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Source: *The Condor*, 114(2):258-267. 2012.

Published By: Cooper Ornithological Society

URL: <http://www.bioone.org/doi/full/10.1525/cond.2012.110029>

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RESEARCH PAPERS

The Condor 114(2):258–267
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A CENTURY OF AVIAN COMMUNITY TURNOVER IN AN URBAN GREEN SPACE IN NORTHERN CALIFORNIA

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Abstract. Over long time periods, urbanization is expected to have a negative effect on species diversity. Predicted effects generally follow one of three competing paradigms: diversity decay, homogenization, or community-composition turnover. However, it has been hypothesized that urban green spaces may provide a means by which urban areas can maintain or increase their species diversity over time. We used surveys conducted in 1913–18, 1938–39, and 2006–07 on the campus of the University of California, Berkeley, to evaluate how an avian community has changed over time in the context of urban growth. In each of the three periods the community differed greatly, yet we found no evidence for a decline in species or functional diversity. Despite the birds of the 1913–18 community having a greater affinity for native habitats than birds of later periods, we found no further evidence that specialists were being replaced by generalists. Of the three paradigms, our results strongly supported community-composition turnover. Parsimoniously, the habitat preferences of groups of species that changed over time were concordant with known changes in landscaping. While urbanization often does result in decreased biodiversity, our results provide an example of how an urban green space can mitigate and potentially reverse this trend within the context of dynamic community change. Our results are concordant with the view that urban green spaces can maintain original bird communities and disturbance-sensitive species can reestablish themselves given appropriate conditions.

Key words: *community-composition turnover, diversity decay, green spaces, homogenization, urbanization.*

Un Siglo de Recambio en una Comunidad de Aves de un Espacio Verde Urbano en el Norte de California

Resumen. En períodos de tiempo prolongados, se espera que la urbanización tenga efectos negativos sobre la diversidad de especies. Los efectos que se predicen por lo general se enmarcan en tres paradigmas que compiten entre sí: disminución de la diversidad, homogeneización o recambio en la composición de la comunidad. Sin embargo, se ha hipotetizado que los espacios verdes urbanos pueden representar un medio por el cual las áreas urbanas pueden mantener o aumentar sus diversidades de especies a lo largo del tiempo. Empleamos muestreos realizados en 1913–18, 1938–39 y 2006–07 en el predio de la Universidad de California, Berkeley, para evaluar como una comunidad de aves ha cambiado a lo largo del tiempo en un contexto de crecimiento urbano. En cada uno de los períodos la comunidad varió enormemente, a pesar de lo cual no encontramos evidencia de una disminución en la diversidad de especies o en la diversidad funcional. A pesar de que las aves de la comunidad de 1913–18 tenían una afinidad mayor por los ambientes nativos que las aves de los períodos posteriores, no encontramos mayor evidencia de que los especialistas estaban siendo reemplazados por los generalistas. De los tres paradigmas, nuestros resultados apoyan fuertemente el de recambio en la composición de la comunidad. Las preferencias de hábitat de los grupos de especies que cambiaron a lo largo del tiempo fueron concordantes con los cambios registrados en el paisaje. Mientras que la urbanización por lo general trae como resultado una disminución en la biodiversidad, nuestros resultados brindan un ejemplo de cómo un espacio verde urbano pueden mitigar y potencialmente revertir esta tendencia en el contexto de cambios dinámicos en la comunidad. Nuestros resultados son concordantes con la visión de que las áreas verdes urbanas pueden mantener las comunidades de aves originales y de que las especies sensibles a los disturbios pueden restablecerse si se les brindan las condiciones adecuadas.

Manuscript received 17 February 2011; accepted 7 October 2011.

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INTRODUCTION

Urbanization is a powerful global process that can result in habitat destruction and species extinction. The United States has seen a dramatic increase in the amount of land converted to urban use over the last half-century, and the urbanization rate is predicted to increase by 79% over the next 25 years (Alig 2004). Whereas land-use conversion has a detrimental effect on biodiversity (McKinney 2006), urban green spaces such as parks and gardens may help alleviate these effects (Gill et al. 2009, Goddard et al. 2010). Green spaces can provide a refuge for native species in a rapidly changing environment, and it has been suggested that they could provide long-term biotic stability even in the face of increasing density of the human population (Jim 2004). Nevertheless, to our knowledge, no studies have examined how urban processes within and around green spaces have affected biodiversity and community composition over long periods of time.

Because of the scarcity of long-term detection/non-detection data, there have been few studies of community change over decades in any landscape. While a number of studies have examined changes in undeveloped landscapes (Holmes and Sherry 2001, Etersson et al. 2007, Catterall et al. 2010), a minority have examined changes in areas undergoing urbanization (Walcott 1974, Aldrich and Coffin 1980, Parody et al. 2001, Catterall et al. 2010, Major and Parsons 2010). The results of these previous studies are manifested in three competing paradigms for the effects of urbanization (Catterall et al. 2010): diversity decay, homogenization, and community-composition turnover (Table 1). It is unknown which, if any, of these paradigms drive community changes in urban green spaces.

The paradigm of diversity decay predicts richness to be lost at multiple levels as natural areas become more urban. The slow conversion of natural areas and habitats to human-dominated ones drives a decrease in species richness (Emlen 1974, Walcott 1974, Beissinger and Osborne 1982, Bentley and Catterall 1997, Ford et al. 2001, Melles et al. 2003, Tratalos et al. 2007, Kalinowski and Johnson 2010) and functional diversity (Filippi-Codaccioni et al. 2009) through the loss of habitat structure and variation.

Similar in result, but more specific in mechanism, homogenization predicts that as natural areas become more urban, non-native invaders will replace local, native diversity. These invading species are more likely to be trophic (Parody et al. 2001, McKinney 2006) and habitat generalists (McKinney and Lockwood 1999) than the specialists they replace. While initially this may increase local biodiversity, as urbanization continues on a global scale, all urban areas will become more similar to each other than to their surrounding areas. This results in the same set of human-associated species being found worldwide, decreasing biodiversity both locally and globally (McKinney and Lockwood 1999, Olden et al. 2004, McKinney 2006). Growing global community similarity also leads to functional and genetic homogenization (Olden et al. 2004, Devictor et al. 2007).

In the third paradigm, community-composition turnover, species composition varies depending on what types of habitat are present at any point in time (Vale and Vale 1976, Parody et

TABLE 1. Three major paradigms of urbanization’s effect on biodiversity (Catterall et al. 2010). Each paradigm hypothesizes how different measures of biodiversity should change with increased urbanization. Dashes denote where a paradigm makes no prediction for a measure.

Measure	Paradigm		
	Diversity decay	Homogenization	Community-composition turnover
Species diversity	Decrease	Decrease	Stable
Functional diversity	Decrease	Decrease	Stable
Phylogenetic diversity	Decrease	Decrease	Stable
% Trophic specialists	—	Decrease	—
% Habitat specialists	—	Decrease	—
Community similarity	—	—	Decrease

al. 2001, Etersson et al. 2007, Catterall et al. 2010). In contrast to the first two paradigms, the empirical result of this process is that even while species composition may change drastically over time as urbanization occurs, the underlying diversity of the community remains stable.

In this study, we investigated the effects of green-space development within a context of urbanization over 93 years on a nonbreeding avian community on the campus of the University of California, Berkeley. The time scale of comparison allows inference on urbanization rarely possible in longitudinal studies of any kind (Tingley and Beissinger 2009), and our study is the first to examine bird-community changes in an urban green space. In addition, although an important part of avian biology, assemblages of nonbreeding birds have been studied much less than those of breeding birds (Evans et al. 2009), and rarely have they been studied in a Mediterranean climate (but see Kalinowski and Johnson 2010). We used surveys in three periods, 1913–18, 1938–39, and 2006–07, to examine changes in the composition and diversity of the avian community over time. On the basis of these differences, we tested whether the pattern of avian species change better fit a paradigm of diversity decay, homogenization, or community-composition turnover (Table 1).

METHODS

STUDY AREA

The campus of the University of California, Berkeley, is situated on the eastern edge of the city of Berkeley, Alameda County, and extends into Strawberry Canyon and the Berkeley Hills. The area used for this study is a 34-ha subset of the entire campus (Rodgers and Sibley 1940), encompassing much of what is referred to as the lower, or central campus (Fig. 1). The area contains many of the university’s academic buildings and has been actively landscaped for the duration of this study. A residential area borders the area to the north, a combination of residential and commercial areas borders it to the west and south, and the rest of the university campus, including a more natural area with additional buildings and labs, borders it to the east.

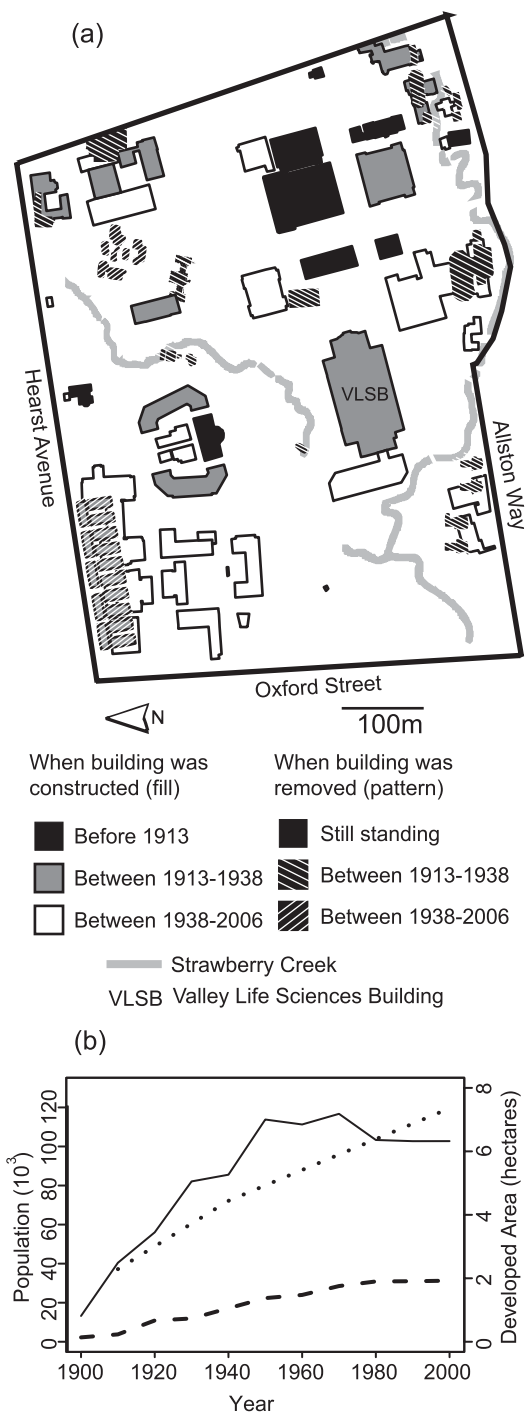


FIGURE 1. Map of the University of California, Berkeley, campus (a) showing the buildings present in each time period. Chart (b) depicts the population growth of the city of Berkeley (solid line; source Metropolitan Transportation Commission, and Association of Bay Area Governments 2010), the student population (dashed line) of the campus from 1900 to 2000 (sources Stadtman and Centennial Publications Staff 1967, University of California 2000, Office of Student Research and Campus Surveys 2010), and the area in hectares (dotted line) within the study area occupied by buildings (sources Stadtman and Centennial Publications Staff 1967, Laurie and Streatfield 1988, Geographic Information Science Center 2000).

Since the inception of the university campus, one prominent feature of the landscape has been Strawberry Creek. The two forks of this creek flow from the northeast and southeast edges of the study area, meeting in the west. Restored from degradation in 1987 (Charbonneau and Resh 1992), Strawberry Creek is the focus of much long-term landscaping, including a eucalyptus grove, redwood grove, and live oak woodland. Most of these trees, along with many other exotics that were part of the Agricultural Experimental Station, were planted in the late 1800s (University of California, Berkeley 2004a). Although there were 300 species of trees on the campus in the 1970s (Cockrell and Warnke 1976), that number has been reduced to about 200 because of building expansions and a lack of replanting (University of California, Berkeley 2004b).

The University of California Botanical Garden was established in 1891 within the northeast sector of the study area and was a source of both exotic and native species, including some chaparral shrubs (University of California, Berkeley 2004a). The botanical garden was moved from its original location to outside the study area in 1924; nevertheless, many specimens remained in situ in the study area until the 1960s, when a manicured lawn replaced many of the remaining plants (Cockrell and Warnke 1976, University of California, Berkeley 2004a).

Relative to much of the United States, Berkeley experiences a mild climate. The average daily high for January, the coldest month, is 13.6 °C, and the average daily low is 6.4 °C. The average daily high for September, the hottest month, is 22 °C, and the average daily low is 13.3 °C. Average annual precipitation is 62.2 cm, with most of the rain falling from November through March (NOAA 2004). Of the years during which bird data were collected, only one (1916–17) was abnormally cold (deviance from long-term average 1.37 °C; Easterling et al. 1999). All survey periods (particularly 1916–18, 1938–39, and 2006–07) were dryer than the long-term average but well within normal annual climatic fluctuations.

The university is situated within an urban context that has become denser over time. By 1910, the modern road and parcel structure of the city was fully laid out, with the city having a population of 40 434 (McClure 1910, Metropolitan Transportation Commission and Association of Bay Area Governments 2010). On the basis of historical maps and aerial photos, development over time consisted of increased density of residential and commercial areas within Berkeley as well as expansion of less dense residential areas farther up into the Berkeley Hills (U.S. Agricultural Adjustment Administration 1939, Laurie and Streatfield 1988, Berkeley Public Library 2011). By 2000, the city of Berkeley had a resident population of 102 743 (Fig. 1b; Metropolitan Transportation Commission and Association of Bay Area Governments 2010). On university property, the campus has become more developed over the study period, with the number of buildings in the study area increasing from 22 in 1913 to 31 in 2006 and many existing structures expanded (Fig. 1a). This expansion has been mirrored by a growth in student population (Fig. 1b).

SURVEYS

All surveys, 1913–18, 1938–39, and 2006–07, extended from October through March. A single observer, Margaret Wythe, made 58 surveys between 1913 and 1918. She recorded all birds seen or heard on half-hour walks through the study area, averaging six surveys per month. Her observations were recorded in field notebooks that have been archived at the Museum of Vertebrate Zoology, University of California, Berkeley.

Thomas L. Rodgers and Charles G. Sibley completed 60 surveys from 1938 to 1939, using a line-transect method to cover three transects per survey day through the study area. Ten days a month, they surveyed one transect each in the morning, at noon, and in the evening. The total time spent across all surveys each day averaged about 2 hr. The data are taken from figure 55 in Rodgers and Sibley (1940), which is a table denoting the presence of each species for each survey day. Rodgers and Sibley made sure to cover all of the main areas of the lower university campus every survey day.

One surveyor, AJS, conducted the 2006 to 2007 surveys. We emulated the methods of Rodgers and Sibley by surveying for ten days a month, three times each day, on transects corresponding to those of 1938–39, for a total of 60 survey days. However, we used a (10-min, variable-distance) point-count survey method to make it easier for future surveyors to duplicate our protocol and gather abundance data. Data from point counts are comparable to line-transect data (DeGraaf et al. 1991). All three campus transects were walked every day the survey was conducted and were assigned randomly to the morning, noon, or evening. The total time spent on point counts was 3 hr per day, although if additional undetected species were observed between buildings at other points during the day, they were also noted.

BIOLOGICAL TRAITS

Habitat affiliations for each species are from the California Wildlife Habitat Dataset (Mayer and Laudenslayer 1988). This dataset provides species’ usage data for 59 different habitats, breaking down usage by the reproductive value, cover value, and foraging value for each species in each habitat. Because our study took place during the nonbreeding season, we used the values for cover and foraging only. We calculated a single habitat-affinity measure for each habitat and species combination by averaging usage scores over the age and size classes within a vegetation type. We limited our analysis to only the 31 habitats found in Alameda County, then eliminated the five habitats that either do not occur on campus (e.g., marine) or that the species recorded do not use. We reduced collinearity between habitats by comparing correlation coefficients of all habitat usages and averaging classes when the correlation was greater than 0.7 and habitats were all either native or non-native. This produced a final assortment of 18 habitat classes, 11 native and 7 non-native (see Table 2 for list), each with a single usage measure for each species.

We based feeding-guild classifications on DeGraaf et al. (1985), who listed the main food item, foraging technique, and

TABLE 2. The coefficients of linear discriminants from the canonical discriminant analysis. Linear discriminant 1 represents 61% of the trace, linear discriminant 2, 39% of the trace.

Habitat	Abbreviation ^a	LD1	LD2
Barren	BA	1.1	-1.9
Chaparral	CH	-2.0	-1.4
Closed cone pine-cypress	PC	-2.5	1.7
Coastal scrub	CS	-0.9	2.5
Deciduous orchard	DO	0.0	0.0
Dryland grain crops	GC	-1.5	0.6
Eucalyptus	EU	1.7	1.2
Evergreen orchard	EO	0.5	-0.8
Hardwood	HW	1.3	-2.9
Irrigated crops	IC	-4.3	-2.1
Nonnative grassland	NG	-3.4	-5.2
Oak woodland	OW	3.3	2.4
Perennial grassland	PG	2.6	4.0
Redwood	RW	1.6	0.9
Riverine	RV	5.6	2.3
Urban	UR	0.2	-0.9
Valley foothill riparian	FR	-1.3	-2.8
Vineyard	VY	2.4	0.0

^aReference for Figure 5.

feeding substrate for each species. They gave either a year-round or nonbreeding classification for most species but both for several; in such cases we used both in subsequent analyses. From the classification information, we created a binary matrix of feeding traits, divided up into all possible food items, foraging techniques, and feeding substrates.

STATISTICAL ANALYSES

We created a species list for each period based on all species recorded. Since abundances were either not recorded (1913–18) or were recorded by different methods (1938–39 vs. 2006–07), we used the total number of survey days a particular species was encountered as an index of its abundance. This metric takes advantage of the mathematical relationship between the frequency with which a species is detected in repeated surveys and the abundance of that species in the survey area, providing an index of abundance that is not comparable across species but within species is consistent through time, given equal sampling (Royle and Nichols 2003). We estimated alpha diversity as the inverse of Simpson’s D ($1/D$; Peet 1974) to incorporate heterogeneity in encounter frequencies, while to compare similarity in avian communities we calculated beta diversity in different survey periods by proportional similarity (S ; Pielou 1977). Although we also calculated other indices of alpha and beta diversity, the results were quite similar to those for $1/D$ and S , so we do not report them.

To explore occurrence trends through time for each species, we used a binomial generalized linear model (GLM) to analyze species occurrence as a function of both survey era

and Julian day. Julian day was included in models as both a linear and quadratic function. First, we analyzed all species with a full model including all parameters: Julian day, Julian day², and survey era (a categorical variable with 3 levels). Using likelihood-ratio tests ($\alpha = 0.05$), we then reduced these models in a backwards-stepwise fashion to significant explanatory factors. If there was no significant difference between periods ($\alpha = 0.05$) we aggregated them, resulting in one, two, or three levels of survey-era effect. We used estimates of point values to analyze patterns of increase or decrease between these eras, then categorized the 13 possible trend patterns into five groups: no change in abundance through time (“no change”), always increasing through time (“up”), always decreasing through time (“down”), occurrence greatest in the middle period (“mid-best”), and occurrence lowest in the middle period (“mid-worst”). We explored associations between habitat affiliations and avian occurrence trends over time with a canonical discriminant analysis (CDA; Williams 1983, James and McCulloch 1990), using only those species that showed “up,” “down,” or “mid-best” patterns.

To test aspects of the homogenization hypotheses, we used four different measures of habitat usage by species to explore differences between generalists and specialists over time. Our first measure (GENERAL1) simply counted the number of habitats each species used in any frequency for foraging and cover. Our second measure (GENERAL2) summed the habitat-affinity scores for each species across all habitats. Our third measure (GENERAL3) calculated the inverse of the sum of the square of the proportion of affinity for each habitat. Our fourth measure (NATIVE) used summed habitat affinities but differentiated between native and non-native habitats, calculating a percentage for each species of native-habitat usage. For all four measures, we performed one-way ANOVAs weighted by species’ occurrence frequency in each era to test for differences in the habitat usage of bird communities over the three time periods. We assessed differences between time periods with Tukey’s HSD.

We calculated functional diversity (Petchey and Gaston 2002) for each time period from a dendrogram based on feeding guild and species’ occurrence. To create the dendrogram, we first created a distance matrix by using the Gower distance metric (Gower 1971) from the matrix of feeding-guild traits. From the distance matrix, we created a dendrogram by the unweighted pair-group clustering method with arithmetic averages (UPGMA). Although the values of functional diversity changed depending on the distance and clustering method used, the results were qualitatively the same. We then tested whether the functional diversities for each era were significantly different from a null model, where equal numbers of species were selected at random from the total pool (simulations were run 10 000 times; Petchey 2004). Finally, we compared functional composition similarity across eras by computing Spearman’s

ρ correlation coefficient on distributions of functional groups’ composition. These we calculated by multiplying the species–functional-group matrix by the community-composition matrix.

All analyses were run in R version 2.11 (R Development Core Team 2010), with the addition of the package Mass (Venables and Ripley 2002) for CDA analysis, the package Cluster (Maechler et al. 2005) for distance-matrix calculations, and the package Vegan (Oksanen et al. 2010) for the functional-diversity analysis and randomizations. All values are reported as means \pm standard error.

RESULTS

SPECIES TRENDS

The distribution of frequencies with which species were encountered during surveys varied across survey eras but did not shift significantly over time. The mean frequency of occurrence was 0.26 ± 0.03 for 1913–18, 0.37 ± 0.05 for 1938–39, and 0.48 ± 0.06 for 2006–07 (Appendix, available at <http://dx.doi.org/10.1525/cond.2012.110029>). From 1913 to 1918 no species was detected on every survey (frequency of 1.0); the maximum frequency was 0.72. The 1938–39 period had a very even distribution of detection frequencies, with two species that were detected every survey. The 2006–07 period showed a pattern split between rare species and common species, with 26% of species detected on less than 10% of surveys and 22% of species detected on every survey. However, Wilcoxon rank-sum tests showed no significant differences between the three distributions (1913–18 to 1938–39: $W = 964.5$, $P = 0.48$; 1913–18 to 2006–07: $W = 786$, $P = 0.07$; 1938–39 to 2006–07: $W = 906$, $P = 0.13$).

Binomial GLMs for species trends showed a range of occurrence patterns over time. Of the 13 possible models for era-abundance trends, 11 were the best-fitting significant model for at least one species (Fig. 2). No species showed the decreasing trend “321” or the mid-worst trend “312.” Of the five major trends, “no change” was followed by 21 species, “up” by 25 species, “down” by 10 species, “mid-best” by 14 species, and “213” by 2 species (Fig. 2). GLMs showed a significant ($P < 0.05$) linear effect of seasonality on the probability of occurrence on 45 species (Appendix online) and a significant ($P < 0.05$) quadratic effect of seasonality on 24 of those 45.

DIVERSITY CHANGES

Alpha diversity was nearly constant over time despite high rates of turnover in species composition. In total, 72 bird species were identified during surveys across all time periods, yet a maximum of only 44, 46, and 48 species was detected in the periods 1913–18, 1938–39, and 2006–07, respectively. Heterogeneity having been accounted for, alpha diversity as measured by $1/D$ remained nearly constant across time (Fig. 3a). In contrast, beta diversity, as measured by S , shows that the avian community of each period diverged greatly from that

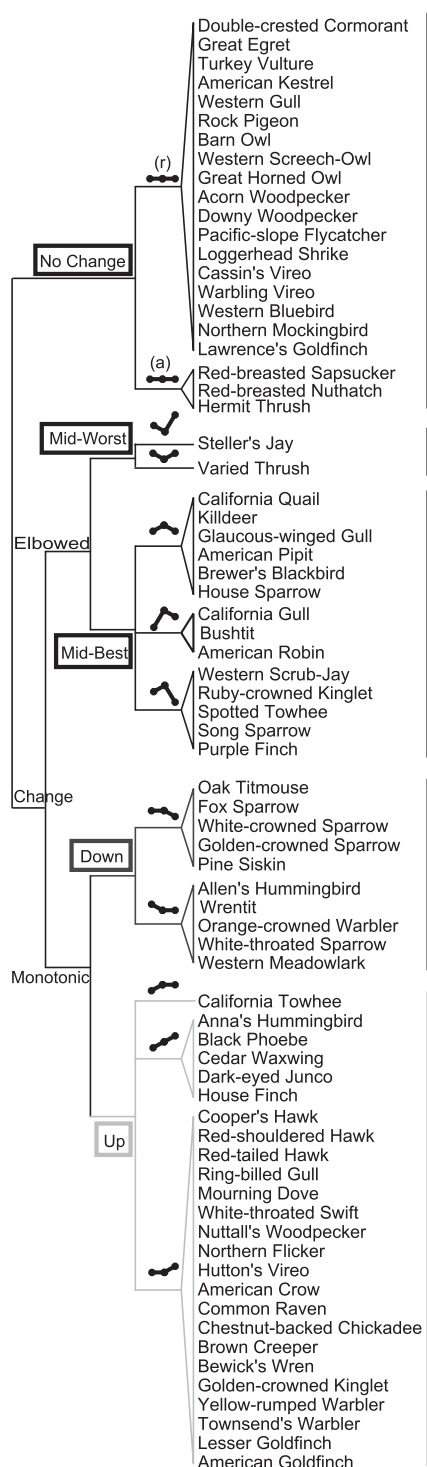


FIGURE 2. Schematic map of frequency-based trends of species' occurrence over time as supported by the GLM analysis. Specific trends (ball-and-stick cartoons) are grouped into five major categories (outlined in boxes): no change, mid-worst, mid-best, down, and up. For the "no change" trends, "a" indicates abundant in all time periods, "r" indicates rare in all time periods. Both of these species groups had best-fitting models for "constant," with "rare" defined by average occurrence frequencies less than 0.05.

of each other period (Fig. 3a). The first two periods were most similar to each other (0.67 similarity), while each was equally dissimilar to the current community (0.45 compared to 1913–18, 0.46 compared to 1938–39).

Measures of functional diversity (Fig. 3b) increased over time, but the trend was not significant (ANOVA, $F_{1,1} = 33.2$, $P = 0.11$). None of the measures was significantly different than the null distribution created by the randomization simulation (1913–18: $z = -1.35$, $P = 0.019$; 1938–39: $z = -0.77$, $P = 0.43$; 2006–07: $z = 1.34$, $P = 0.17$). In addition, functional-group composition in all three periods was very similar (Fig. 3b). Wilcoxon signed-rank tests showed no significant differences between the distributions of functional-group composition in the three periods (1913–18 to 1938–39: $V = 6$, $P = 0.25$; 1913–18 to 2006–07: $V = 6$, $P = 0.25$; 1938–39 to 2006–07: $V = 6$, $P = 0.17$). There were no significant differences between the frequency of omnivores and specialist feeders between any pair of periods (1913–18 to 1938–39: $F_{1,35} = 0.76$,

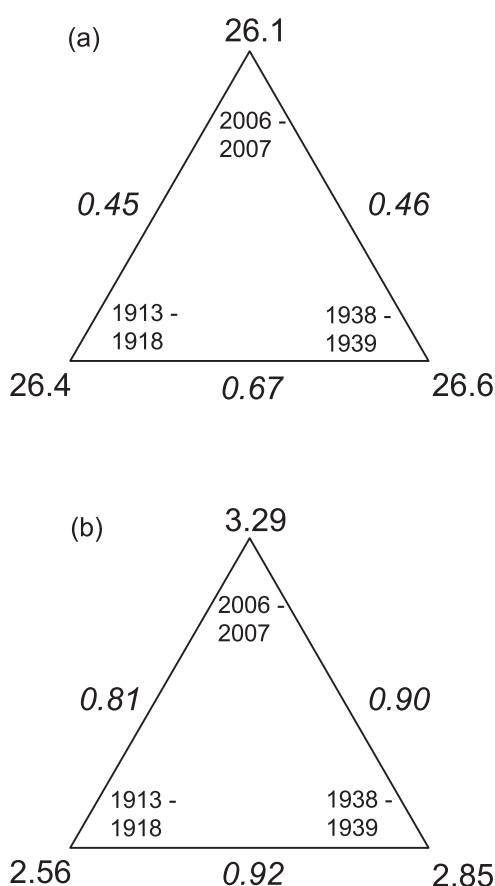


FIGURE 3. Alpha and beta diversity of avian communities in three periods as measured by species diversity (a) and functional diversity (b). Numbers at the triangles' apices show alpha diversity (Simpson's D in [a], functional diversity in [b], see Methods) for each period, whereas numbers between apices show beta diversity (proportional similarity for [a], Spearman's ρ for [b]) between each pair of periods.

$P = 0.39$; 1913–18 to 2006–07: $F_{1,35} = 0.71$, $P = 0.40$; 1938–39 to 2006–07: $F_{1,35} = 0.10$, $P = 0.76$).

HOMOGENIZATION TESTS

Tests of homogenization hypotheses provided varying results (Fig. 4). The three measures differentiating generalists from specialists all failed to show differences between time periods (GENERAL1: $F_{2,135} = 0.13$, $P = 0.88$; GENERAL2: $F_{2,135} = 0.30$, $P = 0.74$; GENERAL3: $F_{2,135} = 0.11$, $P = 0.90$; Fig. 4a). In contrast, differences between survey periods in percent usage of native habitat were marginally significant (NATIVE: $F_{2,135} = 2.97$, $P = 0.054$; Fig. 4b). Species' weighted mean usage of native habitat was highest (0.74) in 1913–18 and significantly greater than in 1938–39 (0.68; Tukey's HSD: $P = 0.043$). The 2006–07 period had species with an intermediate mean weighted usage of native habitat (0.71).

HABITAT COMMUNITIES

On the basis of species-specific habitat affinities, CDA separated the “up,” “down,” and “mid-best” occurrence trends well (Fig. 5a). The discriminant model correctly classified 82% of the species to trend group, with error spread evenly among the classifications. LD1 strongly separated “up”

species from both “down” and “mid-best,” whereas LD2 separated “down” species from “mid-best” species (Fig. 5a). Loadings on the canonical axes (Table 2; Fig. 5b) indicate the relationship between species' trends over time and habitat preferences. A positive loading on LD1, distinguishing the “up” species, was strongly positively associated with riverine, oak woodland, perennial grassland, and vineyard habitats. A positive loading on LD2 separated “down” species from “mid-best” species. Perennial grassland, coastal scrub,

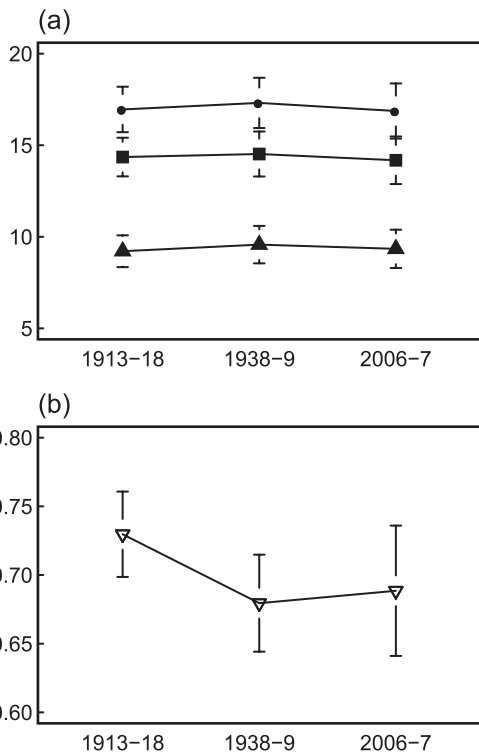


FIGURE 4. Results of four tests for homogenization through time. None of the three measures (a) of habitat generalists versus habitat specialists (circles, GENERAL1; squares, GENERAL2; triangles, GENERAL3) found a significant trend. The fourth measure (b), the percent of native habitat used by species (NATIVE), decreased significantly over time. Plots show era means and 95% confidence intervals.

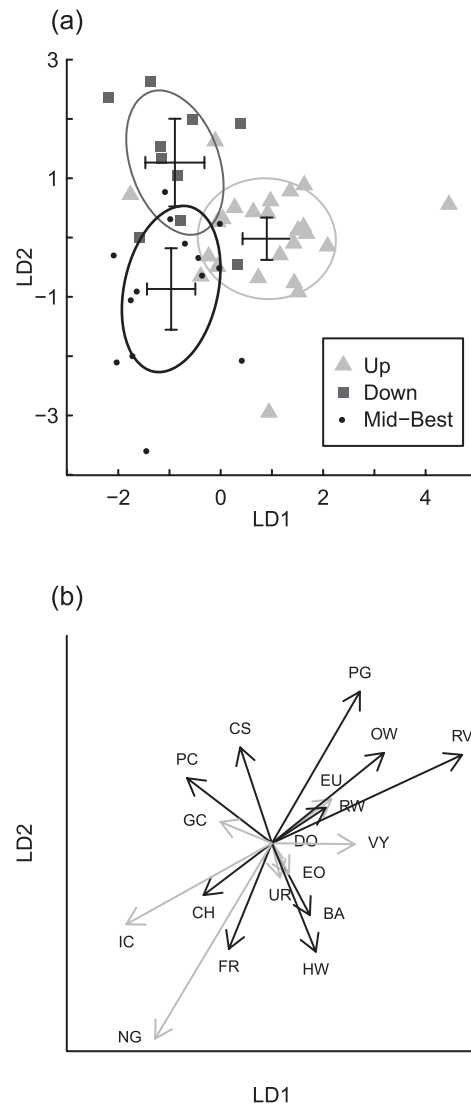


FIGURE 5. Results of the canonical discriminant analysis separating species by scores of affinity for nonbreeding habitat. Species are plotted on two linear discriminant axes (a) and categorized by occurrence trend (“up” in triangles, “down” in squares, “mid-best” in circles). Ellipses encompass 50% point density within each group, and whiskers denote 95% confidence intervals around group means. Habitat-affinity vectors (b) graph proportional loadings of each habitat on relative linear discriminant axes. Habitats are color-coded as either native (black) or non-native (gray). For habitat abbreviations, see Table 2.

oak woodland, and riverine habitat had strong positive loadings on LD2, whereas non-native grassland, hardwood, valley foothill riparian, and irrigated crop habitats had strong negative loadings on LD2.

DISCUSSION

93 YEARS OF CHANGE

The avian community on the campus of the University of California, Berkeley, has retained diversity over the last century, but the species composition of the community has changed substantially. The three survey periods illustrate an avifauna that has shifted over time, with each community being equally different from the other two. The result is a dynamic portrait of a community in flux.

While there was a difference in observer effort (time spent per survey) among the three time periods, we are confident that our results accurately represent the changes in community composition. If increased observer effort biased the findings substantially, one would expect an increase in diversity over time relative to an increase in effort, in addition to increased frequencies of detection of species over time, leading to artificially high numbers of “up” species. However, we saw no increase in species diversity over time (Fig. 3a) and only a marginal increase (from 44 to 48 species) in richness. Additionally, the distributions of occurrence frequencies were only marginally significantly different in the comparison of 1913–18 to 2006–07 ($P = 0.07$) and not significantly different for the other era comparisons. Although there were more species classified as “up” than “down” or “mid-best,” if effort were driving frequencies of occurrence of “up” species, one would expect to find the largest jump in frequency between 1913–18 and 1938–39, resulting in a pattern of “133” or “123” (Fig. 2). However, most species followed a different “up” pattern, “113,” indicating significant differences in occurrence only between 1938–39 and 2006–07, even though survey effort in these latter two periods was almost equal to each other. While we cannot rule out a marginal bias in occurrence frequency for every species individually, we have no evidence that different observer efforts have significantly biased the broad trends that emerge when the community as a whole is examined.

DECAY, HOMOGENIZATION, OR TURNOVER?

A classic tenet of urban ecology is that the more human-dominated a landscape becomes, the less biodiversity that landscape retains (McKinney 2006). The diversity-decay paradigm encapsulates this philosophy, predicting declines in species richness (McKinney 2006) and functional diversity (Olden et al. 2004, Filippi-Codaccioni et al. 2009) with urbanization. At Berkeley, however, we found no evidence of diversity decay. Although some individual species declined or were extirpated over time, these were replaced by other increasing species with similar traits. As a result, both species and functional diversity stayed constant over time, and in each period the similarity of

community feeding guilds was very high (Fig. 3b). Although functional diversity actually increased over time, this increase was proportional to the gain in the species richness for each time period (Petchey et al. 2007, Evans et al. 2009).

As it is similar to diversity decay, community homogenization was not supported by our results. There was no evidence for a decline in richness. With respect to species traits, there was no increase in habitat generalists relative to habitat specialists (McKinney and Lockwood 1999), nor did the distribution of habitat affinities change significantly through time. Additionally, there was no increase in omnivores relative to specialists (Parody et al. 2001, McKinney 2006); in fact, the feeding-guild compositions of the three different communities were quite similar across time. Nevertheless, the community of 1913–18 consisted of species with a higher affinity for native habitats than did those of the later periods (Fig. 4b). Thus the two later communities are made up of species that can better exploit the non-native habitats found in the study area.

In the context of urbanization, our results provide the strongest support for the paradigm of community-composition turnover. While diversity did not change over time, the species makeup of the university campus changed substantially. These shifts in community structure are possibly due to shifts in campus habitat. While we cannot directly test the relationship between community shifts and habitat shifts, we found species' occurrence trends to be strongly associated with habitat groupings that mirror known changes in university landscaping over the last century (Fig. 5). Species with the “up” trend are most positively associated with riparian habitats. The recent restoration of Strawberry Creek and the presence of water year round—unlike what Rodgers and Sibley (1940) reported—may have allowed species to once again make use of that habitat. In recent decades the university has also instituted landscaping policies to increase the native oak woodland (University of California 2004b), which, with the death and removal of about a third of the exotic tree species, could be the reason for the increase in oak-associated bird species.

Species with the “down” trend are positively associated with perennial grassland, oak woodland, and riverine habitat. These native habitats persisted after the founding of the university through landscaping, and sensitive species may have persisted within them. However, as the campus has become more developed and the number of disturbances has increased, sensitive species in these habitats may have decreased or become extirpated. In the case of species associated with oak woodland, sensitive species have decreased, while other, less sensitive species have been able to increase with the additional habitat. In addition, the 1913–18 community had a significantly higher affinity for native habitats than did either of the later communities, indicating that these species might be more dependent on the native habitats, and possibly sensitive to disturbance. Finally, the habitats that are associated with the

“mid-best” trend are those expected to emerge as the trees and plants from the agricultural test station matured, in particular the hardwood trees, non-native grassland, and irrigated crops.

Although it is bordered by increasingly urban areas, the university campus is an example of how biodiversity can be maintained even with continued development. Long-term bird dynamics on Berkeley’s campus do not conform to either of the diversity-loss paradigms, as expected from urbanization, nor does the campus retain the community stability one would expect in the nearby natural areas. Instead, the campus best supports the paradigm of community-composition turnover, demonstrating the importance of long-term landscaping and habitat maintenance within an urban context.

A study of this type, however, requires acknowledgement of its limitations. While our study contains temporal replication and temporal breadth rarely seen in studies of avian ecology, it lacks spatial replication. Without direct comparisons over the same time period to nearby natural areas or urban areas, it is unknown whether changes in the bird community are due to endogenous processes or whether they resulted from larger regional processes. It is likely that other universities and urban green spaces have carefully preserved historical accounts of easily identified taxa such as birds and may provide comparative examples once unearthed. Until that time, our results should not be interpreted as a generalized study of long-term diversity processes, but as a unique case study of a bird community shifting over the course of a century.

GREEN SPACES AS FOCI FOR URBAN DIVERSITY

Nowak and Walton (2005) predicted that by 2050, an additional 5% of land in the United States will be classified as “urban,” a substantial increase from 3.1% in 2000. The future of a large percentage of biodiversity will depend on how well it is maintained within urban or semi-urban areas (Goddard et al. 2010), but this biodiversity will not persist without careful planning and management of the green spaces where it will reside.

The Berkeley campus, despite a context of increasing urbanization, increasing development of the campus, and a 15-fold increase in human use, has maintained and even slightly increased its bird diversity over time. Additionally, the character of the avian community has been demonstrated to be exceptionally malleable, with changes over decadal scales that mirror specific planned choices of landscaping. The greatest potential for urban biodiversity conservation may lie, consequently, in the prescribed management of green spaces to harbor the specific elements of diversity most at risk. It is time for urban green spaces to be thought of not only as hospices for diversity, but also as potential nurseries.

ACKNOWLEDGMENTS

We thank Carla Cicero and C. J. Ralph for advice regarding survey design and Pascal Title for aid in obtaining GIS layers. Helpful comments were provided by Orien Richmond, Adam Smith, Laurie Hall, Pete Epanchin, Toni Lynn-Morelli, Clint Cleveland, Steven Beissinger, and two anonymous reviewers. AJS was supported by a

National Science Foundation Graduate Research Fellowship under grant no. 2008074713.

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