

RESEARCH ARTICLE

Temporal and Taxonomic Variability in Response of Fauna to Riparian Restoration

Gregory H. Golet,^{1,2} Thomas Gardali,³ John W. Hunt,⁴ David A. Koenig,⁴ and Neal M. Williams⁵

Abstract

Evaluating the success of restoration projects requires well-designed studies. Among the decisions that need to be made are what taxonomic groups to study and when to conduct the monitoring. To explore how these decisions can influence assessments of restoration success, we examined species richness and composition data collected over several years on different terrestrial fauna (landbirds, rodents, bees, and beetles) at Sacramento River restoration and remnant riparian sites. Our selection of study organisms enabled us to ask whether variability in species richness among restoration sites is less for vagile taxa than for sedentary taxa, and if invertebrates display greater variability among sites than vertebrates. Our results demonstrate that responses to restoration can vary depending upon the season when it is assessed, and the taxa that are studied. For all taxa except bees, there was considerable

variability in the relative performance of taxa at restoration sites from one sampling date to the next, such that the relative ranking of the sites often changed dramatically. Comparisons of β -diversity (variability in species richness across sites) revealed that certain taxonomic groups were more spatially variable in their response to restoration than others. Among vertebrates, sedentary taxa (rodents) had significantly higher variability in species richness across sites than highly vagile taxa (birds); however, no such pattern was observed for invertebrates. Overall, vertebrates had lower variability than invertebrates, suggesting that evaluations of restoration success based on a few better-known taxonomic groups (e.g., birds, rodents) may be inadequate to represent the biodiversity response of other groups (e.g., insects).

Key words: β -diversity, indicators, monitoring, restoration, richness, riparian.

Introduction

A major goal of ecosystem restoration is the recovery of biodiversity (Young 2000). To assess whether restoration projects have succeeded in meeting this goal, ecologists often compare native species richness and attributes of community composition at restoration and remnant (or reference) sites. Restoration sites that have a fuller complement of native species found at remnant sites are viewed as more successful than those with fewer of these species (SER 2004; Ruiz-Jaen & Aide 2005).

Yet, if species richness and community composition patterns vary temporally, with changes occurring from year to year or from one season to the next, or if restoration sites and remnant habitats vary in different ways, then evaluations of whether restoration has been successful will depend upon when and where these evaluations are made. Also, if certain taxa are

inherently more variable than others, then there are additional complications in interpreting restoration outcomes. These complexities present challenges for assessing the success of restoration projects, and point out the need for clearly specifying project goals (Ehrenfeld 2000; Holl & Cairns 2002).

The existing literature provides valuable information on monitoring in the context of restoration (e.g., Block et al. 2001; Morrison 2002). However, there is a need for more detailed examinations of how the choice of study organisms, and spatial and temporal variability in their response to restoration, influences progress assessments. Some studies of these topics have been conducted on aquatic species (e.g., Jeppesen et al. 2002), but we do not know of any similar investigations that have focused on terrestrial fauna.

To help address these information needs, we studied landbirds, rodents, bees, and beetles over several years at riparian restoration sites and remnant habitats along the Sacramento River, California, U.S.A. In a previous paper, Golet et al. (2008), we reported on the success of this restoration effort for these and other taxa. However, that paper did not explicitly examine variability in taxonomic response to restoration, which is the focus of this paper. Here, we use species richness and community composition data to evaluate the following: (1) whether determinations of restoration success vary depending upon the season in which they are made; (2) whether sites

¹ The Nature Conservancy, Northern Central Valley Office, Chico, CA 95928, U.S.A.

² Address correspondence to G.H. Golet, email ggolet@tnc.org

³ PRBO Conservation Science, Petaluma, CA, U.S.A.

⁴ Terrestrial Ecology Division, Department of Biological Sciences, California State University Chico, CA, U.S.A.

⁵ Department of Biology, Bryn Mawr College, Philadelphia, PA, U.S.A.

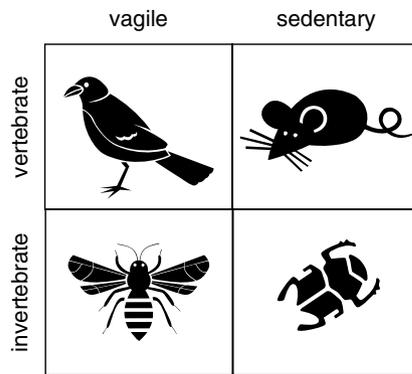


Figure 1. Matrix of study organisms arranged according to taxonomic order and vagility.

rank consistently in the performance of their taxa through time; and (3) whether some taxa are more variable than others in how they respond to restoration.

Our selection of study organisms (Fig. 1) enabled us to ask whether variability in species richness among restoration sites is less for vagile taxa than for sedentary taxa, and if invertebrates display greater variability among sites than vertebrates. Answering these questions can help determine whether all taxonomic groups of interest need to be studied in riparian restoration projects, or if a subset of taxa may be studied as indicators of the larger community (*sensu* Lambeck 1997). The use of a surrogate taxon has become questionable in conservation planning because evidence suggests that the correlation of species richness between pairs of taxa is highly variable both taxonomically and geographically (Prendergast et al. 1993; Prendergast & Eversham 1997; Ricketts et al. 1999; Su et al. 2004), and may depend on the spatial scale examined (Weaver 1994; Blair 1999). Our study begins to address whether the same is true in studies of restoration success.

Methods

Restoration Success Metrics and Methods

Our examination of temporal variability in response of different taxa to restoration was focused on three metrics: species richness, percent representation, and β -diversity. Species richness is the total number of species observed at a site. In the case of birds and rodents, we know whether or not species are native, and thus report native species richness. For beetles and bees, we include non-native species in our richness counts. Percent representation is a community composition metric, defined as the percent of species from remnant habitats that are observed at restoration sites. It provides a complementary characterization to species richness by describing how similar the assemblage of species present at restoration sites are to those observed at reference sites.

β -diversity provides a measure of how variable species richness of different taxa is across sites. Strictly speaking, it is defined as the diversity in richness among sites within a

region of interest. It differs from α -diversity, the diversity in species within individual plots, and γ -diversity, the diversity of species within a whole region (Whittaker 1960). We examined patterns of β -diversity to determine whether certain taxa may be suitable as indicators of restoration success of other co-occurring taxa. Analyses of co-occurrence have been widely used, and analyzed by a variety of methods, in the conservation planning literature. Different researchers have referred to these analyses by different terms including *cross-taxon congruency* (Su et al. 2004), *assemblage fidelity* (Oliver et al. 1998), and *community concordance* (Paszowski & Tonn 2000). We calculated β -diversity for each taxon at both restoration and remnant sites following Harrison et al.'s (1992) adaptation of Whittaker's (1960) original index:

$$\beta - \text{diversity} = (S/a - 1)/(N - 1) \times 100$$

In this index, S is the regional diversity—the total number of species recorded at all sites during a given sampling window (month or season)—and a is the mean number of species recorded at a single site in the collection of N sites. We used this index because it accounts for different sample sizes (Harrison et al. 1992). Low index values indicate that sites share many species, and high values indicate that sites share few species.

It is possible that differences in sampling intensity influenced some of our results. However, we believe that this influence was very small because all taxa were sampled intensively (see Methods), and sampling efforts were identical at restoration sites and remnant habitats.

Although more sophisticated methods and associated metrics (e.g., multivariate techniques such as cluster analysis [Belbin 1992] and ordination [Paller et al. 2000]) are available for assessing the response of different organisms to restoration, we focus on these three basic parameters to enable straightforward comparisons across taxonomic groups, site types, locations, and seasons. No single metric adequately represents the complexity and variety of life in an area (Gaston & Spicer 2004); however, species richness is one of the most commonly used measures to quantify biodiversity (e.g., Bisby 1995; Gaston 2000; Purvis & Hector 2000) and to measure the success of restoration projects (McCoy & Mushinsky 2002). Golet et al. (2008) provide a more diverse range of analysis methods and performance metrics to assess the response of Sacramento River terrestrial fauna to restoration.

Study Sites

We conducted surveys at 12 study sites (Table 1), distributed over 143 river kilometers on the middle Sacramento River, between the towns of Gerber and Colusa, California, U.S.A. (Fig. 2). This is an alluvial stretch of the Sacramento River, which was over 8 km wide in some sections prior to European settlement. Riparian restoration efforts have focused on this reach because degradation is largely reversible. Farms (as opposed to cities) have replaced floodplain forests, and levees, where present, are

often set back from the river by appreciable distances. In some areas, bank revetment (riprap) is absent and the natural processes of bank erosion and point bar deposition are still intact (Buer et al. 1989; Singer & Dunne 2001).

Study sites consisted of riparian restoration and remnant habitats. Remnant riparian habitats arose by natural means (i.e., they were not planted) and were never cleared. Remnant sites represent reference conditions and are used here to evaluate progress toward restoration goals. However, conditions in remnant forests are not ideal; all sites are subjected to a highly altered flow regime, are highly fragmented relative to historic condition, and are degraded to varying degrees by invasive species. Nonetheless, they provide useful benchmarks for drawing comparisons to restoration sites (Gardali et al. 2006).

Restoration sites averaged 124 ha (range: 13–376 ± 127 [SD]). All were located in low-lying floodplain areas embedded in a landscape matrix of natural remnant habitats, fallow land, and agriculture. All restoration sites had some remnant riparian habitat directly adjacent, and all remnant study sites were bordered by restoration, with the exception of Stegeman (Fig. 2). Thus, transboundary influences were likely similar across sites. No restoration or remnant sites were in close proximity to urban areas or dense residential settlements. Nearby agriculture consisted of orchard, row, and field crops, although a few areas were managed as irrigated pasture for livestock. All restoration sites were previously in agriculture, most commonly as walnut or almond orchards, before being revegetated with local ecotypes of indigenous trees, shrubs, and, in a few sites, understory species. A list of planted species is provided in Golet et al. (2008). Restoration approaches were generally consistent across study sites and are described by Griggs & Peterson (1997) and Alpert et al. (1999). Overall, restoration sites have been successful in establishing woody riparian species where soil conditions were suitable (Hujik & Griggs 1995a, 1995b; Griggs & Peterson 1997; Griggs & Golet 2002). However, thus far, native understory recruitment has been minimal (Holl & Crone 2004).

Landbirds. Species richness of landbirds (passerines and near-passerines) was measured by analyzing two different datasets collected from two different field methods. To determine whether taxonomic response to restoration varied seasonally, we computed richness from standardized effort mist-netting capture data (Dunn & Ralph 2004) derived from restored and remnant riparian habitats sampled over three seasons (summer, autumn, and winter) between 1999 and 2006, when restoration sites were aged 8–15 years. At each site, 12-m and 36-mm-mesh mist nets were operated for 5 morning hours per day for approximately 10 days per season. Nets were opened 45 minutes before sunrise. Captured birds were identified, measured, and banded with standard U.S. Fish and Wildlife Service bands before being released.

To determine whether there was consistency in how restoration sites ranked over time, and to compare spatial variability

in the response of different taxa to restoration, we calculated species richness and β -diversity by analyzing point count data during the breeding season at four restoration sites from 1996–2002 when these sites were aged 5–11 years. Point count data comprised a larger and more robust dataset than mist-net data and were better suited to estimating species richness. We established a series of survey stations approximately 200 m apart (Ralph et al. 1993). Point count stations were surveyed three times during the breeding season from 1996 through 2001, and twice in 2002. The duration of each count was 5 minutes, and all birds seen or heard were recorded. We used only those birds noted within 50 m of the observer and assumed that detection probabilities were similar within this distance among site types and years. Counts began at dawn and continued up to 4 hours past sunrise. See Gardali et al. (2006) for additional study details.

Rodents. We determined native rodent species richness from captures and observations made at young (aged 3–4 years) and older (aged 12–15 years) restoration and remnant (>25 years old) sites along a 118-km reach of the Sacramento River (Table 1, Fig. 2). Three replicates of each site type were sampled with Sherman live traps (Wiener & Smith 1972) and with visual surveys (techniques adapted from MELP [2001]) during spring and autumn 2005–2006. At each site, we sampled for five consecutive days using 100 traps arranged in a 10 × 10 trap grid with traps spaced 10 m apart. Once we completed the live trapping, we conducted visual surveys within all cells of the trap grid at each site. See Golet et al. (2007) for additional study details.

Bees. We calculated average bee species richness based on capture data from geographically paired restoration sites (aged 8 years) and remnant forest/scrub habitats distributed along a 66-km reach of the Sacramento River (Table 1, Fig. 2, Williams 2007). Paired sites were separated by 0.5–3.8 km. At each site, 1-ha plots were established where bees were sampled with sweep nets at flowering plants and with water-filled pan traps ($n = 30$) spaced regularly along two crossed 100-m transects (see <http://online.sfsu.edu/~beeplot/> for additional details on trapping methods). Plots were surveyed every 6 weeks from late February through August 2003 (five sampling periods within 1 year).

Beetles. We determined beetle morphospecies richness from captures made at pitfall traps at young (aged 1–3 years) and older (aged 6–10 years) restoration sites and remnant riparian habitats (>25 years old) along a 31-km reach of the Sacramento River (Table 1). Three replicates of each site type were sampled monthly for one full year (December 2000–November 2001), and average morphospecies richness values were calculated for each site type for each sampling period. At each site, 12 traps were placed 15 m apart in a 3 × 4 grid. Traps were left open for collections for seven consecutive days each month. Following collection, beetles were identified to the lowest taxonomic level possible based

Table 1. Study sites, associated habitat types, hectares planted, and taxa studied.

Site Name	Habitat Types (years, hectares planted)	Taxa Studied (years sampled)
Flynn ¹	Restoration site (1996–2000, 144) Remnant riparian	Bees (2003) Bees (2003)
Kopta Slough ²	Restoration site (1989–1992, 134) Remnant riparian	Landbirds (1996–2002, 2004, 2006), Rodents (2005–2006), Beetles (2001) Landbirds (1996–2003)
Rio Vista ¹	Restoration site (1993–2000, 376)	Rodents (2005–2006), Bees (2003), Beetles (2001)
Merril's Landing ³	Remnant riparian	Rodents (2005–2006), Bees (2003), Beetles (2001)
Pine Creek ¹	Restoration site (1997–1999, 226) Remnant riparian	Beetles (2001) Beetles (2001)
Capay ¹	Remnant riparian	Landbirds (2000, 2004, 2006)
Phelan Island ¹	Restoration site (1991–2002, 70) Remnant riparian	Landbirds (1996–2004, 2006), Rodents (2005), Bees (2003), Beetles (2001) Rodents (2005–2006), Bees (2003), Beetles (2001)
Jacinto ³	Restoration site (2001, 15)	Rodents (2005)
Sul Norte ¹	Remnant riparian	Landbirds (1999, 2002–2004, 2006)
Princeton South ³	Restoration site (2001, 13)	Rodents (2005–2006)
Stegeman ³	Remnant riparian	Rodents (2005–2006)
Moulton North ³	Restoration site (2002, 15)	Rodents (2005–2006)

Some sites have multiple habitat types present. Many of the restoration sites are composed of sets of fields that were planted over a series of years. The locations of these sites along the Sacramento River are depicted in Figure 2. Sites are listed according to their locations on the river, from north to south.

¹Units of the USFWS Sacramento River National Wildlife Refuge Complex.

²Properties managed by The Nature Conservancy.

³Units of the Department of Fish and Game Sacramento River Wildlife Area.

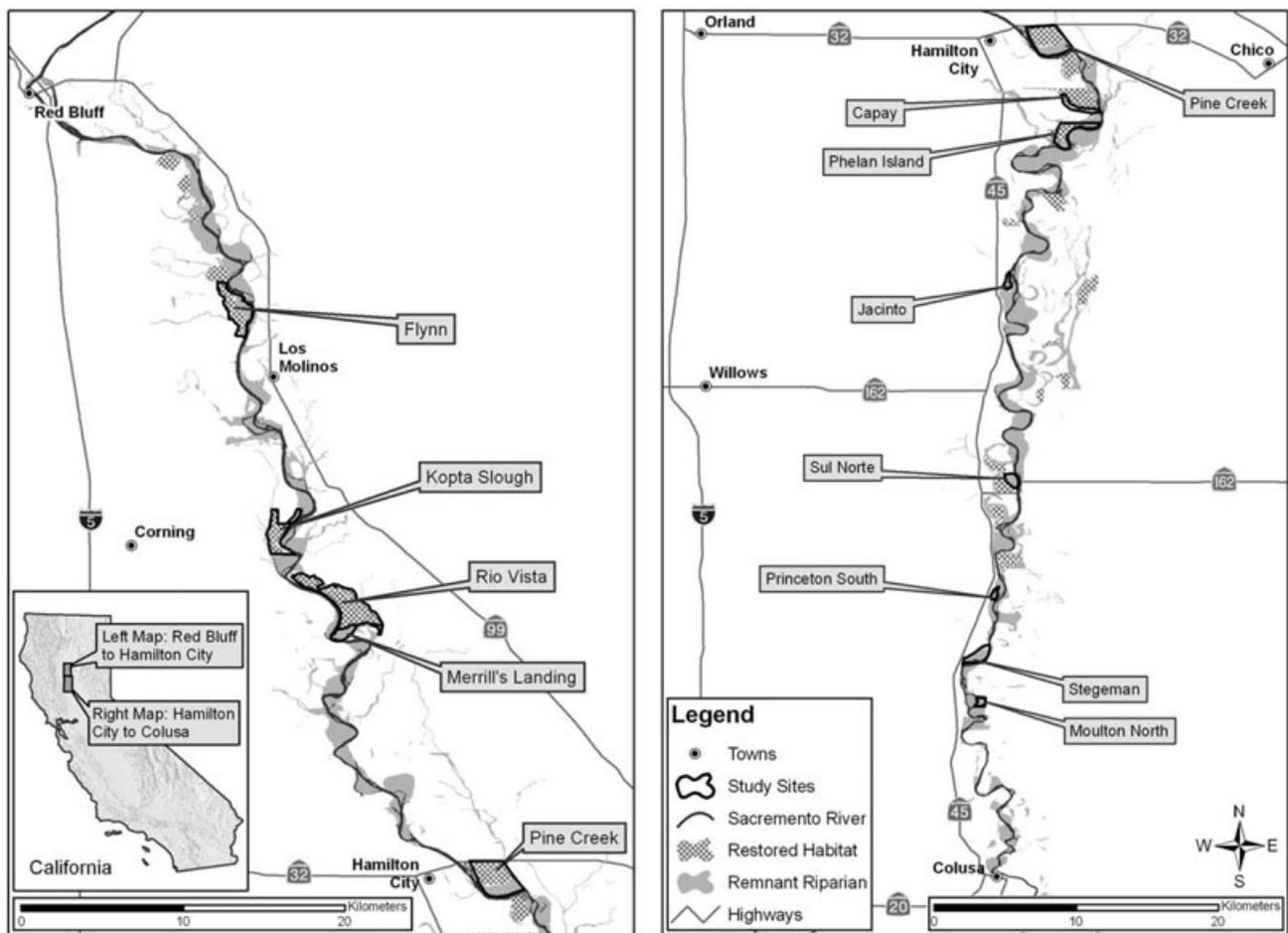


Figure 2. Locations of study sites within the 161-river km Sacramento River Project area. The left map shows the northern half of the Project area and the right map illustrates the southern half. Inset map shows the location of the Project area within California, U.S.A.

on external morphology, and then classified as morphospecies (Oliver and Beattie 1993; Beattie and Oliver 1994). Although distinct morphospecies may not always represent true species, this classification represents the finest division practical for this diverse and relatively unstudied group.

Statistics

For rodents, bees, and beetles, we used univariate repeated measures general linear models (GLM) to test for effects of site type, season, and site on species richness (SYSTAT 1996). In all cases, the assumption of compound symmetry was met, as determined by computation of the Greenhouse–Geisser and Huynh–Feldt statistics (SYSTAT 1996). For birds, we did not incorporate a repeated measures analysis into our GLM because the data structure would not support it (site locations varied among seasons and years, and not all seasons were studied in all years). We used parametric statistics because species richness, percent representation, and β -diversity values were independent, and the residuals of our applied models were approximately normally distributed. Because our values of percent representation were calculated after pooling all samplings of a given season, they lacked variance; hence, they could not be compared among seasons with statistical significance testing. However, we were able to test for statistical differences in present representation among taxa, and between young and older sites, which we did with an analysis of variance (ANOVA). To test for differences among taxa in β -diversity, we used ANOVA and computed Tukey pairwise comparison probabilities (SYSTAT 1996). Percentage data were arc sine transformed. Unless otherwise indicated, means are presented \pm SE, and all tests are two-tailed.

Results

Temporal Variability in the Response of Taxa to Restoration

Landbirds. Restoration success, assessed by comparing landbird species richness between restored sites and remnant riparian habitat, differed depending upon the season when it was assessed (site type \times season interaction: $F_{2,17} = 7.5$, $p = 0.005$, Fig. 3A). During summer and autumn, restoration sites had lower species richness than remnant ones; however, in winter no such difference was observed. Also, in winter, the percent representation of native birds at restoration sites was the highest among seasons studied (Fig. 3A).

Overall, native landbird species richness was significantly higher at remnant sites than at restoration sites ($F_{1,17} = 19.8$, $p < 0.001$, Fig. 3A), and differed seasonally, being highest in autumn, intermediate in summer, and lowest in winter ($F_{1,17} = 21.5$, $p < 0.001$, Fig. 3A).

Over 7 years of study, there was no significant difference in the performance of taxa at individual restoration sites ($F_{2,17} = 2.5$, $p = 0.12$, Fig. 4A), with three of the four restoration sites having taxa with nearly identical performance. KOSL2, the site that had taxa with the lowest overall performance, was an exception. It ranked lowest in the last 5 of the 8 study years. For the other three sites, the relative rankings varied widely among sampling years. Richness at PHIS1 was especially variable. It ranked highest in 3 years, lowest in 2 years, and intermediate in the remaining 3 years.

Rodents. Native rodent species richness was not significantly different between restoration and remnant habitats ($F_{2,6} = 3.0$, $p = 0.12$, Fig. 3B). The restoration success also did not vary seasonally: there was no significant site type \times

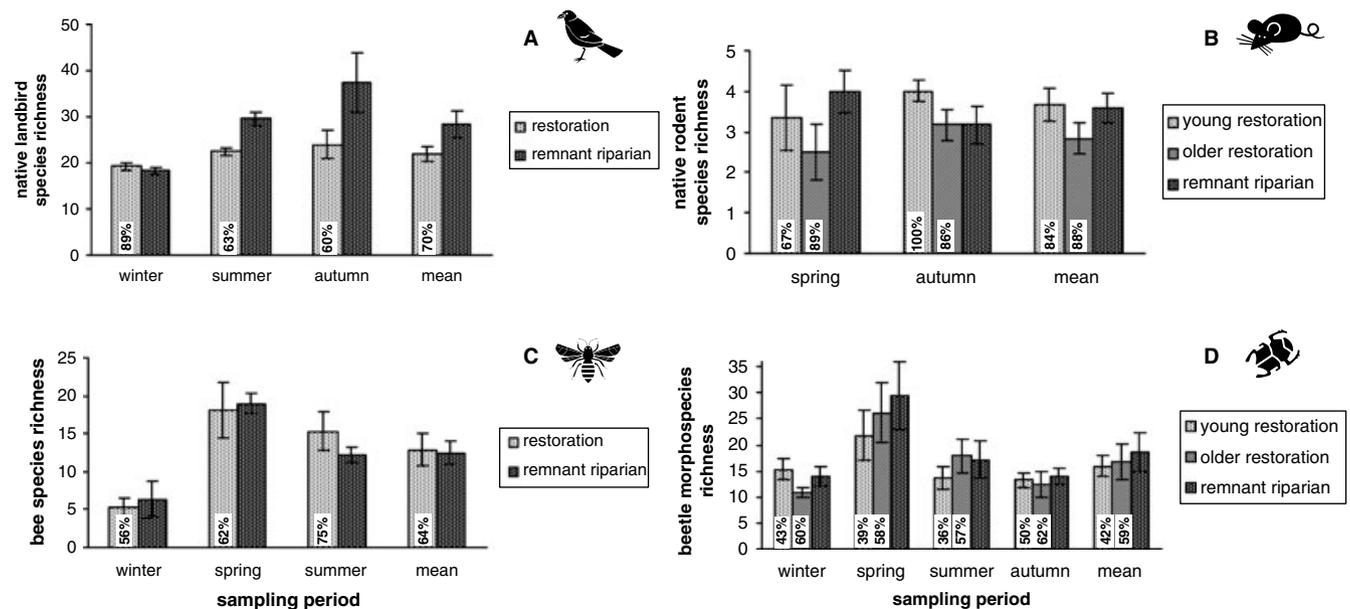


Figure 3. Seasonal species richness patterns for (A) landbirds, (B) rodents, (C) bees, and (D) beetles at Sacramento River riparian restoration sites and remnant habitats. Percent representation (the percent of remnant species that were observed at the restoration sites) for each sampling period is indicated by the values at the base of the bars. See Methods, Table 1, and Figure 2 for ages of restoration sites, years of study, and study site locations.

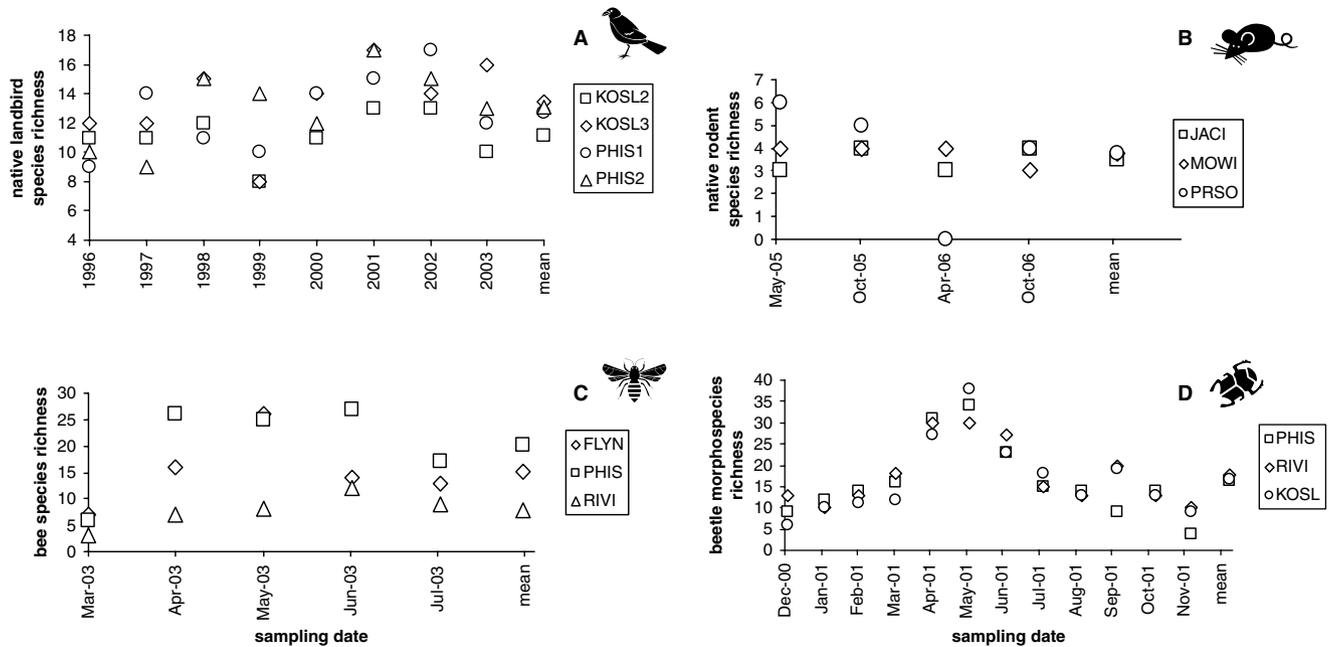


Figure 4. Comparisons of species richness patterns across time at different Sacramento River riparian restoration sites for (A) landbirds, (B) rodents, (C) bees, and (D) beetles. See Methods, Table 1, and Figure 2 for ages of restoration sites, years of study, and study site locations.

season interaction in rodent species richness ($F_{6,18} = 0.7$, $p = 0.65$, Fig. 3B). Percent representation of native rodents at restoration sites was similar among seasons and did not differ between young and older sites ($F_{1,2} = 0.042$, $p = 0.86$, Fig. 3B).

Overall, native species richness varied significantly among sampling periods ($F_{3,18} = 3.6$, $p = 0.035$). This difference appeared to be driven by variability at individual sites (e.g., PRSO, Fig. 4B), as opposed to that by uniform patterns of change across all sites. Mean native species richness was similar among both older (Fig. 4B) and younger (not shown) restoration sites.

Bees. Overall, there was no significant difference in bee species richness between restoration and remnant sites ($F_{1,2} = 0.037$, $p = 0.87$, Fig. 3C). There was, however, a strong seasonal difference in species richness ($F_{4,8} = 19.9$, $p < 0.001$, Fig. 3C), being highest in spring, intermediate in summer, and lowest in winter. During winter and spring, remnant riparian habitats appeared to have slightly higher species richness than restoration sites, while during summer the reverse was true. These differences were small, however, and overall there was no difference in restoration success among seasons (site type \times season interaction: $F_{4,8} = 0.94$, $p = 0.49$, Fig. 3). Percent representation was lowest in winter, intermediate in spring, and highest in summer.

There was also no statistical difference in species richness among sites ($F_{4,8} = 0.94$, $p = 0.49$). Among restoration sites, PHIS typically ranked highest and RIVI consistently ranked lowest (Fig. 4C); however, at paired remnant sites, richness was similar among the three locations.

Beetles. Morphospecies richness varied among site types as a function of the month it was sampled in (significant site type \times month interaction: $F_{22,66} = 3.5$, $p < 0.001$, Fig. 3D), suggesting that restoration success varied seasonally for beetles. We also observed a strong seasonal difference in richness ($F_{11,66} = 46.7$, $p < 0.001$, Fig. 3D) with highest values being observed in spring, as was the case with bees. Overall, remnant habitats appeared to support more morphospecies than restoration sites, and older restoration sites had higher mean richness than young sites. However, these differences were small and statistically insignificant. Percent representation of beetles at restoration sites was similar among seasons and was significantly higher at older restoration sites than at young sites ($F_{1,6} = 30.3$, $p = 0.002$, Fig. 3D).

No significant difference was detected in species richness among sites ($F_{3,3} = 0.41$, $p = 0.76$). Averaged over the course of a year, older restoration sites had nearly identical richness; however, the relative success of individual sites varied depending upon the month when it was studied (Fig. 4D). A very similar pattern was observed for young restoration sites (not shown).

Taxonomic Variability in Response to Restoration

The four taxonomic groups differed significantly in β -diversity ($F_{3,46} = 8.3$, $p < 0.001$). No difference was found among taxa grouped according to vagility (bees and birds vs. beetles and rodents, $F_{1,50} = 2.26$, $p = 0.14$). However, invertebrates had significantly higher β -diversity than vertebrates (bees and beetles vs. birds and rodents, $F_{1,50} = 7.4$, $p = 0.008$). And there was a significant interaction between taxonomic order (vertebrates vs. invertebrates) and vagility

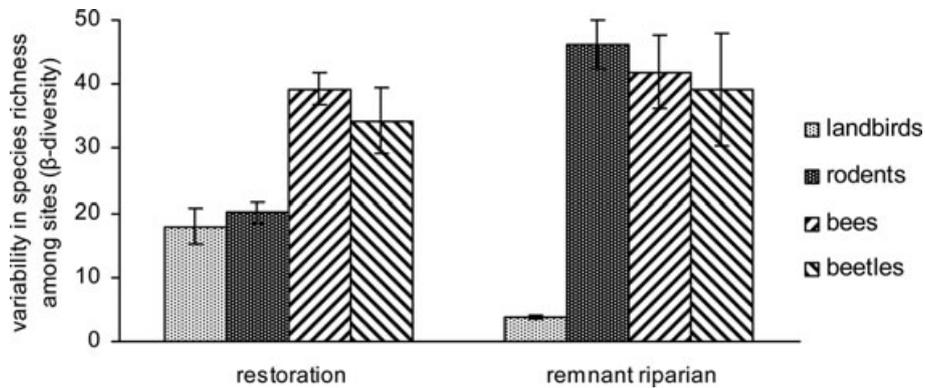


Figure 5. Comparisons of β -diversity among four taxonomic groups at restoration sites and remnant habitats on the Sacramento River, California, U.S.A.

($F_{1,50} = 7.4$, $p = 0.008$), suggesting that among vertebrates more highly vagile taxa (landbirds) have lower β -diversity than less vagile taxa (rodents), although this was not the case among invertebrates. Overall, no difference was found in β -diversity between restoration sites and remnant habitats ($F_{1,46} = 0.66$, $p = 0.42$). However, landbirds at remnant habitats had significantly lower β -diversity than at restoration sites ($t = 5.0$, $p < 0.001$), while the reverse was observed for rodents ($t = 6.2$, $p = 0.025$, Fig. 5).

Percent representation was significantly different among taxa ($F_{3,14} = 6.83$, $p = 0.002$, Fig. 3), and was higher among vertebrates than invertebrates ($F_{1,16} = 13.08$, $p = 0.002$).

Discussion

Variability in Restoration Success among Seasons, Taxa, and Sites

Our results provide strong evidence that determinations of restoration success, made by comparing species richness and percent representation data between restoration and remnant sites, can vary depending upon the season when it is assessed. While this might be an expected result for highly vagile and migratory taxa like birds, we also found this to be true for more sedentary taxa such as beetles.

In the case of landbirds, riparian restoration sites appeared to support as many species as remnant areas in winter, but not during summer or autumn. This suggests that restoration sites were used by as many species as remnant sites for overwintering, but not for summer breeding or autumn migration. This may be because different assemblages of birds use Sacramento River riparian habitats during different seasons (Humble & Geupel 2002), and species that make up the wintering bird communities may be more habitat generalists than those found on the river at other times of the year.

For bees and beetles, there were clear peaks in species richness in spring at both restoration and remnant sites. The generality of this result is unknown, however, as these taxa were studied in only 1 year. If this result is borne out in future studies, then this season should be a priority for future sampling efforts, as it is the most appropriate time to test

whether restoration projects are achieving the goal of increasing the diversity of riparian ecosystem insect functional types (e.g., scavengers, herbivores, detritivores, and predators) and the important ecosystem services they provide (e.g., pollination, decomposition). This recommendation holds whether the increased capture rates are a function of differences in species occurrence at the sites, or simply due to different levels of activity. However, researchers should recognize that determinations of restoration success during spring may differ from those made in other seasons, as we found with beetles. And furthermore, that species assemblages, and the associated ecological functions they perform may vary from one season to the next, such that assessments across multiple seasons are the most desirable.

Previous researchers have identified sedentariness and habitat specificity as biological correlates of high β -diversity (e.g., Shmida & Wilson 1985; Westoby 1985). Our findings with the vertebrates we studied were consistent with this prediction, as we found that the highly vagile taxonomic group that we studied (birds) showed considerably less variability among sites than the more sedentary group (rodents). However, no such difference was found among invertebrates. That a vagility effect was present for vertebrates but not invertebrates may be due to relatively greater dispersal abilities among birds than bees, and/or a function of how the different taxa studied interact with the specific configuration of remnant and riparian habitats in our study area. Both topics deserve further study.

We found no significant differences in species richness among the individual restoration sites studied, and for landbirds, rodents, and beetles, mean species richness at these sites was remarkably similar overall. Yet, despite this uniformity, there was considerable variability in the relative performance of taxa at restoration sites from one sampling event to the next, such that the ranking of the sites often changed quite dramatically. This suggests that sites should be studied over several seasons and years before conclusions are made about success of different restoration sites. Bees were an exception to this rule. Among this group, there were pronounced differences in how taxa at the individual sites performed, and the relative ranking of restoration sites was consistent among sampling periods.

Selection of Metrics and Taxa for Assessing Restoration Success

The Society for Ecological Restoration (SER) recommends that restoration success be assessed by characterizing a suite of biodiversity and ecosystem attributes. The first, and arguably most important attribute, is “. . . a characteristic assemblage of the species that occur in the reference ecosystem and that provide appropriate community structure” (SER 2004). This recommendation suggests that species richness should be complemented with information on community composition and structure to properly characterize restoration outcomes.

We found that percent representation provided useful information on community composition that was complementary to what was conveyed solely by species richness data. In general, percent representation tracked species richness fairly closely, such that percent representation tended to be higher in seasons when restoration site species richness was closer to remnant site species richness. However, variations on this theme are revealed when restoration sites of different ages are compared. These variations provide useful information about the trajectory that restoration sites are on. For example, although beetle species richness was quite similar overall at young and older sites, the older sites had considerably higher percent representation of beetles observed at remnant sites. Similarly, although species richness of rodents at young restoration sites tended to be higher than that at older restoration sites, percent representation was quite similar overall among site types. The implication is that even when older sites do not have more species occurring at them than the younger sites, their species assemblages may more closely approximate what is observed at remnant habitats. This is a desirable outcome from a restoration standpoint, as it implies that restoration sites are becoming more similar to remnant sites as they mature, but is one that would have been obscured if species richness data were considered alone.

Comparisons of species richness between restored and remnant sites may be strongly complemented by similarity analyses that utilize abundance data to compare the frequency distributions of desirable species. Commonly employed approaches include ordination and cluster analyses (e.g., Bray–Curtis, Correspondence Analysis). Applications of these approaches to Sacramento River data show the potential they have for yielding additional insight about how taxa respond to restoration. In the case of bees, we found a similar diversity of bees at restoration and remnant sites, but the communities were quite different as expressed through ordination (Golet et al. 2008), and only about half of the species among paired restoration and remnant sites overlapped. With beetles we saw that overall species richness was not different between young and older restoration sites; however, a cluster analysis demonstrated that older sites have beetle communities more similar to remnant sites than those in the young sites (Golet et al. 2008). Assessments of restoration success for these two taxa clearly benefited from incorporation of both community similarity analyses and diversity indices. In the

absence of species richness data on bees, we might have concluded that the restoration sites were not successful as the communities were dissimilar. And, in the case of beetles, without the similarity analysis, we would not have been able to determine whether or not the beetle community at restoration sites was coming to resemble that of remnant habitats (although percent representation data point to this as well). We therefore concur with Pélissier et al. (2003) that the analysis of species–environment relationships should simultaneously encompass an ordination technique and a consistent measurement of taxonomic diversity.

Each of the taxonomic groups in our study exhibited different patterns of response to restoration, suggesting that the most comprehensive view of restoration success comes from integrating data collected on multiple taxa. However, because doing so may not always be feasible or affordable, the information value that is derived from the investigations of different taxa is worth considering. In our situation, and with the analytical approaches we used, certain taxa stood out as being more valuable to study than others.

Among vertebrates, studies of landbirds were more informative than studies of rodents, largely due to differences in the number of native species in the two groups. For taxa with low species richness, such as rodents on the Sacramento River, it is especially important to analyze abundance patterns in addition to species richness. Low species richness among rodents at both restoration sites and in remnant habitats meant that differences in restoration success among sites and seasons were necessarily slight. In contrast, studies of landbirds, a much more specious group, revealed interesting patterns of response (discussed above) across both seasons and sites.

Among invertebrates, studies of both bees and beetles were very informative, and in fact the contrasting patterns of restoration success exhibited by the two groups greatly increased the value of information that came from either of the single taxa studied in isolation. For example, among beetles but not bees, restoration success varied across seasons. Yet, for bees, but not beetles, there were consistent differences in species richness across sites.

Importantly, our study suggests that the evaluation of restoration success based on the response of vertebrates does not adequately represent the response of invertebrates. Overall, we found that there was less variability in species richness across sites (lower β -diversity) among landbirds and rodents than among bees and beetles. Restored sites that contained similar vertebrate species did not necessarily contain similar invertebrate species. These results parallel those of Oliver et al. (1998), who found lower β -diversity among mammals and birds than invertebrates (and plants) across forest habitats in Australia. The implication of these findings for assessments of restoration success is that there is a need to study insects, as the distribution patterns of birds and mammals do not necessarily mirror those of this group. More generally, it should be concluded that, in studies of restoration success, taxa with low β -diversity cannot be considered as surrogates for those with high β -diversity. The reverse may be possible,

but this needs to be confirmed through studies of cross-taxon congruence.

It has been convincingly demonstrated by various researchers (e.g., Webb & Hopkins 1984; Wilcox et al. 1986; Kremen 1992; Balmford & Long 1995; Oliver et al. 1998; Roberge & Angelstam 2004) that the evaluation of habitat value based on the occurrence patterns of a few better-known taxonomic groups does not adequately represent the biodiversity of other groups that may be uncorrelated with the surrogate taxon. Our study extends these findings to evaluations of restoration success where it may be similarly misleading to draw conclusions of the restoration outcome based upon a limited suite of indicator taxa.

Implications for Practice

- Determinations of restoration success based on species richness data may vary among seasons and taxa.
- Certain taxonomic groups may be more spatially and temporally variable than others in how they respond to restoration.
- The relative performance of taxa at individual restoration sites may change over time.
- Assessments of restoration success are most informative when informed by multiple metrics, including species richness, percent representation, β -diversity, and those derived from community similarity analyses (e.g., ordination, cluster analysis).
- In studies of restoration success, taxa with low β -diversity (variability in species richness across sites) should not be considered as surrogates for those with high β -diversity.
- The evaluation of restoration success based on the occurrence patterns of a few better-known taxonomic groups (e.g., of birds and mammals) does not adequately represent the biodiversity of other groups (e.g., insects) that may be uncorrelated to the surrogate taxon.

Acknowledgments

This paper was improved thanks to the excellent comments of Richard Hobbs, Lynn Lozier, Darren Ryder, Stacey Solie, and two anonymous reviewers. Assistance with statistics was graciously provided by David Wood. For dedicated field assistance, we thank Levi Bateman, Rachelle Boul, Scott Chamberlain, Matt Noel, Anne King, Michelle Hammond, Sherry Hudson, Stacy Small, Jim DeStaebler, Peter Pintz, Joanne Gilchrist, and Michael Rogner. Thanks to Robbin Thorp (UC Davis) for final species determination of bees. We are grateful to Seth Paine for producing the study site figure. Funding for the studies profiled in this paper was provided by the CALFED Bay/Delta Program, California State University Agricultural Research Initiative, The Nature Conservancy, U.S. Fish & Wildlife Service, David and Lucile Packard Foundation, William and Flora Hewlett Foundation, Bella Vista Foundation, National Fish and Wildlife Foundation,

U.S. Bureau of Reclamation, Natural Resource Conservation Service, California Department of Parks and Recreation, California Department of Fish and Game, and through a David Smith Conservation Research Postdoctoral Fellowship. This is PRBO Contribution number 1647.

LITERATURE CITED

- Alpert, P., F. T. Griggs, and D. R. Peterson. 1999. Riparian forest restoration along large rivers: initial results from the Sacramento River Project. *Restoration Ecology* 7:360–368.
- Balmford, A., and A. Long. 1995. Across-country analyses of biodiversity congruence and current conservation effort in the tropics. *Conservation Biology* 9:1539–1547.
- Beattie, A. J., and I. Oliver. 1994. Taxonomic minimalism. *Trends in Ecology & Evolution* 9:488–490.
- Belbin, L. 1992. Comparing two sets of community data: a method for testing reserve adequacy. *Australian Journal of Ecology* 17:255–262.
- Bisby, F. A. 1995. Characterization of biodiversity. Pages 21–106 in V. H. Heywood and R. T. Watson, editors. *Global biodiversity assessment*. Cambridge University Press, Cambridge, United Kingdom.
- Blair, R. B. 1999. Birds and butterflies along an urban gradient: surrogate taxa for assessing biodiversity. *Ecological Applications* 9:164–170.
- Block, W. M., A. B. Franklin, J. P. Ward Jr., J. L. Ganey, and G. C. White. 2001. Design and implementation of monitoring studies to evaluate the success of ecological restoration on wildlife. *Restoration Ecology* 9:293–303.
- Buer, K., D. Forwalter, M. Kissel, and B. Stohler. 1989. The middle Sacramento River: Human impacts on physical and ecological processes along a meandering river. Pages 22–32 in D. L. Abell, editor. *Proceedings of the California riparian systems conference: protection management and restoration for the 1990s*. General Technical Report PSW-110. Pacific Southwest Forest and Range Experiment Station, Forest Service, U. S. Department of Agriculture, Berkeley, California.
- Dunn, E. H., and C. J. Ralph. 2004. Use of mist nets as a tool for bird population monitoring. *Studies in Avian Biology* 29:1–6.
- Ehrenfeld, J. G. 2000. Defining the goals of restoration: honesty is the best policy. *Restoration Ecology* 8:2–9.
- Gardali, T., A. L. Holmes, S. S. Small, N. Nur, G. R. Geupel, and G. H. Golet. 2006. Abundance patterns of landbirds in restored and remnant riparian forests on the Sacramento River, California, U.S.A. *Restoration Ecology* 14:391–403.
- Gaston, K. J. 2000. Global patterns in biodiversity. *Nature* 405:220–227.
- Gaston, K. J., and J. I. Spicer. 2004. *Biodiversity: an introduction*. Blackwell, Oxford, United Kingdom.
- Golet, G. H., R. J. Bogiatto, J. W. Hunt, D. Koenig, and G. Werner. 2007. Effects of riparian restoration on abundances of small mammal agricultural pest species (California). *Ecological Restoration* 25:136–137.
- Golet, G. H., T. Gardali, C. Howell, J. Hunt, R. Luster, B. Rainey, M. Roberts, H. Swagerty, and N. Williams. 2008. *Wildlife Response to Restoration on the Sacramento River*. San Francisco Estuary and Watershed Science, Vol. 6, Issue 2 (June), Article 1. <http://repositories.cdlib.org/jmie/sfew/svol6/iss2/art1>.
- Griggs, F. T., and G. H. Golet. 2002. Riparian valley oak (*Quercus lobata*) forest restoration on the middle Sacramento River. Pages 543–550 in R. B. Standiford, D. McCreary, and K. L. Purcell (technical coordinators). *Proceedings of the fifth symposium on oak woodlands: oaks in California's changing landscape*. October 22–25, 2001, San Diego, California. Gen. Tech. Rep. PSW-GTR-184. US Department of Agriculture, Forest Service, Pacific Southwest Research Station, Albany, California.
- Griggs, F. T., and D. R. Peterson. 1997. Evaluation of techniques and costs for valley oak riparian forest restoration on the Sacramento River. *Proceedings of a symposium on oak woodlands: Ecology, management,*

- and urban interface issues. Gen. Tech. Rep. PSW-GTR-160. US Department of Agriculture, Forest Service, Pacific Southwest Research Station, Albany, California.
- Harrison, S., S. J. Ross, and J. H. Lawton. 1992. Beta diversity on geographic gradients in Britain. *Journal of Animal Ecology* **61**:151–158.
- Holl, K. D., and J. Cairns Jr. 2002. Monitoring and appraisal. Pages 411–432 in M. R. Perrow, and A. J. Davy, editors. *Handbook of ecological restoration*, Vol. 1, Principles of restoration. Cambridge University Press, Cambridge, United Kingdom.
- Holl, K. D., and E. E. Crone. 2004. Applicability of landscape and island biogeography theory to restoration of riparian understory plants. *Journal of Applied Ecology* **41**:922–933.
- Hujik, P., and F. T. Griggs. 1995a. Cutting size, horticultural treatments affects survival and growth of riparian species (California). *Restoration and Management Notes* **13**:219–220.
- Hujik, P., and F. T. Griggs. 1995b. Field-seeded riparian trees and shrubs thrive in non-irrigated plots (California). *Restoration and Management Notes* **13**:220–221.
- Humple, D. L., and G. R. Geupel. 2002. Autumn populations of birds in riparian habitat of California's central valley. *Western Birds* **33**:34–50.
- Jeppesen E., J. P. Jensen, and M. Søndergaard. 2002. Response of phytoplankton, zooplankton, and fish to re-oligotrophication: a 11 year study of 23 Danish lakes. *Aquatic Ecosystem Health and Management* **5**:31–43.
- Kremen, C. 1992. Assessing the indicator properties of species assemblages for natural areas monitoring. *Ecological Applications* **2**:203–217.
- Lambeck, R. J. 1997. Focal species: a multi-species umbrella for nature conservation. *Conservation Biology* **11**:849–856.
- McCoy, E. D., and H. R. Mushinsky. 2002. Measuring the success of wildlife community restoration. *Ecological Applications* **12**:1861–1871.
- MELP (Ministry of Environment, Land and Parks). 2001. Inventory methods for moles and pocket gopher, Version 2.0, No. 26. Retrieved from: <http://ilmbwww.gov.bc.ca/risc/pubs/tebiodiv/molesgophers/mogo%20ml20%20final.pdf>– Last accessed February 8th, 2007.
- Morrison, M. L. 2002. Page. 215 *Wildlife restoration: techniques for habitat analysis and animal monitoring*. Island Press, Washington, DC.
- Oliver, I., and A. H. Beattie. 1993. A possible method for the rapid assessment of biodiversity. *Conservation Biology* **7**:562–568.
- Oliver, I., A. J. Beattie, and A. York. 1998. Spatial fidelity of plant, vertebrate, and invertebrate assemblages in multiple-use forest in Eastern Australia. *Conservation Biology* **12**:822–835.
- Paller, M. H., M. J. M. Reichart, and J. M. Dean. 2000. Use of fish community data to evaluate restoration success of a riparian stream. *Ecological Engineering* **15**(1):S112–118.
- Paszkowski, C. A., and W. M. Tonn. 2000. Community concordance between the fish and aquatic birds of lakes in northern Alberta, Canada: the relative importance of environmental and biotic factors. *Freshwater Biology* **43**:421–437.
- Pélissier, R., P. Couteron, S. Dray, and D. Sabatier. 2003. Consistency between ordination techniques and diversity measurements: two strategies for species occurrence data. *Ecology* **84**:242–251.
- Prendergast, J. R., and B. C. Eversham. 1997. Species richness covariance in higher taxa: empirical tests of the biodiversity indicator concept. *Ecography* **20**:210–216.
- Prendergast, J. R., R. M. Quinn, J. H. Lawton, B. C. Eversham, and D. W. Gibbons. 1993. Rare species, the fidelity of diversity hotspots and conservation strategies. *Nature* **365**:335–337.
- Purvis, A., and A. Hector. 2000. Getting the measure of biodiversity. *Nature* **405**:212–219.
- Ralph, C. J., G. R. Geupel, P. Pyle, T. E. Martin, and D. F. DeSante. 1993. *Handbook of field methods for monitoring landbirds*. Gen. Tech. Rep. PSW-GTR-144, U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station Albany, California.
- Ricketts, T. H., E. Dinerstein, D. O. Olson, and C. Loucks. 1999. Who's where in North America? Patterns of species richness and the utility of indicator taxa for conservation. *Bioscience* **49**:369–381.
- Roberge, J.-M., and P. Angelstam. 2004. Usefulness of the umbrella species concept as a conservation tool. *Conservation Biology* **18**:76–85.
- Ruiz-Jaen, M. C., and T. M. Aide. 2005. Restoration success: how is it being measured?. *Restoration Ecology* **13**:569–577.
- SER (Society for Ecological Restoration International Science & Policy Working Group). 2004. *The SER International Primer on ecological restoration* (available from <http://www.ser.org>) accessed May 2007. Society for Ecological Restoration International, Tucson, Arizona.
- Shmida, A., and Wilson, M. 1985. Biological determinants of species diversity. *Journal of Biogeography* **12**:1–20.
- Singer, M. B., and T. Dunne. 2001. Identifying eroding and depositional reaches of valley by analysis of suspended-sediment transport in the Sacramento River, California. *Water Resources Research* **37**:3371–3381.
- Su, J. C., D. M. Debinski, M. E. Jakubauskas, and K. Kindscher. 2004. Beyond species richness: community similarity as a measure of cross-taxon congruence for coarse-filter conservation. *Conservation Biology* **18**:167–173.
- SYSTAT. 1996. *Statistics, SYSTAT 6.0 for Windows*. SPSS, Inc., Chicago, Illinois.
- Weaver, J. C. 1994. Indicator species and scale of observation. *Conservation Biology* **9**:939–942.
- Webb, N. R., and P. J. Hopkins. 1984. Invertebrate diversity on fragmented Calluna heathland. *Journal of Applied Ecology* **21**:921–933.
- Westoby, M. 1985. Two main relationships among the components of species richness. *Proceedings of the Ecological Society of Australia* **14**:103–107.
- Whittaker, R. M. 1960. Vegetation of the Siskiyou Mountains, Oregon and California. *Ecological Monographs* **30**:279–338.
- Wiener, J. G., and M. H. Smith. 1972. Relative efficiencies of four small mammal traps. *Journal of Mammalogy* **53**:868–873.
- Wilcox, B. A., D. D. Murphy, P. R. Ehrlich, and G. T. Austin. 1986. Insular biogeography of the montane butterfly faunas in the Great Basin: comparison with birds and mammals. *Oecologia* **69**:188–194.
- Williams, N. M. 2007. Restoration of native bee pollinators within the Sacramento River system (California). *Ecological Restoration* **25**:67–68.
- Young, T. P. 2000. Restoration ecology and conservation biology. *Biological Conservation* **92**:73–83.