Betts and others 2008) and, in this case, the pool of potential dispersers into revegetated areas would be greater where more existing habitat occurs. Alternatively, even if the dispersing birds reach all restoration sites, some species may choose dispersal areas in early spring by cueing into landscapes with greater amounts of habitat and/or conspecifics (Reed and others 1999). The actual cues used for selecting breeding habitat are not known and may include social factors, vegetation structure, or an interaction between the two. For herbivores in North Dakota USA, landscape context outweighed local habitat quality in its effects on dispersal (Haynes and others 2006). Revegetated sites do not look like remnant sites when they are young (see Fig. 4 in Gardali and others 2006), suggesting that social cues might be more important than vegetation structure (Betts and others 2008). The role of social information and conspecific attraction remains an important area of research for wildlife restoration.

Rapid or greater opportunity for colonization may not necessarily lead to a trend for greater abundance, yet it is possible that sites where birds colonize quickly benefit from philopatry and the addition of time to reproduce and



populate the restored sites. In addition, restoration sites embedded within a greater amount of existing riparian forest may be of higher quality in terms of reproductive output: less fragmentation and/or a more natural landscape matrix may equate to greater reproductive success (Vander Haegen 2007, Kus and others 2008). A study of the factors that influence reproductive success and annual survival of birds along the Sacramento River would help to identify the underlying mechanisms that drive the observed patterns in abundance.

Several local factors of restoration design also proved to be important. When more tree species were planted, the abundance of several species and overall bird species richness increased at a faster rate. Interestingly, the number of shrub species planted was only supported as a predictive variable in the model set for bird species richness, and the direction of the effect was negative. Confidence intervals for the incident rate ratio widely overlap 1, however, so it is questionable whether this effect is real (Table 3). The relative lack of statistical support and the direction of this relationship is puzzling, as we expected that an increase in shrubs would equate to an increase in the structural diversity of the restoration, and hence its value to birds. During the early years of restoration, however, young stems and overall structure tree species essentially function as shrubs. As these restorations continue to age and trees mature in height, the structural importance of shrubs to birds may increase.

The planting densities of individual species were important to several bird species, but because our data was incomplete for some species (e.g., sycamore) we lack the ability to assess whether one or more of the commonly planted species outperforms others. Valley oak was most frequently supported among the model sets but planting densities for each species that we investigated showed up as important at least once. Habitat elements important to Common Yellowthroats (e.g., emergent plant species) were not well indexed by the information available to us on planting designs, however, so we do not conclude that local design elements are unimportant. The riparian patch density metric may be a good index to availability of edge habitat at a local scale to which this warbler has an affinity.

Abundances of all seven bird species we investigated as well as species richness increased as the age of restoration plantings increased (Fig. 2). This finding is similar to that of previous work that included these as well as other restoration sites in the Sacramento Valley (Gardali and others 2006; Golet and others 2008).

Insights from ecological theory on landscape ecology, and in particular habitat fragmentation and dispersal, were credible guides for the restoration strategy employed in the Sacramento Valley. Local-scale factors also influenced bird abundance and community composition and hence support

the premise that populations respond at multiple spatial scales. Understory plant communities along the Sacramento River also responded at multiple spatial scales but local-scale factors explained more of the variance (Holl and Crone 2004). As a result, Holl and Crone (2004) recommended that managers focus on local-scale restoration methodologies and put less importance on choosing sites near remnant forests. For birds and likely other highly mobile organisms however, we conclude that the value of restoration can be maximized by locating future restoration plots in landscapes with high proportions of existing riparian vegetation. Additionally, for birds in particular, planting palettes should include a diverse suite of tree species.

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