Ecological Restoration

Fifteen Years of Avian Use in a Small Riparian Area Following Restoration

Contents

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Long Term Progress in Riparian Restoration with Concurrent Avian Declines in the Southern San Francisco Bay Area (CA)

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ABSTRACT

The restoration of riparian habitats aims to provide habitat for birds and other environmental benefits; yet the evaluation of long-term outcomes is rare. To address this knowledge gap, we used bird and vegetation data from Coyote Creek Field Station (CCFS), in the southern San Francisco Bay Area, to assess the progress of two riparian revegetation projects (1987 Revegetation, 1993 Revegetation) over nearly two decades. Restoration success was measured by changes in 1) vegetation structure and composition, and 2) avian abundance, diversity, and community composition. We compared the two revegetated areas to a remnant riparian reference site and a managed floodplain overflow channel in three time periods (1996–1998, 2004–2006, 2012–2014) using ANOVA, Tukey's HSD tests, and beta diversity analysis of avian community composition. Over time, the restored areas became more similar to the remnant riparian reference site in four of seven indices. The avian community became more similar across the habitat areas over time, although differences remained. Migratory birds declined across all habitat areas, while resident and wintering birds declined in one revegetated habitat only. Overall we found that different types of data told different stories, indicating both convergence with the reference site and ongoing differences. Our findings highlight the need for multifaceted approaches to evaluating restoration success.

Keywords: California, Coyote Creek, migratory birds, resident birds, restoration success, vegetation

❧ Restoration Recap ❧

- Largest understory changes in revegetated habitats occurred within the first eight years.
- Overstory ecological indices in restored sites were largely determined by initial plantings.
- Ecological indices for vegetative and avian communities in revegetated sites generally became more similar to those of the reference remnant riparian habitat after more than 15 years.
- Long-distance migratory bird species declined across all habitats, while residents and short-distance migrants declined only in one habitat area.
- Riparian restoration for long-distance migratory birds requires a regional perspective.

Riparian ecosystems provide essential ecological functions, ecosystem services, and economic benefits, including wildlife habitat, water quality improvements,

groundwater recharge, mitigation of climate warming, and increased local property values (Dybala et al. 2018, Justice et al. 2017, Kristensen et al. 2013). In water-limited regions, such as the western United States, riparian ecosystems represent biodiversity hotspots and provide key stopover opportunities for migratory birds along the Pacific Flyway (Barton and Sandercock 2017). In California, riparian ecosystems are home to some of the most diverse annual bird communities (Dybala et al. 2018, Lind et al. 2019, Rottenborn 1999) and are important foci for migrant and resident bird conservation efforts (Rockwell and Stephens 2018), even though they account for < 0.5% of the land area (RHJV 2004).

In California, up to 98% of historical riparian habitats have been lost due to rapid habitat destruction (RHJV 2004). In the San Francisco Bay Area, riparian habitat destruction is a consequence of urbanization, population growth (Heppler 2017), industrial farming, and straightening and channelizing local waterways (Okamoto 2015). The impact of these losses is exacerbated by the important role these ecosystems may play in adaptation to climate change (Capon et al. 2013, Seavy et al. 2009), as they are naturally resilient to disturbances (Fremier et al. 2015, Matzek et al. 2018), provide habitat corridors for migrating species (Dybala et al. 2018, Rottenborn 1999), create thermal refugia for wildlife (Seavy et al. 2009), and accumulate carbon stocks at a greater rate than upland forests (Dybala et al. 2019). Concerns over losses of riparian biodiversity and ecosystem services and a growing awareness of their ecological importance have led to greater prioritization of their restoration (Fremier et al. 2015, Rockwell and Stephens, 2018).

While ecological restoration can potentially lead to many desired outcomes, such as reversing land degradation, increasing biodiversity, and providing important ecosystem services, the assessment of long-term restoration success raises complex questions. There is ongoing debate over whether restoration progress is best measured by comparing species composition and physical structure of restored sites to reference sites, or by evaluating changes over time and the recovery of habitat function (Dufour et al. 2007, Suding 2011). Several studies have stressed the importance of before-and-after monitoring, in addition to comparisons with reference sites (Bernhardt et al. 2007, Wortley et al. 2013). The consideration of spatial and temporal scales is also important but poses significant challenges, as the restoration process often spans decades or even centuries, and responses to restoration may be non-linear and spatially variable (Follstad Shah et al. 2007, Trowbridge 2007). Therefore, appropriate metrics and approaches to quantifying key attributes of success, such as ecological structure, abundance, ecosystem functioning, or socioeconomic impacts are difficult to determine for any given site (Bernhardt et al. 2007, Kondolf et al. 2007, Suding 2011, Wortley et al. 2013), and as a result, restoration projects frequently suffer from the absence of clear goals and objective evaluation criteria (Ruiz-Jaén and Aide 2005a, Kondolf et al. 2007). In addition, long-term monitoring campaigns are generally underfunded, further hampering the evaluation of restoration outcomes (González et al. 2015).

Previous studies have emphasized the need for multidecadal assessments of post-restoration success of vegetation and fauna for coastal California habitats to ensure that impactful, stochastic weather events and the highly variable and cyclical hydrology associated with Mediterranean climates are captured in the evaluation period (Follstad Shah et al. 2007, Kondolf et al. 2007). Yet, globally, only 13% of riparian restoration projects are monitored for more

than six years after restoration (González et al. 2015). In practice, restoration progress is usually evaluated using annual vegetation measurements, such as species abundance, species diversity, physical properties, and survival (González et al. 2015). Vegetation structure informs habitat suitability and ecosystem productivity, while plant diversity provides information on the trophic structure necessary for ecosystem resilience and susceptibility to invasions (Ruiz-Jaén and Aide 2005b).

In addition to vegetation metrics, the abundance and diversity of avian communities represent important and widely used monitoring indicators, as birds occupy a high position in the food web, respond to habitat change at multiple spatial scales, and can be monitored with comparative ease (Fjeldså 1991, Carignan and Villard 2002, Gardali et al. 2006, Rockwell and Stephens 2018). Avian community composition, the assembly of unique species present in a community, may indicate how established the vegetation community has become, as some bird species prefer young vegetation, while others prefer mature systems (Dybala et al. 2018), and bird population trends at restored sites can be compared to broader regional trends (Gardali et al. 2006, Dybala et al. 2018). Knowledge of factors that influence habitat selection and utilization by birds in a restored habitat can provide information on how to improve revegetation plans in future restorations (Rockwell and Stephens 2018). However, concurrent assessment of corresponding faunal recovery is uncommon and is assumed to follow revegetation (Ruiz-Jaén and Aide 2005a, Feld et al. 2011, Rockwell and Stephens 2018). The combination of riparian restoration by the Santa Clara Valley Water District and the Coyote Creek Field Station (CCFS), a long-running bird banding station in San Jose, California, provides a unique opportunity to assess how avian communities have responded to medium-to-long-term post-restoration vegetation changes.

Study Goals

Our objective was to evaluate the success of two riparian revegetation projects at CCFS by comparing them against a remnant riparian reference site and a managed floodplain overflow channel over three time periods (1996–1998, 2004–2006, 2012–2014). We predicted that the restored sites would increasingly resemble the reference site, but not the managed floodplain, over time, and that this would be reflected in convergence in measures of vegetation and avian presence (Batisteli et al. 2018, Rockwell and Stephens 2018). Restoration is considered successful when the metrics of restored sites are similar to those of the reference site (Ruiz-Jaén and Aide 2005a). Specifically, we evaluated restoration progress by measuring 1) understory and overstory vegetation structure, composition, and physical characteristics, and 2) the abundance, diversity, and community composition of resident, wintering, and migrant avian species. We assumed that changes in avian

communities following revegetation were at least partly connected to changes in vegetation structure, and that patterns of change are related to known habitat requirements and use (Batisteli et al. 2018).

Methods

Study Site

Coyote Creek Field Station (CCFS) is located along Coyote Creek, a perennial stream flowing from the eastern San Jose foothills into the southern end of the San Francisco (SF) Bay in Santa Clara County, California (Figure 1). The Bay Area is situated within the California Floristic Province, a world biodiversity hotspot (Reilly et al. 2017), with CCFS consistently identified as one of the most diverse birding sites in the South SF Bay Area (www.ebird.org/hotspots). The SF Bay Bird Observatory (SFBBO) has operated a bird-banding station at CCFS since 1983. Climate in the region is Mediterranean, with mild, wet winters (November–April), and warm, dry summers (May–October) (Minnich et al. 2007). Mean annual rainfall is 431.8 mm, with average high temperatures of 22°C and average lows of 11°C.

The Santa Clara Valley was historically dominated by oak (*Quercus*) savanna woodlands, with riparian forests bordering rivers, streams, and marshes (Jaramillo et al. 2003). In the 1930s, the land where the CCFS is located was converted into a pear orchard, with a 2.8 ha strip of remnant riparian forest (hereafter Remnant Riparian), adjacent to the creek (Figure 1). In the absence of alternative mature habitat, we considered it a baseline for riparian species composition and ecosystem function for comparison with the revegetated habitats. Beyond CCFS, the remnant riparian strip continues south along the creek for over 30 km. Beginning in the 1980s, the Santa Clara Valley Water District (SCVWD), which manages most of the local watersheds through water storage and flood protection infrastructure, initiated riparian restoration efforts at several sites along Coyote Creek, including two at CCFS. The restoration at CCFS began with 1.8 ha in 1987, followed by 3.2 ha in 1993 (Figure 1). The combined size of the habitat areas is 14 ha. The species planted included trees, shrubs, and understory plants and are listed in Supplementary Material, Table S1.

Vegetation Structure and Composition

Overstory vegetation were measured in two 5m-wide parallel transects on either side of each mist net to characterize vegetation in the immediate vicinity of each net. The vegetation sampling around all nets in a habitat area taken together documented differences between habitats. Vegetation surveys monitored the relationship between the habitat adjacent to the mist nets and the bird species and number of individuals caught in the mist nets (Dufour et al. 2007).

Understory vegetation was classified as any plant less than 140 cm in height (McClain et al. 2011). Samples of the understory were taken at four equally-spaced points along each net with a meter stick. Sampling began two meters perpendicularly away from each side of the net and using the meter stick, with ten increments 10 cm apart, being held as close to the ground as possible. At each increment, the species of plant or substrate touching the stick was recorded along with its height.

Overstory vegetation was defined as any woody plant greater than 3 m tall and with a trunk diameter of greater than 1.5 cm, 1.5 m above ground (DBH). Overstory vegetation was measured by mapping out all the qualifying woody plants in the two 5m-wide parallel transects. Overstory height was recorded at the tallest point of each plant and was calculated using a telescoping pole for woody plants up to 7 m in height and a clinometer for those that were taller. DBH was measured using a DBH tape 1.5 m above ground. Canopy coverage was measured using a densiometer at the center of each net, and at the creekside end of every net. At each location, readings were taken in each of the four cardinal directions (N, S, E, W) and the number of dots obscured by vegetation were recorded and averaged.

Bird Abundance and Diversity

For more than 35 years, the SF Bay Bird Observatory (SFBBO) has operated a constant-effort bird-banding station at CCFS. Each captured bird was banded, measured, and released. The data included in this study are from 46 permanent mist nets (all 12 m × 2 m except one 6 m × 2 m, 32 mm mesh, manufactured by Avinet, Portland, OR) locations with 12 nets in each of the four habitat types except the Remnant Riparian, which had ten nets. All included nets were 0.5 m to 2.5 m above ground level to avoid confounding effects of variable net height (Tattoni and LaBarbera 2022). Nets are operated year-round with each net opened one day per week for five hours starting 30 minutes before sunrise. Bird capture rates were standardized as the number of birds captured per 100 net-hours (nh) where one net-hour is one net open for one hour. *In situ* capture data allows the tracking of seasonal and long-term population trends of spring- and fall-migrant (April–May and Aug 15–Oct 15), wintering (November–February), and year-round resident species, and for the investigation of avian responses to riparian restoration. More details on bird-banding at CCFS can be found in Jaramillo et al. (2003).

Statistical analysis

Abundance and diversity—Overstory and understory vegetation surveys at CCFS were conducted in eight year intervals starting in 1997. Therefore, vegetation survey data was available for the years 1997, 2005, and 2013. To best match avian capture data to the state of the vegetation we analyzed avian capture data only in three-year
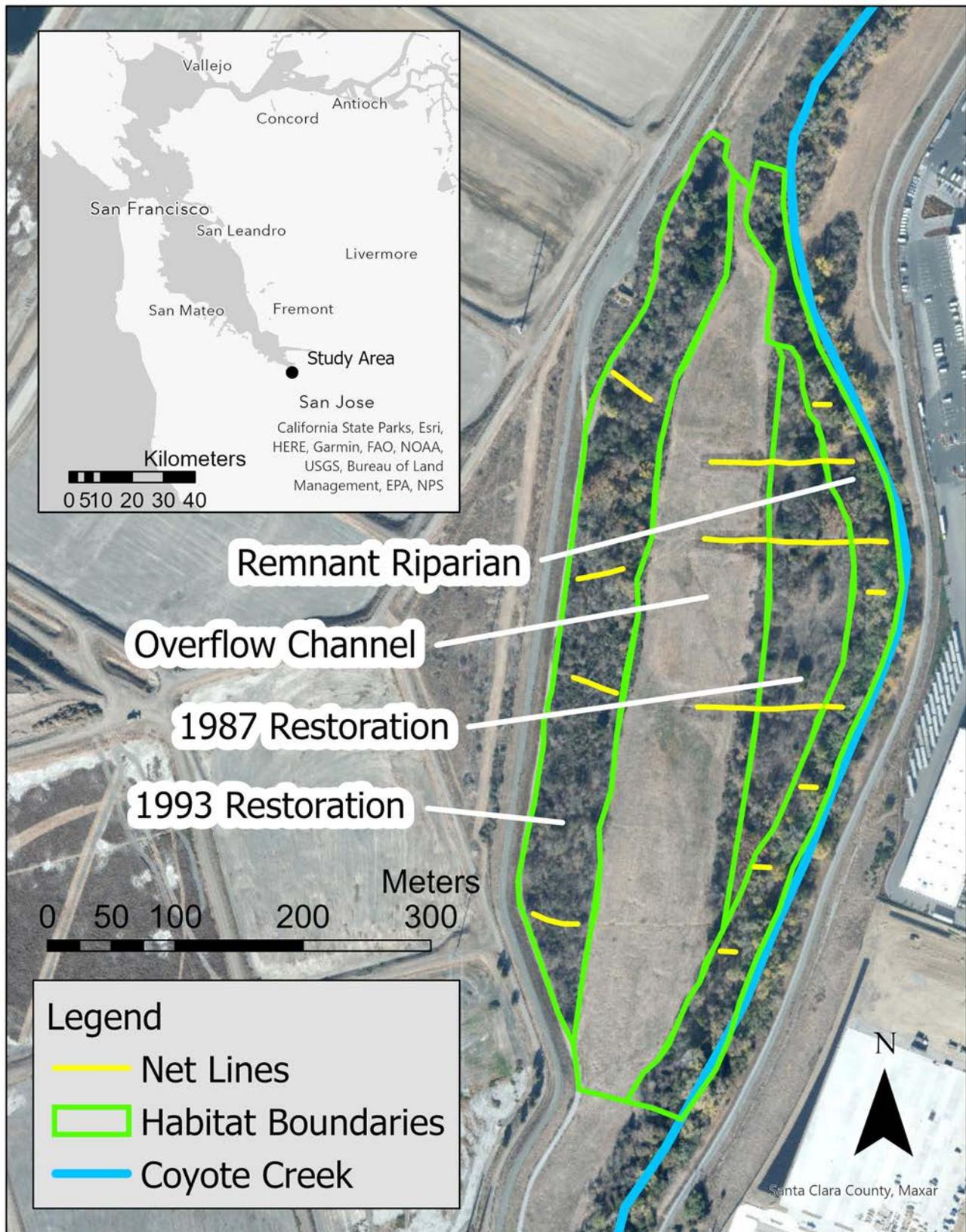
Figure 1. Boundaries of the Coyote Creek Field Station (CCFS) habitat areas and mist net line locations analyzed in this study. The CCFS is located at the southern end of the San Francisco, CA, Bay Area (inset) near the mouth of Coyote Creek, which flows to the right of the remnant riparian habitat. The areas now covered by the 1987 and 1993 revegetation areas and the overflow channel were converted to a pear orchard during the 1930s, such that only a thin strip of a remnant riparian zone remained adjacent to Coyote Creek.

periods centered on the years for which vegetation data exists, namely 1996–1998, 2004–2006, and 2012–2014. Three-year periods represent a compromise between temporal specificity, to match the vegetation survey data, and sample size to reduce the impact of any potential aberrant time periods.

To quantify habitat differences at CCFS, we calculated species abundance and diversity for vegetation understory, overstory, and avian communities with R package *vegan* (Chao et al. 2004, Oksanen et al. 2020). We defined vegetative species abundance as the total number of individuals per net, and avian species abundance as the total number of individuals captured per 100 mist net hours. Species diversity is a quantitative measure that reflects the number of different species (species richness) and how evenly individuals are distributed among those species. We used the Inverse Simpson's Index (ISI), a weighted arithmetic mean of proportional abundance that measures the probability that two individuals randomly selected from a sample will belong to different species. ISI is calculated as:

$ISI = 1 / \Sigma (n_i(n_i-1))/(N_i(N_i-1))$, where n_i is the number of individuals of each of the i species, and N_i is the total number of individuals for the site. The value of ISI ranges from 1 to infinity, with 1 representing no diversity. The ISI was chosen over the Shannon-Wiener Index (SWI), also frequently found in the literature, as the SWI is weighted towards relatively rare species and will thus tend to be highly correlated with richness.

Abundance and ISI were calculated for vegetation understory, overstory, and avian captures in each of the three study periods and for the four habitat types (see Figure 1). Type III Sum of Squares Two-way ANOVA tests were used to determine differences between and interactions among habitat types and time periods for vegetation and birds; the residuals were extracted and then tested for normality using Shapiro-Wilk tests. For distributions of residuals that did not meet normality tests, the data were log transformed. A constant value of one was added to each value prior to log transformation. If log transformations did not pass Shapiro-Wilk tests, Tukey's Ladder of Powers was applied with R package *rcompanion* (Mangiofico 2020). Each ANOVA was also checked for homogeneity of variance, using the Levene's test with R package *car* (Fox et al. 2020). If the ANOVA was significant then Tukey's Honest Significant Difference (HSD) post hoc tests were run to determine which specific groups differed. Vegetation structure (height, DBH, canopy cover) was analyzed in the same manner.

To reduce the risk of a type I (false positive) error when performing multiple statistical tests, the significance level α was adjusted using the Benjamini-Hochberg Correction (BHC) (Benjamini and Hochberg 1995) to hold the type I error rate at 0.05. The BHC was chosen due to its strict α error correction (Voelkl 2019).

Avian communities—Over 100 avian species have been captured and banded at CCFS since 1996 in a process known as Capture Mark Recapture (CMR, Bird et al. 2014). Species were divided into three migratory strategies (resident, wintering, and passage migrant) as a means of examining each group's responses to restoration over time. Recapture rates were 29%, 26%, and 7% for resident, wintering, and migrant species, respectively and recaptures were included in the analysis. A common assumption in CMR analysis is that all individuals in a population have equal availability for sampling (Bird et al. 2014). Therefore, if individuals are able to temporarily leave the sampled population, their absence may result in a downward bias in estimated capture probabilities (Barker et al. 2004). Here, every bird inherently has equal availability for sampling, as we consider migratory, wintering, and resident groups separately. Through counting recaptures we are reducing bias as we include the presence of individuals in all habitat areas they used. For each group, we used two-way ANOVA to test for differences in abundance and diversity between habitats and years and for interactions among habitats and years (see previous section).

Because ANOVA tests used to evaluate differences in avian abundance and diversity are insensitive to differences in species composition, we conducted beta-diversity analysis for each of the three periods using R package *vegan* (Oksanen et al. 2020) to examine the similarity of total avian community compositions between habitats during the 3-year focal periods. Beta-diversity quantifies the variability in species composition among locations of interest: in our case, it measured the (dis)similarity in bird communities among the four habitat types. Following the approach of Anderson et al. (2006), our beta-diversity analysis calculates the differences in bird species composition between each net; plots those differences as distances in a multivariate space, with more similar nets having smaller distances and therefore appearing closer together in the space; finds the centroid for each habitat type by taking the multi-dimensional mean of all nets in that habitat; and then calculates the dispersion, or variability, of species composition in each habitat from the distances of each net to that centroid.

First, pairwise community dissimilarities between all nets were calculated using the quantitative Jaccard dissimilarity index calculated as: $2B/(1+B)$, where B is Bray-Curtis dissimilarity calculated as: $d_{jk} = \Sigma_i |x_{ij} - x_{ik}| / \Sigma_i (x_{ij} + x_{ik})$ (Chao et al. 2004), i is species and j and k are the sites (nets) being compared. Then we used Anderson and Santana-Garcon's (2015) PERMDISP2 procedure to analyze homogeneity of group dispersions (variances) between habitat types. Pairwise Jaccard distances were used to plot each net in a multivariate space defined by principal coordinate axes based upon bird species composition. Nets were grouped by habitat type to calculate group centroids
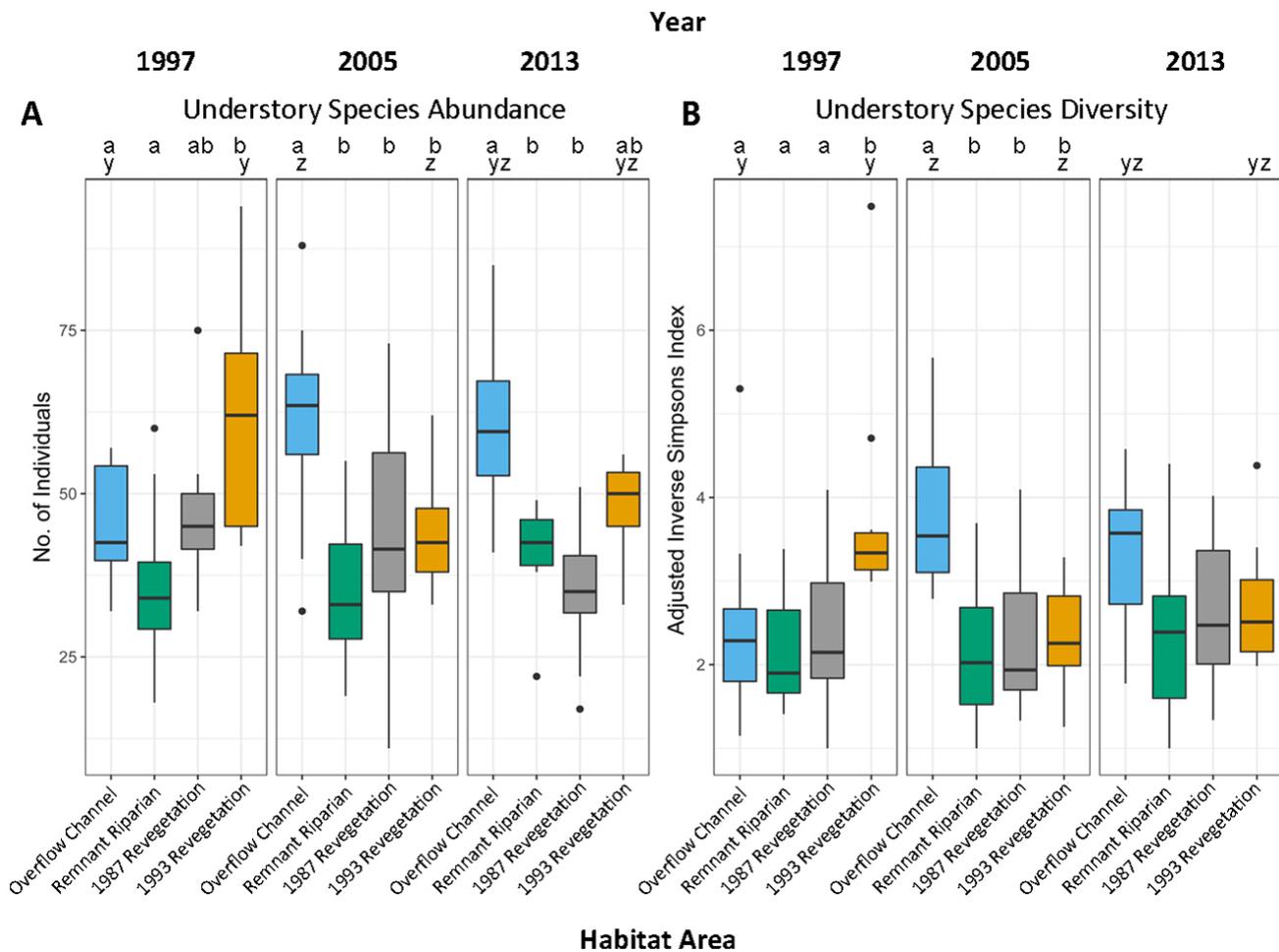
Figure 2. Measures of biodiversity for understory vegetation in each of the four habitat areas and three survey years from a riparian restoration site in the San Francisco Bay Area. Median and range are given for A) species abundance (number of individuals) and B) species diversity measured by the inverse Simpson's index. Significant differences are indicated by letters across the top of each panel. Lowercase a and b indicate comparisons within a year and between habitats (i.e. within a single figure panel), while y and z indicate comparisons within a single habitat over time (i.e. across figure panels).

in this multivariate space, and group dispersion was calculated from each net's distance to its group's centroid. We then used Tukey's Honest Significant Difference (HSD) tests to test whether group dispersions differed between habitat types. For pairs of habitats with homogeneous (non-different) dispersions, we used PERMANOVA with 99,999 permutations to test whether group centroids were different from each other, i.e., whether the species compositions differed. We only tested for centroid differences among habitats with homogenous dispersions because PERMANOVA will indicate a difference if either dispersion or centroids differ.

The above-described analyses tested whether significant differences between the habitat areas can be detected, but do not capture quantitative differences in the similarity between habitat areas. To address this, we also calculated the separation between habitat groups (the mean of the distances between every point in a group to its closest

neighbor in a different group; "separation" in function "cluster.stats" in R package *fpc* [Hennig 2020]) and the overlap between groups, which we defined for a pair of groups as the ratio between the number of points belonging to each group that fall within the standard deviation of the other group and the total number of points belonging to either of the groups (modified from Hong and Wu 2015).

Results

Vegetation

Understory—Models of understory abundance and diversity had significant interactions between habitat and time period (Figure 2, Table 1). In 1997, the 1993 Revegetation had significantly higher abundance and diversity than the Remnant Riparian. Both metrics in the 1993 Revegetation then decreased, such that in 2005 and 2013, the two habitats

Table 1. *P*-values from comparisons of the means between time periods (1996–1998, 2004–2006, 2012–2014), habitat areas within the riparian restoration site in the San Francisco Bay Area and their interaction as determined from two-way ANOVA tests. Determinations were made for canopy coverage and tree size parameters (height and diameter at breast height (DBH), and the abundance and diversity (inverse Simpson's Index, ISI) for over-/under-story and bird species grouped by migratory habit. Asterisks (*) indicate significance after Benjamini-Hochberg correction. Full ANOVA tables are in Supplementary Materials, Table S2.

Variable	Year Periods (*p*)	Habitat (*p*)	Interaction (*p*)
Canopy Coverage[1]	0.078	1.53e-05*	0.029*
Tree Height[1]	0.444	4.18e-09*	0.091
Tree DBH[1]	0.052	2.83e-12*	0.012*
Overstory Abundance[1]	0.479	0.009*	0.270
Overstory ISI[1]	0.810	0.010*	0.925
Understory Abundance	0.866	5.23e-09*	1.85e-05*
Understory ISI	0.731	3.92e-05*	2.05e-04*
Migrant Abundance	8.28e-08*	8.27e-08*	0.469
Resident Abundance	0.017*	1.66e-06*	1.35e-08*
Winter Abundance	0.040	1.52e-06*	8.45e-03*
Migrant ISI	1.38e-05*	1.43e-05*	0.083
Resident ISI	0.033	0.014*	0.003*
Winter ISI	8.47e-06*	6.27e-05*	0.011*

[1]Overflow Channel not included because no tall woody plants are present in that habitat.

no longer differed. Neither metric differed between the Remnant Riparian and 1987 Revegetation in 1997, and they remained constant through 2013. The Overflow Channel had similar abundance and diversity to the Remnant Riparian in 1997, but both metrics then increased to be higher in the Overflow Channel in 2005; in 2013 the Overflow Channel remained higher than the Remnant Riparian in abundance but not diversity.

Overstory—This analysis omits the Overflow Channel, which lacks overstory vegetation. Overstory species abundance was higher in the 1993 Revegetation than in the Remnant Riparian, while overstory species diversity was higher in the 1987 Revegetation than in the Remnant Riparian (Figure 3, Table 1). There was no effect of time on overstory species abundance or diversity. Canopy coverage, DBH, and tree height were all lower in the 1993 Revegetation than in the other two habitat areas; canopy coverage and DBH then increased in the 1993 Revegetation, such that the difference in canopy coverage was no longer significant in 2005, and the difference in DBH was no longer significant in 2013.

Tree composition—While several vegetation metrics for Remnant Riparian, 1987 Revegetation, and 1993 Revegetation areas changed in ways that made these indices more similar with time across habitat areas (Figure 3), tree compositions differed among each of the three habitats with overstory vegetation (Figure 4), and remained different across the study periods (Supplementary Material, Figure S1). In the Remnant Riparian, *Populus fremontii* (Fremont cottonwoods) and *Aesculus californica* (California buckeyes) were more prevalent, the 1993 Revegetation

contained larger numbers of *Sambucus cerulea* (blue elderberry), *Acer negundo* (box elder), and *Baccharis pilularis* (coyote brush), while in the 1987 Revegetation *S. cerulea*, *Quercus agrifolia* (coast live oak), *Fraxinus latifolia* (Oregon ash), and *Quercus lobata* (valley oak) dominated. These differences in tree assemblages between the 1987 and 1993 Revegetation and Remnant Riparian reflect differences in the original restoration plantings (Supplementary Material, Table S1) as well as species differences in survival (Figure 4).

Avian Communities

Abundance and diversity—Metrics for migrant, wintering, and resident species differed across habitat areas and study periods (Figure 5, Table 1). Habitat and time period interacted significantly in models for wintering and resident birds, but not for migrants. Generally, resident and wintering birds declined in the 1993 Revegetation, and migrant birds declined across all habitat areas. The 1993 Revegetation differed from the Remnant Riparian for all birds in 1996–1998, with this difference remaining significant over time for migrants but no longer being significant by 2004–2006 for resident and wintering birds. Migrant abundance was lower in the Overflow Channel than the other three habitats, and higher in the 1993 Revegetation. The Remnant Riparian and 1987 Revegetation did not significantly differ for any bird group in any metric at any time.

Beta diversity and community composition—Avian beta diversity shifted over the time periods studied, with 1993 Revegetation initially showing lower beta diversity than 1987 Revegetation and Remnant Riparian in 1996–1998 (Figure 6 and Table 2), then increasing such
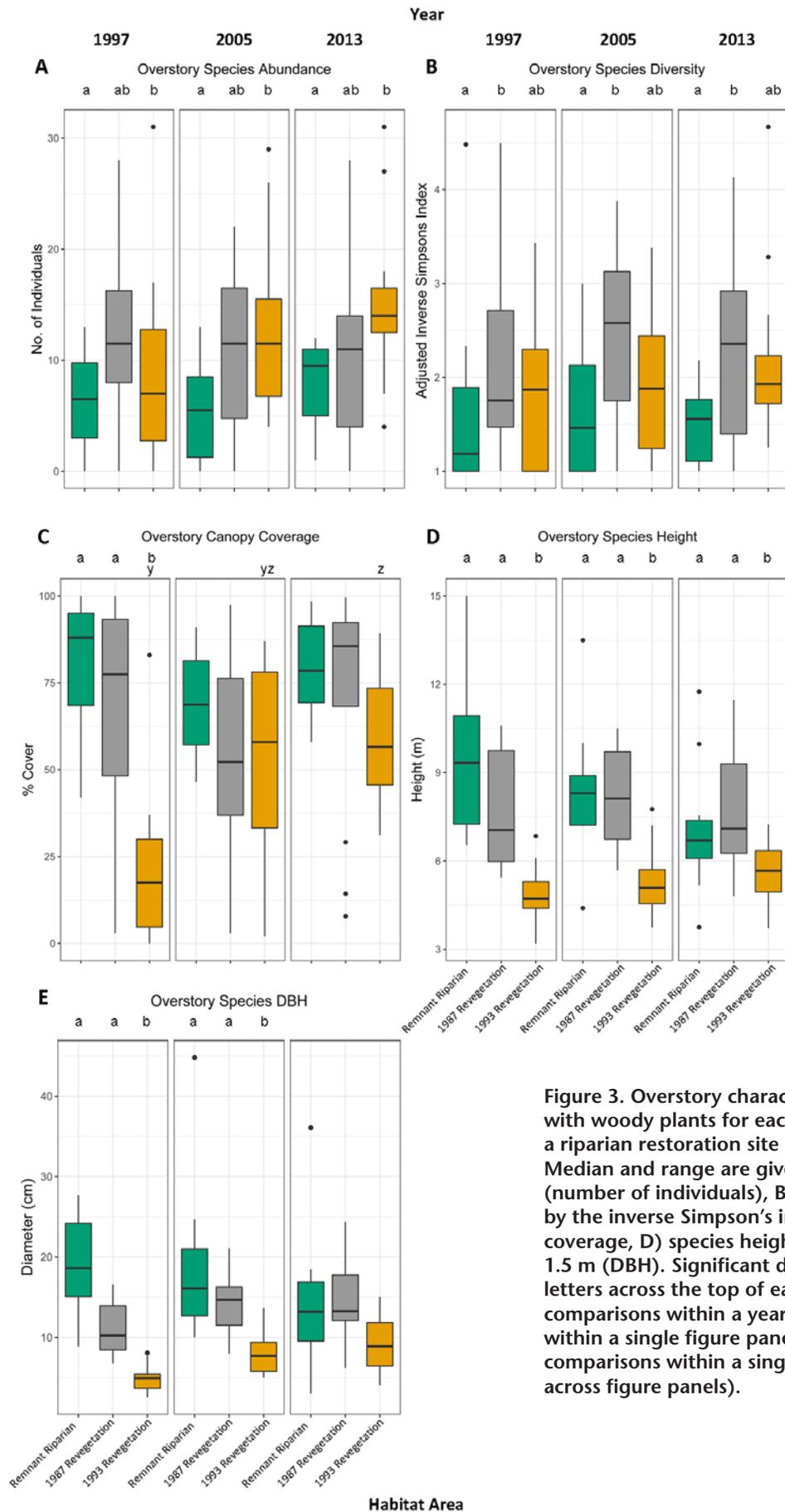
Figure 3. Overstory characteristics in each habitat area with woody plants for each of the three survey years, in a riparian restoration site in the San Francisco Bay Area. Median and range are given for A) species abundance (number of individuals), B) species diversity measured by the inverse Simpson's index, C) percent canopy coverage, D) species height, and E) species diameter at 1.5 m (DBH). Significant differences are indicated by letters across the top of each panel: a and b indicate comparisons within a year and between habitats (i.e. within a single figure panel), while y and z indicate comparisons within a single habitat over time (i.e. across figure panels).
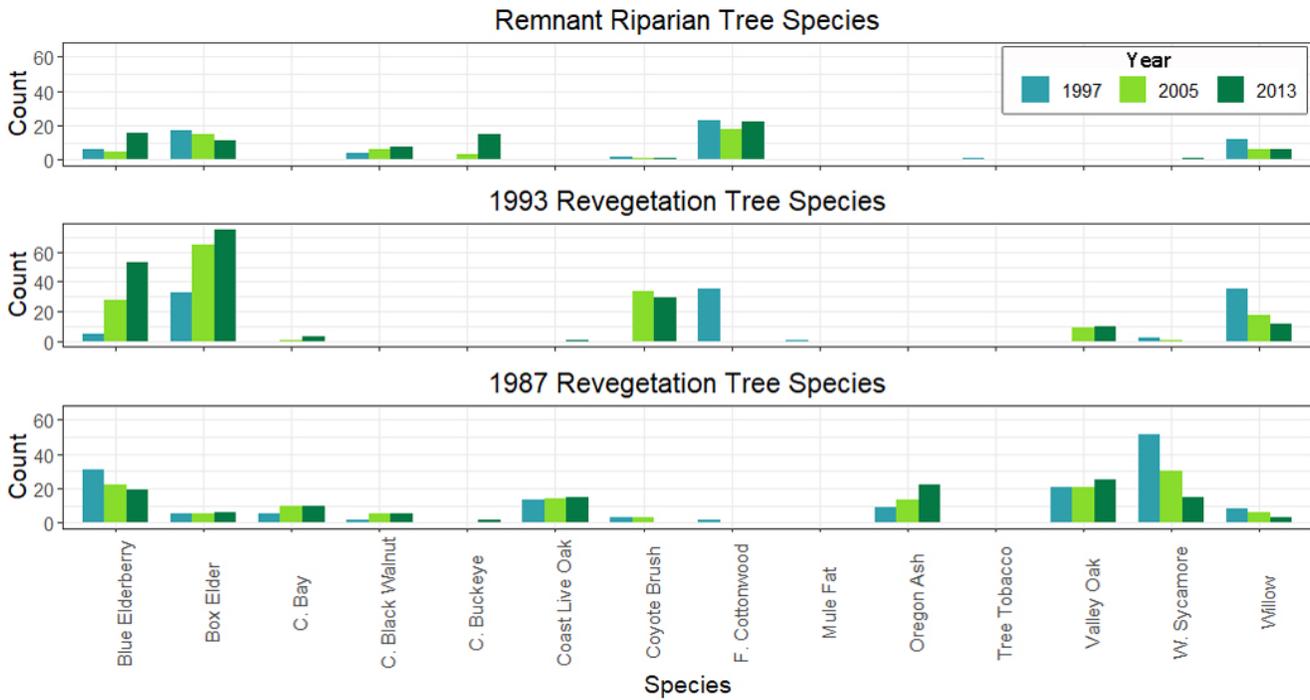
Figure 4. Comparison of the overstory woody plant species assemblages across each habitat area with woody plants and each survey year in a riparian restoration site in the San Francisco Bay Area. The following abbreviations are used: C. Bay = California Bay (*Umbellularia californica*); C. Black Walnut = California Black Walnut (*Juglans hindsii*); C. Buckeye = California Buckeye (*Aesculus californica*); F. Cottonwood = Fremont Cottonwood (*Populus fremontii*); W. Sycamore = Western Sycamore (*Platanus racemosa*).

that in 2004–2006 and 2012–2014 there were no among-habitat differences in beta diversity. In contrast, community composition did not change over time. Community composition significantly differed between all habitat areas with the exception of the Remnant Riparian and the 1987 Revegetation, which did not differ in 1996–1998 or 2004–2006. However, note that in 1996–1998 differences in avian species composition could not be statistically tested between the 1993 Revegetation and either the Remnant Riparian or the 1987 Revegetation due to their differences in dispersion.

Separation decreased over time between the Remnant Riparian and the other three habitat areas. Separation from the Remnant Riparian was initially lower for 1987 Revegetation than 1993 Revegetation, but by 2012–2014 separation values were lower between Remnant Riparian and 1993 Revegetation than 1987 Revegetation. Separation values between the revegetated areas also decreased over time. Overlap followed a complementary pattern, with overlap between Remnant Riparian and the two revegetated areas increasing over time.

Discussion

Over nearly two decades, the two restored sites became broadly more similar to the reference remnant riparian site in vegetation and in some aspects of avian presence. Understory abundance and diversity, canopy coverage,

and tree DBH all became more similar among these three habitat areas over time, as did resident bird abundance and diversity, wintering bird abundance and diversity, and avian community composition. The three vegetation metrics that did not converge (overstory diversity and abundance and tree height) did not become any less similar among the three habitats. Avian metrics, in addition to supporting increasing similarity among the sites, also suggest ongoing differences as well as potentially non-local factors driving change: avian community composition converged but did not become indistinguishable, and all birds, but especially long-distance migrants, showed a decline in diversity and abundance over time.

Our evaluation of decades of vegetative changes highlighted important differences between habitat areas. In the Remnant Riparian, few changes in the physical characteristics of the over- or understory were observed over the 15+ year study period, suggesting stability and lending support to our use of this habitat as a benchmark for assessing the success of the revegetated areas. In the revegetated areas, understory abundance and diversity mostly decreased over the three time periods we studied, as expected with maturation. Previous work found similar understory species declines with increasing site age (Gornish et al. 2017) and canopy coverage (Ruiz-Jaén and Aide 2005b). For the 1993 Revegetation, initial higher values for understory ecological indices were recorded, likely due to the greater importance that was placed on understory species in the
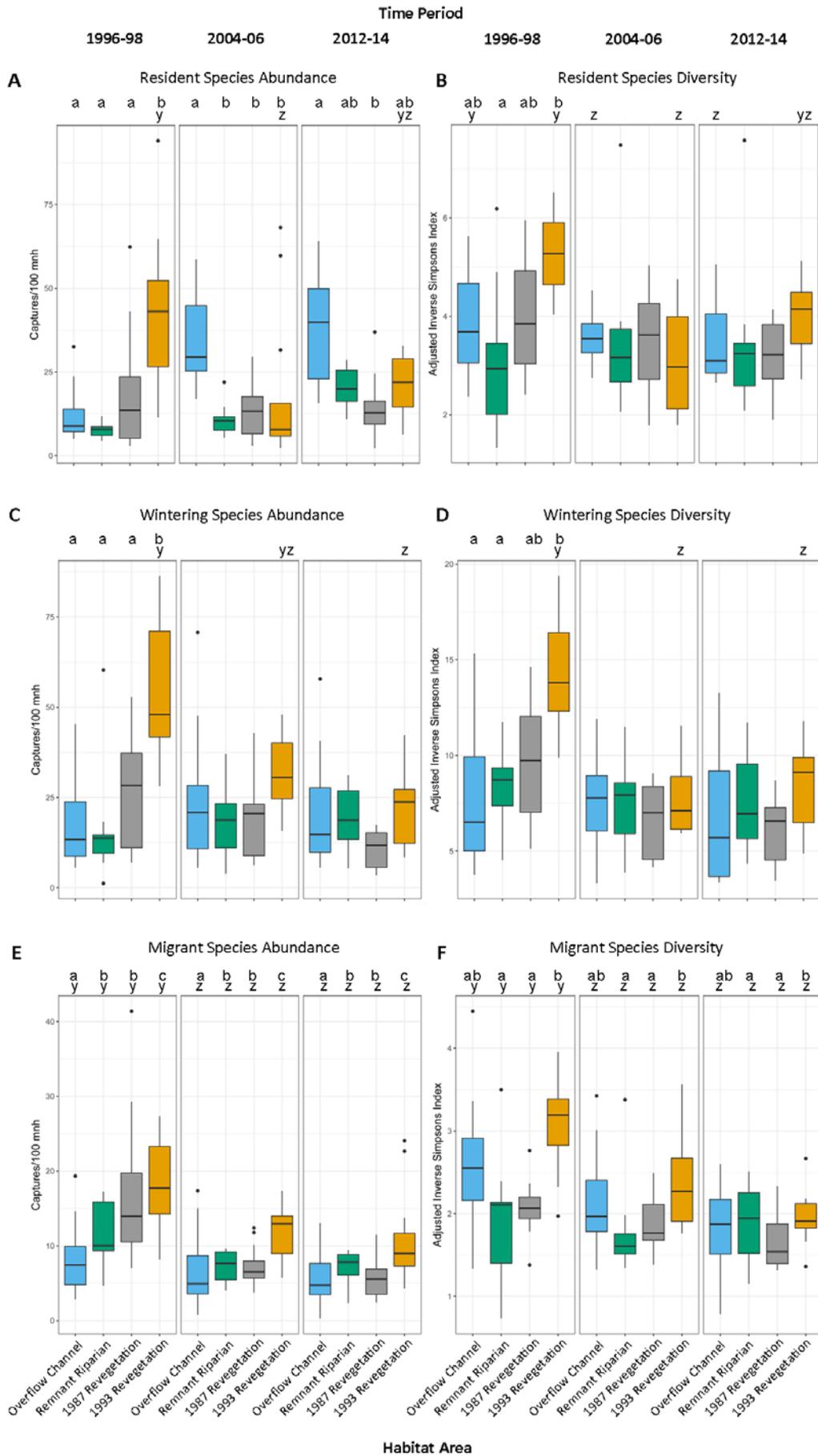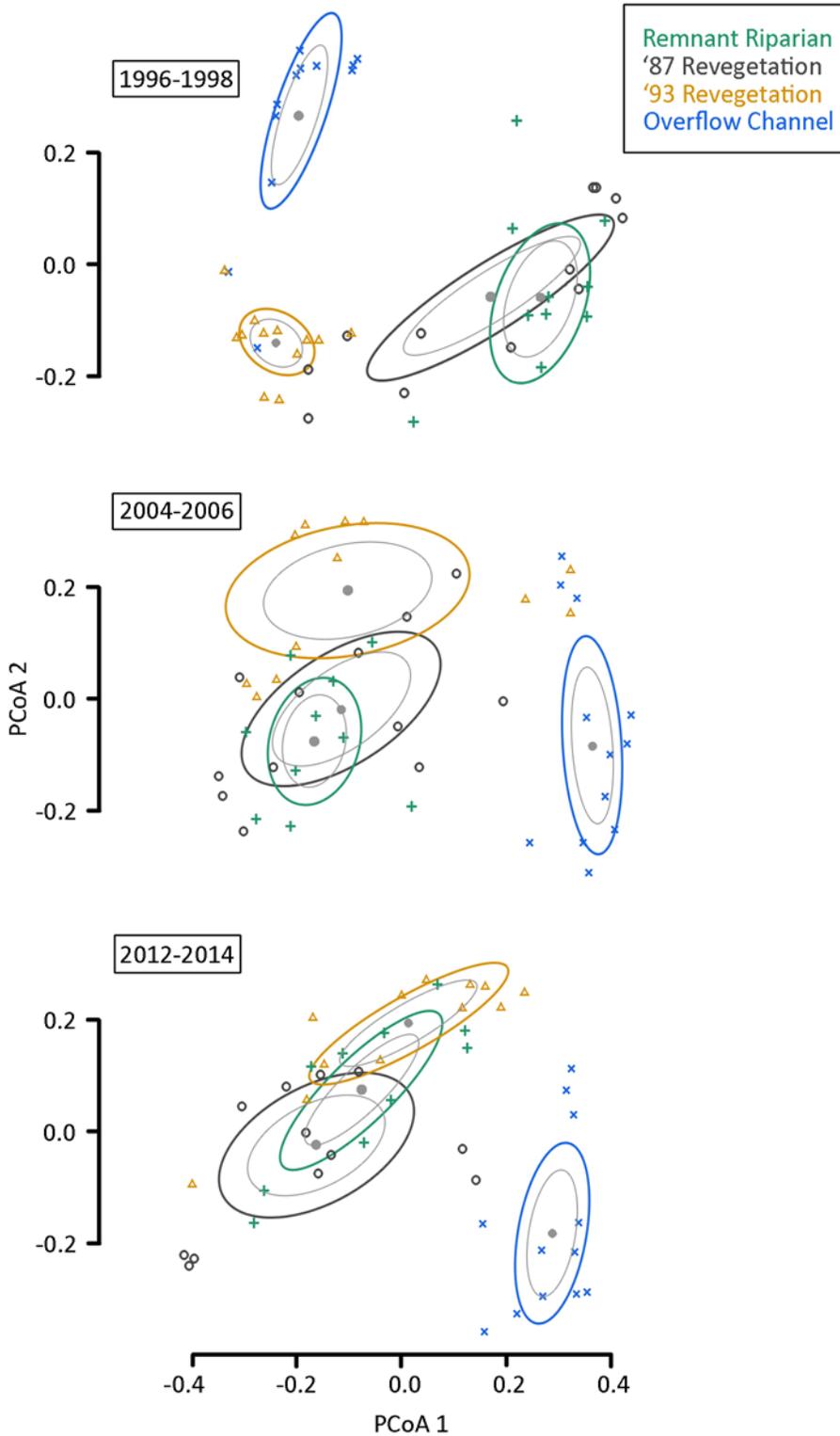
Figure 6 (left): Avian species composition of captures at each net in a riparian restoration site in the San Francisco Bay Area, grouped by habitat type, in each time period, depicted in a multivariate space with principal coordinate axes. Outer ellipses illustrate the standard deviation of that habitat area's captures at each net, indicating the dispersion (avian beta-diversity); inner ellipses illustrate the 95% confidence interval for the centroid location; filled gray points indicate centroid location (avian community composition); plus signs (+) are Remnant Riparian nets; unfilled circles are 1987 Revegetation nets; triangles are 1993 Revegetation nets; x's are Overflow Channel nets.

Figure 5 (pg. 212). Measures of biodiversity for resident (A and B), wintering (C and D), and migrant avian (E and F) species in each of the four habitat areas and the three study periods (1996–1998, 2004–2006, 2012–2014) in a riparian restoration site in the San Francisco Bay Area. A,C,E) Median and range for abundance, captures/100 mnh = # captures for 100 mist net hours. B,D,F) Median and range for the inverse Simpson's index adjusted for sampling effort. Species are sorted according to their migratory strategy at the study site. Significant differences are indicated by letters across the top of each panel: a, b, and c indicate significant differences within a time period and between habitats (i.e. within a single figure panel), while y and z indicate a significant difference within a single habitat over time (i.e. across figure panels).

Table 2. Comparison of avian beta-diversity (dispersion), community composition (centroid location), separation, and overlap in avian captures between habitat areas and for each of the three time periods from a riparian restoration site in the San Francisco Bay Area. Differences between habitat areas in avian beta-diversity were measured as mean distance-to-centroid (dispersion), from Tukey's HSD test with a 95% family-wise confidence interval. A positive difference value indicates that the first-listed habitat has greater beta-diversity than the second-listed habitat. Differences in bird community composition were measured as difference in centroid position between the two habitats, from PERMANOVA. Separation is the mean of the distances between every point in a group to its closest neighbor in a different group; higher separation values indicate greater differences between habitats. Overlap is the ratio between the number of points belonging to each habitat that fall within the standard deviation (outer ellipse in Figure 6) of the other habitat and the total number of points belonging to either of the groups; higher overlap values indicate greater similarity between groups. Asterisks (*) indicate significance after Benjamini-Hochberg correction.

Metric	Habitat areas compared		1996–1998	2004–2006	2012–2014
Beta-diversity (difference, *p*)	Remnant Riparian	'87 Reveg.	–0.023, 0.889	–0.023, 0.921	–0.047, 0.673
		'93 Reveg.	0.098, 0.018*	0.010, 0.993	0.007, 0.998
		Overflow Channel	0.068, 0.152	0.026, 0.888	0.009, 0.996
	'87 Reveg.	'93 Reveg.	0.121, 0.001*	0.013, 0.984	0.054, 0.546
		Overflow Channel	0.091, 0.017	0.049, 0.502	0.056, 0.519
	'93 Reveg.	Overflow Channel	–0.030, 0.741	0.036, 0.729	0.002, 0.999
Community composition (F, P)	Remnant Riparian	'87 Reveg.	1.63, 0.078	1.30, 0.171	2.01, 0.034*
		'93 Reveg.	NA[1]	3.16, <0.001*	2.55, 0.011*
		Overflow Channel	9.56, <0.001*	10.18, <0.001*	8.02, <0.001*
	'87 Reveg.	'93 Reveg.	NA[1]	2.56, 0.009*	3.88, 0.001*
		Overflow Channel	7.84, <0.001*	9.12, <0.001*	8.70, 0.001*
	'93 Reveg.	Overflow Channel	8.10, <0.001*	9.43, <0.001*	9.01, <0.001*
Separation	Remnant Riparian	'87 Reveg.	0.431	0.414	0.397
		'93 Reveg.	0.561	0.414	0.382
		Overflow Channel	0.616	0.509	0.474
	'87 Reveg.	'93 Reveg.	0.377	0.393	0.332
		Overflow Channel	0.454	0.436	0.432
	'93 Reveg.	Overflow Channel	0.356	0.414	0.350
Overlap	Remnant Riparian	'87 Reveg.	0.136	0.364	0.273
		'93 Reveg.	0	0.091	0.227
		Overflow Channel	0	0	0
	'87 Reveg.	'93 Reveg.	0	0.125	0.125
		Overflow Channel	0	0	0
	'93 Reveg.	Overflow Channel	0.042	0	0

[1]No values are given for pairs with significantly different dispersions because PERMANOVA assumes dispersion homogeneity.

1993 Revegetation as compared to the 1987 Revegetation habitat (16 versus four species planted, respectively; Supplementary Material and Table S1). In contrast, in the Overflow Channel where regular mowing prevented the growth of overstory vegetation, ecological indices for understory increased. Therefore, the observed medium-term changes in vegetation at CCFS indicate consistency with the management history at CCFS.

Overstory tree species assemblages reflected the restoration plantings and would be expected to change over longer time scales than the understory. Although much of the overstory assemblages remained constant over the three study periods, indicating successful establishment of the planted species, several changes are noteworthy for the two revegetated areas (Figure 4). The number of *Salix* spp. (willow) individuals decreased over the three study intervals, especially in 1993 Revegetation areas

furthest from the stream channel. Their disappearance could be linked to their role as pioneer woody plants on floodplains (Nakamura and Ohgushi 2004) or the recent warming and droughts in California, and suggests that shallow groundwater or stream seepage were insufficient to support willows beyond the immediate proximity of the creek. In their place, more drought resistant and adaptable coyote brush and box elder have thrived throughout the 1993 Revegetation habitat area. Another noteworthy disappearance is that of the Fremont cottonwood in the 1993 Revegetation, which is consistent with the species' difficulty establishing itself in restored environments (Shafroth et al. 2017). In the 1987 Revegetation, the difference in outcomes for the western sycamores, which experienced die-offs, and the valley oaks, which maintained a stable presence, may be related to differing soil preferences (Griggs 2009).

Bird community data generally followed a pattern of increasing similarity between the Remnant Riparian and two revegetated habitat areas, with the 1987 Revegetation initially more similar to the Remnant Riparian and the 1993 Revegetation converging on the other two over time. The convergence among the 1987 Revegetation, 1993 Revegetation, and Remnant Riparian suggests a growing equivalence in resources available to the birds in those habitats, and increasing similarities in bird-relevant habitat. Notably, however, avian community composition was significantly different among most habitats in most time periods, including all habitat areas in the most recent time period. While the avian communities utilizing the Remnant Riparian and revegetated habitat areas have become more similar to each other, they remain distinguishable. This is possibly due to the younger age of the revegetated areas, or it may indicate that the revegetation was not successful in perfectly reproducing the Remnant Riparian habitat. Although east-west dimensions of the habitat areas in this study are comparatively small, and edge effects are likely, our data supports the idea that habitat differences at this scale are relevant to birds: we documented significant habitat-to-habitat differences in avian communities, as well as changes in these communities. Consistent with expectations, the bird community in the Overflow Channel, which is mowed annually and has no woody vegetation, differed from those of the other three habitats.

Differences in vegetative and avian trajectories highlight the importance of looking beyond plants to assess restoration. The apparent progress in restoration has not bolstered avian abundance or diversity; instead, these measures have decreased over time, particularly for long-distance migrants. One possible cause for any changes in bird abundance as estimated by mist net capture rate is a change in the vegetation structure around the mist nets (Tattoni and LaBarbera 2022); however, the lack of change over time in tree height in any habitat suggests that this is unlikely to account for the observed declines. The avian decline contrasts with previous studies that considered strings of restored riparian sites throughout the Central Valley and North Coast of California, and found bird species diversity (Dybala et al. 2018) and abundance (Gardali et al. 2006, Dybala et al. 2018,) significantly increased as restoration sites matured. The decline of resident and wintering species in the 1993 Revegetation may be related to succession in that habitat, as many bird species prefer early successional habitat (Raphael et al. 1987, Harris and Betts 2021). This illustrates the challenges of using species presence as a marker of habitat quality: succession is a natural process and does not indicate a failure of restoration, yet it may be correlated with declines in abundance and diversity.

As migratory birds are highly vagile, any explanation of population trends should also look to more regional factors, such as bird declines observed nationally to globally, changes in habitat more broadly, drought cycles, increasing warming or climate variability, or the effects of pollution, disturbance, or competition (Møller et al. 2008, Gorta et al. 2019, Rosenberg et al. 2019). Similar evidence for widespread declines in migratory species across North America tied to habitat loss elsewhere has been documented (Rosenburg et al. 2019, Rosamund et al. 2020). Migratory birds are a challenging target for conservation, as they require quality habitat across broad geographies, frequently necessitating international coordination and management. Runge et al. (2015) found that 91% of migratory birds have inadequate protected area coverage in at least one part of their migration cycle. They are also increasingly impacted by climate change-induced phenological mismatch with their prey species (Møller et al. 2008, Northrup et al. 2019) and by extreme weather events (Huntley et al. 2008, Rosamund et al. 2020). Longer-distance migrants face correspondingly greater challenges, which is consistent with our finding that wintering species, which migrate shorter distances than our spring- and fall-migrant species, have exhibited smaller declines than the spring- and fall-migrants over the same time period.

Similar to other restoration success studies, our work was impacted by several limitations. One of the primary determinants of the value of a restoration study is the ability to compare the restored sites to a mature benchmark habitat (Ruiz-Jaén and Aide 2005a). The remnant riparian strip we used for comparison did not appear to change in characteristics during the 15–20 years studied here, but we lack earlier data to determine whether it is genuinely mature. Mist netting for comparatively short periods likely only captures a subset of birds. In addition, the comparatively small habitat areas make edge effects likely, such that birds can easily move between habitat types, and reducing the significance between the different habitat areas. We were unable to replicate any of the control or treatment areas.

The results from our analysis provide several management implications. A number of individuals planted in the 1993 revegetation did not survive the first decade. These plantings were essentially unmanaged after initial establishment; our observations suggest that more active management would benefit certain plant species, and that more frequent monitoring of plant survival could inform future management actions. Although all birds declined in at least one habitat area at CCFS, wintering and resident species were stable in three of the four habitat areas, suggesting that the restorations had some success. Our analysis illustrates the limitations of individual ecological indices, such as avian species abundance or diversity, or a focus on either vegetative or avian communities to determine restoration success. Instead, our work highlights the need to assess restoration success for both different vegetative and wildlife communities over long time periods. The complexity of the restoration process at a given site is likely to encompass both successes and failures and must be viewed holistically.

Acknowledgments

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