

Avian community composition, but not richness, differs between urban and exurban parks

Angela R. Haas,^{1,*} Sara M. Kross^{1,2} and Jamie M. Kneitel¹

¹Department of Biological Sciences, California State University, Sacramento, 6000 J Street, Sacramento, CA 95819, USA and ²Department of Ecology, Evolution & Environmental Biology, Columbia University, 1200 Amsterdam Avenue, New York, NY 10027, USA

*Corresponding author. E-mail: angela.haas88@gmail.com

Submitted: 5 April 2020; Received (in revised form): 15 September 2020. Accepted: 17 September 2020

Abstract

Urban development alters landscape structure and available resources, potentially threatening avian diversity worldwide. However, it is unclear how bird communities respond in areas currently undergoing urban development, particularly in the non-breeding season. We examined avian communities at 8 parks in urban (within established urban matrix; >50% built cover) and 9 parks in exurban (within adjacent grassland; 5–20% built cover) areas in Sacramento County, CA. We measured bird species and abundance, conducting five line-transect surveys per park (85 total). We investigated factors influencing avian assemblage, including local habitat features (land cover, number of trees, fruiting trees and tree species, tree height and diameter at breast height, park size, park age), and landscape features (land cover within 500 m and distance to riparian habitat). Fifty bird species, including 15 migrants, were observed. Total species richness and abundance at urban and exurban parks was not significantly different, but community assemblages differed significantly. Park area positively predicted species richness. Abundance was negatively associated with in-park percent built cover, average number of fruiting trees and landscape-scale percent water cover. Species composition changes were associated with distance to riparian habitat and landscape percent grass cover for all but one exurban park; and with tree height, DBH and park and landscape percent tree cover for urban parks. The expansion of exurban areas in many parts of the world poses a significant risk for natural habitat loss. Parks in such areas should be planned to harbor some of the displaced biodiversity.

Key words: bird species richness, conservation, non-breeding season, urbanization, California, greenspace

Introduction

In densely populated areas, urbanization is a primary cause of species decline (Czech, Krausman, and Devers 2000; McKinney 2002). Urban development fragments, isolates and degrades natural habitats (Alberti 2005; Chamberlain et al. 2009) while simplifying and homogenizing species composition (Lockwood, Brooks, and McKinney 2000; Aronson et al. 2014). Over the last 50 years, the USA has experienced a 29% decrease in bird abundance across species (Rosenberg et al. 2019). About one-fifth of all bird species occur within cities (Aronson et al. 2014); however, species vary in their response to urbanization

(Rebollo-Ifrán et al. 2015; Isaksson 2018; Callaghan et al. 2020). Most are unable to occupy new habitats created by urban development (Rebollo-Ifrán et al. 2015) and the species that disappear quickly after urbanization can be identified with relative ease (Isaksson 2018). Others persist or even increase in density (Rebollo-Ifrán et al. 2015), often responding positively to increased habitat features for perching and nesting (Emlen 1974; Lancaster and Rees 1979; Isaksson 2018). More difficult to detect are gradual changes in populations. Some species are attracted to cities by available resources and warmer temperatures, but their populations decline slowly due to dangers such

as high nest predation rates and incidental collisions (Isaksson 2018).

While not all species can be supported within cities (Shochat et al. 2010), habitat heterogeneity may allow for greater coexistence between prolific urban species and rarer native species (Shochat et al. 2004). The complex mosaic of disturbance and land transformation caused by urban development (Blair 2004; Pautasso 2007) can generate habitat heterogeneity (McKinney 2008). Whether heterogeneity within and between parks can help increase species richness is not yet clear, and questions remain as to the role of green spaces in supporting biodiversity (Lepczyk et al. 2017). However, the argument that parks act as refuges for bird species is well-supported (Fernández-Juricic and Jokimäki 2001). Remnant vegetation within urban areas, especially native cover, facilitates persistence of native species and higher diversity, even at small scales such as along streetscapes (White et al. 2005). Parks can also increase habitat connectivity, acting as stepping-stones between habitats (Fernández-Juricic and Jokimäki 2001). Parks commonly have higher bird species diversity and richness than other urban areas (Jokimäki 1999; Nielsen et al. 2014), highlighting their potentially integral role in maintaining (Savard, Clergeau, and Mennechez 2000) and promoting (Nielsen et al. 2014) biodiversity in urban landscapes.

Avian biodiversity in urban parks has been well-studied within cities and city edges (Jokimäki 1999; Fernández-Juricic 2000; Clergeau, Jokimäki, and Savard 2001; Murgui 2007) and during the breeding season (Blair 1996, 2004; Marzluff, Bowman, and Donnelly 2001; Crooks, Suarez, and Bolger 2004). However, exurban areas [city-adjacent areas that have ~5% to 20% built area and are surrounded by a natural matrix (Marzluff, Bowman, and Donnelly 2001)] and winter bird use of parks by fall migrant and overwintering species is not thoroughly understood (Smith 2007).

In the USA, exurban development has outpaced other development types, and takes up five times more space than urban and suburban development combined (Lenth, Knight, and Gilgert 2006). Despite this phenomenon, parks within exurban areas currently undergoing such development have been largely overlooked in the scientific literature. In a study comparing forest bird communities in forests versus exurban developments in Virginia, USA, Suarez-Rubio, Leimgruber, and Renner (2011) found similar species richness, but significantly different species composition; and a reduction of forest specialists in exurban areas. The study reinforced a differential impact of exurban development on a species-by-species basis, and the need for further investigation of such areas.

The majority of avian studies are conducted during the breeding season (or use data sets such as the American Breeding Bird Survey; e.g. Chocron, Flather, and Kadmon 2015), and the same is true for studies within parks (Blair 1996, Blair 2004; Marzluff, Bowman, and Donnelly 2001; Crooks, Suarez, and Bolger 2004; but see Carbó-Ramírez and Zuria 2011 for their study of greenspaces in Mexico). Less is known about the habitats used by resident (overwintering) and migrant birds during the non-breeding season (Tryjanowski et al. 2015). In areas such as CA, USA, species assemblages shift throughout the year as migrants move along major migration routes, or make more local, seasonal movements. Understanding species richness and abundance during the non-breeding season, which represents the majority of the year and therefore the majority of the life cycle for most species, could provide a more complete picture of the value of urban greenspaces to avian communities.

The Central Valley of California, a 47 000 km² landscape dominated by intensive agriculture and growing cities, has a

rapidly expanding human population (Department of Finance 2017). The associated intensification and expansion of agriculture and urban development have impacted wildlife habitats (Matchett and Fleskes 2017). For instance, over 90% of historic wetlands have been lost (Matchett and Fleskes 2017). Sacramento County alone experienced a net increase in over 202 km² of urban and built-up land between 1988 and 2016 (Department of Conservation 2016). The region contains critical overwintering habitat for many bird species (Matchett and Fleskes 2017) and a diversity of resident species, making this a model system for understanding how expanding urban areas may influence the composition of avian communities. Here, we present the results of a study to investigate species richness and abundance of birds in parks. We predicted that urban parks would have higher richness and abundance. In addition, we expected species richness to be correlated with available foraging substrates within the parks (e.g. trees and grass) and avian abundance would be correlated with a more urban-developed landscape surrounding the parks. To address these hypotheses for avian communities in the non-breeding season, we used avian counts, data on local (within-park), and data on landscape (park surroundings) habitat features.

Methods

Study sites

We conducted this study in Sacramento County, CA, USA. Historically, numerous native-American tribes lived along watercourses in the area, followed by an influx of European miners in the early 1800s (US Forest Service 2003). The four rivers that cross the county (Sacramento, American, Consumnes and Mokelumne) contributed to the development of agriculture and transportation (US Forest Service 2003). The county experienced major population growth in the 1950s, due to local aerospace industry, government services growth and military expansion (County of Sacramento 1996). By 1950, ~245 km² of built landscape existed in the Sacramento region (Sacramento County and adjacent counties with associated urban sprawl) (Wheeler and Beebe 2011). By 2010, developed landscape had increased to 1978 km². The growth pattern includes houses and commercial buildings historically aggregated near the river that expanded into the exurban grassland; this pattern of sprawl continues. Under current land-use patterns, it is estimated that 3691 km² of new development will be required to support an influx of 1.7 million additional residents by 2050 (Wheeler and Beebe 2011).

We collected field data at 17 parks in Sacramento County, CA, within the City of Rancho Cordova or adjacent census-designated areas (Fig. 1). The City of Rancho Cordova, incorporated in 2002, has a population of 70 087 (U.S. Census Bureau 2019). The elevation is ~27 m, mean temperature is 16.22°C with an average annual precipitation of ~500 mm (Arguez et al. 2012). The surrounding biome is the Mediterranean climate region of the Central Valley. Within the urban environment, parks are older, were built near the American River, and tend to have more mature trees and complex vegetation. The natural habitats surrounding the urban core of Rancho Cordova are primarily annual and vernal pool grasslands. An ~15.5 km² area within this grassland is currently in the process of being developed for single family houses and encompasses in some of the newest parks in this study. Parks in exurban areas undergoing residential development tend to be more recently built, and have fewer, smaller trees and less overall vegetation, and are located further

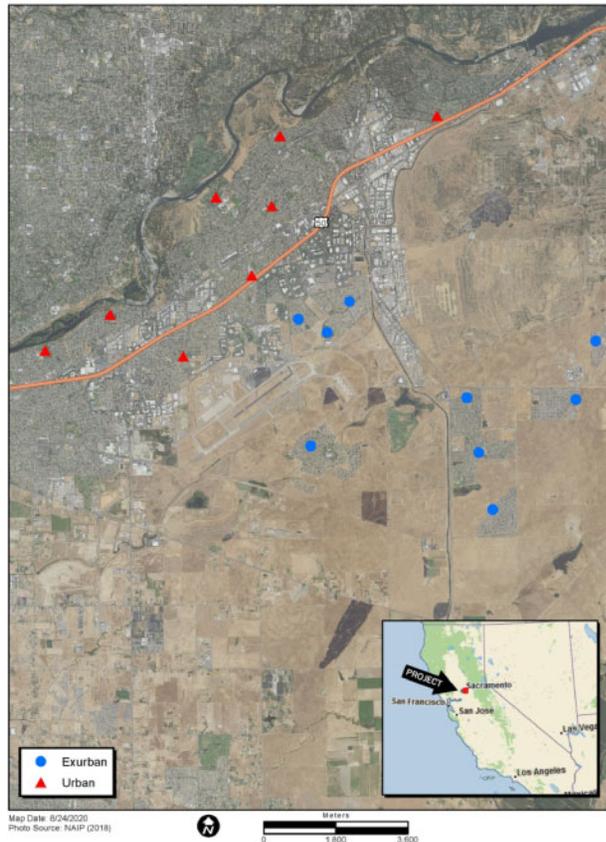


Figure 1: Urban ($n=8$) and exurban ($n=9$) parks of this study in the City of Rancho Cordova and unincorporated areas in Sacramento County, CA, USA

from the river. The locations of the urban and exurban parks share many similarities due to proximity that helped control for spatial aggregation between the two groups, including similar elevation (0–76 m), temperature and rainfall. The youngest exurban park was built in 2016, 1 year before the study took place, and construction of housing developments in the study area is ongoing as of 2020. Because development is current, five of the parks in this study were <10 years old, allowing us to study bird communities after recent disturbance. The remaining undeveloped exurban area adjacent to Rancho Cordova is habitat for several bird species of conservation interest, including Swainson's hawk (*Buteo swainsoni*, California-Threatened and US Fish and Wildlife Service bird of conservation concern [BCC]), tricolored blackbird (*Agelaius tricolor*, California Threatened, a California species of special concern [SSC], and USFWS BCC), short-eared owl (*Asio flammeus*, SSC), burrowing owl (*Athene cucularia*, SSC) and loggerhead shrike (*Lanius ludovicianus*, SSC and BCC) (CDFW 2019).

Data collection

Species surveys

We performed five surveys at each park (e.g. Clergeau, Jokimäki, and Savard 2001; Crooks, Suarez, and Bolger 2004) for a total of 85 surveys. Surveys were conducted once or twice weekly from September to November 2017, between sunrise and 11:00 A.M. to coincide with peak bird activity (Fernández-Juríc 2000). We randomized the order in which parks were visited. Surveys were not conducted during rain or strong winds (Ralph, Sauer, and Droege 1995) or when parks were being irrigated or mowed.

Single-year and single-visit surveys have been deemed appropriate for predicting bird abundances and species richness in urban spaces (Jokimäki and Suhonen 1998; Jokimäki and Kaisanlahti-Jokimäki 2003).

Each survey consisted of a 50 m line-transect (e.g. White et al. 2005) that was walked for 5 min. All birds seen or heard within 50 m of the transect line, and any birds seen or heard beyond the 50 m truncation (Ralph, Sauer, and Droege 1995) were identified to species using binoculars (Monarch 5 8 × 42). All transects started midway along one edge of the park (the edge chosen for each park was determined through random number generation) and a single observer (ARH) walked into the park perpendicular to that edge. All five surveys in each park were repeated along the same transect. Care was taken to avoid counting the same individual twice on each transect. Birds that flew over but not within the habitat were labeled as flyovers. Behavior was opportunistically recorded. For each transect, elevation and geographic coordinates were collected (UTM's; Garmin GPSMAP 64).

Habitat measurements

Parks were labeled as urban (located in the established urban matrix, >25 years of age) or exurban (recently built within the exurban matrix of grassland habitat, <20 years of age). In studying avian communities, the proportions of vegetated open space versus human made structures (e.g. percentage of built area) have been used as surrogates for urbanization (Blair 1996; Clergeau et al. 1998; Lee et al. 2004). Area covered by pavement and area covered by buildings have been shown to be redundant (Blair 1996) and can be combined into a single measure of 'built environment'. According to Stein, Gerstner, and Kreft (2014), plant diversity and land cover are probably suitable for capturing the habitat requirements of many species.

We collected habitat measurements within 50 m on either side of the transect within the park, and at the broader landscape scale of 500 m from the park (e.g. Murgui 2007; Smith, Francis, and Fahrig 2014) since this is an appropriate scale for meaningfully measuring landscape heterogeneity (Litteral and Shochat 2017).

Park-scale, 'local' habitat variables. In each park, we measured a number of ecologically relevant variables shown to predict bird richness and or abundance in previous studies (Blair 1996; Bolger, Scott, and Rotenberry 1997; Jokimäki 1999; Fernández-Juríc 2000; Fernández-Juríc and Jokimäki 2001; Melles, Glenn, and Martin 2003; White 2005; Murgui 2007; Biadun and Zmihorski 2011; Zhou and Chu 2012; Leveau and Leveau 2016). To capture vegetation structure heterogeneity we measured park percent land cover, tree DBH and tree height. We used aerial photographs and Google Earth Pro software to calculate the park area and percent land covers within each park. To gauge anthropogenic disturbance, we recorded the number of pedestrians that entered the survey area per minute, as well as number of cats and dogs because these variables can affect avian species richness (Clergeau, Jokimäki, and Savard. 2001). These data were collected within the survey timeframe (i.e. sunrise to 11:00 A.M.) to coincide with maximum bird activity. Park age was determined by land acquisition dates as provided by the Cordova Recreation and Park District. For a full list of variables measured at the local habitat scale, see Table 1.

Landscape-scale habitat variables. We used Google Earth Pro to measure the distance from each transect to the American River, the large river that runs through Rancho Cordova, to account for

Table 1: Measured variables and inclusion in models

	Variable name	Units	Description	Included in models?
Park characteristics	Park area	Square kilometers	Park size	Yes
	Park age	Years	Years since park was established	No. removed while checking for multicollinearity (VIF > 3)
Local (Park) habitat	Number of fruiting trees	Trees fruiting/park	Mean of count of trees observed bearing fruit over 5 visits to each park	Yes
	DBH	Centimeters	Mean diameter at breast height of all trees within 50 m of transect line	Yes
	Number of trees	Trees/50 m transect	Count of trees per 50 m transect	No. correlated with tree species richness ($r = 0.734$, $P < 0.001$) and removed
	Tree species richness	Tree species/50 m transect	Count of number of tree species per transect	No. removed while checking for multicollinearity (VIF > 3)
	Tree height	Meters	Mean tree height for all trees within 50 m of transect line	No. correlated with tree DBH ($r = 0.88$, $P < 0.001$), and removed
	Built cover	%	% land cover within 50 m of transect that was built structure/surface	Yes
	Water cover	%	% land cover within 50 m of transect that was water	Yes
	Grass cover	%	% land cover within 50 m of transect that was grass	No. removed while checking for multicollinearity (VIF > 3)
	Bare ground cover	%	% land cover within 50 m of transect that was bare ground	No. correlated with park water cover ($r = 0.92$, $P < 0.001$) and removed
	Tree cover	%	% land cover within 50 m of transect that was tree canopy	No. removed while checking for multicollinearity (VIF > 3)
Anthropogenic activity	Individuals/minute		Count of number of people per minute within 50 m of transect	Yes
	Pets	Dogs and cats/minute	Count of number of dogs and cats observed per minute within 50' of transect	No. correlated with anthropogenic activity ($r = 0.69$, $P = 0.002$) and removed
Landscape (500m) habitat	Built cover	%	% land cover within 500 m radius of park that was built structures/surfaces	Yes
	Water cover	%	% land cover within 500 m radius of park	Yes
	Grass cover	%	% land cover within 500 m radius of park that was grass	No. correlated with landscape % tree cover ($r = -0.837$, $P < 0.001$) and removed
	Bare ground cover	%	% land cover within 500 m radius of park that was bare ground	No. removed while checking for multicollinearity (VIF > 3)
	Tree cover	%	% land cover within 500 m radius of park that was tree canopy	No. removed while checking for multicollinearity (VIF > 3)
	Distance to river	Meters	Distance from the park boundary to the nearest river	No. removed while checking for multicollinearity (VIF > 3)

the fact that many of the urban parks are clustered closer to the river than exurban parks, and riparian habitat could introduce different bird species (Sabo et al. 2005) to adjacent parks. We used iTree Canopy (Version 6.1, United States Forest Service 2006), a peer-reviewed software program (Jacobs, Mikhailovich, and Delaney 2014), to generate cover percentages for five relevant habitat characteristics within a 500 m radius of each park (Table 1). We used 400 randomly generated points for our characterization in iTree Canopy, and all standard errors were <3.0%. For a full list of variables measured at the landscape habitat scale, see Table 1.

Statistical analysis

Species richness and abundance

Analyses were carried out on bird species richness (cumulative number of species seen during five surveys) and on avian

abundance (the average number of individuals of each species seen in each park during five surveys, summed across all species observed in the park) (e.g. Crooks, Suarez, and Bolger 2004; White et al. 2005; Biadun and Zmihorski 2011). All avian species were assigned resident or migrant status based on their winter ranges. Flyovers were excluded from analyses (Jokimäki 1999) as were unidentified species.

Because species richness and park area were highly correlated, we used Analysis of Covariance (ANCOVA) to test if species richness varied between urban and exurban parks, controlling for the effect of park size. We used a two-sample t-test to investigate whether maximum abundance differed between the park groups. We used multiple linear regression to investigate what local and landscape-scale habitat features were associated with species richness and abundance.

Dependent variables were tested for normality using the Shapiro–Wilk test (e.g. Husté and Boulinier 2011). We used

frequency histograms and quantile–quantile plots to assess whether the data fit the assumptions of normality and homoscedasticity of residuals. Abundance and park area were log-transformed to meet these assumptions (e.g. Jokimäki 1999; Fernández-Juricic 2000). We examined the Cook's distance to check for outliers. Hagan Community Park has a larger area than all parks and had the highest avian species richness. However, no outliers were found (all Cook's distances were <3) so Hagan was included in all analyses.

To assess the assumptions of ANCOVA, we checked for a linear relationship between species richness and area, the covariate. We checked for homogeneity of regression slopes by verifying that the interaction term was not statistically significant. We used a Shapiro–Wilk test to assess the normality of residuals. We checked for homogeneity of the residual variances using the Levene's Test.

To meet the assumptions of multiple linear regression, and avoid issues of multicollinearity, we used Pearson's coefficient to test for collinearity amongst variables. Several variables were correlated using Pearson's coefficient (see Table 1). In each case, the variable that seemed more biologically relevant and/or had a higher correlation with the dependent variables was selected (Table 1). We then formally checked the remaining independent variables for multicollinearity, and any with variance inflation factors (VIFs) >3 were sequentially removed starting with the covariate with the highest VIF. VIFs were recalculated, and this process was repeated until all VIFs were smaller than 3, a stringent pre-selected threshold (Zuur, Ieno, and Elphick 2010) (Table 1). We included a total of eight variables in our models.

We ran stepwise multiple regression (e.g. Pino et al. 2000; Crooks, Suarez, and Bolger 2004; Carbo-Ramirez and Zuria 2011) using as predictor variables: log park area, park percent built cover, park percent water cover, landscape percent built cover, landscape percent water cover, number of fruiting trees, average tree DBH and average number of pedestrians at parks. Stepwise regression accounts for the contribution each of the independent variables makes to explaining total variance, and thus demonstrates the relative importance of these variables in the regression (Pino et al. 2000). We used a non-automatic variable search (e.g. Carbo-Ramirez and Zuria 2011) using backwards elimination techniques and the Akaike information criterion (AIC) to select the most informative model (e.g. Biadun and Zmihorski 2011; Supplementary Appendix A). The model residuals were examined for deviations from assumptions and none were observed. All analyses were run in R version 3.4.3 (R Core Team 2017), packages vegan (Oksanen et al. 2018), car (Fox and Weisberg 2019) and broom (Robinson 2014).

Community composition

We conducted nonmetric multidimensional scaling (NMDS) to examine differences in avian composition between parks (e.g. Leveau and Leveau 2016). The dissimilarity matrix was calculated using the Bray–Curtis distance metric (e.g. Kneitel 2014; Leveau and Leveau 2016) with species abundance data. Two dimensions were specified. Environmental variables were fitted onto ordination using the envfit function in the R vegan package, and only significant variables ($p < 0.05$) were kept and plotted. This analysis was conducted in R, version 3.4.3 (R Core Team 2017), packages vegan (Oksanen et al. 2018) and ggplot2 (Wickham 2016).

Species densities were used to conduct a one-way analysis of similarity (ANOSIM) to test for differences in community composition between urban and exurban parks. Density was calculated as individual birds per hectare (e.g. Zhou and Chu

2012): using the abundance of birds across the five surveys within 50 m of the transect. Significant ANOSIM results were followed by a Similarity of percentages (SIMPER) test, using Bray–Curtis dissimilarity to determine the relative contribution of each species to differences in community assemblages (e.g. Kneitel 2014) between park types. ANOSIM and SIMPER were conducted using PAST, version 3.19 (Hammer, Harper, and Ryan 2001).

Results

A total of 437 observations of 50 bird species were made during five surveys at 17 parks (Table 2). Thirty-five species were observed at exurban parks, and 36 at urban parks. Exurban parks had an average of 11.56 ± 1.18 (all results are presented \pm standard deviation) species per park, and urban parks averaged 12.75 ± 2.82 species per park. Species richness and area had a linear relationship (Fig. 2). After adjusting for the effect of park size, park types did not differ significantly in total number of species observed (ANCOVA, $F = 0.866$, $df = 1$, $P = 0.368$). Exurban ($\bar{x} = 22.56 \pm 11.05$) and urban ($\bar{x} = 24.4 \pm 17.75$) parks did not differ significantly in the abundance of birds present (two sample Student's *t*-test, $t = -0.043$, $df = 15$, $P = 0.967$). The average number of species observed per survey across all parks varied between 3.4 and 6.6 species.

Exurban parks tended to have been smaller and have lower tree height and DBH; while urban parks tended to be larger and have higher tree height and DBH (Table 3). Exurban parks had more fruiting trees on average and tended to have more grass cover and less tree cover within the parks than their urban counterparts. On a landscape scale, exurban parks tended to have more grass cover and less tree cover in the surrounding environment (Table 3). Age and area of parks were not correlated ($r = 0.35$, $P = 0.16$).

The best model for species richness explained 81% of the variance in the data and included average DBH, landscape percent built cover, landscape percent water cover and park area ($R^2 = 0.81$, $P < 0.001$; Table 4). Park area was a significant, positive predictor of species richness ($t = 6.84$, $P < 0.001$). Although non-significant, landscape percent built cover was retained in the best fit model and was a positive predictor of species richness ($t = 1.33$, $P = 0.207$). Average tree DBH ($t = -1.3$, $P = 0.218$) and landscape percent water cover ($t = -1.69$, $P = 0.117$) were non-significant, negative predictors of species richness. The best linear model for avian abundance explained 75% of the variance in the data and included park percent built cover, landscape percent built cover and landscape percent water cover, average number of fruiting trees at park and park area ($R^2 = 0.75$, $P = 0.004$; Table 4). Park percent built cover ($t = -3.67$, $P = 0.003$), landscape percent water cover ($t = -4.74$, $P < 0.001$), and average number of fruiting trees at park ($t = -2.71$, $P = 0.02$) were all significant and negatively associated with abundance. Landscape percent built cover was also negatively associated with abundance but was non-significant ($t = -2.09$, $P = 0.06$). Park area was the only positive, though non-significant, predictor of abundance ($t = 1.98$, $P = 0.073$).

Communities segregated in NMDS space according to park location type (Stress = 0.15; Fig. 3). When parks were ordinated into multidimensional space, urban and exurban parks segregated along dimension 1. The environmental factors that significantly drove dimension 1 were distance to river ($r^2 = 0.67$, $P = 0.003$) and landscape percent grass cover ($r^2 = 0.55$, $P = 0.002$), which were associated with exurban parks; and tree DBH ($r^2 = 0.57$, $P = 0.007$), tree height ($r^2 = 0.76$, $P < 0.001$), park

Table 2: Bird species observed across all surveys

Common name	Scientific name	Foraging guild	Status	Exurban	Urban
Acorn Woodpecker	<i>M. formicivorus</i>	Insectivore	R	0	1
American Crow	<i>Corvus brachyrhynchos</i>	Omnivore	R	1	2
American Goldfinch	<i>Spinus tristis</i>	Granivore	M	1	1
American Pipit	<i>A. rubescens</i>	Omnivore	M	3	2
American Robin	<i>Turdus migratorius</i>	Omnivore	R	5	3
Anna's Hummingbird	<i>Calypte anna</i>	Omnivore/insectivore	R	3	5
Black Phoebe	<i>Sayornis nigricans</i>	Insectivore/frugivore	R	8	5
Blue-gray Gnatcatcher	<i>Poliophtila caerulea</i>	Insectivore	M	0	1
Brewer's Blackbird	<i>E. cyanocephalus</i>	Omnivore	R	7	1
Brown-headed Cowbird	<i>M. ater</i>	Granivore	R	1	0
Bushtit	<i>Psaltriparus minimus</i>	Omnivore	R	2	0
California Gull	<i>Larus californicus</i>	Carnivore	M	0	1
California Scrub-Jay	<i>Aphelocoma californica</i>	Omnivore	R	5	8
Canada Goose	<i>B. canadensis</i>	Herbivore	M	1	4
Common Merganser	<i>Mergus merganser</i>	Piscivore	M	0	1
Dark-eyed Junco	<i>Junco hyemalis</i>	Granivore	R	1	0
Downy Woodpecker	<i>Picoides pubescens</i>	Insectivore/frugivore	R	0	1
European Starling*	<i>S. vulgaris</i>	Omnivore	R	4	7
Great Egret	<i>Ardea alba</i>	Carnivore/crustaceovore	R	1	1
Great-tailed Grackle	<i>Quiscalus mexicanus</i>	Omnivore	U	3	0
Greater White-fronted Goose	<i>Anser albifrons</i>	Herbivore	M	0	2
Horned Lark	<i>E. alpestris</i>	Granivore	R	3	0
House Finch	<i>H. mexicanus</i>	Granivore	R	5	6
House Sparrow*	<i>Passer domesticus</i>	Granivore	R	2	0
Killdeer	<i>C. vociferus</i>	Insectivore	R	8	5
Lesser Goldfinch	<i>Spinus psaltria</i>	Granivore	R	3	5
Mallard	<i>Anas platyrhynchos</i>	Herbivore/granivore	R	0	1
Northern Flicker	<i>Colaptes auratus</i>	Omnivore	R	2	8
Northern Mockingbird	<i>Mimus polyglottos</i>	Frugivore	R	3	3
Orange-crowned Warbler	<i>Oreothlypis celata</i>	Omnivore	M	0	1
Purple Finch	<i>Haemorhous purpureus</i>	Granivore	R	1	0
Red-tailed Hawk	<i>Buteo jamaicensis</i>	Carnivore	R	1	0
Red-winged Blackbird	<i>A. phoeniceus</i>	Granivore	R	3	0
Ring-billed Gull	<i>Larus delawarensis</i>	Carnivore	M	0	1
Ruby-crowned Kinglet	<i>Regulus calendula</i>	Insectivore	M	0	1
Savannah Sparrow	<i>Passerculus sandwichensis</i>	Granivore	R	6	0
Say's Phoebe	<i>Sayornis saya</i>	Insectivore	M	3	0
Snowy Egret	<i>Egretta thula</i>	Carnivore/crustaceovore	R	0	1
Swainson's Hawk	<i>B. swainsoni</i>	Carnivore	M	1	0
Turkey Vulture	<i>Cathartes aura</i>	Carnivore	R	1	0
Western Bluebird	<i>Sialia mexicana</i>	Omnivore	R	3	5
Western Meadowlark	<i>S. neglecta</i>	Omnivore	R	6	1
White-breasted Nuthatch	<i>Sitta carolinensis</i>	Granivore/insectivore	R	0	1
White-crowned Sparrow	<i>Zonotrichia leucophrys</i>	Granivore	M	1	0
White-tailed Kite	<i>Elanus leucurus</i>	Carnivore	R	2	1
Wild Turkey	<i>M. gallopavo</i>	Herbivore	R	1	2
Yellow Warbler	<i>S. petechia</i>	Insectivore	M	0	1
Yellow-billed Magpie	<i>P. nuttalli</i>	Omnivore	R	0	6
Yellow-rumped Warbler	<i>S. coronata</i>	Omnivore	M	4	6

The number of exurban and urban parks where a species was observed. Foraging guilds shown are non-breeding season/year-round (De Graaf, Tilghman, and Anderson 1985). Asterisks indicate non-native species.

Status: M, migrant; R, resident; U, unestablished.

percent tree cover ($r^2 = 0.51$, $P = 0.005$) and landscape percent tree cover ($r^2 = 0.62$, $P = 0.002$), which were associated with urban parks. The exception (an exurban park that segregated with the urban parks, Fig. 3) was the oldest exurban park, which exhibited similar characteristics to urban parks, such as more mature trees with higher DBH.

Based on Bray-Curtis dissimilarity indices, species composition was significantly different between urban and exurban

parks (ANOSIM: $R = 0.526$, $P \leq 0.001$). SIMPER indicated that the species that contributed the most to these differences were the higher densities of Brewer's blackbird (*Euphagus cyanocephalus*), western meadowlark (*Sturnella neglecta*), wild turkey (*Meleagris gallopavo*), killdeer (*Charadrius vociferus*) and American pipit (*Anthus rubescens*) present at exurban parks; and the higher density of Canada goose (*Branta canadensis*), European starling (*Sturnus vulgaris*), yellow-rumped warbler (*Setophaga coronata*),

house finch (*Haemorhous mexicanus*) and yellow-billed magpie (*Pica nuttalli*) present at urban parks (Table 5). Together, these species explained 75.92% of the dissimilarity in species composition between bird communities at exurban versus urban parks.

There were several bird species observed at only exurban, or only urban, parks (Table 2). Those observed only at exurban parks included red-winged blackbird (*Agelaius phoeniceus*), horned lark (*Eremophila alpestris*) and brown-headed cowbird (*Molothrus ater*); while those observed only at urban parks included acorn woodpecker (*Melanerpes formicivorus*), Canada goose, yellow warbler (*Setophaga petechia*) and yellow-billed magpie. The abundance of migrant species did not differ

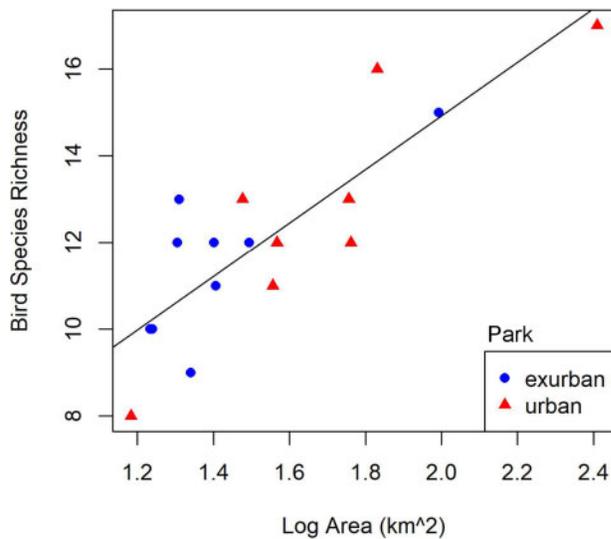


Figure 2: The relationship between bird species richness (total number of species) and park area (log[km²]) at urban and exurban parks. The trendline of the regression is shown

between park types (two sample Student's t-test, $t = -1.83$, $df = 7.1$, $P = 0.108$).

Discussion

Species richness and abundance

Total bird species richness and abundance was not significantly different at urban and exurban parks during the nonbreeding season, suggesting that divergent park structure and landscape characteristics can support similar numbers of birds and species. This was contrary to our hypothesis that urban parks would have higher species richness and abundance. The exurban parks in this study could be experiencing a temporary uptick in both richness and abundance. Bird assemblages contain more species in the initial stages of urbanization (Jokimäki and Suhonen 1993) because moderate disturbance increases bird abundance and richness (Blair 1996, 2004). As expansion into habitats such as grassland occurs, urban adapter species from the regional species pool are seen (Blair 1996; Suarez-Rubio, Leimgruber, and Renner 2011). However, as the developed landscape spreads, abundance remains high while homogenization of bird communities takes place (Aronson et al. 2014; Leveau, Jokimäki, and Kaisanlahti-Jokimäki 2017) and richness decreases. Whether richness and abundance at the parks in this study will remain similar over time is unclear.

Park age has been correlated with richness many times (Fernández-Juricic 2000; Fernández-Juricic and Jokimäki 2001; Biadun and Zmihorski 2011; Carbó-Ramírez and Zuria 2011). As expected, park age was positively associated with habitat complexity measures such as tree size and canopy cover (Table 3); but was excluded from analyses due to correlation with other variables. Park area was positively correlated with species richness, corroborating many studies (Jokimäki 1999; Fernández-Juricic and Jokimäki 2001; Murgui 2007; Carbó-Ramírez and Zuria 2011). Greater area increases the availability of habitats for birds (Fernández-Juricic 2000) and many measures of habitat heterogeneity, including land cover types, tree height and DBH, scale positively with area (Stein, Gerstner, and Kreft 2014). This

Table 3: Mean (± SD) habitat characteristics for exurban (n = 9) versus urban (n = 8) parks

	Variable	Exurban parks	Urban parks
Park characteristics	Park area (km ²)	30.79 ± 24.23	69.68 ± 72.44
	Park age (years)	8.22 ± 4.70	43.13 ± 11.50
Local (transect) habitat	Number of fruiting trees	1.02 ± 1.36	1.33 ± 2.15
	DBH (cm)	12.85 ± 12.58	50.34 ± 23.82
	Number of trees	7.22 ± 6.01	7.38 ± 4.33
	Tree species richness	2.11 ± 1.45	2.75 ± 0.97
Local (park) habitat	Tree height (m)	5.51 ± 3.47	10.70 ± 2.40
	Number of fruiting trees	10.30 ± 13.60	3.70 ± 4.90
	% Built cover	18.01 ± 3.94	13.36 ± 8.73
	% Water cover	1.51 ± 4.20	0.52 ± 1.30
	% Grass cover	67.72 ± 13.63	55.31 ± 12.17
	% Bare ground cover	3.49 ± 7.00	1.43 ± 2.04
	% Tree cover	9.27 ± 8.91	29.39 ± 10.20
Landscape (500 m) habitat	Anthropogenic activity	0.18 ± 0.11	0.23 ± 0.19
	Dogs	0.08 ± 0.09	0.11 ± 0.10
	% Built cover	40.4 ± 11.45	44.19 ± 8.32
	% Water cover	0.08 ± 0.17	3.86 ± 4.91
	% Grass cover	44.1 ± 12.11	22.32 ± 6.24
	% Bare ground cover	7.47 ± 4.81	3.77 ± 3.19
	% Tree cover	5.54 ± 3.89	22.5 ± 3.46
	Distance to river (m)	6803 ± 2174	919.5 ± 711.8

Table 4: Final models (lowest AIC) from stepwise multiple linear regression analyses between bird species richness ($R^2 = 0.81$) or avian abundance ($R^2 = 0.75$) of bird communities at exurban and urban parks, and park and landscape habitat characteristics

Dependent variable		Coefficient	SE	P-value	
Species richness	(Intercept)	-1.280	2.454	0.612	
	Average tree DBH	-0.016	0.012	0.218	
	Landscape % built cover	0.041	0.031	0.207	
	Landscape % water cover	-0.142	0.084	0.117	
	Log park area	3.487	0.510	<0.001***	
Model				<0.001***	
Abundance	(Intercept)	3.872	0.654	<0.001***	
	Park % built cover	-0.045	0.012	0.003**	
	Landscape % built cover	-0.017	0.008	0.060	
	Landscape % water cover	-0.129	0.027	<0.001***	
	Park fruiting trees	-0.021	0.008	0.020*	
	Log park area	0.272	0.137	0.073	
	Model				0.005**

* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

reinforces the importance of size when planning to conserve or restore habitat patches within urban areas (Lepczyk et al. 2017).

Community composition

Although species richness and abundance did not differ between the urban and exurban parks, considering these findings in isolation could lead to misleading interpretations about the similarity of their avian assemblages. Species composition between the parks in urban versus exurban areas in the nonbreeding season was significantly different. This is consistent with other studies, where significant differences in community assemblage were driven by urbanization (Trollope, White, and Cooke 2009; Minor and Urban 2010).

The majority of species seen across parks (48 out of 50 species) were native to California, suggesting that during the nonbreeding season these parks are important habitat for native birds. Urban parks had only one nonnative species, the European Starling, yet it was the second most abundant species at those parks. This may be due to a higher abundance of mature trees and urban structures, which can provide cavities for nesting. The high abundance of starlings, an urban adapter species (Zhou and Chu 2012) that can outcompete native species for nest cavities, suggests that summary statistics such as species richness and abundance should be considered along with species composition data.

Species overwintering in temperate regions in the USA are declining in abundance (Rosenberg et al. 2019). A total of 15 out of the 50 species observed at all parks in our study were migrants, underscoring the potential importance of parks as refuges for migrant species. Because similar abundances of migrants were observed at both park types, this appears to be true in both urban and exurban habitats. Monitoring exurban areas over time could help establish whether this remains true as exurban parks and surrounding areas mature.

Grassland species have shown the greatest declines in abundance since 1970 of any North American bird species, and 74% of grassland species are declining (Rosenberg et al. 2019). The exurban parks, characterized in part by more grassland habitat in the surrounding landscape, tended to be dominated by

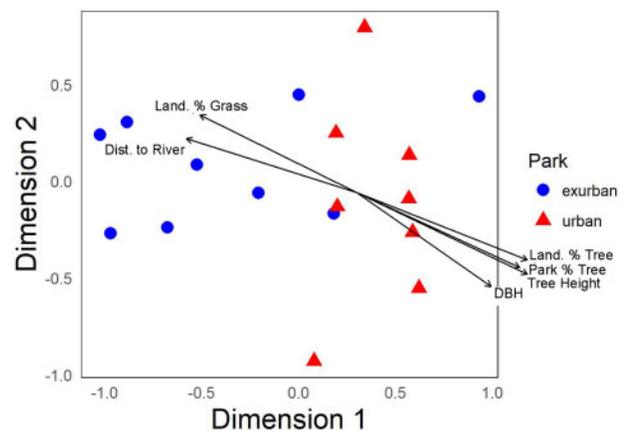


Figure 3: NMDS plot of avian communities at urban and exurban parks using Bray-Curtis dissimilarity. Significant ($P < 0.05$) environmental vectors are fitted onto ordination

grassland species, including Brewer's blackbirds and Western meadowlarks. The Western meadowlark has a habitat requirement of grassland greater than five hectares (Johnson and Igl 2001). One critique of park planning is the tendency to maximize a diversity of habitats within a single park (Aronson et al. 2017). Instead, the management of large, contiguous areas of habitat such as grassland, when multiplied across different habitat types at the broader scale, may be more beneficial to species (Aronson et al. 2017; also see Lepczyk et al. 2017). Recently built parks with young saplings might not support as many migrants or species that forage or roost in dense tree canopies, but they can provide refuge to displaced grassland species whose native habitat was transformed by recent development. Their role as a refuge in this context could be enhanced by increasing park size, perhaps by opting for a single large park within a development complex in lieu of several smaller parks. There are some examples of this in the Central Valley, in the form of Specific or Habitat Conservation Plans, which can promote a common preserve area for multiple development projects. However, as these young parks mature and the adjacent grassland is converted to urban cover, the bird communities will continue to respond and change, and it is possible grassland species will be displaced.

Conclusion

In the study area, bird species showed a spatial organization due to local and landscape habitat features of parks. To support a variety of bird species, no clear patterns emerged on a park-by-park basis. However, parks with divergent features supported comparable species richness and abundances, supporting the assertion that increased environmental heterogeneity between parks can increase bird diversity overall (Lepczyk et al. 2017). The communities of avian species utilizing each habitat type varied, therefore contributing to greater species diversity across the entire study area. Future research could parse these species into their functional groups to explore the relationship between functional diversity and park habitat characteristics. While urban environments pose great challenges to many bird species, they also present new niche opportunities (Shanahan et al. 2014). A diversity of parks or other refuges within urban landscapes, strategically located and prioritized for large, contiguous size, could slow the spread of biotic homogenization and help support native species. Importantly, the development

Table 5: Between park type dissimilarity (SIMPER, dissimilarity = 87.06) for comparisons of urban and exurban parks based on species density

Species	Contribution %	Cumulative %	Higher density
Brewer's Blackbird	20.32	20.32	Exurban
Canada Goose	18.89	39.21	Urban
European Starling*	8.35	47.56	Urban
Western Meadowlark	6.60	54.16	Exurban
Yellow-rumped Warbler	4.40	58.55	Urban
House Finch	4.16	62.72	Urban
Yellow-billed Magpie	3.80	66.52	Urban
Wild Turkey	3.54	70.06	Exurban
Killdeer	3.25	73.30	Exurban
American Pipit	2.62	75.92	Exurban
California Scrub-Jay	2.20	78.12	Urban
Savannah Sparrow	2.14	80.26	Exurban
Northern Flicker	2.12	82.38	Urban
Lesser Goldfinch	1.81	84.19	Urban
Lark Sparrow	1.48	85.67	Urban
Black Phoebe	1.45	87.12	Exurban
American Robin	1.10	88.22	Urban
Western Bluebird	1.09	89.31	Urban
Horned Lark	1.08	90.39	Exurban
Bushtit	1.03	91.42	Exurban
Great-tailed Grackle	1.02	92.44	Exurban
Red-winged Blackbird	0.97	93.41	Exurban
Northern Mockingbird	0.73	94.15	Exurban
Anna's Hummingbird	0.73	94.87	Exurban
Mallard	0.62	95.49	Urban
American Goldfinch	0.48	95.97	Exurban
Brown-headed Cowbird	0.37	96.34	Exurban
American Crow	0.35	96.70	Urban
Ring-billed Gull	0.34	97.04	Urban
Turkey Vulture	0.30	97.34	Exurban
Blue-gray Gnatcatcher	0.27	97.61	Urban
White-tailed Kite	0.23	97.84	Urban
Say's Phoebe	0.21	98.05	Exurban
Snowy Egret	0.21	98.25	Urban
Ruby-crested Kinglet	0.21	98.46	Urban
Acorn Woodpecker	0.19	98.64	Urban
Great Egret	0.17	98.81	Urban
House Sparrow*	0.17	98.99	Exurban
Common Merganser	0.14	99.12	Urban
Greater White-fronted Goose	0.13	99.25	Urban
Yellow Warbler	0.10	99.35	Exurban
White-crowned Sparrow	0.09	99.44	Urban
Orange-crowned Warbler	0.08	99.53	Urban
White-breasted Nuthatch	0.08	99.61	Urban
Purple Finch	0.07	99.69	Exurban
Swainson's Hawk	0.07	99.76	Exurban
Dark-eyed Junco	0.07	99.84	Exurban
Downy Woodpecker	0.07	99.90	Urban
Red-tailed Hawk	0.06	99.97	Exurban
California Gull	0.03	100	Urban

Each species is listed with its contribution to the dissimilarity, the cumulative percentage dissimilarity and park type where it was observed in higher densities. Asterisks indicate non-native species.

of well-designed parks cannot replace preservation of threatened habitats as a strategy to conserve species, so we caution that our results do not support the conversion of natural

grassland habitats in favor of exurban housing development; however, our results do suggest that exurban parks can support some native species.

Supplementary data

Supplementary data are available at JUECOL online.

Acknowledgments

We thank Caroline Hinkelman (ECORP Consulting, Inc.) for GIS assistance, Dr Timothy Davidson (CSUS) for comments and earlier versions, and The Albert Delisle family for a scholarship for gas and equipment. We thank the associate editor, Dr Lucas Leveau, and three anonymous reviewers for comments that improved this manuscript.

Data availability

Data will be made available upon request.

Conflict of interest statement. None declared.

References

- Alberti, M. (2005) 'The Effects of Urban Patterns on Ecosystem Function', *International Regional Science Review*, **28**: 168–92.
- Arguez, A et al. (2012) 'NOAA's 1981–2010 U.S. Climate Normals: An Overview', *Bulletin of the American Meteorological Society*, **93**: 1687–97. [10.1175/BAMS-D-11-00197.1](https://doi.org/10.1175/BAMS-D-11-00197.1)
- Aronson, M. F. et al. (2014) 'A Global Analysis of the Impacts of Urbanization on Bird and Plant Diversity Reveals Key Anthropogenic Drivers', *Proceedings of the Royal Society B: Biological Sciences*, **281**: 20133330.
- et al. (2017) 'Biodiversity in the City: Key Challenges for Urban Green Space Management', *Frontiers in Ecology and the Environment*, **15**: 189–96.
- Biadun, W., and Zmihorski, M. (2011) 'Factors Shaping a Breeding Bird Community along an Urbanization Gradient: 26-Year Study in Medium Size City (Lublin, SE Poland)', *Polish Journal of Ecology*, **59**: 381–9.
- Blair, R. (1996) 'Land Use and Avian Species Diversity along an Urban Gradient', *Ecological Applications*, **6**: 506–19.
- (2004) 'The Effects of Urban Sprawl on Birds at Multiple Levels of Biological Organization', *Ecology and Society*, **9**: 2.
- Bolger, D. T., Scott, T. A., and Rotenberry, J. T. (1997) 'Breeding Bird Abundance in an Urbanizing Landscape in Coastal Southern California', *Conservation Biology*, **11**: 406–21.
- California Department of Fish and Wildlife (CDFW). (2019) *State and Federally Listed Endangered and Threatened Animals of California*. Sacramento, California: Biogeographic Data Branch, California Natural Diversity Database.
- Callaghan, C. T. et al. (2020) 'A Continental Measure of Urbanness Predicts Avian Response to Local Urbanization', *Ecography*, **43**: 528–38.
- Carbó-Ramírez, P., and Zuria, I. (2011) 'The Value of Small Urban Greenspaces for Birds in a Mexican City', *Landscape and Urban Planning*, **100**: 213–22.
- Chamberlain, D. E. et al. (2009) 'Avian Productivity in Urban Landscapes: A Review and Meta-analysis', *IBIS*, **151**: 1–18.
- Chocron, R., Flather, C. H., and Kadmon, R. (2015) 'Bird Diversity and Environmental Heterogeneity in North America: A Test of the Area-heterogeneity Trade-off', *Global Ecology and Biogeography*, **24**: 1225–35.

- Clergeau, P. et al. (1998) 'Bird Abundance and Diversity along an Urban–Rural Gradient: A Comparative Study between Two Cities on Different Continents', *The Condor*, **100**: 413–25.
- , Jokimäki, J., and Savard, J. P. L. (2001) 'Are Urban Bird Communities Influenced by the Bird Diversity of Adjacent Landscapes?', *Journal of Applied Ecology*, **38**: 1122–34.
- County of Sacramento. (1996) *Housing Element of the General Plan*. Sacramento: County of Sacramento, p. 385.
- Crooks, K. R., Suarez, A. V., and Bolger, D. T. (2004) 'Avian Assemblages along a Gradient of Urbanization in a Highly Fragmented Landscape', *Biological Conservation*, **115**: 451–62.
- Czech, B. P., Krausman, R., and Devers, P. K. (2000) 'Economic Associations among Causes of Species Endangerment in the United States', *BioScience*, **50**: 593–601.
- De Graaf, R. M., Tilghman, N. G., and Anderson, S. H. (1985) 'Foraging Guilds of North American Birds', *Environmental Management*, **9**: 493–536.
- Department of Conservation (DOC). (2016) *Sacramento County Historic Land Use Conversion*. Division of Land Resource Protection, Farmland Mapping and Monitoring Program, DOC, Sacramento, California.
- Department of Finance (DOF). (2017) *Population Projections for California and Its Counties, 2016 Baseline Series*. Demographic Research Unit, DOF, Sacramento, California.
- Emlen, J. T. (1974) 'An Urban Bird Community in Tucson, Arizona: Derivation, Structure, Regulation', *The Condor*, **76**: 184–97.
- Fernández-Juricic, E. (2000) 'Bird Community Composition Patterns in Urban Parks of Madrid: The Role of Age, Size and Isolation', *Ecological Research*, **15**: 373–83.
- , and Jokimäki, J. (2001) 'A Habitat Island Approach to Conserving Birds in Urban Landscapes: Case Studies from Southern and Northern Europe', *Biodiversity and Conservation*, **10**: 2023–43.
- Fox, J., and Weisberg, S. (2019) *An R Companion to Applied Regression*, 3rd ed. Thousand Oaks, CA: Sage.
- Hammer, Ø., Harper, D. A. T., and Ryan, P. D. (2001) 'Past: Paleontological Statistics Software Package for Education and Data Analysis', *Palaeontol Electron*, **4**: 9.
- Husté, A., and Boulinier, T. (2011) 'Determinants of Bird Community Composition on Patches in the Suburbs of Paris, France', *Biological Conservation*, **144**: 243–52.
- Isaksson, C. (2018). 'Impact of Urbanization on Birds', in Dieter Thomas Tietze (ed.) *Bird Species: How They Arise, Modify and Vanish*, pp. 235–57. Cham: Springer.
- Jacobs, B., Mikhailovich, N., and Delaney, C. (2014) *Benchmarking Australia's Urban Tree Canopy: An i-Tree Assessment, prepared for Horticulture Australia Limited by the Institute for Sustainable Futures*. Sydney, Australia: University of Technology Sydney.
- Johnson, D. H., and Igl, L. D. (2001) 'Area Requirements of Grassland Birds: A Regional Perspective', *The Auk*, **118**: 24–34.
- Jokimäki, J., and Suhonen, J. (1998) 'Distribution and Habitat Selection of Wintering Birds in Urban Environments', *Landscape and Urban Planning*, **39**: 253–63. [10.1016/S0169-2046\(97\)00089-3](https://doi.org/10.1016/S0169-2046(97)00089-3)
- (1999) 'Occurrence of Breeding Bird Species in Urban Parks: Effects of Park Structure and Broad-scale Variables', *Urban Ecosystems*, **3**: 21–34.
- , and Kaisanlahti-Jokimäki, M. L. (2003) 'Spatial Similarity of Urban Bird Communities: A Multiscale Approach', *Journal of Biogeography*, **30**: 1183–93.
- , and Suhonen, J. (1993) 'Effects of Urbanization on the Breeding Bird Species Richness in Finland: A Biogeographical Comparison', *Ornis Fennica*, **70**: 71–7.
- Kneitel, J. M. (2014) 'Inundation Timing, More than Duration, Affects the Community Structure of California Vernal Pool Mesocosms', *Hydrobiologia*, **732**: 71–83.
- Lancaster, R. K., and Rees, W. E. (1979) 'Bird Communities and the Structure of Urban Habitats', *Canadian Journal of Zoology*, **57**: 2358–68.
- Lee, P. et al. (2004) 'Breeding Bird Species Richness in Taiwan: Distribution on Gradients of Elevation, Primary Productivity and Urbanization', *Journal of Biogeography*, **31**: 307–14.
- Lenth, B. A., Knight, R. L., and Gilgert, W. C. (2006) 'Conservation Value of Clustered Housing Developments', *Conservation Biology : The Journal of the Society for Conservation Biology*, **20**: 1445–56.
- Lepczyk, C. A. et al. (2017) 'Biodiversity in the City: Fundamental Questions for Understanding the Ecology of Urban Green Spaces for Biodiversity Conservation', *BioScience*, **67**: 799–807.
- Leveau, L. M., Jokimäki, J., and Kaisanlahti-Jokimäki, M. (2017) 'Scale Dependence of Biotic Homogenisation by Urbanisation: A Comparison of Urban Bird Communities between Central Argentina and Northern Finland', *European Journal of Ecology*, **3**: 1–18.
- , and Leveau, C. (2016) 'Does Urbanization Affect the Seasonal Dynamics of Bird Communities in Urban Parks?', *Urban Ecosystems*, **19**: 631–47.
- Litteral, J., and Shochat, E. (2017) 'The Role of Landscape-scale Factors in Shaping Urban Bird Communities', in E. Murgui and M. Hedblom (eds) *Ecology and Conservation of Birds in Urban Environments*, pp. 135–59. Cham, Switzerland: Springer International Publishing.
- Lockwood, J. L., Brooks, T. M., and Mckinney, M. L. (2000) 'Taxonomic Homogenization of the Global Avifauna', *Animal Conservation*, **3**: 27–35.
- Marzluff, J. M., Bowman, R., and Donnelly, R. (2001) 'A Historical Perspective on Urban Bird Research: Trends, Terms, and Approaches', in *Avian Ecology and Conservation in an Urbanizing World*, pp. 1–17. Boston, MA: Springer.
- Matchett, E. L., and Fleskes, J. P. (2017) 'Projected Impacts of Climate, Urbanization, Water Management, and Wetland Restoration on Waterbird Habitat in California's Central Valley', *PLoS One*, **12**: e0169780.
- McKinney, M. L. (2002) 'Urbanization, Biodiversity, and Conservation', *BioScience*, **52**: 883–91.
- (2008) 'Effects of Urbanization on Species Richness: A Review of Plants and Animals', *Urban Ecosystems*, **11**: 161–76.
- Melles, S., Glenn, S., and Martin, K. (2003) 'Urban Bird Diversity and Landscape Complexity: Species–Environment Associations along a Multiscale Habitat Gradient', *Conservation Ecology*, **7**: 5.
- Minor, E., and Urban, D. (2010) 'Forest Bird Communities across a Gradient of Urban Development', *Urban Ecosystems*, **13**: 51–71.
- Murgui, E. (2007) 'Effects of Seasonality on the Species–Area Relationship: A Case Study with Birds in Urban Parks', *Global Ecology and Biogeography*, **16**: 319–29.
- Nielsen, A. B. et al. (2014) 'Species Richness in Urban Parks and Its Drivers: A Review of Empirical Evidence', *Urban Ecosystems*, **17**: 305–27.
- Oksanen, J. et al. (2018). *vegan: Community Ecology Package*. R package version 2.4-6. Vienna: R Foundation for Statistical Computing. <<https://CRAN.R-project.org/package=vegan>>. Last accessed August 31, 2020.
- Pautasso, M. (2007) 'Scale Dependence of the Correlation between Human Population Presence and Vertebrate and Plant Species Richness', *Ecology Letters*, **10**: 16–24.

- Pino, J. et al. (2000) 'Landscape Structure and Bird Species Richness: Implications for Conservation in Rural Areas between Natural Parks', *Landscape and Urban Planning*, **49**: 35–48.
- Ralph, C. J., Sauer, J. R., and Droege, S. (1995). *Monitoring Bird Populations by Point Counts: Standards and Applications*. Albany, CA: Pacific Southwest Research Station.
- R Core Team. (2017) *R: A Language and Environment for Statistical Computing*. Vienna, Austria: R Foundation for Statistical Computing.
- Rebolo-Ifrán, N. et al. (2015) 'Links between Fear of Humans, Stress and Survival Support a Non-random Distribution of Birds among Urban and Rural Habitats', *Scientific Reports*, **5**: 13723.
- Robinson, D. (2014) 'broom: An R Package for Converting Statistical Analysis Objects into Tidy Data Frames', *Computation*, arXiv:1412.3565.
- Rosenberg, K. V. et al. (2019) 'Decline of the North American Avifauna', *Science*, **366**: 120–4.
- Sabo, J. L. et al. (2005) 'Riparian Zones Increase Regional Species Richness by Harboring Different, Not More, Species', *Ecology*, **86**: 56–62.
- Savard, J. P. L., Clergeau, P., and Mennechez, G. (2000) 'Biodiversity Concepts and Urban Ecosystems', *Landscape and Urban Planning*, **48**: 131–42.
- Shanahan, D. F. et al. (2014) 'The Challenges of Urban Living', in D. Gill and H. Brumm (eds) *Avian Urban Ecology*, pp. 3–20. Oxford, England: Oxford University Press.
- Shochat, E. et al. (2004) 'Linking Optimal Foraging Behavior to Bird Community Structure in an Urban-desert Landscape: Field Experiments with Artificial Food Patches', *The American Naturalist*, **164**: 232–43.
- et al. (2010) 'Invasion, Competition, and Biodiversity Loss in Urban Ecosystems', *BioScience*, **60**: 199–208.
- Smith, A. C., Francis, C. M., and Fahrig, L. (2014) 'Similar Effects of Residential and Non-residential Vegetation on Bird Diversity in Suburban Neighbourhoods', *Urban Ecosystems*, **17**: 27–44.
- Smith, P. G. (2007) 'Characteristics of Urban Natural Areas Influencing Winter Bird Use in Southern Ontario', *Environmental Management*, **39**: 338–52.
- Stein, A., Gerstner, K., and Kreft, H. (2014) 'Environmental Heterogeneity as a Universal Driver of Species Richness across Taxa, Biomes and Spatial Scales', *Ecology Letters*, **17**: 866–80.
- Suarez-Rubio, M., Leimgruber, P., and Renner, S. C. (2011) 'Influence of Exurban Development on Bird Species Richness and Diversity', *Journal of Ornithology*, **152**: 461–71.
- Trollope, S. T., White, J. G., and Cooke, R. (2009) 'The Response of Ground and Bark Foraging Insectivorous Birds across an Urban-forest Gradient', *Landscape and Urban Planning*, **93**: 142–50.
- Tryjanowski, P. et al. (2015) 'Winter Bird Assemblages in Rural and Urban Environments: A National Survey', *PLoS One*, **10**: e0130299.
- United States Census Bureau. 2019. American Community Survey. Department of Commerce, Suitland, Maryland. <www.census.gov>. Last accessed 18 July 2020.
- United States Forest Service. (2003) *General Technical Report PSW-GTR-187*. Albany, California: Department of Agriculture.
- (2006) *iTree Canopy*, Version 6. Northern Research Station, Madison, Wisconsin. <canopy.itreetools.org> Last accessed April 30, 2018.
- Wheeler, S., and Beebe, C. (2011) 'The Rise of the Postmodern Metropolis: Spatial Evolution of the Sacramento Metropolitan Region', *Journal of Urban Design*, **16**: 307–32.
- White, J. G. et al. (2005) 'Non-uniform Bird Assemblages in Urban Environments: The Influence of Streetscape Vegetation', *Landscape and Urban Planning*, **71**: 123–35.
- Wickham, H. (2016) *ggplot2: Elegant Graphics for Data Analysis*. New York, NY: Springer-Verlag.
- Zhou, D., and Chu, L. M. (2012) 'How Would Size, Age, Human Disturbance, and Vegetation Structure Affect Bird Communities of Urban Parks in Different Seasons?', *Journal of Ornithology*, **153**: 1101–12.
- Zuur, A. F., Ieno, E. N., and Elphick, C. S. (2010) 'A Protocol for Data Exploration to Avoid Common Statistical Problems', *Methods in Ecology and Evolution*, **1**: 3–14.